BEFORE THE SECRETARY OF THE INTERIOR

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PETITION TO PROTECT THE MONARCH BUTTERFLY (*DANAUS PLEXIPPUS PLEXIPPUS*) UNDER THE ENDANGERED SPECIES ACT

Notice of Petition

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PETITIONERS

The Center for Biological Diversity ("Center") is a nonprofit, public interest environmental organization dedicated to the protection of imperiled species and the habitat and climate they need to survive through science, policy, law, and creative media. The Center is supported by more than 775,000 members and activists throughout the country. The Center works to secure a future for all species, great or small, hovering on the brink of extinction.

The **Center for Food Safety** ("CFS") is a nonprofit public interest organization established in 1997 whose mission centers on protecting public health and the environment by curbing the adverse impacts of industrial agriculture and food production systems on public health, the environment, and animal welfare, and by instead promoting sustainable forms of agriculture. As particularly relevant here, CFS is the leading nonprofit working on the adverse impacts of genetically engineered crops and neonicotinoid pesticides. CFS and its over half-a-million members are concerned about the impacts of industrial agriculture on biodiversity generally, and on monarch butterflies specifically. CFS and its members have strong interests in the conservation of monarch butterflies that are impacted, directly and indirectly, by harmful agricultural practices. As part of its mission and member interests, CFS's multifaceted pollinator protection program actively works to reduce the adverse effects of toxic pesticides on important insect and pollinator species, such as monarch butterflies and honey bees. This program utilizes scientific, policy, educational, legislative, regulatory, and grassroots campaigns to spearhead action from government agencies, policymakers, and the public, to protect food security and the environment by requiring robust analyses of these pesticides' adverse impacts, and suspending or curbing their use as needed.

The Xerces Society is a nonprofit organization that protects wildlife through the conservation of invertebrates and their habitat. For forty years, the Society has been at the forefront of invertebrate protection worldwide, harnessing the knowledge of scientists and the enthusiasm of citizens to implement conservation programs.

Dr. Lincoln Brower first began studying monarch butterfly biology in 1954 when he was a graduate student at Yale University. He currently is Distinguished Service Professor of Zoology Emeritus at the University of Florida and Research Professor of Biology at Sweet Briar College. His research includes conservation of endangered biological phenomena and ecosystems, the overwintering and migration biology of the monarch butterfly, chemical defense, mimicry, and scientific film making. He has authored and coauthored more than 200 scientific papers on the monarch butterfly. Since 1977 he has been deeply involved with conservation of the monarch's overwintering and breeding habitats.

Submitted this 26th day of August, 2014

Pursuant to Section 4(b) of the Endangered Species Act ("ESA"), 16 U.S.C. § 1533(b); Section 553(e) of the Administrative Procedure Act, 5 U.S.C. § 553(e); and 50 C.F.R. § 424.14(a), the Center for Biological Diversity and Center for Food Safety as co-lead petitioners joined by the Xerces Society for Invertebrate Conservation and Dr. Lincoln Brower hereby petition the Secretary of the Interior, through the United States Fish and Wildlife Service ("FWS," "Service"), to protect the monarch butterfly (*Danaus plexippus plexippus)* as a threatened species.

FWS has jurisdiction over this petition. This petition sets in motion a specific process, placing definite response requirements on the Service. Specifically, the Service must issue an initial finding as to whether the petition "presents substantial scientific or commercial information indicating that the petitioned action may be warranted." 16 U.S.C. § 1533(b)(3)(A). FWS must make this initial finding "[t]o the maximum extent practicable, within 90 days after receiving the petition." *Id*. Petitioners also request that critical habitat be designated for the monarch butterfly concurrently with the species being listed, pursuant to 16 U.S.C. § 1533(a)(3)(A) and 50 C.F.R. § 424.12.

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EXECUTIVE SUMMARY

The monarch is an iconic large orange and black butterfly that is one of the most familiar butterflies in North America. During summer monarchs can be found throughout the United States and southern Canada in most places where milkweeds (*Asclepias* spp.), their host plants, are available. Each year monarchs undertake a spectacular multi-generational migration of thousands of miles to and from overwintering and breeding areas. Most monarchs east of the Rocky Mountains migrate from southern Canada and the northern United States to the mountains of interior Mexico to overwinter. Most monarchs west of the Continental Divide migrate to coastal California.

Monarchs east and west of the Rocky Mountains now face significant threats to their survival in both their summer and winter ranges, and their numbers have declined precipitously in recent years. Overall the North American monarch population has declined by more than 90 percent in the past two decades based on comparisons of the most recent population size estimates to the 20-year average. Numbers of monarchs east of the Rockies have declined by more than 90 percent since 1995; at most recent count, in winter 2013-2014, monarchs east of the Rockies dropped to the lowest number yet recorded, continuing the progression toward declining numbers seen over the last decade. Similarly, numbers of monarchs west of the Rockies have declined by more than 50 percent since 1997. The significant threats facing the monarch are high in magnitude and ongoing.

In recognition of the dire status of this symbolic animal, in June 2014 the White House issued a Presidential Memorandum creating a federal strategy to promote the health of honey bees and other pollinators including the monarch. Although this is an important acknowledgement of the large-scale issues that are threatening the monarch, much more tangible action is needed to protect the butterfly and its habitat. Specifically, protecting this iconic species under the Endangered Species Act is a step that should be immediately taken to safeguard and recover the monarch.

The Endangered Species Act (ESA) allows species to be listed as “threatened” when they are at risk of becoming endangered in a significant portion of their range. The ESA defines an endangered species as “any species which is in danger of extinction throughout all or a significant portion of its range” and a threatened species as “any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.” As applied here, the language of the statute, its legislative history and congressional intent, and the relevant judicial precedent interpreting and applying the statute all make clear that a species need not be at risk of worldwide extinction to qualify for ESA protection. Rather, in enacting the “significant portion of range” provision, Congress intended to provide a means to protect species before they are on the brink of extinction, which is of paramount importance to species conservation.

The best available scientific information indicates that the monarch butterfly is threatened in a significant portion of its range. The North American monarch population is significant because without it, the redundancy, resiliency, and representation of the species would be so impaired that the monarch would have an increased vulnerability to extinction. The migratory butterflies in eastern and western North America represent the vast majority of all monarchs in the world.

Though monarchs are found in relatively small, peripheral, and introduced populations in tropical and subtropical locations outside of North America (see Appendix A), these non-migrating populations cannot conserve the genetic diversity and spatial distribution of the species, are limited in population growth potential such that they cannot substitute for the abundance of the continental North American population, and are themselves vulnerable to extirpation.

Numerous species have been protected under the ESA that have large ranges and relatively abundant population sizes but that have experienced population decline and that face significant threats to their continued existence. A few examples of such species include the gray bat (*Myotis grisescens),* Indiana bat (*Myotis sodalis),* fat pocketbook mussel (*Potamilus capax),* piping plover (*Charadrius melodus),* Chinook salmon (*Oncorhynchus (=Salmo) tshawytscha)*, and small whorled pogonia flower (*Isotria medeoloides*). A species is not required to have declined to the level of range-wide endangerment in order to qualify for protection under the ESA.

The ESA states that a species shall be determined to be endangered or threatened based on any one of five factors (16 U.S.C. § 1533 (a)(1)): 1) the present or threatened destruction, modification, or curtailment of its habitat or range; 2) overutilization for commercial, recreational, scientific, or educational purposes; 3) disease or predation; 4) the inadequacy of exisiting regulatory mechanisms; and 5) other natural or manmade factors affecting its contined existence. The monarch is threatened by all five of these factors and thus warrants protection under the Act:

Factor One: Modification or Curtailment of Habitat or Range

Monarch habitat has been drastically reduced and degraded throughout the butterfly's summer and winter ranges and threats are ongoing. Monarch habitat is threatened by, among other things, pesticide use from genetically engineered, pesticide-resistant crop systems that kill milkweeds and nectar sources, as well as by development, logging, and climate change.

A primary threat to the monarch is the drastic loss of milkweed caused by increased and later-season use of the herbicide glyphosate in conjunction with widespread planting of genetically-engineered, herbicide-resistant corn and soybeans in the Corn Belt region of the United States and to planting of genetically-engineered cotton in California. In the Midwest, nearly ubiquitous adoption of, glyphosate-resistant "Roundup Ready" corn and soybeans has caused a precipitous decline of common milkweed, and thus of monarchs, which lay their eggs only on milkweeds. The majority of the world's monarchs originate in the Corn Belt region of the United States where milkweed loss has been severe, and the threat that this habitat loss poses to the resiliency, redundancy, and representation of the monarch cannot be overstated.

Monsanto introduced Roundup Ready soybeans in 1996 and Roundup Ready corn in 1998. Genetically-engineered herbicide-resistant varieties (nearly all Roundup Ready) now comprise 94 percent of soybeans and 89 percent of all corn grown in the United States. Glyphosate is not only being applied to vastly more acres than ever before, it is being applied more intensively to the acres that are treated with it. Between 1995, the year before Roundup Ready soybeans were introduced, and 2013, total glyphosate use on corn and soybeans rose from 10 million to 204 million pounds per year, a 20-fold increase. Roundup Ready crops have also shifted the application period later into the growing season when milkweed is more susceptible to glyphosate.

Additional monarch habitat is being lost due to the rapid conversion of grasslands and other milkweed-containing land types to corn and soybean fields to produce biofuels. Most remaining monarch habitat in the Midwest is on Conservation Reserve Program (CRP) lands. This habitat is threatened by ongoing conversion of these lands to corn and soybean production, a change driven by federal biofuels policy. Nationally, CRP acreage has shrunk by 11.2 million acres (30 percent) since 2007, with more than half of this decline occurring in the Midwest, which has lost 6.2 million CRP acres. This land-use change has resulted in the widespread elimination of milkweed from these habitats due to glyphosate use.

Glyphosate used in conjunction with Roundup Ready crops has nearly eliminated milkweed from cropland throughout the monarch's vital Midwest breeding range. It is estimated that in Iowa, for example, cropland lost 98.7 percent of its milkweed from 1999 to 2012. In just the 13 years from 1999 to 2012, it is estimated there was a 64 percent decline in overall milkweed in the Midwest, most of which was from croplands. Because cropland milkweed produces nearly four times as many monarchs as plants in other settings, milkweed loss in corn and soybean fields has had a disproportionate impact on monarch numbers. It is estimated that in 2012, the Midwest produced 88 percent fewer monarchs than it did in 1999.

Monarch habitat is further threatened by the imminent introduction of new herbicide-resistant crops that are genetically engineered to now be resistant to multiple herbicides including for the first time 2,4-D and dicamba, which will be used in addition to glyphosate. Herbicides frequently drift beyond the boundaries of crop fields to affect wild plants growing nearby. These new genetically engineered crops will lead to sharply increased herbicide use, continued elimination of common milkweed from cropland, and reduction via herbicide drift of flowering plants that provide monarch adults with nectar, thereby threatening monarch nectaring habitat. Remnant monarch habitat outside of croplands is also being lost and degraded.

Monarch breeding, nectaring, and wintering habitats have also been lost to development, and this threat is ongoing. Between 1982 and 2010, 43 million acres of land in the United States were newly developed, representing a 58 percent increase in developed land over a roughly 30-year period. Of note, more than 37 percent of developed land in the United States was developed during the last 28 years. East of the Rockies, it has been very roughly estimated that approximately 167 million acres of monarch habitat, an area about the size of Texas, may have been lost since the mid-1990s due to agricultural changes and development including nearly one-third of the monarch's total summer breeding range.

Monarch breeding habitat west of the Continental Divide is being lost due to urban and rural development, aggressive roadside management, herbicides, intensification of agriculture, and long-term drought. Glyphosate is also heavily used in the western portion of the monarch's range, and may be degrading habitat there as well.

The monarch is also threatened in its winter range. Monarch wintering habitat in California is threatened by development and natural senescence. Monarch wintering habitat in Mexico is threatened by logging, forest diseases, and climate change. Though large-scale illegal logging in the Mexican winter range has largely been curtailed, the economy of the monarch butterfly region faces serious economic challenges which catalyze small-scale illegal logging as a short-term option to cope with poverty.

Finally, climate change poses a dire threat to monarch habitat. Several scientists have predicted that the monarch's overwintering habitat in Mexico may be rendered unsuitable by global climate change, and that much of the monarch's summer range may also become unsuitable due to increasing temperatures.

Factor Two: Disease and Predation

Disease and predation are significant sources of mortality for monarchs. In light of recent population declines and the major threats facing monarch habitat, either predation or disease or both could rise to population-level threats putting the monarch butterfly at risk of extinction. Numerous pathogens infect monarchs including viruses, bacteria, and protozoan parasites. The parasite *Ophryocystis elektroscirrha* (OE) is the most studied of monarch parasites and is of particular concern. Monarchs that are infected with these protozoa do not fly as well or live as long as uninfected butterflies. OE disproportionally affects female butterflies and may be responsible for the declining percentage of females in the population, which has long-term implications for monarch survival and recovery. The drastic reduction in milkweed availability in agricultural fields and other factors reducing monarch habitat pushes butterflies into smaller habitat patches where they may be at higher risk of disease transmission. Global climate change magnifies the threat posed to monarchs from disease. Climate change could influence butterfly disease prevalence by affecting pathogen development, survival rates of parasites and hosts, processes of disease transmission, and stress and host susceptibility. The release of commercially-reared monarchs also heightens the threat posed to wild monarchs by disease due to both increased exposure risk and the potential introduction of novel strains of pathogens or pathogens that have evolved higher virulence in captivity.

Decreased monarch population sizes and reduced habitat availability exacerbate the threat of predation and parasitism to monarchs. The protective chemicals monarchs obtain from milkweeds provide some defense against predation, but monarchs have many natural predators, some of which are capable of consuming large numbers of eggs, caterpillars, and butterflies. Ants are a common predator on monarch eggs and have been recorded consuming 100 percent of eggs at some study sites. Monarch caterpillars are subject to high levels of predation and parasitism. A large suite of invertebrate predators including ants, spiders, crab spiders, and wasps prey on developing monarch larvae, and several species of flies and wasps parasitize larvae. Mortality rates as high as 100 percent at study sites have been reported for monarch caterpillars due to parasitism. Overall, only approximately 8 to 12 percent of monarch eggs and larvae survive to become adults. Adult monarch mortality rates as high as 44 percent from bird predation have been reported from winter colonies in Mexico. Overwintering adults are also subject to predation from mice, with mortality rates as high as 5 percent of an overwintering colony. Migrating and breeding adults face predation from birds, wasps, spiders, mantids, and dragonflies. While predation is a natural phenomenon, high levels of predation are of increasing concern given recent dramatic population declines and shrinking availability of both winter and summer habitat.

The high rates of mortality of monarch eggs, caterpillars, and adults from disease and predation underscore the importance to the long-term survival of the species of having a very large population size, and magnify the threat posed to the long-term survival of the species by recent dramatic population declines.

Factor Three: Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

Overutilization poses a significant potential threat to monarchs especially in light of recent dramatic population declines and in conjunction with the many other threats facing monarchs. Millions of monarchs are raised in captivity and sold commercially for primarily educational and entertainment purposes. Capture, sale, transport, and release of monarchs can threaten the wellbeing of wild monarch populations in several ways including disease transmission, loss of genetic diversity, and accumulation of deleterious genetic adaptations, especially when rearing and release is conducted without following careful protocols. Release of captive butterflies can also interfere with studies of the distribution and movement of wild butterflies which are increasingly important in light of habitat loss and climate change. Harvesting wild monarchs also has the potential to exacerbate population decline. In addition, viewing aggregations of wintering monarchs in Mexico and California is a popular tourist activity, and some of these activities may harm wild monarch populations if conducted improperly.

Petitioners recognize the valuable roles that scientific research, citizen monitoring, and classroom and at-home rearing of monarchs can play in monarch conservation and hence request that upon listing, the Service facilitate or waive permitting requirements for such activities that are beneficial to monarch conservation. See Appendix B of this petition for requested rules to facilitate monarch butterfly conservation, science, citizen monitoring, and education.

Factor Four: The Inadequacy of Existing Regulatory Mechanisms

Though numerous voluntary efforts are in place that benefit monarch conservation, there are no existing regulatory mechanisms which adequately address the multitude of complex and synergistic threats that are driving the monarch’s precipitous decline. Some programs are in place at the international, federal, state, and local levels that benefit monarchs, but due to the butterfly’s rapid and severe decline and the significant, ongoing threats to its survival, the monarch needs the comprehensive protection that only the ESA can provide to ensure its persistence and recovery.

Factor Five: Other Natural or Manmade Factors Affecting the Monarch’s Continued Existence

The monarch is threatened by several other factors including global climate change, severe weather events, pesticides, and the spread of invasive species. Unfavorable weather conditions have been identified as a primary factor contributing to the recent drastic declines in monarch populations. Weather that is too hot or too cold at critical times in monarch development can cause massive mortality of caterpillars and adults. A single winter storm event in Mexican overwintering habitat in 2002 killed an estimated 450-500 million monarchs. This high death toll from a single storm event is particularly staggering given that the entire monarch population now numbers only about 35 million butterflies. Because of their narrow thermal tolerance and specific microhabitat requirements, climate change threatens monarchs in their summer and winter ranges. The threat from climate change in the monarch's overwintering habitat in Mexico is so dire that monarchs may no longer occur in the Monarch Butterfly Biosphere Reserve by the end of the century due to climatic changes. The monarch's summer breeding habitat in the United States is also predicted to become too hot in many areas for monarch's to be able to successfully reproduce.

Pesticides are widely used in the United States, with more than one billion pounds applied each year, including in the core of the monarch's breeding range where they threaten all monarch life stages. In particular, monarchs are threatened by pesticides used in agriculture, in lawns and gardens, and for mosquito and grasshopper control. Monarchs are threatened by habitat loss due to increasing use of glyphosate and other herbicides that kill host and nectar plants, and also by lethal and sub-lethal effects of insecticides such as neonicotinoids, which are persistent in the environment and are known to be highly toxic to pollinators.

Monarchs are also threatened by the spread of invasive tropical milkweed species, which are actively planted by gardeners with the intent to attract monarchs to their gardens. Unlike native milkweeds, this species grows year round so may disrupt migratory cues, and monarchs that breed on the same plants year round may have increased pathogen infections.

In sum, monarch butterfly numbers have declined severely and the monarch is threatened by all five of the ESA listing factors.

Accordingly, we hereby request that the Service list the monarch as a threatened species with a 4(d) rule, which would allow for protection of the monarch but also still permit activities to continue that promote the conservation of the species, such as scientific research and monitoring, citizen monitoring and tagging, and non-commercial classroom and household rearing of monarchs for educational purposes.

INTRODUCTION

The charismatic monarch butterfly is an irreplaceable piece of the natural heritage of North America. Yet this butterfly, that was once common across the country, is now plummeting toward extinction and needs protection or is at risk of being lost forever.

The monarch has played a unique and prominent role in the imagination of our country, especially so for an insect. Millions of school children have reared monarchs in classrooms and learned about metamorphosis by watching the caterpillars transform. Monarchs are pivotal in science education and provide a textbook example of the principle of co-evolution and mimicry due to their complex relationship with milkweeds, their sole host plants, and with viceroy butterflies (*Limenitis archippus)*, which are mutual mimics with monarchs, helping both butterflies avert predation. Monarchs have been reared on the international space station and were the first butterflies to have their genome sequenced. They are the official state butterfly of no less than seven states. For generations of Americans and Canadians, these large orange and black butterflies have been symbols of summer time outdoors and have served as ambassadors of nature in people's backyards and gardens. In Mexico, the arrival of monarchs heralds Day of the Dead celebrations, and the beginning of winter.

No other butterfly species on Earth undertakes a migration like the North American monarch. The multi-generational migration of the monarch butterfly can cover thousands of miles and is often described as spectacular, mysterious, and extraordinary. In late summer the butterflies begin their journey from Canada and northern states to the mountains of central Mexico or the coast of California where they will overwinter. The following spring that same generation of butterflies will return north to lay eggs on milkweed plants. Those eggs hatch into caterpillars, which feed on milkweeds, and transform into butterflies that continue to fly north in search of newly emerging milkweeds. This process is repeated for several generations, until the last generation—the "great-great-grandchildren" of the butterflies that departed overwintering sites the previous spring—returns to winter roosts the following autumn. Scientists are still trying to understand exactly how monarchs—multiple generations later—find their way to the very same winter roosts that hosted their ancestors. Visitation of overwintering monarch groves is of economic value in California and in Mexico, where such tourism is an important source of revenue for rural communities.

Monarchs are important not only educationally and scientifically, but also within the ecosystem. The monarch plays a valuable role in the food web. Despite the toxins they accumulate from milkweeds, monarchs provide food for overwintering migratory songbirds, especially for orioles, grosbeaks, and towhees. Many invertebrate animals prey on monarch eggs and caterpillars including numerous species of ants, spiders, beetles, true bugs, lacewings, and wasps. Overwintering adults also provide food for small mammals in the forest.

Monarchs visit many different species of flowers to drink nectar and probably act as incidental pollinators in many cases. While the monarch's contribution to plant pollination has not been well studied, it may play an important role in the long distance transfer of pollen for some plants, and, due to its historical abundance, its contribution to the pollination of some plants may be significant.

The monarch was very recently a highly abundant species, and its population reduction indicates environmental change on a large and rapid scale. The factors that are causing monarch numbers to plummet also threaten many other species of butterflies and bees, which in turn threatens the wellbeing of people because the food security of humans is dependent on the ecological services that pollinators provide.

In their overwintering groves there were once so many monarchs that the sound of their fluttering wings was commonly described as a rippling stream or a summer rain. Early newspaper descriptions of monarchs gathered on trees in California described branches breaking under the weight of so many butterflies, and depicted the masses of butterflies as “the personification of happiness” (in Lane 1993, p. 341). As recently as the winter of 1996-1997 the number of monarchs from east of the Rockies alone was estimated at around one billion butterflies. In the course of less than 20 years, that number has fallen to fewer than 35 million monarchs, representing a decline of 97 percent from the 1996-1997 high and a 90 percent decline from the 20-year average. The number of monarchs that overwinter west of the Rockies has also undergone a dramatic recent decline of 90 percent from the 1997 high (when monitoring began) and a 51 percent decline from the 17-year average.

Numerous landscape-level factors have contributed to the decline of the monarch and pose ongoing threats to its continued existence. The monarch is entirely dependent on milkweeds in its summer breeding range, and milkweed availability has been drastically reduced as a result of the increased spraying of herbicides caused by the widespread planting of genetically-engineered, herbicide-resistant crops, as predicted over a decade ago (Brower 2001). Milkweed loss has been exacerbated by the push for increased biofuel production and the planting of millions of acres of land formerly in the Conservation Reserve Program or other milkweed-compatible land uses with genetically-engineered, herbicide-resistant corn and soybean crops. Monarch overwintering habitat is threatened by development in California and by illegal logging in Mexico. Monarchs are further threatened by pesticide use, drought and other severe weather events, and climate change. Monarchs are also threatened by disease, predation, and overutilization, all of which are exacerbated by other stressors.

The total population of monarchs in North America is now approximately 35 million butterflies, which could be misinterpreted to mean that the butterfly is not threatened with extinction. That millions of monarchs still survive, however, does not indicate that the species is secure. While rare species with narrow ranges are often given conservation priority, common species that face multiple environmental stressors, such as those impacting the monarch, can undergo unanticipated rapid decline or extirpation. Monarchs face multiple, synergistic, complex threats that have contributed to an extreme and rapid reduction in population size. Moreover, monarch life history strategy requires a very large population size to compensate for high levels of predation and mortality from multiple factors.

It would be unwise to assume that the monarch is too common to be threatened with extinction. There is a distressing record of the rapid and unexpected decline of once common and widespread species. Examples of extremely abundant species that plummeted to unforeseen extinction include the passenger pigeon (*Ectopistes simigratorius*) and the Rocky Mountain grasshopper (*Melanoplus spretus*) (Schorger 1973). The passenger pigeon went extinct in the early 20th century, yet in the late 19th century it was one of the most abundant birds in the country, with flocks so numerous they darkened the sky and took 14 hours to fly past. Habitat loss and hunting reduced the pigeon from billions of birds to extinction in a matter of decades. Similarly, the Rocky Mountain grasshopper once ranged throughout western North America and was so numerous that a swarm that passed through Nebraska in 1874 numbered more than 12 trillion grasshoppers covering an estimated 198,000 square miles, an area larger than the state of California (Chapco and Litzenberger 2004). Due to habitat loss from plowing and irrigation, the grasshopper plunged to extinction in less than 30 years, and the last living individual was seen in Canada in 1902 (Ibid.).

Unfortunately, there is a long and growing list of abundant species that have undergone precipitous population declines. The once common woodland caribou (*Rangifer tarandus caribou*) once inhabited much of the northern lower 48 states, including the northern Rocky Mountains, upper Midwest and Northeast, but in less than a century habitat alteration and hunting reduced the population to just a few dozen individuals in Idaho and Washington. Numerous native mammalian species in Australia that were at one time abundant and widespread have gone extinct or have been wiped out of more than 95 percent of their historic ranges (Dickman 2007, Bilney et al. 2009). Lindenmayer et al. (2011) document the rapid and unanticipated decline of the common Australian arboreal marsupial, the greater glider (*Petauroides volans*) which was lost from a 6,500-hectare study area in just a 3-year period due to changing environmental conditions. Widespread declines have also been noted in migratory animal populations—such as birds and ungulates—that involve billions of individuals (Bolger et al. 2008, Robbins et al. 1989, Wilcove 2008).

The collapse of numerous species of fishes resulting from overharvesting is a well-documented example of the rapid decline of once-abundant populations (Levin et al. 2006). Four North American bumblebee species with broad geographic ranges have recently declined in abundance by up to 96 percent, some over just a twenty-year period (Cameron et al. 2011). Nearly seven million bats in North America have perished since 2006 due to the rapid spread of a fungal disease known as white nose syndrome (*Geomyces destructans*), which has affected seven species and spread to 25 states, wiping out the majority of some species' populations and causing declines of more than 90 percent within timeframes of less than three years. The once common little brown bat (*Myotis lucifugus*) has nearly been extirpated in the Northeast due to the fungus (Frick et al. 2010). Thousands of frog populations have been decimated by the spread of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) since 1998 including dozens of species extinctions and precipitous declines of even widespread species (La Marca et al. 2005, Skerratt et al. 2007). Many species of well-known birds have undergone recent dramatic decline in agricultural areas in Europe (Vincent 2005, Freeman et al. 2008). In the United States, rusty blackbirds (*Euphagus carolinus*) have experienced one of the most significant declines ever documented among North American birds in recent times. Data from long-term surveys indicate that rusty blackbird numbers have plummeted 85-95 percent since the mid-1900s due to habitat alteration and other factors (Greenberg and Droege 1999).

These examples of the rapid and unanticipated loss of common species illustrate how complacency towards species with large population sizes can have disastrous consequences when timely action is not undertaken to safeguard their populations (Lindenmayer et al. 2011). As a further example, recent failure to act quickly on evidence of rapid population decline led to the extinction of a bat in Australia, the Christmas Island pipistrelle (*Pipistrellus murrayi*), which was a common species as recently as 1984 (Martin et al. 2012, p. 275). By 1994 it was in marked decline and recommendations from scientists to form an emergency response plan were considered but not carried out. Delays in decision making resulted in lack of action and the bat became extinct; the last individual was seen in 2009 ((Martin et al. 2012, p. 274).

Delays in protection for declining species and assumptions about the resiliency of once-common species can lead to lack of timely intervention, further population declines, greater recovery costs, or ultimately, extinction. The downward trajectory of the monarch and the enormity of the threats it is facing plainly show that this charismatic butterfly warrants protection under the ESA. Timely protection is imperative to ensure that the monarch survives for future generations.

NATURAL HISTORY

TAXONOMY

The monarch (*Danaus plexippus plexippus)* is a member of the family Nymphalidae (Rafinesque, 1815), a family characterized in part by small front legs with specialized hairs, giving them the common name “brushfoot butterflies”; they also have particular wing venation patterns, and antennal clubs with two grooves. Monarchs are in the subfamily Danaianae, “milkweed butterflies” (Boisduval, 1833), which lay their eggs only on plants in the family Apocynaceae (dogbane) in the milkweed subfamily Asclepiadoideae, genus *Asclepias* (L.) and related genera. Milkweed butterflies are specialized to accumulate toxins from milkweed plants into their larval and adult bodies for predator defense (Brower 1984).

The monarch was first described in 1758 by Linnaeus in *Systema Naturae* in the genus *Papilio*, and later became the type species for the genus *Danaus* (Kluk 1802), comprised of 12 mostly tropical species that are medium to large butterflies, typically with bright color patterns (Brower and Jeansonne 2004).

There are six currently recognized subspecies of monarch, including the subject of this petition, the nominal subspecies *D. p. plexippus*, which occurs in migratory populations across North America from southern Canada (about 50 degrees N), south to California and Mexico in winter, and also in non-migratory populations in southern Florida and other parts of the extreme southern United States. There are also recently established non-migratory populations of *D. p. plexippus* in Hawaii, and in other countries throughout Oceania in the Pacific and from the Bahamas to coastal Spain in the Atlantic (Smith et al. 2005, *see* Appendix A of this petition).

Danaus plexippus plexippus (Linnaeus, 1758) is a valid and currently recognized subspecies (Pelham 2008). Its standardized common name is simply monarch (*see*: http://lepsurvey.carolinanature.com/sc-nabn/danaids.html). Its Taxonomic Serial Number in the Integrated Taxonomic Information System is 779023.

Genetic research to determine the relationship between monarch populations is ongoing. Lyons et al. (2012) used microsatellite markers to evaluate the genetic structure of the migratory monarch populations in eastern and western North America, as well as the non-migratory populations of Hawaii and New Zealand. They did not find evidence for genetic differentiation between the migratory monarch populations of eastern and western North America, but did find that the migratory populations have diverged genetically from the non-migratory resident populations of Hawaii and New Zealand. However, no taxonomic changes have been made in response to this new research; the monarchs found in Hawaii and New Zealand are still considered to be the same subspecies as the migratory animals of eastern and western North America - *D. p. plexippus*. This petition requests ESA protection for the subspecies *D. p. plexippus*. Should future studies published within the time of review of this petition show that the North American migratory populations of monarch constitute a subspecies distinct from non-migratory populations of Hawaii, New Zealand, or other locations (such as south Florida), then in addition to determining if *D. p. plexippus* the subspecies should be protected, petitioners also request that the Service evaluate whether any newly identified North American subspecies may warrant federal protection.

DESCRIPTION

Photo © Jeffrey E. Belth

Figure 1. Female monarch on ovipositing on common milkweed flower bud.

The monarch, one of the most recognizable butterflies in North America, has several distinctive morphological characteristics (Ackery and Vane-Wright 1984, pp. 201 – 204, and references therein; Oberhauser and Solensky 2004, Commission for Environmental Cooperation 2008). It is a large butterfly that flies with its orange and black wings held in a "v" shape. The upper surfaces of both the forewing and hindwing have black or dark-brown veins outlining an orange background, with two rows of white and whitish-yellow spots at the margins (cover photo). The dark body is also white-spotted. Underwings have a similar color pattern but the hindwing background color is much lighter, from tan to light orange (Figure 1). The forewing is more angular than the hindwing with an elongated apex that has lighter orange spots near the tip. The wingspan is about 10 cm, with males averaging larger wing sizes than females, although there is substantial variability. Males also have a black scent pouch, or androconium, in the center of each hind wing. Females have thicker dark venation than do males.

There appears to be a relationship between wing size and shape and migratory behavior in monarchs. Monarchs east of the Rockies, which migrate longer distances than monarchs from the west, have larger and more angular forewings than their western counterparts on average, even when reared in a common environment, indicating a potential genetic basis for this morphological trait (Altizer and Davis 2010). Monarchs from Hawaii, which do not migrate, have even smaller forewings than western monarchs, although they are just as rounded as in the eastern North American butterflies. Forewings of monarchs from non-migratory monarch populations in South Florida are both smaller and rounder than forewings of migratory populations of *D. p. plexippus* (Dockx 2012).

RANGE

For *D. p. plexippus* in North America, the geographical range encompasses breeding areas, migration routes including staging areas, and winter roosts. During the spring and summer breeding season, *D. p. plexippus* disperses throughout the United States and southern Canada when successive generations migrate and expand north with the availability of suitable milkweeds as summer progresses. During winter, butterflies that primarily originate from east of the Rockies converge on specific locations in Mexico, contracting from a summer range of about 100 million hectares to winter roosts that total 20 hectares at most (Wassenaar and Hobson 1998, Oberhauser and Solensky 2004, p. 79, Commission for Environmental Cooperation 2008). Monarchs that breed along the east coast migrate to Florida (Knight and Brower 2009), where some fly west along the coast of the Gulf of Mexico and continue to Mexico, or apparently integrate into stable populations in Florida. A few continue migrating to Cuba and other islands in the Caribbean (Dockx 2012). Monarchs from west of the Rockies primarily fly to a series of roosting sites centered along coastal areas of south-central California (Jepsen and Black in press), although some migrate to the Mexican roosts used by eastern monarchs (Brower and Pyle 2004, Lyons et al. 2012).

Some monarchs have established small non-migratory populations in southern Florida and areas along the Gulf of Mexico where they reside year-round. Some monarchs that migrate to Florida to overwinter apparently integrate into the stationary populations (Knight and Brower 2009), and some continue to Cuba and integrate into populations of a monarch subspecies found in the Caribbean (*D. p. megalippe)* (Dockx 2002, Dockx 2007, 2012). Since they do not migrate, some researchers classify monarchs in southern Florida as *D. p. megalippe* (Smith et al. 2005), but others consider them to be *D. p. plexippus* (Pelham 2008). The establishment of stationary populations in Florida and other southern areas may be facilitated by the spread of nonnative heat-tolerant milkweeds in the southeastern states (Harvey et al. 2009).

In the past two centuries, *D. p. plexippus* has established small non-migratory populations in non-native habitats outside of continental North America (*see* Appendix A of this petition). Monarchs are thought to have moved both east and west of North America, and between various islands via favorable winds and storms, by hitchhiking on boats, and by intentional human introduction (Clarke and Zalucki 2004, Zalucki et al. 2004). During the mid- to late-1800s, monarchs spread across the Pacific Ocean to Hawaii, Australia, New Zealand, and many other islands (Zalucki and Clarke 2004). During this same time period, monarchs also moved across the Atlantic, colonizing islands including the Azores and Canary Islands, and coastal areas of Spain (Haeger et al. 2011). Various lines of evidence point to more than one introduction event in the Pacific, with populations in Hawaii and Australia likely forming independently (Lyons et al. 2012, Shephard et al. 2002), and other Pacific islands being colonized by radiation from original areas (Zalucki et al. 2004). Introduction and spread in the Atlantic and Spain have not been as well studied.

Based on the short amount of time since the introduction of *D. p. plexippus* outside of North America, these populations are still considered part of the nominal subspecies. Genetic analyses show that they have less genetic diversity than monarchs in North America, and are now genetically isolated (Lyons et al. 2012). Whether or not such differences constitute grounds for ultimately separating these disjunct populations into subspecies, there does appear to be enough reproductive isolation for them to have begun the process of speciation. See Appendix A for more information on populations of monarchs that have become established outside of their traditional North American range.

LIFE HISTORY

The life cycle of the monarch butterfly is intertwined directly with milkweed plants (Oberhauser 2004). The monarch life cycle has been described in great detail in various reports and proceedings (*see*: Malcolm and Zalucki 1993, Oberhauser and Solensky 2004, Commission for Environmental Cooperation 2008, Bériault et al. 2010).

Photo © Jeffrey E. Belth

Figure 2. Monarch egg on common milkweed leaf.

Photo © Jeffrey E. Belth

Figure 3. Monarch caterpillar, fifth instar, chewing on common milkweed leaf.

Photos © Jeffrey E. Belth

Figure 4. Monarch chrysalis in the process of development.

Monarchs lay their eggs only on plants in the Apocynaceae (dogbane family) in the milkweed subfamily Asclepiadoideae, genus *Asclepias* (L.) and related genera. Many milkweeds defend themselves from generalist herbivores by exuding sticky, bitter-tasting latex from cut leaves and other plant parts, and by producing compounds such as cardenolides that are toxic to many animals, including most vertebrates. Larvae of some milkweed butterflies are specialized to tolerate latex and accumulate cardenolides and/or other secondary compounds of the host plants into their bodies. They use the plant's chemicals for their own defense against predators (Brower 1984), for pheromone production, and for other specific functions during their lifecycle (Brower et al. 2010, Agrawal et al. 2012).

After mating a female must soon find milkweed plants of a suitable species on which to lay her eggs. Some milkweed-family species have such high levels of toxins that even the larvae of milkweed-adapted species such as monarchs will not thrive (Zalucki et al. 2001a, b). Other milkweed species have such low cardenolide levels that larvae and subsequent adults may not be chemically protected from predation (Lynch and Martin 1993). Nutrient content of milkweeds varies with environment, and declines during the season (Oyeyele and Zalucki 1990, Agrawal et al. 2012), so a female needs to locate healthy plants young enough to support the full development of her offspring.

Eggs are laid singly, on the underside of a young leaf or on a flower bud. The eggs are cream-colored or light green, ovate to conical in shape, and about 1.2 by 0.9 mm in size (Figure 2). The eggs weigh less than 0.5 mg each and have ridges running longitudinally from the pointed top to the truncated base. Eggs take three to eight days to develop and hatch into larvae (caterpillars). Larval monarchs take nine to 14 days to go through five instar stages before pupating. Instar stages can be distinguished by larval coloration and tentacle length, size of the head capsule, and other characteristics (Details of life history stages in this and following paragraphs, unless otherwise noted, are from the Monarch Larva Monitoring Project "Larval Field Guide," available at: http://www.mlmp.org/Resources/LarvalFieldGuide/Default.aspx; and the Larval Monitoring Handbook, available at: http://www.mlmp.org/Resources/pdf/Monarch-Monitoring_en.pdf).

The first instar larva, just out of the egg, is solid pale green and translucent, without banding coloration or tentacles. It eats the nutritious egg capsule first, and then uses a circular motion to eat milkweed leaf tissue without eliciting an overwhelming amount of latex that could entrap it. After the first molt, the second instar larva develops a characteristic pattern of white, yellow and black transverse bands. The opaque body is covered in short setae, and pairs of black tentacles start to grow, one pair on the thorax and another pair on the abdomen. The third instar larva has more distinct bands, particularly on the abdomen, and the two pairs of tentacles continue to elongate. Legs on the thorax differentiate into a smaller pair near the head and two larger pairs further back. These third-stage caterpillars begin to eat along leaf edges. The fourth instar is characterized by a new banding pattern on the thorax, and white spots on the prolegs near the back of the caterpillar.

The fifth and last instar larva (Figure 3) has a more complex banding pattern and white dots on the prolegs, with front legs that are small and very close to the head. The fifth instar is large relative to the earlier instars; the body is 25 to 45 mm long and 5 to 8 mm wide, compared to the tiny first instar that is only 2 to 6 mm long and 0.5 to 1.5 mm wide. The body mass of fifth stage caterpillars has increased about 2000-fold from first stage instars. Fifth stage instar larvae often cut the petiole or midrib of milkweed leaves to restrict the latex flow so that they can eat more leaf tissue to support the last growth period before pupation. Larvae must eat constantly to ingest enough milkweed to increase in mass so dramatically within a few weeks.

Larvae in the final stages of development stop feeding to search for a location to form a pupa, or chrysalis, the last stage of development before the emergence of the adult butterfly (Figure 4). The fifth stage larva attaches itself securely to a chosen leaf or branch with a silk pad, latching on with its hind legs and hanging down. The larva then molts to reveal an opaque, blue-green chrysalis adorned with gold dots. At normal summer temperatures, adult morphology develops within a few weeks. The cuticle of the chrysalis becomes transparent and the monarch's characteristic orange and black wings become visible. At the end of metamorphosis, the adult emerges from the chrysalis, expands its wings and flies away.

Monarch metamorphosis from egg to adult occurs in as little as 25 days during warm summer temperatures, to as many as 7 weeks during cool spring conditions. During the development period both larvae and their milkweed hosts are vulnerable to weather extremes, predators, parasites and diseases; commonly, fewer than 10 percent of monarch eggs and caterpillars survive.

Breeding adults first mate a few days after emergence. Females lay eggs on milkweed shortly after mating, and only live from two to five weeks, in which a single female may lay hundreds of eggs. During an average summer in North America, several generations of breeding butterflies will be produced.

Monarchs in the fall migratory generation go into reproductive diapause instead of mating. Diapause is usually maintained from late summer or fall through most of the winter, so most females do not mate and lay eggs until just before or during their return trip north in spring.

Diapause studies found that by the last week in August, one-third of wild-caught female monarchs in west-central Wisconsin and east-central Minnesota were in reproductive diapause, presumably in response to changing day length and temperature conditions (Goehring and Oberhauser 2002). By the end of the second week in September, all wild-caught and emerging captive female monarchs were in diapause (Goehring and Oberhauser 2002, Prysby and Oberhauser 2004). Not all migratory monarchs, however, enter reproductive diapause, at least in the southern states (Borland et al. 2004, Knight and Brower 2009, McCord and Davis 2010). Overwintering butterflies can live up to nine months, in contrast to the few-week lifespan of spring and summer generation adults.

Body condition and total fecundity are influenced by the temporal and spatial pattern of milkweed plants in the landscape, which determines how far adults must move in search of host plants for their eggs. Late-season decline in milkweed quality may be one of the triggers for larvae to turn into butterflies that enter diapause in the fall.

Some life history details differ between western and eastern *D. p. plexippus* in North America and elsewhere, in conjunction with their specific habitat requirements.

FEEDING

Adult monarchs obtain sugar from nectar and convert it to lipids to use as their energy source (Brower et al. 2006, Brower et al. in press). Adult monarchs are not directly dependent on milkweeds for food, although they benefit from milkweed-specific cardenolides and other chemicals sequestered during larval growth that make adults distasteful and toxic to predators. Both breeding and migrating adults sip nectar from many native and nonnative flowers including milkweeds, asters (*Asteraceae* spp.*),* forget-me-nots (*Boraginaceae* spp.), lilies (*Liliaceae* spp.), verbenas (*Verbenaceae* spp.), mallows (*Ranunculacea* spp.), wild carrots (*Apiaceae* spp.), legumes (*Fabaceae* spp.), goldenrod (*Solidago* spp.), clover (*Trifolium* spp.), alfalfa (*Medicago* spp.), butterfly bush (*Buddleja* spp.), and numerous others (Tooker et al. 2002, Brower et al. 2006). Tooker et al. (2002) analyzed and updated records from Robertson (1928) of butterfly visits to flowers near Carlinville, Illinois for 33 years. These records show monarchs visiting 61 different flower species in 39 genera from 15 families.

MIGRATION

No stage of development of monarchs can survive freezing temperatures during winters in most of North America, so during autumn, *D. p. plexippus* adults undergo a series of physiological changes that result in reproductive diapause, accumulation of lipids, and directional migration to the south and west (Solensky 2004a, Merlin et al. 2012).

Migrating adults put energy from nectar into lipids for fuel instead of reproduction, and are thus usually heavier than summer butterflies (Brower et al. 2006, Brower et al. in press). They move directionally toward their winter roosts, taking different routes depending on their origins (Brower and Pyle 2004, Howard and Davis 2008), and covering an average of 25 to 30 miles per day (Brower et al. 2006), stopping along the way for nectar and shelter (Davis et al. 2012).

Upon reaching their destination, butterflies cluster together in trees located in specific microclimates that keep them cool enough to conserve lipid reserves, but not so cold that the butterflies freeze (Brower et al. 2011). Monarchs at roosts are vulnerable to storms, freezing, dehydration (Brower et al. 2011), and predation (Arellano et al. 1993, Brower and Calvert 1985, Fink and Brower 1981, Glendinning 1993) that can result in high mortality. Surviving butterflies remain in winter locations until changing environmental conditions alter hormone levels in the spring and spur the butterflies to break diapause, begin mating, and journey north to begin the breeding cycles again (Oberhauser and Frey 1997).

Monarchs that migrate to inland Mexico merge and congregate in huge colonies occupying very small areas of specific habitat. Some mating occurs at these winter roosts before spring dispersal (Oberhauser and Frey 1997, Brower et al. 2007). Most individuals that overwinter colonize northern Mexico and the southern tier of the United States as milkweeds develop, although a few migrate directly to more northern areas (Miller et al. 2012, Flockhart et al. 2013). Because breeding monarch adults typically only live from two to five weeks, successive generations continue north and east as southern areas get too hot and milkweeds decline in number and quality. Remigration in spring must be timed so that females arrive at a particular latitude after milkweed plants have emerged, and when the weather is settled and warm enough so that larvae survive and develop at a healthy rate (Cockrell et al. 1993, Davis and Howard 2005).

Reproductive females generally head north from inland Mexico beginning in late February to early March. They start laying eggs on fresh milkweeds in northern Mexico, Texas, southern Oklahoma and Kansas, and to a lesser extent, Louisiana, Florida and other Gulf states, generally between mid-March and the beginning of May. In late April the first-generation butterflies—offspring of the migrants from Mexico—continue to move north, laying eggs throughout the mid-South into the Midwest and North. Then in June, the main colonization of the Midwest and

North takes place with two to three more generations being produced there before migration south begins in August (Cockrell et al. 1993, Howard and Davis 2004, Flockhart et al. 2013).

The small number of monarchs that migrate to Cuba and the Caribbean apparently do not return to North America (Dockx 2002, Dockx 2007, 2012, Knight and Brower 2009) perhaps because they do not experience the suite of environmental conditions required to trigger migration (Guerra and Reppert 2013).

The fall migratory route of eastern monarchs has been studied since the 1930s (Urquhart and Urquhart 1978) and monitoring continues through the present via several citizen science projects (Howard and Davis 2008 and references therein). Monarchs east of the Rockies follow one main "central" flyway from southern Ontario and Midwest states south-southwest through the states of Kansas, Missouri, Oklahoma and Arkansas to Texas and Northern Mexico (Howard and Davis 2008). There is also a second flyway along the easternmost states and coastal areas. A large gap without monarch roost sightings exists between the central and eastern/coastal flyway (Howard and Davis 2008, *see* Figure 5, below). During spring migration, monarchs do not congregate in roosts and monarch occurrence is largely coincident with breeding habitat and the seasonal development of milkweed (Solensky 2004a).

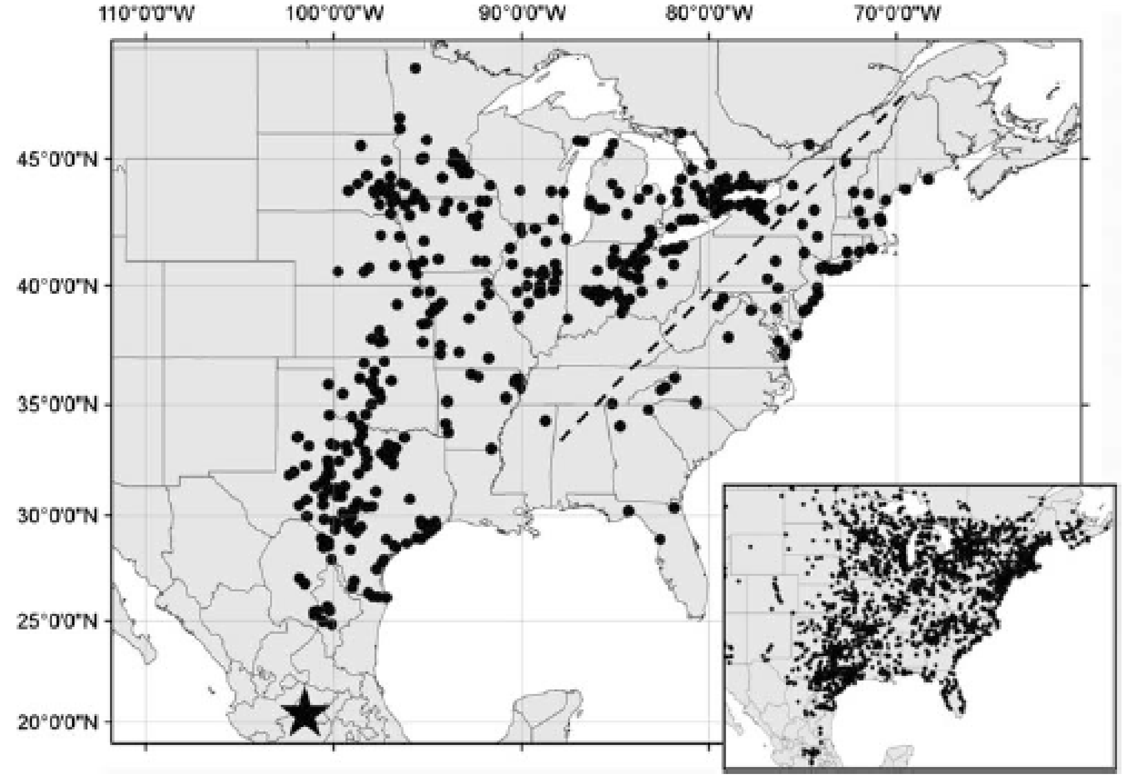


Figure 5. Central and eastern northward migratory flyways of monarchs east of the Rockies. Dots represent observations of roost sightings from Journey North data. The dashed line represents an apparent gap in monarch flyways. The star represents the overwintering sites in inland Mexico. Figure 2 from Howard and Davis 2008, original caption omitted.

Monarch butterflies in western North America migrate to overwintering sites in coastal California and coastal Mexico (Figures 6, 7, 8). Monarchs have historically aggregated in the fall and winter at more than 450 wooded sites scattered along 620 miles of the California coast from northern Mendocino County to as far south as Baja California, Mexico (Lane 1993, Leong et al. 2004, Jepsen and Black in press), although in the past ten years, only 72 of these sites have hosted more than 1,000 butterflies (Figure 7). In the fall of 2013, only 22 sites hosted more than 1,000 butterflies. Smaller aggregations of monarchs consisting of tens to hundreds of butterflies have been reported from Arizona and southeastern California (Monroe et al. 2013, California Natural Diversity Database 2012, Xerces Society 2013).

Figure 6. Winter and potential breeding range of western monarchs. Dots represent western monarch overwintering sites. Shaded areas represent the most likely locations of breeding grounds for migratory monarchs based on late-summer milkweed occurrence and thermal conditions. Lines within state boundaries represent climatic regions. Figure 1 from Stevens and Frey 2010, original caption omitted.

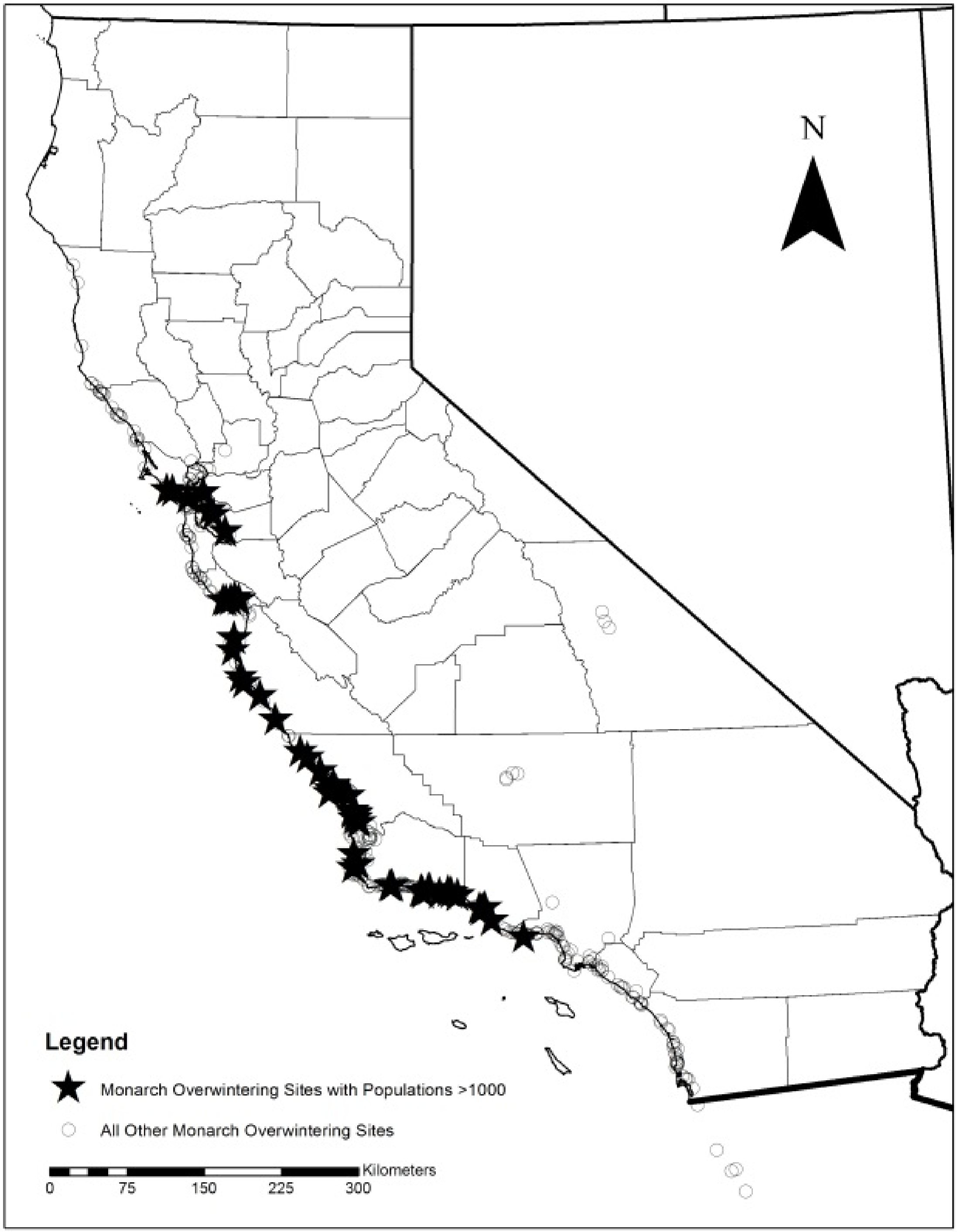


Figure 7. Western monarch overwintering sites. Dots represent all of the 458 recorded western monarch overwintering locations. Stars represent all overwintering sites that have hosted monarch populations of more than 1,000 butterflies at any point from 2003-2013. Figure from Jepsen and Black in press.

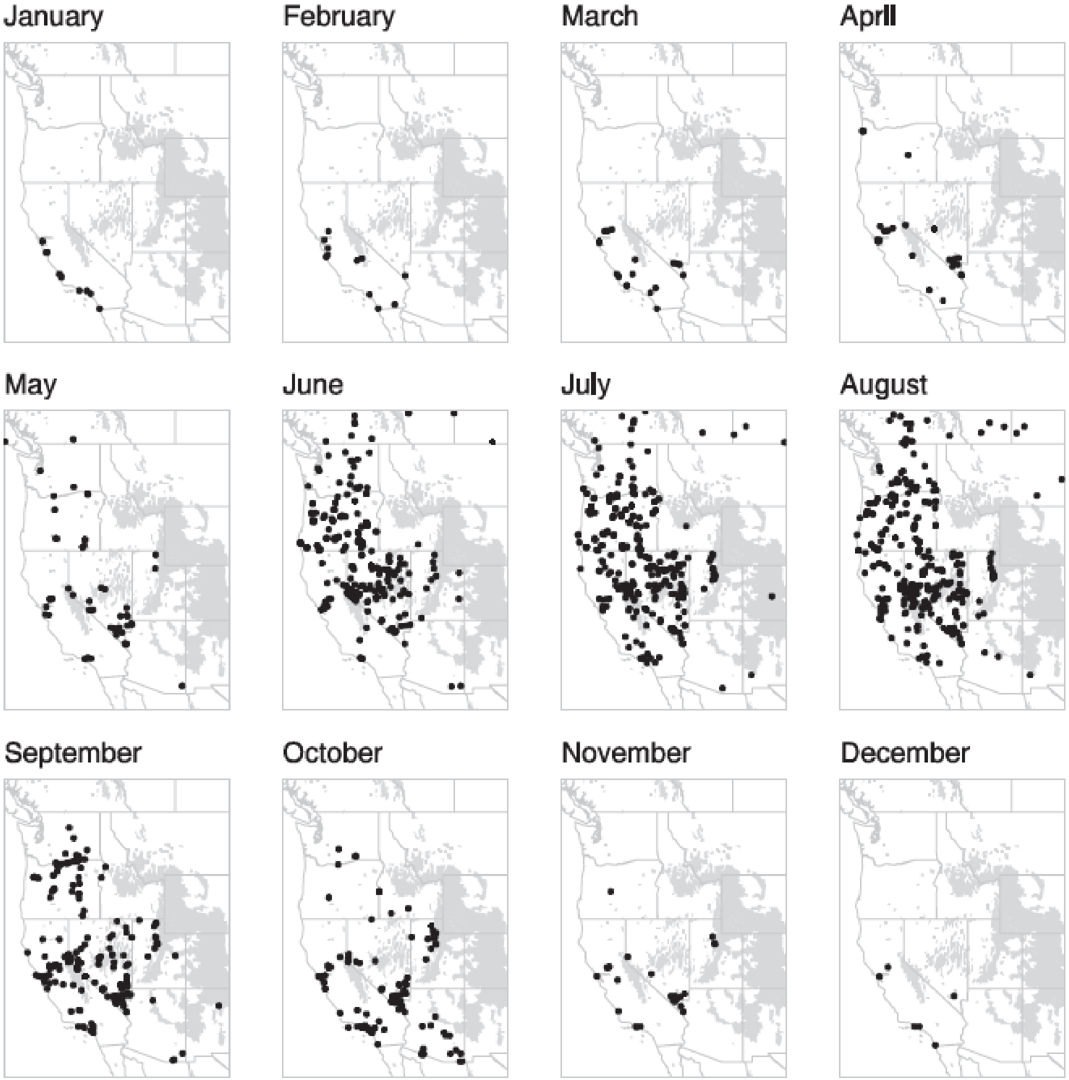


Figure 8. Western monarch collection records across the calendar year. Dots represent monarch specimens. Shaded regions are areas of high elevation (>2000 m). Figure 1 from Dingle et al. 2005, original caption omitted.

HABITAT

In general, butterfly habitat requirements include host plants for larvae, adult nectar sources, and sites for roosting, thermoregulation, mating, hibernation, and predator escape (Zalucki and Lammers 2010). In addition to these, the monarch butterfly requires conditions and resources for initiating and completing migration both to and from winter roosting areas, making them vulnerable to habitat degradation across wide areas. Because monarchs are host-plant specific, they are entirely dependent on the abundance of milkweeds, and threats to milkweed thus threaten their survival, as do threats to the specific forested areas that provide the microclimatic conditions they need to survive the winter. Monarchs and their habitat are also highly vulnerable to erratic climate conditions because their successful survival, metamorphosis and migration are dependent on appropriate temperature and moisture regimes.

In the broadest sense, monarch habitat is defined by the distribution of suitable species of milkweeds and their abundance and condition. Milkweeds contain species-specific suites of toxic secondary compounds used for defense against herbivores that include cardiac glycosides such as cardenolides, and various alkaloids. Monarchs use the toxic chemicals in milkweeds for their own defense, and generally will not lay eggs on any other species; nor will caterpillars eat leaves of other plants (Brower 1984).

Milkweeds are in the family Apocynaceae (dogbane family), subfamily Asclepiadoideae (Rapini et al. 2007). Milkweeds used by monarchs are in the tribe Asclepiadeae, subtribe Asclepiadinae (Nazar et al. 2013). Migrating monarchs evolved in North America using milkweeds in the exclusively American genus *Asclepias* (Fishbein et al. 2011), and also some related vine milkweeds in other genera that most likely dispersed northward from South America (e.g. *Cyanchum*, *Funastrum*, and *Matelea*). Although *D. p. plexippus* can and does thrive on some African milkweed species in non-native habitats (e.g. *Gomphoscarpus* and *Calotropis* species), it did not encounter African milkweeds until the plants were widely dispersed pan-tropically by human colonists, and became naturalized in the 1800s (*see* Appendix A).

Of the 130 species of milkweed in the genus *Asclepias* in North America, including the Caribbean and Mexico (Woodson 1954, Fishbein et al. 2011), monarch larvae have been observed feeding on 34 of these species (Malcolm and Brower 1986, Lynch and Martin 1993). In addition, monarchs have been observed successfully developing on some species of milkweed vines in related genera, such as *Cynanchum laeve* (honeyvine or blue vine milkweed), *Funastrum* (formerly *Sarcostemma*) *crispum* (wavyleaf twinevine), *F. cynanchoides* (fringed twinevine) and some species in the genus *Matelea* (Lynch and Martin 1993). Only a few of the milkweed species that monarchs use, however, are abundant, widely-distributed enough, and of sufficient quality at the right season to maintain large butterfly populations throughout their yearly cycles. The eastern range of *D. p. plexippus* during breeding is mainly coincident with the distribution of the most abundant and widely dispersed milkweeds—the northern species *A. syriaca* (common milkweed) and the southern species *A. asperula* (antelope horn milkweed), *A. viridis* (green or spider milkweed), and *A. humistrata* (pinewoods milkweed) (*see* Fig.1 in Malcolm et al. 1993).

By far the most abundant milkweed species in the northern breeding areas is common milkweed (*A. syriaca*) which is found from southern Canada to Virginia in the east, throughout the Midwest, and west to Kansas and the Dakotas (Woodson 1954, Woods et al. 2012). Common milkweed has recently expanded southward into Georgia, the Carolinas, and Louisiana (Wyatt et al. 1993, Wyatt 1996), and has also become naturalized in parts of the Pacific Northwest. Common milkweed inhabits places that have experienced soil disturbance, such as some cultivated fields, crop fields that have been abandoned or are fallow, pastures, logged land, riparian zones, suburban and urban vacant lots and waste areas, and along trails, railroad tracks, and roadways. It is also intentionally planted in gardens.

Cardenolide fingerprinting of monarchs in their Mexican winter roosts has shown that the majority of the butterflies that migrated there in the fall were raised on *A. syriaca*. Thin-layer chromatography studies found that 85 percent (Seiber et al. 1986) and 92 percent (Malcolm et al. 1993) of nearly 400 monarchs fingerprinted in Mexico in winter had fed as larvae on common milkweed (Brower et al. 2012a, p. 97).

Although *A. syriaca, A. asperula, a viridis*, and *A. humistrata* are the most important species for eastern monarchs, the butterflies also use other milkweed species as they spread throughout their breeding range. In the western portion of the range of eastern monarchs, the butterflies use *A. speciosa* (showy milkweed) and *A. incarnata* (swamp milkweed). In Texas, three of the most important milkweed species for monarchs are antelope horn milkweed, green milkweed, and Zizotes milkweed (*A. oenotheroides).* In eastern Louisiana and other Gulf states, pinewoods milkweed is a common monarch host. Non-native *A. curassavica* (bloodflower, or tropical milkweed) is now a common host in Texas and the southeast, in part due to the intentional planting of this species in gardens. Other southern milkweed vines also occasionally host monarch larvae including *Cyanchum leave* (honeyvine milkweed), *Matelea retiuclata* (green milkweed vine), and *Funastrum crispum* (wavy leaf milkweed vine) (*see* Texas Monarch Watch, http://www.texasento.net/dplex.htm#Milkweed).

The population of *D. p. plexippus* in western North America utilizes multiple species of milkweeds to reproduce, including the broadly distributed *A. fascicularis* and *A. speciosa*, along with other locally common species such as *A. eriocarpa* (woollypod milkweed), *A. cordifolia* (heartleaf milkweed), and *A. vestita* (woolly milkweed) (*see* http://monarchwatch.org/bring-back-the-monarchs/milkweed/milkweed-profiles).

The distribution of milkweeds in the landscape influences monarch productivity. The amount of time a female monarch spends searching for host plants, the number of eggs laid in a given area, and the degree of parasitism and predation of immature stages can be affected by the density and size of milkweed patches in different habitats (Zalucki and Lammers 2010, Pleasants and Oberhauser 2012). Monarchs lay more eggs per plant on milkweeds that occur in smaller milkweed patches (Oberhauser et al. 2001, Zalucki and Lammers 2010).

In studies of the distribution of common milkweed (*A. syriaca*) in Iowa, Maryland, Minnesota, Wisconsin, and Ontario, researchers found that milkweed density was higher and patch size was larger in nonagricultural habitats (such as road right of ways, pastures, and abandoned fields) than in cornfields (Oberhauser et al. 2001, Pleasants and Oberhauser 2012), meaning that monarchs are more likely to lay higher numbers of eggs per milkweed in the smaller milkweed patches found within agricultural fields (Zalucki and Lammers 2010). In Iowa, Minnesota, and Wisconsin, egg densities were higher on milkweeds within fields of corn and soybeans than on milkweeds at field edges or in non-agricultural habitats (Oberhauser et al. 2001). Further assessment over four years in Iowa revealed that milkweed growing in cropland harbored on average 3.89 times more eggs per plant versus that growing in other habitats (Pleasants and Oberhauser 2012). Females may prefer agricultural milkweeds because of their higher nitrogen content, because they can locate milkweed plants more readily within a corn or soybean monoculture because milkweed chemical cues stand out more, or because larval success rate may be higher within smaller patches (Ibid.).

By multiplying the number of eggs per milkweed in the growing season by the density of milkweeds in the landscape and the proportion of the landscape in crop fields versus other land uses, Pleasants and Oberhauser (2012), as updated in Pleasants (in press), estimated the total productivity of different habitats for monarchs and found that a significant proportion of the monarchs from the Midwest once originated in cropland. Based on milkweed densities in various habitats in Iowa in 1999 (Hartzler and Buhler 2000), they estimated that corn and soybean fields produced 78 percent of the state's monarchs, with another 16 percent from land enrolled in the Conservation Reserve Program (based on data supplied by John Pleasants).

Milkweeds vary in nutritional quality based on species and age. Southern milkweeds generally have higher cardenolide concentrations than northern milkweeds, which may help protect monarchs from bird predation during much of their breeding cycle and which may thus also influence migration strategy (Malcolm and Brower 1986, Malcolm et al. 1993, Lynch and Martin 1993, Rasmann and Agrawal 2011). Monarchs need milkweeds that are young, nutritious, and that supply the appropriate amount of protective cardenolides. Common milkweed leaves in shaded habitats tend to be larger, less tough, and have lower cardenolide content and lower induced latex production which possibly increases their quality for monarch larvae (Oyeyele and Zalucki 1990, Agrawal et al. 2012). Egg densities on milkweeds with young or re-sprouted leaves tend to be higher than on older leaves (Zalucki and Kitching 1982). The re-sprouting that follows non-glyphosate herbicide application may contribute to higher egg densities on milkweeds in agricultural fields (Oberhauser et al. 2001), though application of any herbicide causes defoliation that prevents development into larvae of monarch eggs laid prior to treatment (Pleasants in press). Some butterflies have been shown to be more likely to oviposit on leaves with higher nitrogen content, though this is not conclusive in monarch studies (Oyeyele and Zalucki 1990). Monarchs can compensate for lower nitrogen content in leaves by consuming more leaves (Lavoie and Oberhauser 2004).

In addition to milkweed, monarch habitat requirements during the breeding and migrating season include trees for roosting. During migration, monarchs have to make frequent stops to rest, to feed on nectar to maintain fat reserves, and during bad weather (Davis and Garland 2004, Brower et al. 2006, McCord and Davis 2010, Davis et al. 2012, Brower et al. in press). Monarchs form communal roosts at some of these stopover sites, particularly during the fall. Based on an analysis of four years of roost data collected by citizen scientists during fall migration for Journey North, a student wildlife monitoring program, monarchs can use trees with different branching patterns and leaf characteristics for roosting (Davis et al. 2012). Monarchs in northern states primarily roost in conifers and maples, while monarchs in the south commonly roost in pecan and oak trees. No particular land cover type is correlated with roosts, however, monarch roost sites are associated with large bodies of water, such as rivers and lakes, although reasons for this are unknown. In the southern part of the flyway, monarchs are found more often in grassland than would be expected by chance. Monarchs do not appear to consistently roost in the same locations within the flyways each year, suggesting that roost site selection is somewhat random (Davis et al. 2012).

The ephemeral nature of monarch roost site selection increases the importance of protecting nectar resources in the flyways, because nectar sources can be more easily predicted by land managers than roost sites (Brower et al. 2006, Howard and Davis 2008, Davis et al. 2012). Though monarch caterpillars are entirely dependent on milkweed, numerous species of flowering plants can provide suitable nectaring habitat for adult monarchs (Tooker et al. 2002).

Climate, including weather patterns and temperature, also plays a significant role in defining monarch habitat seasonally because suitable temperature regimes are required for monarch survival and reproductive success (Zalucki and Rochester 2004, Taylor and Lentz 2005, Stevens and Frey 2010).

Although basic overwintering habitat requirements are common to the subspecies, some details differ for *D. p. plexippus* east and west of the Rocky Mountains. The western monarchs roost in coastal areas of California in the winter, whereas the much larger numbers of monarchs east of the Rockies roost in a small area of Mexico, and these roosting locations have distinctive flora and microclimates.

Overwintering monarchs have very specific microclimatic habitat requirements, such as protection from wind and storms, absence of freezing temperatures, exposure to dappled sunlight, and presence of high humidity (Chaplin and Wells 1982, Calvert et al. 1983, Anderson and Brower 1996, Leong 1999). Fall or winter blooming flowers that provide monarchs with nectar may be important to maintain lipid reserves required for winter survival and the spring migration (Tuskes and Brower 1978).

In inland Mexico, monarchs gather on oyamel (sacred) fir (*Abies religiosa*) trees on the border between Michoacán and Mexico State in the mountains of the Trans-Mexican Volcanic Belt. The high altitude forests provide the microclimatic conditions that monarchs must have to survive the winter. Colonies are ecologically and geographically constrained to densely forested sites that are at high elevations (~2,900–3,300 m [9,500–10,800 ft]) and they are usually restricted to arroyos near streams on southwest-facing slopes that are moderately steep (Slayback et al. 2007, p. 28). The cool temperature and moisture inside the oyamel forests maintain the butterflies in a state of reproductive diapause and allow them to conserve lipid reserves that fuel the wintering period and the spring remigration north (Brower et al. 2011, p. 28). The benefits of the dense canopy and mature trees have been likened to an umbrella, a blanket, and a hot-water bottle, protecting the butterflies from rain and keeping them warm enough not to freeze but cool enough that diapause is not broken (Ibid.). The monarch's overwintering in habitat in Mexico is threatened by logging, forest disease, forest senescence, climate change, and severe weather events. Site fidelity and extreme localization of colonies within such a small area of available habitat heightens monarch vulnerability and highlights the urgent need for protecting the butterflies' habitat (Slayback et al. 2007, p. 38).

In coastal California, most overwintering sites are dominated by exotic blue gum (*Eucalyptus. globulus*) or red river gum *E. camaldulensis*), although many sites also contain native trees such as Monterey pine (*Pinus radiata*), Monterey cypress (*Cupressus macrocarpa*), western sycamore (*Platanus racemosa*) and other species (Xerces Society 2013). Recent research shows that monarchs do not prefer *Eucalyptus* over native tree species (Griffiths and Villablanca 2013), especially later in the season as storms become more severe. Historically, the composition of vegetation on the California coast differed from the contemporary composition, and groves of native trees presumably hosted dense monarch aggregations (Lane 1984, 1993). Monarch overwintering habitat in California is directly threatened by logging and other forest degradation for commercial and municipal development. Habitat alterations, such as tree trimming or tree removal, or natural factors such as fire, severe storms, or disease or senescence of trees, can alter the structure and microclimate of an overwintering site and reduce its suitability for monarchs (Sakai and Calvert 1991, Commission for Environmental Cooperation 2008).

All of the California sites are at low elevations (<300 ft) and in sheltered locations, and many occur within half a mile of the shoreline (Lane 1993). The sites shelter monarchs due to both canopy cover and local topography with most locations being in shallow canyons, gullies, or on the lee side of hills. Sites frequently occur where the coastline runs generally in an east-west direction offering protection from the predominate winds. Underlying shrub and herb layers also likely contribute to the specific microclimatic conditions the butterflies need, similar to conditions in the oyamel fir forests in inland Mexico (Lane 1993, p. 336). The surrounding forest conditions are important to maintain the microhabitat conditions on the “butterfly trees” where the monarchs gather (Lane 1993).

Populations of *D. p. plexippus* outside of North America share basic habitat requirements, but have less complex life histories without migration. They also inhabit areas with fewer species of milkweeds and with different climates (*see* Appendix A).

Because of their complex life history and specific habitat requirements, monarchs are highly vulnerable to habitat loss and degradation. Monarchs are threatened by habitat loss and degradation in their breeding, migrating and overwintering habitats, as discussed in detail in the Threats section of this petition.

POPULATION DISTRIBUTION AND STATUS

The historic distribution and abundance of monarchs is not known with certainty, but would have been broadly defined by the distribution of milkweed. Historically *D. p. plexippus* populations east of the Rockies would have bred mainly in the grasslands and prairies of the Great Plains that were populated by a mix of native milkweed species (Brower 1995) and copious nectar sources (Figure 9). Monarchs likely also inhabited meadows, Native American agricultural fields, and other open areas throughout North America wherever milkweeds occurred and weather conditions permitted. The butterflies would have been rare in heavily forested regions, mountainous areas, and arid zones. Monarchs were almost certainly confined to continental North America from pre-history until the mid- to late-1800s.

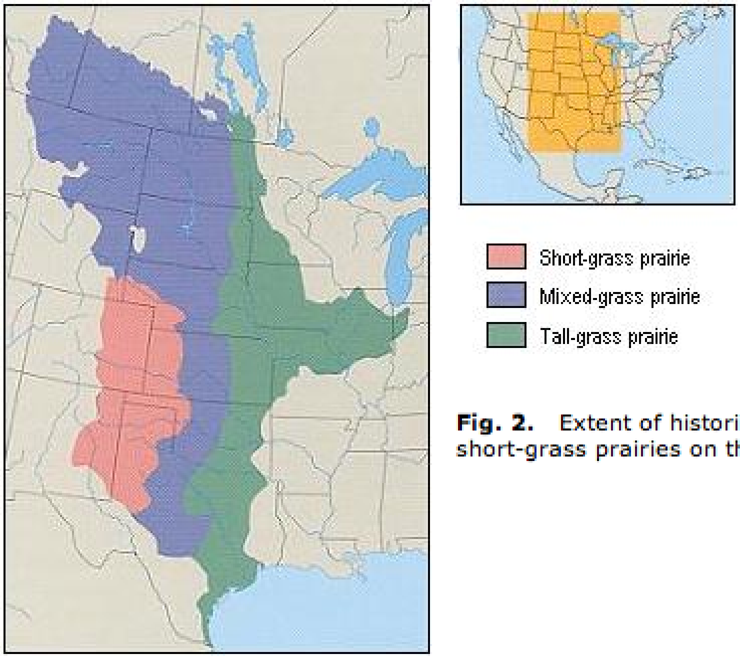
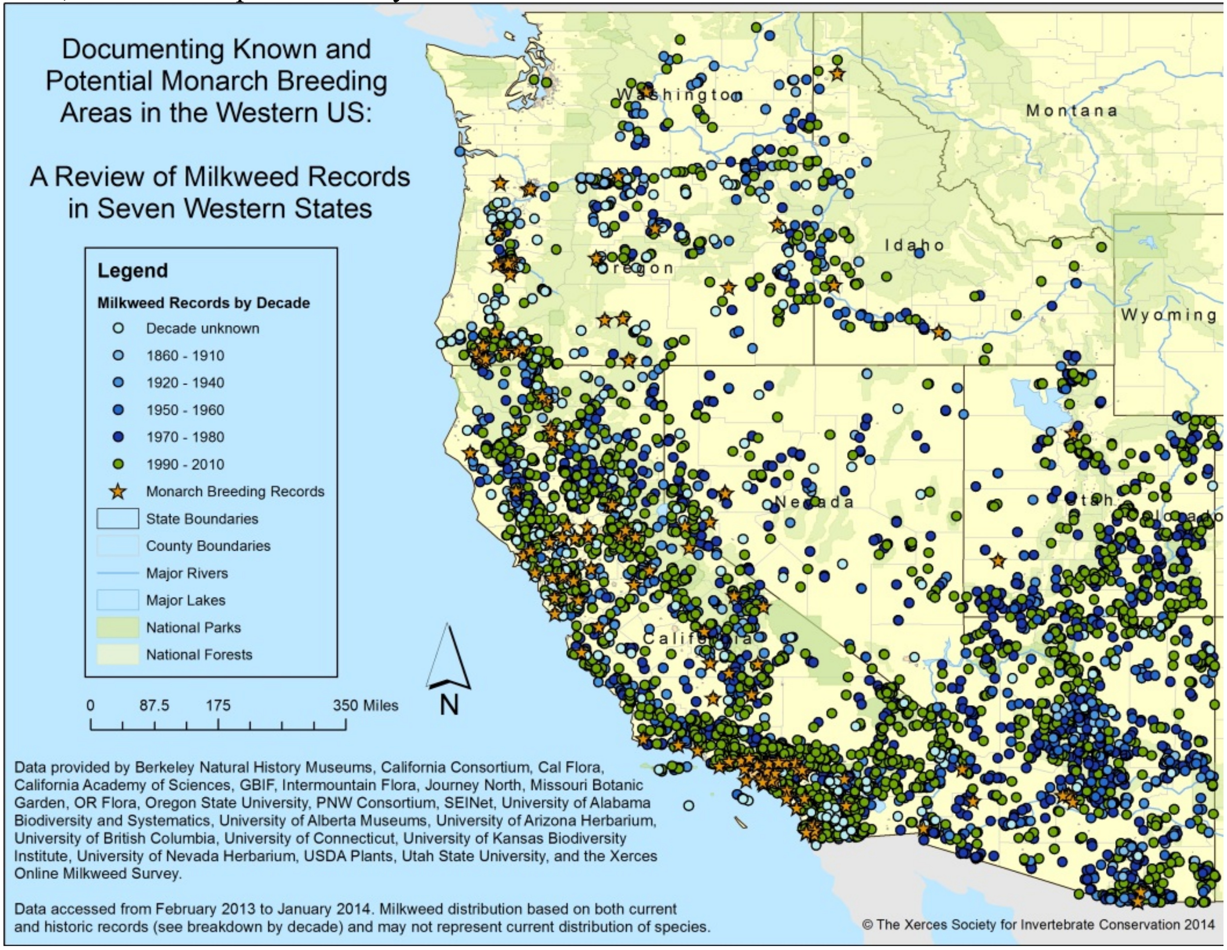


Fig. 2. Extent of historical (pre-European) tall-grass, mixed-grass, and short-grass prairies on the North American Great Plains.

Figure 9. Historic monarch distribution east of the Rockies likely coincided with pre-European prairie extent. Figure 2 from USGS 2013 Prairie Past and Present, caption included: http://www.npwrc.usgs.gov/resource/habitat/grlands/pastpres.htm#table1

It is likely that prairie milkweeds were abundant and supported high monarch populations, though abundance and distribution of particular milkweed species before widespread plowing of the prairies is unknown. Milkweed species and abundance have been measured in some current prairie remnant habitats in Iowa and extrapolated to provide an estimate of pre-agricultural milkweed occurrence. One measure of milkweed abundance is percent coverage of the landscape by milkweeds in relation to all other plant species in an area – how much space they take up. Pleasants (in press) estimates that statewide, the milkweed species in former prairies contributed 0.65 percent of the vegetation coverage in Iowa, which would have provided habitat to support highly abundant monarch populations. As of 1999, common milkweed comprised only 0.194 percent of coverage in Iowa, and that percentage has decreased nearly three-fold, to 0.068 percent by 2012, as the widespread planting of glyphosate-resistant Roundup Ready crops has led to a drastic decline in milkweed abundance in agricultural fields, as discussed in detail in the Threats section of this petition.

In the western United States, milkweeds are distributed across the landscape (Figure 10). More research is needed to understand how milkweed availability may have changed over time in the west, and what impact that may have had on monarchs.



Documenting Known and Potential Monarch Breeding Areas in the Western US:

A Review of Milkweed Records in Seven Western States

Data provided by Berkeley Natural History Museums, California Consortium, Cal Flora, California Academy of Sciences, GBIF, Intermountain Flora, Journey North, Missouri Botanic Garden, OR Flora, Oregon State University, PNW Consortium, SEINet, University of Alabama Biodiversity and Systematics, University of Alberta Museums, University of Arizona Herbarium, University of British Columbia, University of Connecticut, University of Kansas Biodiversity Institute, University of Nevada Herbarium, USDA Plants, Utah State University, and the Xerces Online Milkweed Survey.

Data accessed from February 2013 to January 2014. Milkweed distribution based on both current and historic records (see breakdown by decade) and may not represent current distribution of species.

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Figure 10. Records of milkweeds (multiple *Asclepias* species) from 1860-2010 (blue and green) and records of monarch caterpillars on milkweed (orange). Note that records for Montana and Wyoming are not displayed on this map. Figure courtesy of the Xerces Society, available at: http://monarchjointventure.org/our-work/western-us-milkweed-survey

The grasslands and prairies of North America were rapidly and almost completely converted to rangeland for domesticated animals and to agricultural fields after European settlers moved west beginning in the early to mid-1800s. Most milkweed species would have declined in abundance as a result. At about the same time that grasslands and prairies were being plowed under, forests east of the Mississippi were being cleared. Though most milkweed species declined following prairie conversion, common milkweed (*A. syriaca*), which thrives in areas of soil disturbance, increased in range and abundance in both agricultural and logged areas (Brower 1995). Monarchs thus would have been able to maintain high populations after European colonization of North America by shifting the center of their population east and north as formerly forested land was invaded by common milkweed, and by substituting this one milkweed for most of the others as their main host plant in the northern and eastern breeding range.

Based on the limited historical data that are available, monarchs were highly abundant in the mid- to late-1800s. Brower (1995 and references therein) discusses early observations of monarchs in the Midwest and east by naturalists, journalists, farmers, and scientists. D'Urban (1857) described monarchs appearing in the Mississippi Valley in “such vast numbers as to darken the air by the clouds of them” (in Brower 1995, p. 349). Scudder and Allen (1869) described monarchs gathered in groves of trees bordering the prairie in Iowa “in such vast numbers, on the lee sides of trees, and particularly on the lower branches, as almost to hide the foliage, and give to the trees their own peculiar color” (in Brower 1995, p. 306). In the 1870s swarms of monarchs were reported in New England and the Great Lakes. Saunders (1871) observed “vast numbers-- I might safely say millions” of monarchs clustering on trees on the Canadian shore of Lake Erie (in Brower 1995, p. 308). Scudder (1889) noted endless masses of monarchs migrating through Connecticut in 1871 (Ibid.). In 1872 an immense swarm of monarchs was observed in flight over Cleveland, Ohio (Brower 1995, p. 308).

Prior to monitoring efforts that began in the 1980s, the historic distribution and size of the western monarch population was largely unknown. There are early accounts of overwintering masses of monarchs from Monterey, California in 1869 and 1873, and from Santa Cruz in 1888 (Lane 1993, Brower 1995). In May 1874 the Monterey Weekly Herald published an account from near Pacific Grove of “millions” of monarchs “fluttering around,” “while overhead stout branches of firs dropped with their weight” (in Lane 1993, p. 341). An 1881 letter describes trees near Monterey “over one and a half feet in diameter, and completely covered with live butterflies. To say that there were as many butterflies as leaves upon the trees would not be a very great exaggeration” (in Lane 1993, p. 341). Historic estimates of the western overwintering population size range from 1 to 10 million (Nagano and Lane 1985, Nagano and Freese 1987). Leong et al. (2004) used data from the California Natural Diversity Database (CNDDB) from 1990 to 2000 to estimate the maximum number of overwintering monarchs for a single season to be more than 2.3 million. Historic estimates of monarch population size that are available for a few overwintering sites suggest that the monarch population was larger prior to the onset of a large-scale yearly monitoring effort that began in 1997 (Figure 11.)

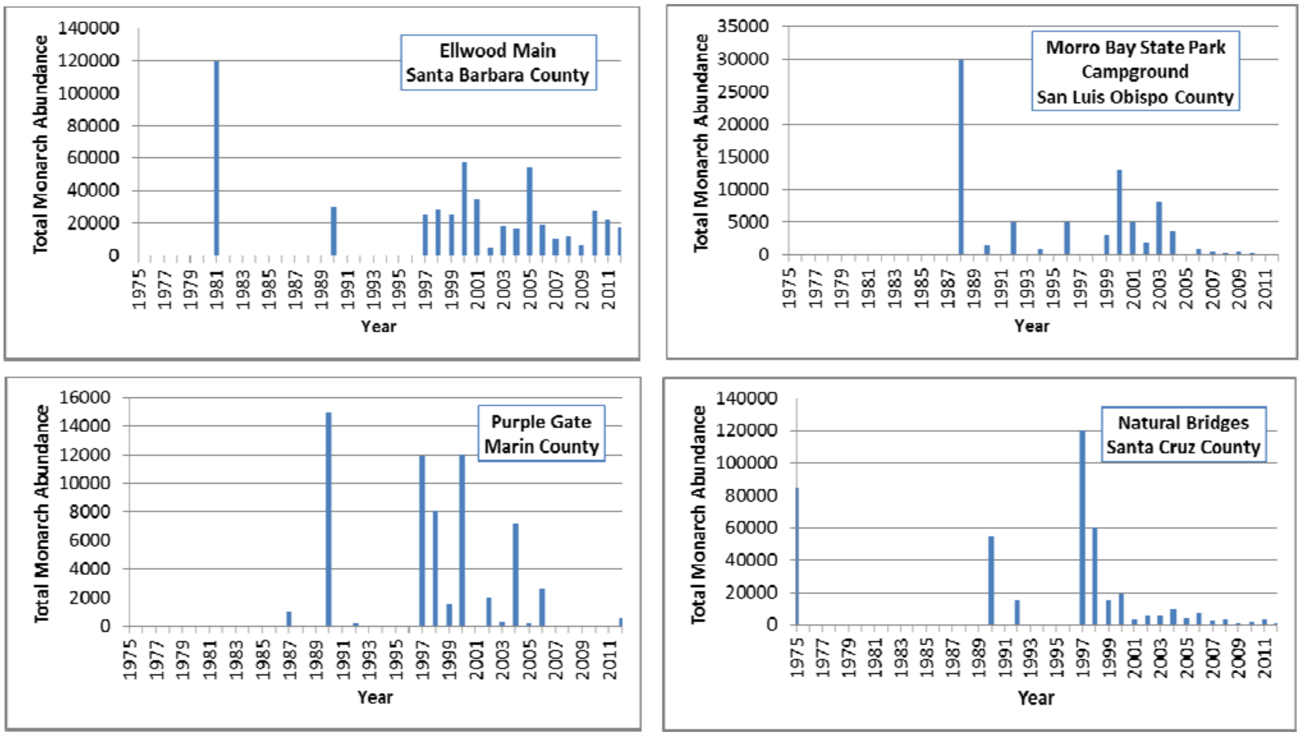


Figure 11. Western monarch population estimates from November 1 - December 15 at four sites: Ellwood Main (Santa Barbara County), Morro Bay State Park Campground (San Luis Obispo County), Purple Gate (Marin County) and Natural Bridges (Santa Cruz County); figure from Jepsen and Black in press.

Thus it is clear that historically monarchs were highly abundant, though annual population sizes were not quantified prior to the late 1990s when monitoring began Though monarchs are still widely distributed, their abundance has declined drastically across their U.S. range, as discussed in detail below. Very recently, the number of monarchs from east of the Rockies has declined from occupying an overwintering area of 7.8 hectares in the 1994-1995 overwintering season (the first year data are considered to be reliable), to occupying an area of only 0.67 hectares in the 2013-2014 overwintering season, a decline of more than 90 percent from the 20-year average, and a decline of 97 percent from the 1996-1997 population high (Rendón-Salinas and Tavera-Alonso 2014).

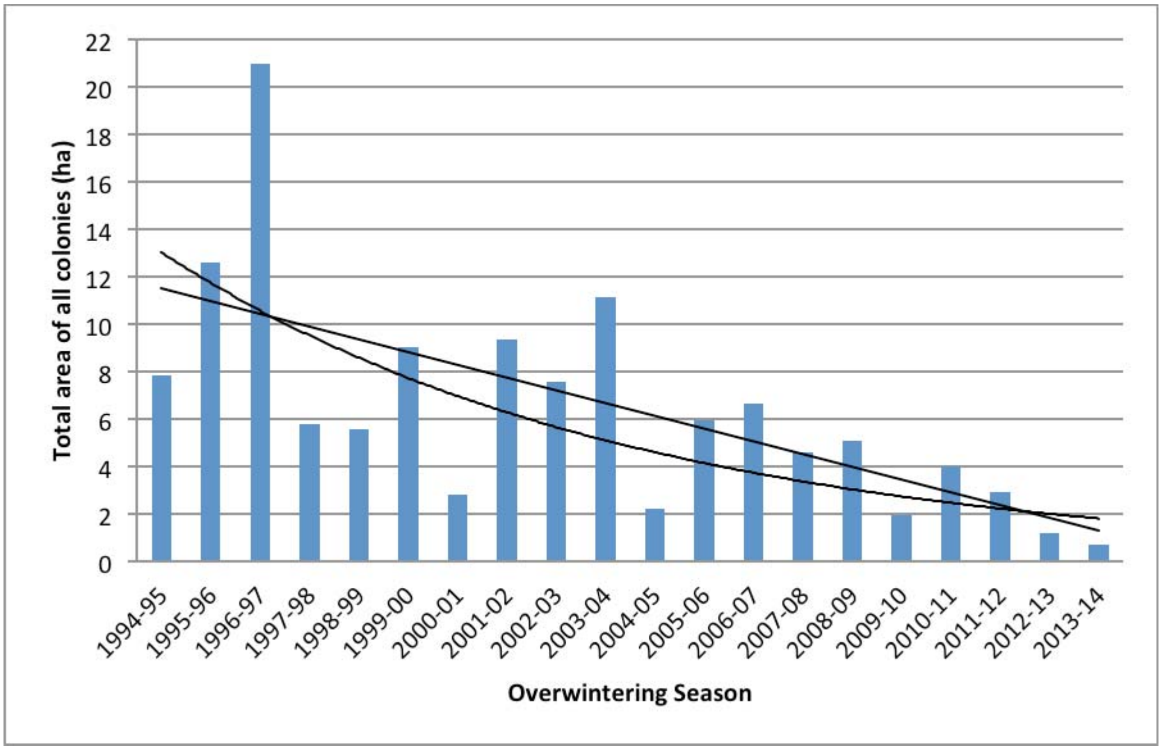
Monarchs from west of the Rockies have also undergone recent significant decline. In the winter of 1997, which is the year that monitoring began, there were more than 1.2 million monarchs overwintering in California (or an average of 12,232 monarchs per site), but in 2013 there were only about 200,000 monarchs counted (an average of 2,151 monarchs per site), representing a decline of 90 percent from the 1997 high and a 51 percent decline from the 17-year average (Monroe et al. 2014, Figure 13). Western monarch numbers have not reached the highs recorded in the late 1990s since that time, and have fluctuated around 200,000 butterflies since 2001 (Monroe et al. 2014). Historical estimates of the overall California overwintering population size range up to 10 million butterflies (Nagano and Lane 1985, Nagano and Freese 1987).

There are several research and citizen science programs that provide data on current monarch distribution and abundance, including the World Wildlife Fund Monarch Monitoring Project in

Mexico, the Monarch Larva Monitoring Project, Peninsula Point Migration Monitoring Project, Cape May Migration Monitoring Project, the Western Monarch Thanksgiving Count, annual censuses of monarchs in the Central Valley and Sierra Nevada by Dr. Art Shapiro, the North American Butterfly Association annual breeding adult surveys, and state-level programs (Monarch Net 2014, *see*: http://monarchnet.uga.edu/).

To estimate overall abundance of monarchs that overwinter in inland Mexico, scientists rely on the combined area of overwintering colonies because it is a direct measure of the entire migratory population (Brower et al. 2012b, p. 328). On-the-ground counts have resulted in estimates of 10 to 60 million butterflies per hectare of trees occupied, with 50 million monarchs per hectare being used as a standard estimate of overwintering butterfly numbers, since measurements are taken at a time of year when butterflies are likely to be most tightly packed, and since the higher density numbers are from more recent and standardized studies (Slayback et al. 2007). Monarch numbers in winter roosts generally correlate with numbers produced during breeding in a given season, although variable mortality does occur during migration. Reliable information on colony sizes and locations in Mexico is available since the 1994–1995 overwintering season for eastern North America; earlier information is considered less reliable because it was gathered on increasing numbers of colonies as they were discovered by diverse groups of investigators with variable expertise. The overall abundance of monarchs that overwinter on the California coast is estimated from counting the actual number of butterflies at each site; 76-162 overwintering sites have been counted each year, and 17 sites have been consistently monitored since 1997 (Figures 13 and 14).

The number of monarchs overwintering in Mexico, primarily representing the eastern migratory population, shows a statistically significant decline over the past twenty years (Figure 12). In winter 1994-1995, monarchs occupied 7.81 hectares of oyamel forest. The highest number observed was in winter 1996-1997 when monarchs occupied 20.97 hectares. By 2004-2005, the number of hectares had dropped to 2.19, and has not since risen to 7.0 hectares, the area covered when standardized counts began in 1994-1995. Regression analyses show statistically significant monarch population decline even when the highest and lowest measurements are removed (linear model, $P = 0.032$ or 0.042; exponential model, $P = 0.040$ or 0.049; Brower et al. 2012a, p. 96). We extended the Brower et al. (2012a, Fig. 1) graph to include the results of the three most recent winter surveys (Figure 12). Regression analysis of the extended data continues to show a statistically significant decline in monarch abundance ($P = 0.01$). In summary, there has been a 91 percent decline in overwintering eastern monarch numbers over the past twenty years, with numbers in winter 2013-2014 being the lowest ever recorded.



linear:	$y = -0.5372x + 12.028$	$R^2 = 0.4493$
exponential:	$y = 14.445e^{-0.104x}$	$R^2 = 0.5502$

Figure 12. Total annual area occupied by overwintering butterflies in Mexico from 1994 through 2013, with linear (upper line) and exponential (lower line) regression analyses. The significant decline charted by Brower et al. (2012a, Fig. 1) through 2010-11 continues through 2013-14.

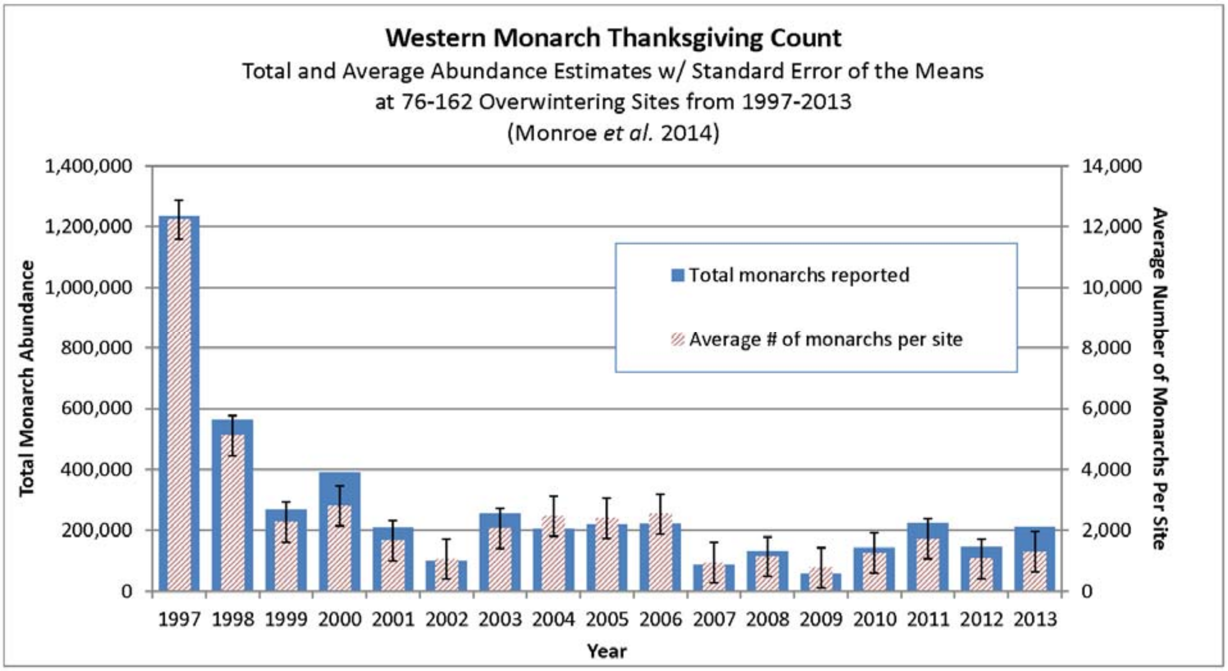


Figure 13. Western Monarch Thanksgiving Count Data 1997-2013. From Monroe et al. 2014

An analysis of the 17 western monarch overwintering sites that have been monitored every year shows that there has been a statistically significant population decline (Griffiths and Villablanca in preparation). There is evidence that a range contraction has also occurred, with significantly more sites declining at the southern and northern extremes of the monarch's winter range (Griffiths and Villablanca in preparation).

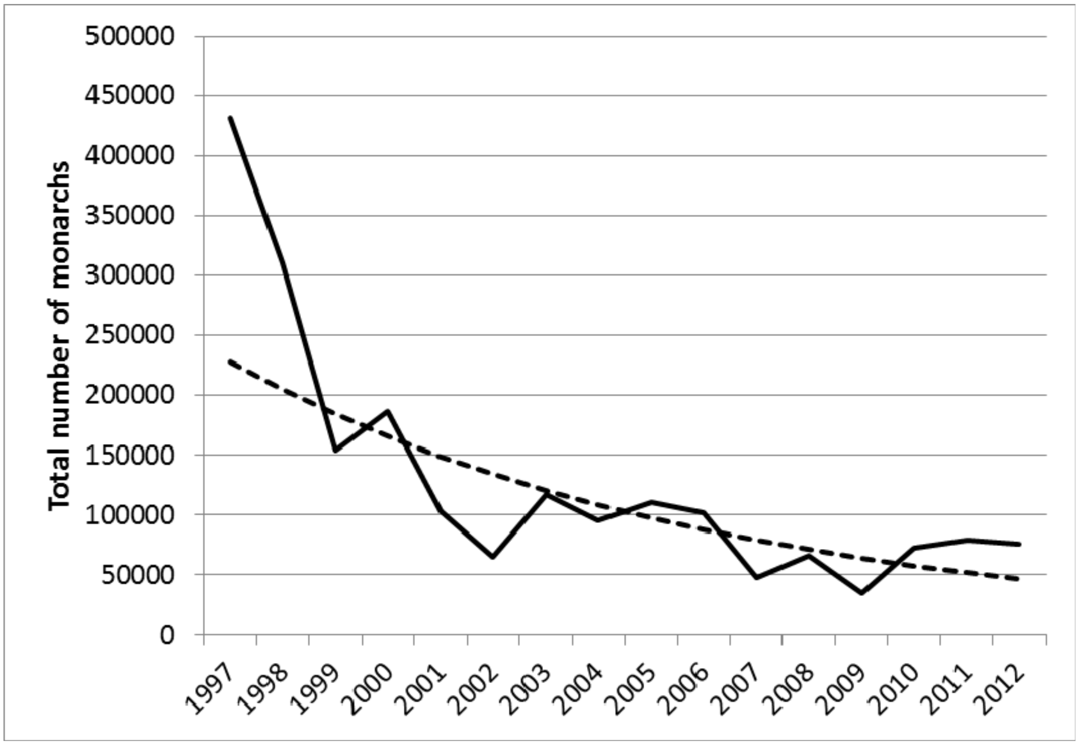


Figure 14. The total number of monarchs counted at 17 monarch overwintering sites during the Western Monarch Thanksgiving Count from 1997-2012. The solid line represents the actual survey data. The dotted line represents the regression function. Figure from Griffiths and Villablanca (in preparation).

Though their numbers have been drastically reduced, monarchs are still widespread in appropriate habitat in the continental United States. Flockhart et al. (2013) predicted where eastern monarchs are most likely to be found during the breeding season by determining the probable range based on amount and kind of vegetation, geographical limits (latitude, longitude, altitude, and slope), temperature, precipitation, and records from Journey North citizen scientist observations collected between 1997 and 2011 (Flockhart et al. 2013, Fig. 1). They determined that the majority of monarchs are found from east- and mid-Texas north into the Midwest, and then at a somewhat lower density throughout the east from southern Canada south to the Gulf. Some monarchs also occur much further west and north.

Although monarchs are distributed throughout the eastern United States during the breeding season, their reproductive success is not uniform across regions. Wassenaar and Hobson (1998) analyzed stable hydrogen and carbon isotope profiles from wings of butterflies overwintering in Mexico to determine the host plants and latitude where the caterpillars had developed. They determined that half of the overwintering monarchs had “originated from a fairly restricted part of the breeding range, including the states of Kansas, Nebraska, Iowa, Missouri, Wisconsin, Illinois, Michigan, Indiana, and Ohio, corresponding to an area of intense corn, soybean, and dairy production in the Midwestern United States” (Figure 15, below). It is important to note that the butterflies they analyzed developed during the 1996 breeding season, and overwintering monarchs from that year covered the largest area in Mexico recorded in the last 20 years, 20.97 hectares. Using the standard estimate of 50 million butterflies per hectare (Slayback et al. 2007), almost a billion individuals were in the population at that time, half of which metamorphosed on common milkweed in regions dominated by agriculture, particularly corn and soybeans.

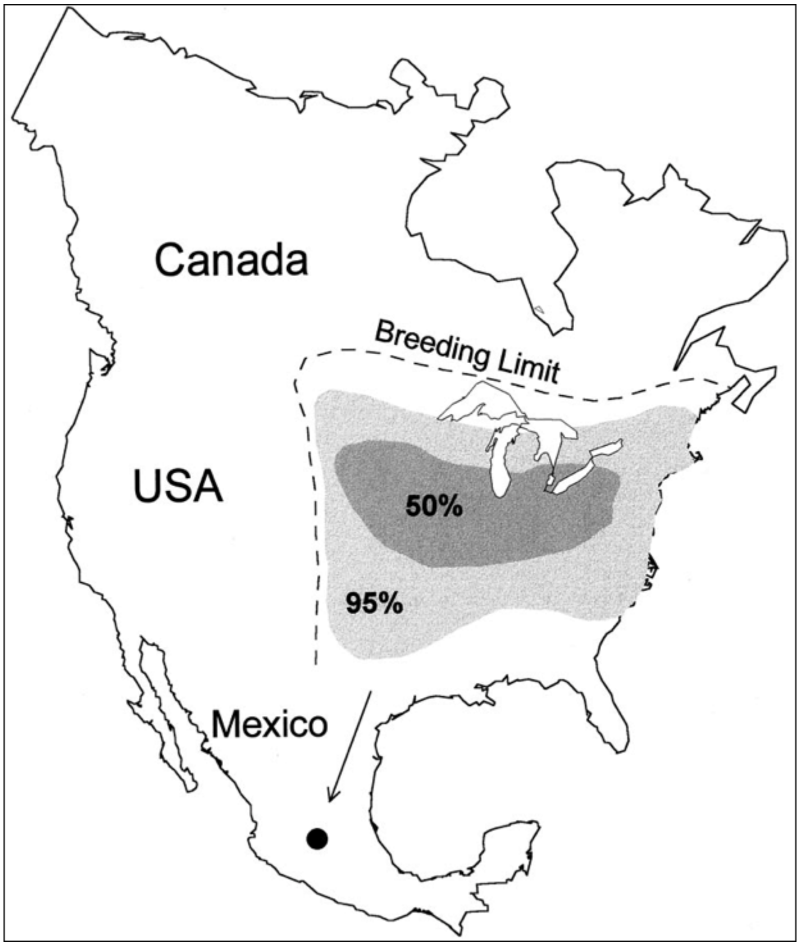


Figure 15. Natal origins of monarch butterflies in Mexico from the 1996 breeding season based on isotope data. The dark and light-shaded areas show the natal origins of 50% and 95% of the one billion monarchs that overwintered in 1996/97. The dashed line approximates the eastern breeding range. The Mexican monarch overwintering colonies are denoted by the solid circle. Figure 3 from Wassenaar and Hobson (1998), original caption omitted.

Flockhart et al. (2013) extended the monarch natal origin studies by measuring isotopes in butterflies collected throughout eastern North America at different times during the 2011 breeding season. Researchers collected monarchs as they arrived in the southern United States from overwintering in Mexico, and then continued to sample butterflies throughout the summer and into fall to determine where each successive generation had originated. They determined that the overwintered generation in 2010 – 2011 had natal origins throughout much of eastern North America, but that most individuals came from a swath running from the northeastern states through the lower Midwest into northern Texas, and that fewer overwintered butterflies had originated in the heart of the Corn Belt as compared to the 1996 season (Flockhart et al. 2013, Fig. 2, panel a: “overwintered generation”). Notably, fewer overwintered butterflies originated in northern Indiana, Illinois, Iowa, Michigan, or the upper Midwest compared to the 1996 breeding season.

Flockhart et al. (2013) went beyond study of the overwintering generation to determine the natal origins of successive monarch generations produced in the east throughout the 2011 breeding season. The natal origins showed a broad spatial distribution that encompassed the entire breeding range in eastern North America, though the preponderance of individuals originated from northern Texas to western Ohio, in a region extending from the southern Great Plains through the Midwestern Corn Belt (Figure 16). Over this particular breeding season, fewer butterflies originated in the upper Midwest, northeastern and eastern states, and southern Canada, than in the Texas-to-Ohio zone. There were few indications of natal origins from Mississippi, Alabama, Georgia and Florida despite the fact that areas located north of these locations were sampled extensively.

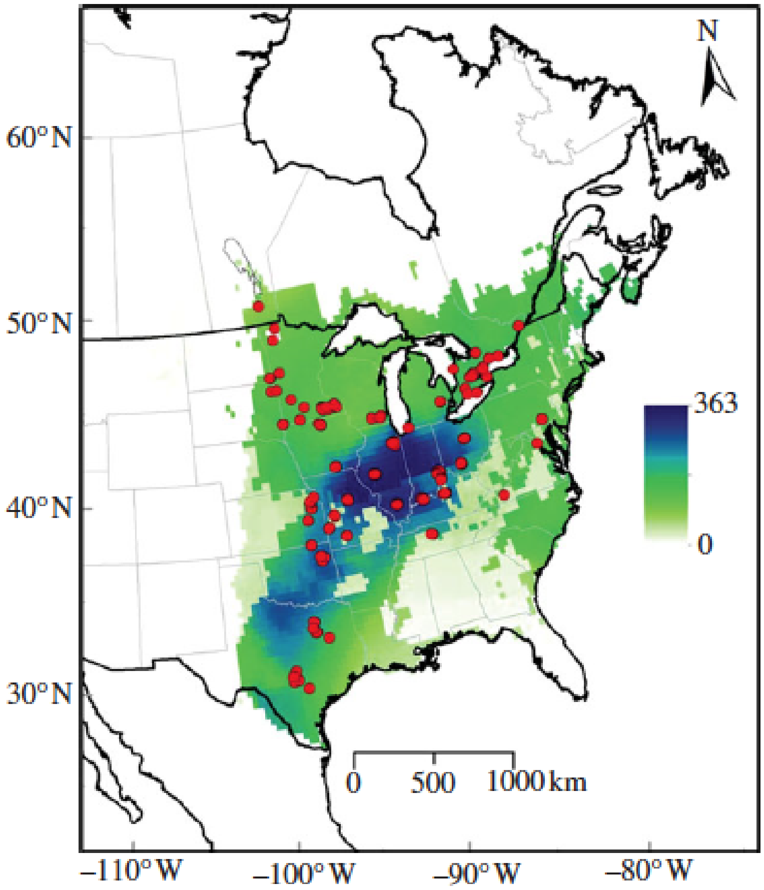


Figure 16. Probability distribution for natal origins of monarchs collected in eastern North America during the 2011 breeding season, based on isotope analysis of butterflies. Red dots represent monarch capture locations. The color gradient on the map (light green to dark blue) represents the natal origins of the 839 butterflies analyzed, with increasing numbers of butterflies born in areas with progressively darker coloration, as indicated by the scaled bar to the right of the map. Figure 3 from Flockhart et al. (2013), original caption omitted.

When butterflies were collected for the Flockhart et al. (2013) study, the overwintering monarch population size was drastically reduced from the 1996-1997 level. During the winter of 2010–2011, the estimated population size was 200 million individuals (Figure 12, above), compared to the estimated billion butterflies at the time of the earlier study. In 2010 almost all soybean and most corn fields were Roundup Ready and few milkweeds remained in those fields to provide habitat for breeding monarchs (as discussed in detail in the Threats—Habitat Loss section of this petition). Overwintering butterfly numbers have continued to decline, as discussed above, coinciding with the greatly reduced availability of common milkweed in agricultural fields as a result of the large increase in use of the herbicide glyphosate made possible by widespread planting of genetically-engineered, herbicide-resistant (Roundup Ready) crops (Pleasants and Oberhauser 2012).

To predict monarch risk of extinction, Flockhart et al. (2014) "developed a spatially-structured, stochastic and density-dependent periodic projection matrix model that integrates patterns of migratory connectivity and demographic vital rates across the annual cycle" (p. 2). Their "year-round population model predicted population declines of an additional 14 percent," from already drastically reduced population size, and a quasi-extinction probability (meaning less than 1000 surviving individuals) of greater than five percent within the next 100 years (p. 2). This "non-trivial" extinction risk (*see*: http://theconversation.com/iconic-monarch-butterflies-under-threat-from-rising-herbicide-use-27596) demonstrates that monarchs are threatened in the foreseeable future. The model is a conservative, yet realistic, minimum estimate of quasi-extinction of eastern monarch butterflies, and provides strong published evidence that breeding season habitat loss is driving monarch population decline.

Yet the model also underestimates the extinction risk facing monarchs for several reasons. The model does not incorporate further expected losses of milkweed in Conservation Reserve Program lands which are being rapidly converted to crop production, primarily Roundup Ready corn and soybeans, due to Program cutbacks and continuing strong demand for biofuels (*See* Threats…Habitat Loss and Degradation, Loss of Monarch Habitat Due to Agricultural Intensification to Produce Biofuels). It does not consider the imminent release of new genetically-engineered herbicide-resistant crops, which will reduce nectar resources for monarch adults via herbicide drift and continue to eliminate milkweed from cropland once commercialized (*See* Threats- Habitat Loss and Degradation, New Herbicide-Resistant Crops Promise Further Habitat Degradation). Nor does it take into consideration the release of new pesticides that are in development that will be harmful to monarchs (*See* Threats…Other Factors).

The model also underestimates the risk that climate change poses to monarch butterflies. The model is based on the assumption that there will be a reduced probability of catastrophic mortality events on the wintering grounds in Mexico, but other authors have predicted increased probability of winter mortality due to climate change (Brower et al. 2011, p. 28, Barve et al. 2012, p. 820, Brower et al. 2012a, p. 98). In fact, other models have predicted that the entire Mexican overwintering grounds could become unsuitable to support monarchs in the foreseeable future (Oberhauser and Peterson 2003, p. 14067, Saenz-Romero et al. 2012, p. 98). The model also underestimates climate risk because it uses temperatures from weather stations that are on average 274 m (~900 ft) below the elevation at which butterflies cluster (Flockhart et al. 2014, supporting materials, p. 30). The model is based on the assumption that increasing temperatures from climate change will decrease the risk of severe winter storm events, yet this assumption is not supported by other climate models. The model also fails to take into account the influence of predicted warmer temperatures on lipid depletion during overwintering which reduces butterfly fitness (*See* Threats…Other Factors, Global Climate Change).

Thus, the Flockhart et al. (2014) model demonstrates that the monarch is threatened, yet certainly still underestimates extinction risk. The model demonstrates that ongoing population declines will be driven by land-use change and global climate change, and identifies as a top priority for slowing future population declines the need to reduce the loss of milkweed host plants in the Midwest and Southern U.S. breeding grounds, which they determine is the primary driving force behind the current population decline (p. 3, 14). The model also demonstrates that the drastically reduced current population size of monarchs makes the species even more vulnerable to catastrophic events. The overall population of monarchs in North America is exhibiting a significant decline and the butterflies are facing high magnitude, imminent threats from multiple factors across their range.

THE MONARCH BUTTERFLY WARRANTS ESA PROTECTION

The Endangered Species Act states that a species shall be determined to be endangered or threatened based on any one of five factors (16 U.S.C. § 1533 (a)(1)). In this case, the monarch is threatened by all five of these factors and warrants protection under the Act. The monarch is threatened by the first factor, the modification and curtailment of habitat and range, due to the drastic reduction of milkweed in its summer breeding habitat that has occurred due to increased herbicide spraying caused by the widespread adoption of genetically-engineered, herbicide-resistant corn and soybean crops (Pleasants and Oberhauser 2012, Flockhart et al. 2014). Monarch habitat has also been reduced due to increased production of ethanol since 2007 that has resulted in conversion of grasslands to corn and eliminated milkweed from those habitats (Brower et al. 2012a), and by other factors such as urban development and aggressive management of roadside vegetation (Commission on Environmental Cooperation 2008). East of the Rockies, it has been very roughly estimated that approximately 167 million acres of monarch habitat, an area about the size of Texas, may have been lost since the mid-1990s due to agricultural changes and development, including nearly one-third of the monarch’s total summer breeding range (Taylor 2014). The monarch’s wintering grounds are threatened by illegal logging, legal wood gathering, water diversion, and agricultural conversion of forest land in Mexico, and by development, aging forests, and other threats in California. The butterfly is potentially threatened by the second factor, overutilization, due to commercial production and release of large numbers of butterflies, which threatens to spread disease and undesirable genetic traits to wild populations. The monarch is also threatened by the third factor, disease or predation. High levels of predation are a significant threat at all life stages, especially in synergy with habitat loss and declining populations. Disease further threatens the monarch, and the spread of one protozoan parasite in particular may be reducing the proportion of females in the population and thus reducing the monarch’s potential for population growth and recovery (Davis and Rendón-Salinas 2010). The fourth factor, inadequacy of existing regulatory mechanisms, is a threat because voluntary efforts undertaken have not been able to stop and reverse population decline. Finally, monarchs are also threatened by the fifth factor, other natural and manmade factors affecting their continued existence, including pesticides, invasive species, global climate change, and stochastic weather events. Severe weather conditions have been identified as one of the primary factors in the recent precipitous decline in monarch numbers (Brower et al. 2012a,b).

Synergies between all of these factors magnify the intensity of threats facing monarchs. Climate change, for example, will exacerbate other threat factors such as disease and habitat loss, and habitat loss will increase threats from other factors including disease and predation. There are no existing regulatory mechanisms that are adequate to protect the monarch butterfly from all of these threat factors. As discussed in detail in the Significant Portion of Range section of this petition, below, the monarch is at risk of extinction in a significant portion of its range in North America because without the significant North American population, the redundancy, resiliency, and representation of the species would be so impaired that the monarch would have an increased vulnerability to threats to the point that the overall species would be likely to become endangered in the foreseeable future. The monarch butterfly needs ESA protection as a threatened species to address landscape level threats to its existence before its population declines to the level of endangerment.

THREATS

FACTOR ONE: MODIFICATION OR CURTAILMENT OF HABITAT OR RANGE

Monarch Habitat Loss Due to Pesticides

The monarch butterfly is threatened by modification and curtailment of habitat and range due to the drastic loss of milkweeds, especially common milkweed (*Asclepias syriaca* L.), caused by increased and later-season use of the herbicide glyphosate. Glyphosate use has increased dramatically because of the widespread planting of genetically-engineered, herbicide-resistant corn and soybeans in the Corn Belt region of the United States and to planting of genetically-engineered cotton in the southern United States and California. In the Midwest, nearly ubiquitous commercial planting of, glyphosate-resistant Roundup Ready corn and soybeans has caused a precipitous decline of common milkweed, and thus of monarchs, which lay their eggs only on milkweeds. Moreover, milkweed from crop fields is particularly significant for maintaining monarch abundance (Oberhauser et al. 2001, Pleasants and Oberhauser 2012, Flockhart et al. 2014).

On top of the loss of milkweed in crop fields, much habitat that once hosted milkweed, particularly Conservation Reserve Program land, has recently been converted to genetically-engineered, glyphosate-resistant corn and soybeans to produce biofuels. In addition, new multiple genetically-engineered, herbicide-resistant crops, soon to be introduced, will further degrade monarch habitat by reducing nectar resources for monarch adults via increased herbicide drift damage, and causing further loss of milkweed in agricultural fields. Threats posed to monarchs from pesticides in addition to habitat loss are discussed in the petition section Other Factors- Pesticides.

As discussed in detail in the Natural History section of this petition, the majority of the world’s monarchs originate in the Corn Belt region of the United States, and the demographic importance of this region to the resiliency, redundancy, and representation of *Danaus plexippus plexippus* cannot be overstated (Wassenaar and Hobson 1998, Oberhauser et al. 2001, Brower et al. 2012a, b; Flockhart et al. 2013, 2014; Pleasants and Oberhauser 2013, Pleasants in press). The dramatic loss of milkweed from the monarch's summer breeding grounds thus puts the monarch at risk of extinction (Flockhart et al. 2014), and this risk is magnified by other ongoing threat factors such as climate change, severe weather events, and habitat loss to development (Brower et al. 2011, 2012a, b; Saenz Romero et al. 2012, Vidal et al. 2013).

Loss of Monarch Habitat in Croplands Due to Increased Use of Glyphosate With Roundup Ready Crops

First introduced by the Monsanto Company in 1974, glyphosate is an extremely effective herbicide that kills a broader range of plants than most weed-killers (Duke and Powles 2008). This is because glyphosate inhibits a critical enzyme—5-enolpyruvyl-shikimate-3-phosphate synthase (EPSPS) —that is found in virtually all green plants, and which helps the plant synthesize various compounds it requires for growth and survival. Glyphosate is thought to kill plants by inducing shortages of these essential compounds (Henderson et al. 2010), though other potentially complementary mechanisms have been proposed (Lorentz et al. 2011, Johal and Rahe 1984, Duke et al. 2007).

Glyphosate is a systemic herbicide that has unparalleled effectiveness on perennial weeds—such as common milkweed—that most other herbicides fail to kill (Franz et al. 1997). When glyphosate is sprayed on a weed, it is absorbed by the leaves and stems and then translocated (moved) inside the plant to concentrate in actively growing meristematic tissues, including the plant's roots and developing buds (Duke and Powles 2008). By killing common milkweed at the root, regrowth the following year is largely prevented (Bhowmik 1994).

In 1996 Monsanto introduced the first of a series of Roundup Ready crops, which are genetically engineered to survive direct broadcast application of glyphosate, sold under the brand name of Roundup, but also in many generic versions produced by other firms. Roundup Ready crops enable glyphosate to be used post-emergence (to the growing crop) to kill weeds through much of the growing season without crop injury. Glyphosate is particularly lethal to milkweed when used in conjunction with Roundup Ready crops because it is applied more frequently, at higher rates, and later in the season—during milkweed's most vulnerable flowering stage of growth—than when used with traditional crops. The increasingly common practice of growing Roundup Ready crops continuously and sequentially (corn, soybean, corn, and so on) on the same fields means that milkweed is exposed to glyphosate every year, with no opportunity to recover.

Prior to the Roundup Ready crop era, glyphosate was little used in corn and soybean production. From 1990 to 1995, glyphosate was applied to only 5-20 percent of national soybean acres and from 1-6 percent of corn acres each year [U.S. Department of Agriculture National Agricultural Statistics Service (USDA NASS) 1991-2008]. Monsanto introduced Roundup Ready soybeans in 1996 and Roundup Ready corn in 1998. Herbicide-resistant varieties (nearly all Roundup Ready) comprised 93 percent of soybeans and 85 percent of all corn grown in the United States in 2013 (USDA ERS 2014a).

Pesticide usage figures from USDA's National Agricultural Statistics Service (NASS) and the U.S. Geological Survey (USGS) show the dramatically increasing use of glyphosate in American agriculture triggered by Roundup Ready corn and soybeans. The glyphosate data discussed below are based primarily on NASS, which surveys thousands of farmers to arrive at the best available estimates of pesticide use in American agriculture (USDA NASS Advisory 2006). NASS reports pesticide use by crop—including percent of total crop acres treated, application rate, number of applications, and total amount used—for the "Program States" where most of the crop (corn or soybeans) is grown in the survey year. Several operations were required to derive the figures reported below. First, use figures for different types (salts) of glyphosate (these include "sulfosate," which is the trimethylsulfonium salt of glyphosate, *see*: http://www.weeds.iastate.edu/mgmt/qtr00-1/touchdown2.htm) as reported by NASS were combined: total amounts and percent area treated of different types were summed, while weighted averages were calculated for application rates and frequencies. Second, because NASS figures on total amount of glyphosate reflect usage only in those Program States surveyed in a given year, the totals are normalized to estimate national usage, and to enable valid comparisons from year to year. On average, NASS surveyed pesticide use on 88 percent of corn acres and 88 percent of soybean acres for the reported time period (USDA NASS 2013, 2011, 1991-2008). Thus, for example, if total glyphosate use as reported by NASS is 50.00 million pounds on corn in a year in which 90 percent of corn acres were surveyed, national glyphosate use on corn is 55.56 million pounds (50.00 million lbs./0.90). Third, because NASS did not survey pesticide use on corn and soybeans every year (particularly after 2005), glyphosate figures are interpolated or extrapolated for un-surveyed years. USGS also reports use of pesticides, including glyphosate, based primarily on proprietary data from GfK Kynetec, Inc. (Thelin and Stone 2012), and these data corroborate our NASS-derived figures.

Between 1995, the year before Roundup Ready soybeans were introduced, and 2013, total glyphosate use on corn and soybeans rose from 10 million to 205 million pounds per year, a 20-fold increase (*see* Figure 17). USGS figures on national glyphosate use on corn and soybeans agree closely with those derived from NASS data (*see* Figures 17 and 18). This dramatic increase is attributable to increased acreage treated, more glyphosate being applied per acre, and increasingly frequent applications in a single year and over the course of years. Each of these factors and its relevance to common milkweed is discussed below.

From 1995 to 2013, combined corn and soybean acreage treated with glyphosate increased from 17 to 157 million acres, a nine-fold increase (*see* Figure 19), tracking the rising adoption of Roundup Ready varieties (*see* Figure 20). For perspective, these 157 million glyphosate-treated acres represent half of all harvested cropland in the entire country in 2012 (315 million acres), an area nearly the size of Texas (USDA Census 2012, Table 8).

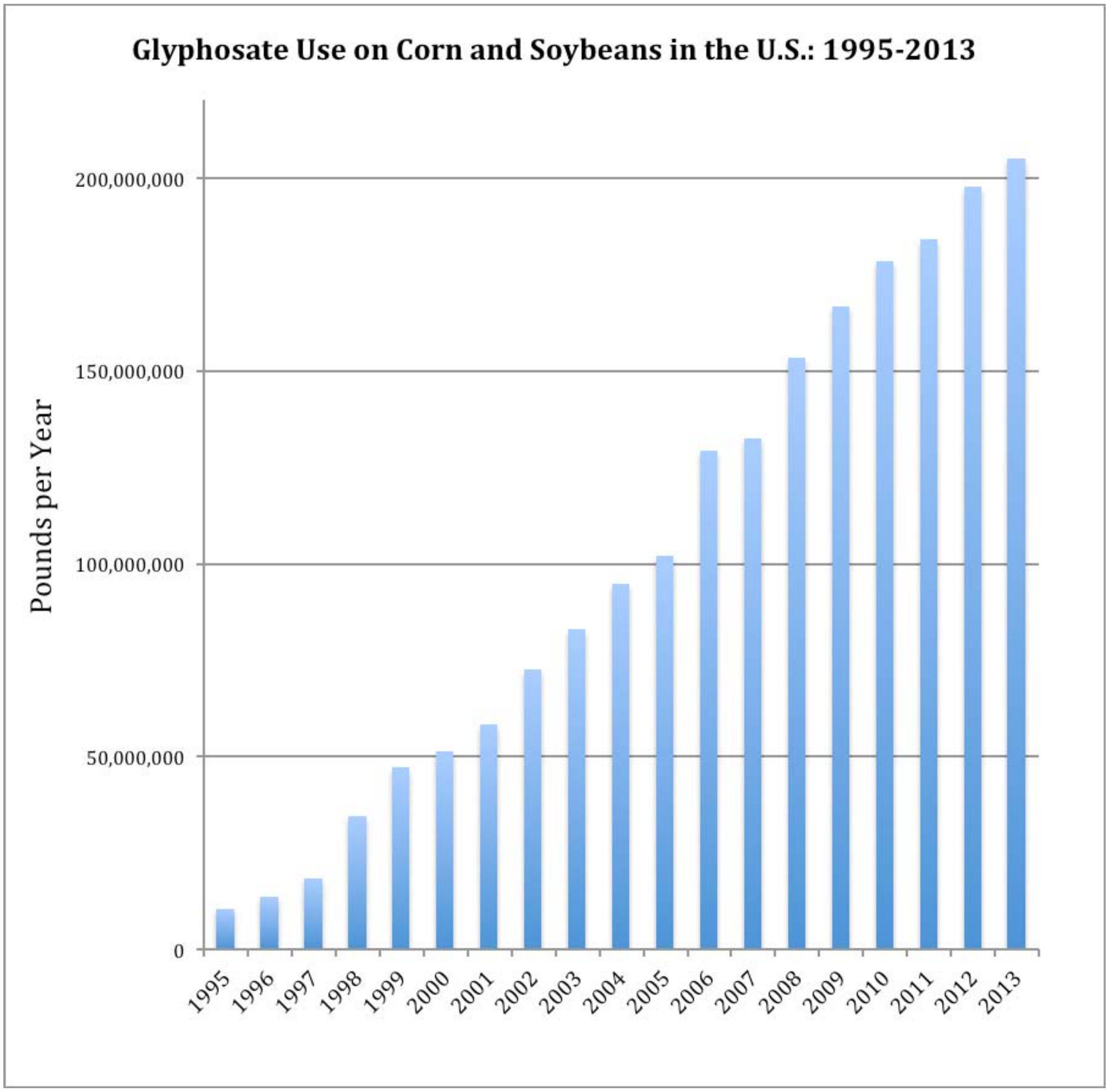


Figure 17. Glyphosate use on corn and soybeans: 1995-2013. Sources: USDA NASS (2013, 2011, 1991-2008).

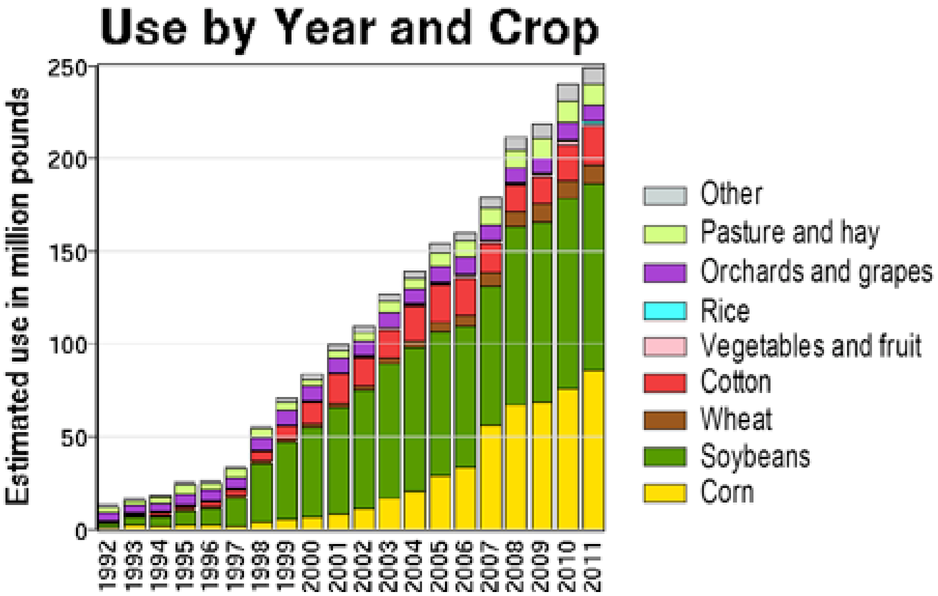


Figure 18. Estimated Agricultural Use of Glyphosate: Epest-Low. U.S. Geological Survey. *Compare* yellow and green bars for corn and soybean *with* NASS-derived data in preceding figure. http://water.usgs.gov/nawqa/pnsp/usage/maps/show_map.php?year=2005&map=GLYPHOSATE&hilo=L, accessed July 29, 2014.

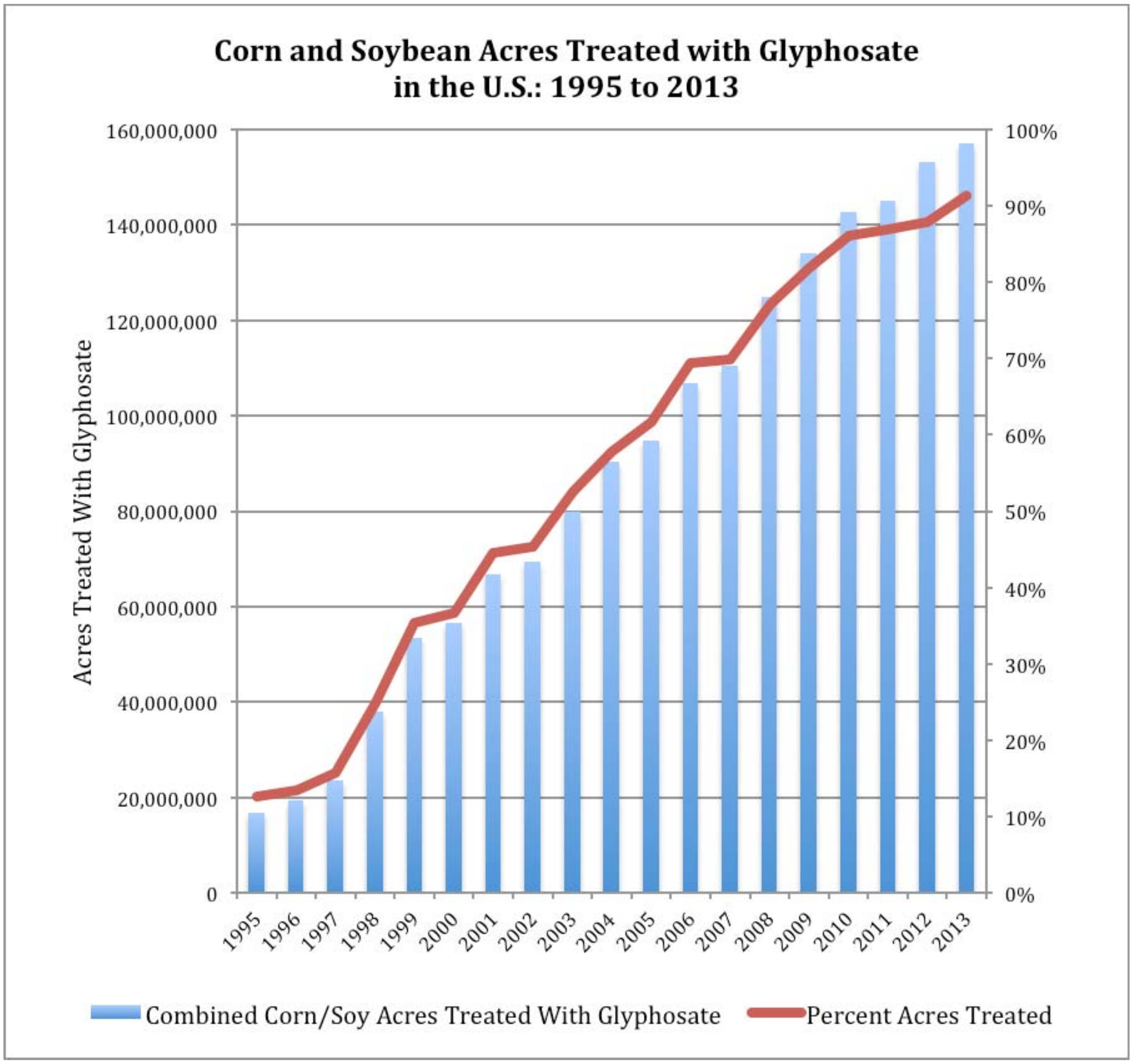


Figure 19. U.S. Corn and Soybean Acres Treated with Glyphosate: 1995-2013. Sources: USDA NASS (2014, 2013, 2011, 1991-2008).

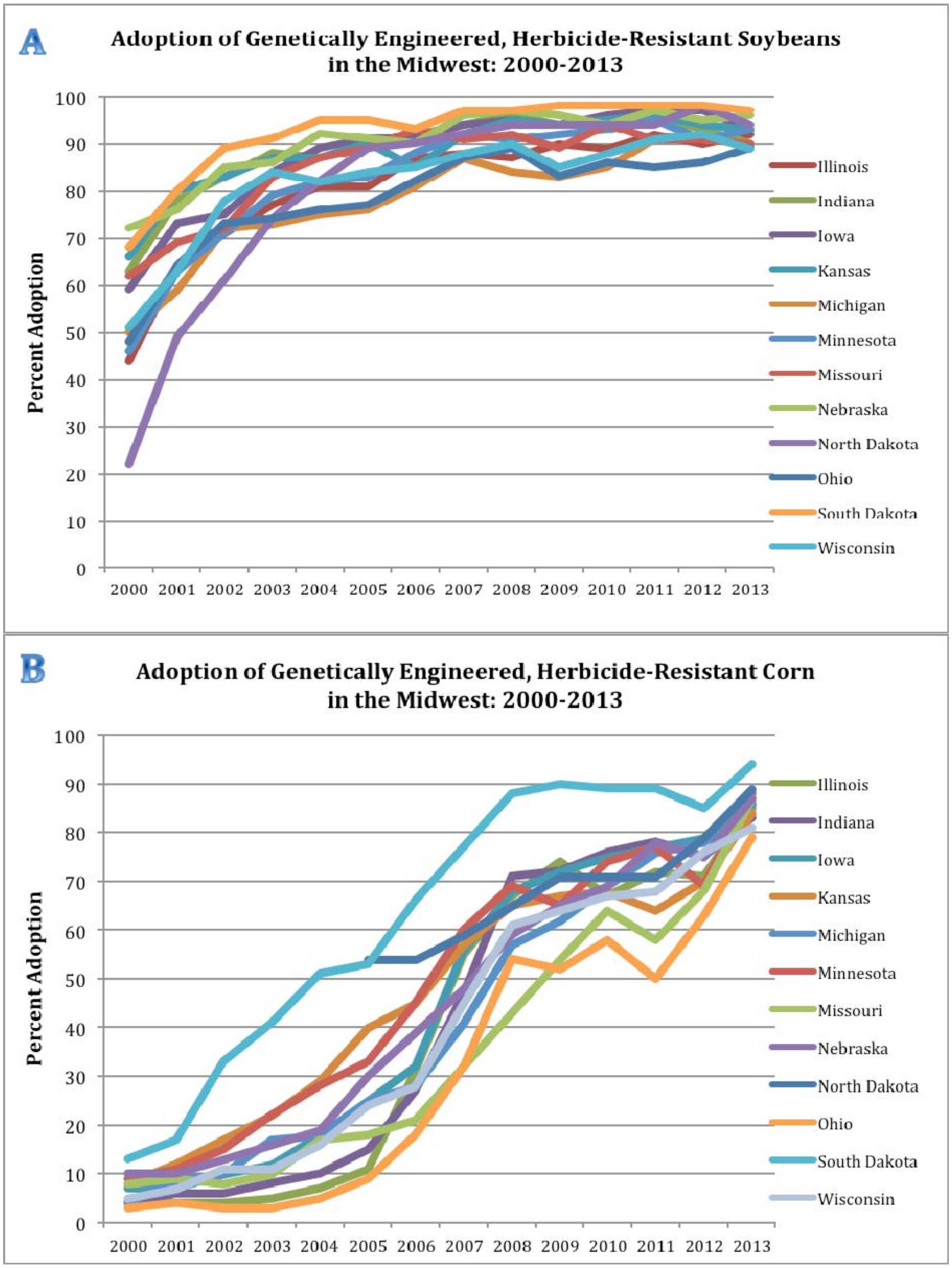


Figure 20. A: Percentage of U.S. soybean acreage planted to genetically engineered, herbicide-resistant soybeans. B: Percentage of U.S. corn acreage planted to genetically engineered, herbicide-resistant corn. Source: USDA ERS (2014b).

Glyphosate is not only being applied to vastly more acres than ever before, it is also being applied more intensively to the acres that are treated with it. From 1995 to 2013, the average glyphosate application rate increased by 58 percent on soybeans, from 0.60 to 0.95 pounds per acre, and increased by 41 percent on corn, from 0.61 to 0.86 pounds per acre (USDA NASS 2013, 2011, 1991-2008). Because higher rates of glyphosate are recommended to kill perennial weeds like common milkweed more effectively (Monsanto 2009, 12.7 and 12.8), this rising intensity of use is one factor in common milkweed's demise in cropland.

The average frequency of glyphosate applications has also increased over this same period: from 1.0 to 1.64 applications per year on soybeans (a 64 percent increase), and from 1.1 to 1.27 applications per year on corn (a 15 percent increase) (USDA NASS 2013, 2011, 1991-2008). This means that progressively more acres of Roundup Ready corn, and especially Roundup Ready soybeans, have been treated twice rather than once per season. Because perennial weeds like common milkweed that regenerate from roots are more effectively killed by "repeat treatments" of glyphosate than by just one treatment (Monsanto 2009, 15.0), increased application frequency is another factor in common milkweed's disappearance from cropland.

Over three decades ago, weed scientists in Nebraska recommended glyphosate to control common milkweed, but noted that production practices to decrease common milkweed must be continued over a number of years to have a significant impact on the plant (Cramer and Burnside 1981). Roundup Ready crops have greatly facilitated continual use of such milkweed-killing practices. From the late 1990s to early 2000s, most farmers grew only Roundup Ready (RR) soybeans (*see* Figure 20A). Because most soybeans are rotated (grown in alternating years) with corn (USDA ERS 2012), any milkweed that survived glyphosate spraying in Roundup Ready soybeans had a chance to recover in the non-Roundup Ready corn year. That opportunity to recover was lost as Roundup Ready corn adoption rose after the mid-2000s (*see* Figure 20B), and common milkweed was increasingly exposed to glyphosate every year in now ubiquitous Roundup Ready corn/Roundup Ready soybean rotations.

Roundup Ready crops have not only increased the extent, intensity, and frequency of glyphosate use, they have also shifted the application period later into the growing season, when milkweed is more susceptible to glyphosate (Loux et al. 2001). When used with traditional corn and soybeans, glyphosate is usually applied pre-emergence, around planting time, in order to avoid injuring the growing crop. In Iowa, this corresponds to late April to mid-May for corn, and the month of May for soybeans (USDA NASS 2010). This early-season use occurs predominantly before milkweed's reproductive phase (formation of buds and flowering), which in the Midwest occurs from the latter part of May to mid-July (Sauer and Feir 1974, Martin and Burnside 1977/1984). In contrast, Roundup Ready soybeans are sprayed once or twice, two to eight weeks after planting (Monsanto 2009, 12.0, 12.7, 12.8). Roundup Ready corn is typically sprayed once or twice, two to six weeks after planting (Johnson and Leer 2006, Monsanto 2009, Section 12.0). These later application periods coincide with common milkweed's reproductive phase, when it is more vulnerable to glyphosate's killing effects (Bhowmik 1982, Martin and Burnside 1977/1984).

In sum, the limited and early-season use of glyphosate with traditional crops had little effect on common milkweed populations. As used with Roundup Ready crops, however, glyphosate has nearly eliminated milkweeds from cropland throughout the monarch's Midwest breeding range.

The loss of milkweed habitat in recent decades has been dramatic. In 1980, common milkweed was found on at least 26 million acres of land in the 13 north central states (Cramer and Burnside 1980). The two crops harboring the most milkweed were corn (12 million acres) and soybeans (6 million acres), although given the common practice of rotating these two crops the difference in reported acreage may not be very significant. Milkweed was also found to a much lesser extent in small grains, pastures, roadsides and sorghum (Bhowmik 1994). Iowa, Nebraska and Wisconsin had the most land occupied by milkweed (Cramer and Burnside 1980). Common milkweed continued to be a common inhabitant of Midwestern cropland throughout the 1980s and 1990s in Iowa (Hartzler and Buhler 2000), Minnesota and Wisconsin (Oberhauser et al. 2001), southwestern Ontario (Frick and Thomas 1992), and other areas. Milkweed acreage was expanding into the late 1990s in parts of North Dakota (Zollinger 1998), Wisconsin (Doll 1998), and likely other states. Despite its wide distribution, however, common milkweed was far less prevalent than many more agriculturally significant weeds even before the Roundup Ready crop era, and for the most part was not problematic for farmers (Doll 2001, Hartzler 2010).

Common milkweed's success in 20th century corn and soybean fields is attributable in large part to its tolerance to commonly used herbicides of the period (Martin and Burnside 1977/1984). While these non-glyphosate herbicides wither milkweed leaves, the plant usually recovers in two to three weeks by sprouting new branches from leaf axils and new stems from the perennial root; in contrast, with glyphosate treatment most plants do not recover (Pleasants in press).

Iowa is the state where common milkweed was once most abundant, occupying more than five million acres in 1980 (Cramer and Burnside 1980). In 1999 and again in 2009, Iowa State University scientists conducted surveys that established the prevalence and distribution of common milkweed in both crop fields and other land types throughout the state (n = 859 fields in 1999, n = 432 fields in 2009) (Hartzler and Buhler 2000, Hartzler 2010). In 1999, common milkweed was detected in half (51 percent) of Iowa corn and soybean fields, but by 2009 it was detected in just eight percent of fields, a more than six-fold reduction. In addition, the average milkweed density in fields where it was present declined by nearly five-fold, from 23 to just five square meters per hectare. The declining number of fields with milkweed, and the reduced density where it was found, translate to a 96.5 percent decline in milkweed in Iowa corn and soybean fields from 1999 to 2009 (based on Hartzler and Buhler 2000, Hartzler 2010, *see* Figure 21).

These survey results are corroborated by a second, more limited survey conducted by entomologist John Pleasants in Iowa from 2000 to 2008 (Pleasants and Oberhauser 2012). Pleasants charted declining milkweed populations in seven fields surveyed over a nine-year period. Of roughly 1,000 milkweed stems counted in 2000, none remained by 2009 (Pleasants in press) (Figure 21). Milkweed loss has continued since 2009, and it is estimated that Iowa cropland lost 98.7 percent of its milkweed from 1999 to 2012 (Pleasants in press).

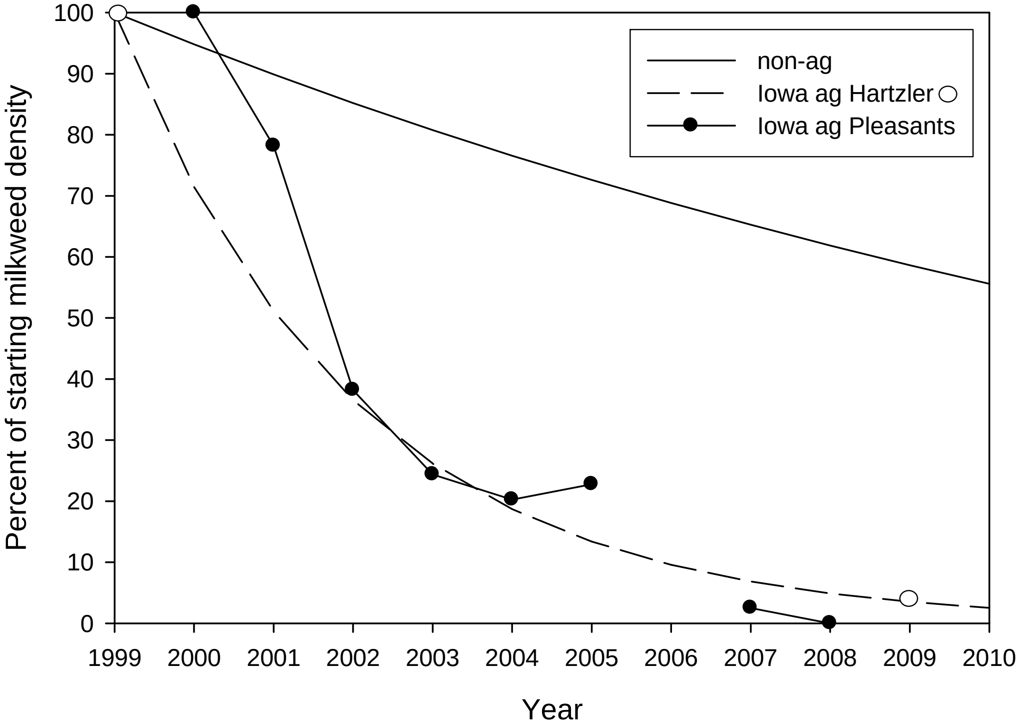


Figure 21. Change in milkweed density in Iowa: agricultural and non-agricultural habitats (updated from Pleasants and Oberhauser 2012, Figure 1, supplied by authors).

Data from Minnesota also indicate widespread milkweed decline. Extensive milkweed surveys were conducted from 2003 to 2005 in Minnesota crop fields (Koch 2005). The survey covered 72 Minnesota counties with appreciable acreage planted to corn and soybeans, with an average of six to seven fields surveyed per county. Each year 453 fields were surveyed on average, equally divided between soybeans and corn. Averaged over the three years, milkweed was detected in just 3.4 percent of surveyed fields, and those fields harbored 0.084 milkweed plants/m^2. Averaged over all fields (including those with no milkweed), milkweed density came to just 30 plants per hectare. Milkweed plants were much more numerous in this area just three to five years before the Koch surveys. In the year 2000, Oberhauser et al. (2001) studied milkweed in five cornfields in east central Minnesota/west central Wisconsin, finding on average 2,850 milkweed plants per hectare, roughly two orders of magnitude (100-fold) higher than the level found in the Koch (2003-2005) surveys. Although these sites were not necessarily representative of landscape milkweed prevalence because candidate fields with less than 10 milkweed stems/ha were excluded, the authors report that the majority of sites visited during their site selection process had some milkweed (Karen Oberhauser, personal communication to Bill Freese, 3/20/14), as opposed to only 3.4 percent of fields with milkweed in the 2003-2005 Minnesota surveys. Dr. Oberhauser reported that the study fields in 2000 had never been planted with herbicide-resistant soybeans or corn, and attributed the drop in milkweed numbers by 2003-2005 to the widespread planting of genetically engineered, glyphosate-resistant soybeans and corn (personal communication to Bill Freese, 3/20/14, Pleasants and Oberhauser 2012).

The Iowa and Minnesota surveys exemplify the broader picture of milkweed decline throughout the major monarch breeding grounds in the Midwest due to the similarity in land use. The entire region is dominated by corn and soybean fields (Figure 22), the vast majority of which are Roundup Ready varieties. Figure 20 shows that adoption trends for genetically engineered, herbicide-resistant corn and soybeans (nearly all Roundup Ready) are quite similar in the 12 Midwestern states, with 89 to 97 percent of soybeans, and 81 to 94 percent of corn, herbicide-resistant by 2013. Anecdotal evidence reported by farmers and scientists of common milkweed's absence from or rarity in crop fields in Nebraska, Kansas, Michigan and North Dakota—all states where it was once quite prevalent—provide further corroboration of the near eradication of milkweed from cropland by glyphosate use with Roundup Ready crops (Center for Food Safety 2014a).

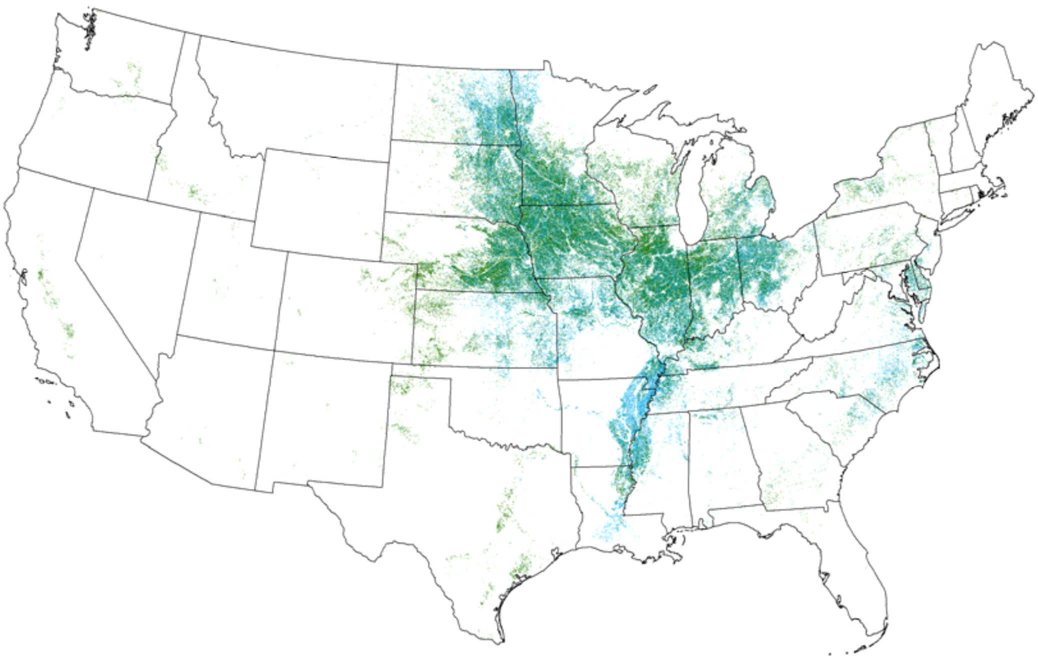


Figure 22. Corn and soybean production in the United States 2013. Source: USDA CropScape (2013). Green represents corn, blue represents soybeans. Depth of color signifies intensity of cultivation.

The extensive loss of milkweed from croplands has contributed significantly to the dramatic decline in monarch abundance since the mid-1990s. Common milkweed in crop fields is of particular importance to monarchs because it produces considerably more monarchs per plant than milkweeds growing elsewhere. Oberhauser et al. (2001) analyzed milkweed distribution and per-plant monarch productivity and found that in Iowa, Minnesota, and Wisconsin, the number of eggs deposited per milkweed plant was higher on milkweeds in corn fields than on milkweeds in old fields, pastures and field edges. Pleasants and Oberhauser (2012) extended this analysis over four years (2000-2003) in Iowa, and found that per-plant egg density on milkweed was on average 3.89 times greater when growing in corn and soybean fields versus non-agricultural habitats. Survival of eggs to adulthood was similar between habitats.

In just the 13 years from 1999 to 2012, it is estimated there was a 64 percent decline in overall milkweed in the Midwest, most of which was from croplands (Pleasants in press). However, because cropland milkweed produces nearly four times as many monarchs as plants in other settings, their loss has a disproportionate impact on monarch numbers. Pleasants (in press) estimates that in 2012, the Midwest produced 88 percent fewer monarchs than it did in 1999.

Loss of Western Monarch Habitat Due to Glyphosate

Glyphosate is also heavily used in the western portion of the monarch's range, and may be degrading habitat there as well. In 2012 in California, glyphosate was among the top five pesticides (and the top herbicide) in terms of amount used (California Department of Pesticide Regulation 2014, p. 15), and the leading pesticide as measured by cumulative acres treated (California Department of Pesticide Regulation 2014, pp. 66-67; Figure 11, p. 70). In addition to almonds and wine grapes, leading crops treated with glyphosate include cotton and alfalfa. Glyphosate accounts for 74 percent of total pounds of herbicides applied to cotton "due to the large acreage of Roundup Ready cotton," and its use is rising on alfalfa "because of increased planting of Roundup Ready alfalfa" (California Department of Pesticide Regulation 2014, pp. 85, 89). Genetically engineered, herbicide-resistant cotton rose from 21 percent to 68 percent of total California cotton acres from 2000 to 2013 (USDA ERS 2014b). Heavy use of glyphosate in California, a state with extensive agriculture production, threatens the multiple species of milkweed that provide habitat in California, and thus monarch reproduction and survival west of the Rockies.

Loss of Monarch Habitat Due to Agricultural Intensification to Produce Biofuels

The 88 percent decline in Midwest monarch production discussed above means that the Midwest produces only 12 percent as many monarchs as it did in 1999. This dramatic decline is driven primarily by loss of milkweed in cropland, which is being lost at the astonishing rate of nearly 50 percent every two years (Figure 21, based on data supplied by John Pleasants). Without conservation and restoration efforts, common milkweed will for all practical purposes disappear from the largely Roundup Ready corn and soybean fields that dominate the Midwest landscape (Pleasants and Oberhauser 2012). Moreover, monarch habitat outside of crop fields is also being rapidly degraded.

The majority of remaining Midwest monarch habitat is today found on lands enrolled in the Conservation Reserve Program (CRP). The CRP is a program administered by the U.S. Department of Agriculture that compensates farmers for taking environmentally sensitive land out of crop production for 10-15 year periods and instead planting species (usually grasses) that improve environmental quality by reducing soil erosion, providing wildlife habitat and improving water quality (USDA Farm Service Agency 2014). Because of the precipitous decline in milkweed in cropland, CRP lands that contributed only 16 percent of Midwest monarchs in

1999 accounted for 56 percent of the much-reduced population remaining in 2012 (based on data supplied by John Pleasants).

Conversion of CRP acreage to corn and soybean production is being driven by federal biofuels policy. The 2005 Energy Policy Act and the 2007 Energy Independence and Security Act established subsidies and quotas for biofuels production, chiefly ethanol from corn. These incentives drove construction of new ethanol plants, increased demand for corn, sharply rising corn prices, and huge increases in corn acreage (USDA ERS Corn 2014). The share of the U.S. corn harvest processed for ethanol rose from 6 percent in the year 2000 and 14 percent in 2005 to 43 percent in the drought year 2012, and a still substantial 36 percent in 2013 (USDA ERS Feed Grains 2014). To meet this increased demand, corn acreage has increased by 17 million acres since 2006 (USDA NASS 2014).

While some of this increased corn acreage has come at the expense of other crops (Wallander 2011), a substantial portion has come from the CRP. Enticed by the greater profitability of corn versus CRP payments, farmers have responded to the ethanol-driven "corn rush" by taking their land out of the CRP to grow corn (Love 2012, Cappiello and Apuzzo 2013). These land conversions are reflected in CRP enrollment figures. Nationally, CRP acreage has shrunk by 11.2 million acres (30 percent) since 2007 (USDA FAS CRP 2014). Over half of this decline has taken place in the twelve Midwest states, which have lost 6.2 million CRP acres (Figure 23). Wright and Wimberly (2013) estimate that 1.3 million acres of grassland in the western Corn Belt (much of it CRP land) was converted to corn and soybean production from 2006 to 2011. CRP acreage has declined substantially since 2011 (Figure 23), suggesting a continuation of this disturbing trend.

CRP lands will continue to shrink in the future. In the 2014 Farm Bill, Congress sharply reduced the maximum acreage that can be enrolled in the program. This "CRP cap," which stood at 39.2 million acres from 2002 to 2009, will decline by 39 percent to just 24 million acres by 2017 and 2018 (National Sustainable Agriculture Coalition undated, National Council of Farmer Cooperatives 2014), ensuring that each year progressively more of monarchs' most important breeding habitat will be converted to corn and soybean fields stripped of common milkweed by use of glyphosate and other herbicides.

CRP land is the major remaining habitat for Midwest monarchs, and conversion to corn and soybeans that are engineered to be resistant to glyphosate (and other herbicides, *see* next section) will continue to drive monarch population decline in the core of the species' range.

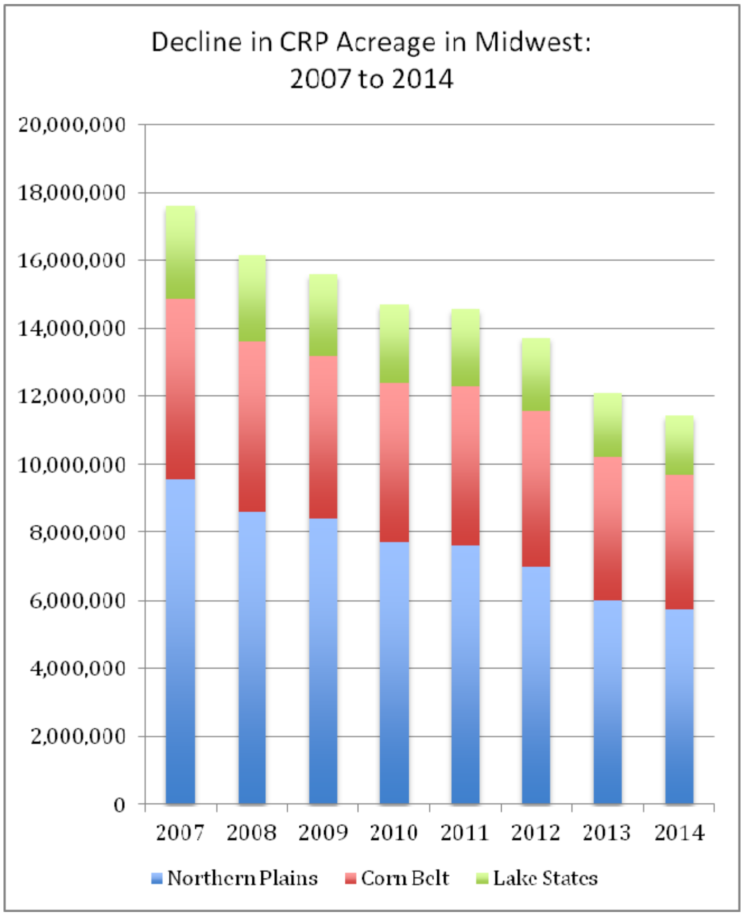


Figure 23. Decline in Acreage Enrolled in Conservation Reserve Program: 2007-2014. Source: USDA FAS CRP (2014). Midwest here defined as the 12 states of the Corn Belt (IA, IL, IN, MO, OH), the Lake States (MI, MN, WI) and the Northern Plains (KS, NE, ND, SD).

New Herbicide-Resistant Crops Promise Further Habitat Degradation

Monarch habitat is further threatened by the imminent introduction of new herbicide-resistant crops that are genetically engineered to be resistant to multiple herbicides. These new crops pose two distinct risks: (1) continued elimination of common milkweed from cropland, and (2) reduction via herbicide drift of flowering plants that provide monarch adults with nectar.

The widespread use of glyphosate with Roundup Ready crops has spawned an epidemic of glyphosate-resistant weeds (Benbrook 2009). In the United States, 135 populations of 14 different weed species in 36 states have evolved resistance to glyphosate (International Survey of Herbicide Resistant Weeds 2014), and they infest an estimated 50-62 million acres of U.S. cropland (Benbrook 2012, Fraser 2012), an area the size of Wyoming. A recent survey found that the problem is expanding, with 49 percent of farmers reporting glyphosate-resistant weeds in 2012, up from 34 percent in 2011 (Fraser 2012).

In response, all of the major agricultural biotechnology companies have developed "next-generation" crops resistant to other herbicides that will still kill glyphosate-resistant weeds, at least for a time (Kilman 2010, Table 1). The most popular are expected to be corn, soybeans and cotton engineered by Dow AgroSciences for resistance to 2,4-D-dichlorophenoxyacetic acid (2,4-D), and the Monsanto Company's dicamba-resistant soybeans and cotton, which collectively will likely supplant a substantial portion of Roundup Ready crop acreage (Mortensen et al 2012). Genetically engineered 2,4-D-resistant corn and soybeans were recently approved by USDA, which also gave preliminary approval to the genetically engineered dicamba-resistant crops (Table 1, *see*: http://www.aphis.usda.gov/biotechnology/petitions_table_pending.shtml). Commercial introduction is expected in the next two years.

GE Herbicide-Resistant Crops Approved or Pending Approval by USDA

Petition No.	Company	Crop	Herbicides	Status
13-262-01p	Dow	Cotton	2,4-D, glufosinate, ***glyphosate***	Pending approval
12-251-01p	Syngenta	Soybeans	HPPD inhibitors, glufosinate, ***glyphosate***	Approved 2014
12-185-01p	Monsanto	Cotton	Dicamba, glufosinate, ***glyphosate***	Pending approval
11-234-01p	Dow	Soybean	2,4-D, glufosinate, glyphosate	Approved 2014
10-188-01p	Monsanto	Soybean	Dicamba, ***glyphosate***	Preliminary approval
09-349-01p	Dow	Soybean	2,4-D, glufosinate, ***glyphosate***	Approved 2014
09-328-01p	Bayer	Soybean	Isoxaflutole, glyphosate	Approved 2013
09-233-01p	Dow	Corn	2,4-D, ACCase inhibitors, ***glyphosate***	Approved 2014
09-015-01p	BASF	Soybean	Imidazolinones	Approved 2014
07-152-01p	DuPont Pioneer	Corn	Imidazolinones, glyphosate	Approved 2009

Table 1. Partial list of genetically engineered, herbicide-resistant crops recently approved or pending approval by USDA. Source: USDA's Petitions for Determination of Nonregulated Status, http://www.aphis.usda.gov/biotechnology/petitions_table_pending.shtml, accessed August 6, 2014. Where glyphosate is bolded and italicized, the company has not genetically engineered glyphosate resistance into the GE crop for its review by USDA, but has announced plans to breed a glyphosate resistance trait into commercial cultivars to be sold to farmers.

At present, 2,4-D and dicamba are minor corn and soybean herbicides (USDA NASS 2013, 2011), and where used they are applied early in the season at relatively low rates to avoid crop injury. However the high-level resistance conferred by genetic engineering to the new crops will facilitate application of several-fold higher rates of 2,4-D and dicamba than are used at present. Applications will also be made more frequently, and later in the season, similar to the use pattern of glyphosate with Roundup Ready crops (Center for Food Safety 2012b, Center for Food Safety 2012c).

2,4-D and dicamba will not displace glyphosate where these crops are grown, for several reasons. First, the new crops will come with additional resistance to glyphosate (and in some cases still other herbicides) (Table 1). Second, glyphosate will continue to be used because it kills certain weeds (e.g. grass family and perennial weeds) more effectively than either 2,4-D or dicamba. Third, the chemical companies will market dual products specifically for use with the resistant crops: Dow's Enlist Duo (a combination of 2,4-D and glyphosate) and Monsanto's Roundup Xtend (a dicamba/glyphosate mix). Thus, Roundup Ready farmers who switch over to these next-generation seeds will be applying high rates of 2,4-D or dicamba *in addition to* glyphosate at rates currently used (Center for Food Safety 2014b, Monsanto 2012).

Herbicide efficacy trials show that application of high rates of either 2,4-D or dicamba alone cause considerable lasting damage to common milkweed, though not as much as glyphosate (Zollinger 1998). Ohio agronomists recommend either glyphosate or dicamba alone, or a mix of 2,4-D and glyphosate, to kill common milkweed (Loux et al. 2001). Thus, the application of the dual herbicide products (Enlist Duo or Roundup Xtend) to crops resistant to them will continue to eliminate what little common milkweed remains in corn and soybean fields at least as effectively as glyphosate has with Roundup Ready crops.

The second major threat posed by these new multiple herbicide-resistant crops is a reduction in flowering plant communities that supply nectar to monarch adults.

Loss of Habitat Due to Pesticide Drift

Although monarch larvae can only thrive on milkweeds, adult butterflies feed on a wide variety of nectar-producing flowers (Tooker et al. 2002). They depend on flowers that are in bloom in their breeding habitat during the spring and summer, and then along migration routes to their winter roosts (Brower and Pyle 2004, Brower et al. in press). Monarchs that are breeding during spring and summer require energy derived from nectar for flying, laying eggs, mating, and other activities. In addition, the generation that migrates in the fall depends on nectar sugars (stored in the form of fat) to sustain themselves while overwintering, and perhaps also to fuel their northern migration the following spring (Brower et al. 2006).

Herbicides, by definition, are toxic to plants, and they frequently drift beyond the boundaries of crop fields to affect wild plants growing nearby. Various models of herbicide spray drift suggest that from one percent (commonly) to 25 percent (occasionally) of the applied herbicide dose drifts beyond field boundaries to reach wild plants growing nearby (Holterman et al. 1997, Wang and Rautmann 2008, Boutin et al. 2014). Areas surrounding cropland provide most of the biodiversity in agriculture-dominated landscapes (e.g. Boutin and Jobin 1998) such as the Midwest. Herbicide drift threatens the wild plants monarchs depend upon for nectar. The imminent introduction of next-generation herbicide-resistant crops, such as those resistant to 2,4-D and dicamba, discussed above, will lead to sharply increased herbicide use, drift, and associated damage to wild plants, reducing monarch nectaring habitat.

Herbicide drift is greatly exacerbated by herbicide-resistant crops. This is demonstrated quite clearly by experience with Roundup Ready crops. Glyphosate has relatively low volatility and is not regarded as a drift-prone weed killer (Lee et al. 2005, p. 135). Nevertheless, it has become one of the top two herbicides (along with 2,4-D) implicated in herbicide drift complaints nationwide since the Roundup Ready era began (Association of American Pesticide Control Officials 1999, 2005). The high incidence of glyphosate drift injury is partly attributable to the expanded acreage and increased volume of use with Roundup Ready crops. The late application period—mid-season with Roundup Ready crops versus early season with conventional varieties—also increases the risk of drift injury. In a comprehensive study of the potential for herbicide drift to injure crops in Fresno, CA, scientists from the U.S. Environmental Protection Agency found that:

> Increased use of herbicide-resistant technology by producers creates the possibility of off-site movement onto adjacent conventional crops . . . Post-emergence application of herbicide to a genetically-modified (GM) crop often occurs when non-GM plants are in the early reproductive growth stage and are most susceptible to damage from herbicide drift (Ghosheh et al.,1994; Hurst, 1982; Snipes et al., 1991, 1992). Consequently, most drift complaints occur in spring and summer as the use of post-emergence herbicide applications increases (Lee et al. 2005, p. 15).

Glyphosate drift from Roundup Ready crops has repeatedly caused extensive damage to wheat (Baldwin 2011) and rice (Scott 2009) in Arkansas, to rice (Wagner 2011) and corn (Dodds et al. 2007) in Mississippi, to rice in Louisiana (Bennett 2008), and to tomatoes in Indiana and adjacent states (Smith 2010), to cite just a few of many examples. A search of the online farm publication Delta Farm Press using the search term "glyphosate drift" yields 127 articles (search conducted June 5, 2014, *see*: www.deltafarmpress.com). Drift episodes sometimes give rise to lawsuits, as when farmers won compensation for onions damaged by glyphosate applied to Roundup Ready soybeans in Ontario, Canada (Lockery vs. Hayter 2006).

Glyphosate drift injury can be extensive. In Mississippi, damage was reported on 30,000 to 50,000 acres of rice in 2006 (Wagner 2011). Glyphosate drift damage to wheat has prompted suggestions that it simply not be grown in Arkansas (Baldwin 2011). Tomato growers in Indiana, Michigan and Ohio suffered more than $1 million in glyphosate drift damage over four years (Smith 2010). Arkansas corn growers felt so threatened by drift that they switched to Roundup Ready varieties out of "self-defense" against glyphosate drifting from Roundup Ready soybean and cotton fields (Baldwin 2010).

The frequency of crop injury from glyphosate drift demonstrates the threat that genetically engineered, herbicide-resistant crops pose to monarch habitat. Several studies suggest that glyphosate applied to crops engineered with resistance may have already reduced the abundance and diversity of nectar plants in and around agricultural fields, from direct applications as well as spray drift (e.g. Blackburn and Boutin 2003, Gove et al. 2007). Next-generation, genetically engineered, herbicide-resistant crops will greatly exacerbate these impacts.

2,4-D and dicamba are volatile herbicides prone not only to spray drift (like glyphosate), but also vapor drift, which is much more unpredictable and difficult to control (Behrens and Lueschen 1979, Sciumbato et al. 2004). While spray drift happens only while the herbicide is being applied, vapor drift occurs when an herbicide previously deposited on plant surfaces and the ground volatilizes and moves off-site, and is favored by hot conditions and temperature inversions (Johnson and VanGressel 2012, United States Geological Survey 2003). Vapor drift helps explain why 2,4-D and dicamba, though much less heavily used than glyphosate, have been leading culprits in drift-related crop injury, with 2,4-D ranking first or second along with glyphosate (Association of American Pesticide Control Officials 1999, 2005).

Crops damaged by 2,4-D and dicamba drift, often at quite low levels, include grapes, cotton, soybeans, sunflowers, and many fruits and vegetables (Hebert 2004, Egan et al. 2014a, Doohan et al. 2014). Despite numerous restrictions on formulation types and application methods intended to mitigate drift, 2,4-D continues to cause widespread crop injury (Hebert 2004). Though damage often occurs to crops in adjacent fields, area-wide impacts are not uncommon. For instance, in 2006 volatilization of 2,4-D damaged cotton on upwards of 200,000 to 250,000 acres in five counties in Arkansas, likely due to multiple applications in the area and weather conditions that promoted vapor drift (Bennett 2006). In 2012, a single 2,4-D application damaged 15,000 acres of California cotton as well as a pomegranate orchard, with cotton damage verified as far as 100 miles from the application site (Cline 2012).

In the Canadian Prairies, 2,4-D, dicamba and other herbicides are frequently found in the air and in rain (Tuduri et al. 2006). At the high end of concentrations detected in rainfall in Alberta, Canada, a mixture of four herbicides (2,4-D, dicamba, MCPA and bromoxynil) was found to negatively impact test plants, leading the researchers to conclude that "occasional high levels of herbicides detected in rainfall in southern Alberta could harm beans and tomatoes grown in the area" (Hill et al. 2002). Extensive monitoring in Washington State has shown that 2,4-D injury to grapes occurs "from regional nonpoint sources estimated to be as far as 10 to 50 miles away, and correlates with airborne 2,4-D concentrations rather than local pesticide use" (Hebert 2004).

The frequency of such area-wide impacts, including those from regional off-target movement and "toxic rainfall," will increase dramatically with the surge in use anticipated with the planting of resistant crops. USDA has projected that 2,4-D-resistant corn and soybeans would increase annual agricultural use of 2,4-D by three- to seven-fold: from 25.6 million pounds at present to anywhere from 77.8 to 176 million lbs./year by 2020, depending on how widely they are grown (Figure 24). Pennsylvania State University weed scientists have projected a similarly large increase in 2,4-D and dicamba applications if soybeans resistant to them are approved (Mortensen et al. 2012).

Increased drift injury will not be limited to sensitive crops, but will affect wild plants as well. 2,4-D and dicamba selectively kill broadleaf plants, and are less effective on grasses (Rasmussen 2001, US EPA 2006, Center for Food Safety 2012a). This will make them particularly injurious to butterflies, especially with frequent application over a broad area, as would occur with 2,4-D and dicamba-resistant crops. A study of pesticide effects on butterflies in agricultural areas of England showed that restricting the use of “persistent broadleaf herbicides” near field edges would result in more butterflies in the landscape. In one experiment, researchers sprayed the bulk of the field with the usual complement of pesticides, but modified the spraying apparatus such that only selective grass-killing herbicides were applied to the field edges. They found that there were indeed more butterflies after implementing this measure, and also that there were more flowering plants, “thereby increasing the availability of nectar resources for butterfly species,” as well as more biodiversity in general (Longley and Sotherton 1997, pp. 8-9).

Several new field studies in the United States—undertaken to assess the potential effects of dicamba use with dicamba-resistant crops—support the English findings. Bohnenblust (2014) found that drift-level doses of dicamba delayed flowering of alfalfa, and both delayed and reduced flowering of common boneset (*Eupatorium perfoliatum*), a wildflower that provides resources to many insect species. In addition, common boneset flowers were less visited by all pollinators when treated with dicamba at rates simulating drift.

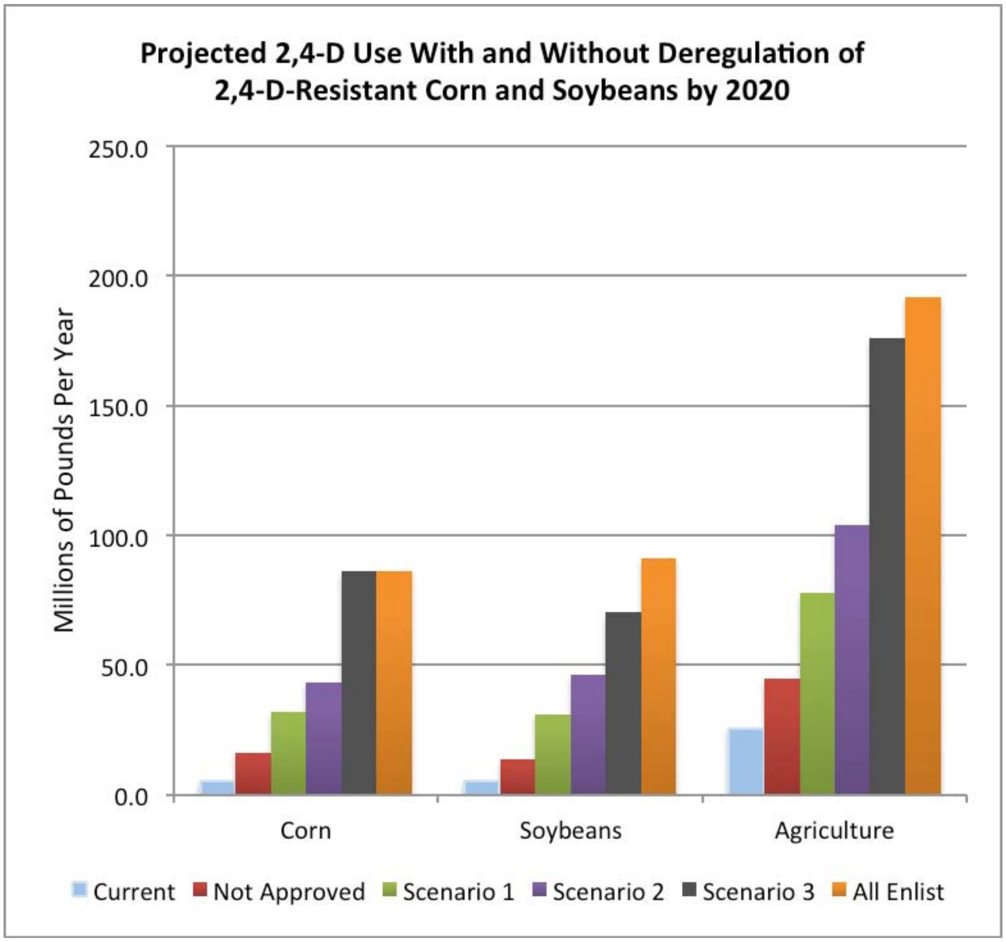


Figure 24. Projected Use of 2,4-D With and Without USDA Approval of 2,4-D-Resistant Corn and Soybeans by 2020. Source: CFS (2014a), based on projections made by Dow in USDA APHIS (2013), Appendix 4. Scenarios 1, 2, 3 and All Enlist represent 2,4-D use based on various adoption scenarios for 2,4-D-resistant corn and soybeans by 2020. Scenario 1: 30% of corn and soybean acres are 2,4-D-resistant and sprayed with 2,4-D; Scenario 2: 40.5% of corn and 45% of soybean acres are 2,4-D-resistant and sprayed with 2,4-D; Scenario 3: 80% of corn and 68% of soybean acres are 2,4-D-resistant and sprayed with 2,4-D; All Enlist: 85% of corn and 89% of soybean acres are 2,4-D-resistant and sprayed with 2,4-D (representing complete displacement of glyphosate-resistant varieties by 2,4-D-resistant corn and soybeans). *See* CFS (2014a) for more details.

A second study explored the impact of a range of drift-level dicamba doses on the plant and arthropod communities in agricultural "edge" habitats (Egan et al. 2014b). The most striking result was a significant decline in the abundance of broadleaf plants over time and with increasing dicamba dose. Impacts were observed at substantially lower levels (about one percent of the dicamba field application rate) than have been reported to affect plant communities in other studies. This study was conservative in design: dicamba alone was applied just once per year over two years. More severe impacts would be expected with longer-term use, and with the dicamba-glyphosate mix to be used with dicamba-resistant crops, which could be applied up to three times per year according to the proposed label (CFS 2012c). In general, the complementary action of glyphosate and either 2,4-D or dicamba, applied in the form of Enlist Duo or Roundup Xtend to resistant crops, would kill or injure a broader range of plants more effectively, and over a broader range of plant growth stages, than either component alone.

The implications of these studies are plain for use of dicamba and 2,4-D with crops engineered for resistance: these are herbicides that selectively kill broadleaf plants, the main nectar source for adult butterflies, including monarchs. Dicamba and 2,4-D will be used more often during a season, more extensively in an area, and more continuously over years with resistant crops than they are currently used in agriculture. This is precisely the use pattern that the studies discussed above suggest would have long-term, harmful effects on butterflies and other species. Herbicide drift thus poses a present and increasing threat to monarch habitat.

Remnant Monarch Habitat Insufficient to Sustain Monarch Populations

Remnant monarch habitats have become increasingly important, because of the overwhelming loss of milkweed from crop fields and CRP lands. Remnant habitats include pasturelands, roadsides, and field edges, though milkweeds in these habitats produce fewer monarchs per stem than milkweeds in crop fields (Oberhauser et al. 2001, Pleasants and Oberhauser 2012). All of these habitats are threatened by pesticide drift or direct application.

Pastureland represents the most abundant non-cropland habitat for milkweed, but milkweed is very sparse in pastures (Hartzler and Buhler 2000), probably because it does not compete well with long-established grasses. The already-low milkweed density in pastures in 1999 declined by half by 2012, and it is estimated that milkweeds in pastures now account for just three percent of monarch production in the Midwest breeding range (based on data supplied by John Pleasants). Pastures are also often sprayed with broadleaf herbicides (Johnson and VanGressel 2012), which kill flowering plants that provide nectar to monarch adults and may also be a factor in milkweed decline. For instance, the largest single use of 2,4-D and one of the major uses of dicamba is on pasturelands (US EPA BEAD 2012, Monsanto 2010, Table VIII-12, p. 199).

In light of milkweed loss from other areas, roadsides have become an important component of remnant monarch habitat (Flockhart et al. 2014). When crop fields had more milkweed in 1999, roadside plants accounted for only six percent of monarchs (based on Hartzler and Buhler 2000 and data supplied by John Pleasants). Because of the decimation of cropland milkweed, roadsides now produce 35 percent of Midwest monarchs, second only to CRP lands (based on data supplied by John Pleasants). Monarch habitat on roadsides is threatened by aggressive management (e.g., mowing and herbicide applications) of roadside vegetation (Commission for Environmental Cooperation 2008), and also potentially by application of road salt (Snell-Rood et al. 2014). Field edges that do not abut roads may also harbor milkweed, but increasing farm and field size has sharply reduced such fencerow habitat (Doll 1998; R. Hartzler personal communication to Martha Crouch, January 21, 2014), which becomes incorporated into cropland planted primarily to Roundup Ready corn and soybeans, where any milkweed is eliminated through glyphosate use.

In sum, the resiliency and extinction risk of monarchs is largely driven by availability of milkweed and nectar sources and appropriate weather conditions on the breeding grounds in the

Corn Belt region (Wassenaar and Hobson 1998, Oberhauser et al. 2001, Brower et al. 2012a, b; Flockhart et al. 2013, Pleasants and Oberhauser 2012). Due to the loss of common milkweed, Pleasants (in press) estimates that in 2012, the Midwest produced 88 percent fewer monarchs than it did in 1999. Increased herbicide use and drift with new herbicide-resistant crops further threatens continuing loss of milkweed for monarch larvae and loss of nectar resources for monarch adults. Remnant monarch habitat outside of croplands is also shrinking. Habitat loss in the monarch's U.S. breeding grounds threatens the monarch with extinction because of the significance of this portion of the range to the redundancy, resiliency, and representation of *Danaus plexippus plexippus* overall, as discussed further in the Significant Portion of Range section of this petition. The rapid loss of milkweed attributable to increased pesticide use and land cover changes puts the monarch at risk of extinction in the foreseeable future (Hartzler 2010, Brower et al. 2012a, b; Pleasants and Oberhauser 2012, Flockhart et al. 2014, p. 18). Extensive loss of milkweed due to increased use of glyphosate and near ubiquitous planting of Roundup Ready crops has contributed substantially to the drastic population decline of eastern monarchs of 90 percent from the twenty-year average, and glyphosate use in California has also likely contributed to the decline of western monarchs. Because monarch survival is dependent on maintaining a large population size, the relatively low remaining population size puts the species at heightened risk of extinction from global climate change, stochastic weather events, disease, predation, and other habitat-destroying activities including further loss of nectar sources from next-generation genetically engineered, herbicide-resistant crops.

Development

Monarchs are also threatened by habitat loss due to residential, industrial, commercial, and other development activities that cause conversion of habitat. Between 1982 and 2010, 43 million acres of land in the United States were newly developed, bringing the total acreage of developed land to approximately 113 million acres, a 58 percent increase in developed land over a roughly 30-year period (U.S. Department of Agriculture 2013, p. 8). Of note, more than 37 percent of developed land in the 48 conterminous states, Hawaii, Puerto Rico and the U.S. Virgin Islands was developed during the last 28 years, with every one of the 48 conterminous states, Hawaii, and the Caribbean having statistically significant increases in developed land area since 1982 (U.S. Department of Agriculture 2013, p. 8).

Development causes direct loss of monarch butterfly habitat. It threatens monarch overwintering sites in coastal California and breeding, nectaring, and roosting sites throughout the country. For example, trees required for winter roosts are uprooted to make way for housing and other urban and suburban infrastructure. Areas with milkweed are converted to lawns, covered with concrete and asphalt, and otherwise made unsuitable for breeding and nectaring. Development also contributes to increased pesticide use which can be harmful to monarchs.

More than two decades ago, a California statewide report documented the loss or destruction of 38 overwintering sites in the state, 16 of which were lost to housing developments (Sakai and Calvert 1991). Then, in the 1990s, housing developments replaced 11 additional monarch overwintering sites (Meade 1999). At present, at least three California overwintering sites are slated for housing developments (Sarina Jepsen personal observation).

Though the total area of monarch habitat that has been lost to development has not been quantified, it is certainly substantial and is a threat factor that has been noted by several authors.

Brower et al. (2012a) identify loss of breeding habitat due to land development as one of the primary factors implicated in the drastic downward trend in monarch abundance in recent years (in conjunction with other threat factors, including severe weather events and loss of milkweed due to increased herbicide use caused by the cultivation of genetically-engineered, herbicide-resistant crops) (p. 96). Flockhart et al. (2014) also identify urbanization as a contributing factor in the land-use change that is driving monarch declines (p. 4).

Development of roads causes direct loss of monarch habitat, and chemicals sprayed on roadsides can also be harmful to monarchs including herbicides. Road maintenance and other related activities may also impact the butterflies. For instance, the application of road salt to melt snow and ice during winter can affect butterflies the following summer. Road salts are applied widely during winter months. For example, in Minnesota in the metropolitan area of Minneapolis and St. Paul, approximately 300,000 tons of sodium chloride are applied to roads each winter (Snell-Rood et al. 2014, p. 1).

Sodium is important for the function of neural and muscle tissue and influences brain size and other traits, but can have varying effects at different life stages. Sodium availability is limited in most ecosystems, which likely led to the evolution of sodium cravings and sodium foraging behaviors. For example, adult male butterflies of many species engage in "puddling" to get sodium that they then transfer to females as part of mating practices (Snell-Rood et al. 2014, p. 1). Changes in sodium availability translate into physiological effects on butterflies including effects on neural and muscle tissue development.

Excessive sodium, however, appears to have detrimental impacts on monarch larvae. Snell-Rood et al. (2014) reared monarchs on milkweed collected from roadsides or milkweed collected from prairies and found that milkweeds readily take up roadside sodium which is then taken up by larvae. They found that the survival rates of monarch caterpillars were significantly lower on roadside milkweed leaves than on milkweed leaves from prairies (40.5% vs. 58.2%, $P = 0.02$). In surviving butterflies, the fitness effects of the induced physiological changes were unclear. They also reared cabbage white butterflies (*Pieris rapae*) on diets with varying levels of sodium and found that butterfly survival was significantly lower on a high-sodium artificial diet than on a medium- or low-sodium diet (high: 10.9%; medium: 34.3%; low: 41.7%; $P < 0.0001$).

Due to widespread loss of milkweed in agricultural fields attributable to increased use of herbicides resulting from near-ubiquitous planting of genetically engineered, herbicide-resistant corn and soybeans, roadside milkweeds are becoming increasingly important habitat for monarchs. Flockhart et al. (2014) estimate that roadside habitats now harbor 10 percent of all milkweeds in eastern North America (p. 16). It is estimated that in Iowa, which is representative of the monarch's Midwest breeding grounds, roadsides harbored 13 percent of milkweed in 1999, and 36 percent of milkweed in 2012 (based on data supplied by John Pleasants). Reduced caterpillar survival due to road salt could thus have significant effects on monarch populations, particularly so given the newly heightened reliance on roadside milkweed for recruitment.

Loss and Degradation of Overwintering Habitat in Mexico

The eastern monarch population primarily overwinters in oyamel (sacred) fir (*Abies religiosa*) forests in the mountains of the Trans-Mexican Volcanic Belt in Central Mexico. The high altitude forests provide the microclimatic conditions that monarchs must have to survive the winter. Loss of overwintering habitat threatens the survival of the monarch because the butterflies are limited to very specific habitat areas. Because of ecological and geographical requirements, colonies are only found in densely forested sites at high elevations (~2,900–3,300 m [9,500–10,800 ft]), and they are usually restricted to arroyos near stream headwaters located on moderately steep southwest-facing slopes (Slayback et al. 2007, p. 28). The cool temperature and moisture inside the oyamel forests maintain the butterflies in a state of reproductive diapause and allow them to conserve lipid reserves that fuel the wintering period and the spring remigration north (Brower et al. 2011, p. 28). The benefits that the dense canopy provide to monarchs have been likened to an umbrella, a blanket, and a hot-water bottle, protecting the butterflies from rain and keeping them warm enough not to freeze but cool enough that diapause is not broken which would deplete lipid reserves (Ibid.).

The monarch's overwintering habitat in Mexico is threatened by illegal and legal logging, water diversion, forest disease, and forest senescence. The habitat is also threatened by climate change and severe weather events, which are discussed further in the petition section on Other Factors Affecting the Species' Continued Existence.

The overwintering monarch colonies in Mexico were discovered in 1975 (Brower 1995). In 1980 a reserve was established for monarch protection, but exact protected locations were not specified, and logging was only restricted during winter months when monarchs were on site. A presidential decree in 1986 established the Monarch Butterfly Special Biosphere Reserve which protected five isolated areas in Mexico State and Michoacán comprising 16,110 ha, including 4,491 ha of core zone where all extractive activities were prohibited, and 11,619 ha of buffer zone where extractive activities were permitted if they were deemed sustainable.

Forest loss and degradation continued after the establishment of the 1986 reserve. The reserve did not protect all important overwintering sites, failed to compensate local landowners for imposed restrictions, offered no effective economic alternatives to subsistence uses including logging and agriculture, and angered indigenous communities who then set forest fires in protest (Solensky 2004b, p. 118, Vidal et al. 2013, p. 178). Based on aerial photographic comparisons of forest cover, between 1971 and 1999, the size of the largest patch of high quality forest was reduced by 75 percent, and 44 percent of forest patches with greater than 80 percent cover were degraded (Brower et al. 2002). The annual rate of degradation from 1971 to 1984 was 1.70 percent and increased to 2.41 percent from 1984 to 1999 (Brower et al. 2002).

In 2000 the current Monarch Butterfly Biosphere Reserve (Reserva de la Biosfera Mariposa Monarca) was established, linking the five areas from the 1986 decree and protecting 56,259 ha of forest including 13,552 ha in three core zones and 42,707 ha in two buffer zones (Vidal et al. 2013, p. 178).

Even though the habitat has been under some form of protected status since 1980, logging is known to have eliminated considerable habitat for the monarchs. On the 12 known massifs that host butterfly colonies, illegal logging has eliminated overwintering habitats on several and severely degraded habitat on others. Logging has eliminated colony areas including several on the north face of Cerro Pelon and at least three areas in Lomas de Aparacio on the southern portion of Sierra Campanario. Logging has severely degraded colony areas including the west face of Cerro Pelon and the south face of Cerro Altamirano (Brower et al. 2012a, p. 97). As recently as 2008, a small overwintering colony was documented to have been lost due to logging on the property of Crescencio Morales (Vidal et al. 2013, p. 183). Incremental logging has degraded habitat even in the two principal ecotourism colony areas, Rosario and the Sierra Chincua (Brower et al. 2012a, p. 97).

Due to increased enforcement efforts and economic support, large-scale logging has mostly been curtailed in the monarch reserve since 2007, but forest loss and degradation resulting from small-scale logging, forest diseases, water diversion, severe weather events, climate change, and edge effects continue to threaten the monarch's overwintering habitat.

Vidal et al. (2013) used aerial photographs, satellite images, and field surveys to monitor forest cover in the core zones of the Reserve from 2001 to 2012. They found that from 2001-2012, 1,254 ha were deforested (defined as areas with less than ten percent canopy cover remaining), 925 ha were degraded (defined as areas in which canopy forest decreased), and 122 ha were negatively affected by climatic conditions including winds, drought, fire, and floods (p. 180). Of the total 2,179 ha of affected area, 2,057 ha were affected by illegal logging, 1,503 ha of which were affected by large-scale logging and 554 ha of which were affected by small-scale logging. They found that Mexican authorities were effectively enforcing efforts to protect the monarch reserve, particularly from 2007 to 2012, and that together with financial support to create local alternative income generation and employment, large-scale illegal logging had decreased from 731 ha affected in 2005–2007 to none affected by large-scale logging in 2012. Small-scale logging, however, remains a present and growing concern (Vidal et al. 2013, p. 177).

Small-scale illegal logging for subsistence represents more than one-fourth of the total forest area that was lost and degraded from 2001-2012, and has severely affected the monarch core zones (Vidal et al. 2013, p. 183). Illegally logged wood is used mainly for local housing construction and firewood, and is primarily sold locally as the primary source of fuel in villages that lack electricity (Vidal et al. 2013, p. 184). As of 2010 approximately 27,000 people lived in 93 agrarian communities within the reserve's buffer zones, and more than one million people live around the reserve. The economy of the monarch butterfly region faces serious economic challenges which catalyze illegal logging as a short-term option to cope with poverty (Vidal et al. 2013, p. 184).

The monarch's winter habitat is threatened by degradation from edge effects from forest loss in the buffer zones and in surrounding habitats. The forests in the buffer zones have been, and continue to be, significantly degraded by logging, grazing, fires, and agricultural expansion. Habitat degradation in the buffer zones also harms habitat in the core zones due to edge effects and climatic effects (Vidal et al. 2013, p. 184).

Even small openings in the forest canopy can cause a lessening in temperature buffering effects that protect the microhabitat conditions monarchs require to remain at the correct temperatures for diapause. Opening of the forest canopy increases the daily temperature range at all heights in the forest, which can directly affect monarch physiology. Denser forest provides more optimal habitat than thinned forest and provides important temperature buffering effects, especially during severe weather events (Brower et al. 2011, p. 27, 42).

The integrity of the high-elevation cloud forest that supports the monarchs depends upon an extensive and dense forest structure to capture moisture (Brooks et al. 1997). Ongoing logging and canopy loss threatens to undermine the hydrological integrity of the ecosystem, which threatens the continued survival of the overwintering monarchs (Calvert et al. 1979, Slayback et al. 2007, p. 39). Small canopy openings also increase edge effects which increase the risks of wildfire, tree mortality, changes in plant and animal species, and increased human use of the land (Vidal et al. 2013, p. 8).

In addition to small-scale logging, the monarch's overwintering forest habitat is threatened by senescence and forest diseases. There has been a recent increase in the level of bark-beetle-induced tree mortality in the overwintering grounds. Several species of beetles are causing tree mortality including *Scolytus mundus* Wood, *Psuedohylesinus variegatus* [Blandford], *Pityopthorus* spp., and *Dendroctonus mexicanus* Hopkins (Steed and Willhite 2011, p. 12). Most tree mortality in the core area is in oyamel firs that have been attacked by *P. variegatus*, which was "observed in the lower bole of every examined dead and dying fir greater than 5 inches in diameter at breast height" during a recent forest health assessment (Steed and Willhite 2011, p. 3). Although only a small area has been affected, the beetle outbreak is occurring in multiple sites within the reserve. In an attempt to stop the spread of the beetle, 9,000 trees were felled in 2009 alone. It is estimated that 15 years of continued beetle population growth could decimate the fir trees in the reserve (COSEWIC 2010, p. 12).

Other disease agents are also contributing to increased levels of mortality of firs, pines, and other trees in the reserve including annosus root disease (*Heterobasidion annosum,* P-group [now *H. occidentale*]) and dwarf mistletoes (*Arceuthobium abietis-religiosae* Heil, *A. globosum* Hawksw. and Wiens) (Steed and Willhite 2011, p. 12). In field visits from 2011-2012, Vidal et al. (2013) identified 14 ha of forest that had been impacted by drought and parasitic plants (*Arceuthobium* spp. and *Psittacanthus calyculatus)* and an additional 7 ha that had been logged for disease control (p. 181). In addition to tree loss due to disease and disease-control activities, natural forest aging also threatens the reserve because monarchs typically form colonies in mature forests and as forest patches age, it is unclear whether they will be replaced (Keiman and Franco 2004).

Water diversion for human and domestic animal use may also pose a significant threat to overwintering habitat in Mexico (Commission for Environmental Cooperation 2008). At one major water source for monarchs—the Ojo de Aqua ravine on the south side of Cerro Pelón—water has been diverted so extensively that the stream is now dry for more than 1 km. Monarchs now have to fly farther distances to obtain water, which may deplete the lipid reserves needed to survive the winter and sustain the spring migration (Ibid).

As discussed in more detail in the Other Factors Affecting the Monarch's Continued Existence Section of this petition, severe weather events threaten the monarchs with direct mortality and with habitat degradation when trees fall down due to ice, wind, fire, floods, or drought. From 2009-2011, 115 hectares of forest were impacted by floods, strong winds, droughts, and fires, and 21 additional hectares were impacted by drought and parasitic plants in 2012 (Vidal et al. 2013, p. 182). From 2008 to 2011, the monarch reserve was affected by extreme drought which likely stressed the trees and made them more vulnerable to disease (Vidal et al. 2013, p. 182).

Climate change threatens to eliminate the monarch's current overwintering habitat. Oberhauser and Peterson (2003) used ecological niche modeling to identify areas suitable for overwintering monarch colonies under both current and future climate scenarios. The models predicted current monarch presence with a high degree of accuracy, and indicated that precipitation and diurnal temperature range are key environmental factors in making locations suitable for monarchs. The models predicted that future conditions are likely to become unsuitable across the entire current winter range, particularly owing to increased cool-weather precipitation that could cause increased mortality events (Oberhauser and Peterson 2003, p. 14063).

Saenz-Romero et al. (2012) likewise found that the forests which currently support monarchs are likely to become unsuitable habitat by the end of this century in the face of global climate change. They projected the contemporary climate niche into future climates provided by three General Circulation Models and found that the area occupied by the current climate niche will diminish rapidly in the next one hundred years. The models predicted a decrease in suitable climatic habitat conditions of 69.2 percent by the decade surrounding 2030, a decrease of 87.6 percent for the decade surrounding 2060, and a decrease of 96.5 percent for the decade surrounding 2090. Direly, "the projections show that by the end of the century, suitable habitat for the monarch butterfly may no longer occur inside the [Monarch] Biosphere Reserve" (Saenz-Romero et al. 2012, p. 98). Thus appropriate habitat for overwintering monarchs could be eradicated entirely within the century because the forests outside the reserve have largely been lost and degraded.

Loss and Degradation of Overwintering Habitat in California

In the western United States, hundreds of thousands of monarchs coalesce every fall at forested groves along the Pacific Coast. Monarchs generally begin to arrive to the California coast in mid-October (Hill et al. 1976) but may arrive as early as September (Leong 1990). These groves have historically been distributed as far north as Mendocino County, and south into Baja California, although the monarch's overwintering range has contracted in recent years (Griffiths and Villablanca unpublished data), and monarchs are rarely found overwintering in the far northern and southern extremes of their overwintering range. Similar to the monarchs that overwinter in Mexico, monarchs return to many of the same locations in California year after year. There are 458 distinct locations where overwintering monarchs have clustered, although currently only about 30 sites host more 1,000 monarchs annually (Xerces Monarch Overwintering Database 2014).

Historically, the composition of vegetation on the California coast differed from the contemporary composition, and groves of native trees presumably hosted dense monarch aggregations in the past (Lane 1984, 1993). At present, most overwintering sites in California are dominated by nonnative blue gum (*Eucalyptus globulus*) or red river gum (*E. camaldulensis*), although many sites also contain native trees such as Monterey pine (*Pinus radiata*), Monterey cypress (*Cupressus macrocarpa*), western sycamore (*Platanus racemosa*), coast redwood

(*Sequoia sempervirens*), coast live oak (*Quercus agrifolia*), and other native tree species (Xerces Monarch Overwintering Database 2014).

The mild environmental conditions at forested groves along the California coast provide the microclimate that monarchs require to survive the winter in western North America. The majority of these sites are at low elevations (below 200-300 feet), within 1.5 miles (about 2.37 km) from the Pacific Ocean or San Francisco Bay (Leong et al. 2004), where these water bodies moderate temperature fluctuations (Chaplin and Wells 1982), and in shallow canyons or gullies (Lane 1993). Many groves occur on slopes that are oriented to the south, southwest, or west, which likely offers the most favorable solar radiation exposure and wind shelter (Leong et al. 2004).

The suitability of habitat for overwintering monarchs is likely also influenced by landscape- and site-level characteristics that create very specific environmental conditions. These conditions include: protection from winds and storms, absence of freezing temperatures, exposure to dappled sunlight, high humidity, and access to nectar and water (Chaplin and Wells 1982, Calvert et al. 1983, Anderson and Brower 1996, Masters et al. 1988, Leong 1999). Monarch habitat includes the cluster trees that monarchs roost on as well as surrounding trees (Leong 1989, Leong et al. 1991). Fall or winter blooming flowers that provide monarchs with nectar are likely important in maintaining the lipid reserves required for the spring migration (Tuskes and Brower 1978).

Pyle and Monroe (2004) suggest that the most vulnerable element of the monarch annual cycle is the overwintering stage. Monarch overwintering habitat in California is directly threatened by urban development, and to a lesser extent, agricultural development. Habitat alterations, such as tree trimming or tree removal, and natural factors such as fire, severe storms, or disease or senescence of trees, can alter the structure and microclimate of an overwintering site and reduce its suitability for monarchs (Sakai and Calvert 1991, Commission for Environmental Cooperation 2008).

More than two decades ago, a statewide report documented the loss or destruction of 38 overwintering sites, 16 of which were lost to housing developments (Sakai and Calvert 1991). Eleven of these sites were lost in the period from 1985 to 1991; the remaining 27 sites were lost prior to 1985 (Sakai and Calvert 1991). In the 1990s, housing developments replaced 11 additional monarch overwintering sites (Meade 1999). The Xerces Society Database currently lists 62 sites that have likely been made unsuitable for monarchs, but many of those localities need to be monitored to determine whether monarchs have returned and assess the condition of the habitat. At present, at least three California overwintering sites are slated for housing developments (Sarina Jepsen personal observation). Anecdotal reports suggest that overwintering sites have been lost due to tree cutting or trimming (Sakai and Calvert 1991), or that the monarch population has declined after tree trimming, although this assertion can be difficult to demonstrate (*see* discussion in Villablanca 2010).

Most western overwintering sites are dominated by *Eucalyptus*, which are exotic invasive species that were introduced to California from Australia in 1853 (Butterfield 1935), and have been shown to reduce biodiversity (Bossard et al. 2000). *Eucalyptus* removal is a restoration goal for some natural areas (International Environmental Law Project and Xerces Society 2012), and conflicts can emerge between monarch habitat conservation and *Eucalyptus* removal. However, recent research suggests that monarchs do not prefer *Eucalyptus* trees. They use native tree species more than would be expected, given the low density of native trees relative to *Eucalyptus* in many overwintering groves (Griffiths 2012).

Many monarch overwintering sites contain aging or diseased trees. For example, Monterey pine is affected by pitch canker (*Fusarium circinatum),* a fungus that causes swollen lesions that girdle branches, trunks, and exposed roots. The disease was first observed in California in Santa Cruz County in 1986 and has since spread to 18 coastal counties (Winkler et al. 2003). As aging or diseased trees lose limbs or die, sites can become less suitable for monarchs and pose a public safety hazard. In 2004, a limb from a diseased tree within the Pacific Grove monarch sanctuary fell on a visitor and killed her. Her family subsequently sued the city and was awarded a settlement of $1 million (Chawkins 2010). To ameliorate safety hazards, land managers prune aging or diseased trees, yet the removal of tree limbs may result in microclimatic changes that make a site unsuitable for overwintering monarchs.

In sum, development, tree senescence, vegetation management activities, and severe weather events pose ongoing threats to monarch habitat in California.

FACTOR TWO: OVERUTILIZATION FOR COMMERCIAL, RECREATIONAL, SCIENTIFIC, OR EDUCATIONAL PURPOSES

Risks associated with overutilization may pose a threat to the monarch, especially in light of recent dramatic population declines and in conjunction with the many other threats facing monarchs such as habitat loss and degradation and other factors.

Monarchs are reared in captivity and sold commercially for entertainment and educational purposes, such as for live releases at events including weddings, graduations, and funerals. Monarch adults and caterpillars are readily available for purchase on the internet and from catalogues. Monarchs are also sold in kits as “pets.”

Capture, sell, transport, and release of monarchs can threaten the wellbeing of wild monarch populations in several ways, as illustrated by several monarch scientists and other lepidopterists (Brower et al. 1995, Altizer et al. 2014, Young-Isebrand et al. 2015).

Releasing commercially-bred monarchs outside, where they can interact with wild monarchs, poses the following risks to wild monarchs: disease transmission, loss of genetic diversity, and introduction of deleterious genetic adaptations. Given that millions of monarchs are likely released each year, there is a significant opportunity for captive-bred and wild monarchs to interact.

Release of captive-bred butterflies can also interfere with studies of the distribution and movement of wild butterflies which are essential to understanding their conservation needs, and increasingly important in light of climate change. Harvesting wild monarchs, a common practice of the commercial butterfly industry to attempt to sustain the genetic diversity within commercial populations, also has the potential to exacerbate population decline.

Monarchs are very susceptible to diseases that can be transmitted among larvae, and mass production of monarchs facilitates disease transmission. Release of infected monarchs into the environment could threaten wild monarchs with increased exposure and infection (Altizer and de Roode 2010, p. 25). There are currently no requirements that butterfly breeders follow specific disease-prevention protocols, or that outside agencies conduct routine tests of captive stocks for diseases. Commercially-reared monarchs can be heavily infested with the parasite *Ophyrocystis elektroscirrha* (OE) (*see*: http://www.learner.org/jnorth/tm/monarch/conservation_action_release.html), discussed in the Disease section of this petition, below. Monarchs reared in captivity can also carry other pathogens including *Serratia*, *Nosema* and cytoplasmic viruses (Ibid.). A recent increase in disease in laboratory monarchs since 2004 coincides with an increase in the release of commercially-bred monarchs (Ibid). The spread of disease from captive-reared monarchs has high potential to negatively impact wild monarch populations, as has occurred with native bee species (Pyle et al. 2012).

The levels of genetic diversity among commercially-reared monarchs are not known or regulated, and the release of large numbers of captive monarchs with low genetic diversity threatens wild populations with deleterious effects such as inbreeding depression. It could also contribute to the accumulation of deleterious genetic adaptations due to the accumulation of alleles in captivity that are mal-adaptive in the wild, as has been observed with hatchery salmon These deleterious adaptations can accumulate rapidly and can contribute to reduced survivorship of wild monarchs (Frankham 2008).

The potential for captive-reared monarchs to transmit disease or undesirable genetic traits is high because of the vast number of commercially reared monarchs compared to wild monarchs. Though the exact number of monarchs sold commercially is unknown, there are an estimated 45 –60 butterfly farms in operation in the United States that distribute more than 11 million butterflies per year, most of which are monarchs or painted ladies (*Vanessa cardui*) (Altizer and de Roode 2010, p. 26; Pyle et al. 2012). Thus, it is likely that at least a few million monarchs are released into the wild annually, representing a substantial proportion of the overall monarch population (33.5 million wild monarchs estimated in the overwintering eastern population in 2013-2014, and less than half a million total western monarchs). A recent investigative report on this industry suggests that the commercial monarch industry is rapidly growing, in part due to the increasing popularity of releasing monarchs at weddings (Federman 2008).

Overutilization via tourism activities should also be considered as a potential threat to monarch populations. Tourists gather annually to view monarch wintering colonies. While these activities have educational benefits, if conducted inappropriately they could also be harmful to monarch colonies. Ecotourism is a significant source of income for people living in and around the Monarch Butterfly Biosphere Reserve in Mexico (Vidal et al. 2013). From 2002 to 2013 visitation numbers at monarch colonies in Mexico ranged from 54,500 to 133,000 people (Vidal et al. 2013, p. 184). To ensure the long-term conservation of overwintering forests in Mexico, the international community and Mexican communities and authorities must take action to address the region's pressing social and economic problems (Vidal et al. 2013, p. 184).

Monarchs are widely used in scientific research for a number of purposes including studies of predation, mimicry, toxicology and chemical defense, physiology, neuroscience, development, pathology, and ecology, among others. A large and growing body of scientific research has contributed hundreds of publications relevant to monarch life history and habitat needs, population status, and conservation. Scientific research clearly contributes to monarch conservation and permitted research activities should continue after the monarch is protected under the ESA in a manner that ensures that wild populations are not harmed by research activities and that facilitates the permitting process for scientists.

Monarchs are also popular subjects of citizen scientists, who engage in such activities as: observing and/or photographing all life stages of monarchs and milkweed and reporting these observations; censuses of eggs, larvae, and adults; collecting eggs and larvae and rearing them indoors, then releasing the adults; and collecting adults and tagging, then releasing, them. In addition to the valuable educational role that citizen science projects fulfill, many of these projects provide data that is helpful to understanding monarch conservation needs. Some of these citizen science programs include: Journey North, the Monarch Larval Monitoring Project, Monarch Alert, Correo Real, Monarchs in the Classroom, The Monarch Teacher Network, Monarch Watch, Southwest Monarch Study, the Western Monarch Thanksgiving Count, Monarchs Across Georgia, Monarch Monitoring Project, Monarch Health, and Monarchs Without Borders. Should the Fish and Wildlife Service list the monarch butterfly as a threatened species under the ESA, the agency should recognize the valuable role that citizen scientists play in monarch conservation and either waive the permit requirement for citizen scientists or make the permitting process easy, so that the listing will not hinder these activities.

Children often rear monarch caterpillars at home. Petitioners request that upon listing, the Service develop guidance such that any take associated with rearing of up to ten wild monarchs per year by any person not engaged in commercial activity is not prohibited or subject to permitting requirements.

See Appendix B of this petition for proposed rules to facilitate monarch butterfly conservation, science, citizen monitoring, and education.

FACTOR THREE: DISEASE OR PREDATION

Disease and predation are significant sources of mortality for monarchs. In light of recent population declines and the major threats facing monarch habitat, either predation or disease or both could quickly rise to population-level threats putting the monarch butterfly at risk of extinction.

Disease

Monarchs are threatened by disease, and this threat factor is magnified by habitat loss, reduced population size, global climate change, and release of captive-reared monarchs. Numerous pathogens infect monarchs including viruses, bacteria, and protozoan parasites. Common monarch infectious agents include *Pseudomonas* bacteria, a nuclear polyhedrosis virus, the protozoan parasite *Ophryocystis elektroscirrha* (OE), and a microsporidian *Nosema* species (McLaughlin and Myers 2007).

The protozoan parasite *O. elektroscirrha* has been relatively well studied and has significant lethal and sub-lethal effects on monarch populations. Monarchs that are infected with this parasite have reduced flight ability and reduced longevity (Altizer and de Roode 2010, p. 23). Female butterflies appear to be more susceptible to OE infection than males. In general, female butterflies exhibit higher infection intensities (de Roode et al. 2008) and greater reductions in body size due to infection than males (de Roode et al. 2007) (Davis and Rendon-Salinas 2010, p. 47), though on the Hawaiian Islands, Pierce et al. (2014) found that 49 percent of males were infected, but only 44 percent of females were infected (p. 7).

The OE parasite has become so prevalent that it may be responsible for the increasingly skewed sex ratio of monarchs with declining proportions of females. An analysis of 30 years of monarch population data reveals that between 1976 and 1985, 53 percent of overwintering monarchs in Mexico were female, but since the year 2000, the proportion of females has declined to 43 percent (Davis and Rendon-Salinas 2010). The proportion of females in the fall migration has also declined (Ibid., p. 45). Declining proportion of females is of conservation concern and could have serious ramifications for population growth and recovery.

The recent drastic reduction in the availability of milkweed in agricultural fields exacerbates the threat posed to monarchs by OE infection. OE spores can persist for years and accumulate in the environment as they are spread in milkweed patches by male and female adult butterflies (Zalucki 1993, de Roode et al. 2009). Ingestion of a single OE spore can cause heavy infections in adult butterflies (de Roode et al. 2007). Because of OE's environmental persistence, its high capacity to be spread by adult butterflies, and the low exposure rate needed for infection, there is high potential for rapid increases in infection among monarchs that use the same milkweed patches in multiple overlapping generations (Bartel et al. 2011, p. 345). Reduced availability of milkweed will push monarchs into smaller habitat patches and thus increase their infection risk.

Non-migrating monarchs can suffer especially high rates of infection. Along the Gulf and southern Atlantic coasts, monarchs are subject to very high rates of disease prevalence and reductions in overall population health due to their dependence on patches of tropical milkweeds that produce vegetation year-round (Bartel et al. 2011, p. 349). On the Hawaiian archipelago, Pierce et al. (2014) found that on average, 35.5 percent of monarchs across islands were heavily infected with OE across all study sites and years. They found high variation in prevalence both within and among islands, with the average proportion of heavily infected monarchs per site per year ranging from as low as zero to as high as 88 percent (Pierce et al. 2014, p. 7).

Human activities are influencing parasite dynamics in monarch populations due to several factors including the loss of breeding and overwintering habitat, the release of captive-bred butterflies, and factors related to global climate change including the spread of tropical milkweed (*A. currasavica*) and increased stress due to drought and severe temperatures (Bartel et al. 2011, p. 349). Where tropical milkweed has been widely planted, especially in the southern United States and California, monarchs are able to breed through the winter. These year round patches of tropical milkweed facilitate increased transmission of OE (Monarch Joint Venture 2014, *see*: http://monarchjointventure.org/images/uploads/documents/Oe_fact_sheet.pdf).

Overall, climate change will have serious ramifications for disease in monarchs. Global climate change will influence butterfly diseases by affecting pathogen development, survival rates of parasites and hosts, processes of disease transmission, and stress and host susceptibility. Increasingly warm winters in North America will prevent the die-off of pathogens that would otherwise be killed by cold weather. Warmer temperatures and reduced seasonality will likely lead to increased pathogen survival and transmission (Altizer and de Roode 2010, p. 25).

Modification and curtailment of habitat and range will crowd monarchs into smaller habitat patches, increasing the risk of disease transmission, and also increasing competition and exposure to pesticides and other environmental stressors that will heighten the susceptibility of monarchs to infection (Altizer and de Roode 2010, p. 25).

In sum, increasingly small population size, less habitat availability, and high magnitude ongoing threats to monarch habitat make disease a very real threat to the persistence of monarch butterflies, and one that could increase rapidly in synergy with other threat factors.

Predation

Though monarchs are important in the food web and predation occurs naturally, monarchs are increasingly threatened by predation due to declining populations and reduced habitat. The protective chemicals monarchs obtain from milkweeds provide some defense against predation, but monarchs have many natural predators, some of whom are capable of consuming large numbers of eggs, caterpillars, and butterflies. Predators exhibit differing levels of sensitivity to monarch toxins.

Avian predation of monarch adults at overwintering sites has been reported in Mexico and in California (Tuskes and Brower 1978, Sakai 1994) and can result in very high levels of mortality. At overwintering sites in Mexico, birds including black-backed orioles (*Icterus abeillei*) and black-headed grosbeaks (*Pheucticus melanocephalus*) consume very large numbers of monarchs (Fink and Brower 1981). These two species in particular are capable of circumventing the monarch's chemical defense by avoiding eating the cuticle and/or by taking a recovery period after accumulating large amounts of cardenolides (Arellano et al. 1993, p. 315). Grosbeaks detach and consume the monarch's abdomen, and orioles strip out the abdominal contents and thoracic muscles (Arellano et al. 1993, p. 316). Brower and Calvert (1985) reported that orioles and grosbeaks consumed more than 2 million monarchs over the course of the winter at a 2.25 hectare colony in Sierra Chincua, Mexico. Estimates of bird mortality at winter colonies range from 9 to 44 percent (Arellano et al. 1993, p. 315). Also, Calvert et al. (1979) found that the smaller the colonies, the greater was the percent bird predation. During especially cold winters, birds consume even more butterflies than in moderate years (Arellano et al. 1993). While predation is a natural phenomenon, high levels of predation such as those reported in overwintering colonies are of increasing concern given recent dramatic population declines and shrinking availability of forest habitat due to illegal logging, climate change, and forest diseases.

Mice also kill large numbers of wintering monarchs. Mice are estimated to kill about 5 percent of butterflies in a given overwintering colony (Brower et al. 1985, Glendinning et al. 1988). One species in particular, the black-eared mouse (*Peromyscus melanotis*), preys extensively on monarchs, establishing residency inside monarch colonies, and feeding on live, moribund, and recently dead monarchs on the forest floor (Glendinning 1993, p. 324). In cold conditions, monarchs fall to the ground at night, and though some re-animate once the sun rises, those that have fallen to the ground are exceedingly vulnerable to predation. Overwintering adults are also subject to predation from wasps (Leong et al. 1990). Monarchs are susceptible to very high levels of predation when they are clustered during the winter, but adults also face a number of predators during migration and the breeding season including birds, wasps, spiders, mantids, and dragonflies (Smithers 1973, White and Sexton 1989, in Prysby 2004, p. 27).

Monarch caterpillars and eggs are also subject to extremely high levels of both predation and parasitism. A large suite of invertebrate predators including ants, spiders, crab spiders, and wasps prey on developing monarch larvae, and several species of flies and wasps parasitize larvae. Monarch toxins do not stave off the very high levels of predation and parasitism from invertebrate natural enemies (Prysby 2004, p. 36). Only approximately 8 to 12 percent of monarch eggs and larvae survive through metamorphosis (Borkin 1982, Oberhauser et al. 2001, Prysby 2004, p. 27), indicating that a large population size is required to maintain population growth.

Twelve species of tachinid flies, and brachonid and pteromalid wasps are known to parasitize monarch caterpillars, with the tachinid fly *Lespesia archippivora* (Order Diptera) being a primary predator responsible for high rates of parasitism (Oberhauser 2012, p. 20). A single monarch pupa can host up to ten tachinid fly maggots (Altizer and de Roode 2010, p. 20). Studies of parasitism rates from tachinid flies have been reported from many regions and include mortality rates in the study area of one percent in southern Ontario, 12 percent in Wisconsin, 42 percent in Hawaii, 43 percent in Texas and Louisiana, 70 – 98 percent in central Mexico, and 100 percent in study sites in Australia (Prysby 2004, p. 28). Parasitoid flies alone comprise a very significant source of mortality for monarch caterpillars, and have been identified as a major factor regulating wild monarch populations (Altizer and de Roode 2010, p. 20). In addition to parasitoid flies, developing monarchs have numerous other predators (Prysby 2004, p. 35, Oberhauser et al. 2007, Oberhauser 2012, p. 20).

Spiders and ants have also been identified as contributing to high levels of early mortality, with ants being a significant predator during the egg stage (Lynch and Martin 1993, Prysby 2004, p. 36). Calvert (1996) reported 100 percent mortality of monarch eggs and larvae in a one-hectare Texas prairie due likely to predation from fire ants (*Solenapsis invicta* Buren, Formicidae) (p. 149).

The high rates of mortality of monarch eggs, caterpillars, and adults from predation underline the importance to the long-term survival of the species of having a very large population size, and magnify the threat posed to the long-term survival of the species of recent population declines of more than 50 percent from the 17-year average in the west and more than 90 percent from the 20-year average east of the Rockies. Monarch reproductive success is dependent on large numbers of butterflies being in the population. The threat of predation is greatly exacerbated by declining numbers of monarchs resulting from habitat loss and degradation, loss of milkweed, climate change, and other threats.

FACTOR FOUR: INADEQUACY OF EXISTING REGULATORY MECHANISMS

There are no existing regulatory mechanisms that adequately protect the monarch butterfly. This section analyzes voluntary mechanisms and existing monarch protective measures on federal, state, local, and private lands. Additionally, it reviews international monarch protection agreements and protective mechanisms established in other nations. To conduct this analysis, in the past year, petitioners sought, received, cataloged, and then evaluated both publicly available information and literally thousands of pages of documents obtained from federal and state agencies pursuant to Freedom of Information Act and similar state public records requests. Although these voluntary efforts are notable, they are not regulatory, nor are they sufficient to recover the monarch butterfly. Accordingly the lack of effective regulatory mechanisms for monarchs, in concert with the species' downward population trend, underscores the critical need to provide monarchs protection under the Act.

Voluntary Mechanisms

Numerous voluntary programs and partnerships exist that are contributing to monarch conservation, but none of these plans are regulatory mechanisms that are capable of addressing the high magnitude, range-wide threats to monarchs. Most monarch conservation measures are voluntary and are inadequate to reverse the butterfly's precipitous population decline and the range-wide threat factors driving this decline. Moreover, most of these programs lack reliable funding. Relying solely on voluntary measures to protect the monarch will delay the implementation of regulatory protection that the butterfly needs to survive and recover. Moreover, the Service cannot rely on voluntary measures to deny listing of species. Voluntary and unenforceable conservation efforts are simply *per se* insufficient as "regulatory mechanisms" under 16 U.S.C. 1533(a)(1)(d):

> [T]he Secretary may not rely on plans for future actions to reduce threats and protect a species as a basis for deciding that listing is not currently warranted . . . . For the same reason that the Secretary may not rely on future actions, he should not be able to rely on unenforceable efforts. Absent some method of enforcing compliance, protection of a species can never be assured. Voluntary actions, like those planned in the future, are necessarily speculative . . . . Therefore, voluntary or future conservation efforts by a state should be given no weight in the listing decision (*Oregon Natural Resources Council v. Daley,* 6 F. Supp.2d 1139, 1154-155 (D. Or. 1998).

The existence of numerous monarch conservation plans illustrates that many entities understand the importance of monarchs and the need for urgent action to protect them. A broad array of public and private entities have undertaken voluntary monarch conservation efforts including milkweed seed production and planting activities, education and outreach efforts, tagging and monitoring, habitat creation programs, work plans, innovative collaborations, and reports. Yet monarch numbers continue to decline steeply despite the fact that many of the existing conservation plans have been in place for many years or even decades. This is not to say that the measures currently in place are insignificant, but the most significant current threats to monarchs are landscape-scale issues that can only be properly addressed by protecting the monarch under the ESA. Existing plans and piecemeal voluntary efforts simply cannot adequately address the complex and synergistic threats in the manner needed to reverse the decline of monarchs.

Federal Mechanisms

There are no existing federal mechanisms which are adequate to ensure the monarch's long-term survival and recovery. The Service is required to take into account other federal agencies' actions when considering the adequacy of existing regulatory mechanisms.

The genetically-engineered, herbicide-resistant varieties of crops that have decimated milkweed in the Midwest and hence monarch butterfly populations are approved by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (APHIS). That agency regulates these genetically-engineered crops under the Plant Protection Act (PPA), 7 U.S.C. §§ 7701-7772, which provides APHIS authority to "prohibit or restrict . . . movement in interstate commerce of any plant" as necessary to prevent either "plant pest" or "noxious weed" harms. 7 U.S.C. § 7712(a). In the United States, there is no single overarching law or federal agency that oversees the products of biotechnology. There are no laws that were drafted and passed with the intent to regulate genetically engineered organisms. Instead, federal agencies apply their pre-existing legislative authorities to genetically engineered organisms in order to oversee them, laws that were never intended for that purpose, implemented by several agencies, including APHIS. The PPA's purpose is to protect not only agriculture, but also the "environment, and economy of the United States" through the "detection, control, eradication, suppression, prevention, or retardation" of these harms. 7 U.S.C. § 7701(1). Genetically engineered crops are classified as presumptive plant pests, and cannot be sold and grown commercially until approved, or deregulated, by APHIS. 7 C.F.R. 340.1, 340.2, 340.6; *Monsanto Co. v. Geertson Seed Farms*, 561 U.S. 139, 130 S. Ct. 2743, 2749-50 (2010) (explaining APHIS's regulation). Once a genetically engineered crop is approved by APHIS, the agency ceases to monitor it or regulate it in any way.

Unfortunately, APHIS's regulatory approach in applying the PPA to genetically engineered crops has been to narrowly cabin its statutory authority. As a result it has never denied a petition to deregulate a genetically engineered crop, or put restrictions on their use or planting post-commercialization. APHIS has claimed that the significant herbicide impacts of genetically engineered, herbicide resistant crop systems, despite their intertwined nature with the engineered plant (and its sole, engineered purpose) are beyond their purview. Further, in so approving some genetically engineered crops, including "Roundup Ready" crops, APHIS has claimed its approval decision is non-discretionary and thus it could not consult under the Endangered Species Act's Section 7 mandates, despite admitting that the genetically engineered, "Roundup Ready" crops might cause harm to protected species or their habitat. In summary, APHIS's regulatory approach in approving numerous genetically engineered, "Roundup Ready" crops at issue here has been wholly inadequate to protect monarch butterflies and their habitat, and instead has directly contributed to the need for their ESA listing, as shown in the section of this

Petition, Loss of Monarch Habitat in Croplands Due to Increased Use of Glyphosate With Roundup Ready Crops, *supra*.

Similarly, the U.S. Environmental Protection Agency (EPA) licenses the sale and use of the herbicides and insecticides that threaten monarch butterflies as explained *supra*. EPA regulates these pesticides under the Federal Insecticide, Fungicide and Rodenticide Act (FIFRA), 7 U.S.C. § 136 *et seq*. FIFRA directs EPA to register a pesticide only upon determining that "when used in accordance with widespread and commonly recognized practice it will not generally cause unreasonable adverse effects on the environment". 7 U.S.C § 136a(c)(5)(D). Unfortunately, to date, EPA has not considered the broad suite of population-level impacts on monarch butterflies (or other insects) like those described herein as an "unreasonable adverse effect on the environment," or otherwise as a basis for denying, suspending, re-classifying, or otherwise limiting any pesticide registration approvals or use determinations, despite having the ongoing authority to take such actions.

The culmination of the FIFRA registration process is EPA's approval of a label for the pesticide, including use directions and appropriate warnings or cautions on safety and environmental risks. FIFRA, 7 U.S.C. § 136(q)(1), is explicit in requiring EPA to find a product is misbranded and may not be used if:

> (F) the labeling accompanying it does not contain directions for use which are necessary for effecting the purpose for which the product is intended and if complied with, together with any requirements imposed under section 136a(d) of this title, are adequate to protect health and the environment; [or]
> (G) the label does not contain a warning or caution statement which may be necessary and if complied with, together with any requirements imposed under section 136a(d) of this title, is adequate to protect health and the environment.

A review of the labels for the various glyphosate, neonicotinoid and other pesticides at issue here because of their harm to monarchs reveals no use directions, warnings or cautions aimed at protecting monarch butterflies.

In short, FIFRA's regulatory measures, as implemented by EPA in registering and labeling the large number of glyphosate and the other herbicidal and insecticidal products at issue, have been wholly inadequate to protect monarch butterflies. As with APHIS's actions, EPA's regulatory actions have instead directly contributed to the need for ESA listing.

Though some protective mechanisms for monarchs are in place on federal lands, including efforts of the Monarch Joint Venture (MJV) and various programs on National Wildlife Refuges, on U.S. Forest Service lands, and on National Park Service lands, none of these federal programs provide regulatory measures to give monarchs adequate protection.

The Monarch Joint Venture (MJV) is a partnership of entities across the United States that is guided by the North American Monarch Conservation Plan (NAMCP) (described below in the 'international mechanisms' section). The Monarch Joint Venture is a partnership of federal and state agencies, non-governmental organizations, and academic programs that are working together to support and coordinate efforts to protect the monarch migration across the lower 48 United States (http://www.monarchjointventure.org/). While some of these entities are working to further the conservation of monarchs and their habitat, the implementation of the MJV is not a regulatory mechanism because it is a voluntary and unenforceable effort.

Several programs exist on National Wildlife Refuges (NWRs) to foster monarch conservation. Refuges across the nation engage in monarch related activities, but all such activities are voluntary and none of them are adequate to provide monarchs with meaningful protections. Each NWR makes its own determination on how to manage monarchs. Many programs involve activities such as monarch festivals and citizen surveys. These voluntary efforts, while beneficial, are by their nature inadequate and not cognizable as regulatory mechanisms for purposes of ESA listing..

The U.S. Department of Agriculture's (USDA) Natural Resources Conservation Service (NRCS) is part of the Monarch Joint Venture. Through a Conservation Innovation Grant, the NRCS has partnered with the Xerces Society and the seed industry to increase the availability of native milkweed seed for large-scale restoration efforts in the several states including California, Nevada, Arizona, New Mexico, Texas, and Florida. While this is an important program for monarch habitat creation, it is not a regulatory mechanism that can protect monarchs from the landscape level threats that they face (*see*: www.xerces.org/milkweed/).

The U.S. Forest Service has some programs that benefit monarchs, but it does not have an agency-wide mandate or policy on monarch protection. The Forest Services' efforts at protecting monarchs are inadequate regulatory mechanisms because the majority of the agency's efforts are voluntary, the policies that protect animals such as monarchs provide only minor benefits, and the agency cannot utilize its authority to address significant threats across the range of monarchs. An example of a Forest Service policy that tangentially benefits monarchs is the regulation requiring a permit for the collection of plants and animals on Forest Service lands. While in theory this could protect individual monarchs from being collected, it does not provide protection for the monarch's habitat.

The Forest Service also maintains several webpages containing information on monarch butterflies that are focused on education and monitoring. Under the Monarch Joint Venture, an organization comprised of numerous stakeholders and initiated by the U.S.Forest Service International Programs, some National Forests have made efforts on behalf of monarchs including the creation of gardens designed to attract pollinators at ranger stations, controlling weeds and encouraging native plants, conducting butterfly surveys, restoring overwintering sites, and endeavoring to use thinning and prescribed burns to create conditions that foster native plants. Though useful, these voluntary and unenforceable efforts cannot be considered adequate regulatory mechanisms to protect and recover monarch butterflies.

Several units of the National Park system in California contain monarch overwintering sites. National Park lands are protected from the development pressures facing other monarch habitats in California, but measures are not in place that specifically provide for monarch protection on Park Service lands.

Additionally, FWS will phase out the use of all genetically-engineered crops to feed wildlife and will ban neonicotinoid insecticides from all Wildlife Refuges nationwide, effective January 2016. The decision, applicable NWR System-wide, was announced on July 17, 2014, via a policy Memorandum issued by the Chief of the NWR System, James W. Kurth (http://www.centerforfoodsafety.com/files/agricultural-practices-in-wildlife-management_20849.pdf). While not specifically for monarch butterfly protection, the policy provides a strong monarch protection model, as it will largely eliminate the threat of genetically-engineered herbicide-resistant varieties and neonicotinoids on National Wildlife Refuges. However, the protected land area of these Refuges is minor in relation to the area of protected land needed to conserve monarch populations from further decline.

In sum, though some programs are in place on federally- managed lands that provide some benefit to monarchs, there are no existing regulatory mechanisms at the federal level which are adequate to safeguard the species.

In addition, there are no mechanisms to protect monarchs from overutilization or activities that facilitate the spread of disease. Although the USDA regulates the interstate shipment of live butterflies, existing permits do not track the number of butterflies transported nor do they require the butterflies to be screened for disease. The spread of parasites and diseases is a major factor of concern for monarch conservation. Given the growing popularity of butterfly releases, lack of required screening for parasites, and potential for cross-species transmission in operations where multiple butterfly species are reared together, the lack of regulatory mechanisms governing the commercial rearing and release of wild butterflies poses a significant threat to monarchs (*see* Altizer and de Roode 2010, p. 26).

In June 2014, the White House issued a Presidential Memorandum (2014) conceding that monarchs faced "an imminent risk of failed migration." The Memorandum established a federal strategy to address the alarming declines in populations of honey bees and other pollinators, including the monarch. Although the Memorandum is an important acknowledgement of the monarch crisis, it does not constitute a regulatory mechanism.

State Mechanisms

There are also no existing regulatory mechanisms at the state level that are adequate to protect monarchs. Some states have plans in place to protect some monarch habitat, but these protections are limited to specific sites and fail to provide monarchs with the landscape-scale protections necessary to stem their precipitous decline.

Because they are easily identifiable and charismatic, monarchs have been officially listed as state insects or butterflies across the country. Seven states list monarch butterflies as their official state insect or butterfly including Alabama, Idaho, Illinois, Minnesota, Texas, Vermont, and West Virginia. These designations do not, however, confer substantive protections to the monarch.

At the state level, Iowa and California provide examples of measures states have taken that can benefit butterflies, but because of its broad geographic range and the widespread environmental stressors affecting monarchs, piecemeal state programs are not adequate to safeguard the species.

The Iowa Department of Natural Resources and the Iowa Prairie Resource Center are members of the Monarch Joint Venture and have active programs for monarch protection. The Prairie Resource Center has focused its efforts on generating native prairie seeds, including milkweeds, and their engagement with the Monarch Joint Venture has generated additional funding for milkweed seeds that will be propagated through prairie habitat in Iowa. While certainly helpful, these programs cannot be considered as regulatory mechanisms that are adequate to safeguard the monarch.

California does not have a statewide plan to benefit monarchs, but monarch overwintering sites occur in many State Parks and on other land managed by state agencies in California. State Park rules prohibit visitors from collecting animals and disturbing monarch roost trees, which provides the butterflies with some protection from collection and disturbance. Each park has a General Plan which guides management, but only one of these plans specifically considers monarch protection. The Leo Carrillo State Park General Plan considers monarchs and focuses on issues such as restoring native plants and maintaining overwintering sites for monarchs in non-native eucalyptus groves. None of the other parks specifically provide for monarch protection in their management plan, even if they are known to support large numbers of butterflies. Pismo State Beach, for example, provides a significant overwintering site for migratory monarchs, yet Pismo's General Plan does not include any monarch specific management measures (International Environmental Law Project and Xerces Society 2012). While many parks do make good faith efforts to protect monarchs, the California State Park system does not provide an adequate regulatory mechanism for the protection of monarchs both due to the voluntary nature of monarch protection efforts and because it cannot provide protections for monarchs at the landscape scale.

Local Mechanisms

This petition does not attempt to analyze all county or city-level mechanisms that could provide some conservation benefit to monarchs because of the broad geographic range of monarchs. Though some areas may have programs in place that consider monarchs, these isolated programs are not an adequate replacement for range-wide regulatory protection. One example of a strong city ordinance that is beneficial to monarchs is the city of Capitola, California, which has adopted a year-round prohibition on the removal of trees within monarch habitat (with limited exceptions). The ordinance bars construction during monarch season, limits development in monarch habitat, requires developers to provide monarch-friendly landscaping, and mandates the collection of data both before and three years after construction to help develop a database for understanding environmental parameters associated with butterfly behavior (International Environmental Law Project and Xerces Society 2012). Unfortunately, this type of protection applies to a very small number of monarch sites and is an exception to the rule of weak or lacking protections. The vast majority of California's monarch sites remain unprotected, with almost all jurisdictions allowing tree trimming without appropriate protection for monarchs. Overall, monarchs remain inadequately protected on city and county lands throughout the country.

Private Lands

The vast majority of monarchs are dependent on habitat on private land where no existing regulatory mechanisms are in place to protect them. The breeding range of summer monarchs is largely on private agricultural land where protection is entirely lacking. Part of the winter range of western monarchs is on private lands in California, where they are threatened by development and disturbance and there are no existing regulatory mechanisms that are adequate to protect them. Monarchs on California's private lands do enjoy slightly more protection than monarchs in other states because many of California's monarch overwintering sites occur primarily within the coastal zone, generally defined as areas within 1,000 yards of the high tide line. Under the Coastal Zone Management Act, cities and counties are required to develop Local Coastal Programs (LCPs) for these areas. Most LCPs do not provide specific protections for monarch overwintering sites, but even the ones that do generally only provide protection during winter months when monarchs are actually overwintering, leaving vital habitat unprotected during the rest of the year (International Environmental Law Project and Xerces Society 2012). This means that landowners can cut limbs, trees, or even entire groves utilized by monarchs for overwintering habitat as long as they don't do the cutting during the time monarchs may be physically present. Further, many overwintering sites are not even within the coastal zone, thus they don't even benefit from this limited protection. Across the country, monarch habitat on private lands is under-protected or unprotected.

International Mechanisms

Monarchs migrate from Canada to Mexico, and the monarch migration is the subject of international attention and processes that reflect significant concern on the part of international bodies for the plight of monarchs. None of these endeavors, however, are adequate regulatory mechanisms due to their voluntary nature, their considerable reliance on anticipated future action, and because they are not equipped to address the most significant threats to monarchs.

The North American Monarch Conservation Plan (NAMCP)

Parties in Canada, Mexico, and the United States produced the North American Monarch Conservation Plan (NAMCP) in 2008 (Commission for Environmental Cooperation 2008). Like other efforts discussed *supra*, the NAMCP is not a cognizable "regulatory mechanism" for purposes of determining whether ESA listing is warranted because it is voluntary and relies on plans for future actions. Though the plan cannot be considered as a regulatory mechanism, it reflects a solid research effort and contains useful information on threats to migratory monarchs and recommended conservation actions to remedy such threats. The NAMCP is described by the U.S. Forest Service as a long-term cooperative agenda for monarch conservation, and it offers a list of key tri-national collaborative conservation actions, priorities, and targets to be considered for adoption by the three countries. The Commission for Economic Cooperation, an international body created by the North American Agreement on Environmental Cooperation at the same time as the North American Free Trade Agreement, released the plan. The NAMCP provides a status review of monarchs, and details the current factors causing monarch decline. It notes that the proliferation of genetically engineered, glyphosate-resistant crops in the Midwestern United

States is one of the most significant factors leading to the loss and degradation of monarch breeding habitat.

The NAMCP provides recommendations for the three party nations to consider implementing, but explicitly does not impose any obligations on the parties, and its recommended actions primarily focus on developing studies and recommendations, not specific actions. For example, while the NAMCP identifies genetically engineered crop glyphosate use as a significant threat to migratory monarchs, its recommended action is to study and limit impacts of herbicides and insecticides on monarch populations and their habitat. In general the NAMCP establishes goals for study and future actions that as such cannot be considered adequate regulatory mechanisms.

Monarch Butterfly Biosphere Reserve

The first reserve to protect overwintering monarchs in Mexico was established in 1986. In 2008, the United Nations Education, Scientific, and Cultural Organization (UNESCO) added Mexico's Monarch Butterfly Biosphere Reserve to its list of World Heritage sites. UNESCO's listing brought recognition of the significance of this site and efforts to protect the millions of monarchs who rely on it for overwintering habitat. However this effort is not a cognizable regulatory mechanism because it only requires voluntary actions, and because by its inherently-focused nature it cannot adequately address range-wide threats to monarchs, particularly those in the monarch's summer breeding habitat in the United States.

UNESCO recommends a principal focus on prevention of illegal logging on the property; additional areas of focus include achieving sustainable use of the property by making tourism to it more sustainable, involving local communities in benefit-sharing programs to incentivize conservation, and continued investment in continent-wide management of the migratory phenomenon. A 2011 UNESCO report indicates that these efforts have resulted in large reductions in illegal logging. The effort has also helped to develop infrastructure to better manage tourism. However efforts pursuant to this designation are voluntary and come in the form of recommendations. For example, in its list of requirements for protection and management at the site, UNESCO is careful to use "should" instead of "shall" when it offers suggestions such as "[t]he principal focus of protection and management should be to prevent illegal logging on the property" (*see*: http://whc.unesco.org/en/list/1290/). In addition, UNESCO's efforts do not adequately address the threats faced by migratory monarchs across their range, because its focus is on this one reserve and the surrounding area.

Small-scale logging in particular remains a problem in the Monarch Reserve. Vidal et al. (2013) used aerial photographs, satellite images, and field surveys to monitor forest cover in the core zones of the Reserve from 2001 to 2012. They found that from 2001-2012, 1,254 ha were deforested (defined as areas with less than ten percent canopy cover remaining), 925 ha were degraded (defined as areas in which canopy forest decreased), and 122 ha were negatively affected by climatic conditions including winds, drought, fire, and floods (p. 180). Of the total 2,179 ha of affected area, 2,057 ha were affected by illegal logging, 1,503 ha of which were affected by large-scale logging and 554 ha of which were affected by small-scale logging.

Vidal et al. (2013) identify small-scale logging as an increasing problem for the Monarch Reserve, and suggest that a strategy needs to be devised and implemented as a matter of urgency to address the socioeconomic and environmental problem of both the monarch reserve and the region as a whole which suffers from severe poverty and lack of basic services:

> We suggest a substantive increase and more focused and coordinated action with regards to the payments for environmental services to the local communities and ejidos by the federal and state authorities as part of a long-term investment in sustainable economic activities, such as ecotourism and production of trees. Those investments should be better coordinated with the financial support provided by private donors and the monarch fund. Simultaneously, federal, state, and municipal authorities should implement a year-round and effective on-the-ground surveillance and law-enforcement strategy to avoid the resurgence of large-scale logging and to stop small-scale logging. Finally, we suggest implementation of a comprehensive, regional plan to create (and maintain) new and better job opportunities, improve and expand basic education for children and youth, improve basic services (e.g., sanitation, electricity, and water), all of which should be in partnership with the people living in the region and take full account of their needs and aspirations (p. 184).

Slayback et al. (2007) also conclude that more protections need to be in place to safeguard the monarch reserve, stating: "The extraordinary site fidelity and extreme localization of colonies within such a small amount of available habitat underscores the urgency of implementing an ironclad conservation policy for this unique biological phenomenon" (p. 38).

Direly, global climate change models predict that the entire current Mexican winter range for monarchs could become unsuitable habitat by the end of the century (Oberhauser and Peterson 2003, p. 14063, Saenz-Romero et al. 2012, p. 98). There are currently no existing regulatory mechanisms in place to reduce greenhouse gas emissions and avoid impending climate catastrophes such as the entire loss of the Monarch Butterfly Biosphere Reserve. Just as Joshua Tree National Park is becoming unsuitable habitat for Joshua trees, the monarch reserve is undergoing climatic changes that are expected to entirely undermine its ability to provide appropriate climatic conditions for monarchs.

FWS and USFS International Efforts

The FWS and the U.S. Forest Service both support international monarch protection efforts. FWS' International Affairs office has been engaged in migratory monarch protection efforts through its Wildlife Without Borders-Mexico program since 1995 (*see*: http://www.fws.gov/international/animals/monarch-butterfly.html). This is a voluntary program and is focused on just a small portion of the monarch's range; it is not a regulatory program. This program entails FWS partnering with and providing funding to groups in Mexico that support communities around the Monarch Butterfly Biosphere Reserve to protect this overwintering habitat. FWS is providing useful support to a training program administered by a local non-governmental organization. The agency does not utilize its authority under this program to conserve monarchs or their habitat in their summer range in the United States where they are currently most threatened.

In addition to initiating the Monarch Joint Venture, the U.S. Forest Service International Programs runs a monarch protection campaign that unites partners across Canada, the United States, and Mexico, and coordinates habitat conservation efforts through training and community outreach (*see*: http://www.fs.fed.us/global/wings/butterflies/welcome.htm). These efforts rely on the voluntary participation of conservation partners, school children, and other agencies, and are not attached to any legal mandate. The agency also participates in efforts to conserve and restore monarch habitat in all three nations, on public lands, and on private lands, and is making plans to form partnerships with farming organizations to conserve milkweed as part of its international monarch protection program. Though important, these programs cannot be considered as cognizable regulatory mechanisms for ESA purposes.

Canadian Species of Special Concern

Monarchs were designated a “species of special concern” in Canada in 1997, 2001, and 2010 (*see*: http://www.sararegistry.gc.ca/document/default_e.cfm?documentID=2027). A species of special concern is a “wildlife species that may become threatened or endangered because of a combination of biological characteristics and special threats” (http://www.cosewic.gc.ca/eng/sct2/sct2_6_e.cfm). This status does not come with substantive protections and indeed the latest monarch status report does not include any discussion of how Canadian officials intend to provide monarchs with any substantive protections; thus it is not an adequate regulatory mechanism. Furthermore, the majority of this species’ breeding habitat occurs in the United States, and threats in the States must be addressed in order for the butterfly to recover.

Importantly, the Assessment and Status Report published by Canadian authorities and associated with the most recent listing notes that herbicide and pesticide use across North America is a threat to monarchs, but the Report does not indicate that Canadian authorities are mandating or even strongly recommending any significant action to protect milkweed habitat from this threat; indeed, milkweeds remain listed under the noxious weed acts of multiple provinces. The continued inclusion of milkweed as a noxious weed in parts of Canada is another indication that a Canadian species of special concern status cannot be considered an adequate regulatory mechanism.

In sum, no existing regulatory mechanisms exist to adequately protect monarchs because the vast majority of monarch protection comes from voluntary measures, and even when measures are enforceable, they do not address monarch conservation on a rangewide scale. Some existing conservation efforts have undoubtedly increased and protected monarch habitat, but the continuing trend of steep decline plainly demonstrates that these existing measures are wholly insufficient to overcome the myriad threats to monarchs. Herbicide and pesticide use in summer habitat, development, climate change, and other synergistic threats are landscape-scale problems that cannot be adequately addressed through a mix of voluntary conservation measures. Rather, monarchs face threats that can only be adequately addressed through the comprehensive protections of the ESA.

As explained elsewhere in this petition (*see* Threats- Overutilization), upon listing the monarch butterfly, petitioners request that the Service implement measures that promote the continuance of activities that benefit monarch conservation such as citizen tagging and monitoring, scientific research, classroom rearing, education, and other activities that are beneficial for monarch conservation (*see* Appendix B).

Petitioners also recognize the valuable role that the native seed industry plays, and will continue to play, in propagating milkweed seed and plants to facilitate monarch habitat recovery. Take of monarch caterpillars, eggs, and pupae routinely occurs as part of normal milkweed production activities. Should the Fish and Wildlife Service list the monarch butterfly as a threatened species under the ESA, we strongly recommend that the agency recognize the valuable role that milkweed producers will play in monarch habitat recovery and streamline the permitting process for incidental take permits for milkweed producers, so that the listing will not hinder milkweed production efforts.

FACTOR FIVE: OTHER FACTORS AFFECTING THE MONARCH'S CONTINUED EXISTENCE

Several other factors also threaten the monarch butterfly including increased pesticide use, global climate change, severe weather events, the spread of invasive species, and mortality at solar energy facilities.

Pesticides

Monarchs face threats at all life stages from pesticides used throughout their range. The term "pesticides" encompasses herbicides, insecticides, fungicides, nematocides, rodenticides, and all of the other biocides. Impacts of pesticides on monarchs can occur from indirect and direct effects, and from lethal and sub-lethal injuries (e.g., Kohler and Triegskorn 2013).

Monarchs are harmed from widespread loss and degradation of habitat as a result of herbicide use that kills host milkweeds and alters nectar plant quality and abundance (e.g., Pleasants and Oberhauser 2012). As discussed in detail in the Modification and Curtailment of Habitat or Range section of this petition, use of glyphosate on genetically engineered, Roundup Ready corn and soybeans has been identified as the major cause of the precipitous drop in monarch numbers over the last 15 years, and this threat to the population continues as new areas are converted to corn and soybeans for biofuels, in addition to upcoming threats from the imminent introduction of new genetically engineered, herbicide-resistant crops (*see* discussion in Loss and Curtailment of Habitat and Range section of this petition).

Larvae and adults, and under some circumstances, eggs and pupae, of monarch butterflies can be killed or impaired by exposure to pesticides via contact from overspray, drift of spray particles and vapor, runoff, dust, and through ingestion of pesticide-contaminated food and water. Pesticides also have "inert" ingredients, many of which are also toxic to butterflies (Stark et al. 2012).

Pesticide use is ubiquitous in North America. In the United States, pesticide use reached 1.1 billion pounds in 2007, the latest year for which EPA has released records (U.S. Envrionmental Protection Agency 2007). Pesticides are widely used in agriculture, on rangelands, woodlands and other natural areas, waterways, golf courses, residential lawns and gardens, sports fields, roadsides, and on street trees. Pesticides are applied as granules, dusts, and liquids. They are sprayed from ground rigs, planes and helicopters; from backpack sprayers or dusters; used to coat seeds; and are injected into tree trunks and soils. Within the breeding range of the monarch butterfly, most pesticide applications are made during the crop-growing season, so exposure from applications overlap the migration and breeding of monarchs. In addition, exposure to persistent pesticides occurs well after applications are made, extending risk throughout the monarch's residence time in the United States. In some cases, pesticides are active for multiple years.

Insecticides

Since the active ingredients of most compounds are optimized to kill insects, and monarchs are in the class Insecta, they are vulnerable to many insecticides. Furthermore, since many insecticides were designed to control lepidopteran crop pests, they are especially toxic to many butterflies, which are in the Order Lepidoptera.

Larvae of a variety butterflies have proven to be extremely sensitive to insecticides used in agriculture (Groenendijk et al. 2002). A risk analysis in the Netherlands showed that butterflies in field margins were at risk from insecticide use on nearby crops (Ibid.). Butterflies and moths can be indirectly affected by drift from pesticides applied aerially (Sinha et al. 1990).

Although the U.S. Environmental Protection Agency regulates pesticide use in order to attempt to minimize impacts to non-target organisms such as monarchs, its regulations do not provide adequate protection. Currently, pesticide companies are not required to evaluate non-target effects of new pesticides on butterflies before registering their product. Incidents of harm to non-target organisms from pesticides are common, both from legal (following label directions) and illegal (not following label directions) applications (Mineau and Palmer 2013, Hopwood et al. 2012, 2013, also *see* Habitat Loss Due to Pesticide Drift section of this petition). Incidents that involve wild organisms such as butterflies are undoubtedly greatly underreported. Sub-lethal impacts to insects are unlikely to be recognized or reported at all, even when impacts are severe.

Insecticides of particular concern that directly impact monarchs include, but are not limited to, the increasingly used neonicotinoid insecticides, organophosphates, and pyrethroids.

Neonicotinoid insecticides

Neonicotinoids are a relatively new class of insecticides, introduced in the 1990s, which irreversibly block post-synaptic nicotinic acetylcholine receptors (nAChRs) in the central nervous system of insects and other animals (Jeschke and Nauen 2008, Jeschke et al. 2011). They are lethal to insects and other arthropods at very low doses, and cause serious sub-lethal impacts at even lower exposures (Hopwood et al. 2012, 2013, Goulson 2013, Mason et al. 2013, Van der Sluijs et al. 2013).

Neonicotinoids include imidacloprid, clothianidin, thiamethoxam, acetamiprid, thiacloprid,and dinotefuran. New insecticides that are not in the neonicotinoid class, but that have the same mode of action continue to be registered, such as sulfoxaflor (Cutler et al. 2012). Although they share a common mechanism of action, specific neonicotinoids differ in solubility, degree of persistence in soil and water, types of insects that can be killed at particular concentrations, and some other properties (Fishel 2005, Jeschke and Nauen 2008).

Neonicotinoids are applied as seed coatings to many crops such as corn and soybeans, before planting, are used in agriculture and landscaping as soil drenches and trunk injections, spread as granules in pastures and turf, added to irrigation water, and are sprayed on leaves of crops and ornamentals (Jeschke et al. 2011).

These chemicals pose a significant threat to monarchs for the following reasons: (adapted from Hopwood et al. 2012, 2013):

- Neonicotinoids, especially imidacloprid, clothianidin, dinotefuran, and thiamethoxam (four of the most widely used neonicotinoids) are highly toxic to a variety of insects. Some of the breakdown products are just as toxic.

- Sub-lethal levels of neonicotinoids can damage the ability of insects to function. This includes the ability to fly, navigate, and learn new tasks, which can impair their foraging ability and in the case of monarchs may impair migration.

- These products have a systemic mode of action: they translocate into every part of the plant including nectar and pollen. For monarchs this means they can be negatively impacted as both larvae (feeding on plant tissue) and as adults feeding on nectar.

- Neonicotinoids can persist for long periods of time in plants and soil. They can persist in soil for months or years after a single application. Also untreated plants may absorb chemical residues in the soil from the previous year. Measurable amounts of residues were found in woody plants up to six years after a single application.

- Neonicotinoids are now one of the most widely used classes of agricultural chemicals in this country.

- The toxic nature of these products, the mode of action that allows for these products to build up in plants, the fact that they are so long-lived in the environment, and that they are used across such large geographic areas and in such large quantities makes these chemicals a considerable threat to monarchs.

It is notable that the monarch decline has occurred during the same time period that the use of neonicotinoid insecticides in the key monarch breeding areas has dramatically increased, although, to our knowledge no one has tested the hypothesis that neonicotinoid use is a significant driver of monarch population dynamics, in addition to habitat loss.

The specific toxicity of each neonicotinoid insecticide to the monarch butterfly has not been investigated, but it is likely that monarchs are vulnerable to one or more of these compounds as larvae or adults, or possibly even as eggs or pupae, given the toxicity of neonicotinoids to so many other butterfly species. Several lepidopteran pests of crops and trees are on the lists of specific insects that can be controlled by neonicotinoid applications. For example, sampling a few product labels, imidacloprid applied in CoreTect Tree and Shrub Tablets controls pine tip moth larvae (Bayer CropScience 2007), and Gaucho 600 Flowable seed treatment controls black cutworm (Bayer CropScience 2010); acetamiprid applied in TriStar 30 SG foliar spray controls caterpillars of gypsy moth, tobacco bud worm, fall army worm, southern army worm, cabbage looper, and diamondback moth (Cleary Chemical Corporation 2006). Since neonicotinoids are the most widely applied insecticides in the world (Jeschke et al. 2011) and their use overlaps with monarch breeding areas, there is an urgent need to investigate the lethal and sub-lethal toxicity of these compounds to monarchs.

In the Midwestern Corn Belt, neonicotinoid use skyrocketed in the last decade, mainly as a result of almost all corn and most soybean seeds being sold having been pre-treated with neonicotinoid coatings (Krupke et al. 2012), despite questionable efficacy (Stevens and Jenkins 2014). Figures 25 through 29 illustrate this dramatic increase.

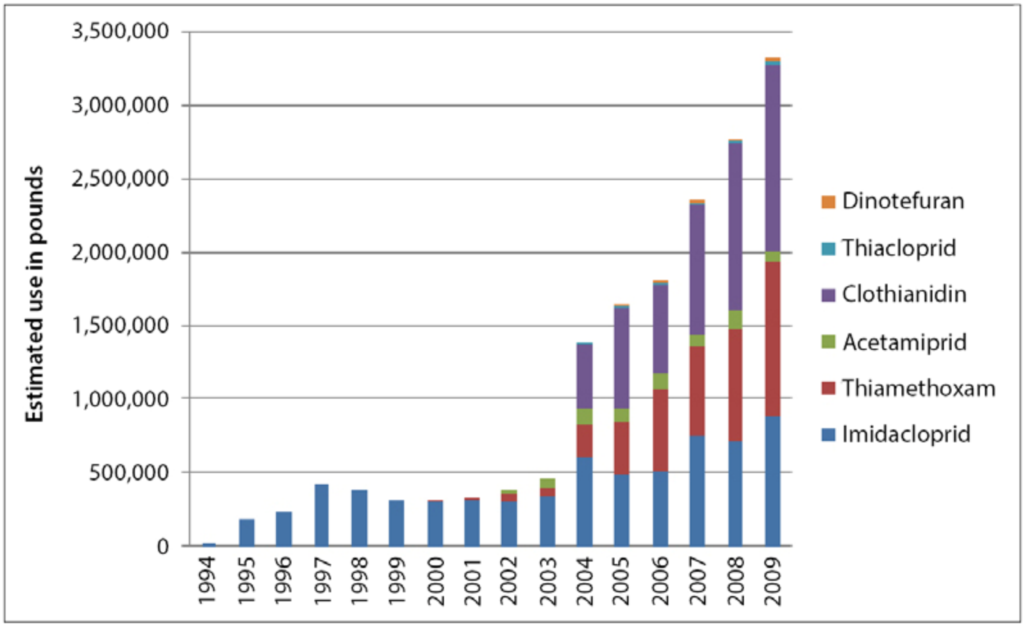


Figure 25. Estimated annual agricultural use in pounds of neonicotinoids in the United States, 1994-2009 (Data from: Stone, W.W. 2013. Estimated annual agricultural pesticide use for counties of the conterminous United States, 1992–2009. U.S. Geological Survey Data Series 752.

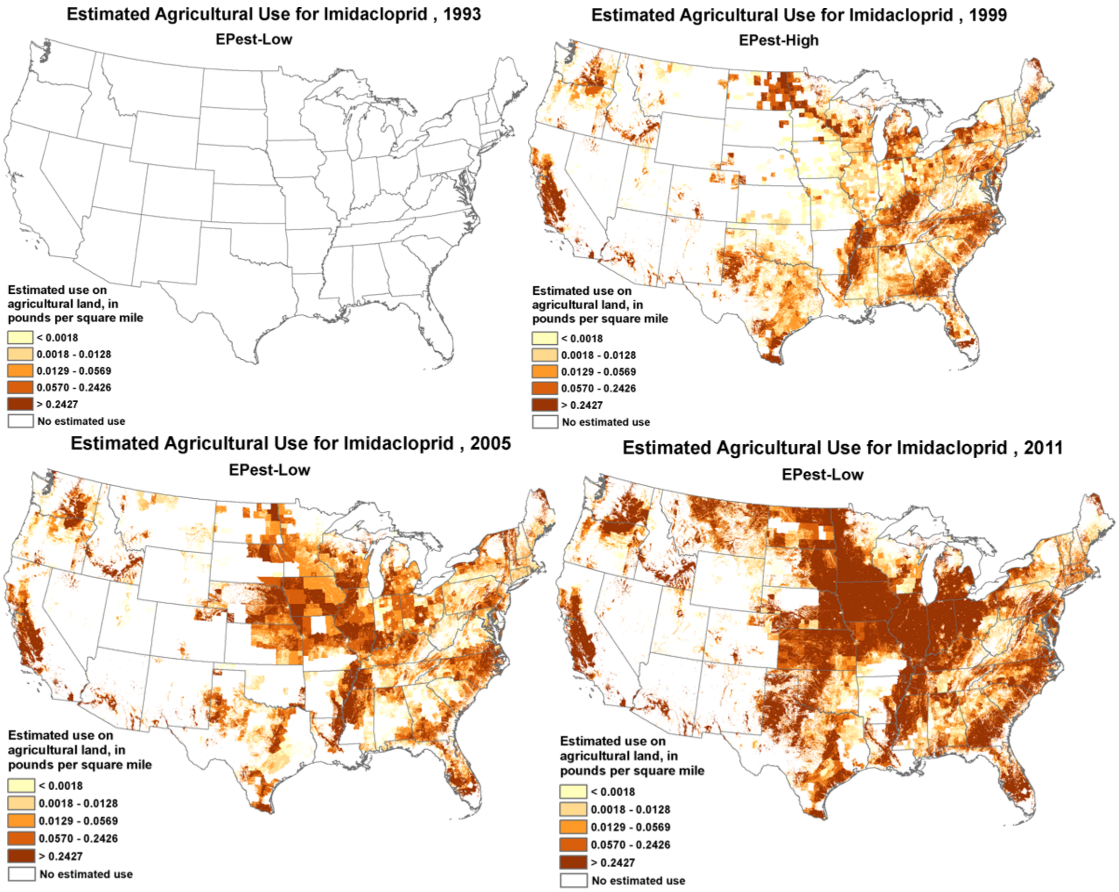


Figure 26. Increasing imidacloprid use in the United States in 1993, 1999, 2005, and 2011. Data from the USGS Pesticide National Synthesis Project, available from: http://water.usgs.gov/nawqa/pnsp/usage/maps/show_map.php?year=1992&map=IMIDACLOPRID&hilo=L

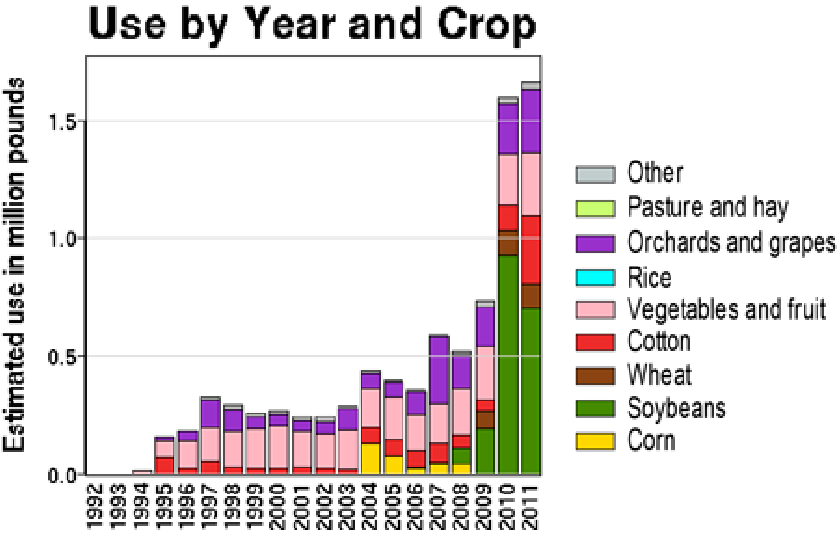


Figure 27. Imidacloprid use by crop from 1992-2011 in the United States. Data from: http://water.usgs.gov/nawqa/pnsp/usage/maps/

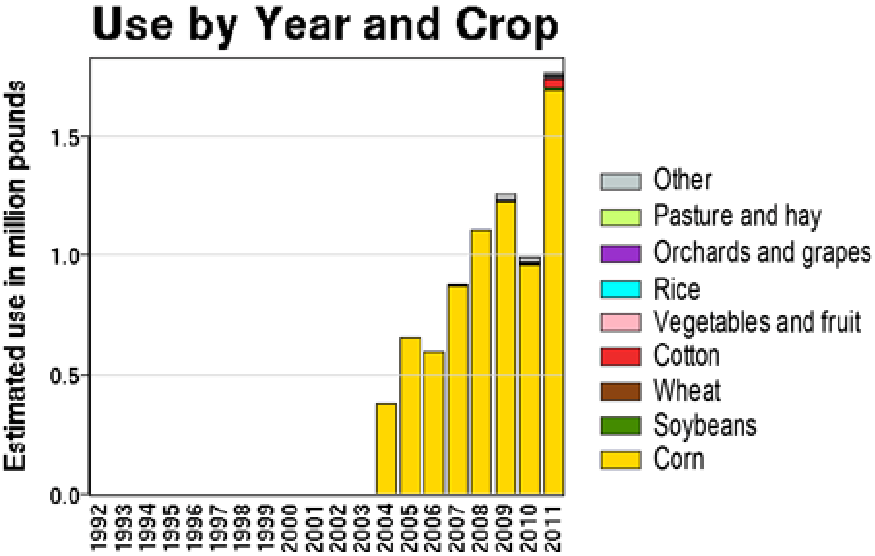


Figure 28. Clothianidin use by crop from 1992-2011 in the United States. Data from: http://water.usgs.gov/nawqa/pnsp/usage/maps/

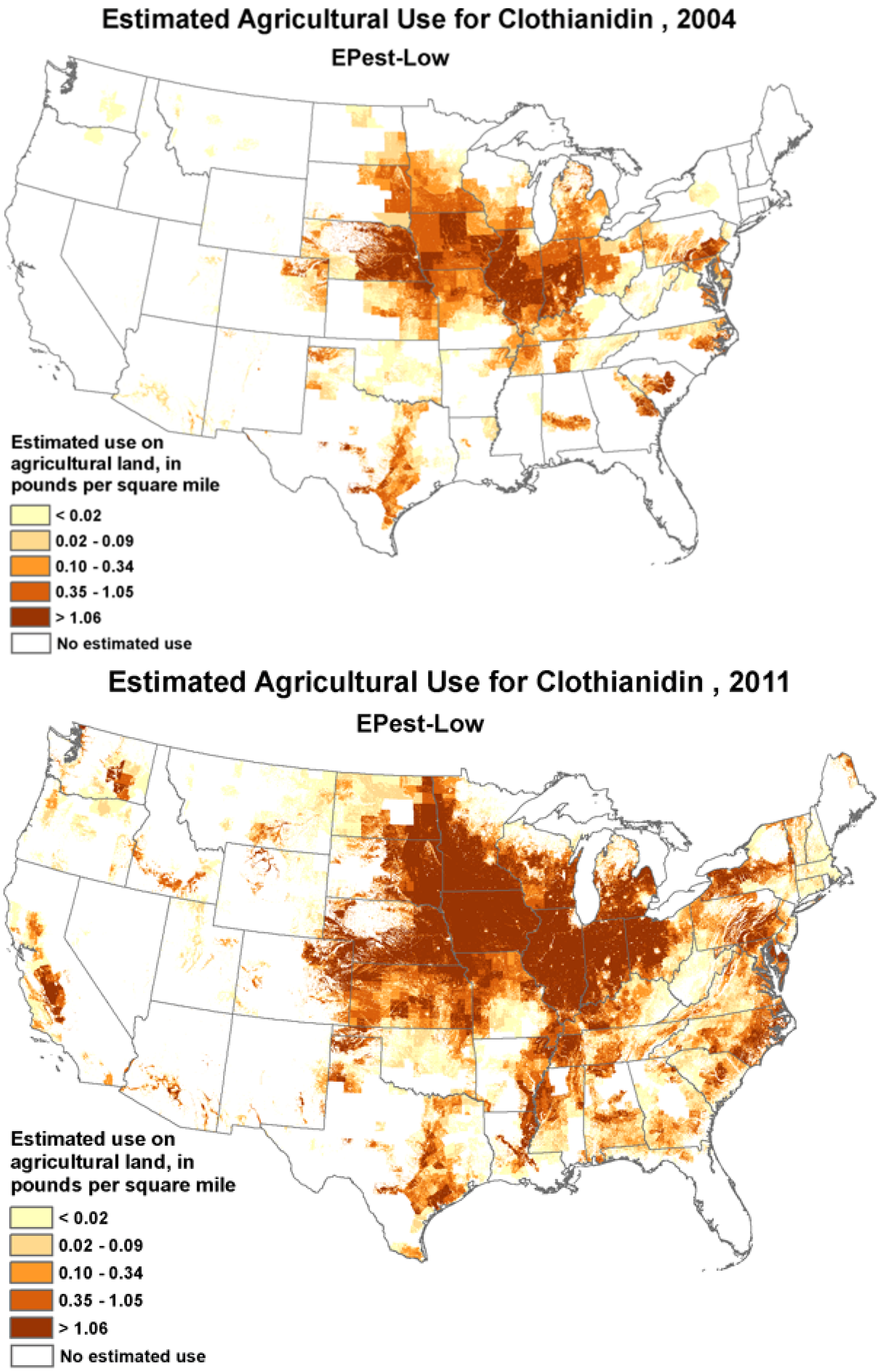


Figure 29. Increasing clothianidin use in 2004 and 2011 in the United States. Data from: USGS Pesticide Synthesis Project, *see*: http://water.usgs.gov/nawqa/pnsp/usage/maps/show_map.php?year=2011&map=CLOTHIANIDIN&hilo=L&disp=Clothianidin

Increasing neonicotinoid use is of particular concern to monarchs in the East because their main breeding range is coincident with the area of greatest neonicotinoid use in the Corn Belt.

Seeds of other crops, such as cotton, which is a significant crop in many states where monarchs breed (including Texas, Arizona and California), are also now pre-treated with neonicotinoids. After leaving overwintering sites in Mexico, many first-generation monarchs breed in Texas, and thus quality and quantity of habitat in that state is extremely important to the size of the monarch population.

Monarchs can be exposed to neonicotinoids in a variety of ways, and at different stages of their lifecycle. In brief, monarch adults can be exposed via direct contact with spray, residues on plants and other surfaces, particles released during the planting of treated seeds, contaminated water; and neonicotinoid-containing pollen, floral and extra-floral nectar and guttation liquid. Larvae can be exposed by direct contact with spray and residues, and also by eating milkweed tissues that have been contaminated, either by overspray or drift directly onto leaves, or by milkweed taking up insecticide from contaminated soil and/or water (Hopwood et al. 2012).

In more detail, systemic movement of neonicotinoid insecticides increases the number of routes by which monarchs can be exposed. Neonicotinoids are taken up by plants and move through the vascular system to all tissues and organs, including flower buds, pollen, nectar, roots, leaves, and stems. They are then slowly metabolized within plant tissues, and some of the metabolites are also toxic; residues and metabolites kill insect pests for weeks, months, or sometimes for years (Oliver et al. 2010, Goulson 2013). Thus, if host milkweed plants take up neonicotinoids from adjacent treated crops (as described below), monarch larvae will be exposed. Adult monarch butterflies feed on a wide variety of flowering plants, and if they sip nectar or guttation liquids or eat pollen from treated plants, they can also be exposed to systemic neonicotinoids.

As with most pesticides, only a fraction of neonicotinoid applications generally end up on or in targeted plants (Sur and Stork 2003, Goulson 2013), depending on the type of application. Also, a portion of neonicotinoids that does enter target plants is released into the environment as those plants decay. Environmental contamination with neonicotinoids occurs via several routes and thus poses risks to monarchs in different contexts:

- Neonicotinoids that do not contact or are not taken up by the plants during applications leach or run off directly into soil and water, where residues and metabolites can persist, remaining active for months to years (e.g. Huseth and Groves 2014). They regularly contaminate ground and surface waters near treated fields, impacting natural areas some distance from application sites at concentrations high enough to reduce insect populations (Mineau and Palmer 2013, Main et al. 2014). Monarchs can drink contaminated water, consume milkweed plants that have taken up neonicotinoids from contaminated soil and water, or drink nectar from a wide variety of plants that have taken up neonicotinoids from contaminated soil or water.

- Seed coatings form dust during planting as abraded seed tissues mix with talc or other carriers and are expelled from planting machines (Krupke et al. 2012, Tapparo et al.

2012, Nuyttens et al. 2013). This dust can contact monarch larvae and adults directly during the planting operation. Dust also settles on plants, soil and water in and around fields, where it can expose monarchs (both larvae and adults) after planting.

- Unharvested plant material from crops that have taken up neonicotinoids from foliar sprays, seed treatments, soil drenches, or other application methods contains residues and metabolites that can be released into soil (Hopwood et al. 2013) and water as the roots, stalks, and other plant parts decay, adding to environmental contamination.

Given the widespread use of neonicotinoid insecticides, especially as seed treatments, it can be assumed that milkweeds and nectar plants in monarch habitats could be contaminated with neonicotinoids. According to Goulson (2013, p. 981): "Given their persistence and accumulation in soils, we might predict hedgerow plants and trees, field margin vegetation and naturally regenerating fallows to take up neonicotinoids."

Very low concentrations of neonicotinoids and other pesticides have been shown to cause sub-lethal effects in other insects. For example, studies show sub-lethal impacts of pesticides on bee species that include changes in foraging behavior, navigation ability, reduced reproduction, and many other processes (Blacquière et al. 2012, Bryden et al. 2013, Goulson 2013), as well as increased susceptibility to pathogens (Pettis et al. 2013). Sub-lethal effects of neonicotinoids on fruit flies include a disruption of mating behavior (Charpentier et al. 2014). These types of effects are of obvious relevance to monarch populations.

Several studies suggest that levels of neonicotinoids in milkweed and nectar plants that have been exposed to contaminated soil, water, dust, or spray drift may reach concentrations that are toxic to monarchs in some situations, based on studies so far:

> The evidence presented here [in this review] suggests that the annually increasing use of neonicotinoids may be playing a role in driving these declines [of farmland insects and other taxa]. The concentrations accumulating in soil (1 to >100 ppb), waterways (often in excess of 1 ppb, sometimes up to 200 ppb), field margin plants (1–9 ppb) and nectar and pollen of flowering crops (1–50 ppb) exceed levels in crop tissues needed to control pest insects (5–10 ppb) and overlap with LC50 values for a range of non-target insects. They would appear to be sufficient to cause both direct mortality in the more sensitive nontarget species and chronic sublethal effects in many more. The groups most at risk are likely to include soil-dwelling insects, benthic aquatic insects, granivorous vertebrates and pollinators. Herbivorous insects feeding on field margin and hedgerow plants may also be exposed (Goulson 2013, p. 985).

Monarchs are in the "pollinator" risk category as adults, and the "herbivorous insects feeding on field margin and hedgerow plants" risk category as larvae. Milkweeds have largely been eradicated from corn and soybean fields, but thelands enrolled in the Conservation Reserve Program and roadsides where common milkweed now hosts most monarch larvae and where nectaring occurs are largely within agroecosystems where neonicotinoids are widely used.

New research shows that neonicotinoids are common in streams and rivers of the Midwest (Hladik et al. 2014), where they have been found in a number of samples at levels associated with toxicity to insects, and thus may be a threat to monarchs in this central breeding region. In one of the first major investigations of water contamination from multiple neonicotinoids in the United States, Hladik et al. (2014) sampled surface waters in corn and soybean regions centered in Iowa and found that neonicotinoids are mobile and that they persist in the environment. The amounts and kinds of neonicotinoids applied, timing of their use, and precipitation events determined the pattern of neonicotinoids in streams (p. 191). Neonicotinoids were detected at all of the sites sampled, including large and small watersheds draining regions with different percentages of corn and soybeans (p. 192). Small watersheds with large percentages of row crops had the highest levels of neonicotinoids in surface waters. Summarizing the results (p. 189), "[m]aximum and median concentrations (maxiumum:median) across all sites and samples followed the same pattern as detection frequencies with clothianidin (257 ng/L; 8.2 ng/L) > thiamethoxam (185 ng/L; < 2 ng/ L) > imidacloprid (42.7 ng/L; < 2 ng/L) (Table 2). Multiple neonicotinoids were common, with three neonicotinoids detected in 23% of the samples." Many samples had levels that are in the range known to be toxic to insects (e.g. Goulson 2013, p. 905: 5 - 10 ppb neonicotinoids in crop tissues control insect pests), and at levels that are associated with declining bird populations in Holland (Hallman et al. 2014: greater than 20 ppb imidicloprid in surface water is correlated with 3.5% annual decline in birds).

Another threat from neonicotinoids to monarchs comes from some nursery-grown milkweeds and nectar plants purchased from garden centers. As public awareness of the plight of monarchs grows, increasingly monarchs are being encouraged to lay eggs and sip nectar in butterfly-attracting gardens, both as a conservation measure and as a source of entertainment. Neonicotinoids have been detected in approximately half of nursery-grown plants tested (Brown et al. 2014), and there are anecdotal accounts of monarch larvae not surviving on nursery-grown milkweed plants, consistent with toxicity from systemic insecticides.

In California alone, where the state's Department of Pesticide Regulation collects detailed pesticide use data, 2,447 pounds of imidacloprid were applied to nursery plants in 2012 (California Department of Pesticide Regulation 2014, p. 414-415). These products are also widely used around homes, and products approved for home and garden use may be applied to ornamental and landscape plants, as well as turf, at significantly higher rates (up to 32 times higher) than those approved for agricultural crops (Hopwood et al. 2012).
Taken together, the cumulative impacts of these exposures to neonicotinoids throughout the monarch's habitat, particularly in their main breeding range, pose a significant ongoing and increasing threat.

Mosquito Control Programs

Insecticides are used in many areas of North America to attempt to manage mosquito larvae and adults, often in response to mosquito-borne diseases such as West Nile virus and dengue fever, or to control nuisance populations. Some models suggest that higher global temperatures will extend the geographic ranges of some mosquitos that vector diseases (Reiter 2001), which will likely lead to an increased use of insecticides targeting mosquitos. Mosquito control is done using agents that kill the adult (adulticides) or immature (larvicides) forms of the insect. The most commonly used adulticides are organophosphate (e.g., malathion, naled) and pyrethroid (e.g., pyrethrin, permethrin, resmethrin, sumithrin, prallethrin) insecticides (Mazzacano and Black 2013). These compounds have broad -spectrum toxicity and can cause severe impacts to non-target animals including butterflies.

General losses of biodiversity in insect communities that affect a wide range of orders and families have been noted by some researchers in areas where mosquito adulticides are sprayed (Eliazar and Emmel 1991, Kwan et al. 2009). Multiple studies have also shown negative impacts of mosquito treatments specifically on butterfly populations. Barrier treatments, in which pesticide applied as a spray to foliage forms a coating that kills adults that come into contact with it, can have lethal and sub-lethal effects on adult or immature butterflies.

The decline of the federally endangered Schaus swallowtail butterfly (*Heraclides aristodemus ponceanus*), endemic to southern Florida, has been linked to pesticide applications for mosquito control (Eliazar and Emmel 1991), as has the decline of the Miami blue butterfly (*Cyclargus thomasi bethunebakeri*) (USFWS 2012, 77 FR 20948). Mosquito-control pesticides are also considered to be a contributing factor in the extinctions of the Florida zestos skipper (*Epargyreus zestos)* and rockland grass skipper (*Hesperia meskei pinocayo*) (*see*: http://www.fws.gov/southeast/news/2013/032.html).

In areas that are being treated for mosquitoes, monarchs can be exposed to the insecticides at the larval stage if the insecticides are over-sprayed or drift onto milkweed hosts, or as adults if butterflies are flying or visiting nectar plants during or after applications.
Researchers at the University of Minnesota investigated toxicity to monarchs of two insecticides often used to control mosquitos (Oberhauser et al. 2006, Monarch Joint Venture 2014), and found that monarchs did have higher mortality when exposed:

> The University of Minnesota conducted research on how monarch larvae and adults were affected by exposure to insecticides commonly used in mosquito control (resmethrin and permethrin). These pyrethroids can be sprayed as ultra-low volume treatments or as barrier treatments. Ultra-low volume treatments intended to affect insects as they are flying, whereas the barrier treatments remain on leaves, providing a barrier to mosquitoes that may not be out foraging during the day. Both the ultra-low resmethrin study and the barrier permethrin study showed negative impacts on monarch larvae and adults. Leaves from the barrier treatments resulted in higher mortality to monarch larvae than control leaves up to 3 weeks after the initial application (Monarch Joint Venture 2014).

Increased mortality of monarchs from mosquito control programs is thus a significant potential threat, although impacts have not been assessed.

Grasshopper Control on Rangelands in the Western United States

Insecticides are commonly used in rangeland areas across many western states to control native grasshoppers that compete with cattle for forage. When grasshopper numbers are high, the Animal Plant Health Inspection Service (APHIS) routinely facilitates spraying of insecticides to control Mormon crickets and grasshoppers on public and private lands. APHIS lists three pesticides commonly used for Mormon cricket and grasshopper control: diflubenzuron (Dimilin), carbaryl (spray and granular formulations), and malathion (USDA APHIS 2002).

All pesticides that can be used to control native grasshoppers are thought to be highly toxic to all life stages of the monarch butterfly, since they are broad-spectrum insecticides, with the exception of diflubenzuron which is primarily toxic to the larval stage. Carbaryl is a carbamate insecticide that inhibits the action of the enzyme acetyl cholinesterase (AChE) that is an essential component of insect, bird, fish, and mammal nervous systems. Carbaryl has “very high” toxicity levels for terrestrial invertebrates (Cox 1993), including butterflies. Malathion is an organophosphate insecticide and is highly toxic to a broad range of insects including butterflies. Dimilin is the trade name for the pesticide diflubenzuron. Dimilin acts as an insect growth inhibitor by arresting chitin synthesis, i.e., the formation of an insect’s exoskeleton. Dimilin is lethal to lepidoptera caterpillars at extremely small quantities (Martinat et al. 1987). Dimilin caused 100 percent mortality of Douglas-fir tussock moth larvae up to seven weeks following application (Robertson and Boelter 1979). Another study found residue on foliage 21 days after application (Martinat et al. 1987). Sample et al. (1993) found that after Dimilin spraying, the number of lepidoptera larvae was reduced at treated sites.

Herbicides

In addition to indirect effects of herbicides on the monarch population via loss of milkweeds, as described in the Modification and Curtailment of Habitat section of this petition, some herbicides also exert toxic lethal and sub-lethal effects against butterflies (Russell and Shultz 2009).

Herbicides may directly harm exposed insects, such as monarchs. Some herbicides have been shown to leave residues that cause lepidopteran larvae to stop feeding on herbicide- exposed plants, and also some herbicides directly inhibit enzymes within the exposed insects (Russell and Shultz 2009, Bohnenblust et al. 2013). For example, glufosinate may have direct effects on lepidopteran pollinators when larvae eat glufosinate-containing pollen, nectar or leaves, either after direct over-spray or from drift. Glufosinate is one of the herbicides utilized on several currently grown genetically engineered, herbicide-resistant crops, and several new genetically engineered crops resistant to glufosinate and oher herbicides are slated for introduction in the coming years (Table 1); should these crops be approved for planting, glufosinate use could rise significantly.

Laboratory experiments with the skipper butterfly (*Calpodes ethlias)* showed that larvae fed glufosinate-coated leaves were injured or killed by inhibition of glutamine synthase, at doses comparable to the amount that might realistically be acquired by feeding on GLA [glufosinate]-treated crops. These studies were done with the active ingredient, not a full formulation, and so may have underestimated field toxicity (Kutlesa and Caveney 2001). Although monarchs will not use these crops as host plants for larvae, glufosinate may accumulate in nectar, pollen and guttation liquid of treated crops and be consumed by monarch butterflies. Also, glufosinate may drift onto milkweeds, exposing immature stages of monarchs to residues.

In sum, a plethora of pesticides used in a variety of applications threaten monarch adults and larvae across their range.

Global Climate Change

The monarch butterfly and its habitat are threatened by global climate change which will have significant physiological and ecological ramifications for monarchs (York and Oberhauser 2002, p. 297, Oberhauser and Peterson 2003, p. 14063, Zalucki and Rochester 2004, Batalden et al. 2007, Stevens and Frey 2010, Saenz-Romero et al. 2012). Global climate change threatens monarchs and their habitat due to increasing temperatures, increased frequency and intensity of severe drought and storm events, and curtailment of both summer and winter range due to changes in vegetation and climatic conditions.

The terms ‘‘climate’’ and ‘‘climate change’’ are defined by the Intergovernmental Panel on Climate Change (IPCC). The term ‘‘climate’’ refers to the mean and variability of different types of weather conditions over time, with 30 years being a typical period for such measurements, although shorter or longer periods also may be used (IPCC 2013a). The term ‘‘climate change’’ thus refers to a change in the mean or variability of one or more measures of climate (for example, temperature or precipitation) that persists for an extended period, typically decades or longer (Ibid.).

Climatic conditions influence monarch population dynamics with weather conditions directly affecting monarch reproductive success (York and Oberhauser 2002, Zalucki and Rochester 2004, Batalden et al. 2007). Zipkin et al. (2012) identify climate as a major driver of monarch population dynamics. Monarch butterfly recruitment is constrained by both regional temperatures and milkweed distribution (Zalucki and Rochester 2004). Prolonged cold and rainy conditions can reduce egg-laying and increase development time, but prolonged dry, hot conditions can reduce fecundity and adult lifespan (Zalucki 1981). Climate change poses a significant threat to long-term monarch survival because of the profound influence that climate has on monarch phenology and fecundity (Zalucki and Rochester 2004).

Climate can directly affect adult activity and larval development, or indirectly impact monarchs by reducing the growth and vitality of milkweed, nectar sources, and/or the forests monarchs use to overwinter (Zalucki and Rochester 2004, Zipkin et al. 2012, p. 3041). As climatic changes affect habitats, monarchs will have to adjust their seasonal movement patterns to attempt to accommodate changing conditions as currently suitable locations for breeding, nectaring, and overwintering are lost (Batalden et al. 2007, p. 1371).

Climate change models predict an increase in summer mean temperatures across the United States (IPCC 2013b). Increasing summer temperatures directly threaten monarchs and their habitat. Monarch summer breeding range is likely to be curtailed due to increasingly hot temperatures and loss of milkweed. High temperatures limit monarch reproductive success, and temperature rises expected from global climate change could reduce the area of suitable breeding habitat available for monarchs. Climate change models predict that annual mean maximum temperature is expected to increase across the continental United States, with mean predicted increases ranging from 3.6˚F to 9.0˚F (Alder and Hostetler 2013).

Increased temperatures threaten monarchs with direct mortality and with reduced reproductive success. Constant temperatures between 31°C and 35.5°C (88-96°F) are lethal for monarch larvae in laboratory conditions (Rawlins and Lederhouse 1981, Zalucki 1982). Exposure to temperatures above 29˚C (84°F) can be detrimental to the development of monarch larvae, with effects being dependent on length of exposure (York and Oberhauser 2002, p. 290). Increasing lengths of constant exposure to high temperatures result in increasingly higher mortality, longer development time, and lighter adult mass (Ibid.). Increasing temperatures threaten to disrupt the monarch migration. Larvae could be subjected to high-temperature conditions of longer duration which could compromise fitness by increasing pre-adult mortality, increasing development time, or decreasing adult size (York and Oberhauser 2002, p. 297). Generally speaking, areas south of Ohio are already too warm to support optimal larval growth during summer months (Malcolm et al. 1987; Batalden et al. 2007). Increasingly high temperatures and more frequent, more intense, and longer duration heat waves threaten monarchs in both their eastern and western range (Christensen et al. 2007, IPCC 2013b). Increasing temperatures could make the monarch's current summer habitat unsuitable (Batalden et al. 2007, p. 1371).

In addition to threatening the migratory populations in North America, climate change could eradicate the peripheral monarch populations that are not part of the main eastern or western migrations such as the stationery population in south Florida and populations found outside the United States on Pacific Islands and in Australia. In Miami, Florida, for example, the mean monthly maximum temperature recorded at the Miami airport from 1961–1990 (April to September) was 31.7°C (Knight and Brower 2009, p. 821). This mean temperature is already high enough to have direct negative effects on monarch larvae (Rawlins and Lederhouse 1981, Zalucki 1982, York and Oberhauser 2002), and global climate change is expected to cause an increase in mean maximum temperatures throughout Florida (Alder and Hostetler 2013). From 2050-2074, the annual mean maximum temperature in Miami-Dade County is expected to increase by 4.1˚F, with models predicting mean temperature increases of 2.3˚F - 5.9˚F (Alder and Hostetler 2013). This increase would render the area unsuitable for monarchs and could eradicate the non-migratory resident monarch population. In many parts of Florida, temperatures may already often exceed the threshold that is lethal to developing monarchs (Knight and Brower 2009, p. 821). In Gainesville, for example, the mean monthly maximum temperature from 1961–1990 from April to September was 32.6°C (Ibid.). Even increases at the lowest end of predictions would make the Gainesville area unsuitable for breeding monarchs, as temperatures in Alachua County are expected to increase by a mean of 5.0˚F, with models predicting increases ranging from 2.5˚F-7.4˚F (Ibid). Other outlying monarch populations could also be wiped out by climate change impacts. Australia, for example, has suffered from a decade-long severe drought and climate change is predicted to increase drought conditions on the continent (Van Dijk et al. 2013). In addition to threats from rising temperatures, island populations are likely to decrease in size as rising seas eliminate habitat.

Increasing temperatures threaten monarchs with direct mortality, and also threaten to alter the distribution of milkweed, the monarch's sole host plant. Due to increasing temperatures, the distribution of common milkweed will likely shift northward, but the plant may not be able to colonize northward as rapidly as monarchs will require if they are displaced from the southern parts of their range due to increasing temperatures (Batalden et al. 2007, p. 1371). Southern species of milkweeds generally become less nutritious or die back during summer and so are unsuitable host plants for the summer generations of butterflies, including those that will migrate in the fall. Monarch breeding and migration are coordinated with and dependent on milkweed availability (Cockrell et al. 1993, Malcolm et al. 1993, Brower 1995, Howard and Davis 2004), making disruption in milkweed distribution a dire threat to their survival and reproductive success.

Climate change is also expected to cause increased frequency and intensity of drought, which threatens monarchs in several ways. Climate change models predict increasing drought and reduced water availability across much of temperate western North America by 2050 (Christensen et al. 2007; IPCC 2013b). Moreover, it is generally expected that the duration and intensity of droughts will increase in the future (Glick et al. 2011, p. 45). Drought has already been identified as a primary contributing factor in population declines of western monarchs (Stevens and Frey 2004, Stevens and Frey 2010, p. 733). Stevens and Frey (2010) found that variation in moisture availability (as measured by Palmer's drought severity index) predicted monarch abundance patterns across the western United States, and determined that moisture regimes act as a strong bottom-up driver of monarch population dynamics; essentially, years of severe drought across the western monarch breeding range were associated with the lowest monarch population estimates in the western United States (p. 731). Stevens and Frey (2010) suggest that drought reduces the abundance and quality of milkweed, thus leading to lower monarch populations. Milkweed quality for developing larvae deteriorates at high temperatures (Batalden et al. 2007, p. 1365). Drought reduces milkweed germination, survivorship, growth, and seed production (Stevens and Frey 2010, p. 740). Reduced water availability can also cause changes in the properties of milkweed plants. Milkweed plants with low water availability may cause declines in larval survival because the latex is more viscous and can make leaf-eating more difficult (Stevens and Frey 2010, p. 740).

Climate change also threatens monarchs in their winter ranges in California and Mexico. Monarchs east of the Rockies migrate to Mexico each fall where they overwinter in conifer forests in the Trans-Mexican Volcanic Belt. The monarchs require very specific habitat conditions in these forests so that they do not freeze or become too warm and break diapause. The climate change models for the monarch's overwintering habitat predict that the currently occupied habitat will become unsuitable for monarchs by the end of the century.

Saenz-Romero et al. (2012) found that, by the end of the century, the climate will no longer support the forested habitat conditions upon which monarchs depend for overwintering in Mexico. In this study, the authors projected the monarch's contemporary Mexican overwintering climate niche into future climates provided by three General Circulation Models and two greenhouse gas emission scenarios and found that the area occupied by the niche will diminish rapidly over the course of the century. They predicted a decrease of suitable conditions of 69.2 percent by the decade surrounding 2030, a decrease of 87.6 percent for that surrounding 2060, and a decrease of 96.5 percent by 2090 (p. 98). In Mexico by the end of the century, temperatures are expected to increase by an average of 3.7˚C, and precipitation is expected to decrease by 18.2 percent (Ibid.). By 2100, suitable habitat for the monarch butterfly may no longer occur inside the Monarch Butterfly Biosphere Reserve (Ibid.). Drought is already causing tree loss and increased susceptibility to forest diseases within the Reserve (Saenz-Romero et al. 2012, p. 99).

Oberhauser and Peterson (2003) projected current monarch overwintering distribution onto future climate scenarios (Hadley Centre climate models) and found that conditions are likely to become inadequate to support monarchs across their entire current winter range in Mexico, particularly owing to increased cool-weather precipitation that could cause increased mortality (Oberhauser and Peterson 2003, p. 14063). For example, a winter storm in 2002 killed an estimated 468-500 million monarchs representing colony losses of 75 percent (Brower et al. 2004, p. 162). Oberhauser and Peterson (2003) predict that climate change effects will cause current overwintering sites to become considerably less suitable for monarchs by 2050; in fact, when current oyamel fir forest distribution was included in models to be projected to future climates, none of the present overwintering sites were predicted to be suitable in 50 years (Oberhauser and Peterson 2003, p. 14067).

Increased occurrence of severe weather events also threaten monarchs in their overwintering habitat where they cluster together in small areas, and the frequency of severe winter precipitation events that could kill monarchs is expected to increase with climate change (Brower et al. 2012a, p. 98). Barve et al. (2012) report a regional climate change signal in Mexican overwintering areas that is trending consistently toward conditions that are inimical to monarch survival including downward temperatures that put butterflies at risk of freezing during winter storms which are expected to increase in frequency (p. 820, 821). Shrinking of forested habitat areas due to logging, drought, and tree diseases further increases the risk of exposure of overwintering monarch clusters to hazardous weather conditions (Brower et al. 2011, p. 28).

Extreme weather events can kill large numbers of monarchs, as discussed in detail in the petition section Other Factors—Severe Weather and Stochastic Events, below. A recent compilation of climate change models predicts that the southern United States will become drier and that extreme events such as heavier storms, heat waves, and regional droughts, may become more frequent across the United States (Glick et al. 2011, p. 7, IPCC 2013b).

In contrast to the findings of other authors, in a recent population model Flockhart et al. (2014) assume that climate change in Mexican overwintering habitat will reduce mortality levels on the overwintering grounds, but some assumptions behind the model are likely to result in an underestimate of climate change threats (discussed further in the Population Status section of this petition). The model assumes that increasing overall temperatures will benefit monarchs by reducing the risk of freezing, but fails to take into account increased risk of stochastic weather events due to climate change, ongoing degradation of the monarch’s forest habitat in Mexico which will alter microhabitat conditions, and climate change impacts which will harm forest health and decrease the climatic suitability of the habitat. The model also underestimates climate risk because it uses temperatures from weather stations that are on average 274 m (~900 ft) below the elevation at which butterflies cluster (Flockhart et al. 2014 supporting materials, p. 30). The model also fails to take into account the influence of predicted warmer temperatures on lipid depletion during overwintering which decreases monarch fitness and reproductive success.

In sum, climate change is a primary threat to monarch butterflies throughout their range. Climate change exacerbates the threat posed to monarchs from drought and other severe weather events, and the threat is heightened even further in light of drastically reduced population size due to recent population declines.

Severe Weather and Catastrophic Events

Periodic extreme weather conditions and catastrophic events have been identified as a primary threat to monarch butterflies (Slayback et al. 2007, p. 38, Brower et al. 2012a, p. 95, Vidal et al. 2013, p. 178). Monarchs are threatened by severe weather conditions and catastrophic events including high and low temperatures, drought, winds, storms, fires, and flooding. To complete their multi-generational migration, monarchs depend on moderate temperature conditions during the various stages of their life cycle, and aberrant temperatures can kill larvae and adults. Severe cold threatens the survivorship of overwintering monarchs, and spring and summer weather that is too cold or too hot lowers breeding season survivorship and fecundity and alters larval growth rates (York and Oberhauser 2002, p. 294, Brower et al. 2012a, p. 97).

Milkweed host plants are also sensitive to temperature extremes. Late frosts can kill milkweed shoots during the early breeding season for monarchs (Brower 2009). Droughts also harm milkweed both by resulting in fewer milkweed plants and by causing plants to be of lower quality (e.g. Craig, as quoted in Mulvaney 2013; *see also* Climate Change section of this petition, *supra*).

A series of severe weather conditions in recent years demonstrates the significant threat that stochastic weather poses to monarch survival, especially in light of drastically reduced population sizes due to other threat factors. For example, above normal temperatures in Texas in spring 2009 reduced first-generation migrating monarch numbers. Then below normal temperatures in the Midwest limited numbers of summer generations produced in the Corn Belt region. Combined, these aberrant climate factors severely reduced the number of butterflies in the migrating fall generation (Brower et al. 2012a, p. 97). Already at reduced numbers, the 2009-2010 overwintering monarch population in Mexico was subjected to record-breaking precipitation levels and heavy winds which blew down hundreds of oyamel fir trees in the core of the Monarch Reserve. In addition to habitat loss from flooding, landslides, and freezing temperatures, large numbers of butterflies were killed by the winter storms (Brower et al. 2012a, p. 98).

During winter when monarchs are clustered, stochastic events can kill the vast majority of the population. Calvert et al. (1983), Brower et al. (2004), and Brower et al. (2012a) document storm events that killed very large numbers of overwintering butterflies. A winter storm in 2002 killed an estimated 468-500 million monarchs representing colony losses of 75 percent (Brower et al. 2004, p. 162). When considering that a single winter storm event killed more than 450 million butterflies, it is important to note that the 2013-2014 eastern monarch overwintering population numbered only 35 million butterflies. The drastically reduced current population size of monarchs now makes the species even more vulnerable to catastrophic events.

Stochastic weather events kill monarchs directly and cause habitat degradation. Vidal et al. (2013) found that 115 ha of monarch overwintering grounds in Mexico were degraded by floods, winds, droughts, and fires from 2009-2011 (p. 182). Extreme drought in the monarch reserve from 2008-2011 is thought to have contributed to greater susceptibility to forest diseases and parasitic plants (Ibid.).

Drought has also contributed to declining abundance of monarch's west of the Rockies. Stevens and Frey (2010) attribute declining western monarch populations to increasing drought conditions in the western United States (p. 733). They found that variation in moisture availability, as measured by Palmer's drought severity index (PDSI), across the western region predicted monarch abundance patterns, and that moisture regimes act as a strong bottom-up driver of monarch abundance via resource availability in the western United States (p. 731). Furthermore, climate change models predict that drought severity will increase in large areas of temperate western North America, with 10-30 percent less precipitation and water availability by 2050 (Stevens and Frey 2010, p. 732).

Extreme weather conditions that impact monarchs have become much more frequent and intense in recent years and have contributed to significant reductions in monarch population size (Vidal et al. 2013, p. 179). Moreover, the frequency of severe weather events is expected to increase with climate change (Brower et al. 2012a, p. 98). Barve et al. (2012) used ecological niche estimates and future climate projections to estimate future monarch overwintering distributions and predicted that regional climate change in the monarch's overwintering grounds would result in increased monarch winter mortality because climate conditions in Mexican overwintering areas are trending consistently toward conditions inimical to monarch survival and extreme events appear to be increasing in frequency (Barve et al. 2012, p. 820). Models developed by Oberhauser and Peterson (2003) also predict increased winter season mortality and a likelihood of the monarch's entire current winter range becoming climatically unsuitable habitat for monarchs (Oberhauser and Peterson 2003, p. 14063).

Invasive Species

The spread of invasive species also poses a threat to monarch butterflies. Invasive fire ants prey on monarch eggs and larvae (Calvert 1996), as discussed above in the petition section on predation. Invasive exotic plants threaten monarchs by acting as a sink when oviposition occurs on plants that are unsuitable for larval development, and when invasive plants displace milkweeds.

Tropical or scarlet milkweed (*Asclepias curassavica*) is a non-native milkweed that is often planted in backyard gardens. In parts of the southern United States, *A. curassavica* has become naturalized and is considered invasive (Harvey et al. 2009). Its leaves do not die back at the end of summer as do native milkweeds, and this can have several negative effects on monarchs (McCord and Davis 2010, p. 415, Monarch Joint Venture 2014).

When migrating monarchs encounter tropical milkweed in the fall, they may stop migrating, break diapause and lay eggs, a common occurrence in Florida where tropical milkweed is continuously available (Knight and Brower 2009). Another negative consequence of tropical milkweed is that in the absence of winter dieback, spores of the parasite *Ophryocystis elektroscirrha* accumulate on leaves over time and spread infections to monarch larvae (Altizer et al. 2004). The non-migratory south Florida monarch population is thus heavily infected with the parasite (Altizer et al. 2000).

Invasive swallow-wort species also threaten monarchs by outcompeting and displacing native plant species, including milkweed, and by acting as a sink for monarch oviposition. There are two highly invasive swallow-wort species that are widely distributed in the United States—black swallow-wort (*Vincetoxicum nigrum*, synonym *Cynanchum louiseae L.)* and pale swallow-wort (*V. rossicum*, synonym *C. rossicum*). Black swallow-wort is found from Maine through Kansas and in California. Pale swallow-wort is discontinuously distributed from the Great Lakes through New England and the Mid-Atlantic States. Both swallow-wort species out compete milkweed and also serve as dead-end hosts for monarch oviposition because monarchs lay eggs on them due to chemical cues similar to milkweeds, but larvae do not survive (DiTommaso and Losey 2003, p. 205, Casagrande and Dacey 2007, p. 632, 635).

The threat posed to monarchs by invasive species is likely to be exacerbated by climate change, which is expected to facilitate the spread of exotic species (e.g. Dukes and Mooney 1999).

Mortality at Solar Energy Facilities

Monarch butterflies are threatened by mortality from solar arrays, particularly in southern California and the southwestern United States. In a study of bird mortality at three solar energy facilities in California, Kagan et al. (2014) documented significant monarch mortality at a solar site in Ivanpah, California (p. 2). The authors observed "hundreds upon hundreds" of dead butterflies and concluded that it appears that Ivanpah acts as a "mega-trap" for insects and in turn, insect-eating birds (p. 2, 20). Some butterfly carcasses were singed. Researchers deduced that the butterflies were attracted to a brightly lit area around the boiler at the top of facility (p. 20). Based on the large numbers of monarch carcasses observed at the facility, the authors conclude that solar power towers could have a significant impact on monarch populations in the desert southwest (p. 21). The threat posed to monarchs from solar facilities will likely increase in the future as more facilities are constructed.

Electromagnetic Noise

Monarchs may potentially be threatened by electromagnetic noise. Recent research has demonstrated that monarchs possess an internal magnetic compass, located in their antennae, which may help guide their migration (Guerra et al. 2014). In a recent paper, Guerra et al. (2014) note the possibility that electromagnetic noise emitted from various electronic devices could possibly impair the monarch's migratory ability:

> Taken as a whole, our study reveals another fascinating aspect of monarch butterfly migratory behaviour. Greater knowledge of the mechanisms underlying the fall migration may well aid in its preservation, currently threatened by climate change and by the continuing loss of milkweed and overwintering habitats. Another vulnerability to now consider is the potential disruption of the magnetic compass in monarchs by human-induced electromagnetic noise, which can apparently disrupt geomagnetic orientation in a migratory bird (Engels et al. 2014) (Guerra et al. 2014).

Electromagnetic noise from AM radio signals and some electronic equipment can disrupt the magnetic compasses that migratory birds use to navigate (Engels et al. 2014). Human-induced electromagnetic noise presents a potential threat to the monarch migration and should be further investigated.

SIGNIFICANT PORTION OF RANGE

As explained in detail above, the monarch butterfly, *Danaus plexippus plexippus*, is threatened range-wide with extinction in the foreseeable future due to loss and curtailment of habitat and range, disease, predation, other factors including climate change and pesticide use, and the lack of existing regulations to safeguard the butterfly. North American populations have declined precipitously and are threatened by all five listing factors. Populations outside of North America are also threatened with extinction due to a variety of factors including small population size, host plant eradication, development, disease, global climate change, stochastic weather events including drought and excessive heat, and sea-level rise. The monarch butterfly thus warrants listing due to range-wide threats. Should the Service conclude, however, that the monarch is not threatened range-wide, then the Service must examine whether the monarch is threatened in a significant portion of its range (SPR). The best available scientific information indicates that the monarch plainly is threatened with extinction in the foreseeable future in a significant portion of its range.

On July 1, 2014, the Service issued a Final Policy on Interpretation of the Phrase ‘‘Significant Portion of Its Range’’ in the Endangered Species Act’s Definitions of ‘‘Endangered Species’’ and ‘‘Threatened Species’’ (79 FR 37578). According to the policy, a portion of the range of a species is “significant” if its contribution to the viability of the species is so important that, without the members in that portion, the species would be in danger of extinction, or likely to become so in the foreseeable future, throughout all of its range.

As an initial matter, this definition violates the Endangered Species Act and relevant judicial precedent. In a case concerning the flat-tailed horned lizard (*Phrynosoma mcallii*), the Ninth Circuit Court of Appeals specifically rejected a definition of Significant Portion of Range that requires risk of extinction to the species as a whole, stating:

> If, however, the effect of extinction throughout ‘a significant portion of its range’ is the threat of extinction everywhere, then the threat of extinction throughout ‘a significant portion of its range’ is equivalent to the threat of extinction throughout all its range. Because the statute already defines ‘endangered species’ as those that are ‘in danger of extinction throughout all ... of [their] range,’ the Secretary's interpretation of ‘a significant portion of its range’ has the effect of rendering the phrase superfluous. Such a redundant reading of a significant statutory phrase is unacceptable. *Defenders of Wildlife, et al. v. Norton*, 258 F.3d 1136, 1145 (9th Cir. 2001).

In essentially defining the significant portion of range language out of existence, the Service’s new policy undercuts a critical component of the Act. Indeed, Congress expressly noted that the “significant portion of its range” provision marked “a significant shift in the definition in existing law which considers a species to be endangered only when it is threatened with worldwide extinction” (H.R.Rep. No. 412, 93rd Cong., 1 Sess. (1973).

The monarch is a case in point. As this petition demonstrates, the monarch is at risk of extinction in North America, but also occurs as an introduced species in a number of other parts of the world, including Europe, Australia and a number of island nations. A conclusion by the Service that the entire North American range of an iconic species like the monarch is not significant would provide the clearest of examples of the fact that the policy is fundamentally at odds with the purposes of the Endangered Species Act to protect species before they are at risk of "worldwide extinction" and to conserve the ecosystems upon which species depend.

Even under the overly restrictive revised policy, however, the North American monarch population qualifies as significant, and warrants listing as a threatened species. The policy describes the threshold for "significant" in terms of an increase in the risk of extinction for the species based on the principles of conservation biology using the concepts of redundancy, resiliency, and representation. The North American population of the monarch butterfly meets this standard of significance, because North America is the core of the monarch's range and its loss would cause imperilment everywhere due to the exacerbated risk of extinction to the species if it were only represented by the peripheral, introduced, and vulnerable non-migratory populations found outside continental North America.

The North American monarch population is significant because without it, the redundancy, resiliency, and representation of the species would be so impaired that the monarch would have an increased vulnerability to threats to the point that the overall species would be likely to become endangered in the foreseeable future. The loss of the North American portion of the monarch's range clearly would increase the vulnerability to extinction of the entire species. Monarch populations outside of North America are relatively small and less genetically diverse and already at risk of extinction from stochastic weather events, climate change, habitat loss from development and intentional host plant eradication, disease, sea-level rise, and other factors as discussed in Appendix A. The monarch population in North America is the heart of the species range and if it were to be lost, the species would be vulnerable to extinction on a global scale. In other words, the hypothetical loss of the North American monarch population would cause the species to become endangered, for several reasons: without the North American population, which harbors the vast majority of all monarchs, the population in the remainder of the monarch's range would not be large enough to be resilient to environmental catastrophes or random variations in environmental conditions; the spatial structure of the entire species would be disrupted and only isolated tangential populations would remain; potentially important elements of genetic diversity would be lost; the overall redundancy, resiliency and representation of the species would be severely compromised.

Redundancy (having multiple populations distributed across the landscape; abundance, spatial distribution) provides a margin of safety for a species to withstand catastrophic events. Resiliency (abundance, spatial distribution, productivity) describes the characteristics of a species that allow it to recover from periodic disturbance. Representation (the range of variation found in a species; spatial distribution, diversity) ensures that a species' adaptive capabilities are conserved. Redundancy, resiliency, and representation are not independent of each other, and some characteristic of a species or area may contribute to all three. For example, distribution across a wide variety of habitats is an indicator of representation, but it may also indicate a broad geographic distribution contributing to redundancy (decreasing the chance that any one event affects the entire species), and the likelihood that some habitat types are less susceptible to certain threats, contributing to resiliency (the ability of the species to recover from disturbance).

The North American monarch population is biologically significant because without it, the redundancy of the species would be drastically curtailed. North America is the core of the monarch's range and the North American population as recently as the mid-1990s numbered nearly one billion butterflies. The loss of milkweed due to increased spraying of particular herbicides and development and the degradation of overwintering sites has reduced the population to approximately 35 million butterflies as of winter 2013-2014. The migratory populations in eastern and western North America still represent the vast majority of all monarchs in the world. Though monarchs are found in relatively small, peripheral, and introduced populations in tropical and subtropical locations such as Bermuda, the Canary Islands, and Australia (*see* Appendix A), these non-migrating populations cannot conserve the spatial distribution of the species over the core of its range in North America, and are limited in population growth potential such that they cannot substitute for the abundance of the continental North American population.

In terms of resiliency, the North American monarch population is biologically significant because if it were to be lost, the resiliency of the species would be so reduced that the monarch would be at risk of extinction. North America is home to nearly all monarchs. Within North America, the population from east of the Rockies that overwinters in the mountains of Mexico is the largest monarch population in the world representing by far the majority of all monarchs. Within the eastern population, in the spring most monarchs breed in Texas, Oklahoma, Arkansas, and Kansas. Summer breeding occurs mainly in the Corn Belt states (Iowa, Illinois, Indiana, northern Missouri, Ohio), the eastern portions of the Northern Plains states (Kansas, Nebraska, South Dakota), and the southern parts of the Lake States (Minnesota, Michigan and Wisconsin) (Wassenaar and Hobson 1998, Miller et al. 2011, Flockhart et al. 2013). The Corn Belt states are particularly important for production of butterflies that will overwinter (Wassenaar and Hobson 1998, p. 15439). In population models, Flockhart et al. (2014, p. 15) found that at a regional scale total monarch abundance was most sensitive to changes in vital rates in this central eastern breeding region, and in the Corn Belt in particular (p. 18). They concluded (Flockhart et al. 2014, p. 16) that the loss of milkweed due to the increased use of pesticides on herbicide-resistant crops in the Midwest has increased the current and future extinction probability for monarchs. The Corn Belt region is pivotal to monarch resiliency because it is a source population for monarchs in other regions including along the East Coast and Florida, and also provides genetic influx to the western monarchs that migrate to Mexico in lieu of overwintering in California, and presumably to many of the peripheral populations (Appendix A).

Numerous scientific studies have identified the importance of the eastern monarch population in supporting other monarch populations in North America. Miller et al. (2011, p. 43) used isotope measurements to estimate natal origins of monarchs collected from 17 sites along the East Coast and found that 88 percent of the coastal monarchs had originated in the Midwest and Great Lakes regions before completing a west to east longitudinal migration across the Appalachian mountains. The Florida monarch population is also apparently supplemented by monarchs with Midwestern origins. Though non-migratory monarchs reside in southern Florida throughout the year, this population too receives an influx of individuals each fall from the eastern migratory population (Knight 1997, Altizer 2001). In addition, the demographic success of monarchs in the Corn Belt region is directly linked to overwintering population size in Mexico (Wassenaar and Hobson 1998, Oberhauser et al. 2001, Brower et al. 2012a, b; Flockhart et al. 2013, Pleasants and Oberhauser 2012). There is also strong evidence for significant mixing of eastern monarchs with the western monarch population in California (Lyons et al. 2012, p. 3341). The productivity of monarchs as a species is thus largely dependent on the monarchs in the eastern North American population.

Monarchs from the east, and some from the west, overwinter in a small area in the mountains of central Mexico where they are highly vulnerable to severe weather events and predation from birds and mice. In fact, winter storms and predation in some years have killed the majority of overwintering monarchs. If the overwintering population were lost due to stochastic events, climate change, or high levels of predation, the majority of the monarch's habitat in North America would be unoccupied the following summer, as the entire breeding range east of the Rockies would not be repopulated by remigration. The western population and resident southern populations are likely too small to provide this function, and are themselves vulnerable to development, disease, climate change, and other factors. Also, non-migrating populations in southern areas are not subject to environmental cues that would cause them to migrate long distances in spring to re-populate the full range (e.g. Guerra and Reppert 2013).

Moreover, there is no question that the resiliency of monarchs as a species would be at risk if the North American population overall were to be lost. Without the North American population, the survival of monarchs as a species would be dependent on isolated, introduced, vulnerable populations that are themselves threatened with extinction. In Australia, for example, the monarch population has declined below the 1960s population size and is threatened by coastal development, active removal of milkweed by ranchers, severe drought, and record heat waves. Monarchs have narrow thermal tolerance, and populations in tropical and sub-tropical areas are vulnerable to rising temperatures from climate change and also to severe storm events, drought, and sea-level rise.

In terms of representation, the North American monarch population is biologically significant because the spatial distribution and diversity of the species would be severely disrupted without it. The continental North American population harbors high genetic diversity and the migrations and intermingling of the eastern and western populations maintain genetic diversity that has been lost in peripheral and isolated populations from other areas. For example, Hawaiian monarchs are smaller than North American migratory monarchs, and microsatellite markers show that Hawaiian monarchs are genetically distinct from those in North America and New Zealand (Pierce et al. 2014, p. 2). The range of variation, spatial distribution, and diversity of monarchs as a species are dependent on the survival of North American monarchs. The overall North American population of monarchs is biologically significant, and within this population, the eastern migratory population is also biologically significant. The redundancy, resiliency, and representation of the monarch species would be gravely compromised without North American monarchs.

After determining that the North American monarch population constitutes a significant portion of the species' range, the Service must then examine whether the North American SPR is threatened by any of the five listing factors. As discussed in detail in previous sections of this petition *supra*, monarch butterflies in eastern and western North America have undergone precipitous decline and are threatened by modification or curtailment of habitat and range, disease and predation, overutilization, other factors including climate change, pesticides, and severe weather events, and by a lack of existing regulations which would be adequate to safeguard the species. The monarch is threatened range-wide, and in addition, there is no question that the monarch is severely threatened in the North American portion of its range.

Though the newly finalized SPR policy is overly restrictive and illegal, even under that new policy, the North American monarch qualifies as significant. In addition, when examined under the original policy, there is no doubt that the North American monarch qualifies as a significant population. The Endangered Species Act defines an endangered species as “any species which is in danger of extinction throughout all or a significant portion of its range” and a threatened species as “any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.” The language of the statute, legislative history, congressional intent, and relevant judicial precedent all instruct that a species need not be at risk of worldwide extinction to qualify for Endangered Species Act protection. Rather, as noted in the draft policy, a species can qualify as an endangered species in two ways: if it is in danger of extinction “throughout all of its range,” or if it is in danger of extinction “in a significant portion of its range.” In enacting this provision, Congress intended to provide a means to protect species before they are on the brink of extinction, which is of paramount importance to species conservation.

In sum, the monarch butterfly is threatened with extinction across its range and thus whether it is threatened in a significant portion of its range is ancillary. The monarch, however, is threatened with extinction in a significant portion of its range, the North American population, and meets the threshold of significance as defined in the July 2014 SPR policy and under the original interpretation of the SPR policy.

CONCLUSION

The Endangered Species Act requires that the Service promptly issue an initial finding as to whether this petition “presents substantial scientific or commercial information indicating that the petitioned action may be warranted.” 16 U.S.C. § 1533(b)(3)(A). There is no question that under the five listing factors of the Act, protecting the monarch butterfly may be warranted. The monarch is threatened by loss or curtailment of habitat or range, disease and predation, and other factors including global climate change, pesticides, and drought. There are no existing regulatory mechanisms which are adequate to protect the monarch butterfly. The Service must act promptly to protect this iconic species and to designate critical habitat in order to reverse its precipitous decline and to plan for the monarch’s long-term survival and recovery.

REQUEST FOR CRITICAL HABITAT DESIGNATION

Petitioners urge the Service to designate critical habitat for the monarch butterfly concurrently with its listing. Critical habitat as defined by Section 3 of the ESA is: (i) the specific areas within the geographical area occupied by a species, at the time it is listed in accordance with the provisions of section 1533 of this title, on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection; and (ii) the specific areas outside the geographical area occupied by the species at the time it is listed in accordance with the provisions of section 1533 of this title, upon a determination by the Secretary that such areas are essential for the conservation of the species. 16 U.S.C. § 1532(5).

Congress recognized that the protection of habitat is essential to the recovery and/or survival of listed species, stating that: "classifying a species as endangered or threatened is only the first step in ensuring its survival. Of equal or more importance is the determination of the habitat necessary for that species' continued existence… If the protection of endangered and threatened species depends in large measure on the preservation of the species' habitat, then the ultimate effectiveness of the Endangered Species Act will depend on the designation of critical habitat." H. Rep. No. 94-887 at 3 (1976).

Critical habitat is an effective and important component of the ESA, without which the monarch's chance for survival diminishes. Petitioners thus request that the Service propose critical habitat for the butterfly concurrently with its proposed listing.

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Appendix A: Non-migratory Populations of *Danaus plexippus plexippus*

Non-migratory populations of *Danaus plexippus plexippus* outside of the Americas

During the mid- to late-1800's and into the 1900's monarchs spread across the Pacific to Hawaii, New Zealand, Australia, and many islands of Oceania (Brower 1995, Zalucki and Clarke 2004, Fig. 1, p. 114; *see* Figures 1 and 2 below). During this same time period, monarchs also colonized islands across the Atlantic, such as Bermuda and the Madeira and Canary Islands, and are now resident in the Azores and coastal areas of Spain as well (Haeger et al. 2011). Various lines of evidence point to more than one introduction event in the Pacific, with populations in Hawaii and Australia likely forming independently (Shephard et al. 2002, Lyons et al. 2012), and other Pacific islands being colonized by radiation from original areas (Zalucki and Clarke 2004, Fig. 1). Introduction and spread in the Atlantic and Spain have not been as well studied, but monarchs are regularly found off-course during fall migrations as far as the United Kingdom (Vane-Wright 1993, Brower 1995, p. 354).

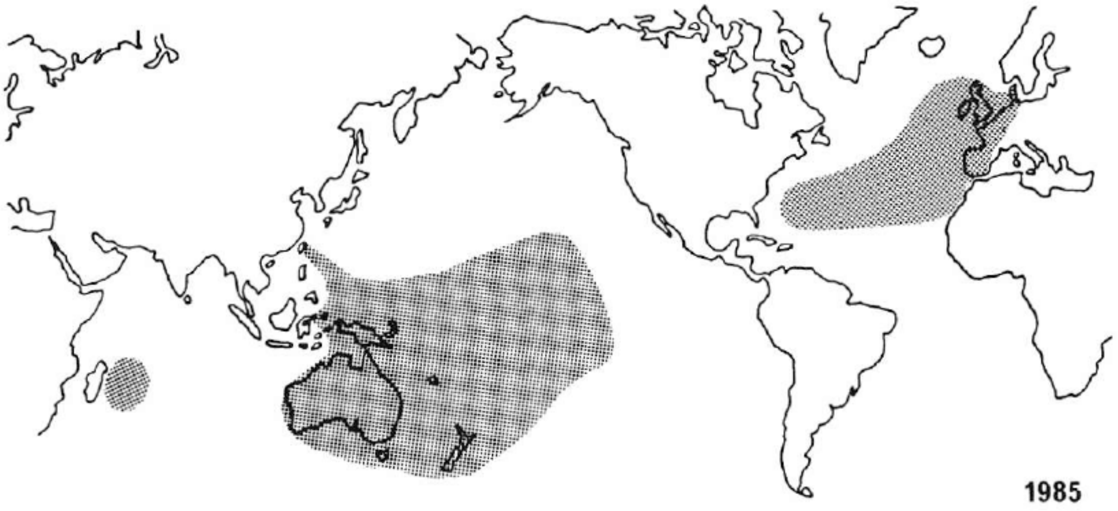

Figure 2. Current (1985) known range of *D. p. plexippus* outside the Americas. [Note: Apart from the east coast region of Spain (Edwards, 1988) monarchs are not known to breed in the British Isles or continental Europe, but they still occur as more or less occasional vagrants on western coasts (e.g. Bretherton and Chalmers-Hunt, 1982).]

Figure 1, Appendix A. 1985 Range of *Danaus plexippus plexippus* outside the Americas. Figure 2 from Vane-Wright 1993, original legend.

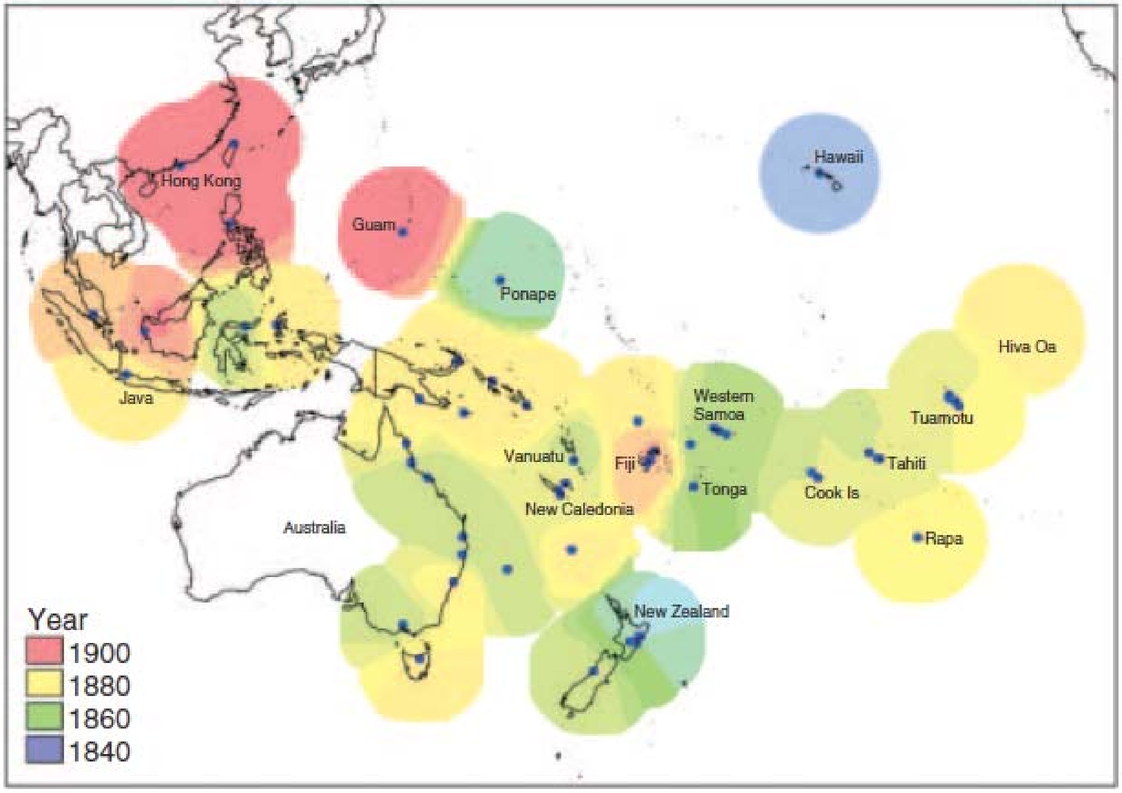

Figure 2, Appendix A. The spread of monarch butterflies, *Danaus plexippus plexippus*, across the Pacific in the 1800s. The map is generated by assuming that each new population was derived from the nearest neighboring population (in any direction) with a confirmed earlier arrival, unless an intervening island group was known to be free of the butterfly. Note that populations appear to stem from one or two incursion points in the South Pacific. Figure 1 from Zalucki and Clarke 2004, original legend.

Based on the short amount of time since these introductions of *D. p. plexippus* outside of North America, the new populations are still considered part of the subspecies. However, genetic analyses show that they have less genetic diversity than monarchs in North America (Shephard et al. 2002, Lyons et al. 2012, Pierce et al. 2014), and most are now likely to be genetically isolated from the main North American population (Lyons et al. 2012).

There is debate about how and why these dispersals occurred when they did, both east and west (Brower 1995, pp. 352 – 357). Host plants in the milkweed family had been introduced to the Pacific and Atlantic during this same time frame. Given sightings of vagrant monarchs far from North America over the years, it is plausible that some monarchs have always ventured far from their native habitat during migrations but would not have been able to establish breeding populations in the absence of suitable milkweeds. Such milkweeds were absent before colonial times.

In both the Atlantic and Pacific islands and coastal areas, non-native tropical milkweeds were introduced by colonists and travelers, intentionally as garden flowers and for medicinal uses, and unintentionally in packing materials and as seed contaminants (Brower 1995, Zalucki and Clarke

2004). These milkweeds also have become naturalized to greater or lesser extents, usually in disturbed areas such as pastures and roadsides, or along watercourses, and are now considered to be pan-tropical. The most common are *Asclepias curassavica* (tropical milkweed, scarlet milkweed) (*see*: http://www.cabi.org/isc/datasheetreport?dsid=7248), native to South America; *Gomphocarpus physocarp*a (balloon plant, giant swan plant) and *G. fruticosus* (swan plant, cotton bush), native to South Africa; and *Calotropis procera* (apple of Sodom, giant milkweed) (*see*: http://www.cabi.org/isc/datasheetreport?dsid=16848), originally from Africa, India and Southeast Asia. In addition, *C. gigantea* (crown flower, tree calotrope), also from Asia, is found in many areas of the Pacific (*see*: http://www.hear.org/pier/species/calotropis_gigantea.htm); and the non-tropical *A. incarnata* (swamp milkweed) from North America is cultivated specifically to feed monarch larvae in New Zealand (Elliot et al. 2009).

In some islands, naturalists report boom and bust cycles accompanying monarch introductions, as monarchs first thrive on and then decimate the introduced host plant populations:

> From the records of early naturalists we get a clue as to how the introductions and rapid spread may have proceeded. A number of commentators (Semper, 1873; Sturm, 1878; Walker, 1886; Collenette, 1925) point out that monarchs on some islands reached very high levels shortly after introduction. For Upolu, in the Samoan group, Semper (1873) wrote '. . . it was observed in 1869 for the first time. On Upolu the species became quickly very frequent and in 1870 it was one of the most common butterflies.' On New Caledonia, one writer reported 'millions of butterflies' (Walker, 1914). Initial 'boom' commonly appears to have been followed by 'bust', however, as large caterpillar populations appear to have eaten out their host plants, e.g. 'In New Caledonia, . . . it became very abundant some years ago, but is now comparatively scarce, owing, . . . to the destruction of nearly all the food-plant by the larvae' (Walker, 1886). Collenette (1925) reported that this butterfly had changed from being common, to rare or absent, on Hiva-Oa, Tahuata and Nuka-Hiva Islands, in the Marquesas, on Papeete, Tahiti, and on Moorea Island in the Society Islands. Diggle (Marks, 1963) went so far as to use the recently introduced (to Australia) monarch to illustrate perhaps the first ever talk on biological control using herbivorous insects (Zalucki and Clark 2004, p. 114).

Decimation of host plants results in cycles of monarch abundance, depending on the particular milkweed species and their capacity to rebound:

> Such variation in abundance still happens: on Oahu (Hawaiian archipelago) butterfly numbers fluctuate widely during the year, with periods when caterpillars are so abundant that host plants (*Calotropis* spp.) are defoliated, alternating with periods when numbers are low (M. P. Zalucki, pers. observ.; John Stimpson, University of Hawaii, pers. comm.). Thus, it appears likely that once monarchs successfully colonized an island, their populations increased rapidly until the local carrying capacity was exhausted. Subsequent outbreaks only appear to be possible with hosts that can recover relatively quickly from defoliation (e.g. *Calotropis*). Blakley & Dingle (1978) reported the virtual elimination of *A. curassavica* by monarchs on Barbados. Initial outbreaks following colonization would have resulted in high levels of non-directional local dispersion, probably resulting in high levels of population mortality, until the next island was chanced upon and the cycle repeated (Zalucki and Clarke 2004, p. 114).

Monarchs are thought to have moved between islands via favorable winds and storms, by hitchhiking on boats, and sometimes by intentional human introduction (Clarke and Zalucki 2004, Zalucki and Clarke 2004, p. 115). None of the non-North American monarch populations migrate as a regular part of their lifecycle, although they may move in response to habitat changes. There are reports and studies of migratory behavior of monarchs in Australia and New Zealand during winter from colder to warmer areas (Ramsay 1964, James 1993). These movements, however, are not comparable to the yearly two-way migrations in North America.

Establishing a population on the "next island" in this way is only possible if non-native milkweed host plants are already present when monarchs arrive. Although widespread, to our knowledge the distribution of these milkweeds, and thus the potential for resident monarch populations, is incomplete. There are surveys of milkweeds on some but not all islands in the Pacific and Atlantic, so the proportion of islands inhabited by milkweeds and that are thus potentially suitable for monarchs is unknown.

There are no published estimates of the total number of monarchs outside of North America as there have not been any comprehensive surveys or censuses. Nor are there regular studies of particular populations specifically to determine their relative status and threats. However, some information about status and threats can be gleaned from more general studies of monarch biology in various non-North American locations, both west and east of the continent.

Polynesia

Polynesia consists of more than a thousand islands scattered over the central and southern Pacific Ocean. Monarchs were first described in this region in the Hawaiian Islands in 1840's, and monarchs were reported from New Zealand then, as well. Genetic studies support the contention that these were separate introductions (Pierce et al. 2014). Monarchs are widely reported throughout Polynesia (e.g. Clarke and Zalucki 2004, Appendix), including Tonga, Vanuatu, the Marquesas, Samoa, and Tahiti, although current status on particular islands is not generally known.

Hawaii

There are resident populations of *D. p. plexippus* on all the major Hawaiian islands, and they use a variety of introduced host plants, mainly *Asclepias curassavica*, *Gomphocarpus physocarpa*, *Calotropis procera*, and *C. gigantea*. Both *Calotropis* species are planted widely around houses and in gardens. In fact, flowers of *C. gigantea* are prized and grown for leis, and were reputed to be the favorite of Queen Lili'uokalani (b. 1838 – d. 1917) (Cook 2013). All are naturalized.

Monarchs were reported in Hawaii by the mid-1800's: "…*A. curassavica* is believed to have been introduced to Hawaii in the period 1845–1850 (Wagner et al. 1990), with monarchs recorded there somewhere between 1841 and 1852, but after the milkweed (Scudder 1875)" (Zalucki and Clarke 2004, p. 114). Whether they arrived on their own or hitchhiked on a ship is not known.

Recent genetic studies using microsatellite markers show little genetic differentiation between monarchs on the four Hawaiian islands sampled, indicating that they form one admixed population (Pierce et al. 2014). The Hawaiian monarch population has fewer alleles at the loci studied than the North American population (Pierce et al. 2014), consistent with being founded by one or a few butterflies and then being separated from the main population, and in line with genetic diversity studies using allozymes (Shepard et al. 2002).

There are no estimates of numbers of monarchs in Hawaii. Numbers fluctuate, as discussed above, based on milkweed status. Threats to introduced milkweeds and monarchs in Hawaii have not been studied.

New Zealand

Monarchs were first reported in New Zealand in the 1840's (Ramsay 1964). There are no native milkweeds in New Zealand (Elliot et al. 2009, p. 603). Hosts for monarchs that have been introduced to New Zealand are *Gomphocarpus fruticosis*, *G. physocarpus*, *Asclepias curassavica*, and *A. incarnata.* These milkweeds are specifically cultivated to host monarchs because New Zealanders are so fond of these butterflies (Wise 1980, p. 157; Monarch Butterfly NZ Trust 2009, as cited in Elliot et al. 2009): "Although the monarch butterfly *D. plexippus*, is exotic in New Zealand, it is an iconic species" (Elliot et al. 2009, p. 606).

Although it appears that most monarchs are raised on garden plants, *G. fruticosus* is listed as "naturalized" in New Zealand, confined to waste places and old gardens around habitations, *see*: http://floraseries.landcareresearch.co.nz/pages/Taxon.aspx?id=_06b0c40c-3461-40bf-b826-6f3d9d5fc4cc&fileName=Flora%204.xml

There are no estimates of the monarch population size, their status, or threats.

Micronesia

Micronesia is comprised of thousands of small islands in the western Pacific Ocean, such as the Caroline Islands, including Palau, Gilbert Islands, Mariana Islands, Marshal Islands, Nauru, and Wake Island.

Monarchs are widespread, occurring on all major island or island groups with the possible exception of Kosrae (Schreiner and Nafus 1997). Monarchs were first reported in 1857, introduced from Hawaii via a shipment that contained milkweed seed (likely *A. curassavica*) to Pohnpei (Kilonia = Ponape), Caroline Islands (Scudder 1875). The main host now is *Calotropis gigantea*. There is no information on status or threats.

In Guam, monarchs seem to have reduced their original host plant population, but the effect on monarchs themselves is not noted. According to Shreiner and Nafus (1997, p. 34 – 35):

> On Pacific islands this butterfly shows up soon after host plants arrive. In 1936, Swezey noted that the weed *A. curassavica* was very abundant on Guam, forming dense stands almost acres in extent, and the butterfly was also very abundant. Possibly the butterflies provided some control of the weed, as it now never forms dense stands.

Monarchs have recently been described in Nauru (Buden and Tennent 2008) using *Calotropis gigantia*, where they are commonly found near host plants along roadsides and yards in the coastal belt. There are seasonal fluctuations in numbers of monarchs, but status and threats are unknown.

Melanesia

Melanesia is made up of islands in the western Pacific, including thousands of islands north and east of Australia to Fiji, notably Papua and West New Guinea, Fiji, Vanuatu, the Solomon Islands, and New Caledonia. Monarchs are widespread in these islands.

Australia

Monarchs are widely distributed in coastal areas of Australia:

> Since the early 1870s, *D. plexippus* has colonized most parts of eastern Australia, the Adelaide area and a small portion of Western Australia (Zalucki, 1986; James, 1993). There is a temperature-induced behavioural distinction among the Australian populations in that the majority of Queensland populations breed continuously throughout the year, whilst a range contraction occurs from southern Queensland and northern New South Wales with the onset of autumn, leading to the development of three eastern population centres: the southern Queensland/Northern New South Wales coastal strip extending up in to the tropics, the Sydney Basin/Hunter Valley region, and the Adelaide area (James, 1979; James, 1993; Zalucki & Rochester, 1999) (Shepard et al. 2002, p. 438).

Although monarchs were first noted in 1870, they were common by 1873 (Clarke and Zalucki 2004). Monarchs may have first arrived in Australia during a series of cyclones, from Vanuatu and New Caledonia where they were already established. They originally used the deliberately introduced *Asclepias curassavica* as a host plant, although *Calotropis* species were also present early:

> Calotrope is thought to have been introduced into Australia during one of the Queensland gold rushes in the late 1800s or early 1900s. It is not known exactly how it was introduced, but it may have been deliberately introduced as an ornamental or accidentally introduced in the packing of camel saddles. Calotrope was first recorded as naturalised in semi-arid northern Queensland in 1935, but was probably present for some time prior to this (Parsons & Cuthbertson 2001), *see*: http://www.environment.gov.au/cgi-bin/biodiversity/invasive/weeds/weeddetails.pl?taxon_id=2767

Monarchs currently use *Gomphocarpus fruticosus*, *G. physocarpus*, and *Calotropis procera,* in addition to *A. curassavica* (James 1993). Each of these milkweeds is considered invasive in some parts of Australia (Ward and Johnson 2013), and there are attempts at eradication (https://www.agric.wa.gov.au/declared-plants/calotropis-declared-pest).

Based on allozyme studies, Australian monarchs do not represent the full genetic diversity of the North American population (Shepard et al. 2002).

Monarchs breed year round in parts of Australia, and overwinter in other parts (Zalucki and Rochester 2004). Roughly, the population size of monarchs is Australia is estimated to be less than 250,000, much smaller than in the 1960's (personal communication, David James to Sarina Jepsen, June 18, 2014); and monarchs may be threatened by coastal development, drought and increasing temperatures, and by eradication of milkweed from pastures due to concerns about toxicity to grazing animals (James 1983, p. 197).

Philippines

Although monarchs were reported from the Philippines in about 1900 (Vane-Wright 1993, as cited in Zalucki and Clarke 2004, p. 121), they have not been found recently.

Southeast China

Monarchs were reported in Hong Kong the 1890's (Walker 1914, as cited in Zalucki and Clarke 2004, p. 121), but recent descriptions of milkweed butterflies in Hong Kong (Wong et al. 2004) and adjacent Macau (Easton and Pun 1997) do not list *D. plexippus*.

Galapagos

The Galapagos Islands are a thousand kilometers off the coast of Ecuador. No native milkweed hosts for monarchs were present before 1905 when *Asclepias currasavica* was introduced. It now grows in gardens, and has naturalized, mainly in the agricultural areas around towns on certain islands. Monarchs were first reported in the 1920's (Roque 1998). Their population size, status and threats are unknown.

Bermuda

Bermuda consists of a cluster of islands about 1000 km east-southeast of Cape Hatteras, North Carolina. According to Hilburn (1989), *Gomphocarpus physocarpa* and *Asclepias curassavica* were introduced and became naturalized by the time the first monarchs were reported in 1850's. By the late 1800's monarchs were very abundant throughout the year, but are much less common now. Milkweeds have been displaced by intense development, resulting in a very restricted distribution (Hilburn 1989). In addition, both caterpillars and adults are preyed upon by giant toads, *Bufo marinus* L. (p. 498). In 1988, the government started a Monarch Conservation Project to encourage citizens to plant *A. curassavica* and *G. physocarpa* in gardens, and commissioned a study of monarchs in the islands (Hilburn 1989, p. 495). Total numbers of monarchs have not been determined. However, the population may be replenished by monarchs that have been seen arriving over the ocean from the north, and also leaving from the south, in September and October, presumably migrants from North America.

Macaronesia

Several islands in the North Atlantic off the coast of Europe and Africa have resident monarch populations. These have been described by Neves et al. (2001, p. 19).

Canary Islands

> …in the Canary Islands, a local monarch population has been listed at least since 1880 (Higgins and Riley 1970) or 1887 (Leestmans 1975; Baez 1998). It inhabits the entire archipelago except for Lanzarote Island, and adults are observed flying throughout the year (Baez 1998). The larvae feed on *Asclepias curassavica* L. (Lesstmans 1975; Baez 1998), *G. fruticosus* (Asclepiadaceae) and *G. arboreum* (Malvaceae) (Baez 1998).

In addition, Brandes (2005) has reported recent introductions of *Calotropis procera* in some of the Canary Islands, since the 1990's.

Madeira Islands

> In Madeira island, it was first observed in 1860 (Leestmans 1975), and after this date several observations were published (*see* Meyer 1993 for review). It has recently become resident (Sousa 1984-85, 1991), and larvae are observed through the entire year (Tatjana Anselm, Caniço, Madeira, pers. comm.). The species occurs in some numbers on Porto Santo Island (Gardner and Classey 1960; Vieira 1999).

Azores

> [In the Azores] … As *Gomphocarpus* sp. is never found in large numbers, the availability of the food plant might be a limiting factor for the increasing population of monarch in these islands (Neves et al. 2001, p. 19).

In fact, large numbers of monarch caterpillars have been observed completely defoliating *G. fruticosus* host plants in the Azores (Neves et al. 2001, pp. 22 – 23).

Spain and Portugal

Resident monarch populations have been present in southern Spain since at least the 1990's, and perhaps much longer. Monarchs have been occasionally reported in coastal Spain since the late 1800's, and now share patches of introduced milkweed, *Asclepias curassavica* and *Gomphocarpus fruticosus*, with another milkweed butterfly from Africa, *Danaus chrysippus* (Haeger et al. 2011, p. 364). Near the Strait of Gibraltar in southern Spain, these milkweeds are naturalized in moist disturbed areas, such as farmlands. In some locations, host plants are threatened by eradication campaigns:

> … both species of milkweed are included on the checklist of invasive plants of Southern Spain (Dana et al. 2005). Therefore, in the ''Natural Park of the Alcornocales'' which was part of our study area, control of these plants is occasionally undertaken and one of the biggest mixed patches of *G. fruticosus* and *A. curassavica* was cleared in 2007. In this patch *D. plexippus* was only sporadically seen, but we registered up to 45 *D. chrysippus* flying during the summer of 2009. In the National Park of Doñana (150 km to the NW of the area) both plants have been systematically uprooted. In 1983 the monarch butterfly was not included on the checklist of this National Park, but both species of *Danaus* have been detected in past years. At least one flourishing colony was eradicated in 2004 (Fernández Haeger and Jordano 2009). Nevertheless the total extinction of plants is not easy. Patches recovered in a few months after being cleared, because both species resprout easily from roots, from seed already in the soil and the arrival of seeds from surrounding patches might be frequent and germination rates of seeds are high (unpublished data). Therefore, if herbivore density and water availability does not change, recovery of patches occurs in a short period of time. In any case, there is a conflict between the conservation of these specialist butterflies and the eradication of their foodplants considered as invasive species (Haeger et al. 2011, p. 364).

Resident monarchs have also been studied in the Mediterranean coastal areas of Spain, from Málaga and Granada to Almeria in southeastern Spain. The first colony was reported in Malaga Province in 1979. Throughout the 1980's monarchs expanded along the Malaga coast. However, numbers of monarchs were extirpated from Malaga Provence in the late 1980's, perhaps due to rapid development of their breeding area and loss of host plants, or in response to cycles of drought and high temperatures (Gil-T 2006, pp. 144 – 145). Monarchs reestablished in southeastern Spain in the 2000's, and were reported to be using a new host plant, native *Cynanchum acutum,* in addition to the introduced host species (Gil-T 2006, p. 145 – 146).

There also are reports of monarchs in coastal Portugal, although their status has not been carefully studied, and they may be visiting migrants rather than residents.

Non-migratory Populations of *D. p. plexippus* in the Southeastern United States, Cuba, and elsewhere in the Caribbean

There are small populations of monarchs that have been overwintering in the United States near the Gulf of Mexico and in Florida. Populations reside in these locations year round. Since they don't migrate, some researchers classify them as *D. p. megalippe* (Smith et al. 2005). At least in the best-studied Florida locations, it appears that migratory *D. p. plexippus* individuals coming from the east coast in the fall integrate into the stationary populations (Knight and Brower 2009). Some continue to Cuba and appear to integrate into the *D. p. megalippe* population there (Dockx 2002, Dockx 2007, Dockx 2012), or continue to other Caribbean islands. Also, with the spread of non-native milkweeds in the southeastern states, more migratory individuals may be forming transient year-round populations on these more heat-tolerant milkweeds (Harvey et al. 2009). Resident populations in south Florida are threatened by development and by increasing temperatures from climate change (Knight and Brower 2009, and *see* Threats—Other Factors, Climate Change section of this petition).

There also are some monarchs that breed year round in Southern California (Urquhart et al. 1968).

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Appendix B: Proposed Rules to Facilitate Monarch Butterfly Conservation, Science, Citizen Monitoring, and Education

To avoid concerns that protecting monarchs under the ESA would curtail education about the species in classrooms as well as scientific research, citizen monitoring, and beneficial household rearing endeavors, we propose the Fish and Wildlife Service adopt a version of the following rules along with any findings on this petition and/or proposal to list the species.

If monarchs are listed as a threatened species, under Section 4(d) of the ESA the Service can create a rule exempting certain activities from the prohibitions in Section 9 when those activities are necessary and advisable for the conservation of the species. 16 U.S.C. § 1533(d). The Service should use its Section 4(d) authority to carve out limited exemptions from the prohibitions on take, transport in commerce, and transport during a commercial activity for scientific research, citizen research and rearing, and conservation education activities that are necessary and advisable for the conservation of the species.

The following is a basic outline for the rule:

§ 17.47(b) Monarchs.

(1) The provisions of § 17.31(a) apply to this species, regardless of whether members of the species are in the wild or in captivity, and also apply to the progeny of any such butterfly.
(2) Any violation of State law will also be a violation of the Act.
(3) Paragraph (b)(1) will not apply to individuals engaged in scientific research on monarchs and/or their habitat that:
    (i) is beneficial to the conservation of the species or aimed at understanding monarch biology in ways that could benefit future monarch conservation;
    (ii) does not entail collection of the species for commercial display or commercial breeding;
(4) Paragraph (b)(1) will not apply to individuals engaged in citizen monitoring designed to conserve monarchs or scientific research designed to conserve the species or better understand monarch biology that:
    (i) is overseen by a scientist, conservation organization, or other entity dedicated to the conservation of the species;
    (ii) does not require capture of members of the species for commercial display or commercial breeding;
(5) Paragraph (b)(1) will not apply to conservation education activities that enhance the survival or propagation of the species, including but not limited to:
    (i) the rearing of monarchs in school classrooms provided that the monarchs are not provided by commercial suppliers;
    (ii) the rearing of monarchs at nature centers or other facilities designed to educate the public about the ecological role and conservation needs of the species provided that the monarchs are not provided by commercial suppliers;
(6) Paragraph (b)(1) will not apply to the collection of wild members of the species and rearing of fewer than ten monarchs per year by any individual, household, or educational entity.

Reptile and Amphibian Response to Hardwood Forest Management and Early Successional Habitats

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Chapter 11: Reptile and Amphibian Response to Hardwood Forest Management and Early Successional Habitats

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Abstract Herpetofauna responses to forest management and early successional habitats are influenced by species-specific adaptations to historical disturbance regimes. It can take decades for woodland salamander diversity to recover after heavy overstory removal for even-aged forest regeneration or hot fires that yield higher light, drier microclimates, and reduced leaf litter cover, but some frog and toad species may tolerate or even increase after disturbances. In particular, disturbances that retain some canopy cover, such as selection harvests or low intensity burns, can mitigate effects on terrestrial salamanders. The same early successional conditions that are detrimental to salamanders can benefit many reptile species, such as fence lizards (*Sceloporus undulatus*). Maintaining stand age diversity across central hardwood forest landscapes, including retention of mature forest communities, should provide habitats for both early successional wildlife and mature forest species.

11.1 Relevant environmental changes following disturbance

The extent and frequency of historical disturbances in central hardwood forests varied widely depending on slope position, aspect, stand age, and stand composition (White et al., Chapter 3). Gap phase disturbances following wind events, ice storms, and insect outbreaks were more common than the large-scale changes that followed hurricanes and wildfires in other regions of North America (White et al., Chapter 3). Amphibian and reptile species associated with mature hardwood forest presumably were common across much of the landscape, whereas those associated with early succession habitats were much more variable because they depended upon infrequent natural disturbance to create ephemeral patches of suitable habitat (Greenberg 2001).

Natural and anthropogenic disturbances that create young forest by removing or reducing canopy cover can greatly alter the microclimate at or just below the soil surface, where most amphibian and reptile species reside (but see Brooks and Kyker-Snowman 2008). Following overstory removal, light penetration increases, raising soil temperatures and evaporation rates and decreasing litter depth and moisture until it is replenished by leaf-fall and shade from the recovering vegetation (Greenberg et al., Chapter 8). Fire also can consume leaf litter and reduce leaf-fall input levels (Petranka et al. 1994). Increased light levels near the ground promote development of a grass and forb layer and establishment of shrubs or regenerating trees (Russell et al. 2004). These environmental changes can alter herpetofaunal movement patterns, survival rates, and prey abundance (Moseley et al. 2004).

Down wood or coarse woody debris (CWD) is used by many reptile and amphibian species for mating sites, egg-laying, feeding, and thermoregulation (Whiles and Grubaugh 1996). Down wood volume typically follows a U-shaped chrono-sequence in central hardwood forests, with highest levels in the 5 to 10 years following disturbance (i.e., downed trees following windthrow or logging slash following timber harvest) and again during late-succession or old growth stages when aging trees senesce (Gore and Patterson 1986). However, larger, more decayed logs may be more abundant in mature or old growth hardwood forest (Petranka et al. 1994). Webster and Jenkens (2005) reported that primary forests in the Southern Appalachians contained more large-diameter, highly decayed CWD compared to forests subjected to anthropogenic disturbances. Furthermore, among sites with similar disturbance histories, higher levels of CWD were associated with mesic conditions and higher elevations (Webster and Jenkens 2005, Keyser, Chapter 15). Therefore, reptile and amphibian species that use down wood heavily may be most abundant early (e.g., some reptiles) or late (e.g., salamanders) in stand development. However, the degree to which salamanders and other amphibians specifically rely on CWD is likely influenced by the availability of other surface cover. For example, salamanders may use cover objects less in undisturbed stands with intact leaf litter and vegetation cover compared to stands where leaf litter and vegetative cover is reduced from prescribed burning and herbivory (Ford et al. 2010).

Machinery associated with timber harvest operations can cause soil compaction or erosion. Disturbances of the subterranean environment, as occurs with most types of mechanical site preparation, can cause direct mortality or degrade habitat conditions for fossorial snakes and other species that spend portions of their life cycle below ground (Russell et al. 2004, Todd and Andrews 2008). However, mechanical site preparation and other forms of intensive forest management are uncommon in the Central Hardwood Region as compared to other regions such as the southeastern Coastal Plain (e.g., Russell et al. 2002).

Amphibians and reptiles often are generically lumped together as “herpetofauna,” but in fact are as phylogenetically distinct from one another as are mammals and birds. Amphibians (class *Amphibia*) have permeable, moist skin that is used for respiration and increases vulnerability to desiccation. Amphibians have a two-stage or “biphasic” life cycle that includes morphologically distinct larval and adult stages. Most require water for egg deposition and development of larvae, which eventually metamorphose into adults that can be largely terrestrial (Duellman and Trueb 1986). Amphibian taxa vary considerably in their vulnerability to desiccation. For example, some frogs and toads can tolerate higher temperatures (Stebbins and Cohen 1995) and can store and reabsorb larger amounts of water in their bladders than salamanders (Zug 1993). Some salamanders are lungless, and some are completely terrestrial (deMaynadier and Hunter 1995). Many amphibian species have small home ranges (Duellman and Trueb 1986) and poor dispersal capabilities (Sinsch 1990). Conversely, most reptiles (class *Reptilia*) require warm temperatures (associated with higher light levels) for egg incubation and successful development of hatchlings (Deeming and Ferguson 1991). Reptiles have dry scaly skin that protects them from desiccation. Clearly, response to disturbance and early successional habitats might be expected to differ between the two taxonomic classes, and among species within them. Within *Amphibia*, salamanders tend to decline following disturbances that reduce canopy cover because of their increased risk of desiccation, whereas some toad and frog species may tolerate higher temperatures and lower moisture in early successional habitats (Russell et al. 2004). Many reptile species increase in recently disturbed areas, likely because of improved opportunity for thermoregulation and foraging (Russell et al. 2004).

11.2 Amphibian and reptile response to timber harvest

11.2.1 Amphibian response

Heavy overstory removal for forest regeneration treatments (e.g., clearcut or shelterwood regeneration harvests) can adversely affect amphibians, especially terrestrial salamanders (Pough et al. 1987, Petranka et al. 1993, 1994, deMaynadier and Hunter 1995, Ash 1997, Harpole and Haas 1999, Reichenbach and Sattler 2007). Canopy removal results in higher light levels, a warmer, drier microclimate, and reduced leaf litter cover, which could cause salamanders to desiccate (deMaynadier and Hunter 1995, Renken 2006). In the Southern Appalachians, terrestrial salamander abundance declines following clearcutting (Ash 1988, Ash 1997, Petranka et al. 1993, Petranka et al. 1994; but see Adams et al. 1996).

There has been considerable debate about the time that it takes salamander populations to recover to pre-disturbance levels following canopy removal (Ash and Pollock 1999, Petranka 1999). Estimates range from approximately 20 years to more than 100 years (Table 11.1). Discrepancies in documented recovery periods likely are related to differences in study designs, salamander communities, and site and landscape characteristics. But, research suggests that post-disturbance recovery of salamander abundance is closely correlated with litter layer recovery (Pough et al. 1987, Ash 1997, Crawford and Semlitsch 2008a). Longer recovery periods may be required on drier aspects and ridge tops than on mesic sites where soil moisture remains relatively high even after disturbance (Harper and Guynn 1999, Petranka 1999). However, the former sites generally are poorer sites for woodland salamanders. Disturbances that retain heavy canopy cover such as midstory removal, selection harvest, firewood cutting, thinning, and heavy browsing by white-tailed deer (*Odocoileus virginianus*) are less likely to affect salamander abundance (Pough et al. 1987, Adams et al. 1996, Messere and Ducey 1998, Brooks 1999, Ford et al. 2000, Harpole and Haas 1999, Moseley et al. 2003, Knapp et al. 2003, Homyack and Haas 2009, Semlitsch et al. 2009). Yet, salamander density may decline following partial canopy reduction (e.g., Duguay and Wood 2002), and reductions in canopy cover by as little as 41% can cause local declines in salamander abundance (Knapp et al. 2003).

The exact mechanisms for the disappearance of terrestrial salamanders from disturbed sites remain in question. Semlitsch et al. (2008) proposed three hypotheses to explain amphibian declines following timber harvest: (1) retreat to underground refugia; (2) mortality from desiccation or starvation; and (3) evacuation to adjacent forest. Although a percentage of pond-breeding mole salamanders (*Ambystoma* spp.) may disperse out of disturbed environments, it is not known how they fare once they reach adjacent forest (Semlitsch et al. 2008). Mortality is the most likely cause of declines in terrestrial salamander density following clearcutting because plethodontid salamanders primarily are surface feeders and individuals eventually would starve unless they came to the surface where they could desiccate. Adult plethodontid salamanders lack lungs and depend on cutaneous respiration for gas exchange. Because moist skin is necessary to facilitate respiration, salamanders are most active where the forest floor is moist or at night when relative humidity is highest (Petranka et al. 1993). Salamander desiccation results from reduced leaf litter cover and depth, and higher ground temperatures following clearcutting, rather than changes in soil moisture (Pough et al. 1987, Ash 1997, Rothermel and Luhring 2005).

Rothermel and Luhring (2005) showed that salamander survival was 100% in uncut forest, but individuals could survive in clearcuts only by gaining access to protective underground burrows. Some researchers have speculated that salamanders are unlikely to evacuate to adjacent forested areas that already are saturated with territorial adults (e.g., Petranka 1999). For example, Bartman et al. (2001) did not detect any post-harvest emigration of plethodontid salamanders from sites that had been subjected to shelterwood harvests in western North Carolina. Interestingly, Ash (1997) speculated that adult salamanders disperse into early successional habitats such as clearcuts to avoid competition from smaller or immature salamanders that are restricted to mature forests with abundant, moist litter.

Juvenile frogs and salamanders typically exhibit higher rates of mortality than adults following canopy removal because their high surface:volume ratios make them prone to desiccation (Jaeger 1980, Ash et al. 2003, Marsh and Goicochea 2003). Additionally, the high adult:juvenile ratio of salamanders in clearcuts indicates low reproduction by adults or higher rates of mortality in juveniles (Ash 1997, Ash et al. 2003). Adults of some salamander species are better adapted to withstand the hot, dry conditions of recently disturbed sites or more exposed ridge top environments (Ash 1997, Ash et al. 2003, Ford et al. 2010). For example, Ford et al. (2010) reported that larger-bodied slimy salamanders (*Plethodon glutinosis*) were less affected by leaf litter reduction following fire than smaller-bodied red-backed salamanders (*P. cinereus*) or mountain dusky salamanders (*Desmognathus ocropheaus*). Riedel et al. (2008) documented high densities of both adult and juvenile eastern red-backed salamanders within former deciduous forests of West Virginia that had been converted to silvopastures, traditional pastures, and ungrazed meadows, indicating that this species may be more resilient to the creation of early successional habitats than previously thought. Interestingly, the physiological condition and sex ratios of salamanders within these open, early successional habitats were similar to those of salamanders in adjacent mature forest, although adults were significantly more abundant than juveniles (Riedel 2006). Riedel et al. (2008) suggested that the presence of artificial cover in these open, early successional habitats, in combination with moisture trapped by dense herbaceous vegetation, facilitated woodland salamander persistence. In addition, Marsh et al. (2004) showed that dispersal of *P. cinereus* was not limited by the presence of forest cover, and suggested that this species may be relatively insensitive to the creation of small, intervening, open habitats within deciduous forests such as fields, power line corridors, and even small residential areas. Accordingly, at least some species of woodland salamanders may tolerate the creation of small patches of early successional habitats within mature deciduous forests (Marsh et al. 2004, Riedel et al. 2008, Moseley et al. 2009), yet others can be highly sensitive to forest road edges (Semlitsch et al. 2007). However, individuals forced to forage in areas with reduced cover may be more exposed to predation (Moseley et al. 2004).

Timber harvest can affect stream-breeding salamanders by eliminating terrestrial habitat for adults and by degrading aquatic habitats required for larval development (Perkins and Hunter 2006, Crawford and Semlitsch 2008a, Peterman and Semlitsch 2009). Adult stream-breeding salamanders (e.g., *Desmognathus* and *Eurycea*) use terrestrial habitats some distance away from streams for foraging and overwintering habitat (Ashton and Ashton 1978, Crawford and Semlitsch 2007). Similar to terrestrial salamanders, adult stream salamander (e.g., Blue Ridge two-lined salamander [*E. wilderae*]) abundance may be reduced following timber harvest because of decrease in leaf litter depth, soil moisture, and overstory cover (Crawford and Semlitsch 2008a, b). Increased water temperatures and reduced litter input following canopy removal and sedimentation from logging roads (Vose and Ford Chapter 14) are detrimental to larval salamanders that occur in the streams (Semlitsch 2000, Peterman and Semlitsch 2009). Stream sedimentation can fill interstitial spaces between rocks at the stream bottom, thus potentially reducing abundance of salamanders that use the spaces for cover, such as *Eurycea* and *Desmognathus* species (Lowe and Bolger 2002, Miller et al. 2007, Moseley et al. 2008, Peterman and Semlitsch 2009). However, retention of an uncut riparian buffer may mitigate the effects of clearcut harvests on larval salamanders (Peterman and Semlitsch 2009).

Frogs and toads tend to be more tolerant of canopy removal and elevated ground temperatures than salamanders (Gibbs 1998, Ross et al. 2000, Russell et al. 2004, Patrick et al. 2006). Additionally, tadpoles of some frog species may develop faster or survive better in ponds within clearcuts (Semlitsch et al. 2009, Felix et al. 2010). Some anuran species likely are attracted to the higher coverage of herbaceous vegetation around ponds in open environments (Felix et al. 2010). Response to canopy removal around breeding ponds differs among anuran species. Species associated with open habitats, such as gray treefrogs (*Hyla versicolor*), deposit more eggs in ponds in areas with heavy canopy removal. In contrast, species that require cooler water temperatures, such as mountain chorus frogs (*Pseudacris brachyphona*) and spotted salamanders (*Ambystoma maculatum*) only deposit eggs where at least 75% of the canopy is retained (Semlitsch et al. 2009, Felix et al. 2010). However, gray treefrogs oviposited more eggs in ponds in clearcuts close to forest edge than in ponds 50 m into clearcuts (Hocking and Semlitsch 2007), because adult treefrogs require mature trees for foraging (Johnson et al. 2007, 2008). Adult wood frogs (*Rana sylvatica*) were able to travel through clearcuts when dispersing between breeding ponds and non-breeding habitats in mature forest, but their rate of travel increased in response to the degraded micro-climatic conditions (Rittenhouse and Semlitsch 2009). Some anurans, especially juveniles, may experience increased predation or desiccation risks following timber harvests (Patrick et al. 2006, Rittenhouse and Semlitsch 2009, Rittenhouse et al. 2009). Species response to the creation of young forest may vary regionally. For example, adult wood frogs did not use hot, dry clearcuts in Missouri but did use moist areas within clearcuts as non-breeding habitat in Maine (Patrick et al. 2006, Rittenhouse and Semlitsch 2009).

11.2.2 Reptile response

The same conditions following timber harvest that may be detrimental to amphibians appear to benefit many reptiles (Greenberg 2002, Adams et al. 1996). Most reptile species require the warm temperatures associated with higher light levels for egg incubation and successful development of hatchlings (Goin and Goin 1971, Deeming and Ferguson 1991). The hotter, drier microclimate in open, disturbed sites also may facilitate movement and thermoregulation for many reptile species (Greenberg 2001). Lizards, particularly fence lizards (*Sceloporus undulatus*), generally increase following canopy reduction (McLeod and Gates 1998, Greenberg 2001, Renken et al. 2004). Following timber harvests, Renken et al. (2004) determined that juvenile abundance of *S. undulatus* was twice as high as that of adults, suggesting that the lizards experienced an immediate boost in reproductive rates in disturbed sites or that the recently disturbed sites were colonized primarily by juveniles. In predominantly forested landscapes in Pennsylvania, snake abundance and richness increased with decreasing tree basal area (Ross et al. 2000).

However, there is evidence that some forest-dwelling reptile species may decline following timber harvest (Russell et al. 2004). In Coastal Plain pine forests, abundance of several small-bodied leaf litter snake species was lower in clearcuts than unharvested and thinned pine stands, but snake abundance was highest in thinned stands where habitat heterogeneity and presumably prey abundance was highest (Todd and Andrews 2008). In contrast with the management of deciduous forests, the intensive mechanical site preparation associated with Coastal Plain pine management not only removes surface cover used by small-bodied snakes but also likely results in direct destruction of nest sites (Russell et al. 2002).

11.3 Response to prescribed fire

Over the past 500 years, fire was a common forest disturbance across much of the Central Hardwood Region (Spetich et al. Chapter 4). Fire effects on vegetation structure likely varied with fire intensity and frequency, which in turn was influenced by topography, weather conditions, and population distribution of Native Americans or European settlers who intentionally burned to promote forage for game or livestock (Spetich et al. Chapter 4). Hot fires certainly reduced leaf litter and often killed overstory trees, creating patchy, heterogeneous early successional conditions with some snags and trees remaining. In contrast, cool, patchy burns likely had minimal impact on overstory trees or leaf litter depth and cover, but reduced shrub cover or killed midstory trees where it burned. In ecosystems such as longleaf pine-wiregrass or sand pine-scrub where lightning-ignited fires created and maintained "fire climax" habitat conditions, many species of reptiles and amphibians are behaviorally adapted to survive wildfire or prescribed burns, and require fire maintained habitat conditions (Russell et al. 1999; Greenberg 2002). Less is known about fire effects on herpetofauna of upland hardwood forest, where the majority of fires were historically human-caused. Fire is thought to have little direct effect on amphibians and reptiles, but the likelihood of individual mortality during a fire depends on the species' behavior, fire intensity, and season of burn (Russell et al. 1999). Negative indirect impacts of prescribed fire likely are most severe for species that require leaf litter or other forest debris that is consumed (Russell et al. 1999).

Relatively few studies have addressed fire effects on herpetofauna in hardwood forests (Russell et al. 2004, Renken 2006). Several studies have reported no difference between amphibian populations on prescribed burned sites and unburned controls (Ford et al. 1999, Floyd et al. 2001, Moseley et al. 2003, Keyser et al. 2004, Greenberg and Waldrop 2008, Ford et al. 2010, Matthews et al. 2010). Others have indicated that toad abundance may increase following fire (Kirkland et al. 1996, Greenberg and Waldrop 2008). Conversely, intense prescribed fires that cause immediate or delayed reduction in canopy cover following overstory tree mortality can produce micro-habitat changes near the forest floor (e.g., reduced leaf litter cover and depth, more sunlight, higher ground temperatures) that negatively impact salamander populations (Matthews et al. 2010).

Reptiles, lizards in particular, may increase after prescribed burns, especially after hot fires that reduce canopy cover (Moseley et al. 2003, Keyser et al. 2004; Greenberg and Waldrop 2008, Matthews et al. 2010). Litter removal, midstory and canopy reduction, and higher ground temperatures following intense fires likely create thermoregulatory conditions favorable for lizards (Moseley et al. 2003). Overstory mortality following intense fires also generates down wood that may be used as basking sites by lizards and large-bodied snakes (Matthews et al. 2010). However, it is not known whether these same changes negatively affect small-bodied fossorial snakes that depend on leaf litter.

Prescribed fire effects on wetland and stream-associated amphibians in central hardwood forests have not been well studied (Renken 2006). Intense fires that kill trees and reduce canopy cover in the uplands adjacent to streams or amphibian breeding ponds could result in higher water temperatures increased sedimentation rates, or runoff of ash that changes water pH, potentially killing amphibian adults, eggs, or larvae (Renken 2006). However, other temperature and sediment-sensitive aquatic vertebrates in the Appalachians, such as brook trout (*Salvelinus fontinalis*), have been reported to respond positively to adjacent forest disturbances, presumably in response to greater abundance of macroinvertebrate prey after partial canopy removal (Nislow and Lowe 2006). In short, more research is needed on the effects of fire and other forest disturbances on aquatic and riparian reptiles and amphibians in central hardwood forests.

11.4 Mitigation strategies

11.4.1 Stream and wetland buffers

Riparian buffers between upland timber harvests and adjacent streams or wetlands have been recommended to mitigate impacts on sensitive amphibian species (Semlitsch 2000). Buffers shade water, contribute leaf litter to streams, filter sediment, provide terrestrial habitats for biphasic amphibians and reptiles, and possibly provide refuge for individuals dispersing out of harvested areas (Mitchell et al. 1997, Semlitsch 2000, Perkins and Hunter 2006). Crawford and Semlitsch (2007) recommended a 92-m buffer adjacent to Southern Appalachian streams to provide core habitat free of edge effects for the widest ranging stream salamander species. Effects of timber harvest on sensitive amphibian species may extend at least 25 m into adjacent mature forest, possibly because of the reduced canopy and litter cover along edges created by timber harvests (deMaynadier and Hunter 1998). To provide the core biphasic habitat needs, Semlitsch and Bodie (2003) recommended 159-290 m buffers for amphibians and 127-289 m buffers for reptiles around wetlands and streams. However, it has been speculated that narrower 30-m buffers may provide adequate protection to larval salamanders (Peterman and Semlitsch 2009). Alternatively, a two-tiered approach has been recommended to protect aquatic herpetofauna, with unharvested 10-25 m buffers around streams surrounded by a wider partial harvest zone (deMaynadier and Hunter 1995). To date, however, the actual community and demographic responses of stream-dwelling herpetofauna to adjacent forest disturbance remain poorly characterized. Therefore, few data are available to evaluate the efficacy of specific buffer widths recommended to protect herpetofauna within deciduous forests of the Central Hardwood Region.

11.4.2 Coarse woody debris retention

Salamander populations are positively linked to CWD abundance, especially on drier sites and where leaf litter cover is sparse, so retention of CWD may help mitigate the effects of disturbance on amphibians and provide critical habitat or refuge to a number of reptile species (Pough et al. 1987, Petranka et al. 1994, Brooks 1999, Herbeck and Larsen 1999, Russell et al. 2004). Retention of CWD and brush piles in clearcuts may decrease the proportion of salamanders leaving clearcuts and could contribute to increased juvenile amphibian survival by providing cool, moist refugia (Patrick et al. 2006, Rittenhouse et al. 2008, Semlitsch et al. 2008). Todd and Andrews (2008) captured more small snakes in clearcuts with CWD retention than in clearcuts without retention. However, CWD retention appears to provide only short-term benefits to sensitive amphibians by providing refuge from desiccating conditions immediately post-harvest, and may not prevent declines (Mosely et al. 2004, Semlitsch et al. 2009). Coarse woody debris diameter and degree of decay is generally much lower, and thus not used by salamanders, in recently harvested sites than in old growth stands (Herbeck and Larsen 1999). Additionally, several studies failed to show benefits of CWD retention for amphibians (Greenberg 2001, Ford et al. 2002a, Rothermel and Luhring 2005, Rittenhouse and Semlitsch 2009). Similarly, higher abundance of lizards and snakes in small canopy gaps was not related to CWD abundance (Greenberg 2001).

11.4.3 Overstory retention

Small forest openings such as group selection harvests and wind-created downburst gaps with multiple treefalls, or partial harvests that retain a large percentage of the overstory, can mitigate the negative effects of timber harvest on amphibians by maintaining shade and leaf litter input and providing refuge and recolonization sources (Pough et al. 1987, Ford et al. 2000, Greenberg 2001, Lowe and Bolger 2002, Homyack and Haas 2009). Overstory retention adjacent to wetlands can be critical to maintaining connectivity between aquatic reproduction sites and other habitat features required by amphibians, as many, especially salamanders, avoid timber harvests when emigrating from breeding pools (Todd et al. 2009). In Maine, partial harvests adjacent to headwater streams had less effect on amphibian communities than clearcuts (Perkins and Hunter 2006). Increased growth of herbaceous plants or shrubs near the forest floor following small overstory reductions might improve habitat conditions for some herpetofaunal species and mitigate changes to the microclimate that are problematic for disturbance-sensitive species such as salamanders (Ross et al. 2000, Semlitsch et al. 2009). Retention of at least 50% of the overstory is recommended to minimize negative effects on amphibian populations (Ross et al. 2000, Semlitsch et al. 2009). However, as little as 41% reduction in the overstory may result in declines in the abundance of plethodontid woodland salamanders similar to clearcuts (Knapp et al. 2003). Group-selection harvests require more frequent stand entries across a larger land base to extract the same amount of wood fiber as a clearcut (Homyack and Haas 2009). We suggest that the relationships between partial overstory reduction and response by amphibian populations require more study.

11.4.4 Small stand sizes and longer rotations

Smaller harvest units may help to minimize the deleterious effects of timber harvest on wood frogs and other sensitive amphibians, especially juveniles (Patrick et al. 2006, Rittenhouse and Semlitsch 2009). The distance that dispersing individuals must traverse across smaller clearcuts could lessen the risks of desiccation and predation. Additionally, small timber harvests may facilitate evacuation by individuals from harvested areas into adjacent uncut areas (Semlitsch et al. 2008). Ford et al. (2002a) demonstrated that the amount of cove hardwood habitat surrounding harvested patches is an important determinant of woodland salamander population response to the disturbance, so designated no-harvest areas on the landscape could serve as sources for repopulating nearby harvest units (Petranka et al. 2004). Additionally, breeding pools in small timber harvest openings could provide ideal locations for rapid larval development for larvae of some disturbance-adapted or early successional amphibians and be in close proximity to the mature forest required by adults (Barry et al. 2008, Semlitsch et al. 2009). Further, small harvest openings (< 2 ha) provide habitat for lizards and other reptiles (Greenberg

2001). Similar to group-selection harvests, however, harvest of the same timber volume in smaller units requires more roads, potentially leading to sediment loading in streams and disturbance to a larger percentage of the land base.

Increasing the rotation length of managed forest stands would ensure that a portion of the landscape contained large trees, high accumulations of large diameter CWD, and other structural characteristics associated with late-seral forest (Herbeck and Larsen 1999). Alternatively, employing forest management practices that retain and enhance structural components of habitats important for herpetofauna (e.g., retention of CWD, green and legacy tree retention, selection harvest systems) may provide suitable conditions for these species while contributing to economic and other resource objectives. Additionally, management practices that mimic historical disturbance regimes may be used to promote a diversity of cover types across the landscape, which in turn would provide habitat for a variety of reptiles and amphibians. Examples of historical disturbance conditions include more frequent prescribed fires on xeric ridge tops in the Southern Appalachians and less disturbance on moist, north-facing slopes and ravines.

11.5 Research challenges

More focus on reptile response to disturbance. Reptile response to disturbance from forest management has been studied much less than amphibian response. For example, a database search of journal articles using the keywords *salamander* and *clearcut* generated 64 citations; conversely, a search using the same database with the keyword *lizard* in place of *salamander* generated three citations and replacement of *salamander* with *snake* generated one citation. We can only speculate that the cause for the discrepancy is due in large part to the direction of response by amphibians and reptiles in previous studies. Because amphibians, especially woodland plethodontid salamanders, typically decline locally following disturbance, they have received the majority of research emphasis in the past two decades. However, some reptile species such as small fossorial snakes similarly show negative response; other reptile species, such as fence lizards increase in abundance following disturbance. We suggest that there may be a bias in the scientific literature attributable to a greater attraction by scientists to studying taxa that respond negatively to forest management, and journals to accept manuscripts that report significant results.

Longer study durations. Deleterious effects of canopy reduction on salamanders and other amphibians may be delayed for up to five years after timber harvest (Ash 1988, Reichenbach and Sattler 2007, Homyack and Haas 2009). Some species may experience a greater time lag in the demographic changes that occur following disturbance (Homyack and Haas 2009). Greenberg and Waldrop (2008) reported that a single prescribed burn that killed trees and reduced canopy cover did not reduce the relative abundance of terrestrial salamanders (*Plethodon* spp.), but salamander abundance was lower in the same treatment units compared to control plots after a second burn 5 years later in the same study area (Matthews et al. 2010). The delayed changes in salamander abundance following the fuel reduction treatments could either have been a result of additive effects of the treatments on environmental conditions, or the result of delayed changes in demographic parameters (Matthews et al. 2010). Lastly, long-term studies also should address the effects of forest management on population demography at large spatial scales (Homyack and Haas 2009).

More accurate assessment of detection bias. Most reptile and amphibian studies assume that sampled individuals represent the entire population (deMaynadier and Hunter 1995). This assumption is unlikely for salamanders because surface populations represent only a small percentage of the total population (Bailey et al. 2004a). Additionally, detection probabilities often differ among treatment areas because of variable habitat conditions, which in turn could influence abundance estimates for reptile and amphibian populations (Bailey et al. 2004b). For example, reduction of leaf litter from prescribed fire or timber harvest could cause individual salamanders to move more frequently and for longer periods (Mosely et al. 2004), or cause them to aggregate under coverboards being used to assess population response to burning or other disturbances (Ford et al. 2010). Few studies of reptile and amphibian response to forest management have accounted for detection bias (except see Bailey et al. 2004b, Ford et al. 2010). Mark-recapture methodologies can be used to account for detection probability, but recapture rates, especially with terrestrial salamanders, can be low and capture-recapture methods can be costly when used in large-scale field experiments (Bailey et al. 2004a). In the case of large-scale studies, researchers can use a double-sampling design that uses capture-recapture analysis on a subset of sites to estimate detection probability and calibrate counts for the complete set of sampling locations (Bailey et al. 2004a, Bailey et al. 2004c).

More focus on site conditions, landscape position, and abiotic features. There is evidence that elevation, slope, concavity, and other landform characteristics may be important determinants of woodland salamander occurrence and abundance in central hardwood forests (Ford et al. 2002a, b). Many studies of amphibian response to forest management do not account for landscape position and associated conditions such as moist, concave, lower-slope positions with a thicker leaf litter layer and drier, warmer ridge tops or south-facing slopes that could influence amphibian or reptile species composition and their response to disturbance. When compared to other vertebrates, patterns of amphibian distribution across landscape scales remain poorly known (Johnson et al. 2002, Dillard et al. 2008a). Because amphibians have limited dispersal abilities and small home ranges, site-specific habitat factors often are assumed to have an overriding influence on patterns of amphibian distribution. However, there is increasing evidence that abiotic habitat characteristics measured at broad spatial scales are important predictors of amphibian occurrence and abundance within forest ecosystems. Although disturbance and succession of vegetation exert a strong influence on amphibian distribution and abundance (deMaynadier and Hunter 1995, Russell et al. 2004), recent research indicates that the importance of abiotic habitat features such as geology, topography, and climate have not been sufficiently recognized (Russell et al. 2005, Harper 2007, Dillard et al. 2008a, b). For example, Dillard et al. (2008a, b) showed that elevation, slope, aspect, and parent geology were better predictors of the occurrence of the threatened Cheat Mountain salamander (*P. nettingi*) in deciduous forests of West Virginia than were the composition or successional stage of overstory vegetation. Moseley et al. (2009) determined that the effects of canopy openings (e.g., edge effects) on woodland salamanders within deciduous forests of West Virginia depended on site aspect.

Landscape-level population effects. Most studies of amphibian and reptile response to forest management have been conducted at the scale of an individual stream, forest stand, or wetland. Therefore, more research is needed to assess the persistence of reptile and amphibian communities at the landscape or watershed scale (Perkins and Hunter 2006). Renken et al. (2004) recorded similar responses by reptiles and amphibians to clearcuts as in other studies, but the researchers failed to detect larger-scale impacts given the relatively small percentage of the landscape that was harvested. Ford et al. (2002a) suggested that salamander populations in small, isolated cove hardwood stands might be more vulnerable to extirpation by timber harvests than populations in larger, less isolated coves. Because juvenile amphibians are more susceptible to habitat change, management activities that fragment habitats likely will have the greatest impact on species for which juveniles conduct the majority of dispersal among breeding and non-breeding locations (Patrick et al. 2008). Some amphibian species avoid roads likely because of reduced soil moisture and cover, so landscape-level conservation strategies should account for these increasingly prominent movement barriers (Gibbs 1998, Marsh and Beckman 2004, Semlitsch et al. 2007). In contrast, anecdotal evidence indicates that secondary forest roads and trails with little use may not have negative impacts on herpetofauna and in some cases be used as habitat (e.g., Dillard et al. 2008c). More information is needed to better understand how landscape factors influence amphibian and reptile response to the creation of early successional habitats in upland hardwood forest (Ford et al. 2002a).

11.6 Literature cited

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Table 11.1 Estimated recovery periods for terrestrial plethodontid salamander populations following timber harvest.

Authors	Recovery Period	Disturbance	Comments
Ash 1997	20-24 years	Clearcut	Monitored salamanders in 3 clearcuts using night searches on 225-m^2 plots for 15 years post-harvest and recovery times estimated from regression curves
Harper and Guynn 1999	13-39 years	Clearcut	Used a terrestrial vacuum to sample leaf litter and associated fauna in 120, 0.04-ha plots in 3 stand age classes (0-12, 23-39, and ≥40 years old)
Pough et al. 1987	<60 years	Clearcut	Conducted nighttime surveys for salamanders in 50- x 2-m transects in 4 disturbed stand types of different ages and in 4 paired old-growth sites
Homyack and Haas 2009	>60 years	Various Harvests	Conducted nighttime searches of 15- x 2-m transects for 13 years following 7 canopy removal treatments and estimated population recovery from demographic models
Petranka et al. 1993	50-70 years	Clearcut	Surveyed salamanders in 50- x 50-m plots at 47 sites ranging in age from 2 to 120 years old
Herbeck and Larsen 1999	>80 years	Regeneration cut	Conducted area- and time-constrained searches for salamanders in 21 144-m^2 plots located in 3 age classes (<5, 70-80, >120 years old)
Ford et al. 2002	>85 years	Clearcut	Captured salamanders in drift fence arrays in 13 cove hardwood stands ranging in age from 15 years old to >85 years old
Petranka et al. 1994	120 years	Clearcut	Conducted daytime searches for salamanders in 50 x 50-m plots at 52 forest sites ranging from <5 years old to approximately 200 years old

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Coarse woody debris and pine litter manipulation effects on movement and microhabitat use of *Ambystoma talpoideum* in a *Pinus taeda* stand

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Abstract

We examined effects of coarse woody debris (CWD) and pine litter (PL) manipulations on movement and microhabitat use by mole salamanders (*Ambystoma talpoideum*) in the upper Coastal Plain of South Carolina. Individuals were tracked within field enclosures using harmonic radar detection from 3 December 2002 to 1 August 2003. Enclosure study one (ES1) consisted of three treatments: (1) high CWD/high PL; (2) low CWD/low PL; (3) high CWD/low PL. Enclosure study two (ES2) consisted of two treatment types: complete PL removal and unmanipulated control. Activity of *A. talpoideum* within ES1 high CWD/low PL, low CWD/high PL and high CWD/high PL treatments did not differ. Individuals subject to ES2 PL removal treatments moved during more nights than individuals in control treatments. During night surveys ES2 PL removal treatments moved on a greater percentage of nights, and were active for longer periods of time, than individuals in control treatments. *A. talpoideum* exposed to low PL treatments may have utilized CWD as a means of compensating for inadequate microclimate conditions provided by reduced pine litter depth. Our results suggest that reduction of CWD and pine litter has little effect on *A. talpoideum* activity levels. Conversely, complete pine litter removal prompts individual salamanders to move more frequently and for longer periods, thereby potentially being subjected to increased desiccation and predation risk. Within managed pine forests in the southeastern United States, forest management practices that minimize pine litter and CWD removal can help to maintain suitable habitat for amphibian groups such as ambystomatid salamanders.

Keywords: Ambystomidae; *Ambystoma talpoideum*; Coarse woody debris; Pine litter; Plantation silviculture

1. Introduction

Alteration and destruction of forest habitat has been cited as a major factor in the decline of many amphibian populations (Blaustein and Wake, 1990, 1995; Wyman, 1990). Conversion of natural forests to intensively managed plantations is increasing to meet burgeoning demand for wood fiber products. In the southeastern United States, these intensively managed plantations typically contain a less diverse and abundant amphibian assemblage as those in less disturbed unmanaged pine or hardwood stands (Bennett et al., 1980; Grant et al., 1994; Hanlin et al., 2000). Reduction of microhabitat features through use of intensive harvesting and subsequent plantation reestablishment methods are believed to be a major factor leading to the

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decrease of amphibian populations within these stands (Enge and Marion, 1986).

Pine plantations account for 15% of timberland in the southeastern United States, occurring predominately in the Coastal Plain and Piedmont physiographic regions. These stands are generally much younger than natural pine stands, with 81% less than 23 years old (Conner and Hartsell, 2002). Because plantations are managed on short rotation lengths, disturbance occurs more frequently than in unmanaged pine stands. Plantations generally are subject to clearcut harvesting followed by intensive site preparation such as stump removal, roller chopping and mechanical bedding (Hunter, 1990; Smith et al., 1997). Even-aged harvest methods and subsequent site preparation compact soil, reduce litter depth and cover, displace mineral soil and reduce volume of coarse woody debris (CWD) (Harmon et al., 1986; Reisinger et al., 1988; deMaynadier and Hunter, 1995), leading to the development of more homogenous and structurally simplified forest stands. Reduction of these microhabitat features diminishes on-site moisture, a critical component for amphibians which require moist skin to respire (Duellman and Trueb, 1994), and reduces favorable cover sites used to escape extreme temperature and dry surface conditions (Russell et al., 2002). While response of amphibian species to forest management in the southeastern Coastal Plain region has been documented, little information exists on the underlying causal mechanisms, especially for members of the family Ambystomatidae.

Existing information indicates that establishment of pine plantations has an adverse affect on *Ambystoma* populations. Means et al. (1996) found that a breeding population of flatwoods salamanders (*Ambystoma cingulatum*) drastically declined after their terrestrial habitat, a natural longleaf pine (*Pinus palustris*)–wiregrass (*Aristida* spp.) forest in Florida, had been converted into an intensively managed slash pine (*Pinus elliottii*) plantation. Raymond and Hardy (1991) documented a reduction in survival of adult mole salamanders (*Ambystoma talpoideum*) at a Louisiana pond that migrated from an adjacent portion of forest that had been clearcut. Management practices that produce sites with increased climatic variation and inadequate microhabitat may result in reduced survival of individuals within altered forest stands. However, effects of microhabitat alterations on *Ambystoma* species are not well understood because of their highly fossorial behavior.

Although ambystomatid salamanders primarily utilize underground retreat sites, surface cover conditions can have a significant influence on microclimate within burrows by buffering against temperature and moisture extremes in the soil (Williams and Gray, 1974; Geiger et al., 1995). The objectives of our study were to determine how alterations in pine litter depth and CWD volume affect movement, activity levels, and microhabitat use of *A. talpoideum*. Because individuals of this species are too small for radiotransmitters and because of difficulty in obtaining permits to use radioisotope tagging, a new tracking technique called harmonic radar detection (HRD) was employed to track movement of individuals within an enclosed area.

2. Study site and methods

2.1. Site description

Our study was conducted in a 50-year-old loblolly pine (*Pinus taeda*) stand on the US Department of Energy's Savannah River Site (SRS), a 78,000 ha National Environmental Research Park in Aiken, Barnwell and Allendale Counties, South Carolina (33°0–25′N, 81°25–50′W). The SRS is located on the upper Coastal Plain physiographic region in an area known as the Sandhills. Historically, the longleaf pine–wiregrass community dominated upland areas of the SRS before being cleared for agriculture in the early 1800s. Upon acquisition of the land comprising the SRS by the Atomic Energy Agency in 1951, the US Forest Service planted abandoned agricultural fields in loblolly and slash pine. Stands were established on these sites primarily by hand planting. Our study stand was located on a well-drained Sandhill at an elevation of 100 m. Soils were of the Blanton–Lakeland association. Understory vegetation was sparse, consisting mostly of poison oak (*Toxicodendron radicans*), black cherry (*Prunus serotina*), muscadine (*Vitis rotundifolia*) and broomsedge (*Andropogon virginicus*). Our study stand was last prescribed burned in 1993 (D. Shea, USFS Savannah River Site, pers. commun.). Mean annual temperature is 18 °C and mean annual precipitation is 122.5 cm.

2.2. Treatments and experimental design

Our first enclosure study (ES1) consisted of three replicate sets of three enclosure treatments of high CWD/high pine litter (PL), low CWD/low PL and high CWD/low PL. We added three pieces of similarly sized, slightly decayed CWD with mostly shed bark to the center of each enclosure. High CWD treatments had a volume of $91,730 \pm 6736\ \text{cm}^3$, whereas those with low CWD treatments had a volume of $25,061 \pm 3190\ \text{cm}^3$. We removed the L, F1, and F2 layers of the A-horizon (Millar, 1974) within each treatment enclosure and replaced it with pine litter collected from the pine stand. Pine litter in high and low PL enclosures had a mean depth of 2.98 ± 1.02 and 0.78 ± 0.43 cm, respectively. Because of soil disturbance caused by removal of pine litter, we created 16 burrows at 64 cm intervals with a 0.64 cm diameter lead pipe. We randomly assigned treatments for one set of enclosures; we then assigned treatment types in remaining enclosures depending upon which treatment had been assigned to enclosures in the first set. This was to ensure that center enclosures, which share walls with adjoining enclosures, received each of the three treatment types in order to eliminate any possible bias associated with having two common walls with adjoining enclosures as opposed to one shared by outside enclosures.

We constructed enclosures for ES1 of 0.635 cm plastic hardware cloth to prevent salamanders from escaping while permitting prey items, primarily insects, to move freely through enclosures. We buried hardware cloth to a depth of 30 cm with an above ground height of 30 cm. We attached polyvinyl chloride (PVC) pipe to the top of fences as well as 12.7 cm above the ground to create a barrier to salamanders attempting to climb out. We then attached a 12.7 cm piece of hardware cloth to the bottom of each side of enclosures to reduce hole size. Each enclosure was $4.57\ \text{m} \times 4.57\ \text{m}$, with a total area of $20.88\ \text{m}^2$. We oriented all enclosures with each side facing one of the cardinal directions. We completed enclosures and treatments for ES1 on 25 July 2002.

Our second enclosure study (ES2) consisted of nine pairs of two enclosure treatments, total pine litter removal and unmanipulated controls. We constructed enclosures from aluminum flashing buried 15 cm below ground with 15 cm above ground. We bent tops of enclosure walls to create a lip to prevent climbing salamanders from escaping. Each enclosure measured $3\ \text{m} \times 3\ \text{m}$. We randomly assigned treatments to each enclosure pair. For PL removal treatments, we removed all pine litter to expose mineral soil while control enclosures were left undisturbed. Pine litter in control enclosures had a mean depth of 4.04 (± 1.23) cm. We completed enclosures and treatments on 15 February 2002.

We collected individual *A. talpoideum* during breeding migrations at nearby Carolina Bay wetlands (Sharitz and Gibbons, 1982) from November 2002 until cessation of emigration from wetlands in April 2003. We used only females for ES1 because they stay at breeding sites for shorter periods than males and therefore spend more time in terrestrial environments (Semlitsch, 1981). In ES2, we used both male and female *A. talpoideum* captured emigrating from wetlands. We kept captured individuals in $20\ \text{cm} \times 15\ \text{cm} \times 5\ \text{cm}$ containers with moist paper towels at 21 °C and natural L:D periods. We did not keep individuals in captivity longer than 21 days. We constructed harmonic radar tags from Zener-telefunken BAT85S schottky-barrier diodes with two 11 mm antennae (total length: 25.9 mm) and a total weight of 0.1 g. We subcutaneously implanted one into each salamander. HRD consists of a hand held transceiver and a diode tag. The transceiver emits a 1.7 W continuous microwave frequency of 917 MHz. When the microwaves strike a diode attached to an animal they are reflected at double the frequency (1834 MHz), which is detected by the receiver. We recorded snout-vent-length (SVL, cm), total length (cm), sex and weight (g) of individuals. We allowed individuals to recover for 7–10 days post-implantation and following a random assignment to treatment, we released animals at night into 10.2 cm deep artificially constructed burrows (initial burrow). If a tagged salamander in an enclosure died, escaped, or lost its tag, and was not subsequently recovered, we replaced that individual. If individuals expelled tags and were recovered, we implanted new tags and released them back into enclosures. Because adult *A. talpoideum* are not easily found once breeding migrations have ended, we collected a group of individuals from a breeding wetland on 9 April 2003 ($n = 12$) and placed them in a $2\ \text{m} \times 2\ \text{m}$ enclosure in the study area for use in replacing lost, dead, or escaped individuals.

2.3. Sampling

We located individuals in ES1 using harmonic radar once during daylight (0800–1800 h) and once during night (2100–0200 h), 2–7 days a week from 3 December 2002 to 3 August 2003 ($n = 241$ days). We located individuals in ES2 during the same time periods from 15 February 2003 to 3 August 2003 ($n = 166$ days). We conducted intensive night surveys when heavy precipitation occurred and movement seemed likely. During night surveys we located individuals once every 60–90 min from sunset until sunrise. We collected daily temperature and rainfall at the study site during daily readings from a thermometer (°C) and rain gauge (cm) located 30 cm above ground level. We conducted night surveys on 26 February (ES1 only), 15 March (ES1 only), 8 April, 6 May (ES1 only), 18 May, 22 May, and 1 July 2003. We marked the location of each individual and time was recorded for each reading. We measured nearest point of locations (cm) using an *XY* coordinate with the southwest corner of enclosures serving as the origin. We then plotted coordinates and total distance moved (cm) was measured for each individual in QuickCAD 8.0.

2.4. Statistical analysis

We converted measured variables during each 24 h sampling period and analyzed them on a per day basis because some enclosures were occupied longer than others. We did not count individuals occupying enclosures for less than 14 days in final analysis. We compared number of activity areas and number of nights moved during 24 h sampling periods among treatments in ES1 using one-way analysis of variance (ANOVA) with individuals nested within treatments. We also compared movement rate, defined as distance moved (cm) per minute, and total minutes of activity during night surveys among treatments in ES1 using one-way ANOVA with individuals nested within treatments. We considered an activity area to be any point occupied by an individual for ≥ 1 day. We compared percent of nights an individual was active within enclosures during night surveys among treatments in ES1 using a one-way ANOVA. We compared percent of days in which individuals occupied pine litter and CWD among treatments using a one-way ANOVA. We used linear contrasts to compare high PL with low PL treatments and high CWD with low CWD treatments for all variables in ES1. For ES2, we compared number of activity areas and number of nights moved during 24 h sampling periods and movement rate and total minutes of activity during night surveys between treatments using one-way ANOVA with individuals nested within treatments. We compared percent of nights an individual was active within enclosures during night surveys between treatments in ES2 with a two-sample *t*-test. Effect of sex on number of activity areas and nights moved were compared using a two-sample *t*-test. All variables were tested for normality with Shapiro-wilk's test for normal distribution. Percentage data were arcsine transformed. Data that were not normally distributed and that could not be successfully transformed were ranked and analysis was performed on the ranks. All analyses were performed in SAS statistical analysis software (SAS Institute, 1997).

3. Results

There was a total of 618, 628, and 640 salamander nights in high CWD/low PL, low CWD/low PL, and high CWD/high PL, respectively. Number of activity areas and number of nights moved during daily locations for ES1 did not differ among treatments (Table 1). Percent use of pine litter and CWD were not different among treatments (Table 2). However, linear contrasts revealed that individuals in low CWD treatments utilized CWD to a greater extent than individuals in high CWD treatments ($F = 6.94$, $P = 0.0388$). Time active (min), movement rate and percent of nights active in ES1 during night surveys were not different among treatments (Table 1).

In ES2 there was a total of 835 and 987 salamander nights for PL removal and control treatments, respectively. Number of activity areas for ES2 did not differ between treatments (Table 3). However, individuals in PL removal treatments moved more frequently than control individuals during night surveys (Fig. 1). Individuals in PL removal enclosures also were active for longer periods and moved during a larger percentage of night surveys than control individuals (Table 3). Males and females did not differ in any other variables measured.

Table 1
Mean (±S.E.) number of activity areas and nights moved per day during daily locations, and mean (±S.E.) time active, movement rate, and nights active during night surveys for *A. talpoideum* in high CWD/low pine litter (PL) ($n = 618$ salamander days), low CWD/low PL ($n = 628$ salamander days), and high CWD/high PL ($n = 640$ salamander days) enclosures at the Savannah River Site, Aiken County, South Carolina, from 3 December 2002 to 1 August 2003

Variable	High CWD/low PL, mean ± S.E. (n)	Low CWD/low PL, mean ± S.E. (n)	High CWD/high PL, mean ± S.E. (n)	F (d.f.)	P
Daily locations					
Activity areas[a]	0.06 ± 0.03 (3)	0.04 ± 0.01 (3)	0.04 ± 0.01 (3)	0.29 (2.6)	0.7586
Nights moved[a]	0.06 ± 0.03 (3)	0.04 ± 0.01 (3)	0.02 ± 0.01 (3)	0.66 (2.6)	0.5491
Night surveys					
Time active (min)	445 ± 96.1 (3)	423 ± 82.3 (3)	261 ± 32.2 (2)	1.86 (2.5)	0.2485
Movement rate (cm/min)	2.65 ± 0.6 (3)	2.85 ± 0.6 (3)	2.07 ± 0.7 (2)	0.19 (2.5)	0.8345
Nights active (%)	42.86 ± 20.53 (3)	29.21 ± 7.7 (3)	18.89 ± 14.2 (2)	0.74 (2.5)	0.5146

[a] ANOVA performed on ranked data.

Table 2
Mean (±S.E.) percentage of days pine litter and coarse woody debris were used by *A. talpoideum* during daily locations in high CWD/low pine litter (PL) ($n = 618$ salamander days), low CWD/low PL ($n = 628$ salamander days), and high CWD/high PL ($n = 640$ salamander days) enclosures at the Savannah River Site, Aiken County, South Carolina, from 3 December 2002 to 1 August 2003

Variable	High CWD/low PL, mean ± S.E. (n)	Low CWD/low PL, mean ± S.E. (n)	High CWD/high PL, mean ± S.E. (n)	F (d.f.)	P
Pine litter use (%)	49.72 ± 16.96 (3)	45.46 ± 11.91 (3)	35.64 ± 21.03 (3)	0.18 (2.6)	0.8410
CWD use (%)	16.81 ± 12.75 (3)	37.62 ± 7.40 (3)	2.15 ± 2.15 (3)	4.17 (2.6)	0.0732

4. Discussion

Pine litter removal had a significant effect on movement and activity levels of *A. talpoideum*. Individuals within ES2 PL removal enclosures were active an average 91.7% of nights surveyed, 32% more than those within control enclosures, and moved 61.6% more than controls during the 166-day sampling period. Increased activity is likely due to absence of adequate microclimate conditions within removal enclosures. Litter acts as an insulating layer for soil, buffering against extreme surface temperatures and retaining moisture during dry periods (Williams and Gray, 1974; Geiger et al., 1995). Elimination of ground cover reduces availability of suitable temperature and moisture conditions for salamanders (Pough

Table 3
Mean (±S.E.) number of activity areas and nights moved per day during daily locations, and mean (±S.E.) time active, movement rate, and nights active during night surveys for *A. talpoideum* in pine litter removal ($n = 835$ salamander days) and control ($n = 987$ salamander days) enclosures at the Savannah River Site, Aiken County, South Carolina, from 15 February 2003 to 1 August 2003

Variable	Pine litter removal, mean ± S.E. (n)	Control, mean ± S.E. (n)	F (d.f.)	P
Daily locations				
Activity areas	0.06 ± 0.01 (9)	0.05 ± 0.01 (9)	0.01 (1.16)	0.9171
Nights moved[a]	0.06 ± 0.01 (9)	0.03 ± 0.01 (9)	5.21 (1.16)	0.0365
Night surveys				
Time active (min)	463 ± 32.83 (7)	272 ± 56.05 (6)	13.21 (1.11)	0.0039
Movement rate (cm/min)	2.45 ± 0.14 (7)	2.54 ± 0.25 (6)	0.14 (1.11)	0.7110

[a] ANOVA performed on ranked data.

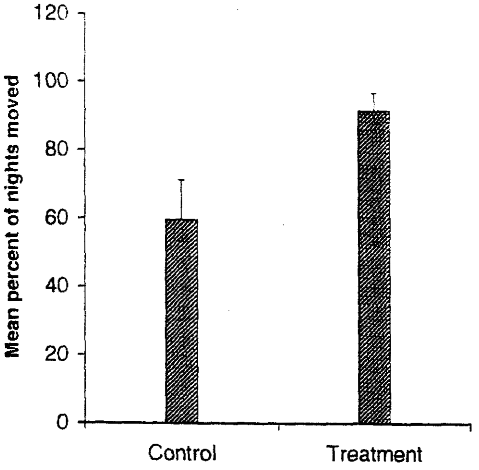

Fig. 1. Percent of nights in which *A. talpoideum* in pine litter removal ($n = 835$ salamander days) and control ($n = 987$ salamander days) treatment enclosures were active on the forest floor during night surveys conducted on 8 April, 18 May, 22 May, and 1 July 2003. Treatments were compared by ranks with a two-sample *t*-test (*t*-value = −2.42, $P = 0.0341$).

et al., 1987). Reduction of forest floor litter depth also has been found to reduce abundance of arthropod prey (Seastedt and Crossley, 1981; Shure and Phillips, 1991; Siira-Pietikainen et al., 2003). Initial burrows within PL removal treatments were not insulated from fluctuations in ambient climatic conditions, prompting individuals to attempt relocation more frequently during rainy nights. Exposure of the soil surface to rain further decreased available microhabitats by eroding burrow entrances, forcing individuals to maintain occupancy in suboptimal initial burrows. Reductions in microhabitat and arthropod density may have been responsible for the increased surface activity of individuals in PL removal enclosures. In contrast, *A. talpoideum* within control treatments were exposed to more suitable microenvironments, enabling them to spend less time on the surface where they were at risk of being consumed by predators.

During our study, snakes consumed two individuals. The first was depredated on 12 May 2003 by a southern hognose snake (*Heterodon simus*) and another on 1 August 2003 by an eastern garter snake (*Thamnophis sirtalis*). While neither depredation occurred in ES2 removal enclosures (both depredations occurred within plots of ES1), they illustrate the predation risk encountered during surface activity and while occupying burrows with an exposed entrance. Increased surface activity time also may subject individuals to desiccation (Semlitsch, 1983a). One individual in an ES2 removal plot was found exposed on the surface alive during daylight hours, and two were found dead more than 30 days after being put into enclosures from what appeared to be desiccation. Although PL removal treatments were mostly devoid of suitable habitat, *A. talpoideum* were able to exploit several microhabitats including plant root systems and shallow patches of pine litter that collected in small depressions.

Unlike conditions in ES2 PL removal treatments, ES1 enclosures containing pine litter and CWD appeared to have provided more suitable microhabitats for *A. talpoideum* to exploit. No differences were found among movement variables measured. Use of CWD compared to availability was greater for individuals in low PL treatments (Fig. 2). Individuals in low PL treatments were found under CWD 22.73% of days located, whereas those in high PL treatments occupied CWD only 2.15% of days located (Table 2). Increased pine litter depth in high PL treatments probably provided adequate moisture for individuals, reducing their need to utilize CWD as an alternative microhabitat. Inability of individuals in low PL treatments to find adequate moisture and temperature conditions under pine litter was probably mitigated through use of CWD.

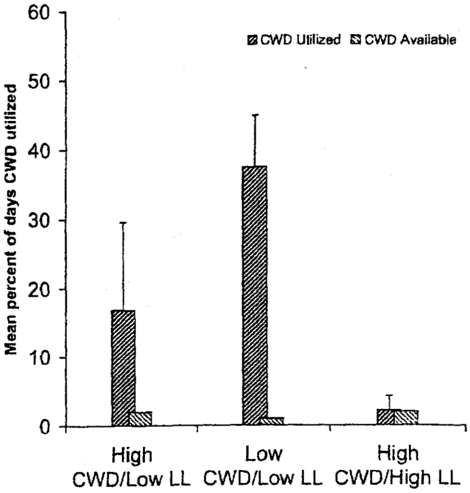

Fig. 2. Mean percent of days, with standard error, in which *A. talpoideum* were located under coarse woody debris within enclosures containing high CWD/low pine litter ($n = 618$ salamander days), low CWD/low PL ($n = 628$ salamander days), and high CWD/high PL ($n = 640$ salamander days) from 3 December 2002 to 1 August 2003.

Like pine litter, CWD buffers against extreme temperature fluctuations, retains moisture during dry periods (Boddy, 1983; Harmon et al., 1986) and contains abundant insect prey (Hanula, 1995). Coarse woody debris has been found to play an important role in the terrestrial ecology of plethodontid salamanders (Kleeberger and Werner, 1982; Aubrey et al., 1988; Bury and Corn, 1988; Dupuis et al., 1995; Maidens et al., 1998). However, CWD may be of less significance in the terrestrial ecology of ambystomatid salamanders, which prefer underground burrow systems (Williams, 1970; Semlitsch, 1983b; Douglas, 1981; Loredo et al., 1996; Madison, 1997; Madison and Farrand, 1998; Trenham, 2001) that are generally independent of CWD (Semlitsch, 1981). Locally, subterranean burrows created by small mammals such as moles (Talpidae) and *Peromyscus* spp., as well as preexisting cracks and crevices in the soil, can be exploited by *A. talpoideum* (Semlitsch, 1983a). However, if pine litter depth becomes inadequate in regulating burrow conditions from extreme climatic variation, individuals may seek refuge under CWD. At the Savannah River Site, Chazal and Niewiarowski (1998) compared juvenile *A. talpoideum* within enclosures in a 4-month-old clearcut to individuals maintained in an adjacent 40-year-old loblolly pine stand. Juveniles did not differ in abundance, body mass, snout-vent-length, clutch size, percent whole-body nonpolar storage lipid, or percent storage lipid of eggs after 5–6 months of exposure to enclosure conditions. Lack of difference between the two treatments was attributed partially to the large amounts of CWD in clearcut enclosures, which were believed to have ameliorated clearcut surface conditions by retaining on-site moisture.

In most natural situations where pine litter is sufficient, use of CWD by *A. talpoideum* probably is low. Following clearcutting and subsequent site preparation pine litter depth and cover is significantly reduced (Russell et al., 2002). During this stage, amount of residual CWD on-site may play a significant role in providing necessary microhabitat for *A. talpoideum*.

5. Conclusion

Availability of microhabitat is greatly influenced by silvicultural techniques used during harvesting and site preparation. Intensive mechanical treatments such as disking, harrowing and rollerchopping are frequently used in the southeastern Coastal Plain. The primary goal of these techniques is to reduce logging slash and competing vegetation, and expose mineral soil. Mechanical site preparation treatments likely produce the most harm by increasing bare ground cover, reducing forest floor depth, disturbing and compacting mineral soil, and eliminating much of the CWD left on-site following tree harvesting (Harmon et al., 1986; deMaynadier and Hunter, 1995; Russell et al., in press). Mechanical operations also mix organic material with mineral soil, accelerating decomposition (Salonius, 1983), and destroy underground burrows preferred by ambystomatid salamanders. Alteration of terrestrial habitat through intensive site preparation of a slash pine stand is believed to have been responsible for a 22 year decline in a breeding population of *A. cingulatum* within the disturbed stand (Means et al., 1996). Because *A. talpoideum* in our study were subject to pine litter and CWD manipulation within an intact 50-year-old slash pine stand, our results should be interpreted cautiously when applied to stand conditions produced by harvesting and site preparation. However, retaining some woody debris as refugia following site preparation (American Forest and Paper Association, 2002) may mitigate effects of inadequate pine litter depth and destruction of underground burrows.

Most CWD remaining after harvest and site preparation is generally lost through decay (Barber and Van Lear, 1984), prescribed fire and deficiency of new inputs by mid-rotation (Van Lear and Waldrop, 1994). However, loss of CWD at this period of stand development is probably not detrimental to ambystomatid salamanders, which favor use of underground burrows. Pine litter increases rapidly during the first 15-years following establishment of pine plantations due to the low decomposition rate of pine litter (Gholz et al., 1985). Once sufficient pine litter is available, *A. talpoideum* will become less dependent upon CWD for refugia. Increased pine litter facilitates recovery of soil structure (Switzer et al., 1979) and stabilizes microclimate in underground burrows. Therefore rapid recovery of pine litter depth ensures rapid restoration of preferred ambystomatid habitat.

Throughout the duration of stand development in much of the Southeast, land managers often employ practices that reduce forest floor material. Prescribed fire is frequently used to create wildlife habitat, reduce heavy fuel accumulation, expose mineral soil and control competing vegetation, insects and diseases (Hunter, 1990). Although prescribed burns reduce litter depth, they are generally not intense enough to remove all organic material on the forest floor. Organic matter in uneven-aged loblolly and shortleaf (*Pinus echinata*) pine stands in southeastern Arkansas was only 15% lower 1 year after a prescribed fire than in similar stands which had not been burned for 6-years or in unburned control stands (Cain et al., 1998). In the Atlantic Coastal Plain of Maryland, a 50-year-old stand dominated by loblolly pine and subject to eight prescribed burns in 13 years had a litter depth of 1.7 ± 0.8 cm, 46% deeper than litter depth in low PL enclosures of our study, whereas a similar unburned pine stand contained a depth of 4.9 ± 0.4 cm (McLeod and Gates, 1998). While prescribed fire reduces pine litter depth, remaining organic material should provide adequate buffering of the soil from climatic extremes and maintain integrity of underground burrows. However, reduction of pine litter through other removal practices, such as pine straw harvesting for horticultural and landscaping markets may have a negative impact on ambystomatid salamanders due to increased disturbance to the organic soil layer.

Demand for pine straw in natural landscaping is increasing (Morris et al., 1992). Harvesting of pine litter reduces litter depth and may increase soil bulk density (McLeod et al., 1979; Haywood et al., 1994); however, if removals are performed at 2–3 year intervals these effects should be negligible, leaving partially decomposed and fragmented needle litter intact. Although soil compaction may be a problem depending on techniques and equipment used, it is regarded as unlikely (Morris et al., 1992). Nonetheless, if removals are conducted too frequently, exposure of mineral soil may result (Morris et al., 1992), compelling resident *A. talpoideum*, or other ambystomatids, to move more frequently. Sustainable pine straw harvests should limit removal to 20% of pine litter (Duryea and Edwards, 2002), thereby leaving adequate litter depth and minimizing disturbance to underground burrows of *A. talpoideum*.

A. talpoideum are capable of exploiting a variety of refugia, responding to depletion of one microhabitat by utilizing another. Our study supports sustainable forestry initiative guidelines, which suggest leaving logging slash on-site following harvesting in order to provide refugia for salamander species (American Forest and Paper Association, 2002). Although our study demonstrated the ability of *A. talpoideum* to survive adverse conditions, immediate and long-term effects of frequent, mechanized habitat disturbance may have profound impacts on breeding populations of ambystomatid species. Quality of terrestrial habitat is important for maintaining viable amphibian populations (Semlitsch, 2000). Plantation forest management practices that minimize mechanical disturbance and retain adequate microhabitat throughout stand development will provide necessary habitat for resident fossorial salamander species.

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Northern Pine Snake

North Carolina Wildlife Profiles

Photo by Jeff Hall

Northern Pine Snake

(Pituophis melanoleucus melanoleucus)

The Northern pine snake is a large, non-venomous snake with a variety of common names, including bullsnake, black and white snake, pilot snake, horned snake, and white gopher snake. While there are three subspecies of pine snakes in North America, only one — the Northern pine snake — is found in North Carolina.

Description

Northern pine snakes are large, heavy-bodied snakes with a white, tan or yellowish background color and dark brown or black markings that begin as heavy mottling on the head and gradually become distinct blotches toward the tail. The belly is white or yellowish and may contain some light mottling of brown, orange or pink. They average about 4 to 5 feet in length; however, some specimens measure more than 6 feet in length.

History and Status

Northern pine snakes are a burrowing species, spending much of their life underground and, therefore, are seldom seen. Despite this secretiveness, Northern pine snakes are thought to be declining throughout much of their range. In North Carolina, the pine snake is state listed as a Threatened species and is identified in the N.C. Wildlife Action Plan as a Species of Greatest Conservation Need. As a state-listed species, pine snakes are protected in North Carolina and cannot be collected or taken from the wild without a special permit issued by the Wildlife Commission's Executive Director.

For more information on this species, visit ncwildlife.org/pinesnake.

Habitats & Habits

In North Carolina, pine snakes are found mostly in the Sandhills and southern Coastal Plain. A few specimens have been found in the southern mountains, specifically in Cherokee and Swain counties. In Swain County, one was spotted swimming in Fontana Lake.

Pine snakes prefer open areas within pine-oak forests with well-drained and sandy soils. In the Coastal Plain, they are found within the longleaf pine ecosystem. While they typically dig their own burrows, they also will use mammal burrows and tree root cavities or stumps.

Because pine snakes spend the majority of their time underground, they are seldom seen, even in areas where they are known to occur. If they are observed, it is usually during the day in the spring and early summer, as they go from burrow to burrow looking for rodents and other small mammals to eat. They also will eat birds and bird eggs. If disturbed or provoked, pine snakes will hiss loudly, vibrate their

Pine snakes are seldom seen because of their burrowing tendencies.

The Wildlife Commission Needs Your Help!

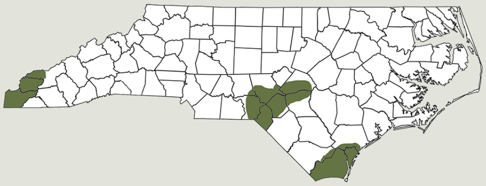
If you see a pine snake in the wild, Wildlife Commission biologists want to know. Email pinesnake@ncwildlife.org with the following:

- A photo (if possible)
- Date and time the snake was observed
- The location (GPS coordinates are best, but a detailed location description is acceptable)

Range and Distribution

The Northern pine snake's range includes New Jersey, West Virginia, Virginia, Kentucky, Tennessee, North Carolina, South Carolina, Georgia, and Alabama. In North Carolina, it is found mainly in the Sandhills and Coastal Plain, and potentially in a few locations in Cherokee and Swain counties.

Range Map



● Northern Pine Snake Range

tails and may bite. Predators include raptors and mammals, such as shrews, raccoons, foxes, skunks, coyotes, dogs, and cats.

Pine snakes are oviparous, meaning they lay eggs. Eggs from this species are larger than any other North Carolina species, and are among the largest of any North American species, at up to over 3 inches long and 1.5 inches wide. Mating occurs in the spring with females laying 5 to 12 eggs in early summer, usually in sandy, open areas. The female will excavate her own nest burrow — a task that can take hours or days to accomplish. Often, females will share the nesting burrow with other females and may use the same burrow for multiple years. Eggs hatch in about 50 to 100 days and hatchlings are about 17 inches long. There is no parental care once the young hatch.

NCWRC/Human Interactions

Pine snakes have a home range that can be as large as 100 acres. Because of this expansive home range, pine snake populations have plummeted in recent years, due to roads and habitat loss from development. In North Carolina, the pine snake is listed as a Threatened species and identified in the N.C. Wildlife Action Plan as a Species of Greatest Conservation Need.

In the southern mountains, where pine snakes are extremely rare, Commission biologists, working with the Eastern Band of Cherokee Indians, have been conducting surveys for pine snakes and their habitat. In areas where pine snakes have been seen recently or in areas with potentially suitable habitat, they have constructed drift fences, which are long, continuous barriers to interrupt movement by the snakes, and set them with trail cameras in hopes of documenting a snake.


Drift fence used to trap pine snakes in the southern mountains

In the Sandhills and the Coastal Plain, Commission biologists, along with biologists from the North Carolina State Museum of Natural Sciences (NCSM), have been monitoring pine snake populations. This monitoring has included walking areas searching for snakes, driving roads hoping to encounter them, and marking animals for potential recapture. Staff from the NCSM have also tracked numerous individual snakes using radio-telemetry over the past decade in partnership with the Commission to help understand management needs and determine conservation actions that might benefit the species.

Sources:
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Peterson Field Guide to Reptiles and Amphibians of Eastern and Central North America, 4th Ed. by R. Powell, R. Conant, and J. T. Collins, 2016
Longevity of reptiles and amphibians in North American collections, 2nd Ed. S.S.A.R. Herpetol. Circ. (21): 40 pp.

Wild Facts

Classification
Class: Reptilia
Order: Squamata

Average Size
Length: 52 inches although can grow as large as 7 ½ feet

Food
Small- to medium-sized mammals; birds and bird eggs.

Breeding/Young
Females lay a single clutch of 5 to 12 leathery, large eggs in spring to early summer. Eggs are laid in a burrow that the female has excavated herself. Eggs hatch in about 50 to 100 days with no parental care. Hatchlings are about 17 inches in length and look similar to the adult.

Life Expectancy
Relatively long-lived, pine snakes are known to live 10-15 years in the wild. In captivity, the record is over 20 years.


Pine snake hatchlings (Photo: Jeff Hall)

Credits
Written by Sam McCoy, Jeff Hall, North Carolina Wildlife Resources Commission. August 2019

Recovery Plan

Noonday Snail
(*Mesodon clarki nantahala*)

RECOVERY PLAN
FOR THE
NOONDAY SNAIL
MESODON CLARKI NANTAHALA

PREPARED BY
AMY SHRADER VAN DEVENDER

FOR
U.S. FISH AND WILDLIFE SERVICE
SOUTHEAST REGION, ATLANTA, GEORGIA

APPROVED: ______________________________
Acting Regional Director, Southeast Region

DATE: September 7, 1984

DISCLAIMER

This is the completed Noonday Snail Recovery Plan. It has been approved by the U.S. Fish and Wildlife Service. It does not necessarily represent official positions or approvals of cooperating agencies who played a role in preparing this plan. This plan is subject to modification as dictated by new findings, changes in species status, and completion of tasks described in the plan. Goals and objectives will be attained and funds expended contingent upon appropriations, priorities, and other constraints.

Additional copies are for sale from:

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1776 E. Jefferson Street
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Rockville, Maryland 20852

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1-800-582-3421

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PART I - INTRODUCTION

The noonday snail, *Mesodon clarki nantahala*, was described by Clench and Banks in 1932 from the cliff ridges of the Blowing Springs area in the Nantahala Gorge, Swain County, North Carolina. This area lies mostly within the Nantahala National Forest. The snail was listed as threatened in the July 3, 1978 *Federal Register* because of a proposal to widen U.S. Route 19 through the Nantahala Gorge. This would have damaged or destroyed most of the species' known habitat.

Clench and Banks (1932a) named this taxon *Polygyra* (*Triodopsis*) *nantahala* and mentioned that it occurs in the subgeneric group that includes *Polygyra elevata* Say, *P. clarki* Lea, and *P. pennsylvanica* Green. Pilsbry (1940), in his monograph on United States land snails, placed this taxon as a subspecies of *Mesodon clarki*. Neither Clench and Banks nor Pilsbry gave anatomical drawings or descriptions to substantiate their taxonomic conclusions. Hubricht (1980) believes the taxonomic status of *M. c. nantahala* to be somewhat uncertain. Essentially nothing is known of the snail's biology.

Description: *Mesodon clarki nantahala* (Figure 1a, b, c) has a subglobose, imperforate shell of about 5 1/2 whorls. It measures 17 to 18 mm in width and because of its depressed spire is only 11 mm in height. The shell is reddish and can be quite shiny when fresh. The lip of the aperture is sharply reflected and the peristome is white. The peristome of the basal area of the aperture is thickened to form an almost blade-like tooth. The

Figure 1 - Shell Morphology of Similar Mesodons

(a) _Mesodon clarki nantahala_, lateral view

(b) ventral view

(c) dorsal view

(d) _Mesodon clarki clarki_, lateral view

(e) ventral view

(f) dorsal view

(g) _Mesodon wheatleyi_, lateral view

(h) ventral view

(i) dorsal view

Note: Scale at side represents millimeters.

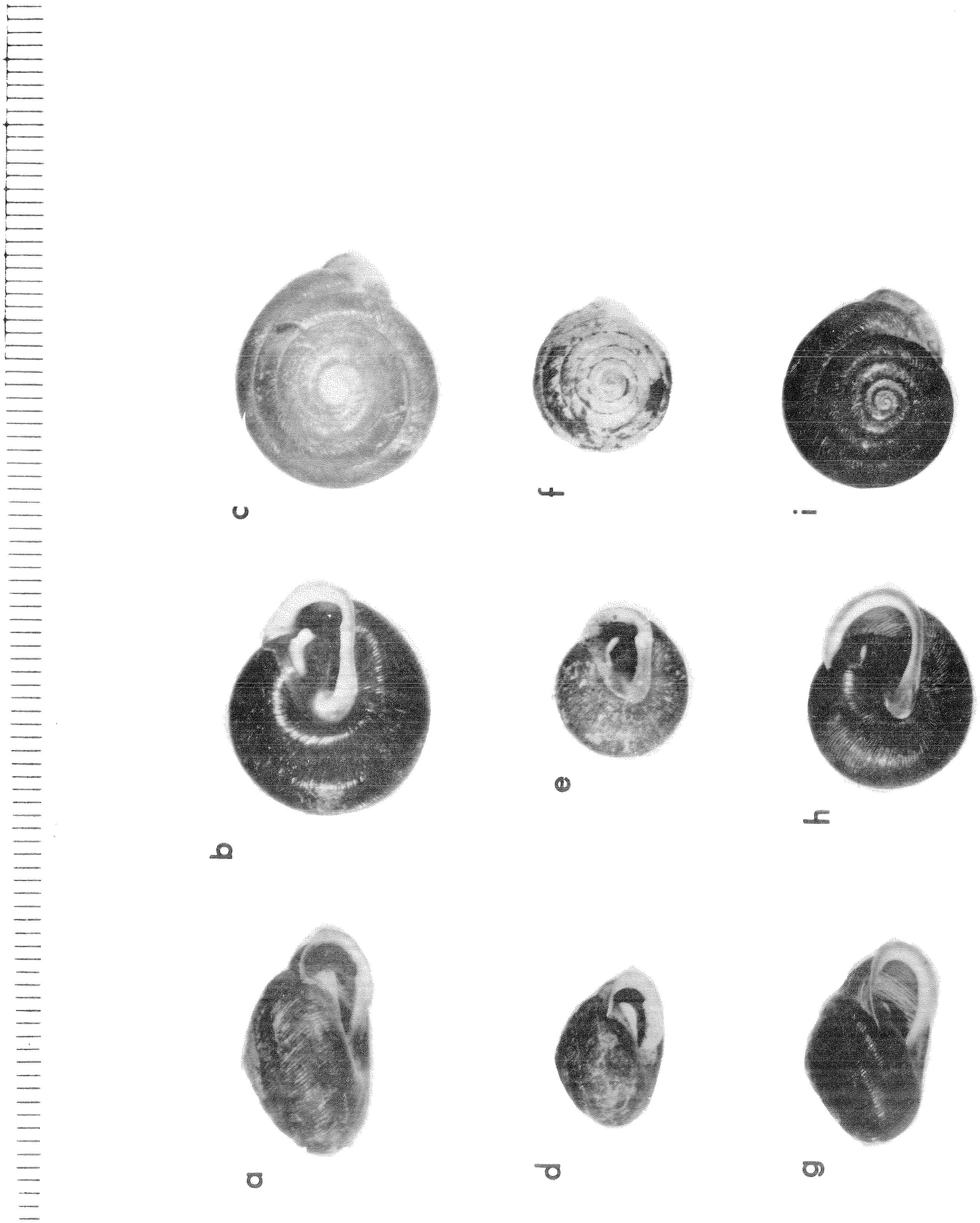
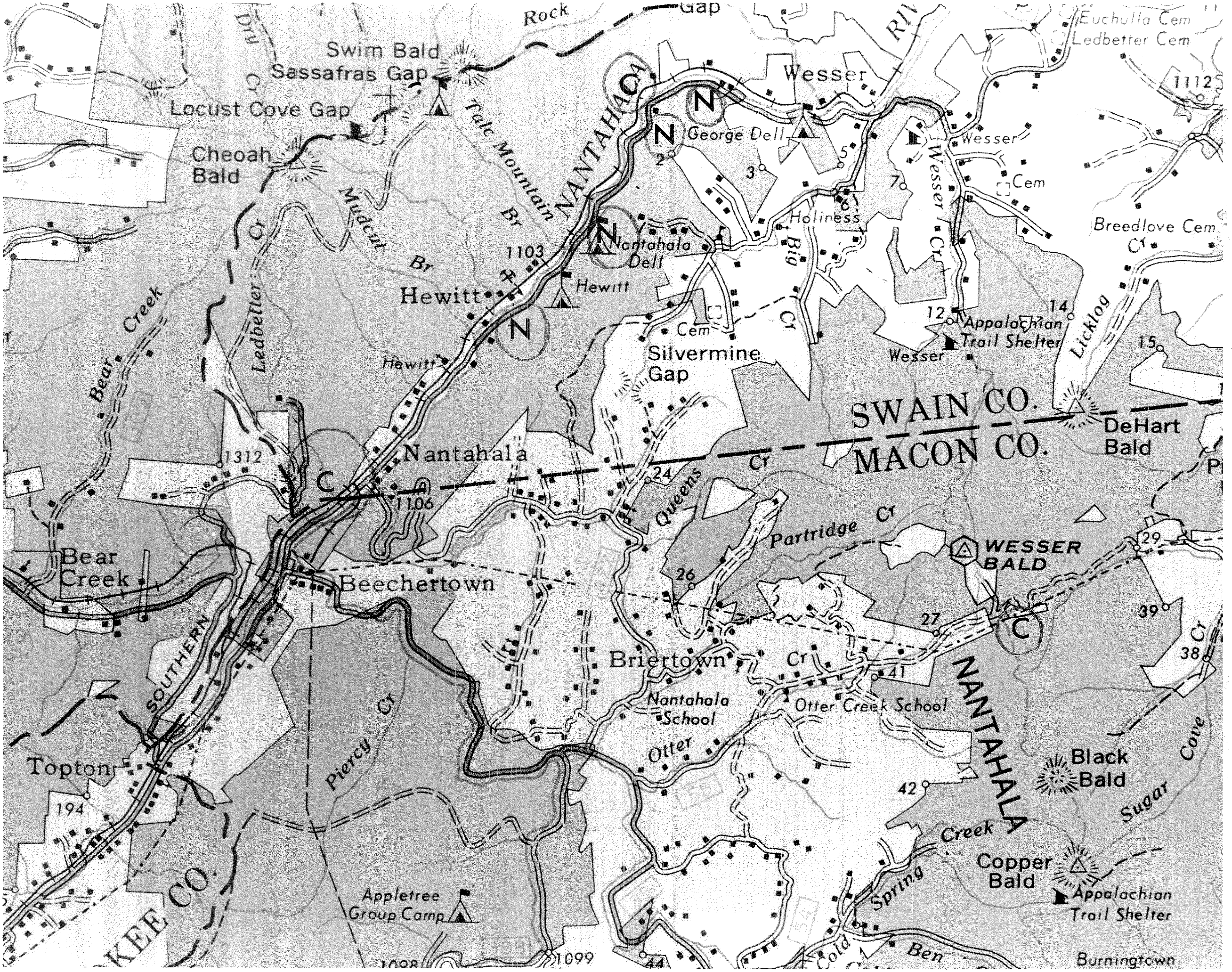


Figure 1

southeastern Tennessee, the extreme western counties of North Carolina and a few sites in northern Georgia. It is generally distributed in this area but is rather uncommon. *Mesodon clarki nantahala* is known from a much more limited area, having been reported only from the high cliffs (rising from 1,900 to 3,100 feet in only one-half mile) along the southeast bank of the Nantahala River in the Nantahala Gorge. It occurs for about a mile up and a mile down river from the type locality of Blowing Springs. The cliffs are very mesic, interrupted frequently by small streams and waterfalls. There is much exposed rock and the forest floor often has a thick humus layer. During an on-site inspection in the spring of 1983, the area around Blowing Springs was checked for living snails (author). Searches, which began in the vegetation at the very edge of the road and continued for a few hundred feet up the cliff, were attempted where stream cuts gave access to steep areas. The noonday snail was found at all stations, but the distribution was spotty and clumped. Searches were also done on the northwest side of the gorge especially at Handpole Branch, a site mentioned in the Federal listing. No specimens of *M. c. nantahala* were found on that side of the river, but typical (though quite small) *Mesodon c. clarki* specimens were found in several places.

Habitat: *Mesodon clarki nantahala* has only been reported from specific areas of the Nantahala Gorge. The gorge lies at the southern end of the Appalachian Mountains where the Nantahala River cuts between Cheoah Bald and Wesser Bald in the Nantahala Mountains (Figure 2). The Southern Appalachians are very old and are deeply dissected by the Little Tennessee

Figure 2 - Map of Blowing Springs area, Nantahala National Forest, North Carolina (1981). Compiled by U.S. Forest Service. Note that *Mesodon clarki clarki* (C) and *Mesodon clarki nantahala* (N) sites are indicated on the map.



Rock
Gap
Swim Bald
Sassafras Gap
Locust Cove Gap
Cheoah Bald
Dry Cr
Talc Mountain
NANTAHALA
Wesser
RIV
Euchulla Cem
Ledbetter Cem
1112
George Dell
Wesser
Cem
Breedlove Cem
Cr
Wesser Cr
Holiness
Big Cr
Nantahala Dell
1103
Hewitt
Hewitt
Hewitt
Mudcut Br
Br
Ledbetter Cr
381
Bear Creek
309
1312
Nantahala
1106
Silvermine Gap
Cem
12
14
15
Appalachian Trail Shelter
Wesser
Licklog
SWAIN CO.
MACON CO.
DeHart Bald
24
Cr
Queens
Partridge Cr
WESSER BALD
29
39
38
Cr
26
27
Bear Creek
Beechertown
422
Briertown
Cr
41
Otter Creek School
Nantahala School
Otter
NANTAHALA
SOUTHERN
Topton
194
Piercy Cr
55
42
Black Bald
Sugar
Cove
Creek
Spring
Copper Bald
Appalachian Trail Shelter
Appletree Group Camp
308
1098
1099
44
35
54
Cold
Ben
Burningtown
KEE CO.
29
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River and its tributaries, including the Nantahala River (Braun, 1967). In general, the region is dominated by oak-hickory forest; but in coves and other very mesic areas, the oak-hickory forest tends to be replaced by mixed mesophytic elements with rich herbaceous undergrowth. The cliff ridge with its steep north-facing slopes seems to be a very special example of this replacement. In a 1.5-acre area immediately around Blowing Springs (Morrow, 1983), the dominant trees include *Fagus grandifolia* (American beech), *Ulmus americana* (American elm). *Tilia heterophylla* (basswood), *Betula lutea* and *Betula lenta* (yellow and sweet birch), *Liriodendron tulipifera* (tulip poplar), *Aesculus octandra* (buckeye), *Carpinus caroliniana* (blue beech), and *Tsuga canadensis* (hemlock). *Acer saccharum* (sugar maple) and *Carya ovata* (shagbark hickory) were common seedlings. The herbaceous undergrowth includes many ferns (ten species) and such pronounced mesophytes as *Trillium*, *Uvularia*, *Disporum*, *Caulophyllum*, *Astilbe*, *Dicentra*, *Tiarella*, *Viola*, *Phacelia*, *Hydrophyllum*, *Asimina*, *Rubus odoratus*, and *Aristolochia*. (Some ericaceous elements such as *Rhodendron* and *Leucothoe* usually associated with oak-hickory forests are also present). Plants present that are considered rare in North Carolina (Roe and Moore, 1983) include *Cymophyllus fraseri* (Fraser's sedge), *Arabis patens* (spreading rockcress), *Panax trifolium* (dwarf ginseng), *Adlumia fungosa* (climbing fumatory), *Stellaria corei* (Core's starwort). Braun (1967) mentioned that this area is strikingly different from the immediately surrounding slopes and speculated that its outstanding richness (when compared to other very moist slopes nearby) is due to underlying "calcareous" rock as well as slope exposure.

Indeed near Blowing Springs is the only location on the steep eastern side of the gorge where there is an incursion of the Murphy marble geological formation. The Murphy marble (mined nearby at Talc Mountain to the south) forms a band of rock for miles along the western edge of the Nantahala River (Roe and Moore, 1983).

The habitat itself has undergone some change within the last 50 years with unknown results. The railroad and the road (U.S. 19) were put through the gorge, causing an increase in openness of the forest canopy and perhaps different water runoff patterns. The forest, once dominated by chestnut, is different in character due to the destruction of these trees by blight. Non-native plants such as Kudzu and honeysuckle are encroaching particularly along the roadsides.

Exposed rock that produces a rich soil, a complex association of plants, and moist conditions are the very elements that often contribute to a diverse snail community. Clench and Banks (1932b) reported 29 species of snails from the cliff ridges at Blowing Springs, including 5 species of *Mesodon*. Interestingly enough, specimens of *Mesodon clarki nantahala* and *Stenotrema stentotrema* (*f. voluminosa*) from Blowing Springs are the largest known examples for each species.

Population Numbers and Trends: No estimates of population size have been made since the exact range has never been determined. Apparently suitable habitat occurs for several miles along the gorge and far higher up the cliffs than has been surveyed. Live snails in several size classes were found, indicating recent recruitment. Mature individuals that had lived two or more winters were rarer than juveniles or newly mature adults.

Food and Foraging Behavior: Nothing is known about the snail's food preferences or feeding behavior. Other species of *Mesodon* are believed to eat fungal mycelia (Pilsbry, 1940). The snails seem to be active during wet weather, as they were frequently out on the surface of the vegetation (rather than under the litter) during an on-site investigation in mid-April 1983 (author). The weather during that site visit was quite mild and rainy. No activity differences were noticed between day and night.

Shelter Requirements: *Mesodon c. nantahala* was found in tangles of vegetation or occasionally under rocks or in the leaf litter but never under fallen logs. The area where the noonday snail lives had deeper litter and was wetter and undoubtedly cooler than areas of southern exposure within the gorge.

Reproductive Behavior: Unknown.

Oviposition and Incubation Requirements: Unknown.

Predation and Other Natural Pressures: The snail's predators are not well known though shrews and other small mammals, feral hogs, certain beetles (lampyrid larvae), and some birds (e.g., wood thrushes) have been documented eating snails. Shells of *Mesodon clarki clarki* that had been cached and gnawed by rodents were found at Handpole Branch. There is one report of *Haplotrema concavum*, a very common and carnivorous land snail, eating a noonday snail (personal communication, R. W. Van Devender).

Reasons for Current Status: The snail is known at present only from a very limited habitat within the Nantahala Gorge. Human activity within the gorge has increased dramatically over the years as the Nantahala River has become a very popular canoeing and kayaking spot. This increase of activity enhances the threat of forest fire or trampling, which would damage the unusual habitat that the snails need.

PART II - RECOVERY

A. Recovery Objectives

The purpose of this recovery plan is to identify those actions that should be undertaken for the protection and recovery of *Mesodon clarki nantahala* to the point that it can be delisted. The immediate dangers are those threats to its limited and specialized habitat. Unless significant populations (dependent upon population size and condition) of *Mesodon clarki nantahala* are found outside the Nantahala Gorge, precluding the need for further protection of the species, delisting of the species may not be considered until the following conditions are met:

1. *M. c. nantahala* and its habitat are protected from human-related or foreseeable natural threats that would jeopardize the species' existence,

2. A population monitoring program is established and conducted for at least five years to establish distribution and baseline abundance for the species and that no downward trend is evident,

3. A means is established to assure that population monitoring will be conducted periodically after delisting, and

4. Collection of the species for scientific or other purposes is controlled or is proven not to threaten the species' continued existence.

B. Step-down Outline

1. Protect, evaluate, and manage the known populations of _Mesodon clarki nantahala_ within the Nantahala Gorge.

    1.1. Protect the snail's essential habitat on the northwest facing cliffs within the Nantahala Gorge by cooperative agreements with the U.S. Forest Service and State authorities, by designating at least some portion of this area as critical habitat or other feasible means.

        1.1.1. Aid to the U.S. Forest Service in caring for this unusual area.

        1.1.2. Continue to utilize existing legislation and regulations (Federal and State endangered species laws) to protect the species and its habitat.

    1.2. Assess and monitor population levels and habitat quality.

        1.2.1. Develop monitoring techniques.

        - 1.2.2. Implement monitoring program.

    - 1.3. Manage the snail's habitat if justified.

        - 1.3.1. Conduct preliminary evaluations as to the necessity for management.

        - 1.3.2. Study limiting factors and develop management techniques.

    - 1.4. Determine present and foreseeable threats to the species.

        - 1.4.1. Evaluate potential for overuse of area (especially at Blowing Springs).

        - 1.4.2. Assess other threats.

- 2. Cooperate with current studies on the status of the noonday snail.

    - 2.1. Contact research scientists such as those at the Invertebrate Section of the Chicago Field Museum of Natural History for results of taxonomic studies.

   2.2. Evaluate impact of findings on the current status of the taxon.

3. Determine if populations of Mesodon clarki nantahala exist outside the Nantahala Gorge.

   3.1. Contact major museums and recognized authorities for existence of additional material.

   3.2. Locate sites in the Southern Appalachians where similar habitats exist.

   3.3. Survey sites for populations of the noonday snail.

   3.4. Investigate status of any newly found population.

4. Reevaluate Recovery Plan if the noonday snail and its habitat are stable and protected or if other populations are found.

C. Narrative

1. Protect, evaluate, and manage the known populations of Mesodon clarki nantahala within the Nantahala gorge. Since the cliff ridges on the northwestern facing side of the Nantahala Gorge

contains the only known population of *M. c. nantahala*, it is essential to recovery that the snail population and its habitat be protected from disturbance. Forest fires, logging, the destruction of the cliff face for widening the road, the possible exploration for minerals (talc is mined close by), and the increased trampling of the area as human pressures increase are all potential hazards.

1.1. Protect the snail's essential habitat on the northwest facing cliffs within the Nantahala Gorge by cooperative agreements with the U.S. Forest Service and State authorities by designating at least some portion of this areas as critical habitat or other feasible means. This part of the project will probably need to be implemented by the Forest Service with help from the U.S. Fish and Wildlife Service. The North Carolina Natural Heritage Program is drafting a proposal to recommend that the Forest Service designate the area around Blowing Springs as a National Forest Special-Interest Biological Management Area. The State authorities also plan to place the site on the Registry of Natural Heritage Areas (Roe and Moore, 1983). Access to the area and protection may not be a major problem since all the currently known range lies in the Nantahala National Forest.

1.1.1. Aid the U.S. Forest Service in caring for this unusual area. The Natural Heritage Program is especially concerned that intensive visitation to the area be discouraged. Therefore, publicity about the site (even locational signs along the road) should be kept to a minimum. The Forest Service should be encouraged to continue to defer the area from timber harvest.

1.1.2. Continue to utilize existing legislation and regulations (Federal and State endangered species laws) to protect the species and its habitat. During implementation of this recovery plan the species can be protected by the full enforcement of existing laws and regulations (such as Section 7 of the Endangered Species Act).

1.2. Assess and monitor population levels and habitat quality. Techniques for population monitoring must be developed and baseline population data established if the status of the snail is to be adequately managed. The population in the present habitat is presumed to be healthy (it can be documented to have occurred in the same biological assemblage for more than 30 years). Establishment of a baseline will help pinpoint any population fluctuations.

1.2.1. Develop monitoring techniques. Initial work should concentrate on finding the distribution of the snail within the gorge and estimating population size. The cliff face has been explored only in a few selected sites (see map) and only to a height of 200 to 300 feet above the river. The cliffs in some places extend up another 1,500 feet. Knowledge of the distribution of noonday snails is incomplete, though the present implication is that a single population occurs in a continuous band along one side of the river. Systematic searches must be done further along the gorge for several miles in both directions from Blowing Springs, higher up the cliff face, and on the opposite side of the river. The snails should be censused. Mark-recapture studies need to be initiated during the first season if possible. Monthly samples are probably necessary at first with additional spot checks in unusual conditions to identify activity patterns. After four or five years of data collection, estimates can be made of the population's stability. All samples (usually this will only be shell material) should be marked as to the exact locality and altitude and held for identification.

1.2.2. Implement monitoring program. After baseline data have been established, it will be necessary to continue at least periodic monitoring to assure that the population and habitat remain within acceptable limits.

1.3. Manage the snail's habitat if justified. The need for management will depend on preliminary status results.

1.3.1. Conduct preliminary evaluations as to the necessity for management. The snail was found alive in reasonable numbers. There was no evidence that the present U.S. 19, the railroad, talc mining in the gorge, increased river traffic, or the encroachment of non-native plants (kudzu or Japanese honeysuckle) were causing the snail any present harm. Therefore, unless surveys and censusing turn up severe population depletions, perhaps the best management is to restrict access.

1.3.2. Study limiting factors and develop management techniques. Once sufficient data are available on the life history (reproduction, activity patterns, food and habitat requirements, predation, etc.) and population dynamics of the snail, an evaluation should be made on the possibility of applying management action. Recommendations should be prepared as needed.

1.4. Determine present and foreseeable threats to the taxon. The present threat is destruction of habitat, but other threats may become apparent to the investigator working in the area.

1.4.1. Evaluate potential for overuse of area (especially at Blowing Springs). The Blowing Springs itself is a gathering place where people stop to sample the fresh water. If the trampling by many people causes habitat destruction, the spring water should be made more accessible by piping the water to the roadside. Though the cliffs themselves are too steep for trails, access to them could be restricted by fencing.

1.4.2. Assess other threats. One possible danger is that the ownership (and control) of the habitat could pass out of Federal hands. Alternative land uses such as logging and mining should be investigated to determine the probability of these activities occurring in snail habitat. The effects of these activities on this unique habitat are unknown.

1. Cooperate with current studies on the status of the noonday snail. The taxonomic status of the noonday snail is uncertain and needs clarification.

    2.1. Contact research scientists such as those at the Invertebrate Section of the Chicago Field Museum of Natural History for results of taxonomic studies. Taxonomic work is currently being conducted at the Chicago Field Museum on all species of *Allongona*, *Triodopsis*, and *Mesodon* (the large polygyrids) using anatomy, electrophoretic data, and shell morphology. The preliminary data are conflicting. The results of comparing six separate populations according to Emberton (1984) of "*Mesodon clarki*" from Cocke County, Tennessee, to as far south as Tusquitee Bald, Macon County, North Carolina, implies that more than one taxon (species) is involved. The shell size follows a decreasing cline (larger to the north, smaller to the south) that is interrupted by huge shells of the noonday snail. The genetic differences between some of the populations is immense (Nei distances greater than 0.4--see Nei, 1972) with *M. c. nantahala* again quite different from nearby populations. The penial morphology is somewhat similar to species from Tellico Gap but quite unlike snails from Handpole Branch. None of this evidence is conclusive, but it seems that the noonday snail is not a subspecies of *Mesodon clarki* but a full species in itself. Also it is possible that the very small Mesodon clarki specimens from Handpole Branch represent another distinct species.

This interpretation differs greatly from Leslie Hubricht's (1980) viewpoint, which denies even subspecific status to the noonday snail. He believes he has found this to be a widespread ecological variant. To settle this problem, more field work and analysis is needed and more live M. c. nantahala will be needed for comparison.

2.2. Evaluate impact of findings on the current status of the taxon. Researchers at the Field Museum believe more variation exists in this population complex than was previously thought. The appropriateness of threatened status may need reevaluation if further systematic studies question the validity of the taxon, or if more variation exists, the new (and unnamed) taxa may need some form of protection.

3. Determine if populations of the noonday snail exist outside the Nantahala Gorge. Discovery of new populations would require reevaluation of recovery objectives and could lead to delisting in the near future. The evaluation of other potential habitat areas could be undertaken along with natural history studies of the noonday snail in the gorge.

3.1. Contact major museums and recognized authorities for existence of additional material. Contact with curators at the Philadelphia Academy of Natural Science, the National Museum of Natural History, the Chicago Field Museum of Natural History, and the University of Michigan turned up very few specimens--none from outside the gorge. Specimens reported from Tusquitee Bald from University of Michigan Museum of Zoology were misidentified. Leslie Hubricht (1980) believes the noonday snail to be an ecological variant not even worthy of subspecific status. He claims to have found it in at least 12 sites (unspecified) in North Carolina and Tennessee. Hubricht should be encouraged to make his specimens and data available for study.

3.2. Locate sites in the Southern Appalachians where similar habitats exist. Incursions of "calcareous" rock with available water that support a rich, mixed mesophytic forest may be indicators of potential habitat. Perhaps the Forest Service, U.S. Geological Survey, or trained naturalists (e.g., Steve Morrow who compiled a plant list for this study and lives in Topton near the gorge) would be of assistance in finding such "islands."

3.3. Survey sites for populations of the noonday snail. Likely areas in extreme western North Carolina, southeastern Tennessee, and northern Georgia should be searched for the noonday snail. The assistance of qualified taxonomists may be required to verify the identification of specimens. Series of dead shells should be collected and later compared with known material.

3.4. Investigate status of any newly found population. Data on population density and range will be required for any new areas prior to any consideration for delisting.

4. Reevaluate Recovery Plan if the noonday snail and its habitat are stable and protected or if other populations are found. The present actions assume that the snail is threatened because of threats to its restricted habitat. If new information leads to a different view of the snail's systematic or population status, the recovery objectives may require revision.

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KEY TO IMPLEMENTATION SCHEDULE COLUMNS 1 AND 4

General Category (Column 1):

Information Gathering - I or R (research)

1. Population status
2. Habitat status
3. Habitat requirements
4. Management techniques
5. Taxonomic studies
6. Demographic studies
7. Propagation
8. Migration
9. Predation
10. Competition
11. Disease
12. Environmental contaminant
13. Reintroduction
14. Other information

Acquisition - A

1. Lease
2. Easement
3. Management agreement
4. Exchange
5. Withdrawal
6. Fee title
7. Other

Other - O

1. Information and education
2. Law enforcement
3. Regulations
4. Administration

Management - M

1. Propagation
2. Reintroduction
3. Habitat maintenance and manipulation
4. Predator and competitor control
5. Depradation control
6. Disease control
7. Other management

Priority (Column 4):

1 - Those actions absolutely necessary to prevent extinction of the species.

2 - Those actions necessary to maintain the species' current population status.

3 - All other actions necessary to provide for full recovery of the species.

Noonday snail (Mesodon clarki nantahala) Part III Implementation Schedule

*1 General Category	Plan Task	Task Number	Priority	Task Duration	Responsible Agency *2			Estimated Fiscal Year Costs			Comments/Notes
					FWS						
					Region	Program	Other	FY 1	FY 2	FY 3	
M3,O1 O4	Work with the U.S. Forest Service in protecting the snail's habitat, within the Nantahala Gorge, from disturbance.	1.1.1	1	Continuous	4	SE	U.S. Forest Service (FS), North Carolina Resources Commission (NCWRC), and North Carolina Natural Heritage Program (NCNHP)	1,000	1,000	1,000	*1. See general categories for Implementation Schedules. *2. Other agencies' responsibility would be of a cooperative nature or projects funded under a contract or grant program. In some cases contracts could be let to universities or private enterprises.
O1-O4	Continue to utilize existing legislation and regulations to protect the species and habitat.	1.1.2	1	Continuous	4	SE	FS,NCWRC, and NCNHP	500	500	500	
R1	Develop monitoring techniques.	1.2.1	3	1 yr.	4	SE	FS, NCWRC, and NCNHP	---	4,000	---	
I1-I2	Implement monitoring program.	1.2.2	3	Continuous	4	SE	FS, NCWRC, and NCNHP	---	---	2,000	
R2	Evaluate necessity for management.	1.3.1	3	1 yr.	4	SE	FS, NCWRC, and NCNHP	---	2,000	---	
R4	Develop management techniques	1.3.2	3	1 yr.	4	SE	FS, NCWRC, and NCNHP	---	---	Unknown	
M3	Manage habitat if needed.	1.3	3	Unknown	4	SE	FS	---	---	Unknown	
I14, M7	Evaluate overuse of area (especially at Blowing Springs); develop necessary controls.	1.4.1	2	1 yr.	4	SE	FS, NCWRC, and NCNHP	---	1,000	---	
I2,I9 I11	Assess other threats.	1.4.2	2	1 yr.	4	SE	FS, NCNHP, and NCNHP	---	1,000	---	

Noonday snail (<u>Mesodon clarki nantahala</u>) Part III Implementation Schedule

General Category	Plan Task	Task Number	Priority	Task Duration	Responsible Agency			Estimated Fiscal Year Costs			Comments/Notes
					FWS						
					Region	Program	Other	FY 1	FY 2	FY 3	
R5	Investigate results of taxonomic studies and evaluate impact of findings on current status of taxon.	2.1 & 2.2	3	1 yr.	4	SE	FS, NCWRC, and NCNHP	---	1,000	---	
I1,I3. I6	Investigate existence of additional material.	3.1	3	1 yr.	4	SE	FS, NCWRC, and NCNHP	1,000	---	---	
I6	Determine potential habitat sites outside Nantahala Gorge.	3.2	3	1 yr.	4	SE	FS, NCWRC, and NCNHP	1,000	---	---	
I1-I2	Survey potential habitat.	3.3	3	2 yr.	4	SE	FS, NCWRC, and NCNHP	2,500	2,500	---	
I1	Evaluate any new populations.	3.4	3	Unknown	4	SE	FS, NCWRC,	---	2,500	2,500	
04	Reevaluate recovery objectives if the noonday snail and habitat are stable or if new populations are found.	4.	3	Continuous	4	SE	FS, NCWRC, and NCNHP	250	250	250	

IV. APPENDIX

List of Reviewers for the Noonday Snail Recovery Plan

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CALIFORNIA ENVIRONMENTAL PROTECTION AGENCY
OFFICE OF ENVIRONMENTAL HEALTH HAZARD ASSESSMENT

SAFE DRINKING WATER AND TOXIC ENFORCEMENT ACT OF 1986
(Proposition 65)

NOTICE TO INTERESTED PARTIES
JULY 7, 2017

CHEMICAL LISTED EFFECTIVE **JULY 7, 2017** AS KNOWN TO THE STATE OF CALIFORNIA TO CAUSE CANCER: GLYPHOSATE

On March 28, 2017**,** the Office of Environmental Health Hazard Assessment (OEHHA) posted a Notice on its website[1] that *glyphosate (CAS No. 1071-83-6)* would be added to the list of chemicals known to the state to cause cancer for purposes of Proposition 65[2] with a delayed effective date due to the pending case *Monsanto v OEHHA*.[3] Monsanto's challenge was unsuccessful in the trial court. Although the case has been appealed, no stay of the listing has been granted. Therefore, glyphosate is being added to the Proposition 65 list on July 7, 2017.

In summary, glyphosate is listed under Proposition 65 effective July 7, 2017 as known to the state to cause cancer, as follows:

Chemical	CAS No.	Endpoint	Listing Mechanism*
Glyphosate**	1071-83-6	Cancer	LC

*Listing mechanism: LC – "Labor Code" mechanism (Health and Safety Code section 25249.8(a) and Title 27 Cal. Code of Regs. section 25904)

** The International Agency for Research on Cancer (IARC) indicates the following chemicals are "also relevant: 38641-94-0 (glyphosate-isopropylamine salt) 40465-66-5 (monoammonium salt) 69254-40-6 (diammonium salt) 34494-03-6 (glyphosate-sodium) 81591-81-3 (glyphosate-trimesium)" (IARC, 2015b), because these salts dissociate to free glyphosate.

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[1] The Notice was published in the California Notice Register on April 7, 2017.

[2] The Safe Drinking Water and Toxic Enforcement Act of 1986, Health and Safety Code section 25249.5 et seq.

[3] *Monsanto et al v OEHHA et al*., Fifth District Court of Appeal, case number F075362.

Effects of Timber Harvesting on Southern Appalachian Salamanders

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Abstract: *We compared the species richness and abundance of salamanders on six recent clearcuts (<10 years old) with that of salamanders on 34 mature forest stands (>50 years old) in southern Appalachian forests in western North Carolina, U.S.A. Catches of salamanders from plots in mature forest stands were about five times higher than those on recent clearcuts. Almost all species and major taxonomic groups of salamanders were adversely affected by timber removal. Mean number of species collected per plot was about twice as great in mature forest stands as in clearcuts. Analyses of stand age versus salamander catch for 47 plots indicate that 50–70 years are required for populations to return to predisturbance levels following cutting. We conservatively estimate that clearcutting in U.S. national forests in western North Carolina results in a loss of nearly 14 million salamanders annually. It also is chronically reducing regional populations by more than a quarter of a billion salamanders (9%) below that which could be sustained if mature forests were not cut.*

Efectos de la tala del bosque sobre las salamandras en el sur de los Apalaches

Resumen: *Nosotros comparamos la riqueza de especies y abundancia de las salamandras en seis recientes cortas totales de bosque (<10 años) con la de rodales maduros (>50 años) en los bosques del sur de los Apalaches, en el oeste de Carolina del Norte, Estados Unidos. La captura de salamandras por plot en bosques de rodales maduros fue aproximádamente cinco veces mayor que en aquellos cortados reciéntemente. Casi todas las especies y los mayores grupos taxonómicos de salamandras fueron adversamente afectados por la tala. La media del número de especies capturada por plot fue aproximádamente dos veces mayor en los rodales de bosques maduros que en los cortados reciéntemente. Los análisis de edad del rodal versus captura de salamandras para 47 plots indican que entre 50-70 años son necesarios para que las poblaciones retornen a los niveles previos a la perturbación ocasionada por la tala del bosque.*

Nosotros estimamos en una forma conservadora que la tala de los Bosques Nacionales en el oeste de Carolina del Norte trae como consecuencia una pérdida de alrededor de 14 millones de salamandras anualmente. La tala también está reduciendo crónicamente las poblaciones a nivel regional en más de un cuarto de billones de salamandras (9%) por debajo del nivel que podría ser sostenido por los bosques maduros si no hubieran sido cortados.

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Introduction

Salamanders are important ecological components of many forest ecosystems in North America. In mesic forests in the eastern U.S., salamanders are often the most abundant group of vertebrates in both numbers and biomass (Burton & Likens 1975*a*, 1975*b*; Hairston 1987). Salamanders also play important roles in food webs, where they prey upon small invertebrates and serve as a food source for an array of larger predators (Pough et al. 1987; Corn & Bury 1989).

Despite their importance in many forest systems, salamanders have often been neglected in forest management studies (Bury et al. 1980; Pough et al. 1987). Studies in the Pacific Northwest indicate that many salamander species are adversely affected by timber harvesting (see Bury & Corn 1988; Raphael 1988; Welsch & Lind 1988; Corn & Bury 1989; Welsh 1990). Relatively few studies have been conducted in the eastern United States (Bennett et al. 1980; Enge & Marion 1986; Blymer & McGinnes 1977; Pough et al. 1987; Ash 1988; Buhlmann et al. 1988), and most are difficult to interpret because of lack of replication or pseudoreplication (Hurlbert 1984). Nonetheless, these studies collectively suggest that timber harvesting is detrimental to salamanders in eastern forests.

The southern Appalachians have an extraordinarily rich and and abundant salamander fauna that in many respects is unparalleled worldwide. As many as 35 species belonging to five families occur in the Appalachian region of North Carolina alone (Conant & Collins 1991). In addition, the local biomass of salamanders in southern Appalachian forest communities often exceeds that of all other vertebrate predators combined (Hairston 1987). Prior to the 1960s, timber harvesting often involved intense selective cutting in which all but a few large trees were removed from timbered tracts. Since the 1960s, clearcutting has almost completely replaced selective cutting as the preferred method of timber harvesting by the U.S. Forest Service in the southern Appalachians. Although most clearcuts are relatively small (typically <10–12 ha), they are often cut in larger blocks that are separated by narrow belts of uncut forest.

Almost no published data are available on the impact of clearcutting on southern Appalachian salamanders other than that of Ash (1988), who found that cutting completely eliminated a local population of *Plethodon jordani*. Here, we report on the effects of clearcutting on salamanders in western North Carolina. We also provide data on the recovery times of local populations following timber removal, and on the regional impact of timber removal on salamander abundance.

Methods

Salamanders were sampled between May 16 and August 8, 1991, from 47 sample plots in and adjoining the Craggy Mountains, Pisgah National Forest, Buncombe County, North Carolina (Fig. 1). The work was part of a collaborative effort to document and monitor long-term changes in biodiversity in the southern Appalachians. The study area is located about 25 km northeast of Asheville and encompasses about 6000 ha of mostly mixed mesophytic deciduous forests (Fig. 1). Forty-one sample sites were selected from equidistant points established by randomly placing a grid on a topographic map of the study area. These stands were selected to provide an unbiased estimate of the relative abundance and diversity of salamanders in different communities within the Craggy Mountains. The stands varied in age from 19 to 120 years and ranged in elevation from 817 to 1667 m. Six clearcuts between 2 and 10 years old were also sampled to determine the effects of timber harvesting on species abundance and diversity (Fig. 1). These ranged in elevation from 969 to 1280 m.

At all sites, a 50 × 50 m plot was established parallel and perpendicular to prevailing contours. Plots were centered on permanent plot markers, and each was sampled once by walking roughly parallel transects and turning all movable rocks, logs, bark, and other surface objects that could provide cover for salamanders. Cracks and crevices in rock outcrops were inspected for crevice-dwelling salamanders, and unsubmerged stones and logs in streams or seepages were turned and searched. Search time varied from 1.33 to 4 people-

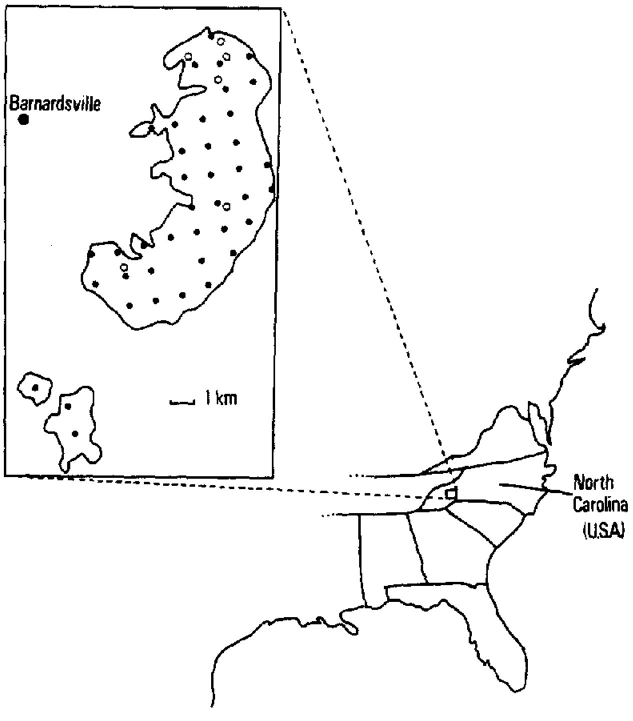

Figure 1. Location of the general study area in western North Carolina. Closed circles indicate the location of plots along grid coordinates. Open circles indicate the location of clearcuts.

hours/plot (mean = 2.38 people hours/plot). Conditions for collecting salamanders were ideal throughout the entire sampling period because of normal to above normal monthly precipitation during the summer of 1991. Specimens were identified to species except in a few instances where large *Desmognathus* specimens could not be captured. Plots in clearcuts were selected haphazardly and were located a minimum of 20 m from adjoining uncut forests. Sampling of clearcuts was staggered throughout the summer to prevent potential bias associated with seasonal changes in the surface activity of certain species.

Ages of forest stands were estimated from U.S. Forest Service CISC (Continuous Inventory of Stand Condition) data, which estimate stand age based on the age of canopy dominants. At four sites CISC data were lacking, and increment borings of the 2–6 largest trees in each stand were used to estimate stand age as a factor.

The effects of clearcutting on salamander populations were analyzed by comparing six clearcut sites less than 10 years old with 34 forest stands more than 50 years old. Stands more than 50 years old were selected for comparison because populations of most species appear to require a minimum of 50 years after mature stands are cut to return to predisturbance levels (see results). Analyses were restricted to the five most abundant species and to major taxonomic groupings. The remaining species were encountered so infrequently that meaningful statistical analyses were not possible.

An analysis of salamander catch as a function of plot age was conducted to provide a first-order approximation of the time required for populations to return to predisturbance levels following the harvesting of mature stands. Plots were grouped into six age categories (<10 years, 11–30 years, 31–50 years, 51–70 years, 71–90 years, >90 years) to allow sufficient sample sizes for detecting overall trends. Regression analysis using data from all 47 plots was used to determine whether salamander catch was dependent on stand age.

Because of the absence or rarity of certain species on clearcut plots, the assumptions of normality and homogeneity of variances were violated in some cases and could not be corrected by data transformations. The assumption of identical distributions for nonparametric rank tests such as the Mann-Whitney test was also clearly violated (see Petranka 1988). Since neither the assumptions of parametric nor of nonparametric tests were met in some instances, we elected to compare group means with the t-test for unequal variances whenever variances among groups differed significantly. All other comparisons were with standard t-tests.

Results

Effects of Stream Presence and Clearcutting on Salamander Abundance and Diversity

A total of 12 species of salamanders ($n = 828$ animals) was collected on the 47 sample plots (Table 1). Total number of salamanders collected per plot varied from 3 to 49 and averaged 17.6 ± 1.8 (±1 *SE*). Total number of species per plot varied from 1 to 7 and averaged 3.6 ± 0.2.

In mature forests, plots with streams or large seepages (hereafter referred to as "wet sites") averaged 5.0 ± 0.5 species per plot, compared to 3.7 ± 0.2 species per plot on "dry sites" that lacked streams or seepages ($t = -2.59$, $p = 0.01$). The mean number of salamanders collected from wet sites was also significantly higher than that collected from dry sites (31.1 ± 3.48 versus 16.9 ± 1.89; $t = -3.18$, $p = 0.003$). The significantly higher number of species and individuals collected on wet sites is primarily due to the greater abundance of *Desmognathus* species on these plots. *Desmognathus ochrophaeus* averaged 19.7 ± 3.6 individuals/plot on wet sites, compared to 5.3 ± 1.0 individuals/plot on dry sites ($t = -5.17$, $p < 0.0001$). In contrast, *Plethodon jordani* was significantly more abundant on dry sites compared to wet sites (mean = 6.9 ± 1.3 versus 2.9 ± 0.9 animals/plot, $p = 0.01$). The other large *Plethodon*

Table 1. Number and frequency of occurrence of amphibians found on plots.

Taxon	*Common name*	*Number (% of total) collected*	*Frequency of occurrence in plots*
Plethodon jordani	Jordan's salamander	263 (32)	72%
Plethodon glutinosus	slimy salamander	61 (7)	57%
Plethodon yonahlossee	yonahlossee salamander	58 (7)	45%
Plethodon cinereus	red-backed salamander	14 (2)	17%
Desmognathus ochrophaeus	mountain dusky salamander	338 (41)	70%
Desmognathus quadramaculatus	black-bellied salamander	13 (2)	11%
Desmognathus monticola	Seal salamander	2 (<1)	2%
Demognathus wrighti	pigmy salamander	26 (3)	30%
Desmognathus spp.	dusky salamanders	13 (2)	4%
Eurycea wilderae	Blue Ridge two-lined salamander	29 (3)	34%
Gyrinophilus porphyriticus	Spring salamander	3 (<1)	4%
Notophthalmus viridescens	red-spotted newt	8 (1)	13%

species showed similar tendencies, although none of the comparisons was significant. Overall, number of *Plethodon* (*P. jordani, yonahlossee, glutinosus, cinereus*) collected from dry sites was nearly twice than of wet sites (mean = 10.3 versus 4.6 *Plethodon* per plot; $t = -5.16$, $p = 0.0002$). Because the proportion of sites that were wet differed substantially among clearcut and mature forest stands (33% for clearcuts versus 15% for mature stands), wet and dry sites were analyzed separately to prevent confounding of the effects of cutting with those of stream presence.

Overall, clearcuts contained significantly fewer salamanders than mature forest stands did (Fig. 2). Trends for wet sites were generally similar to those of dry sites, although small sample sizes ($n = 2$ clearcuts and 5 mature forest sites) reduced the power of many tests to the point where differences were not significant. Groups that did differ significantly were *P. jordani* ($p = 0.03$), *Eurycea wilderae* ($p = 0.005$), total number of *Plethodon* ($p > 0.001$), and total number of salamanders ($p = 0.01$). Clearcuts on wet sites also had significantly fewer species of amphibians than did mature forest sites on wet sites (respective means = 2.0 versus 4.6 species, $p = 0.007$).

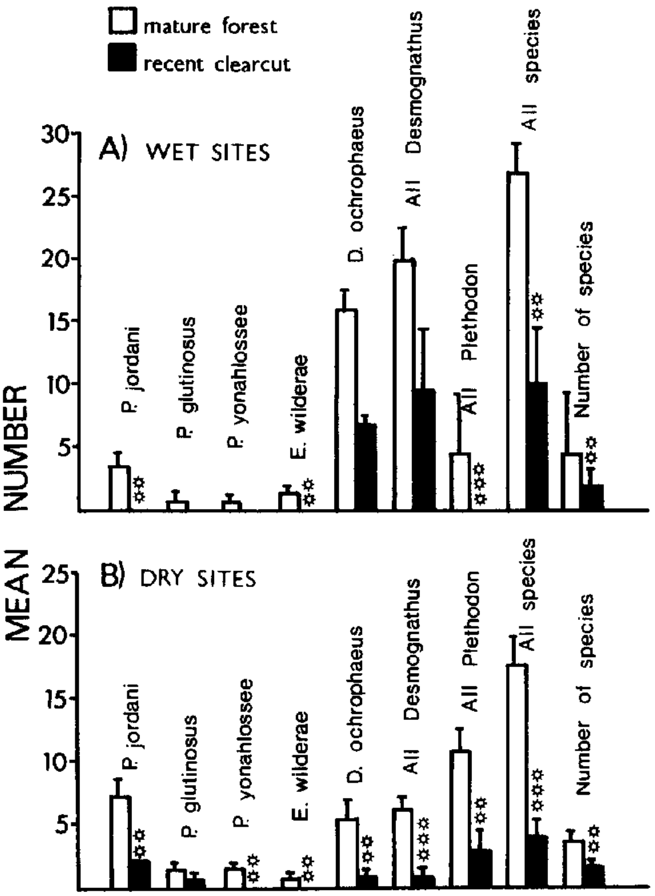

Figure 2. Numeric abundance and species richness of salamanders on recent clearcuts versus mature forest sites. Data on abundance are shown for the five most abundant species, all Desmognathus, *all* Plethodon, *and all species of salamanders combined. The bars on the far right are mean number of species collected per plot. Upper bars are* ±1 SE, *and asterisks indicate means that differ:* * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

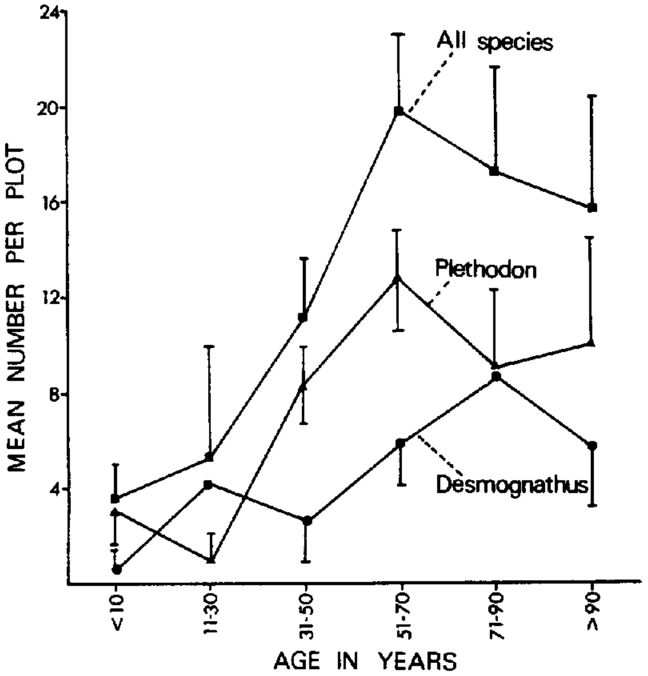

Figure 3. Relationship between stand age and salamander catch on dry sites. Trends are illustrated for total catch of all Desmognathus, *all* Plethodon, *and all species combined. Bars are* ±1 SE.

For dry sites, clearcuts contained significantly fewer *P. jordani* ($p = 0.02$), *P. yonahlossee* ($p = 0.006$), *Eurycea wilderae* ($p = 0.01$), and *D. ochrophaeus* ($p = 0.002$) than did mature stands (Fig. 2). These sites also differed significantly in the total number of *Plethodon* ($p = 0.003$), total number of *Desmognathus* ($p = 0.001$), and total number of all salamanders ($p < 0.0001$) found on plots. *Plethodon glutinosus* was the only species tested that did not differ significantly ($p = 0.58$). Overall, densities of salamanders in mature stands were about five times higher than those on recent clearcuts. Total number of species found on clearcuts was also significantly lower ($p = 0.01$), with clearcuts averaging about half as many species of amphibians as mature forest sites (Fig. 2).

Estimates of Recovery Times for Disturbed Communities

General trends among age classes suggest that most salamander species require several decades to return to predisturbance levels (Fig. 3). Overall, total catch per plot increased with stand age for the first 70 years of regrowth ($p = 0.001$), with stand age explaining about 37% of the among-plot variation in total catch. For stands more than 70 years old, total catch of salamanders was independent of stand age ($p = 0.63$). Total number of *Desmognathus* ($p = 0.05$; $r^2 = 0.15$) and total number of *Plethodon* ($p = 0.0004$; $r^2 = 0.35$) captures also correlated significantly with age for stands less than 70 years old, but not for stands more than 70 years old ($p = 0.93$ for *Plethodon*; $p = 0.25$ for *Desmognathus*). Maximum catch per plot occurred in stands 51–70 years old, and was slightly less in older plots. General trends for total *Plethodon* caught and total *Desmognathus* caught were similar (Fig. 3) and suggest that salamander communities require about 50–70 years to recover to preharvest levels. This estimate may be conservative for clearcut sites because it is based on combined data for clearcut and selectively cut sites. Complete estimates of recovery rates on clearcut stands are not available because most clearcut sites are currently less than 30 years old.

Discussion

Impact of Clearcutting on Local Populations and Communities

We found that clearcutting strongly depletes local populations of salamanders and reduces local species richness. We estimate that about 75–80% of salamanders in mature stands are lost following timber harvesting by clearcutting. This estimate is conservative because it includes plots as old as 10 years that may have undergone partial recovery. Although the fate of salamanders on recent clearcuts is unclear, we assume that most died following timber removal and that few salamanders dispersed to surrounding forests.

Most southern Appalachian salamanders are sensitive to environmental disturbances that modify prevailing temperature, humidity, or soil moisture regimes because adults lack lungs and exchange gases almost entirely by cutaneous respiration. Because their skin must be kept moist to facilitate gas exchange, adults generally restrict their activity to moist forest-floor microhabitats and are active on the ground surface only at night when relative humidities are high. Adult plethodontid salamanders may rapidly dehydrate if microhabitats become too dry (see Duellman & Trueb 1986). Clearcutting degrades forest-floor microhabitats for salamanders by eliminating shading, reducing leaf litter, increasing soil-surface temperature, and reducing soil-surface moisture (Bury 1983; Ash 1988; Raphael 1988; Welsch 1990). Consequently, it is likely that most animals died from physiological stress following the removal of trees from sites. Increased sedimentation and general deterioration of stream quality may also have contributed to the decline of species with aquatic larval stages (Corn & Bury 1989).

Dispersal of plethodontid salamanders from plots following cutting is unlikely because adults have small home ranges and are strongly philopatric. Experimentally displaced *Plethodon* and *Desmognathus* species readily home back to their place of capture, and show no tendency to disperse away from home ranges when disturbed or handled (Duellman & Trueb 1986; Hairston 1987). Although certain plethodontids, such as *Desmognathus* and *Eurycea*, move seasonally to and from breeding sites, they are highly sedentary during most of the year.

Because we relied on surface counts to estimate relative population size, it is possible that the reduction in numbers that we observed on clearcuts does not reflect true population declines. One alternative explanation for the apparent decline in salamanders on clearcuts is that decreases in surface moisture following timber removal forced salamanders to move into subsurface retreats during the day. If this were the case, relatively few animals would be expected to be taken in daytime searches. However, studies by Ash (1988) based on nighttime searches of clearcut sites indicate that this is not the case. Ash (1988) intensively studied the effects of clearcutting on *P. jordani* on Rich Mountain South near Highlands, North Carolina, and noted a near complete elimination of this species the second summer after cutting. After the fourth summer, no salamanders were found on cut plots during nighttime searches. Changes associated with the decline of *P. jordani* included elimination of most shading during the first summer and a significant increase in the amount of bare soil. Our findings are consistent with those of Ash (1988) and others (Blymer & McGinnes 1977; Bury 1983; Enge & Marion 1986; Pough et al. 1987; Bury & Corn 1988; Corn & Bury 1989), which indicate that logging significantly reduces amphibian species abundance and diversity.

Impact of Clearcutting on Regional Populations

Because most individuals of forest-floor species such as *Plethodon jordani* and *Desmognathus ochrophaeus* are underground at any given time, daytime surface searches usually uncover only a small percentage of the existing population. Direct counts and mark-recapture studies show that many species in Appalachian forests occur at very high densities. Large *Plethodon* species like *P. jordani* and *P. glutinosus* typically have densities of 0.2–0.9 animals/m^2 of forest floor, while densities of *Desmognathus* species can be much higher on rock faces and near streams and seepages (Table 2). These estimates are conservative because they exclude larval stages of *Desmognathus* as well as young *Plethodon* that spend their first year or so after hatching underground (Hairston 1983).

Based on data provided in Table 2, we conservatively

Table 2. Estimated densities of salamander species based on mark-recapture or direct counts of populations in the Appalachian Mountains.

Species	*Location*	*Number/m²*	*Source*
P. jordani	southern Blue Ridge	0.18	Ash 1988
P. jordani	Great Smoky Mountains	0.26	Ash 1988
P. jordani	Balsam Mountains	0.33	Ash 1988
P. jordani	Great Smoky Mountains	0.86	Merchant 1972
P. jordani	Howards' Knob (Boone, N.C.)	0.50	Howard 1987
P. jordani	(average of all sites)	0.43	
P. glutinosus	Great Smoky Mountains	0.23	Merchant 1972
P. cinereus	Blackrock Mountain, Virginia	2.2	Jaeger 1980
D. ochrophaeus	Howards' Knob (Boone, N.C.)	2.05	Howard 1987
D. ochrophaeus	southern Blue Ridge	18–41*	Huheey & Brandon 1973
D. ochrophaeus	southern Blue Ridge	6–7*	Tilley 1980
D. ochrophaeus	Nantahala Mountains	0.70**	Hairston 1986

* *Rock-face populations whose densities are generally much higher than populations found on the forest floor.*
** *Estimate of forest-floor density based on repeated removals during a single night. Removal of 0.7 animals/m² did not significantly reduce the number of animals emerging from underground retreats, so the actually density was presumably far greater.*
All sites are in North Carolina except where noted.

estimate that *Plethodon* species collectively average 0.5 animals/m^2 of forest floor in southern Appalachian forests. In the Craggy Mountains, *Plethodon* species constituted only 48% of all salamanders collected (Table 1). Thus, a conservative estimate is that there is at least one salamander/m^2 of forest floor or about 10,000 salamanders/ha in mature forest stands in the Craggy Mountains. This value seems a reasonable first-order approximation of average densities of salamanders in the southern Appalachians as a whole, although in optimal habitats such as mesic cove forests or stream banks, local densities may be much higher. Howard (1987) estimated 22,608 salamanders/ha in mesic forests near Boone, North Carolina. However, densities of salamanders on dry ridgetops and low-elevation forests with sandy soils are presumably much lower.

Timber harvesting by clearcutting of national forests in western North Carolina has averaged 1,709 ha per year between 1981 and 1990 (personal communication from Ed Brown of the U.S. Forest Service). Assuming an 80% loss of resident animals following cutting and an average density of 10,000 salamanders/ha, we estimate that clearcutting on U.S. Forest Service lands in western North Carolina has eliminated an average of 13.7 million salamanders annually in recent years. Although the absolute number of animals being lost annually is substantial, it constitutes only about 0.34% of the estimated total number of salamanders found in national forests in western North Carolina. (This estimate is based on the percent of national forest holdings cut annually, after correcting for 20% survival in clearcuts).

Despite the fact that the annual loss of animals is less than 0.5%, significant reductions in regional populations could occur because of the long recovery period required for populations to return to predisturbance levels following timber harvesting. An estimate of the long-term effects of cutting on southern Appalachian populations can be obtained by using data on current stand age together with age-specific recovery rates derived from the regression of total salamander catch versus stand age. Using the regression model for stands less than 70 years old, we estimate that if forests continue to be cut at 1981–1990 rates, regional populations will be chronically reduced by about 8.5%, or 267 million animals below the numbers which could be sustained in mature forests. This estimate assumes that 80% of the salamanders are lost after removing timber, that 0.34% of the total salamanders on national forests are eliminated annually by cutting, and that populations fully recover in 50 years. This reduction percentage is similar to that which has occurred historically during the last 50 years, based on a current estimate that 16% of U.S. Forest Service lands in western North Carolina are less than 50 years old (data provided by E. Brown, U.S. Forest Service). Although these estimates are intended only as rough approximations, they provide a feel for the magnitude of losses related to timber harvesting.

Stiven and Bruce (1988) provided evidence that timber harvesting may influence the genetic diversity of local populations of black-bellied salamanders in the southern Appalachians. Our data suggest that the depletion of local populations of terrestrial species by clearcutting may be of sufficient magnitude to produce bottlenecks that would significantly alter genetic diversity. There are now conflicting theoretical views as to how population bottlenecks affect genetic diversity. Some have argued that bottlenecks should lower genetic diversity (Nei et al. 1975), while others have taken the opposite stance (Bryant et al. 1986; Goodnight 1987). Any resolution of the problem will require a more complete understanding of how patch dynamics, the scale of disturbance, and local population dynamics interact to influence regional genetic diversity.

We consider the chronic depletion of populations in national forests in western North Carolina by more than a quarter of a billion animals (9%) to be significant from a regional perspective, particularly when one considers that a significant portion of the eastern U.S. has been deforested since its colonization by Europeans. These losses seem to be sustainable in the sense that none of the species studied is in eminent danger of extinction. However, the chronic depletion of salamanders is clearly contributing to a decline in the general health of south Appalachian forest communities, particularly at the local level were salamander communities are severely perturbed during timber removal.

The estimated average reduction of 9% in numbers does not reflect the fact that the intensity of logging varies regionally. Timber removal tends to be concentrated in areas with moderate slopes that are outside of designated wilderness or recreation areas. Consequently, chronic reductions of salamander numbers in many regions far exceeds 9%. Whether alternative harvesting methods would reduce those losses is uncertain. Selective cutting would presumably have less impact on local salamander populations because the loss of shade and leaf litter following cutting would be reduced. In order to harvest a specific volume of timber, however, selective cutting requires that more acreage be cut than when clearcutting. Exactly how this tradeoff would ultimately affect salamander abundance remains to be determined.

Acknowledgments

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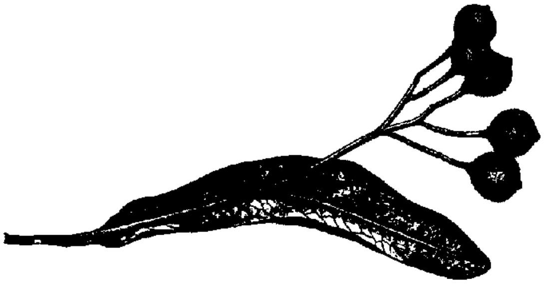


PROTECTED WILDLIFE SPECIES
OF NORTH CAROLINA

North Carolina Wildlife Resources Commission
ncwildlife.org
October 1, 2021

The species listed in this document have been recognized as needing additional conservation by the North Carolina Wildlife Resources Commission under the State Endangered Species Act (G.S. 113-331 to 113-337) and by the U.S. Fish and Wildlife Service, under the Federal Endangered Species Act (16 U.S.C. 1531 to 1543). The N.C. General Statute refers to this list as the Protected Animal List.

This publication was produced by the N.C. Wildlife Resources Commission for informational purposes only. It reflects the most current information available in the NCAC 10I.0100 Endangered and Threatened Species listings.

State-listed species are separated into three categories: North Carolina Endangered; North Carolina Threatened; and North Carolina Special Concern. State designations and their definitions are listed below:

North Carolina Endangered. Any native or once-native species of wild animal whose continued existence as a viable component of the State's fauna is determined by the Wildlife Resources Commission to be in jeopardy or any wild animal determined to be an "endangered species" pursuant to the Federal Endangered Species Act.

North Carolina Threatened. Any native or once-native species of wild animal that is likely to become an endangered species within the forseeable future throughout all or a significant portion of its range or one that is designated as a threatened species pursuant to the Federal Endangered Species Act.

North Carolina Special Concern. Any species of wild animal native or once native to North Carolina that is determined by the Wildlife Resources Commission to require monitoring but that may be taken under regulations adopted under the provisions of Article 25.

Following each species' state listing in this document are the species' federal listing, as designated by the U.S. Fish and Wildlife Service, (if applicable). Federal designations and their definitions are listed below.

Federal Listing Designation Definitions

FE - Federally Listed as Endangered. Any native or once native species of wild animal whose continued existence as a viable component of the state's fauna is determined by the U.S. Fish and Wildlife Service to be in jeopardy or any wild animal determined to be an "endangered animal" pursuant to the Endangered Species Act.

FT - Federally Listed as Threatened. Any native or once native species of wild animal that is likely to become an endangered species within the forseeable future throughout all, or significant portions of its range, or one that is designated "threatened" pursuant to the Endangered Species Act.

Learn more about federally listed species in North Carolina by visiting: fws.gov/raleigh/es_tes.html
Learn more about the U.S. Fish and Wildlife Service's Endangered Species Program by visiting: fws.gov/endangered/

NORTH CAROLINA ENDANGERED SPECIES

FE - Federally Listed as Endangered

Amphibians (4)

Gopher frog (*Rana* [=*Lithobates*] *capito*)
Hickory Nut Gorge green salamander (*Aneides caryaenis*)
Ornate chorus frog (*Pseudacris ornata*)
River frog (*Rana* [=*Lithobates*] *heckscheri*)

Hickory Nut Gorge green salamander (J.Apadoca)

Birds (8)

American peregrine falcon (*Falco peregrinus anatum*)
Bewick's wren (*Thryomanes bewickii*)
Common tern (*Sterna hirundo*)
Henslow's sparrow (*Centronyx henslowii)*
Piping plover (*Charadrius melodus circumcinctus*) FE
Red-cockaded woodpecker (*Dryobates borealis*) FE
Roseate tern (*Sterna dougallii dougallii*) FE
Wayne's black-throated green warbler (*Setophaga virens waynei*)

Piping plover & chick (Randy G. Lubischer)

Crustacea (2)

Bennett's Mill cave water slater (*Caecidotea carolinensis*)
Waccamaw crayfish (*Procambarus braswelli*)

Fish (12)

Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) -
when found in inland fishing waters FE
Blotchside logperch (*Percina burtoni*)
Bridle shiner (*Notropis bifrenatus*)
Cape Fear shiner (*Notropis mekistocholas*) FE
Orangefin madtom (*Noturus gilberti*)
Paddlefish (*Polyodon spathula*)
Roanoke logperch (*Percina rex*) FE
Robust redhorse (*Moxostoma robustum*)
Rustyside sucker (*Thoburnia hamiltoni*)
Sharpnose darter (*Percina oxyrhynchus*)
Shortnose sturgeon (*Acipenser brevirostrum*) -
when found in inland fishing waters as defined
in G.S. 113-129(9)a and (9)b FE
Stonecat (*Noturus flavus*)

Orangefin madtom (NCWRC)

NORTH CAROLINA ENDANGERED SPECIES

FE - Federally Listed as Endangered

Mammals (6)

- Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*) FE
- Eastern cougar (*Puma concolor*) FE
- Gray bat (*Myotis grisescens*) FE
- Indiana bat (*Myotis sodalis*) FE
- Manatee (*Trichechus manatus*) - when found in inland fishing waters FE
- Virginia big-eared bat (*Corynorhinus townsendii virginianus*) FE

Mollusks (24)

- Appalachian elktoe (*Alasmidonta raveneliana*) FE
- Barrel floater (*Utterbackiana couperiana*)
- Brook floater (*Alasmidonta varicosa*)
- Carolina creekshell (*Villosa vaughaniana*)
- Carolina heelsplitter (*Lasmigona decorata*) FE
- Dwarf wedgemussel (*Alasmidonta heterodon*) FE
- Fragile glyph (*Glyphyalinia clingmani*)
- Green floater (*Lasmigona subviridis*)
- Greenfield rams-horn (*Helisoma eucosmium*)
- James spinymussel (*Parvaspina collina*) FE
- Knotty elimia (*Elimia christyi*)
- Littlewing pearlymussel (*Pegias fabula*) FE
- Longsolid (*Fusconaia subrotunda*)
- Magnificent rams-horn (*Planorbella magnifica*)
- Purple wartyback (*Cyclonaias tuberculata*)
- Savannah lilliput (*Toxolasma pullus*)
- Slippershell mussel (*Alasmidonta viridis*)
- Tan riffleshell (*Epioblasma florentina walkeri*) FE
- Tar River spinymussel (*Parvaspina steinstansana*) FE
- Tennessee clubshell (*Pleurobema oviforme*)
- Tennessee heelsplitter (*Lasmigona holstonia*)
- Tennessee pigtoe (*Pleuronaia barnesiana*)
- Yellow lampmussel (*Lampsilis cariosa*)

Reptiles (6)

- Atlantic hawksbill seaturtle (*Eretmochelys imbricata imbricata*) FE
- Eastern coral snake (*Micrurus fulvius fulvius*)
- Eastern diamondback rattlesnake (*Crotalus adamanteus*)
- Kemp's ridley seaturtle (*Lepidochelys kempii*) FE
- Leatherback seaturtle (*Dermochelys coriacea*) FE
- Mimic glass lizard (*Ophisaurus mimicus*)


Gray bats (Katherine Etchison)

Tar River spinymussels (NCWRC)


Mimic glass lizard (Jeff Hall)


Eastern diamondback rattlesnake (Jeff Hall)

NORTH CAROLINA THREATENED SPECIES

FE - Federally Listed as Threatened

Amphibians (7)

Eastern tiger salamander (*Ambystoma tigrinum tigrinum*)
Green salamander (*Aneides aeneus*)
Junaluska salamander (*Eurycea junaluska*)
Long-tailed salamander (*Eurycea longicauda longicauda*)
Mabee's salamander (*Ambystoma mabeei*)
Pine Barrens treefrog (*Hyla andersonii*)
Wehrle's salamander (*Plethodon wehrlei*)

Birds (8)

Bald eagle (*Haliaeetus leucocephalus*)
Caspian tern (*Hydroprogne caspia*)
Eastern black rail (*Laterallus jamaicensis jamaicensis*) FT
Gull-billed tern (*Gelochelidon nilotica aranea*)
Northern saw-whet owl (*Aegolius acadicus*)
Piping plover (*Charadrius melodus melodus*) FT
Red knot (*Calidris canutus rufa*) FT
Wood stork (*Mycteria americana*) FT

Crustacea (5)

Broad River spiny crayfish (*Cambarus spicatus*)
French Broad crayfish (*Cambarus reburrus*)
Pamlico crayfish (*Procambarus medialis*)
Sandhills crayfish (*Procambarus pearsei*)
South Mountains crayfish (*Cambarus franklini*)

Fish (14)

Bigeye jumprock (*Moxostoma ariommum*)
Carolina madtom (*Noturus furiosus*)
Carolina pygmy sunfish (*Elassoma boehlkei*)
Carolina redhorse (*Moxostoma* sp.)
Least brook lamprey (*Lampetra aepyptera*)
Logperch (*Percina caprodes*)
Mimic shiner (*Notropis volucellus*)
Rosyface chub (*Hybopsis rubrifrons*)
Sharphead darter (*Etheostoma acuticeps*)
Sicklefin redhorse (*Moxostoma* sp.,)
Spotfin chub (*Erimonax monachus*) FT
Turquoise darter (*Etheostoma inscriptum*)
Waccamaw darter (*Etheostoma perlongum*)
Waccamaw silverside (*Menidia extensa*) FT

Pine Barrens treefrog (Jay Ondreicka)

Northern saw-whet owl (Shutterstock)

Red knot (Ray Hennessy)

Sicklefin redhorse (Ray Hennessy)

NORTH CAROLINA THREATENED SPECIES

FE - Federally Listed as Threatened

Mammals (4)

Eastern woodrat (*Neotoma floridana floridana*)
Northern long-eared bat (*Myotis septentrionalis*) FT
Rafinesque's big-eared bat (*Corynorhinus rafinesquii rafinesquii*)
Red wolf (*Canis rufus*)

Mollusks (18)

Alewife floater (*Utterbackiana implicata*)
Atlantic pigtoe (*Fusconaia masoni*) FT
Big-tooth covert (*Fumonelix jonesiana*)
Cape Fear threetooth (*Triodopsis soelneri*)
Creeper (*Strophitus undulatus*)
Eastern lampmussel (*Lampsilis radiata*)
Eastern pondmussel (*Ligumia nasuta*)
Engraved covert (*Fumonelix orestes*)
Mountain creekshell (*Villosa vanuxemensis*)
Noonday globe (*Patera clarki nantahala*) FT
Notched rainbow (*Villosa constricta*)
Rainbow (*Villosa iris*)
Roan supercoil (*Paravitrea varidens*)
Sculpted supercoil (*Paravitrea ternaria*)
Smoky Mountain covert (*Inflectarius ferrissi*)
Tidewater mucket (*Leptodea ochracea*)
Triangle floater (*Alasmidonta undulata*)
Waccamaw ambersnail (*Catinella waccamawensis*)
Yellow Lance (*Elliptio lanceolata*) FT

Reptiles (6)

Bog turtle (*Glyptemys muhlenbergii*) FT
American alligator (*Alligator mississipiensis*) FT
Green seaturtle (*Chelonia mydas*) FT
Loggerhead seaturtle (*Caretta caretta*) FT
Northern pine snake (*Pituophis melanoleucus melanoleucus*)
Southern hognose snake (*Heterodon simus*)

Northern long-eared bat (Dave Thomas)

Yellow lance (NCWRC)

Southern hognose snake (Jeff Hall)

Loggerhead seaturtle hatchling (Sarah Finn)

NORTH CAROLINA SPECIAL CONCERN SPECIES

Amphibians (13)

Crevice salamander (*Plethodon longicrus*)
Dwarf black-bellied salamander (*Desmognathus folkertsi*)
Dwarf salamander (*Eurycea quadridigitata*)
Eastern hellbender (*Cryptobranchus alleganiensis alleganiensis*)
Four-toed salamander (*Hemidactylium scutatum*)
Northern gray treefrog (*Hyla versicolor*)
Mole salamander (*Ambystoma talpoideum*)
Mountain chorus frog (*Pseudacris brachyphona*)
Mudpuppy (*Necturus maculosus*)
Neuse River waterdog (*Necturus lewisi*)
Southern chorus frog (*Pseudacris nigrita*)
Southern zigzag salamander (*Plethodon ventralis*)
Weller's salamander (*Plethodon welleri*)

Birds (19)

American oystercatcher (*Haematopus palliatus*)
Bachman's sparrow (*Peucaea aestivalis*)
Barn Owl (*Tyto alba*)
Black-capped chickadee (*Poecile atricapillus*)
Black skimmer (*Rynchops niger*)
Brown creeper (*Certhia americana nigrescens*)
Cerulean warbler (*Setophaga cerulea*)
Glossy ibis (*Plegadis falcinellus*)
Golden-winged warbler (*Vermivora chrysoptera*)
Least bittern (*Ixobrychus exilis*)
Least tern (*Sternula antillarum*)
Little blue heron (*Egretta caerulea*)
Loggerhead shrike (*Lanius ludovicianus*)
Painted bunting (*Passerina ciris*)
Red crossbill (*Loxia curvirostra*)
Snowy egret (*Egretta thula*)
Tricolored heron (*Egretta tricolor*)
Vesper sparrow (*Pooecetes gramineus*)
Wilson's plover (*Charadrius wilsonia*)


Eastern hellbender (Lori Williams)


Red crossbill (Wang LiQuiang)


Golden-winged warbler (Agami Photo Agency)

NORTH CAROLINA SPECIAL CONCERN SPECIES

Crustacea (9)

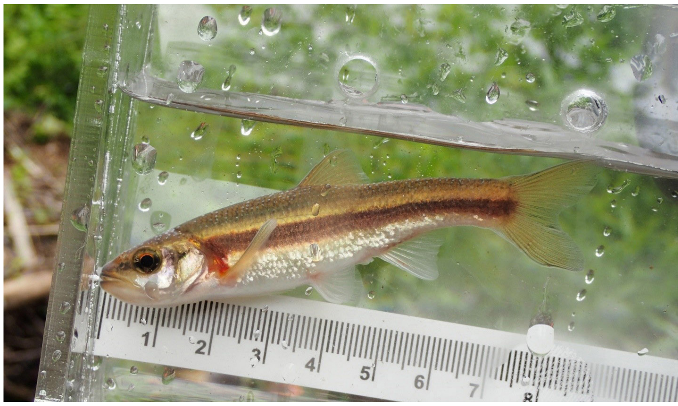
Carolina skistodiaptomus (*Skistodiaptomus carolinensis*)
Carolina well diacyclops (*Diacyclops jeannelli putei*)
Chowanoke crayfish (*Faxonius virginiensis*)
Graceful clam shrimp (*Lynceus gracilicornis*)
Greensboro burrowing crayfish (*Cambarus catagius*)
Hiwassee headwaters crayfish (*Cambarus parrishi*)
Little Tennessee River crayfish (*Cambarus georgiae*)
North Carolina spiny crayfish (*Faxonius carolinensis*)
Oconee stream crayfish (*Cambarus chaugaensis*)

Fish (28)

American brook lamprey (*Lethenteron* appendix)
“Atlantic” Highfin carpsucker (*Carpiodes* sp., c.f. velifer)
Banded sculpin (*Cottus carolinae*)
Blue Ridge sculpin (*Cottus caeruleomentum*)
Blueside darter (*Etheostoma jessiae*)
Broadtail madtom (*Noturus* sp.)
Carolina darter (*Etheostoma collis*)
Cutlip minnow (*Exoglossum maxillingua*)
Freshwater drum (*Aplodinotus grunniens*)
Kanawha minnow (*Phenacobius teretulus*)
Lake sturgeon (*Acipenser fulvescens*)
Least killifish (*Heterandria formosa*)
Mooneye (*Hiodon tergisus*)
Mountain madtom (*Noturus eleutherus*)
Ohio lamprey (*Ichthyomyzon bdellium*)
Olive darter (*Percina squamata*)
Pinewoods darter (*Etheostoma mariae*)
River carpsucker (*Carpiodes carpio*)
Sandhills chub (*Semotilus lumbee*)
Sickle darter (*Percina williamsi*)
Smoky dace (*Clinostomus* sp.)
Striped shiner (*Luxilus chrysocephalus*)
Snubnose darter (*Etheostoma simoterum*)
“Thinlip” chub (*Cyprinella* sp., c.f. zanema)
Waccamaw killifish (*Fundulus waccamensis*)
Westfall’s Darter (*Percina westfalli*)
Wounded darter (*Etheostoma vulneratum*)
Yellowfin shiner (*Notropis lutipinnis*)


Chowanoke crayfish (Tyler Black)


Lake sturgeon (Dr. Luke Etchison)


Smoky dace (Dr. Luke Etchison)

NORTH CAROLINA SPECIAL CONCERN SPECIES

Mammals (10)

- Allegheny woodrat (*Neotoma magister*)
- Buxton Woods white-footed mouse (*Peromyscus leucopus buxtoni*)
- Coleman's oldfield mouse (*Peromyscus polionotus colemani*)
- Eastern big-eared bat (*Corynorhinus rafinesquii macrotis*)
- Eastern small-footed bat (*Myotis leibii leibii*)
- Florida yellow bat (*Lasiurus intermedius floridanus*)
- Pungo white-footed mouse (*Peromyscus leucopus easti*)
- Southeastern bat (*Myotis austroriparius*)
- Southern rock vole (*Microtus chrotorrhinus carolinensis*)
- Star-nosed mole (*Condylura cristata parva*)


Star-nosed mole (Agnieszka Bacal)

Mollusks (32)

- Appalachian gloss (*Zonitoides patuloides*)
- Bidentate dome (*Ventridens coelaxis*)
- Black mantleslug (*Pallifera hemphilli*)
- Blackwater ancylid (*Ferrissia hendersoni*)
- Blue-foot lancetooth (*Haplotrema kendeighi*)
- Cape Fear spike (*Elliptio marsupiobesa*)
- Clingman covert (*Fumonelix wheatleyi clingmanicus*)
- Dark glyph (*Glyphyalinia junaluskana*)
- Dwarf proud globe (*Patera clarki clarki*)
- Dwarf threetooth (*Triodopsis fulciden*)
- Fringed coil (*Helicodiscus fimbriatus*)
- Glossy supercoil (*Paravitrea placentula*)
- Great Smoky slitmouth (*Stenotrema depilatum*)
- High mountain supercoil (*Paravitrea andrewsae*)
- Honey glyph (*Glyphyalinia vanattai*)
- Lamellate supercoil (*Paravitrea lamellidens*)
- Mirey Ridge supercoil (*Paravitrea clappi*)
- Open supercoil (*Paravitrea umbilicaris*)
- Pink glyph (*Glyphyalinia pentadelphia*)
- Pod lance (*Elliptio folliculata*)
- Queen crater (*Appalachina chilhoweensis*)
- Ramp Cove supercoil (*Paravitrea lacteodens*)
- Ridged lioplax (*Lioplax subcarinata*)
- Roanoke slabshell (*Elliptio roanokensis*)
- Saw-tooth disc (*Discus bryanti*)
- Seep mudalia (*Leptoxis dilatata*)
- Spike (*Eurynia dilatata*)
- Spiral coil (*Helicodiscus bonamicus*)


Southeastern bats (USFWS)


Spike (NCWRC)

Mollusks (continued)

Velvet covert (*Inflectarius subpalliatus*)
Waccamaw amnicola (*Amnicola* sp.)
Waccamaw siltsnail (*Cincinnatia* sp.)
Wavy-rayed lampmussel (*Lampsilis fasciola*)


Wavy-rayed lampmussel (NCWRC)

Reptiles (13)

Carolina pigmy rattlesnake (*Sistrurus miliarius miliarius*)
Carolina swamp snake (*Seminatrix [=Liodytes] pygaea paludis*)
Carolina water snake (*Nerodia sipedon williamengelsi*)
Cumberland slider (*Trachemys scripta troostii*)
Diamondback terrapin (*Malaclemys terrapin*)
Eastern chicken turtle (*Deirochelys reticularia reticularia*)
Eastern coachwhip (*Masticophis [=Coluber] flagellum flagellum*)
Eastern slender glass lizard (*Ophisaurus attenuatus longicaudus*)
Eastern spiny softshell (*Apalone spinifera spinifera*)
Northern map turtle (*Graptemys geographica*)
Outer Banks kingsnake (*Lampropeltis getula sticticeps*)
Stripeneck musk turtle (*Sternotherus minor peltifer*)
Timber rattlesnake (*Crotalus horridus*)


Eastern coachwhip (Jeff Hall)

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The Environmental Consequences of Forest Roads and Achieving a Sustainable Road System

March 2020

Table of Contents

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Cover photos credits: Mt. Baker-Snoqualmie National Forest, 2016. WildEarth Guardians.

Introduction

The Forest Service faces many challenges with its vastly oversized, under-maintained, and unaffordable transportation system. With 370,643 miles of system roads and 137,409 miles of system trails (USDA Forest Service 2019), the network extends broadly across every national forest and grassland and through a variety of habitats, ecosystems and terrains. An impressive body of scientific literature addresses the various effects of roads on the physical, biological and cultural environment. Numerous studies demonstrate the harmful environmental consequences to water, fish, wildlife, and ecosystems.

In recent years, the scientific literature has expanded to address the effects of roads on climate change adaptation and conversely the effects of climate change on roads, as well as the multiple benefits of road removal on the physical, biological and cultural environments.

The first section of this paper provides a literature review summarizing the most recent science related to the environmental impacts of forest roads and motorized trails. The second section focuses on climate change effects and strategies to address the growing ecological consequences to forest resources. The third section provides background and specific direction for the Forest Service to provide for an ecologically and economically sustainable road system, including recommendations for future action.

I. Impacts of Transportation Infrastructure and Access to the Ecological Integrity of Terrestrial and Aquatic Ecosystems and Watersheds

It is well understood that transportation infrastructure provides access to national forests and grasslands and also harms aquatic and terrestrial environments at multiple scales. In general, the more roads and motorized trails the greater the impacts. Since its emergence, the field of road ecology and the resulting research has proven the magnitude and breadth of ecological issues related to roads; entire books have been written on the topic (e.g., Forman et al. 2003, van der Ree et al. 2015), and research centers continue to expand their case studies, including the Western Transportation Institute at Montana State University and the Road Ecology Center at the University of California - Davis.[1]

Below, we provide a summary of the current understanding of the impacts of roads and motorized access on terrestrial and aquatic ecosystems, supplementing long-established, peer-reviewed literature reviews on the topic, including Gucinski et al. (2000), Trombulak and Frissell (2000), Coffin (2007), and Robinson et al. (2010). More targeted reviews have been published on the effects of roads on insects (Munoz et al. 2015), vertebrates (da Rosa 2013), and animal abundance (Fahrig and Rytwinski 2009, Benítez-López et al. 2010). Literature reviews on the ecological and social impacts of motorized recreation include Gaines et al. (2003), Davenport and Switalski (2006), Ouren

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[1] See http://www.westerntransportationinstitute.org/programs/road-ecology and http://roadecology.ucdavis.edu/

et al. (2007), Switalski and Jones (2012), and, more recently, Switalski (2017). In addition to the physical and environmental impacts of roads, increased visitation has resulted in intentional and unintentional damage to many cultural and historic sites (Spangler and Yentsch 2008, Sampson 2009, Hedquist et al. 2014).

A. Impacts on geomorphology and hydrology

The construction and presence of forest roads can dramatically change the hydrology and geomorphology of a forest system leading to reductions in the quantity and quality of aquatic habitat (Al-Chokhachy et al. 2016). While there are several mechanisms that cause these impacts (Wemple et al. 2001, Figure 1), most fundamentally, compacted roadbeds reduce rainfall infiltration, intercepting and concentrating water, and providing a ready source of sediment for transport (Wemple et al. 2001). In fact, roads contribute more sediment to streams than any other land management activities on Forest Service lands (Gucinski et al. 2000). Surface erosion rates from roads can be up to three orders of magnitude greater than erosion rates from undisturbed forest soils (Endicott 2008).

Erosion and sediment produced from roads occur both chronically and catastrophically. Every time it rains, sediment from the road surface and from cut-and fill-slopes is picked up by rainwater that flows into and on roads (fluvial erosion). The sediment that is entrained in surface flows are often concentrated into road ditches and culverts and directed into streams. The degree of fluvial erosion varies by geology and geography, and increases with increased motorized use (Robichaud et al. 2010). Closed roads produce significantly less sediment than open drivable roads (Sosa Pérez and Macdonald 2017, Foltz et al. 2009).

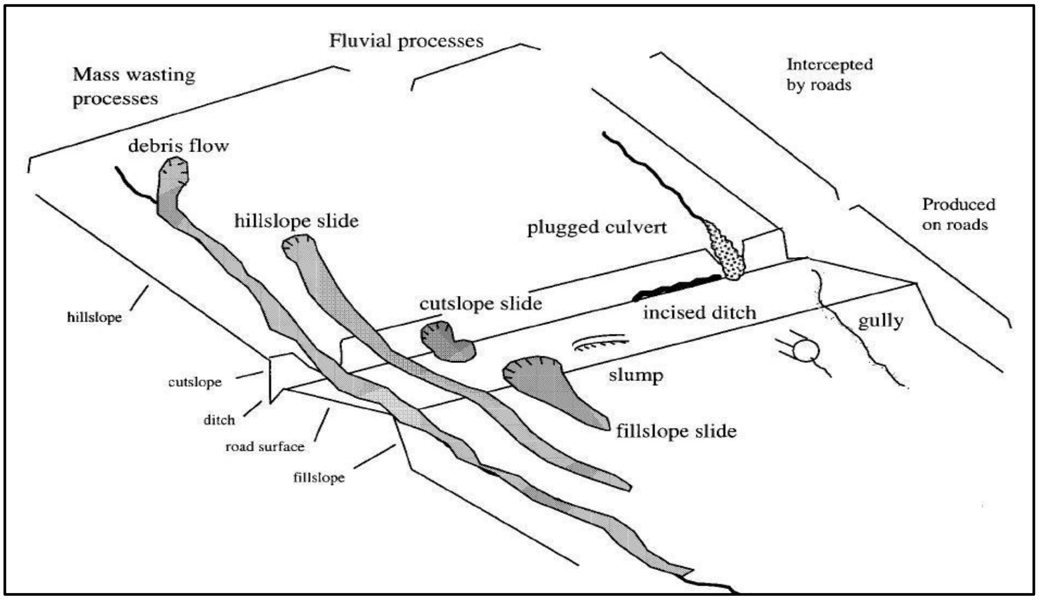

Figure 1: Typology of erosional and depositional features produced by mass-wasting and fluvial processes associated with forest roads (reprinted from Wemple et al. 2001).

Roads also precipitate catastrophic failures of road beds and fills (mass wasting) during large storm events leading to massive slugs of sediment moving into waterways (Gucinski et al. 2000, Endicott 2008). This typically occurs when culverts are undersized and cannot handle the volume of water funneled through them, or they simply become plugged with debris and sediment. The saturated roadbed can fail entirely and result in a landslide, or the blocked stream crossing can erode the entire fill down to the original stream channel.

The erosion of road- and trail-related sediment and its subsequent movement into stream systems affects the geomorphology of the drainage system in a number of ways. It directly alters channel morphology by embedding larger gravels as well as filling pools. It can also have the opposite effect of increasing peak discharges and scouring channels, which can lead to disconnection of the channel and floodplain, and lowered base flows (Gucinski et al. 2000). The width/depth ratio of the stream changes can trigger changes in water temperature, sinuosity and other geomorphic factors important for aquatic species survival (Trombulak and Frissell 2000).

B. Impacts on aquatic habitat and fish

Roads can have dramatic and lasting impacts on fish and aquatic habitat. Increased sedimentation in stream beds has been linked to decreased fry emergence, decreased juvenile densities, loss of winter carrying capacity, increased predation of fish, and reductions in macro-invertebrate populations that are a food source to many fish species (Gucinski et al. 2000, Endicott 2008). Roads close to streams reduce the number of trees available for large wood recruitment, and reduce stream-side shade (Meredith et al. 2014.) On a landscape scale, these effects add up to: changes in the frequency, timing and magnitude of disturbance to aquatic habitat and changes to aquatic habitat structures (e.g., pools, riffles, spawning gravels and in-channel debris), and conditions (food sources, refugia, and water temperature; Gucinski et al. 2000).

River fragmentation

Roads also act as barriers to migration and fragment habitat of aquatic species (Gucinski et al. 2000). Where roads cross streams, road engineers usually place culverts or bridges. Undersized culverts interfere with sediment transport and channel processes such that the road/stream crossing becomes a barrier for fish and aquatic species movement up and down stream (Erikinaro et al. 2017). For instance, a culvert may scour on the downstream side of the crossing, actually forming a waterfall up which fish cannot move. Undersized culverts can infringe upon the channel or floodplain and trap sediment causing the stream to become too shallow and/or warm such that fish will not migrate past the structure. Or, the water can move through the culvert at too high a gradient or velocity to allow fish passage (Endicott 2008).

River fragmentation is problematic for many aquatic species but especially for anadromous species that must migrate upstream to spawn. Well-known native aquatic species affected by roads include salmon such as coho (*Oncorhynchus kisutch*), Chinook (*O. tshawytscha*), and chum (*O. keta*); steelhead

(*O. mykiss*), a variety of trout species including bull trout (*Salvelinus confluentus*) and cutthroat trout (*O. clarki*), as well as other native fish and amphibians (Endicott 2008). The restoration and mitigation of impassable road culverts has been found to restore connectivity and increase available aquatic habitat (Erikinaro et al. 2017), and the quality of aquatic habitat (McCaffery et al. 2007).

C. Impacts on terrestrial habitat and wildlife

Roads and trails impact wildlife through a number of mechanisms including: direct mortality (poaching, hunting/trapping), changes in movement and habitat-use patterns (disturbance/avoidance), as well as indirect impacts including altering adjacent habitat and interference with predator/prey relationships (Coffin 2007, Fahrig and Rytwinski 2009, Robinson et al. 2010, da Rosa and Bager 2013). Some of these impacts result from the road itself, and some result from the uses on and around the roads (access). Ultimately, numerous studies show that roads reduce the abundance, diversity, and distribution of several forest species (Fayrig and Ritwinski 2009, Benítez-López et al. 2010, Munoz et al. 2015).

Abundance and distribution

The extensive research on roads and wildlife establish clear trends of wildlife population declines. Fahrig and Rytwinski (2009) reviewed the empirical literature on the effects of roads and traffic on animal abundance and distribution looking at 79 studies that addressed 131 species. They found that the number of documented negative effects of roads on animal abundance outnumbered the number of positive effects by a factor of 5. Amphibians, reptiles, and most birds tended to show negative effects. Small mammals generally showed either positive effects or no effect, mid-sized mammals showed either negative effects or no effect, and large mammals showed predominantly negative effects. Benítez-López et al. (2010) conducted a meta-analysis on the effects of roads and infrastructure proximity on mammal and bird populations. They found a significant pattern of avoidance and a reduction in bird and mammal populations in the vicinity of infrastructure. Muñoz et al. (2015) found that many insect populations have declined as well.

Direct mortality, disturbance, and habitat modification

Road and motorized trail use affect many different types of species. For example, trapping, poaching, collisions, negative human interactions, disturbance and displacement significantly impact wide ranging carnivores (Gaines et al. 2003, Table 1). Hunted game species such as elk (Cervus canadensis), become more vulnerable from access allowed by roads and motorized trails resulting in a reduction in effective habitat among other impacts (Rowland et al. 2005). Slow-moving migratory animals such as amphibians, and reptiles who use roads to regulate temperature, are also vulnerable (Gucinski et al. 2000, Brehme et al. 2013). Roads and motorized trails also affect ecosystems and habitats because they are major vectors of non-native plant and animal species (Gelbard and Harrison 2003). This can have significant ecological and economic impacts when aggressive invading species overwhelm or significantly alter native species and systems.

Table 1: Road- and recreation trail-associated factors for wide-ranging carnivores (Reprinted from Gaines et al. (2003)[2]

Focal species	**Road-associated factors**	**Motorized trail-associated factors**	**Nonmotorized trail-associated factors**
Grizzly bear	Poaching Collisions Negative human interactions Displacement or avoidance	Poaching Negative human interactions Displacement or avoidance	Poaching Negative human interactions Displacement or avoidance
Lynx	Down log reduction Trapping Collisions Disturbance at a specific site	Disturbance at a specific site Trapping	Disturbance at a specific site
Gray wolf	Trapping Poaching Collisions Negative human interactions Disturbance at a specific site Displacement or avoidance	Trapping Disturbance at a specific site	Trapping Disturbance at a specific site
Wolverine	Down log reduction Trapping Disturbance at a specific site Collisions	Trapping Disturbance at a specific site	Trapping Disturbance at a specific site

Habitat fragmentation

At the landscape scale, roads fragment habitat blocks into smaller patches that may not be able to support interior forest species. Smaller habitat patches result in diminished genetic variability, increased inbreeding, and at times local extinctions (Gucinski et al. 2000; Trombulak and Frissell 2000). For example, a narrow forest road with little traffic was a barrier in Arizona to the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*; Chen and Koprowski 2013). Fragmentation intensifies concerns about grizzly bear population viability, especially since roads increase human/bear interactions exacerbating the problem of excessive mortality (Proctor et al, 2012)

Roads also change the composition and structure of ecosystems along buffer zones, called edge-affected zones. The width of edge-affected zones varies by what metric is being discussed; however, researchers have documented road-avoidance zones a kilometer or more away from a road (Robinson et al.2010; Table 2). In heavily roaded landscapes, edge-affected acres can be a significant percentage of total acres. For example, in a landscape where the road density is 3 mi/mi^2 and where the edge-affected zone is estimated to be 500 ft from the center of the road to each side, the edge-affected zone is 56% of the total acreage.

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[2] For a list of citations see Gaines et al. (2003).

Table 2: A summary of some documented road-avoidance zones for various species (adapted from Robinson et al. 2010).

Species	**Avoidance zone m (ft)**	**Type of disturbance**	**Reference**
Snakes	650 (2133)	Forestry roads	Bowles (1997)
Salamander	35 (115)	Narrow forestry road, light traffic	Semlitsch (2003)
Woodland birds	150 (492)	Unpaved roads	Ortega and Capen (2002)
Spotted owl	400 (1312)	Forestry roads, light traffic	Wasser et al. (1997)
Marten	<100 (<328)	Any forest opening	Hargis et al. (1999)
Elk	500–1000 (1640-3281)	Logging roads, light traffic	Edge and Marcum (1985)
Grizzly bear	3000 (9840)	Fall	Mattson et al. (1996)
	500 (1640)	Spring and summer	
	1122 (3681)	Open road	Kasworm and Manley (1990)
	665 (2182)	Closed road	
Black bear	274 (899)	Spring, unpaved roads	Kasworm and Manley (1990)
	914 (2999)	Fall, unpaved roads	

Migration disruption

Roads disrupt migration of large ungulates, such as elk, impeding travel at multiple scales, including seasonal home range use and migration to winter range (Buchanan et al. 2014, Prokopenko et al. 2017). For example, a recent study found migrating elk changed their behavior and stopover use on migration routes that were roaded (Paton et al. 2017). The authors suggest this disturbance may lead to decreased foraging, displacement of high-quality habitat, and affect the permeability of the migration route. In addition, roads disrupt grizzly bear movements influencing dispersal away from the maternal home range and ultimately influencing population-level fragmentation." (Proctor et al. 2018).

Oil and gas development (and associated roads) reduced the effectiveness of both mule deer and pronghorn migration corridors in western Wyoming. (Sawyer et al. 2005). Multiple studies found that mule deer increased their rate of travel during migrations, reducing stop over time and their use of important foraging habitats (Sawyer et al. 2012, Lendrum et al. 2012; Ledrum et al. 2013;). A study in Colorado found that female mule deer changed their migration timing which may change alignment with vegetative phenology and potentially result in energetic and demographic costs (Lendrum et al. 2013).

D. Road density thresholds for fish and wildlife[3]

It is well documented that, beyond specific road density thresholds, certain species will be negatively affected, and some risk being extirpated (Robinson et al. 2000, Table 3). Most studies that look into the relationship between road density and wildlife focus on the impacts to large endangered carnivores or hunted game species, although high road densities certainly affect other species. Grizzly bears have been found to have a higher mortality risk as road density increases (Boulanger and Stenhouse 2014). Gray wolves (*Canis lupus*) in the Great Lakes region and elk in Montana and Idaho also face increased mortality risk, and have undergone the most long-term and in-depth analysis. Forman and Hersperger (1996) found that in order to maintain a naturally functioning landscape with sustained populations of large mammals, road density must be below 0.6 km/km^2 (1.0 mi/mi^2).

A number of studies show that higher road densities also impact aquatic habitats and fish (Table 3). Carnefix and Frissell (2009) provide a concise review of studies that correlate cold water fish abundance and road density, and from the cited evidence concluded that:

> 1) no truly "safe" threshold road density exists, but rather negative impacts begin to accrue and be expressed with incursion of the very first road segment; and 2) highly significant impacts (e.g., threat of extirpation of sensitive species) are already apparent at road densities on the order of 0.6 km/km^2 (1.0 mi/mi^2) or less, (Carnefix and Frissell (2009), p. 1).

Cold water salmonids such as threatened bull trout, are particularly sensitive to the impacts of forest roads. The U.S. Fish and Wildlife Service's Final Rule listing bull trout as threatened (USDI Fish and Wildlife Service 1999) addressed road density stating:

> … assessment of the interior Columbia Basin ecosystem revealed that increasing road densities were associated with declines in four non-anadromous salmonid species (bull trout, Yellowstone cutthroat trout, westslope cutthroat trout, and redband trout) within the Columbia River Basin, likely through a variety of factors associated with roads (Quigley & Arbelbide 1997). Bull trout were less likely to use highly roaded basins for spawning and rearing, and if present, were likely to be at lower population levels (Quigley and Arbelbide 1997). Quigley et al. (1996) demonstrated that when average road densities were between 0.4 to 1.1 km/km^2 (0.7 and 1.7 mi/mi^2) on USFS lands, the proportion of subwatersheds supporting "strong" populations of key salmonids dropped substantially. Higher road densities were associated with further declines (USDI Fish and Wildlife Service (1999), p. 58922).

Anderson et al. (2012) showed that watershed conditions tend to be best in areas protected from road construction and development. Using the U.S. Forest Service's Watershed Condition Framework assessment data, they showed that National Forest lands protected under the Wilderness Act tend to have

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[3] We intend for the term "road density" to refer to the density of all roads within national forests, including system roads, closed roads, non-system roads, temporary roads and motorized trails, and roads administered by other jurisdictions (private, county, state).

the healthiest watersheds. In support of this conclusion, McCaffery et al. (2005) found that streams in roadless watersheds had less fine sediment and higher quality habitat than roaded watersheds. Miller et al. (2017) showed that in 20 years of monitoring forests managed by the Northwest Forest Plan there were measurable improvements in watershed conditions as a result of road decommissioning, finding "...the decommissioning of roads in riparian areas has multiple benefits, including improving the riparian scores directly and typically the sedimentation scores."

Table 3: A summary of some road-density thresholds and correlations for terrestrial and aquatic species and ecosystems (reprinted from Robinson et al. 2010).

Species (Location)	**Road density (mean, guideline, threshold, correlation)**	**Reference**
Wolf (Minnesota)	0.36 km/km2 (mean road density in primary range); 0.54 km/km^2 (mean road density in peripheral range)	Mech et al. (1988)
Wolf	>0.6 km/km^2 (absent at this density)	Jalkotzy et al. (1997)
Wolf (Northern Great Lakes region)	>0.45 km/km^2 (few packs exist above this threshold); >1.0 km/km^2 (no pack exist above this threshold)	Mladenoff et al. (1995)
Wolf (Wisconsin)	0.63 km/km^2 (increasing due to greater human tolerance	Wydeven et al. (2001)
Wolf, mountain lion (Minnesota, Wisconsin, Michigan)	0.6 km/km^2 (apparent threshold value for a naturally functioning landscape containing sustained populations)	Thiel (1985); van Dyke et al. (1986); Jensen et al. (1986); Mech et al. (1988); Mech (1989)
Elk (Idaho)	1.9 km/km^2 (density standard for habitat effectiveness)	Woodley 2000 cited in Beazley et al. 2004
Elk (Northern US)	1.24 km/km^2 (habitat effectiveness decline by at least 50%)	Lyon (1983)
Elk, bear, wolverine, lynx, and others	0.63 km/km^2 (reduced habitat security and increased mortality)	Wisdom et al. (2000)
Moose (Ontario)	0.2-0.4 km/km2 (threshold for pronounced response)	Beyer et al. (2013)
Grizzly bear (Montana)	>0.6 km/km^2	Mace et al. (1996); Mattson et al. (1996)
Black bear (North Carolina)	>1.25 km/km^2 (open roads); >0.5 km/km2 (logging roads); (interference with use of habitat)	Brody and Pelton (1989)
Black bear	0.25 km/km^2 (road density should not exceed)	Jalkotzy et al. (1997)
Bobcat (Wisconsin)	1.5 km/km^2 (density of all road types in home range)	Jalkotzy et al. (1997)
Large mammals	>0.6 km/km^2 (apparent threshold value for a naturally functioning landscape containing sustained populations)	Forman and Hersperger (1996)
Bull trout (Montana)	Inverse relationship of population and road density	Rieman et al. (1997); Baxter et al. (1999)

Fish populations (Medicine Bow National Forest)	(1) Positive correlation of numbers of culverts and stream crossings and amount of fine sediment in stream channels (2) Negative correlation of fish density and numbers of culverts	Eaglin and Hubert (1993) cited in Gucinski et al. (2001)
Macroinvertebrates	Species richness negatively correlated with an index of road density	McGurk and Fong (1995)
Non-anadromous salmonids (Upper Columbia River basin)	(1) Negative correlation likelihood of spawning and rearing and road density (2) Negative correlation of fish density and road density	Lee et al. (1997)

E. Roads and Fires

Wildland forest fire plays an essential role in many forest ecosystems, and with climate change, fire will increasingly shape National Forest lands. Humans have made fire more common on the landscape, and studies have found that forest roads can affect fire regimes and localized fuel regimes. Changes in the timing and location of fire can alter the natural fire regime and has negative, cascading effects in ecological communities. For example, a change in timing and frequency of fire can result in habitat loss and fragmentation, shift forest composition, and affect predator-prey interactions (DellaSalla et al. 2004). Following a fire, exposed bare ground on roads can result in chronic erosion, catastrophic culvert failures, and noxious weed invasion.

Forest roads can increase the occurrence of human-caused fires, whether by accident or arson, and road access has been correlated with the number of fire ignitions (Syphard et al. 2007, Yang et al., 2007, Narayanaraj and Wimberly 2012, Nagy et al. 2018). A recent study found that humans ignited four times as many fires as lightning. This represented 92% of the fires in the eastern United States and 65% of the fire ignitions in the western U.S. (Nagy et al. 2018). Another study that reviewed 1.5 million fire records over 20 years found human-caused fires were responsible for 84% of wildfires and 44% of the total area burned (Balch et al. 2017).

In addition to changes in frequency, human-caused fires change the timing of fire occurring when fuel moisture is significantly higher than lightning-started fires (Nagy et al. 2018.). Forest roads may also limit fire growth acting as a fire break and providing access for suppression (Narayanaraj and Wimberly 2011, Robbinne et al. 2016). The result is a spatial and temporal distribution of fire that differs from historical fire regimes.

Roaded areas create a distinct fire fuels profile which may influence ignition risk and burn severity (Narayanaraj and Wimberly 2013). Forest roads create linear gaps with reduced canopy cover, and increased solar radiation, temperature, and wind speed. Invasive weeds and grasses common along roadsides also create fine fuels that are highly combustible. These edge effects can change microclimates far into the forest (Narayanaraj and Wimberly 2012, Ricotta et al. 2018). While there is little definitive research on roads and burn severity, an increase in the prevalence of lightning-caused fires in roaded areas may be due to roadside edge effects (Arienti et al 2009, Narayanaraj and Wimberly 2012). Furthermore, watersheds that have been heavily roaded have typically received intensive management in the past leaving forests in a condition of high fire vulnerability (Hessburg and Agee 2003).

Roadless areas are remote and secure from many human impacts such as unintentional fire starts or arson. A forest fire is almost twice as likely to occur in a roaded area than a roadless area (USDA Forest Service 2000). In fact, human-ignited wildfire is almost five times more likely to occur in a roaded area than in a roadless area. (USDA Forest Service 2000). Higher road density correlates with an increased probability of human-caused ignitions. (Syphard et al. 2007).

After a forest fire, roads that were previously well vegetated often burn or are bladed for fire suppression access or firebreaks leaving them highly susceptible to erosion and weed invasion. Roads are a source of chronic erosion following a fire, and pulses of hillslope sediment and large woody debris can result in culvert failures (Bisson et al. 2003). Fine sediment is frequently delivered to streams and reduces the quality of aquatic habitat. Noxious weeds are established on many forest roads, and post-fire weed invasion can be facilitated by creating a disturbance, reducing competition, and increasing resource availability (Birdsaw et al. 2012).

II. Climate Change and Transportation Infrastructure

Before the Trump administration took office, the Forest Service recognized the importance of considering and adapting to changing climate conditions. The USDA Strategic Plan for Fiscal Years 2014-2018 set a goal to: "Ensure our national forests and private working lands are conserved, restored, and made more resilient to climate change, while enhancing our water resources." (USDA 2014, p 3). As climate change impacts grow more profound, forest managers must consider the impacts *on* the transportation system as well as *from* the transportation system. In terms of the former, changes in precipitation and hydrologic patterns will strain infrastructure, resulting in damage to streams, fish habitat, and water quality as well as threats to public safety and loss of access. As to the latter, the fragmenting effect of roads on habitat will impede the movement of species which is a fundamental element of adaptation. Through planning, forest managers can proactively address threats to infrastructure, and can actually enhance forest resilience by removing unneeded roads to create larger patches of connected habitat.

A. Climate change, forest roads, and fragmented habitat

It is expected that climate change will be responsible for more extreme weather events, leading to increasing flood severity, more frequent landslides, changing hydrographs, and changes in erosion and sedimentation rates and delivery processes (Schwartz et al. 2014, USDA FS 2018). The Forest

Service Office of Sustainability and Climate has compiled climate change vulnerability assessments for several regions of the Forest Service discussing near-term consequences for managers to consider. (Halofsky et al. 2017, 2018a, 2018b, 2019, with additional vulnerabilities displayed below in Table 4).

> Warmer locations will experience more runoff in winter months and early spring, whereas colder locations will experience more runoff in late spring and early summer. In both cases, future peakflows will be higher and more frequent, (Halofsky et al. 2018b at ii).
>
> The frequency and extent of midwinter flooding are expected to increase. Flood magnitudes are also expected to increase because rain-on-snow-driven peak flows will become more common," (*Id.* at 83).
>
> Roads and other infrastructure that are near or beyond their design life are at considerable risk to damage from flooding and geomorphic disturbance (e.g., debris slides). If road damage increases as expected, it will have a profound impact on access to Federal lands and on repair costs, (*Id.* at viii).

Magnifying these consequences is the fact that roads, culverts and trails in national forests were designed for storms and water flows typical of past decades, and may not be designed for the storms in future decades. Hence, climate driven changes may cause transportation infrastructure to malfunction or fail (USDA Forest Service 2010, ASHTO 2012). The likelihood is higher for facilities in high-risk settings—such as rain-on-snow zones, coastal areas, and landscapes with unstable geology. The following consequences may occur (USDA Forest Service 2010):

- access to national forests will be interrupted temporarily or permanently as roads wash-out due to landslides or blown-out culverts during events of heavier precipitation or flooding;
- public safety will be compromised as roads, trails and bridges become unstable due to landslides, undercut slopes, or erosion of water-logged slopes due to heavy rainfall; and
- infrastructure may be compromised or abandoned along coastal areas or low-lying estuaries when inundated during high tides and coastal storms as sea-levels rise.

Forests fragmented by roads will likely demonstrate less resistance and resilience to stressors, like those associated with climate change (Noss 2001, see also Table 4. below). First, the more a forest is fragmented (and therefore the higher the edge/interior ratio), the more the forest loses its inertia characteristic, and becomes less resilient and resistant to climate change. Second, the more a forest is fragmented, characterized by isolated patches, the more likely the fragmentation will interfere with the ability of species to track shifting climatic conditions over time and space.

> Hence, roads may impede the movement of many species in response to climate change. Closing unnecessary roads and providing wildlife crossings on roads with heavy traffic might mitigate some of these effects (Noss 1993; Clevenger & Waltho 2000), (Noss (2001) p. 584).

Watershed types within national forests may change which will impact hydrology and when high streamflows occur (Halofsky et. al. 2011). A study in Washington's Mt. Baker-Snoqualmie National

Forest (MBSNF) shows that currently 27% of the roads are in watersheds classified as rain-dominated but that will increase to 75% by 2080 - increasing risk of damage to infrastructure (Strauch 2014). By 2040, 300 miles of forest roads in this forest will be located in watersheds that are projected to see a 50% increase in 100-year floods. Landslide risk will be higher during the winter and spring and decline during summer and autumn. These changes reinforce the importance of transportation analysis that incorporates the impacts of climate change.

Earlier snowmelt may open previously snow-closed roaded areas for a greater portion of the year. While this may appear to benefit visitors that wish to access trails and camps early in the spring, this may also put them in harm's way with melting snow-bridges, avalanche chutes and flooding events (Strauch 2015). Wildlife historically protected by snow-closed roads would be more vulnerable.

B. Modifying infrastructure to increase resilience

To prevent or reduce road-triggered landslides and culvert failures, and other associated hazards, forest managers will need to take a series of actions. In December 2012, the USDA Forest Service published a report entitled, *Assessing the Vulnerability of Watersheds to Climate Change* (USDA FS 2012) which reinforces that forest managers need to be proactive in reducing erosion potential from roads:

> Road improvements were identified as a key action to improve condition and resilience of watersheds on all the pilot forests. In addition to treatments that reduce erosion, road improvements can reduce the delivery of runoff from road segments to channels, prevent diversion of flow during large events, and restore aquatic habitat connectivity by providing for passage of aquatic organisms. As stated previously, watershed sensitivity is determined by both inherent and management-related factors. Managers have no control over the inherent factors, so to improve resilience, efforts must be directed at anthropogenic influences such as instream flows, roads, rangeland, and vegetation management…. [Watershed Vulnerability Analysis (WVA)] results can also help guide implementation of travel management planning by informing priority setting for decommissioning roads and road reconstruction/maintenance. As with the Ouachita NF example, disconnecting roads from the stream network is a key objective of such work. Similarly, WVA analysis could also help prioritize aquatic organism passage projects at road-stream crossings to allow migration by aquatic residents to suitable habitat as streamflow and temperatures change, (USDA Forest Service 2012a, p. 22-23).

Other Forest Service reports support road-related actions to increase climate resilience including replacing undersized culverts with larger ones, prioritizing maintenance and upgrades, and restoring roads to a natural state when they are no longer needed and pose erosion hazards (USDA Forest Service 2010, USDA Forest Service 2011a USDA Forest Service 2012a, USDA FS 2018, Halofsky et al. 2018a).

The Forest Service has developed several resources to identify and mitigate climate change impacts on forests and infrastructure. The aforementioned climate change vulnerability assessments for each region focus on causes, consequences, and options to address them. For example, Halofsky et al.

(2018a) reviews the effects and adaptation options for Region 1 (Northern Region) of the Forest Service, and identifies the increased magnitude of peak streamflows as a primary impact to road infrastructure. Adaptation strategies identified in the report include:

> ...increasing the resilience of stream crossings, culverts, and bridges to higher peakflows and facilitating response to higher peakflows by reducing the road system and disconnecting roads from streams. Tactics include completing geospatial databases of infrastructure (and drainage) components, installing higher capacity culverts, and decommissioning roads or converting them to alternative uses. (Halofsky et al. 2018a)

U.S. Forest Service Transportation Resiliency Guidebook provides a review of the impacts of climate change on Forest Service infrastructure, and a process to assess and address climate change impacts at local and regional levels (USDA FS 2018; Table 4). Included in the guidebook is a step-by-step guide for identifying vulnerabilities and preparedness planning within their transportation network (USDA FS 2018). In addition, the guidebook recommends using the forest plan revision process as "an opportunity to analyze baseline conditions and climate change vulnerabilities and to develop climate resilient strategies for the future." (USDA FS 2018). The Forest Service should use the transportation resilience guidebook to inform forest plan revision analysis and plan components to address climate change in the context of the forest's transportation system.

Table 4. Role of adaptation strategies in reducing climate change impacts of Forest Service lands (reprinted from USDA FS 2018).

	Impacts on Transportation	**Example Strategies to Reduce Impacts**
Heavy Precipitation / Flooding	Flooded roadways interrupting service Damage/destruction of roads and bridges Pavement buckling Erosion comprising soil stability and transportation assets Slope failures Landslides damaging and disrupting routes Plugged or blown out culverts	Retrofit facilities Relocate facilities Upgrade culverts and drainage facilities Build new facilities to climate ready standards Protect existing infrastructure Divest in assets
Wildfires	Additional woody debris that plug culverts Reduced slope stability causing increased landslides Increased heavy vehicle traffic wear and tear on FS roadways	Sustain forest ecology Protect forests from severe fire and wind disturbance
Tree Mortality	Fallen trees disrupt access along transportation routes Increased need for clearing hazard trees along roadways Provide forest fuel for wildfire	Facilitate Forest community adjustments through species transitions

Individual forests have also drafted climate mitigation strategies. The Olympic National Forest in Washington, has developed documents oriented at protecting watershed health and species in the face of climate change, including a 2003 travel management strategy and a report entitled, *Adapting to Climate Change in Olympic National Park and National Forest* (USDA FS 2011a). The report calls for road decommissioning, relocation of roads away from streams, enlarging culverts as well as replacing culverts with fish-friendly crossings (Table 5). In the travel management strategy, Olympic National Forest recommended that one third of its road system be decommissioned and obliterated. In addition, the plan called for addressing fish migration barriers in a prioritized and strategic way – most of these are associated with roads.

Table 5: Current and expected sensitivities of fish to climate change and associated adaptation strategies and action for fisheries and fish habitat management and relevant to transportation management at Olympic National Forest and Olympic National Park (reprinted from USDA Forest Service 2011a).

Current and expected sensitivities	**Adaptation strategies and actions**
Changes in habitat quantity and quality	Implement habitat restoration projects that focus on re-creating watershed processes and functions and that create diverse, resilient habitat.
Increase in culvert failures, fill-slope failures, stream adjacent road failures, and encroachment from stream-adjacent road segments	Decommission unneeded roads. Remove sidecast, improve drainage, and increase culvert sizing on remaining roads. Relocate stream-adjacent roads.
Greater difficulty disconnecting roads from stream channels	Design more resilient stream crossing structures.
Major changes in quantity and timing of streamflow in transitional watersheds	Make road and culvert designs more conservative in transitional watersheds to accommodate expected changes.
Decrease in area of headwater streams	Continue to correct culvert fish passage barriers. Consider re-prioritizing culvert fish barrier correction projects.
Decrease in habitat quantity and connectivity for species that use headwater streams	Restore habitat in degraded headwater streams that are expected to retain adequate summer streamflow (ONF).

C. Reducing fragmentation to enhance aquatic and terrestrial species adaptation

Reconnecting fragmented forests has been shown to benefit native species (e.g., Damschen et al. 2019). Decommissioning and upgrading roads can reduce fragmentation of both aquatic and terrestrial systems. For example, reducing the amount of road-generated fine sediment deposited on salmonid nests can increase the likelihood of egg survival and spawning success (Switalski et al. 2004, McCaffery et al. 2007). Strategically removing or mitigating barriers such as culverts has been shown to restore aquatic connectivity and expand habitat (Erkinaro et al. 2017). Decommissioning roads in riparian areas may provide further benefits to salmon and other aquatic organisms by permitting reestablishment of streamside vegetation, which provides shade and maintains a cooler, more moderated microclimate over the stream (Battin et al. 2007, Meridith et al. 2014). Coordinating the repair of an aging road system with the mitigation of aquatic organism passage may allow for restoring connectivity while improving infrastructure (Nesson et al. 2018).

One of the most well documented impacts of climate change on wildlife is a shift in the ranges of species (Parmesan 2006). As animals migrate, landscape connectivity will be increasingly important (Holman et al. 2005), and restoring and mitigating migration routes in key wildlife corridors will increase wildlife resiliency. Access management in important elk migration sites would reduce disturbance and improve connectivity (Parton et al. 2017). Similarly, a recent study found grizzly bear population density increased 50 percent following the restriction of motorized recreation (Lamb et al. 2018). Decommissioning roads in key wildlife corridors will also reduce the many road-related stressors. Road decommissioning restores wildlife habitat by providing security and food such as grasses, forbs, and fruiting shrubs (Switalski and Nelson 2011, Tarvainen and Tolvanen 2016).

Forests fragmented by roads and motorized trail networks will likely demonstrate less resistance and resilience to stressors, such as weeds. As a forest is fragmented and there is more edge habitat, Noss (2001) predicts that weedy species with effective dispersal mechanisms will increasingly benefit at the expense of native species. However, decommissioned roads when seeded with native species can reduce the spread of invasive species (Grant et al. 2011), and help restore fragmented forestlands. Off-road vehicles with large knobby tires and large undercarriages are also a key vector for weed spread (e.g., Rooney 2006). Strategically closing and decommissioning motorized routes, especially in roadless areas, will reduce the spread of weeds on forestlands (Gelbard and Harrison 2003).

D. Transportation infrastructure and carbon sequestration

The relationship of road restoration and carbon has only recently been explored. There is the potential for large amounts of carbon (C) to be sequestered by restoring roads to a more natural state. When roads are decompacted during reclamation, vegetation and soils can develop more rapidly and sequester large amounts of carbon. Research on the Clearwater National Forest in Idaho estimated total soil C storage increased 6-fold compared to untreated abandoned roads (Lloyd et al. 2013). Another study concluded that reclaiming 425 km (264 miles) of logging roads over the last 30 years in Redwood National Park in Northern California resulted in net carbon savings of 49,000 Megagrams (54,013 tons) of carbon to date (Madej et al. 2013, Table 5). A further analysis found that recontouring roads had higher soil organic carbon than ripping (decompacting) the roads (Seney and Madej 2015). Finally, a recent study in Colorado found that adding mulch or biochar to decommissioned roads can increase the amount of carbon stored in soil (Ramlow et al. 2018).

Kerekvliet et al. (2008) used Forest Service estimates of the fraction of road miles that are unneeded, and calculated that restoring 126,000 miles of roads (i.e. 30% of the road system) to a natural state would be equivalent to revegetating an area larger than Rhode Island. In addition, they calculate that the net economic benefit of road treatments are always positive and range from US $0.925-1.444 billion.

Table 6. Carbon budget implications in road decommissioning projects (reprinted from Madej et al. 2013).

Road Decommissioning Activities and Processes	Carbon Cost	Carbon Savings
Transportation of staff to restoration sites (fuel emissions)	X	
Use of heavy equipment in excavations (fuel emissions)	X	
Cutting trees along road alignment during hillslope recontouring	X	
Excavation of road fill from stream crossings		X
Removal of road fill from unstable locations		X
Reduces risk of mass movement		X
Post-restoration channel erosion at excavation sites	X	
Natural revegetation following road decompaction		X
Replanting trees		X
Soil development following decompaction		X

E. The importance of Roadless Areas and intact mature forests

Undeveloped natural lands provide numerous ecological benefits. They contribute to biodiversity, enhance ecosystem representation, and facilitate connectivity and provide high quality or undisturbed water, soil and air (Strittholt and Dellasala 2001, DeVelice and Martin 2001, Crist and Wilmer 2002, Loucks et al. 2003, Dellasalla et al. 2011, Anderson et al. 2012, Selva et al. 2015). They can also serve as ecological baselines to help us better understand our impacts to other landscapes, and contribute to landscape resilience in the face of climate change.

Forest Service roadless lands, in particular, are heralded for the conservation values they provide. The benefits are described at length in the preamble of the Roadless Area Conservation Rule (RACR)[4] as well as in the Final Environmental Impact Statement (FEIS) for the RACR[5], and include: high quality or undisturbed soil, water, and air; sources of public drinking water; diversity of plant and animal communities; habitat for threatened, endangered, proposed, candidate, and sensitive species and for those species dependent on large, undisturbed areas of land; primitive, semi-primitive non- motorized, and semi-primitive motorized classes of dispersed recreation; reference landscapes; natural appearing landscapes with high scenic quality; traditional cultural properties and sacred sites; and other locally identified unique characteristics (e.g., include uncommon geological formations, unique wetland complexes, exceptional hunting and fishing opportunities).

The Forest Service, National Park Service, and the U.S. Fish and Wildlife Service recognize that protecting and connecting roadless or lightly roaded areas is an important action agencies can take to enhance climate change adaptation. For example, the *Forest Service National Roadmap for Responding to Climate Change* (USDA Forest Service 2011b) establishes that increasing connectivity and reducing fragmentation are short- and long-term actions the Forest Service should take to facilitate adaptation

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[4] Federal Register, Vol. 66, No. 9. January 12, 2001. Pages 3245-3247.

[5] Final Environmental Impact Statement, Vol. 1, 3–3 to 3–7

to climate change. The National Park Service also identifies connectivity as a key factor for climate change adaptation along with establishing "blocks of natural landscapes large enough to be resilient to large-scale disturbances and long-term changes," and other factors. The agency states that: "The success of adaptation strategies will be enhanced by taking a broad approach that identifies connections and barriers across the landscape. Networks of protected areas within a larger mixed landscape can provide the highest level of resilience to climate change."[6] Similarly, the *National Fish, Wildlife and Plants Climate Adaptation Partnership's Adaptation Strategy* (2012) calls for creating an ecologically-connected network of conservation areas.[7]

Crist and Wilmer (2002) looked at the ecological value of roadless lands in the Northern Rockies and found that protection of national forest roadless areas, when added to existing federal conservation lands in the study area, would 1) increase the representation of virtually all land cover types on conservation lands at both the regional and ecosystem scales, some by more than 100%; 2) help protect rare, species-rich, and often-declining vegetation communities; and 3) connect conservation units to create bigger and more cohesive habitat "patches."

Roadless lands also are responsible for higher quality water and watersheds. Anderson et al. (2012) assessed the relationship of watershed condition and land management status and found a strong spatial association between watershed health and protective designations. Dellasalla et al. (2011) found that undeveloped and roadless watersheds are important for supplying downstream users with high-quality drinking water, and developing these watersheds comes at significant costs associated with declining water quality and availability. The authors recommend a light-touch ecological footprint to sustain the many values that derive from roadless areas including healthy watersheds.

Allowing roadless and other intact forested areas to reach their full ecological potential is an effective and crucial strategy for atmospheric carbon dioxide removal. Moomaw et al (2019) termed this approach as "proforestation" and explained,

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[6] National Park Service. Climate Change Response Program Brief. http://www.nature.nps.gov/climatechange/adaptationplanning.cfm. Also see: National Park Service, 2010. Climate Change Response Strategy. http://www.nature.nps.gov/climatechange/docs/NPS_CCRS.pdf. Objective 6.3 is to "Collaborate to develop cross-jurisdictional conservation plans to protect and restore connectivity and other landscape-scale components of resilience."

[7] See http://www.wildlifeadaptationstrategy.gov/pdf/NFWPCAS-Chapter-3.pdf. Pages 55- 59. The first goal and related strategies are:

Goal 1: Conserve habitat to support healthy fish, wildlife, and plant populations and ecosystem functions in a changing climate.
Strategy 1.1: identify areas for an ecologically-connected network of terrestrial, freshwater, coastal, and marine conservation areas that are likely to be resilient to climate change and to support a broad range of fish, wildlife, and plants under changed conditions.
Strategy 1.2: Secure appropriate conservation status on areas identified in Strategy 1.1 to complete an ecologically-connected network of public and private conservation areas that will be resilient to climate change and support a broad range of species under changed conditions.
Strategy 1.4: Conserve, restore, and as appropriate and practicable, establish new ecological connections among conservation areas to facilitate fish, wildlife, and plant migration, range shifts, and other transitions caused by climate change.

> [f]ar from plateauing in terms of carbon sequestration (or added wood) at a relatively young age as was long believed, older forests (e.g., >200 years of age without intervention) contain a variety of habitats, typically continue to sequester additional carbon for many decades or even centuries, and sequester significantly more carbon than younger and managed stands, (Luyssaert et al., 2008; Askins, 2014; McGarvey et al., 2015; Keeton, 2018).

The authors recommend "scaling up" proforestation, which includes both protecting and expanding designations of intact forested areas, as a cost-effective means to increase atmospheric carbon sequestration.

III. Achieving a Sustainable Minimum Road System on National Forest Lands

A. Background

For two decades, the Travel Management Rule, 36 C.F.R. Part 212, has guided Forest Service road management and use by motorized vehicles. It is divided into three parts: Subpart A, the administration of the forest transportation system; Subpart B, designation of roads, trails, and areas for motor vehicle use; and Subpart C, use by over-snow vehicles. *See* 36 C.F.R. Part 212.

Table 7. Travel Management Rule Subparts – Objectives, Requirements & Products

36 C.F.R. §212	Objective:	Requires:	Product(s):
Subpart A; Roads Rule 2001	To achieve a sustainable national forest road system.	Use a science-based analysis to identify the minimum road system and roads for decommissioning	- Travel Analysis Report - Map with roads identified as "likely needed" and "likely unneeded"
Subpart B; Travel Management Rule 2005	To protect forests from unmanaged off-road vehicle use by ending cross-country travel and ensuring the agency minimizes the harmful effects from motorized recreation.	Designating a system of roads, trails and areas available for off-road vehicle use according to general and specific criteria.	- Motor Vehicle Use Maps that indicate what roads/trails are open for motorized travel
Subpart C; Travel Management Rule	To protect forests from unmanaged over-snow vehicle use in a manner that minimizes their harmful effects.	Designating specific roads, trails and/or areas for oversnow vehicle use according to the criteria per Subpart B.	- Oversnow vehicle maps designating trails and areas for winter motorized recreation

This broad-based national rule is needed because at over 370,000 miles, the Forest Service road system is long enough to circle the earth over 14 times and it is over twice the size of the National Highway System.[8] It is also indisputably unsustainable from ecological, economic and management perspectives. The majority of the roads were constructed decades ago when design and management techniques did not meet current standards (Gucinski et al. 2000, Endicott 2008), making them more vulnerable to erosion and decay. Further, current design standards and best management practices have not been updated to address climate change realities. Exacerbating the problem are massive Forest Service road maintenance backlogs that forces the agency to forego actions necessary to ensure proper watershed function, such as preventing sediment pollution and sustaining aquatic organism passages. Nationally, the total deferred maintenance backlog reached $5.5 billion in FY 2019 of which $3.1 billion is associated with roads.[9] As a result, the road network is not only a massive economic liability, it is also actively harming National Forest System lands, waters, fish and wildlife.

Over the past two decades the Forest Service - largely due to the Travel Management Rule - has made some limited efforts to identify and implement a sustainable transportation system. Yet, overall the agency has yet to meet the requirements of Subpart A. The challenge for forest managers is figuring out what is a sustainable road system and how to achieve it – a challenge exacerbated by climate change. It is reasonable to define a sustainable transportation system as one where all the roads and trails are located, constructed, and maintained in a manner that minimizes harmful environmental consequences while providing social benefits and within budget constraints. This could potentially be achieved through the use of effective best management practices. However, the reality is that even the best transportation networks can be problematic simply because they exist and usher in land uses that, without the access, would not occur (Trombulak and Frissell 2000, Carnefix and Frissell 2009, USDA Forest Service 1996), and when they are not maintained to the designed level they result in environmental problems (Endicott 2008; Gucinski et al. 2000). Moreover, what was sustainable yesterday may no longer be sustainable under climate change realities since roads designed to meet older climate criteria may no longer hold up under new scenarios (USDA Forest Service 2010, USDA Forest Service 2011b, USDA Forest Service 2012a, AASHTO 2012, Schwartz et al. 2014, USDA FS 2018, Halofsky et al. 2018a, 2018b).

Given consistent budget shortfalls and increasing risks from climate change vulnerabilities, it is clear the agency has an urgent need to both identify and implement a minimum road system, one that will ensure the protection of all Forest Service system lands. However, without specific direction from the Forest Service's Washington D.C. office or Congress, it is reasonable to expect the agency will continue to rely on piecemeal, project-level analyses to identify the minimum road system. Such an approach is inefficient, and insufficient to achieve a sustainable road system forestwide.

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[8] USDOT Federal Highway Administration, Office of Highway Policy Information. https://www.fhwa.dot.gov/policyinformation/pubs/hf/pl11028/chapter1.cfm

[9] USDA Forest Service. 2019. FY2020 Budget Justification. p.83.

Further, where the Forest Service does act to comply with Subpart A, it typically fails to consider shortcoming in its previous travel analysis processes. In fact, an independent review of 38 Travel Analysis Processes and corresponding reports conducted in 2016 by the U.S. Department of Transportation John A. Volpe National Transportation Systems Center found three overarching concerns:

- A lack of clarity regarding the process;
- Failure to follow 36 CFR 212.5(b) direction and Washington Office guidance; and
- Omission of required documents, referenced appendices, or key supporting materials.

Compounding these concerns is the fact that not only do project-level NEPA analyses fail to account for the TAP shortcomings, they also fail to consider real road/motorized densities when identifying the minimum road system. Moreover, these analyses erroneously assume best management practices and project-specific design features will be effective when the Forest Service authorizes actions to achieve a sustainable road system. Finally, if the project-level decision includes actual road decommissioning, the analysis typically fails to consider or specify treatments, resulting in a legacy of ghost-roads persisting on the landscape. The following sections expand on these shortcomings, which the Forest Service must consider in all project-level analyses, and when revising its land and travel management plans.

B. Using Real Road and Motorized Trail Densities to Identify a Minimum Road System

As the Forest Service works to comply with Subpart A, it is crucial that the agency incorporate the true road and motorized trail densities in both its travel analysis process and NEPA-level analyses. Further, the agency must establish standards in land management plan revisions and amendments to ensure each forest achieves an ecologically sustainable minimum road system. Road density analyses should include closed roads, non-system roads, temporary roads, and motorized trails. Typically, the Forest Service calculates road density by looking only at open system road density. From an ecological standpoint, this is a flawed approach since it leaves out the density calculations of a significant percent of roads and motorized trails on the landscape. These additional roads and motorized trails impact fish, wildlife, and water quality, and in some cases, have more of an impact than open system roads. In this section, we provide justification for why a road density analyses should include more than just open road density whenever the Forest Service evaluates the ecological health of an area during NEPA-level analysis or other processes such as for watershed assessments, forest plan revisions or during travel analysis.

Impacts of closed roads

It is crucial to distinguish the density of roads physically present on the landscape, whether closed to vehicle use or not, from “open-road density.” An open-road density of 1.5 mi/mi^2 has been established as a standard in some national forests as protective of some terrestrial wildlife species. However, many areas with an open road density of 1.5 mi/mi^2 often have more miles of closed roads which are still hydrologically connected and negatively affecting aquatic and wildlife habitat. This higher density occurs because many road "closures" may block vehicle access, but do nothing to mitigate the hydrologic alterations the road causes. The problem is often further compounded by the existence of "ghost" roads that are not captured in agency inventories, but that are nevertheless physically present and causing hydrologic alteration (Pacific Watershed Associates 2005).

Closing a road to public motorized use can mitigate the impacts on water, wildlife, and soils only if proper closure and storage techniques are followed. Flow diversions, sediment runoff, and illegal incursions will continue unabated if the road is not hydrologically stabilized and adequately blocked from motorized traffic. The Forest Service's National Best Management Practices for non-point source pollution recommends the following management techniques for minimizing the aquatic impacts from closed system roads: eliminate flow diversion onto the road surface, reshape the channel and streambanks at the crossing-site to pass expected flows without scouring or ponding, maintain continuation of channel dimensions and longitudinal profile through the crossing site, and remove culverts, fill material, and other structures that present a risk of failure or diversion (USDA Forest Service 2012b).

As noted above, many species benefit when roads are closed to motorized use. However, the fact remains that closed system roads are often breached resulting in impacts to fish and wildlife. A significant portion of gates and closure devices are ineffective at preventing motorized use (Griffin 2004, USFWS 2007). For example, in a legal decision from the Utah District Court, *Sierra Club v. USFS*, Case No. 1:09-cv-131 CW (D. Utah March 7, 2012), the court found that, as part of analyzing alternatives in a proposed travel management plan, the Forest Service failed to examine the impact of continued illegal use. In part, the court based its decision on the Forest Service's acknowledgement that illegal motorized use is a significant problem and that the mere presence of roads is likely to result in illegal use.

In addition to the disturbance to wildlife from motorized use, incursions and the accompanying human access can also result in illegal hunting and trapping of animals. The Tongass National Forest refers to this in its EIS to amend the Land and Resources Management Plan. Specifically, the Forest Service notes in the EIS that Alexander Archipelago wolf mortality due to legal and illegal hunting and trapping is related not only to roads open to motorized access, but to all roads, and that *total road densities* of 0.7-1.0 mi/mi^2 or less may be necessary (USDA Forest Service 2008).

Impacts of unauthorized (non-system) roads

As of 1998, there were approximately 130,000 miles of non-system roads in national forests (USDA Forest Service, 1998). However, the creation of unauthorized roads continues to be a problem as the Forest Service struggles to properly enforce travel management plans protecting areas from motorized travel. No requirements are in place directing the agency to track or inventory unauthorized roads, therefore currently their precise number is unknown. These roads contribute significantly to the environmental impacts of the transportation system on forest resources, just as forest system roads do. Because the purpose of a road density analysis is to measure the impacts of roads at a landscape level, the only way to do this is for the Forest Service to include all roads, including non-system roads, when measuring impacts. An all-inclusive analysis will provide a more accurate representation of the environmental impacts of the road network within the analysis area.

Impacts of temporary roads

Temporary roads are not considered system roads. Most often they are constructed in conjunction with timber sales. Temporary roads have the same types of environmental impacts as system roads, although at times the impacts can be worse if the road persists on the landscape because they are not built to last. It is important to note that although they are termed temporary roads, their impacts are not temporary. According to Forest Service Manual (FSM) 7703.1, the agency is required to "Reestablish vegetative cover on any unnecessary roadway or area disturbed by road construction on National Forest System lands within 10 years after the termination of the activity that required its use and construction."

Regardless of the FSM 10-year direction, temporary roads often remain for much longer because timber sale contracts typically last 3-5 years or more. If the timber purchaser builds a temporary road in the first year of a five-year contract, its intended use may not end until the full project is complete, which can include post-harvest actions such as prescribed burning. Even though the contract often requires the purchaser to close, obliterate and seed the roadbed with native vegetation, this work typically occurs after a few years of treatment activities. The temporary road, therefore, could remain open for 7-8 years or longer before the FSM ten-year clock starts ticking. Therefore, temporary roads can legally remain on the ground for up to 20 years or more, yet they are constructed with fewer environmental safeguards than modern system roads. Exacerbating the problem is the rise of landscape-scale projects that last between 10-20 years. Unless there is explicit direction requiring temporary road removal within a certain time after treatment activities, it is likely these roads could persist for decades.

Impacts of motorized trails

Motorized use on trails has serious harmful effects similar to roads, and it is crucial for the Forest Service to include motorized trails in its density calculations. As we note several times in Section I above, scientific research and agency publications find similar impacts between motorized trails and roads. Off-road vehicle (ORV) use on trails impact multiple resources, resulting in soil compaction and erosion, trampling of vegetation, as well as wildlife habitat loss, disturbance, and direct mortality. Many of these impacts increase on trails not planned or designed for vehicles, as is often the case when the Forest Service designates ORVs on trails built for hiking or equestrian uses. In many instances the agency designates motorized use on unauthorized trails created through illegal use or from a legacy of unmanaged cross-country travel, further exacerbating the related harmful effects. For a full review of the environmental and cultural impacts on forest lands see Switalski and Jones (2012), and for a review of impacts in arid environments see Switalski (2018).

C. Using Best Management Practices to Achieve a Sustainable Road System

Numerous Best Management Practices (BMPs) were developed to help create a more sustainable transportation system and identify restoration opportunities. BMPs provide science-based criteria and direction that land managers follow in making and implementing decisions about human uses and projects that affect natural resources. Several states have developed BMPs for road construction, maintenance, and decommissioning practices (e.g., Logan 2001, Merrill and Cassaday 2003). The report entitled, National Best Management Practices for Water Quality Management on National Forest System Lands, includes specific road BMPs for controlling erosion and sediment delivery into waterbodies and maintaining water quality (USDA FS 2012b). These BMPs cover road system planning, design, construction, maintenance, and decommissioning as well as other transportation-related activities.

Forest Service BMPs - Implementation and Effectiveness

While national BMPs have been established, the effectiveness of individual BMPs, and whether they are implemented at all, is in question. Furthermore, design features are increasingly replacing BMPs for project-level mitigation of road-related environmental impacts. These design features are not consistent among projects, but rather adapted from forest plans and state BMPs, rather than national Forest Service guidelines. Design features need to be standardized, and their rate of implementation and effectiveness systematically reviewed.

When considering how effective BMPs are at controlling nonpoint pollution on roads, both the rate of implementation, and their effectiveness should both be considered. The Forest Service tracks the rate of implementation and the relative effectiveness of BMPs from in-house audits. This information is summarized in the *National BMP Monitoring Summary Report* with the most recent data being the fiscal years 2013-2014 (Carlson et al. 2015). The rating categories for implementation are "fully implemented," "mostly implemented," "marginally implemented," "not implemented," and "no BMPs." "No BMPs" represents a failure to consider BMPs in the planning process. More than a hundred evaluations on roads were conducted in FY2014. Of these evaluations, only about one third of the road BMPs were found to be "fully implemented" (Carlson et al. 2015, p. 12).

The monitoring audit also rated the relative effectiveness of the BMP. The rating categories for effectiveness are "effective," "mostly effective," "marginally effective," and "not effective." "Effective" indicates no adverse impacts to water from project or activities were evident. When treated roads were evaluated for effectiveness, almost half of the road BMPs were scored as either "marginally effective" or "not effective" (Carlson et al. 2015, p. 13). However, BMPs for completed road decommissioning projects showed approximately 60 percent were effective and mostly effective combined, but it was unclear what specific BMPs account for this success (Carlson et al.

2015, p. 35). As explained below, road recontouring that restores natural hillside slopes is a more effective treatment compared to those that leave road features intact.

A recent technical report by the Forest Service entitled, *Effectiveness of Best Management Practices that Have Application to Forest Roads: A Literature Synthesis* summarized research and monitoring on the effectiveness of different BMP treatments for road construction, presence and use (Edwards et al. 2016). They found that while several studies have found some road BMPs are effective at reducing delivery of sediment to streams, the degree of each treatment has not been rigorously evaluated (Edwards et al. 2016). Few road BMPS have been evaluated under a variety of conditions, and much more research is needed to determine the site-specific suitability of different BMPs (Edwards et al. 2016, also see Anderson et al. 2011).

Edwards et al. (2016) cites several reasons for why BMPs may not be as effective as commonly thought. Most watershed-scale studies are short-term and do not account for variation over time, sediment measurements taken at the mouth of a watershed do not account for in-channel sediment storage and lag times, and it is impossible to measure the impact of individual BMPs when taken at the watershed scale. When individual BMPs are examined there is rarely broad-scale testing in different geologic, topographic, physiological, and climatic conditions. Further, Edwards et al. (2016) observes, "The similarity of forest road BMPs used in many different states' forestry BMP manuals and handbooks suggests a degree of confidence validation that may not be justified," because they rely on just a single study. Therefore, BMP effectiveness would require matching the site conditions found in that single study, a factor land managers rarely consider.

Climate change will further put into question the effectiveness of many road BMPs (Edwards et al. 2016). While the impacts of climate will vary from region to region (Furniss et al. 2010), more extreme weather is expected across the country which will increase the frequency of flooding, soil erosion, stream channel erosion, and variability of streamflow (Furniss et al. 2010). BMPs designed to limit erosion and stream sediment for current weather conditions may not be effective in the future. Edwards et al. (2016) states, "More-intense events, more frequent events, and longer duration events that accompany climate change may demonstrate that BMPs perform even more poorly in these situations. Research is urgently needed to identify BMP weaknesses under extreme events so that refinements, modifications, and development of BMPs do not lag behind the need."

The uncertainties about BMP effectiveness as a result of climate change, compounded by the inconsistencies revealed by BMP evaluations, suggest that the Forest Service cannot simply rely on them, or design features/criteria, as a means to mitigate project-level activities. This is especially relevant where the Forest Service relies on the use of BMPs instead of fully analyzing potentially harmful environmental consequences from road design, construction, maintenance or use, in studies and/or programmatic and site-specific NEPA analyses.

D. Effectiveness of Road Decommissioning Treatments

In order to truly achieve a sustainable minimum road system, the Forest Service must effectively remove unneeded roads. According to the Forest Service, the objective of road decommissioning is to "stabilize, restore, and revegetate unneeded roads to a more natural state to protect and enhance NFS lands" (FSM 7734.0). However, rather than actively removing roads, the Forest Service is increasingly relying on abandoning roads to reach decommissioning treatment objectives (Apodaca et al.2018). Simply closing or abandoning roads will lead to continued resource damage. Other treatments such as ripping the roadbed or installing drainage such as waterbars or dips, have limited and often short-term benefits to natural resources (e.g., Luce 1997, Switalski et al. 2004, Nelson et al. 2010). Recontouring roads is the only proven method to attain the intended outcome of road decommissioning.

Several studies have documented the benefits of fully recontouring roads for ecological restoration. Lloyd et al. (2013) found that rooting depths were much deeper in recontoured roads than in abandoned roads in Idaho, and soil organic matter was an order of magnitude higher on recontoured roads than abandoned roads. Further studies show that soil carbon storage is much higher on recontoured roads as well. A study in Northern California found that recontouring roads resulted in higher soil organic carbon than ripping the roads (Seney and Madej 2015). Higher tree growth and wildlife use has also been found on and near recontoured roads than ripped or abandoned roads (Kolka and Smidt 2004, Switalski and Nelson 2011). Switalski and Nelson (2011) found increased use by black bears on recontoured roads than closed or abandoned roads due to increased food availability and increased habitat security. In addition, removing culverts at stream crossings results in restoring aquatic connectivity and expanding habitat (Erkinaro et al. 2017).

Legacy Roads Monitoring Project

Since 2008, the Forest Service Rocky Mountain Research Station has conducted systematic monitoring on the effectiveness of decommissioned roads in reducing hydrologic and geomorphic impacts from the Forest Service road network. One intent of the monitoring project was to gauge the success of the Legacy Roads and Trails Program that Congress established to provide dedicated funding for the treatment and removal of unnecessary forest roads. The monitoring found that recontouring roads and restoring stream crossings results in dramatic declines in road-generated sediment. Storm-proofing treatments lead to fewer benefits, and on control sites (untreated or abandoned roads), high levels of sediment delivery continued, and the risk of culvert failures remained. For example, a study on the Lolo Creek Watershed on the Clearwater National Forest found a 97% reduction in road/stream connectivity following road recontour (Cissel et al. 2011). Using field observations and the Geomorphic Roads Analysis and Inventory Package (GRAIP), they found a reduction of fine sediments from 38.1 tonnes/year to 1.3 tonnes/year along 3.5 miles of road. Furthermore, they found that restoring road/stream crossings eliminated the risk of culverts plugging, stream diversions, and fill lost at culverts (Table 8).

On the other hand, monitoring conducted on the Caribou-Targhee National Forest found only a 59% reduction of fine sediment delivery from a combination of storm proofing (installation of drain dips), ripping, tilling, and outsloping techniques. There was a reduction of 34.9 tons/year to 14.1 ton/year – leaving a significant amount of sediment continuing to be delivered to streams. Additionally, some stream crossing culverts were not treated and the risk of plugging remained leaving 330 m^3 of fill material at risk. While trail conversion and decommissioning treatments reduced slope failure risks, in some cases storage treatments actually increased the risk of failure (Nelson et al. 2010). Additional monitoring studies conducted in Montana, Idaho, Washington, Oregon, and Utah have similar results.[10]

Table 8. Summary of GRAIP road risk predictions for a watershed on the Clearwater National Forest road decommissioning treatment project (reprinted from Cissel et al. 2011).

IMPACT/RISK TYPE	**EFFECT OF TREATMENT: INITIAL GRAIP PREDICTION**
Road-stream hydrologic connectivity	-97%, -2510 m
Fine Sediment Delivery	-97%, -36.8 tonnes/yr.
Landslide Risk	Reduced to near natural condition
Gully Risk	Reduced from very low to negligible
Stream Crossing Risk -plug potential -fill at risk -diversion potential	 -100% eliminated at 9 sites -100%, 268 m^3 fill removed -100%, eliminated at 3 sites
Drain Point Problems	17 problems removed, 4 new problems

The Forest Service recognizes that fundamental to road decommissioning is revegetating the roadbed. FSM 7734 states, "Decommission a road by reestablishing vegetation and, if necessary, initiating restoration of ecological processes interrupted or adversely impacted by the unneeded road." However, roads are inherently difficult to revegetate because of compaction, lack of soil and organic material, low native seedbank, and presence of noxious weeds (Simmers and Galatowitsch 2010, Ramlow et al. 2018). Many recently acquired industrial timberlands (e.g. Legacy Lands) have

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[10] For reports visit https://www.fs.fed.us/GRAIP/LegacyRoadsMonitoringStudies.shtml

road systems with limited canopy cover, little woody debris available, and a large weed seedbank. Thus, revegetation is going to be particularly challenging on these lands.

Consistent application of BMPs that direct recontouring roads for decommissioning will be essential to ensure the treatments best achieve improvements in ecological conditions. More than any other treatment, road recontouring ensures complete decompaction of the roadbed, incorporates native soils that were side-cast during construction, and prevents motorized use. This in turn increases plant rooting depths, soil carbon storage, tree growth, and wildlife use. Any earth disturbing activity can create conditions favorable to noxious weeds, so treating weeds before any treatment and ensuring quick revegetation can limit weeds spread. Applying road recontour BMPs that also mitigate risks associated with noxious weed expansion will help prevent their spread

Conclusion

Numerous studies show that roads and motorized trails negatively impact the ecological integrity of terrestrial and aquatic ecosystems and watersheds. There is ample evidence to confirm the harm to wildlife, aquatic species, water quality, and natural processes from forest roads and motorized use. In addition, the evolving science surrounding roads and wildfire demonstrate a direct link between access and human-caused ignitions, and also suggests that land managers must consider how roads affect fire behavior. Minimizing these impacts by reducing road densities could be an effective solution.

An increasing body of literature exists demonstrating that not only is the Forest Service's transportation infrastructure highly vulnerable to climate change, but also that roads exacerbate climate change's harmful effects to other resources. The agency itself has published multiple reports and guidelines for adaptation, yet few forests are fully translating the information into tangible actions. The Forest Service must implement climate change adaptations as soon as possible, including protecting and expanding intact forests as part of a growing effort to promote natural climate change solutions. Opportunities exist to reduce fragmentation, sequester carbon, and expand roadless areas by implementing a minimum road system.

The Forest Service must fulfil its mandate to achieve an ecologically and economically sustainable forest road system by fully complying with the Roads Rule's requirement to identify a minimum road system. Inconsistent policy interpretations, inadequate travel analysis reports and lack of accountability has largely left this goal wholly out of reach. Yet this work remains vitally important, especially in the context of climate change. The Forest Service should reinvigorate its efforts to comply with the rule's requirements. Towards this end, the agency must include current science, particularly related to future climate conditions. All road and motorized trail densities should be included in the analysis. When the agency actually does identify a minimum road system and proposes to remove unneeded roads, it must carefully evaluate the effectiveness of all proposed BMPs and design features, and fully implement the most effective decommissioning treatments to maximize restoring ecological integrity to the area. These actions will ensure the Forest Service finally achieves its goal to establish a truly sustainable forest road system.

Recontoured road, Olympic National Forest - Skokomish Watershed, 2017. By WildEarth Guardians

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Forestry and Tree Planting in North Carolina

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Abstract

North Carolina's forests cover more than 18.6 million acres (7.5 million hectares), equaling more than 59 percent of the State's land area. Nearly 97 percent of this forest land is capable of timber production. Forestry contributes more than $6 billion annually to the State's economy. The State's forests are genetically and commercially diverse and support more than 60 major tree species. Many other species are also important to the State's native forest ecosystems. Major forest types are oak and hickory; loblolly and shortleaf pine; oak, gum, and cypress; oak and pine; and longleaf pine. State forestry programs support these species, other important species, and ecosystem restoration efforts. More than 50 million tree seedlings are planted annually, 16 million of which are produced by State nurseries. While most of these seedlings are softwoods, local hardwood seed is also collected and expansion of container seedling operations continues. Inroads have been made in growing more specialty species for wetland and streambank restoration needs. Understory herbaceous plants are also being grown for longleaf pine ecosystem restoration projects. Support for the State nursery is still strong, and landowners are encouraged to plant and reforest lands as part of their long-term forest management.

Introduction

Forestry in North Carolina has a long history, beginning with the naval stores industry of colonial times. From 1720 to 1860, North Carolina's pine forests were plentiful, and the resin extracted from longleaf pine was used for tar, pitch, and turpentine. This use was unsustainable, however, and partially led to the industry's demise. The State is considered the birthplace of professional forestry in America. In 1892, Gifford Pinchot, who later became the first Chief of the Federal agency that would become the Forest Service, served as the first Forest Manager for George W. Vanderbilt's Biltmore Estate where he developed and implemented a forest management plan (Goodwin 1969). Subsequently, in 1895, German forester Dr. Carl A. Schenck went to North Carolina to succeed Gifford Pinchot as manager, and 3 years later, in 1898, Schenck founded the Biltmore Forest School. About 300 students attended the school during Schenck's tenure, including Fredrick Weyerhaeuser. The students managed a nursery at Brevard that produced a wide variety of tree species. During this time, the first North Carolina (and possibly the United States) commercial forest tree plantings occurred.

In 1891, W.W. Ashe became the first State employee to carry out timber assessments for the North Carolina Geologic Survey. Ashe became the first forestry expert in 1908 when a separate State Forestry Division was created as part of the N.C. Geological and Economic Survey. In 1909, J.S. Holmes was appointed as the first State employed graduate forester. The early establishment of the State forestry agency occurred in 1921 when forest protection from pests and wildfires was the driving public concern in North Carolina.

The founding of the Civilian Conservation Corps (CCC) ushered in a period of extensive tree planting in the State. CCC crews within North Carolina planted about 15 million seedlings from 1933 to 1938. The Soil Bank days of the 1950s increased the amount of tree planting and, by the 1960s, private forestry companies began plantation management on a large scale in the State. Georgia-Pacific, Weyerhaeuser, and Federal Paperboard, among other companies, planted millions of seedlings on their land holdings. The North Carolina State nurseries produced the bulk of these seedlings by supplying more than 100 million annually. Within a short time period, Weyerhaeuser and Federal Paperboard began operating their own nurseries and the planting of genetically improved seedlings became common in the State. In 1977, the State Forest Development cost-share program was authorized by the North Carolina General Assembly and, in 2004, the one-millionth acre was planted in the State using this program.

Forestry has developed and been recognized for its outreach into management of other natural resources in addition to the scientific management of forest ecosystems. Forestry, logging, wood products manufacturing, and forest recreation contribute more than $6 billion annually to the North Carolina economy (Brown 2007, NCDFR 2009a).

North Carolina's Environment

North Carolina is one of the most physiographically diverse States in the Eastern United States. Three distinct physiographic provinces exist: the Coastal Plain, the Piedmont, and the Mountains (figure 1). Elevations range from sea level to 6,684 ft

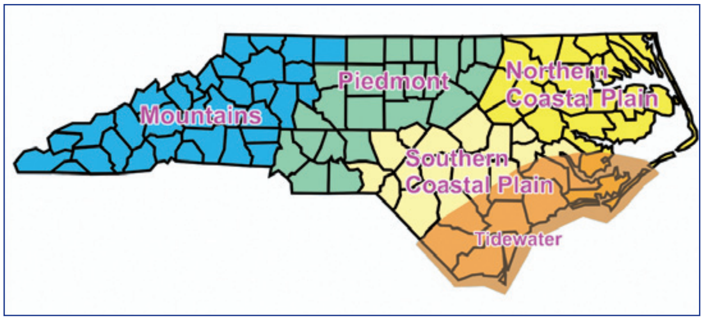

Figure 1. The three physiographic regions of North Carolina based on survey unit (county) boundaries. The tidewater area in the coastal plain is a poorly drained area adjacent to the coast (Source: Unpublished North Carolina Division of Forest Resources, 2011).

(2,037 m), the highest point east of the Rocky Mountains. The State also has more peaks higher than 6,000 ft (1,830 m) than any State east of the Mississippi River (SCONC 2011) and possesses the most extensive system of barrier islands in the United States. These islands extend east into the Atlantic Ocean and are subject to frequent exposure to Atlantic Ocean storms, including hurricanes and nor'easters. Not far inland are pocosins and Carolina bays, more concentrated in North Carolina than in any other State (NCDSS 2011). Deep swamp areas are also common in the eastern one-third of the State.

The climate in North Carolina is also diverse and varies from the Atlantic coast in the east to the Appalachian Mountain range in the west. The mountains often act as a shield by blocking cold temperatures and storms from the Midwest from entering the Piedmont region of North Carolina (SCONC 2011). Temperatures rarely go above 100 °F (38 °C) or fall below 10 °F (-12 °C), but differences in altitude and proximity to the ocean create significant local variations. Rainfall ranges from 35 to 40 in (89 to 102 cm) annually in the Piedmont region, to larger amounts along the coast (70 to 80 in [178 to 203 cm]), to greater than 100 in (254 cm) in the Great Smoky Mountains in the southwest of the State (C-DC 2010). The Mountains are as likely to experience the effects of tropical storms originating from the Gulf of Mexico as the Coastal Plain is likely to experience the effects of tropical storms originating from the Atlantic.

Natural Areas

North Carolina occupies 31.2 million acres (12.6 million hectares) (figure 2). Of this area, 59 percent is forested (Bardon and others 2010). The remaining land consists of urban and industrial development, farmland, and inland water. Of the forested areas, 2 percent are classified as reserved forest land. These forest lands extend across the 17 major river basins in North Carolina (figure 3) (NCDWR 2011).

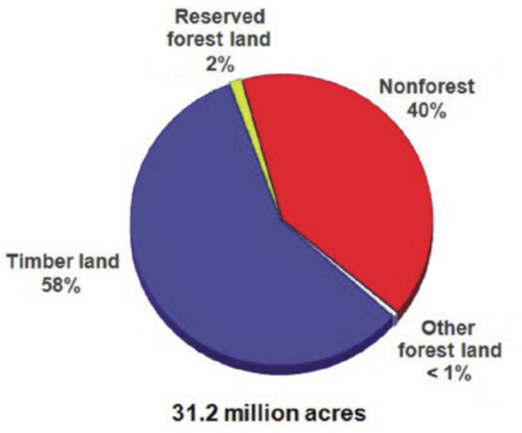

Figure 2. Classification of land area in North Carolina (Source: Bardon and others, 2010).

Figure 3. North Carolina river basins (Source: North Carolina Department of Environment and Natural Resources, 2011 available on Web: http://www.ee.enr.state.nc.us/public/ecoaddress/riverbasins/riverbasinmapinteractive.htm).

The North Carolina Division of Forest Resources (NCDFR) recognizes 13 major forest types; 5 are softwood types and 8 are hardwood types (table 1). The oak/hickory (upland hardwood type) and the loblolly/shortleaf pine (upland softwood type) are the most abundant forest types in the State. Planted stands account for about one-half of the loblolly/shortleaf area (figure 4). Planted oak/pine stands usually result from significant hardwood competition and pine stocking levels that precluded classification as a pine type. Many of these stands originated as pine plantations. Over time and due to natural succession, hardwood species have invaded and thrived, and the distribution of species has changed to a mixed stand.

The 13 forest types are more practically consolidated into six management units based on species, stocking, and stand origin. The six management units are upland hardwood, natural pine, plantation pine, lowland hardwood, oak-pine, and nonstocked (table 2).

Coastal Plain

The land and inland water areas of the Coastal Plain comprise nearly one-half of the State's land area and are divided into northern and southern subregions (figure 1). It can be further subdivided into two sections based on drainage: the tidewater area, which is along the coast and in large part low, flat, and swampy; and the interior portion, which is gently sloping and, for the most part, naturally well drained. Throughout the Coastal Plain, soils consist of soft sediment, with little or no underlying hard rock near the surface. The elevation ranges from about 200 ft (60 m) at the fall line, or western boundary, to less than 50 ft (15 m) higher than the tidewater area (SCONC 2011).

The Coastal Plain is 59 percent forested and contains almost 49 percent of the State's timber land (tables 1 and 2). Because the Coastal Plain contains the State's lowest elevations and has the smallest gradients in elevation, this area contains most of North Carolina's swamps and pocosins. Riverine systems are typically slow, more meandering, and of blackwater type if originating from within the region. Because of these features, most North Carolina bottomland hardwood and cypress forests (a combined 84 percent) are found in the Coastal Plain. Loblolly pine (*Pinus taeda* L.) is the most prevalent softwood type in the region, and nearly all of the State's longleaf pine (*Pinus palustris* Mill.) and pond pine (*Pinus serotina* Michx.) are found there. Unique to this region of the State, Atlantic white cedar (sometimes referred to as AWC or juniper) (*Chamaecyparis thyoides* L. [B.S. & P.]) once covered

Table 1. North Carolina timber land area by forest plant community type and survey unit (2007 survey data).

Forest plant community type	North Carolina physiographic province			
	Coastal Plain	Piedmont	Mountains	Total
	Acres (hectares)			
Hardwoods				
Aspen/birch	0 (0)	0 (0)	1,508 (610)	1,508 (610)
Elm/ash/cottonwood	253,448 (102,567)	250,686 (101,450)	12,164 (4,923)	516,298 (208,938)
Exotic hardwoods	3,775 (1,528)	0 (0)	2,948 (1,993)	6,723 (2,721)
Maple/beech/birch	0 (0)	0 (0)	56,895 (23,025)	56,895 (23,025)
Oak/gum/cypress	1,763,321 (713,590)	123,951 (50,161)	0 (0)	1,887,272 (763,752)
Oak/hickory	1,388,073 (561,733)	2,790,366 (1,129,221)	3,110,179 (1,258,645)	7,288,618 (2,949,600)
Oak/pine	1,141,857 (462,093)	792,957 (320,898)	380,836 (154,119)	2,315,650 (937,110)
Other hardwoods	5,810 (2,351)	0 (0)	109,279 (44,224)	115,089 (46,575)
Hardwoods total	4,556,284 (1,843,863)	3,957,960 (1,601,729)	3,673,809 (1,486,738)	12,188,053 (4,932,330)
Softwoods				
Loblolly/shortleaf	3,807,672 (1,540,910)	1,305,697 (528,397)	115,707 (46,825)	5,229,076 (2,116,132)
Longleaf	289,850 (117,298)	257 (104)	0 (0)	290,107 (117,402)
Other eastern softwoods	1,453 (588)	26,769 (10,833)	1,518 (614)	29,740 (12,035)
Spruce/fir	0 (0)	0 (0)	12,063 (4,882)	12,063 (4,882)
White/red/jack pine	0 (0)	1,025 (414)	134,085 (54,262)	135,110 (54,677)
Softwoods total	4,098,975 (1,658,796)	1,333,748 (539,749)	263,373 (106,583)	5,696,096 (2,305,128)
Nonstocked	111,287 (45,036)	35,978 (14,560)	11,644 (4,712)	158,909 (64,308)
Total	8,776,546 (3,551,742)	5,327,686 (2,156,038)	3,948,826 (1,598,033)	18,043,058 (7,301,766)
Total percent	49%	30%	21%	100%

Source: U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis, 2010.

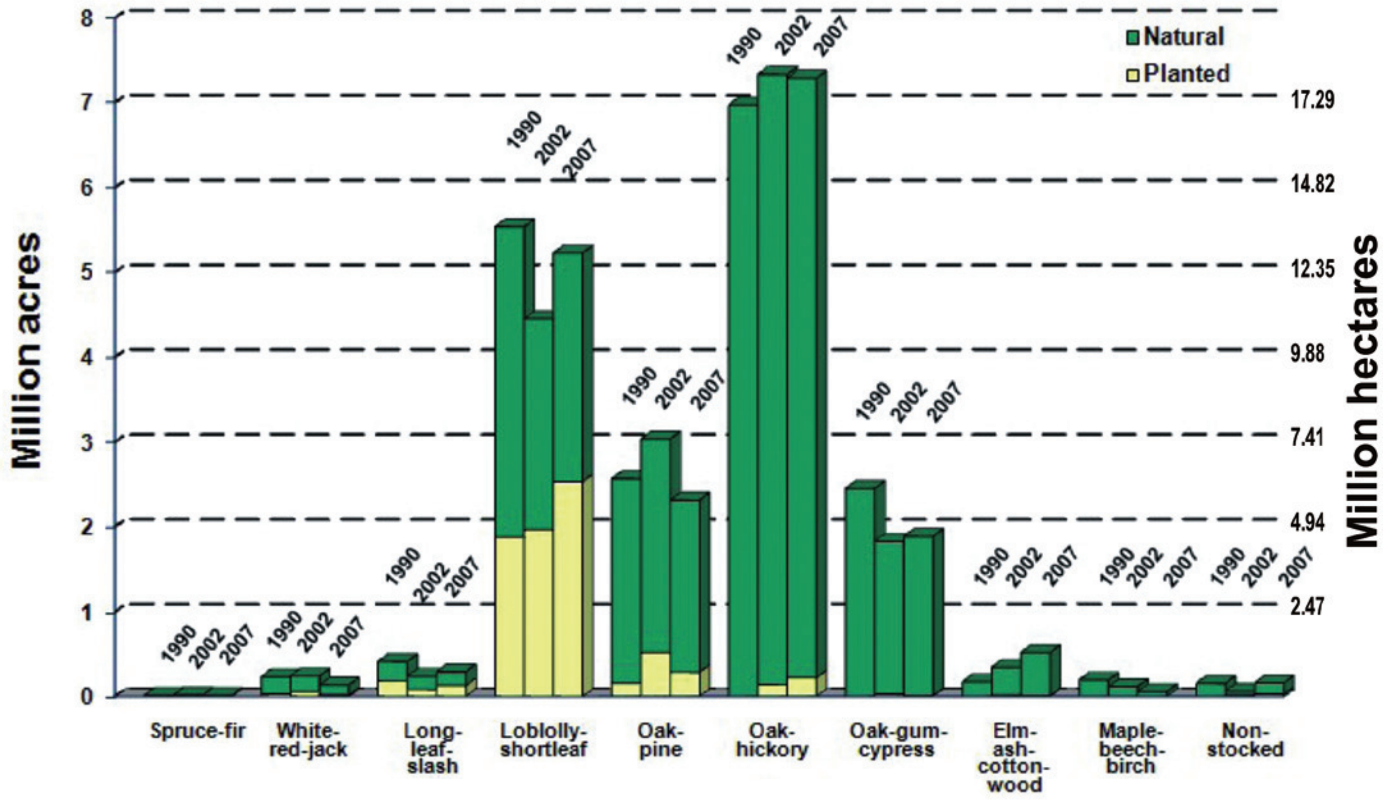

Figure 4. Trends in timber land area by seedling type and forest community type (Source: Bardon and others, 2010).

Table 2. Timber land area by North Carolina physiographic province and forest management type.

Forest management type	North Carolina physiographic province			
	Coastal Plain	Piedmont	Mountains	Total
	Acres (hectares)			
Upland hardwoods	1,397,658 (565,612)	2,790,366 (1,129,221)	3,280,809 (1,327,696)	7,468,833 (3,022,530)
Natural pine	1,956,414 (791,733)	830,384 (336,044)	229,487 (92,870)	3,016,285 (1,220,647)
Planted pine	2,142,560 (867,063)	503,365 (203,705)	33,886 (13,713)	2,679,811 (1,084,481)
Lowland hardwoods	2,016,769 (816,157)	374,637 (151,610)	12,164 (4,923)	2,403,570 (972,690)
Oak-pine	1,141,857 (462,093)	792,957 (320,898)	380,836 (154,119)	2,315,650 (937,110)
Nonstocked	111,287 (45,036)	35,978 (14,560)	11,644 (4,712)	158,909 (64,308)
Total	8,766,545 (3,547,695)	5,327,687 (2,156,038)	3,948,826 (1,598,074)	18,043,058 (7,301,766)

Source: U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis, 2010.

large expanses but is now confined to small areas. Many of the ecosystems found here are fire dependent and will change when fire is excluded.

Piedmont

The Piedmont province is 51 percent forests and represents 30 percent of the State's timber land. The Piedmont province contains the State's largest metropolitan areas, the highest population concentrations, and the most nonforested areas of all the regions in North Carolina. The Piedmont province terrain is much more varied than the Coastal Plain terrain and includes a wide range of tree species. Hardwoods predominate, but mixed stands are common, with loblolly pine the most abundant softwood type and Virginia pine (*Pinus virginiana* Mill.) second (tables 1 and 2). The most common hardwood stands are the white oak-red oak-hickory forest type followed closely by the yellow poplar-oak and the sweetgum-yellow poplar. Riverine systems encounter more gradient here; because of the higher clay mineral content of the soils and movement of these minerals into the drainages, they are referred to as the red river bottom type.

Mountains

The Mountains are 76 percent forested and contain 21 percent of the State's timber land. The region contains most of the State's reserved timber land, primarily in the Great Smoky Mountains National Park. The Mountains have the highest proportion of publicly owned timber land in the State, mainly because the Pisgah and Nantahala National Forests are located here. The Mountains have fewer large cities and urban development than the State's other regions and contain the State's highest elevations and most rugged terrain. Because of the topography, the Mountains are where the headwaters of many streams occur. Waters here are often whitewater in nature, and most are classed as freestone streams—those formed from rainfall and snowmelt. The Mountains are dominated by upland hardwoods, which account for 80 percent of the region's timber land. Chestnut oak, black oak, and scarlet oak stands dominate the region, followed by white oak, red oak, and hickory stands and then by yellow poplar, white oak, and northern red oak stands, in terms of abundance (tables 1 and 2).

The Mountains' highest elevations also contain tree genera typically occurring at more northern latitudes, such as spruce (*Picea*), fir *(Abies*), and birch *(Betula*). Eastern white pine (*Pinus strobus* L.) is the most common softwood type found here.

Forest Land Ownership

Approximately 14.1 million acres (5.7 million hectares), or about 78 percent of the State's timber land, is owned by nonindustrial private forest (NIPF) landowners (figure 5). The proportion of NIPF ownership is 91 percent in the Piedmont, 74 percent across the Coastal Plain, and 70 percent in the Mountains. Ownership by timber investment management organizations has been increasing in the past decade. Forest industry timber land ownership accounts for 8 percent of all timber land (14 percent of Coastal Plain, 3 percent of the Piedmont, and 1 percent of the Mountains).

Timber land ownership by public agencies accounts for 14 percent of all timber land in the State. Public ownership of timber land has increased by about 10 percent since 2002. Public ownership is highest in the mountains, largely due to National Forest System holdings there.

Challenges Facing the State's Forests

Urbanization

As the North Carolina population grows, so does the rural-urban interface. This expanding interface increases demand on forests for water, recreation, and aesthetics, as well as for traditional wood products. Incoming residents in these areas are typically unfamiliar with North Carolina's native forest ecosystems, management practices, and wildfire danger. Green corridors are becoming narrower and disjointed and some forests are becoming smaller. Many of the ownerships in this interface are only a few acres (hectares) in size.

Insects and Diseases

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) is the most destructive forest insect in North Carolina, attacking trees of all age classes. Populations are cyclical; a beetle population-monitoring program is in place. Ips engraver beetle (*Ips* spp.) is the second most destructive insect pest in the State.

Young loblolly pine seedlings are susceptible to pine tip moth (*Rhyacionia* spp.) and to fusiform rust (*Cronartium quercuum* f. sp. *fusiforme* [Hedgc. & N. Hunt] Burdsall & G. Snow), especially when the alternate host is present. Genetic improvement of loblolly pine has made great strides in finding resistant families. These families are now recommended for high rust hazard sites.

Shortleaf pine (*Pinus echinata* Mill.) is susceptible to fusiform rust, pitch canker (*Fusarium subglutinans* (Wollenweb. & Reinking) P.E. Nelson, Toussoun & Marasas f. sp. pini), and littleleaf disease (*Phytophthora cinnamomi* Rands).

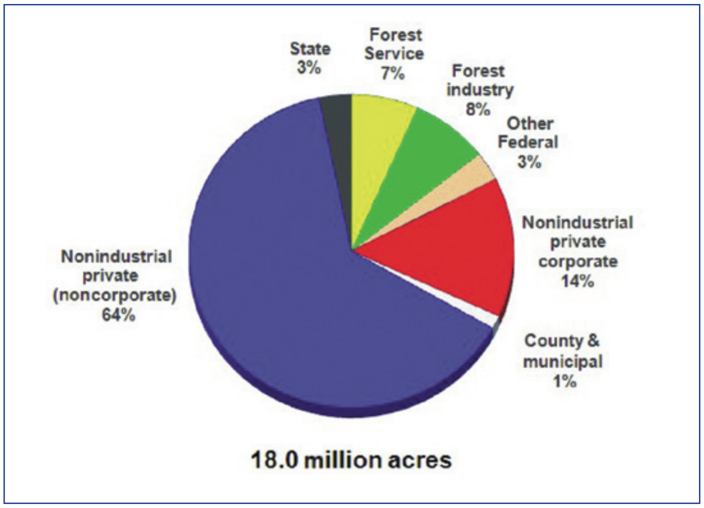

Figure 5. Area of timber land ownership in North Carolina (Source: Bardon and others, 2010).

Phytophthora is becoming endemic and also kills Fraser fir (*Abies fraseri* [Pursh.] Poir.). Eastern white pine is resistant and is recommended as an alternative species to Fraser fir on those sites, which are infected with Phytophthora. Eastern white pine, however, is susceptible to white pine blister rust, (*Cronartium ribicola* J.C.Fisch.) and white pine weevil (*Pissodes strobi* Peck). Combined, these pests reduce the value of white pine in the State.

Longleaf pine shows a high resistance to fusiform rust, tip moth, and fire (Barnard and Mayfield 2009) but is susceptible to pitch canker. Brown-spot needle blight (*Scirrhia acicola* [Dearn.] Siggers.) is also a problem.

More details regarding North Carolina's current forest health are available in the 2010 Forestry Assessment (Bardon and others 2010).

Drought

Currently, most of the North Carolina Piedmont is in a severe drought (NCDMAC 2011). Surrounding areas are designated as being in moderate drought. In recent years, drought has played a significant role in the occurrence and severity of forest fires.

Wildfire

North Carolina has a distinct forest fire season. This season has been extended due to the recent drought conditions affecting the State. In addition, fires have become more serious due to the increase in the number of residents living in the rural-urban interface. This situation is problematic due to the extent of fire-dependent ecosystems that are present.

North Carolina's State Forestry Agency

After preparation of this article, the North Carolina Division of Forest Resources that was under the North Carolina Department of Environment and Natural Resources is now the North Carolina Forest Service as of July 1, 2011, and is now part of the North Carolina Department of Agriculture and Consumer Services.

Founding legislation for NCDFR directs the forest agency to provide the State with forest protection (from wildfires and pests). NCDFR operates out of a Central Office located in the State capital in Raleigh. Forestry operations are organized under three regional offices, one located in each of the physiographic regions of the State (Region 1–Coastal Plain, Region 2–Piedmont, and Region 3–Mountains). Within each region are several districts, each covering several adjacent counties. Regional and district staff provide support to the county level programs. The agency owns and operates very little public land but does manage two operational State forests, seven educational State forests, three training facilities, and three forestry centers. The agency also operates two State nurseries to make forest tree seedlings available to landowners and other citizens across the State. A forest tree improvement program supports the nursery operations to provide the most genetically appropriate seedlings for planting in North Carolina. NCDFR also maintains an aviation program to provide reconnaissance for forest protection efforts and suppression resources for wildland firefighting. Other programs include law enforcement, forest management, forest health, water quality, urban forestry, and other public outreach programs. NCDFR is currently involved in developing a strategic plan to better serve North Carolina citizens. This effort will also evaluate the success and role of tree planting in the State.

The largest State forest NCDFR manages is Bladen Lakes State Forest (BLSF) covering about 32,700 acres (13,233 hectares). BLSF is a working forest that is regularly harvested for timber and reforested, mostly with longleaf pine and AWC. Longleaf pine stand management goals also include pine straw, timber, poles, and charcoal. BLSF typically plants more than 200,000 seedlings annually.

Tree Production and Planting in North Carolina

Across the State, trees are typically planted for traditional forest products such as poles, timber, pulpwood, pine straw, watershed, wildlife, aesthetics, as well as for ecosystem restoration, biomass production, landscape plants, and Christmas trees. Older, natural hardwood stands are usually harvested to supply lumber to the furniture industry and pulpwood.

The most planted species in North Carolina is loblolly pine, which is the economic forestry giant in the State. Essentially all of these seedlings are genetically improved. The next most planted species is longleaf pine. More than 50 million forest tree seedlings are typically planted in North Carolina each year (table 3). These quantities are expected to remain at this level during the next few years.

For stand establishment, weed control is one of the most important cultural practices undertaken before planting (site preparation) and during early stand establishment. If weed control is not vigorously undertaken, an entire young stand can be lost.

Stand spacing depends on site and species. Pine stand spacing ranges from 400 to 600 trees per acre (tpa), while hardwoods are typically planted at 350 to 500 tpa. AWC seedlings are

Table 3. Area of pine and hardwood trees planted in North Carolina for 2004 through 2008. Number of trees planted estimated from areas of trees planted.

	2008		2007		2006		2005		2004	
	Pine	Hardwood	Pine	Hardwood	Pine	Hardwood	Pine	Hardwood	Pine	Hardwood
	Acres (Hectares)									
Non-cost-share	26,883 (10,879)	7,116 (2,879)	28,788 (11,650)	7,337 (2,969)	42,084 (17,030)	10,984 (4,445)	40,859 (16,535)	10,825 (4,380)	32,661 (13,217)	11,468 (4,641)
Cost-share	47,598 (19,262)	438 (177)	50,389 (20,392)	452 (183)	48,351 (19,567)	1,057 (428)	46,397 (18,776)	2,201 (890)	66,746 (27,011)	1,463 (592)
Total NIPFO	74,481 (30,141)	7,552 (3,056)	79,177 (3,204)	7,789 (3,152)	90,435 (36,598)	12,041 (4,872)	87,256 (35,311)	13,026 (5,271)	99,407 (40,228)	12,931 (5,233)
Forest industry	24,000 (9,712)	0 (0)	20,000 (8,094)	0 (0)	21,000 (8,498)	0 (0)	20,000 (8,094)	0 (0)	19,000 (7,689)	0 (0)
Government	411 (166)	0 (0)	642 (260)	0 (0)	599 (242)	0 (0)	879 (356)	0 (0)	426 (172)	0 (0)
Total acres (hectares)	98,892 (40,020)	7,552 (3,056)	99,819 (40,395)	7,789 (3,152)	93,134 (37,690)	12,041 (4,872)	108,135 (43,760)	13,026 (5,271)	118,833 (48,090)	12,931 (5,233)
Total number of trees (estimated)	51,425,000	3,250,000	51,910,000	3,350,000	48,500,000	5,200,000	56,250,000	5,600,000	61,800,000	5,500,000
	54,675,000		55,260,000		53,700,000		61,850,000		67,300,000	

NIPFO = nonindustrial private forest ownership.

Note: Numbers are likely to be underreported.

Source: Georgia Forestry Commission's Annual Reforestation Survey (2009).

typically planted at closer spacings (1,500 to 1,700 tpa). Third cycle loblolly pine require wider spacing to allow the trees to grow more freely.

North Carolina State Nurseries

NCDFR operates two public-sector nurseries. Linville River Nursery (Newland, NC) produces more than 300,000 improved Fraser fir greenhouse container seedlings and 1 million improved bareroot eastern white pine seedlings annually. Claridge Nursery (Goldsboro, NC) is located in the mid-Coastal Plain near the center of the State. This nursery grows several species of southern yellow pine and other conifers, hardwoods, and a few specialty species for forestry, reclamation, and restoration plantings. This includes 12 longleaf ecosystem herbaceous species grown for the Longleaf Pine Ecosystem Restoration Program. In all, NCDFR nurseries collect seed and grow more than 16 million seedlings of more than 40 to 50 species annually, most of which are planted as 1-year-old plants.

Both of the State nurseries grow bareroot and container seedlings (figure 6). New U.S. Environmental Protection Agency regulations for pest management chemicals are expected to severely restrict bareroot seedling production in the near future. This will likely result in a shift to container operations and possible increased seedling costs.

Seed sown in these State nurseries are usually collected and processed internally by NCDFR. Seeds are collected from wild stands, seed production areas, and genetically improved seed orchards and clone banks. Seedlings produced from these seed at these nurseries can be certified as local source material for various restoration projects. Seed production areas of the longleaf understory herbaceous species, like wire grass (*Aristida stricta* Michx.), have also been established to supply additional seed. Seedlings of other species may be grown on request as needed. Rare and hard-to-find species can also be produced if sufficient quantities are required. Claridge Nursery typically contract grows seedlings for the North Carolina Department of Transportation, local military bases, and the USDA Forest Service.

Linville River Nursery produces second generation Fraser fir as field-plantable, greenhouse-bench seedlings in 2 years (figure 7). This is a big change from 5-year-old, 3-2 transplants that the Christmas tree industry has used in the past. These field-plantable seedlings make it possible for NCDFR to move commercial quantities of genetically improved seedling to growers' fields 3 years sooner. Eastern white pine is grown and sold as a 2-year-old seedling.

Figure 6. Claridge Nursery container operation showing longleaf and Atlantic white cedar seedlings (Photo source: Brad Stevens, North Carolina Division of Forest Resources, 2008).

Figure 7. North Carolina Division of Forest Resources 2-year-old field plantable greenhouse-bench Fraser fir seedling; shearing knife is shown for scale (Photo source: Ken Roeder, North Carolina Division of Forest Resources, 2009).

Seedling sales via the Internet are increasing. Sales of seedlings have been helped by offering smaller tree quantities that cater to North Carolina residents owning only a few acres (hectares) in the rural-urban interface.

In addition to the two State nurseries, a few major, and many small nurseries are located in the State that produce about 50 million forest seedlings annually for private and industrial tree planting in North Carolina and other nearby States.

Forest Tree Improvement Program

The forest tree improvement program operates in conjunction with the nursery operation to ensure that seedlings being produced are of the best genetic quality for deployment in North Carolina. The tree improvement program's goals are to maximize forest production on the decreasing number of acres in commercial forests in the State. This set of goals means that, in addition to growth rate and wood quality, disease resistance (i.e., fusiform rust) is also being assessed in selection of improved trees. This selection process will increase stand yields of higher quality products across the State. Species being actively improved under this program are loblolly pine, longleaf pine, shortleaf pine, eastern white pine, Virginia pine, AWC, Fraser fir, and sycamore. The tree improvement program is currently producing open pollinated (half-sib from mother trees) and full-sib crossed seed from NCDFR seed orchards. The full-sib loblolly pine seed is from Mass Controlled Pollination, which produces commercial quantities of the best parental crosses (figure 8).

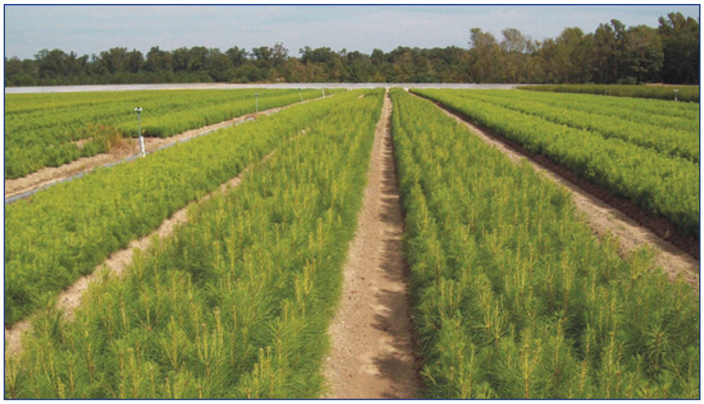

Figure 8. Third Cycle Mass Controlled Pollination seedlings are being grown at Claridge Nursery and are available for planting (Photo source: Ken Roeder, North Carolina Division of Forest Resources, 2009).

Programs Involving Tree Planting

Conservation

Two primary Federal conservation programs are administered in the State by NCDFR. The Forest Stewardship Program provides technical assistance to NIPF landowners to encourage and enable active long-term forest management including reforestation. The primary focus of the program is the development of comprehensive, multiresource management plans that provide landowners with the information they need to manage their forests for a variety of products and services. The Forest Legacy Program is a working forest conservation easement that protects habitat and provides forest products, opportunities for recreation, protection of water quality, and other public benefits.

Cost-Share Programs

Several cost-share tree-planting programs are available through NCDFR and other agencies (table 3). The Forest Development Program (FDP) is one of several cost-share programs providing funding and technical support to promote reforestation and forest improvement activities (NCDFR 2010). More than 1.5 million acres (0.6 million hectares) have been planted under this program. Under current funding levels, this program involves more than 1,500 landowners annually with an average ownership of 37 acres (15.0 hectares) (NCDFR 2009a). These cost-share programs have a large effect on the number of acres (hectares) planted (table 4).

Table 4. Forestry cost-share programs in North Carolina and longleaf pine acres planted under several of these programs.

Short title	Cost-share program title	Program agency	Longleaf pine areas planted under these programs (1997–2007)
			Acres (hectares)
CRP	Conservation Reserve Program	FSA	11,694 (4,732)
FDP	Forest Development Program	NCDFR	25,012 (10,122)
NCA	North Carolina Agricultural Cost-Share Program	NCDSWC	1,779 (720)
CREP	Conservation Reserve Enhancement Program	FSA	1,220 (494)
WRP	Wetland Reserves Program	NRCS	0 (0)
FIP	Forestry Incentive Program	NRCS	244 (99)
EQUIP	Environmental Quality Incentives Program	NRCS	NA
SIP	Stewardship Incentives Program	FS	NA
FLEP	Forest Land Enhancement Program	NCDFR—no longer available	869 (352)
FRRP	Forest Recovery and Rehabilitation Program	NCDFR—no longer available	4,481 (1,813)
FRP	Forest Recovery Program	NCDFR—no longer available	NA
—	No cost-share program	—	13,983 (5,659)

FS = USDA Forest Service. FSA = USDA Farm Service Agency. NA = data not available. NCDSWC = North Carolina Division of Sewer and Water Quality. NCDFR = North Carolina Division of Forest Resources. NRCS = USDA Natural Resources Conservation Service.

Source: NCDFR 2010.

Restoration Projects

Longleaf Pine Restoration

Recognizing the declining longleaf forest acreage, the NCDFR implemented the Longleaf Pine Restoration Initiative. The initiative focuses on artificial forest regeneration as the primary means to restore longleaf pine to sites where it was historically found and adapted to, especially in the southern Piedmont and Coastal Plain (figure 9). An average of 5,000 acres (2,023 hectares) of longleaf pine seedlings are now planted annually (NCDFR 2009b). Longleaf pine ecosystem restoration has also gained importance in recent years with increased production of seedlings and seeds of understory species.

Figure 9. New longleaf pine plantation during summer of second growing season (Photo source: Ken Roeder, North Carolina Division of Forest Resources, 2008).

Shortleaf Pine Restoration

For a variety of reasons, artificial regeneration of shortleaf pine has lagged behind other species. An average of 110 acres (44.5 hectares) of shortleaf was planted each year between 2005 and 2009 on NIPF land (NCDFR 2009a). A number of cost-share assistance programs support shortleaf pine establishment on private lands. North Carolina's FDP is the primary State-administered financial assistance program supporting shortleaf establishment, although the federally funded Environmental Quality Incentives Program, a program of the U.S. Department of Agriculture, Natural Resources Conservation Service, also funds the planting of shortleaf pine. NCDFR helps to develop management plans and provide technical expertise for these programs.

Atlantic White Cedar Restoration

Atlantic white cedar (AWC) was once a common forest type in North Carolina coastal wetlands, but has decreased to less than 10 percent of its original range. Most of the estimated 10,583 acres (4,283 hectares) remaining in North Carolina are on public lands. Exploitive logging, natural regeneration failure, absence of artificial regeneration, drainage effects, fire exclusion, and lack of competition control are cited as reasons behind the decline of AWC forests. North Carolina has identified AWC as a species of concern. NCDFR promotes conservation, restoration, and planting of AWC by providing forest management advice, conducting applied forest management research, and providing workshops and inhouse training.

Future Outlook for Tree Planting in North Carolina

As in most Southern States, urbanization is reducing the land area available for producing traditional forestry products in North Carolina. The acreage of the rural-urban interface is also growing resulting in more people living within native fire ecosystems. Risks to these residents from wildfire have increased. Demand for forest resources is also changing. While the demand for traditional products like pulp, timber, and poles is increasing, more residents also believe more forests are needed to provide clean water, wildlife, aesthetic value, and recreational environments.

More efficient use of North Carolina's forest land base is required. Use of more productive and disease-resistant, genetically improved trees is necessary. The best forest lands must be planted with the best trees and intensively managed with the most appropriate cultural practices. The number of acres planted annually has declined during the past few years. Productivity on every acre has increased, however. Potential productivity of forest land in the State is lost when a site is planted without using appropriate long-term stand management practices.

Some Southern States have closed their nurseries, but support in North Carolina is still strong. In fact, demand for seedlings from the two State nurseries appears to be increasing.

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Burrow Availability and Desiccation Risk of Mole Salamanders (*Ambystoma talpoideum*) in Harvested versus Unharvested Forest Stands

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ABSTRACT.—**Clearcutting and other forest management practices that remove canopy and disturb ground cover may exacerbate the risk of desiccation, particularly for newly metamorphosed amphibians. We examined dehydration rates of juvenile Mole Salamanders (*Ambystoma talpoideum*) in relation to burrow availability in four experimental forest management treatments. Juvenile salamanders ($N = 41$) were confined to small enclosures in four treatments representing a range of habitat disturbance: clearcut with coarse woody debris (CWD) removed; clearcut with CWD retained; thinning; and an unharvested control of second-growth, mature loblolly pine. Half of the salamanders in each habitat treatment were provided with artificial burrows. Water loss over 72 h was significantly higher in the clearcut with CWD retained than in the other three treatments. Most water loss occurred during the first two nights, when salamanders may have been most active. Only 40% of salamanders without burrows survived in the clearcuts, versus 90% in the thinned stand and 100% in the control. Ninety percent of the salamanders with access to a burrow survived in the clearcuts versus 100% in the thinning and control. We found no correlation between soil moisture and water loss and attribute higher desiccation rates in the clearcuts to high temperatures ($>$ 44°C). Although habitat changes resulting from thinning did not lead to increased desiccation, complete canopy removal greatly increased risk of mortality caused by desiccation. Our results also demonstrate that this risk is strongly mediated by the availability of burrows.**

Forest management practices that result in extensive loss of canopy cover and disturbance to ground cover have been associated with reductions in relative abundance of salamanders and other amphibians (deMaynadier and Hunter, 1995). Raymond and Hardy (1991), for example, observed a decline in numbers of Mole Salamanders (*Ambystoma talpoideum*) returning to a breeding pond from the side of the pond adjacent to a recent clearcut. Similarly, Cromer et al. (2002) found fewer Mole and Marbled (*Ambystoma opacum*) Salamanders in gaps resulting from selective logging than in unharvested areas. A proposed mechanism for population declines of some species following logging is an increased risk of desiccation. Amphibians are particularly vulnerable to desiccation because they have a higher ratio of wet surface exposed to the air than any other vertebrate (Spight, 1968). The small size and elongated body shape of many salamanders exacerbates this risk via an increase in their surface-to-volume ratio.

Compared to the more extensive literature on plethodontids (e.g., Heatwole and Lim, 1961; Spotila, 1972; Wisely and Golightly, 2003), there is relatively little information on the factors influencing dehydration rates in ambystomatid salamanders. Despite the presumed importance of desiccation risk in dictating amphibian responses to habitat alteration, few studies have measured dehydration rates or time to desiccation in habitats varying in degree of disturbance. Rothermel and Semlitsch (2002) found that juvenile Spotted (*Ambystoma maculatum*) and Small-Mouthed (*Ambystoma texanum*) Salamanders experienced greater evaporative water loss in fields than in forests over a 24-h period. Although they require wetlands for breeding, ambystomatids are completely terrestrial as juveniles and as adults during the nonbreeding season. The mean maximum migration distance for ambystomatids, calculated from values reported in the literature for seven species, is 253 m (Semlitsch and Bodie, 2003). This makes them vulnerable to clearcutting and other disturbances affecting the upland habitat surrounding wetlands (Faccio, 2003; Semlitsch and Bodie, 2003).

We compared desiccation rates of juvenile *A. talpoideum* among four experimental habitat treatments representing a range of disturbances associated with forest management activities. The treatments, a clearcut with coarse woody debris (CWD) removed, a clearcut with CWD retained, a partial harvest (thinning), and an unharvested control of second growth, mature loblolly pine (*Pinus taeda*), were applied to four 3.8-ha quadrants adjacent to a seasonal wetland. We predicted that the rates of desiccation for the salamanders would increase with the level of disturbance,

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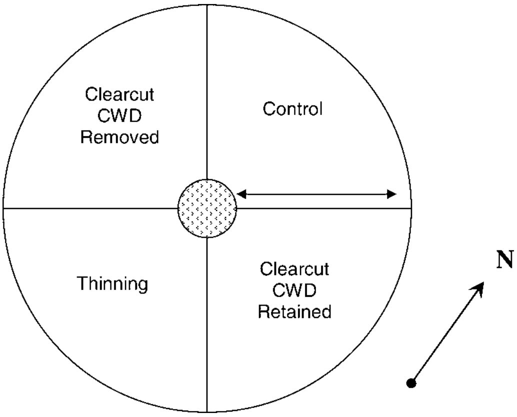

FIG. 1. Diagram showing the arrangement of the four 3.8-ha habitat treatments centered on Bay 1000. CWD = coarse woody debris.

such that salamanders in the clearcuts would experience the highest desiccation rates, followed by the thinning treatment.

We also tested the degree to which burrow availability mitigates the risk of desiccation by providing half the salamanders in each habitat treatment with a burrow. During the terrestrial phases of their life cycle, ambystomatid salamanders are largely fossorial, occupying small home ranges centered on small mammal burrows or other underground refugia (Douglas and Monroe, 1981; Semlitsch, 1981; Madison, 1997; Faccio, 2003). Such refuges provide protection from predators, desiccation, and freezing, and their density may influence terrestrial density of salamanders (Regosin et al., 2003). *Ambystoma talpoideum* are capable of burrowing in loose soil but often rely on existing crevices or burrows made by roots and other animals (Semlitsch, 1983). Thus, the compaction of soil by heavy machinery during logging could not only destroy existing burrows but could make it more difficult for salamanders to create new ones. At the same time, the additional cover provided by logging debris might compensate for the loss of burrows, at least over the short term (Moseley et al., 2004).

MATERIALS AND METHODS

The study site was an area being used for LEAP (Land-use Effects on Amphibian Populations), a multiregional, collaborative study of how land-use practices that degrade and fragment forest habitat affect the migratory success and demographics of pond-breeding amphibians. The study area was a pine-dominated woodland within a 170-m radius of a Carolina bay wetland (Bay 1000) on the Savannah River Site in Barnwell County, South Carolina. The study area was divided into four equal quadrants delineated by two perpendicular transects that intersect at the center of the wetland (Fig. 1). One 3.8-ha quadrant served as a control, whereas each of the others was subjected to one of the three forest management treatments in March, 2004, four months prior to the start of the experiment. Treatments were assigned to each quadrant randomly, with the constraint that the clearcuts could not occur in adjacent quadrants.

The overstory in the control stand consisted of 27-year-old loblolly pine (*Pinus taeda*) with a dense understory of sweetgum (*Liquidambar styraciflua*), wax myrtle (*Morella cerifera*), and holly (*Ilex opaca*) and extensive ground cover dominated by Carolina jessamine (*Gelsemium sempervirens*), poison ivy (*Toxicodendron radicans*), grape (*Vitis* sp.), and grasses. In the thinning stand, the overstory of 51-year-old loblolly pine was uniformly thinned to achieve a 25% reduction in canopy cover relative to the control (67% vs. 89%, respectively). The thinned stand had a sparser understory and less extensive ground cover than the control, both before and after logging.

The clearcut areas were not subjected to site preparation practices or replanted. In the clearcut with CWD removed (CC-removed), logs were skidded to areas off the plot, where they were piled and delimbed. In the clearcut with CWD retained (CC-retained), logs were delimbed, piled, and loaded within the plot. After logging was completed, the woody debris in the CC-retained was spread more evenly across the plot using a bulldozer. By the time our experiment was conducted in July 2004, the regenerating vegetation in the clearcuts comprised a diverse mix of resprouting hardwoods, shrubs, vines, grasses, and herbaceous plants, all generally less than 1 m tall. Approximately 20% of the area of the CC-retained was bare ground, followed by 11% in the CC-removed, 4% in the thinning, and 0% in the control. Litter depth averaged 3.1 cm in the CC-retained, 3.2 cm in the CC-removed, 2.6 cm in the thinning, and 5.0 cm in the control. Although the CC-retained contained higher amounts of woody debris > 10 cm in diameter than the CC-removed (B. B. Rothermel and J. W. Gibbons, unpubl. data), the small size of the salamander enclosures (0.025 m^2) only permitted inclusion of fine woody debris (i.e., smaller sticks and bark) and litter, which consisted predominantly of pine needles. Hence, salamanders in the CC-retained could not benefit directly from the greater volume of CWD in this treatment.

Enclosures for the salamanders were constructed by attaching a cylindrical sleeve of gray fiberglass screening to the rim of a 24-cm section of 18-cm diameter polyvinyl chloride (PVC) pipe. To create the sleeve, we rolled a piece of screening

(55 cm high × 66 cm wide) into a cylinder and sewed the side seam closed with 14-lb. monofilament fishing line. We then used caulk to attach the sleeves to one end of each open-ended section of PVC. Twelve enclosures were placed 1.1 m apart in a 3 × 4 grid in the center of each quadrant. The PVC was buried so the top of the pipe was level with the ground and only the screen was above ground. When the salamanders were added, the enclosure was closed from the top by rolling the screen down, folding in the corners, and securing with binder clips. Burrows were constructed in half of the enclosures by driving a section of 2.2-cm diameter metal conduit 10 cm into the ground at an approximately 30° angle.

Although *A. talpoideum* occur at Bay 1000, the wetland hydroperiod is too short to support larval development and recuitment of this species. Thus, we collected recently metamorphosed juveniles between 8 and 22 June from Ellenton Bay, located 24 km away but also on the Savannah River Site in Barnwell County, South Carolina. We were able to obtain only 41 postmetamorphic *A. talpoideum*, rather than the 48 envisioned in our original study design. We kept the salamanders in plastic trays lined with moist paper towels and stored in a room at 25°C and 50% relative humidity with a 12:12 light:dark cycle until the start of the experiment. The salamanders were fed crickets ad libitum until two days before the experiment to obtain a fully hydrated mass without prey items present in the digestive tract.

Salamanders were transferred to individual, numbered containers containing 1 cm of well water at 1700 h on 7 July 2004, the day the experiment was initiated. Prior to transporting salamanders to the field site, we measured their SVL and mass to the nearest 0.01 g using a Scout II electronic balance (Ohaus Corporation, Florham Park, NJ). Salamanders were then randomly assigned to enclosures, transported to the field site, and added to the enclosures between 1845 and 2130 h. Except for periodic removal for determination of mass, each salamander was confined to its enclosure for 72 h. During this time, we returned every 12 h to obtain salamander mass and measure environmental conditions. Decrease in mass over the 72 h was attributed to water loss and used as a measure of desiccation rate.

Upon checking the enclosures every morning (from 0830–1100 h) or evening (from 1930–2200 h), we noted whether salamanders with burrows were in or out of their burrows. We also noted the location of the salamanders without burrows as either exposed or under litter, as well as their relative position in the enclosure. Each *A. talpoideum* was removed from its enclosure, its mass determined, and immediately returned to the enclosure. Because most burrows were damaged in the process of removing salamanders, all burrows were reconstructed prior to returning the salamander.

At each determination of mass, we measured soil moisture of the top 8 cm of soil inside each enclosure with a TH2O portable soil moisture meter (Dynamax Inc, Houston, TX). We used a sling psychrometer to measure relative humidity in each habitat at the time of addition of salamanders and every 12 h thereafter. We also measured air temperature at 30-min intervals using a Hobo H8 logger (Onset Computer Co., Bourne, MA) mounted 0.5 m above the ground in the middle of each enclosure grid.

We examined the effects of habitat treatment, burrow availability, and their interaction on water loss at 12 h, when all salamanders were still alive, using analysis of variance (ANOVA). We examined changes in water loss over the entire 72-h experiment using repeated-measures ANOVA (Scheiner and Gurevitch, 2001), which included only salamanders for which there was a complete set of measurements (i.e., individuals that survived the entire experiment). We used similar analyses to test for effects of habitat, burrow availability, and time on soil moisture. We used PROC GLM in SAS (SAS Institute, Cary, NC), basing *F*-ratios on Type III sums of squares because of the slightly unequal sample sizes among treatment groups and assessing significance based on $\alpha = 0.05$. To further explore how rates of water loss varied over time, we ran univariate ANOVAs for each successive 12-h time interval, applying a Bonferroni-corrected $\alpha = 0.0083$ to account for the multiple contrasts (PROFILE option in SAS; Scheiner and Gurevitch, 2001). We also calculated Pearson correlation coefficients between soil moisture and salamander water loss for each 12-h interval.

RESULTS

The initial mass of salamanders ranged from 4.9–8.5 g (Table 1), but mean mass did not differ significantly among treatments according to ANOVA (Habitat: $F_{3,33} = 1.20$, $P = 0.3239$; Burrow: $F_{1,33} = 0.92$, $P = 0.3446$). During the first 12 h, water loss (defined as proportional mass loss relative to initial, fully hydrated mass) varied significantly among habitat treatments ($F_{3,33} = 3.06$, $P = 0.0415$, $N = 41$). Salamanders in the CC-retained experienced significantly higher water loss than salamanders in the other three habitats (Scheffe's Test, $P < 0.05$). Salamanders without a burrow lost significantly more water than salamanders provided with a burrow during the first 12 h ($F_{1,33} = 8.78$, $P = 0.0056$). This effect was consistent across habitats; thus, there was no significant habitat × burrow interaction ($F_{3,33} = 0.95$, $P = 0.4269$).

TABLE 1. Mean (SD) initial mass and snout–vent length (SVL) of juvenile Mole Salamanders (*Ambystoma talpoideum*) added to 0.025-m^2 enclosures in each habitat treatment. Half of the salamanders in each habitat were provided with artificial burrows ("Burrow"), and half did not have access to a burrow ("No Burrow").

		Mean (SD) initial mass (g)		Mean (SD) SVL (mm)	
Habitat treatment	*N*	Burrow	No burrow	Burrow	No burrow
Control	11	5.93 (0.45)	5.89 (0.49)	55.8 (1.2)	56.4 (1.7)
Thinning	10	6.67 (1.07)	6.13 (0.49)	57.8 (3.9)	56.2 (2.6)
Clearcut CWD retained	10	5.92 (0.45)	6.82 (0.72)	56.2 (1.1)	57.4 (2.6)
Clearcut CWD removed	10	6.15 (0.81)	6.69 (1.01)	57.0 (3.2)	58.4 (2.4)

The repeated-measures ANOVA was based only on animals that survived the experiment ($N = 32$). Over the entire three-day period, water loss changed significantly with time and varied according to habitat and burrow availability (Table 2, Fig. 2). Individual contrasts revealed significant time effects during only the first two nights (0–12 h: $F_{1,24} = 55.88$, $P < 0.0001$; 24–36 h: $F_{1,24} = 11.84$, $P = 0.0021$). Despite the significant effects of habitat and burrow availability in the multivariate ANOVA, neither of these factors significantly affected water loss within any individual time interval when judged against the adjusted α (all $P > 0.02$).

When available, burrows were heavily used as refuges; we found salamanders outside their burrow on only two occasions (1.6% of the relocations). Salamanders supplied with burrows in the control and thinning areas experienced no mortality over the 72-h period, whereas one salamander with a burrow died in the CC-removed after 72 h, and one salamander with a burrow died in the CC-retained after 60 h (Fig. 3).

Salamanders without burrows fared worse in overall survival, with the exception of the control, in which there were no mortalities (Fig. 3). One salamander without a burrow died in the thinning, whereas three salamanders without burrows died in each of the clearcuts. Although the salamander in the thinning area died after 24 h, it was alive at 12 h after losing 27.5% of its mass. The two surviving *A. talpoideum* without burrows in the CC-removed were located next to a large clump of resprouting sweetgum that shaded their enclosures. They sustained maximum losses of 21.1% and 10.4% of their initial body mass during the 72-h period. Although mean water loss in the clearcuts appeared to level off and even decline after 48 h (Fig. 2), we consider this an artifact of the increasing mortality over time (Fig. 3), which resulted in the

TABLE 2. Results of the repeated-measures analysis of variance of the effects of habitat treatment, burrow availability, and their interaction on water loss of juvenile *Ambystoma talpoideum* over 72 h ($N = 32$).

	df	MS	*F*	*P*
Between-subject				
Habitat	3	0.0317	2.96	0.0524
Burrow	1	0.0683	6.38	0.0186
Habitat × Burrow	3	0.0030	0.28	0.8391
Error	24	0.0107		
	df	Wilks' λ	*F*	*P*
Within-subject				
Time	6, 19	0.1402	19.43	< 0.0001
Time × Habitat	18, 54	0.2345	2.02	0.0244
Time × Burrow	6, 19	0.4254	4.28	0.0068
Time × Habitat × Burrow	18, 54	0.2587	1.85	0.0427

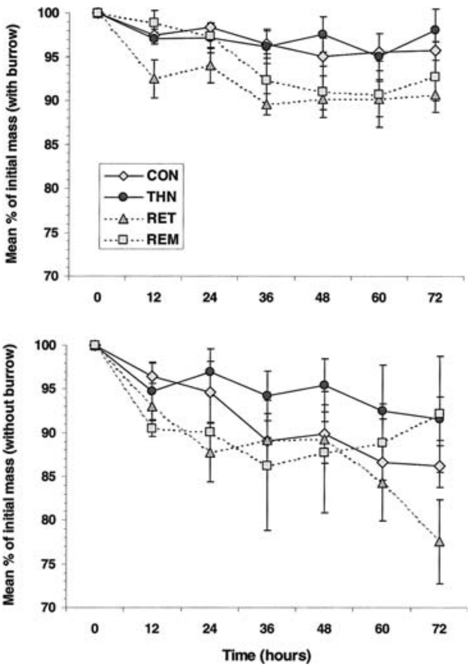

FIG. 2. Mean water loss (percent of initial mass ± SE) for surviving juvenile *Ambystoma talpoideum* with burrows (top) and without burrows (bottom) in four habitat treatments over 72 h. Error bars are standard errors; CON = control, THN = thinning, RET = clearcut with coarse woody debris retained, REM = clearcut with coarse woody debris removed.

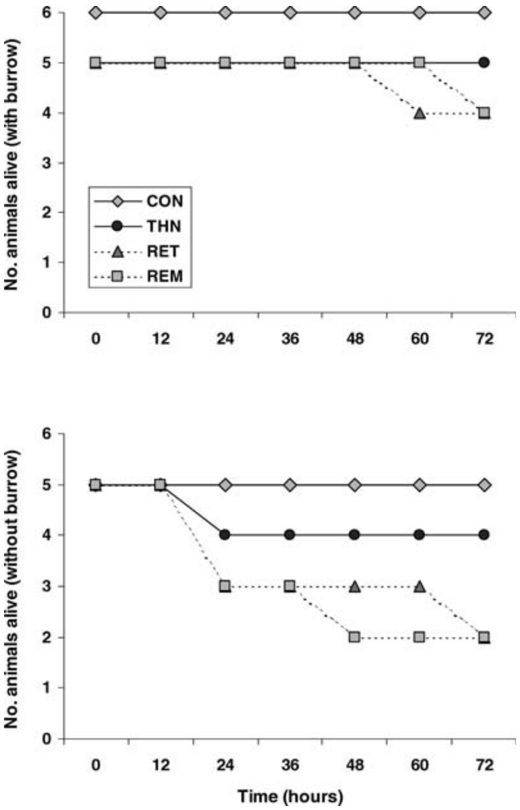

FIG. 3. Survivorship for juvenile *Ambystoma talpoideum* in enclosures with burrows (top) and without burrows (bottom) in four habitat treatments over 72 h. CON = control, THN = thinning, RET = clearcut with coarse woody debris retained, REM = clearcut with coarse woody debris removed.

TABLE 3. Results of the repeated-measures analysis of variance of the effects of habitat treatment, burrow availability, and their interaction on soil moisture over 72 h ($N = 32$).

	df	MS	*F*	*P*
Between-subject				
Habitat	3	941.1380	32.83	< 0.0001
Burrow	1	217.3279	7.58	0.0111
Habitat × Burrow	3	119.9293	4.18	0.0162
Error	24	28.6674		
	df	Wilks' λ	*F*	*P*
Within-subject				
Time	6, 19	0.2501	9.50	< 0.0001
Time × Habitat	18, 54	0.3807	1.23	0.2746
Time × Burrow	6, 19	0.8191	0.70	0.6535
Time × Habitat × Burrow	18, 54	0.4180	1.09	0.3880

censoring of individuals experiencing the most severe water loss.

The two surviving *A. talpoideum* without burrows in the CC-retained lost a maximum of 27.3% and 17.6% of their initial body mass during the 72-h period. We could not locate one salamander in the CC-retained at the final 72-h check. The salamander had access to a burrow and had maintained a fairly steady body mass throughout the experiment. We assumed it had escaped and was still alive, although no measurements could be collected for that individual at the 72-h mark. The four deceased animals in the CC-retained were covered with Fire Ants (*Solenopsis invicta*) when found. The deaths of three of these animals were probably the result of extreme desiccation. The fourth animal, however, seemed well hydrated and was found outside its burrow, suggesting that Fire Ants were the cause of death.

Initial soil moisture varied significantly among habitat treatments ($F_{3,33} = 33.34$, $P < 0.0001$) but not according to burrow availability ($F_{1,33} = 1.68$, $P = 0.2035$), and there was no significant interaction ($F_{3,33} = 2.06$, $P = 0.1250$). At the start of the experiment, soils in the CC-removed were significantly moister than in the other three habitats (Scheffe's Test, $P < 0.05$). Because no measurable precipitation fell during the experiment, the soils gradually dried, resulting in a significant effect of time in the repeated-measures ANOVA (Table 3). Soil moisture over the entire three-day period varied significantly among habitats, remaining consistently higher in the CC-removed (Table 3; Fig. 4). Soils in enclosures with burrows tended to be slightly drier. There were no significant correlations between soil moisture and water loss in any time periods ($P > 0.05$).

The control had the lowest 72-h average temperature as well as the highest average relative humidity of all the habitat treatments (Table 4). Mean daily maximum temperatures in the clearcuts exceeded those in the control by 2.0°C and the thinning area by 7.1°C. The CC-removed had the lowest average relative humidity, although mean humidity varied by less than 4% among habitats (Table 4).

DISCUSSION

Canopy removal and other habitat changes resulting from clearcutting greatly increased the risk of mortality because of desiccation for juvenile *A. talpoideum* in our study. Juvenile *A. talpoideum* in the clearcut treatments suffered 60% mortality in the absence of a burrow. Proximity to shade-providing shrubs may have facilitated survival of remaining salamanders in the clearcuts. The only mortality not in a clearcut was a juvenile without a burrow in the thinning treatment. Thus, salamanders in the recently thinned

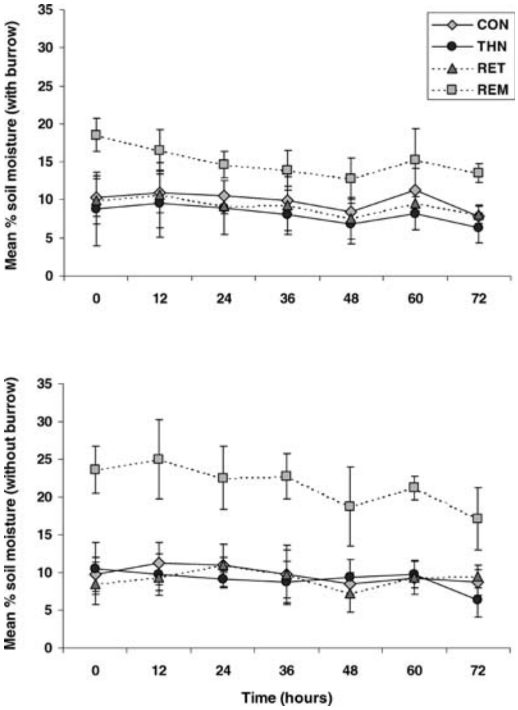

FIG. 4. Mean soil moisture over 72 h in each habitat treatment in enclosures with burrows (top) and without burrows (bottom). Error bars are standard deviations; CON = control, THN = thinning, RET = clearcut with coarse woody debris retained, REM = clearcut with coarse woody debris removed.

stand experienced only a slightly elevated risk of desiccation compared to the unharvested control. We caution that our scope of inference is limited because we did not incorporate replication at the stand level or over time. Our experiment was conducted in July, which is within the migratory period for this species. Juvenile *A. talpoideum* may metamorphose and leave wetlands any time between May and September (Gibbons and Semlitsch 1991), depending on annual and site-specific variation in environmental conditions.

As demonstrated for other amphibians (e.g., *Bufo marinus*; Seebacher and Alford, 2002), the presence of suitable shelters greatly mitigated water loss. In clearcut treatments, the mean maximum dehydration rate in a 12-h period for salamanders with burrows was 80.9 mg/g, 36% less than for salamanders without burrows (125.6 mg/g). Having access to a burrow prevented salamanders from reaching lethal levels of desiccation in at least 19 of 21 (~90%) cases. The death of one salamander with a burrow was likely caused by predation by Fire Ants, which invaded several enclosures in the CC-retained treatment. Increased risk of Fire Ant predation may be another consequence of habitat disturbance for salamanders inhabiting forests of the southeastern United States. The importance of burrows suggests that, for ambystomatids, the time required for habitat quality to be restored following logging depends in part on how compacted the soil is (thus whether salamanders can dig their own burrows), as well as how quickly burrows are reestablished via small mammal activity.

Although ambystomatids lose water at slower rates than plethodontids (Spight, 1968), our results show they are still subject to high rates of desiccation in unsuitable habitats. Six *A. talpoideum* survived after losing more than 20% of their initial body mass. Three salamanders survived after losing more than 27% of their initial body mass. The most water loss tolerated by an *A. talpoideum* in a 12-h period was 28.9%. In laboratory studies, Heatwole and Lim (1961) found that *Plethodon cinereus* can also survive a maximum water loss of 28.9%. Pough and Wilson (1970) determined the average lethal limits for juvenile *A. maculatum* to be 36% of their original body weight (range 23–45%).

The small size of our enclosures prevented us from testing whether retention of CWD mitigates the risk of desiccation. Salamanders in the CC-retained experienced higher dehydration rates than those in the CC-removed. Salamanders in the CC-removed may have benefited from the higher soil moisture in that treatment, although we found no significant correlations between soil moisture and water loss. Although recently harvested sites often have higher soil moisture (e.g., Ash, 1997; Chazal and Niewiarowski, 1998) due to reduced evapotranspiration following tree

TABLE 4. Mean (SD) air temperature and relative humidity in the four habitat treatments over the 72 h of the experiment. CWD = coarse woody debris.

	Temperature (°C)			
Habitat treatment	72-h average	Mean daily maximum	Mean daily minimum	Mean relative humidity (%)
Control	27.7 (6.0)	42.6 (4.0)	21.2 (0.4)	77.6 (7.8)
Thinning	28.1 (5.4)	37.5 (2.0)	21.3 (0.7)	76.4 (11.3)
Clearcut CWD retained	29.9 (9.1)	44.6 (2.3)	19.8 (1.0)	75.4 (7.8)
Clearcut CWD removed	30.3 (8.8)	44.6 (1.0)	20.2 (0.7)	74.3 (7.7)

removal (Williams 1998), this does not account for the difference between our two clearcuts, which may have differed slightly in soil type or compaction caused by skidding.

Dehydration rates of amphibians are determined by the interaction of many factors, including temperature. Dehydration rate increases as temperature increases if relative humidity is held constant (Moore and Sievert, 2001). The high daytime temperatures in the clearcut treatments (Table 4) presumably resulted in greater desiccation, which in turn made animals more susceptible to heat stress. Desiccation lowers an individual's critical thermal maximum, creating a synergistic interaction between temperature and dehydration that poses an additional threat to amphibians in harsh environments (Pough and Wilson, 1970).

Because salamanders migrate at night, when temperature and humidity levels are relatively favorable, an interesting question becomes what cues they use to select habitat. Juvenile Spotted Salamanders (*A. maculatum*) have been shown to select wet substrates over dry ones in laboratory choice tests (Rittenhouse et al., 2004). If salamanders use substrate moisture as a cue indicating habitat suitability, then they may travel into clearcut areas at night and experience high rates of desiccation and mortality the following day. However, *A. talpoideum* tend to migrate only during or immediately after rainfall, when differences in soil moisture are probably minimal (Semlitsch, 1981, 1985). Rittenhouse et al. (2004) found that, moisture levels being equal, juvenile *A. maculatum* discriminated against soil from old fields, spending more time on soil from forested sites. They concluded that ambystomatids must rely heavily on olfactory cues but probably use a variety of information when selecting habitat under natural conditions. Juvenile *A. maculatum* oriented toward forest over old-field habitat in choice tests conducted on habitat edges (Rothermel and Semlitsch, 2002), but the tendency of juvenile *A. talpoideum* to enter clearcut areas and the cues dictating their migratory behavior have not been studied.

If emigrating juveniles fail to avoid recently harvested areas, then their probability of survival hinges on their rate of travel, physiological tolerances, and availability of refuges. Semlitsch (1981) found that newly metamorphosed *A. talpoideum* traveled through undisturbed habitat at a median speed of 3.9 m/h. At this rate, it would have taken a constantly moving juvenile over 57 h to emigrate through our 3.8-ha clearcuts (Fig. 1). Because ambystomatids move only at night, and only when it is raining or the leaf litter is wet (Semlitsch, 1981), the trip would require at least seven days. This trip could be shortened if juvenile ambystomatids exhibit compensatory behavior by traveling faster in unfavorable habitats, as demonstrated in a plethodontid salamander (Rosenberg et al., 1998). However, access to suitable refuges would clearly remain a critical factor determining their migratory success.

Despite high temperatures during the day, patterns of water loss we observed suggest that most water loss occurred during the first two nights. We believe differences in activity level over time may explain this result and highlight the importance of behavior in determining susceptibility to environmental stressors. Salamanders were probably active during the first two nights in the enclosures, incurring high rates of evaporative water loss. During the day and as dehydration became more severe, they probably increased burrow use, if that was an option, or adopted water-conserving behaviors, such as remaining inactive, seeking shade, and positioning themselves to reduce the amount of exposed surface area (Semlitsch, 1983; Rohr and Madison, 2003). Moseley et al. (2004) found that *A. talpoideum* were capable of exploiting different microhabitats depending on what was available. Despite having access to burrows, salamanders in their study exhibited increased surface activity in the absence of pine litter, implying that severe conditions stimulated salamanders to move in search of better habitat. Likewise, if the salamanders in our study had not been confined, they might have been able to find suitable microhabitats (e.g., under logs, in clumps of vegetation) in clearcut areas even if many burrows were destroyed during logging. However, salamanders subjected to dehydrating conditions for long periods would incur high costs in terms of reduced growth (Petranka, 1994) and potentially increased risks of predation (Rohr and Madison, 2003). Although comparing physiological tolerances with environmental parameters may be the first step toward predicting the sensitivity of amphibians to habitat alteration, a complete picture can only be gained by incorporating how animals respond behaviorally to elevated risks of desiccation and predation in disturbed habitats.

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Salamander Abundance along Road Edges and within Abandoned Logging Roads in Appalachian Forests

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Salamander Abundance along Road Edges and within Abandoned Logging Roads in Appalachian Forests

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Abstract: *Roads may be one of the most common disturbances in otherwise continuous forested habitat in the southern Appalachian Mountains. Despite their obvious presence on the landscape, there is limited data on the ecological effects along a road edge or the size of the "road-effect zone." We sampled salamanders at current and abandoned road sites within the Nantahala National Forest, North Carolina (U.S.A.) to determine the road-effect zone for an assemblage of woodland salamanders. Salamander abundance near the road was reduced significantly, and salamanders along the edges were predominantly large individuals. These results indicate that the road-effect zone for these salamanders extended 35 m on either side of the relatively narrow, low-use forest roads along which we sampled. Furthermore, salamander abundance was significantly lower on old, abandoned logging roads compared with the adjacent upslope sites. These results indicate that forest roads and abandoned logging roads have negative effects on forest-dependent species such as plethodontid salamanders. Our results may apply to other protected forests in the southern Appalachians and may exemplify a problem created by current and past land use activities in all forested regions, especially those related to road building for natural-resource extraction. Our results show that the effect of roads reached well beyond their boundary and that abandonment or the decommissioning of roads did not reverse detrimental ecological effects; rather, our results indicate that management decisions have significant repercussions for generations to come. Furthermore, the quantity of suitable forested habitat in the protected areas we studied was significantly reduced: between 28.6% and 36.9% of the area was affected by roads. Management and policy decisions must use current and historical data on land use to understand cumulative impacts on forest-dependent species and to fully protect biodiversity on national lands*

Keywords: amphibian, edge effects, land use, logging, *Plethodon*, road-effect zone

Abundancia de Salamandras a lo Largo de Bordes de Caminos y en Caminos Madereros Abandonados en Bosques Apalaches

Resumen: *Los caminos pueden ser una de las perturbaciones más comunes en bosques otrora continuos en los Montes Apalaches. No obstante su obvia presencia en el paisaje, hay datos limitados sobre los efectos ecológicos a lo largo de un borde de camino o del tamaño de la "zona de efecto del camino." Muestreamos salamandras sitios en caminos vigentes y abandonados en el Parque Nacional Nántala, Carolina del Norte (E.U.A.) para determinar la zona de efecto del camino para un ensamble de salamandras de bosque. La*

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abundancia de salamandras cerca del camino disminuyó significativamente, y las salamandras a lo largo de los bordes eran individuos grandes predominantemente. Estos resultados indican que la zona de efecto de camino para estas salamandras se extiende 35 m a ambos lados de los caminos relativamente angostos, poco utilizados que muestreamos. Más aun, la abundancia de salamandras fue significativamente menor en caminos viejos, abandonados, en comparación con sitios en laderas contiguas. Estos resultados indican que los caminos en los bosques y los caminos madereros abandonados tienen efectos negativos sobre especies dependientes de bosques como las salamandras pletodóntidas. Nuestros resultados se pueden aplicar a otros bosques protegidos en los Apalaches y pueden ejemplificar un problema causado por formas de uso de suelo actuales y pasadas en todas las regiones boscosas, especialmente las relacionadas con la construcción de caminos para la extracción de recursos naturales. Nuestros resultados muestran que el efecto de los caminos rebasó el límite de los mismos y que el abandono de caminos no revirtió los efectos ecológicos perjudiciales; más bien, nuestros resultados indican que las decisiones de gestión tienen repercusiones significativas para las generaciones futuras. Más aun, la cantidad de hábitat boscoso adecuado se redujo significativamente en las áreas protegidas que estudiamos: entre 28.6% y 36.9% de la superficie fue afectada por caminos. Las decisiones políticas y de gestión deben recurrir a datos actuales e históricos sobre el uso de suelo para entender los impactos acumulativos sobre especies dependientes de bosques y para proteger integralmente a la biodiversidad en terrenos nacionales.

Palabras Clave: anfibios, corte de árboles, efectos de borde, *Plethodon*, uso de suelos, zona de efecto de camino

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Introduction

Species declines are often due to decreases in population size, increases in isolation, and edge effects (Kareiva & Wennergren 1995). Edge effects in forests reduce the effective size of remaining patches by creating unsuitable habitat along the boundary due to factors such as increased sunlight, air temperature, wind, soil drying, and the presence of invasive species and predators (reviewed extensively in Saunders et al. 1991; Murcia 1995; Harper et al. 2005). Thus, forest-dependent species, which are sensitive to such factors, may shift activity away from edges and be less abundant or even absent along edges.

Roads may be one of the most common disturbances in otherwise continuous forested habitat, such as protected national forest lands. Most paved roads are used for public transportation (6.2 million km of public roads used by 200 million vehicles in the United States; Forman 2000), but many unpaved roads intersect large areas of forest for access to and removal of natural resources such as timber. Roads can have direct effects on species (e.g., mortality from construction and roadkill; e.g., Langton 1989; Fahrig et al. 1995) or indirect effects due to modification of animal behavior, disruption of the physical environment, alteration of the chemical environment, spread of exotic species, and changes in human use of natural resources (e.g., Trombulak & Frissell 2000). Roads create long and narrow edges that may extend well beyond the road surface or roadsides (Forman 2000). Furthermore, roads may persist for >40 years after abandonment and can be embedded in seemingly continuous forest (Vora 1988). Despite their obvious presence on the landscape, there is limited data on the ecological effects of roads along their edges or on the size of the “road-effect zone” (Forman et al. 1997; Forman & Alexander 1998; Forman & Deblinger 2000). The ecological effects of roads may be just as severe as other edge effects created by habitat loss and alteration (Murcia 1995), both of which have important implications for disrupting the function and diversity of forest ecosystems (Saunders et al. 1991; Harper et al. 2005).

We sought to determine the extent of road effects on an assemblage of woodland salamanders in the southern Appalachian Mountains. Woodland salamanders are small, lungless, sedentary, and strongly dependent on cool, moist forest habitat (e.g., Spight 1968; Spotila 1972), and these characteristics make them excellent indicators of environmental stress or change (e.g., Welsh & Droege 2001; Wyman 2003). We assumed woodland salamanders would be highly sensitive to alterations in the physical environment along roads. We hypothesized that declines in salamander abundance near road edges is due to the reduction of suitable habitat and might correlate with physical changes and lower abundance of macroinvertebrate prey at road edges found in previous studies (e.g., Haskell 2000). Furthermore, because results from the first part of our study on edge effects showed a nonlinear response of salamanders, we tested whether abandoned logging roads embedded in seemingly continuous forest might further fragment the forest by creating linear strips of less-suitable habitat relative to adjacent forested areas. Finally, to determine the loss of habitat by varying sizes of the road-effect zone, we used a GIS analysis to estimate the total area of forest that could be classified unsuitable for woodland salamanders.

Methods

Sampling Design

Our study area was centered within the Highlands Ranger District of the Nantahala National Forest, North Carolina

Table 1. Description of 11 road sites from which salamanders were sampled in the Nantahala National Forest, Highlands, North Carolina.

Site	*Road surface*	*Road width (m)*	*Clearing width (m)*	*Aspect*	*Canopy cover (%)*	*Light (lux)*	*Elevation (m)*	*Cars/ hour*
Norton branch	gravel	3.7	6.4	SSW	57	1030	769	9
Chestnut Mt.	gravel	4.1	7.2	W	32	108,600	831	2
Fodderstack Mt.	dirt/grass	1.9	3.4	NE	55	1482	923	(gated)
Cole gap	paved	6.2	36.1	NW	0	2667	1261	50
Highland Ctr.	paved	5.2	11.4	W	0	32,300	1231	10
Cemetery	paved	6.3	12.1	NNW	0	105,266	769	5
Slick rock	gravel	4.6	9.6	ESE	60	2422	985	12
N. Rich Mt.	gravel	4.8	10.3	SE	12	6200	1200	7
Rattlesnake knob	gravel	4.7	8.6	S	52	134	1231	7
Granite city	gravel	6.2	11.6	SSE	8	2500	923	14
Horse cove	gravel	5.8	12.4	ENE	0	6066	969	7
Mean	—	4.86	11.7	—	25.1	24,424	1008	11.2

(U.S.A.) and encompassed primarily a mature (all >75 years since last logging) southern Appalachian hardwood forest dominated by oaks. To examine edge effects, we used area-constrained searches and cover boards to sample salamanders at 11 road sites within the forest. We selected sites along existing low-use gravel ($n = 8$) and paved ($n = 3$) roads, where mature forest bordered the road, that were at least 200 m away from other active roads or other human activities and had low road banks (<30 cm high; Table 1). Sites were selected haphazardly across the area but were representative of roads commonly found throughout the Nantahala National Forest. From 6 to 12 June 2000, we established paired transects to maximize the area sampled and the number of salamanders collected at each road site. Our sampling protocol followed that of Haskell (2000): transects ran perpendicular from the road edge 100 m into the forest and consisted of six sampling stations at 1, 5, 15, 35, 60, and 100 m along the transect. Transects were started at the road edge, which was defined by the presence of a tree line (trees >30 cm circumference). The paired transects ran parallel to each other and were on average 40 m apart. We revisited transects, opportunistically, six times from June 2000 through August 2003, when surface activity of forest-dwelling plethodontid salamanders is generally high (e.g., Petranka et al. 1993; Ash 1997).

During the initial sampling in June 2000, we laid out a 1.5 × 1.5 m quadrat (2.25 m^2) at each of the sampling stations and conducted a thorough search of the leaf litter and all cover objects (e.g., rocks, bark, tree limbs) within the plot down to the mineral soil or rock. Subsequently, we installed a pair of cover boards (30.5 × 122 × 3.75 cm untreated rough-cut lumber) next to each sampling station in October 2000. At each subsequent sampling date we restricted our salamander sampling to checking beneath the cover boards. The cover boards allowed us to sample stations repeatedly, were less destructive to the habitat, and yielded data on the same species assemblage as raking through natural cover objects in June 2000 (deGraaf & Yamasaki 1992; Marsh & Goicochea 2003), albeit at a lower capture rate (e.g., Smith & Petranka 2000; Hyde & Simons 2001). We recorded the species, sex (if discernable by secondary sexual characteristics), and snout-vent length (SVL in mm: distance from the tip of the snout to the posterior margin of the cloacal aperture) for each individual. All measurements were taken in the field and individuals were released within 5 minutes of capture. All sampling was conducted between the hours of 0800 and 2000 and regardless of weather.

To examine the effects of old, abandoned logging roads, we sampled terrestrial salamanders during May 2005 with area-constrained searches at eight sites within the same area of the Nantahala National Forest. All sites were in closed-canopy forest and were last logged at least 80 years ago. We selected sites haphazardly as they were encountered near our edge transects but they appeared representative of old logging roads in the area. We established two replicate sampling arrays at least 50 m apart at each road site. Each array had two stations on the roadbed separated by 10 m, one off-road station 10 m upslope and one station 10 m downslope adjacent to the road. At each site, we laid out a 1.5 × 1.5 m quadrat (2.25 m^2) at each sampling station on and off the roadbed and conducted a thorough search of the leaf litter and all cover objects (e.g., rocks, bark, tree limbs) within the plot down to the mineral soil or rock. We recorded the species, sex (if discernable by secondary sexual characteristics), and whether the individual was an adult or juvenile based on relative body size. Individuals were released within 5 minutes of capture. All sampling was conducted between 0800 and 1800 hours, regardless of weather.

Physical and Biotic Factors

In the road-edge study at each site, we measured width of the road surface used by vehicles and road shoulder (i.e., edge of the road surface to the treeline), clearing width (road surface plus shoulder), road type (paved or gravel), traffic volume (count of vehicles during the sampling period), and light transmission (determined with a digital EXTECH Instruments light meter) and percent canopy cover (GRS Densitometer) at the center of the road. At each sampling station we measured light transmission (lux), percent soil moisture, litter depth, coarse woody debris (CWD), and macroinvertebrate abundance (number per sample) and richness (number of taxa).

To sample invertebrates we used a corer (4.7 cm diameter; 14.76 cm^2 area) at each station to collect three soil-litter subsamples that were combined in one plastic bag and returned to the laboratory for processing within 4–6 hours (methods after Haskell 2000). Each sample was sifted through a 6.25-mm mesh screen to remove rocks, woody debris, and leaves, and then searched exhaustively by hand to find all invertebrates >1 mm in size. We identified all invertebrates to the level of order except Chilopoda and Diplopoda, which were identified to class.

Using a corer, we collected three soil subsamples at each station and placed samples in a plastic bag. Soil samples were weighed, dried at 45° C for 24 hours, and reweighed to determine percent soil moisture. During one sample period, we estimated stem density along each transect by counting all stems rooted within two 1-m^2 plots at each sampling station and classifying stems as small (<10 cm circumference), medium (10–30 cm circumference), or large (>30 cm circumference).

In the study on abandoned logging roads we measured several characteristics of the road and several physical and biotic parameters at each sampling station on or off the roadbed. At each site we measured width of the road surface and road shoulder. At each sampling station we measured percent soil moisture, soil density (dry soil weight per volume), percent litter moisture, and litter depth with the same methods as in the road edge study.

Statistical Analysis

We initially used Haskell's (2000) correlation analytical method to evaluate whether roads influenced salamander abundance along our transects. We pooled our observations from the paired transects at each site and across all sampling periods to increase sample size for each distance. To account for site differences in the correlations, we calculated the proportion of the total number of captures recorded at each sampling station at each site and tested for differences among sites and distances with a two-way analysis of variance (ANOVA with Type III sums of squares). In this analysis distance from the road was a fixed effect, and sites were treated as blocks yielding a randomized complete block design. To eliminate dependence in the proportions among distances, we dropped the data from 100-m stations. Data from the 100-m stations was also dropped because of biases created by nearby abandoned logging roads. We used the angular transformation to make the proportional values normally distributed. Following Haskell (2000) we conducted correlation analyses for five distances versus invertebrate abundance (number of individuals) and richness (number of taxa) at each site ($n = 11$), with means of the two transects as a response variable. We then tested whether the mean correlation coefficient differed significantly from zero with a one-sample two-tailed t test. Last, to help explain the distribution of salamander along our transects, we conducted Spearman's rank correlations of the abundance of salamanders with invertebrate abundance, invertebrate richness, stem density by size class, light transmission, soil moisture, litter depth, and CWD.

GIS Analysis

To determine the loss of habitat due to the road effect zone, we used a GIS analysis to estimate the total area of forest that could be classified unsuitable for woodland salamanders. We used GIS coverage of forest and roads for the Highlands Ranger District of the Nantahala National Forest (446.76 km^2 = 110,396.9 acres of forest; 1222.8 km of all roads and trails). By using road-effect zones of varying sizes 0, 1, 5, 10, 15, 35, 60, 80, and 100 m (times two sides of the road plus 12 m for the average road clearing from Table 1), we calculated the percentage of forest that was unsuitable for a range of road-effect sizes.

Results

Road Edge Effects

Over the six sampling periods, we collected 199 salamanders at our six sampling stations at each of the 11 paired road transects. A total of seven species was represented in these samples, with the southern gray-cheeked salamander (*Plethodon metcalfi*) representing the majority (77%; Table 2). Of the 11 sites there were 3 negative correlations and 8 positive correlations of salamander abundance with distance, only 2 of which were significant at $p < 0.05$ (Cole Gap and Chestnut Mountain), but the average value was marginally significantly different from zero ($t = 2.03$, df $= 10$, $0.1 > p > 0.05$).

The absence of a strong correlation among transects, however, did not preclude the presence of edge effects because the relationship might be nonlinear and the sampling stations were not continuously distributed. Again, pooling both transects across all sampling periods, we calculated the proportion of the total number of captures recorded at each of the first five sampling stations at each site. We found significant variation both among sites ($p < 0.0001$) and distances ($p = 0.048$) along the transect (Table 3; Fig. 1). Tukey's post hoc comparisons of distance indicated the only significant differences between stations 1 m and 35 m from the road ($p = 0.050$) and between 1 m and 60 m from the road ($p = 0.066$; Fig. 1).

Because *P. metcalfi* was the most common species collected along the transects, the results of the distribution

Table 2. Summary of species and the number of salamanders collected at 11 road sites in the Nantahala National Forest, Highlands, North Carolina during six sampling periods.

Species	*2000* June	*2001* April	May	June	July	August	Total	Proportion
Ambystoma maculatum	0	0	1	0	0	0	1	0.005
Desmognathus ocoee	0	0	1	0	1	1	3	0.015
Eurycea wilderae	1	0	0	1	0	0	2	0.010
Notophthalmus viridescens	2	0	0	1	0	0	3	0.015
Plethodon metcalfi	16	15	41	10	30	41	153	0.769
Plethodon oconalufti	2	8	5	3	4	1	23	0.116
Plethodon serratus	11	2	0	0	0	0	13	0.065
Other (unknown)	1	0	0	0	0	0	1	0.005
Total	33	25	48	15	35	43	199	
Proportion	0.166	0.126	0.241	0.075	0.176	0.216		

analysis were largely due to one species. For this reason we repeated the analysis with only *P. metcalfi* in the ANOVA. Eliminating the other species from the data matrix reduced several site–distance combinations with no observations. Therefore prior to the analysis, we dropped three sites from the data matrix that had fewer than 5% of the total observations of *P. metcalfi*. As in the previous analysis, both the sites ($p = 0.001$) and distances ($p = 0.020$) were significant (Table 3). The pairwise comparisons indicated that the abundance of *P. metcalfi* was significantly lower 1 m from the road compared with 60 m from the road ($p = 0.009$; Fig. 1). Body size of *P. metcalfi* did not differ among sites ($p = 0.720$) but did vary significantly with distance ($p = 0.022$; Table 3). Tukey's pairwise comparisons revealed that individuals found 35 m from the road were significantly smaller than those found 60 m ($p = 0.030$) and 1 m from the road ($p = 0.049$). Notably, these larger salamanders 1 m from the road had relatively little variation in body size (CV = 5.95), whereas all the other sampling distances displayed a much greater degree of variation in body size (CV range 13.86–20.98).

We collected 396 samples for the invertebrate analysis. Neither abundance ($t = 0.352$, df = 10, $p > 0.1$) nor richness ($t = 0.414$, df = 10, $p > 0.1$) was significant. According to goodness-of-fit tests, we could not reject the null hypothesis that an equal number of sites should produce negative and positive correlations for either abundance ($\chi^2 = 0.25$, df = 1, $p > 0.1$) or richness ($\chi^2 = 0.25$, df = 1, $p > 0.1$). Only 5 of 11 sites had positive correlation coefficients for abundance, and the same 5 had positive correlation coefficients for richness. Although six correlation coefficients for individual sites were significant at $p < 0.05$ for abundance, three of these were positive and three were negative correlations. Only three correlation coefficients for individual sites were significant at $p < 0.05$ for richness (two negative and one positive).

The results of the nonparametric regression analysis showed that the abundance of salamanders along the transects was not significantly related to either invertebrate abundance (Spearman $r = 0.20$, $p > 0.05$) or richness ($r = 0.55$, $p > 0.05$). Simple correlation analysis demonstrated that salamander abundance was also not related

Table 3. Summary of analysis of variance statistics for salamander proportion (all salamanders combined; *P. metcalfi* alone) and body size collected along roads in the Nantahala National Forest, Highlands, North Carolina.*

Analysis and source	*df*	*Adjusted SS*	*Adjusted MS*	F	p
All salamanders					
distance	4	0.01450	0.00362	2.64	0.0480
site	10	0.06676	0.00668	4.86	<0.0001
error	40	0.05490	0.00137		
total	54	0.13616			
Plethodon metcalfi					
distance	4	0.02188	0.00547	3.47	0.0200
site	7	0.05312	0.00759	4.81	<0.0001
error	28	0.04418	0.00158		
total	39	0.11918			
Body size					
distance	4	0.06932	0.01733	3.48	0.0220
site	7	0.02224	0.00318	0.64	0.7200
error	25	0.12442	0.00498		
total	36	0.21598			

**Analyses differ in degrees of freedom because some samples were eliminated (see Methods).*

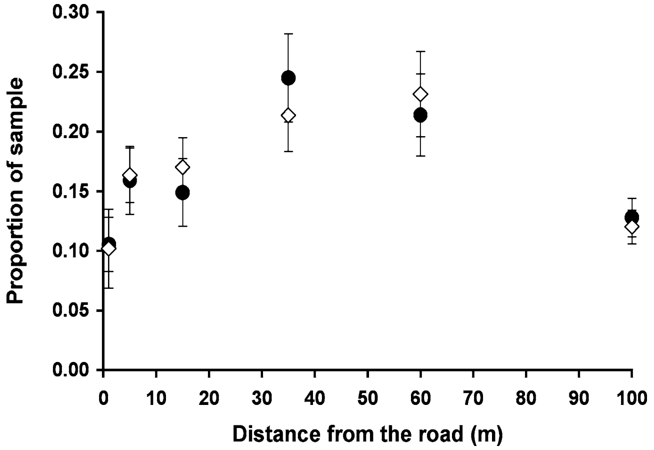

Figure 1. Abundance of salamanders at six distances (1, 5, 15, 35, 60, 100 m) from roads in the Nantahala National Forest, Highlands, North Carolina. Filled circles represent means (+1 SE) of all species combined; open diamonds represent means (+1 SE) of only Plethodon metcalfi *captures.*

to stem density of any size class (Pearson's $r = -0.311$, -0.234, -0.131 for small, medium, and large stem-size classes, respectively; all $p > 0.4$). In a stepwise multiple regression, with the abiotic variables tested against salamander abundance, only litter depth ($t = 3.10, p = 0.053$) and coarse woody debris ($t = 3.87, p = 0.020$) appeared significantly related. None of the abiotic factors were significantly correlated (either positively or negatively) with distance from the road (all $p > 0.05$).

Logging-Road Effects

The eight abandoned roads we sampled were narrow ($\bar{\chi} = 5.4$ m road width) and varied in elevation from 738 m to 1200 m. During the May 2005 sampling period, we collected only 27 salamanders of five species in 64 sample plots. There were no significant differences in the number of salamanders between on- and off-road plots (two-tailed, unpaired t test; $t = 0.8808$, df = 62, $p = 0.3818$). Nevertheless, when we compared the proportion of salamanders collected per plot (to account for twice as many sample plots on roads) on up- and downslope plots separately with on-road plots, there was a significant difference. The upslope plots had significantly higher proportions of salamanders than those on the road ($t = 2.778$, df = 46, $p = 0.0079$), whereas the proportion of salamanders collected downslope was higher but not significantly different than the proportion on the road ($t = 1.3533$, df = 46, $p = 0.1826$). Furthermore, soil density was significantly lower and depth of leaf litter and soil moisture were significantly higher at down- and upslope sites compared with on the road (Table 4). Leaf-litter moisture was also higher at down- and upslope sites compared with the road sites, but not significantly (Table 4).

Reduction in Habitat

After accounting for the average road clearing of 12 m, there was a large initial loss of suitable habitat with a road-edge effect of just 1 m (3.2–15.4%; Fig. 2). After this initial loss there was a steady and linear decrease of suitable habitat (up to a 28.6% loss) using a minimum road-edge effect of 35 m. This edge effect was significant for all salamanders. If we used a road-edge effect of 60 m, which was significant for *P. metcalfi* alone, the loss of suitable habitat increased to 36.9% (Fig. 2).

Discussion

Woodland salamanders showed a significant reduction in abundance near the road, and individuals along the edge were predominantly large in body size. Furthermore, salamander abundance was significantly lower on old, abandoned logging roads compared with adjacent upslope sites. These results indicate that active forest roads and abandoned logging roads have negative effects on forest-dependent species such as lungless plethodontid salamanders.

Although we predicted that based on invertebrate abundance (Haskell 2000), salamander abundance would be lowest next to roads (i.e., 1 m distance) and increase

Table 4. Summary of four physical characteristics (mean + 1 SE) and percent effect of down- and upslope samples compared with those taken from abandoned logging roads in the Nantahala National Forest, Highlands, North Carolina.

Characteristic	*Downslope (% effect)*	*Road (% effect)*	*Upslope (% effect)*
Soil density (g/mL)	0.2519 + 0.0467 (−38.0)*	0.4061 + 0.0758 —	0.2336 + 0.0446 (−42.5)*
Litter depth (cm)	3.09 + 0.20 (+30.3)*	2.38 + 0.19 —	3.44 + 0.19 (+44.7)*
Soil moisture (%)	35.6 + 3.72 (+27.9)*	27.8 + 2.20 —	39.0 + 3.78 (+44.8)*
Litter moisture (%)	30.5 + 4.20 (+12.5)	27.1 + 2.78 —	35.1 + 4.84 (+38.3)

**A* t *test was used to compare road samples with downslope or upslope* (p < *0.05).*

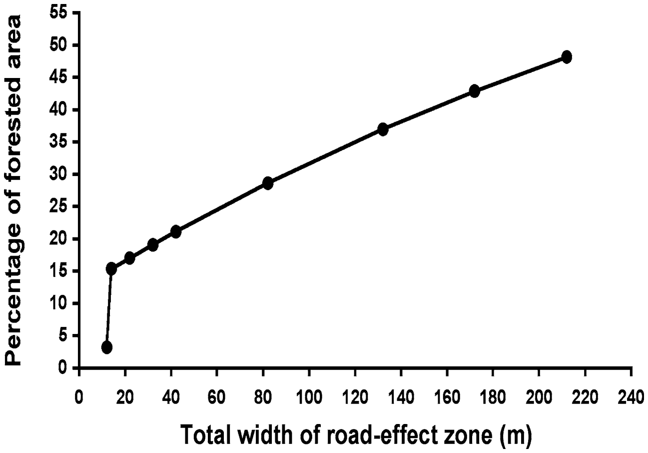

Figure 2. Summary of a GIS analysis showing the percentage of forest area affected by varying sizes of road-effect zone (simulated road edge effects = 0, 1, 5, 10, 15, 35, 60, 80, 100 m) in the Nantahala National Forest, Highlands, North Carolina.

or level off 100 m from roads, abundance was lowest at 1 m, peaked at 35 m from roads for all species and at 60 m for *P. metcalfi*, and declined out to 100 m (Fig. 1). This lack of a correlation with distance and no correlation with invertebrate abundance or richness indicates a road effect is unlikely due to food resources alone.

If one assumes that the scale of road effects in our study was conservatively 35 m, ignoring for the moment the decline at 100 m, this distance was very close to the 20-m road effect found for red-backed salamanders (*Plethodon cinereus*) at two out of three study sites in Virginia but was <the 80-m road effect found at a third site (Marsh & Beckman 2004). Thirty-five meters is also very similar to the edge effects of 20 m found for red-backed salamanders in New Hampshire forests (deGraaf & Yamasaki 2002). Because of such close agreement among three independent studies on the scale of edge effects for salamanders, we suggest that a conservative road-effect zone for terrestrial salamanders likely extends 35 m on either side of these relatively narrow, low-use forest roads (Table 1). We also suggest that the unsuitable habitat for salamanders created by the presence of road clearings plus this road-effect zone (35 m + 12 m road clearing + 35 m = 82 m) can fragment seemingly continuous forest into smaller blocks of suitable habitat.

To illustrate one consequence of a reduction in habitat road edge effects, we conducted a post hoc GIS analysis of the area of forest affected by roads to estimate the area of forest that would be unsuitable for salamanders (Fig. 2). Our estimate, based on the minimum road-effect size of 35 m, was 12,782 ha or 28.6% of the entire Highlands Ranger District. Estimates based on larger values taken from our study (60 m) or Marsh and Beckman (2004) (80 m) show that the amount of forest land that is potentially unsuitable is 36.9–42.8% of this tract of national forest.

Reduced soil moisture and leaf litter or some complex interaction of the two variables appears to decrease the availability of moisture to salamanders near roads. Moisture availability is an important factor for suitable habitat (Jaeger 1971, 1980; Ash 1995, 1997) and is the most likely proximate mechanism driving changes in salamander abundance near edges or limiting use by smaller species and smaller individuals (Ash et al. 2003; Marsh & Beckman 2004; our study). In addition, although data are limited to 1 year, drought conditions can decrease suitability even farther away than 35 m from roads (up to 80 m; Marsh & Beckman 2004), which illustrates the importance of moisture availability as a mechanism driving edge effects. Although explicit tests of this mechanism and further studies are needed, the current data for a broad-range of road effects (e.g., Trombulak & Frissell 2000) would permit a prediction that larger roads with more traffic and a greater drying effect would generate a larger road-effect zone for salamanders (see arguments in Fahrig et al. 1995; Hels & Buchwald 2001; Mazerolle 2004) and likely create even smaller patches of suitable forest habitat.

What is puzzling about our results and those of Marsh and Beckman (2004) is that salamander abundance actually declined after distances of 60 m in our study and 80 m for Marsh and Beckman (2004) from forest roads. A preliminary attempt to explain the declining abundance in our study failed to show any relationship to food resources such as invertebrate abundance or richness, or abiotic factors. Furthermore, salamander abundance did not correlate with shrub cover, as measured by stem density, which might have reflected changes in the availability of night-time foraging surfaces for salamanders (Jaeger 1978). We speculate that two explanations related to habitat change are likely responsible but would require further study. First, our sampling sites at 100 m were often farther up or down a ridge from the road such that the habitat may have been significantly different (e.g., drier on ridges or near outcrops) than at 30–60 m. Nevertheless, our measurements of habitat variables did not detect changes. Second, at 4 of 11 of our initial study sites, old, abandoned logging roads crossed or were adjacent to our transects somewhere between 60 and 100 m into the forest compartment. Although initially the area adjacent to these abandoned roads appeared visually similar to the surrounding forest, data from our study comparing abundance of salamanders on these old roads with samples from up- and downslope sites indicated long-lasting negative effects of roads. The stronger downslope effects relative to upslope sites may be the result of runoff (e.g., chemical pollutants and siltation). Thus, not only do active forest roads have an effect on salamanders but long-abandoned logging roads have an effect as well.

The implications of decreased salamander abundance at distances of 100 m from active roads is that the extraction of timber 80 years ago has created a significant ecological "footprint" in seemingly continuous forest that supercedes regeneration of the forest itself. Such long-lasting ecological effects perpetuate fragmentation of forest habitats and maintain smaller patches of suitable habitat for species than indicated by the presence of mature trees alone. Assuming current timber management practices harvest trees at intervals of 80–100 years in southern Appalachian forests, footprints of logging roads from past harvests will not be gone before a new footprint is laid down, and effects will accumulate over time. Thus, eventually forests could become increasingly fragmented into ever-smaller patches of suitable habitat for salamanders.

We suggest that our results directly apply to other protected forests in the southern Appalachians and exemplify a problem created by current and past land use activities in all forested regions, especially those related to road building for natural resource extraction. The problem we revealed here points to a potential failure of forest managers and policy makers to realize that the effect of roads reaches well beyond their boundary and that abandonment or the decommissioning of roads does not mean detrimental ecological effects disappear. Rather, our results indicate that current management decisions have significant repercussions for generations to come. Furthermore, the quantity of suitable forested habitat in protected areas like national forests is significantly reduced, perhaps as much as 42.8%, when the area encompassed by road effects is taken into account. Thus, we believe that management and policy decisions must use current and historical data on land use to understand accumulative impacts on forest-dependent species and to fully protect biodiversity on national lands.

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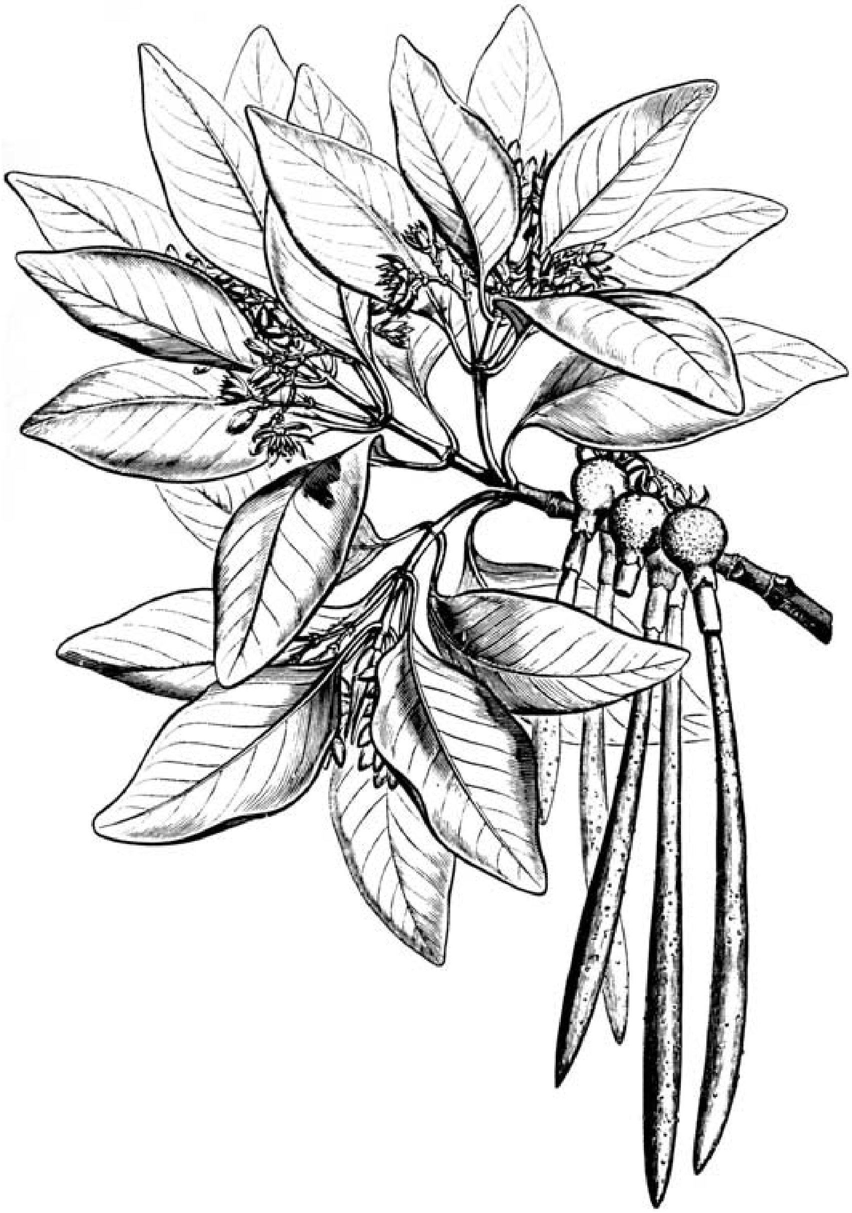

SALAMANDER COMMUNITIES INHABITING EPHEMERAL STREAMS IN A MIXED MESOPHYTIC FOREST OF SOUTHERN APPALACHIA

A Thesis Submitted to the School of Graduate Studies and Research in Partial Fulfillment of the Requirements for the Degree Master of Science

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Indiana University of Pennsylvania

The School of Graduate Studies and Research

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Title: Salamander Communities Inhabiting Ephemeral Streams in a Mixed Mesophytic Forest of Southern Appalachia

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ABSTRACT-

Salamanders are integral parts of forest ecosystems, often exceeding the combined biomass of all other vertebrates. They are often used as indicators of ecosystem health due to their intimate relationship with soils and water and their sensitivity to habitat alteration. This is especially important considering logging practices are un-regulated around ephemeral streams. This study examined salamander community composition in unstudied ephemeral stream areas, in order to identify important habitat characteristics associated with salamander abundance and diversity. Such information may aid in the development of improved forestry practices in and adjacent to ephemeral streams. From March 2007 to May 2008, I surveyed a total of 12 stream segments monthly. I detected 780 salamanders from 10 species, with an average of 65 (±35.8) salamanders per stream segment (minimum 17, maximum 127) with slimy, ravine and eastern newt comprising 78% of the total detections. I also intensively surveyed habitat characteristics in each ephemeral stream channel and along their banks. A linear regression, analyzing salamander species diversity and habitat variables, limited to the inclusion of two habitat variables per model, produced 7 competing models. The important variables (IV >0.4) from those models were density of small rocks and large rocks in the stream bed. When these salamander abundances were compared to habitat data, via redundancy analysis (RDA) and then a forward stepwise variable selection, two habitat variables were revealed to be important to the abundance of the salamander species. These variables included 1) the area of coarse woody debris in the stream; 2) a composite variable consisting of stream width, decay class, and number of coarse woody debris objects in stream. My study revealed that ephemeral streams provide suitable conditions to support diverse forest salamander communities. As such, my findings warrant the development of forestry best management practices for ephemeral streams that consider the maintenance of habitat quality and associated salamander communities.

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Chapter 1

INTRODUCTION

Salamanders often serve as indicators of ecosystem health because of their close relationship with soils and water, as well as their sensitivity to habitat alteration (Wyman and Hawksley-Lescault 1987, deMaynadier and Hunter 1995, Welsh and Droege 2001, Blaustein and Bancroft 2007). Disease, exotic species, chemical pollution, global climate change, increased exposure to UV-B radiation, and most importantly, habitat loss and degradation have been implicated in global population declines of amphibians for the past several decades (Vitt et al. 1990, Adler 2002, Halliday 2002, Blaustein and Wake 2005, Crawford and Semlitsch 2006, Blaustein and Bancroft 2007). The decline of amphibians is of particular conservation concern because they are important components of forested ecosystems, often exceeding the combined biomass of all other vertebrates (Crawford and Semlitsch 2006). Additionally, salamanders affect ecosystem processes including nutrient cycling and food web dynamics (deMaynadier and Hunter 1995).

In light of these declines there has been an increase in the efforts to identify and conserve important salamander habitats (deMaynadier and Hunter 1995, Blaustein and Bancroft 2007). The southern Appalachians have long been recognized as supporting a diverse assemblage of salamander species and is the major geographic center for the evolutionary diversification of the family *Plethodontidae* (National Park Service 2010). Many of the salamander species inhabiting the southern Appalachians are, at least in part, dependent on stream habitats (Behler and King 1979, Conant and Collins 1998, Petranka 1998). As such, a variety of measures have been used to directly and indirectly protect salamanders and their habitat throughout the Appalachian Mountains, including several state and federal regulations (e.g.,Clean Water Act of 1972).

Stream buffers of varying widths and residual basal areas have also been tested and incorporated into forest management plans to protect water quality and biological components (Rudolph and Dickson 1990, McComb et al. 1993, Stringer 2001, Semlitsch and Bodie 2003, Petranka and Smith 2005, Crawford and Semlitsch 2006, Perkins and Hunter 2006). These buffers, often called streamside management zones (SMZs), are primarily designed to protect water quality by acting as physical and chemical filtration for siltation and chemical pollutants (Stringer 2001) and help maintain appropriate water temperature and structural habitat for amphibians, reptiles, birds, mammals (Semlitsch and Bodie 2003), fish (Wesche et al. 1987, Young, 1999, Petranka and Smith 2005), mussels (Petranka and Smith 2005) and invertebrate communities (Newbold et al. 1980, Noel et al. 1986, Collier and Smith 1998, Rask et al. 1998).

While these regulations/practices are intended to protect stream degradation from timber harvest activities, they generally only apply to perennial streams. For example, in Kentucky, regulations prevent timber harvest and timber harvest activities within 7.6 m – 16.8 m (25-55 feet) of a perennial stream depending on the slope of the bank (Stringer 2001). Forestry best management practices (BMPs) intended to protect riparian systems has also been created in Kentucky, where the current study takes place (Stringer 2001). However, BMPs are non-legally binding guidelines that are currently designed to only protect perennial and intermittent streams but not ephemeral streams. Despite the fact that timber harvest activities in and around intermittent and perennial streams are regulated in order to ensure water quality, these stream habitats are often more susceptible to environmental degradation from other factors such as point and not point source pollution, headwater stream degradation, and human development (Sheridan et al.1999, Dosskey et al. 2002).

Although ephemeral streams have limited or no water flow throughout much of the year, their importance to salamander communities and other biodiversity in southern Appalachians should not be overlooked. Ephemeral streams may be at high risk from timber harvest activities because there are no regulations associated with proximity of harvest to this stream type (Stringer 2001). Ephemeral streams (headwater streams) are affected by pollution and human development differently than higher order streams due to several factors such as watershed size, stream connectivity, and water flow volume (Likens, and Bormann 1974, Lowe 2002, Lowe et al. 2006). Hence, the need for SMZs designed to protect water quality and habitat in ephemeral streams warrants investigation.

Salamanders are one taxon that could be negatively impacted by unregulated timber harvest in ephemeral streams. The importance of forested ephemeral streams to salamander populations inhabiting eastern deciduous forests is unknown. While most ephemeral streams are dry throughout the majority of the year, the time of year when water is present coincides with the breeding activities of many eastern salamander species (Petranka 1998). The absence of water during part of the year also limits fish populations in the ephemeral streams allowing many salamanders to complete a successful lifecycle due to reduced predation pressures (Kats et al. 1988, Taylor and Warren 2001, Petranka and Smith 2005). As a result, ephemeral streams may be of great importance for sustaining viable populations of amphibian species inhabiting deciduous forests of the eastern United States.

The objective of my study was to survey salamander communities occupying ephemeral streams in a southern Appalachian forest. Specifically, I collected data regarding salamander species diversity and abundance concomitant with habitat features for several ephemeral streams. These data will serve as a pretreatment baseline for a timber management experiment that will examine the affect of SMZ buffer width and residual basal area on water quality and associated wildlife.

Chapter 2

LITERATURE REVIEW

Amphibian Declines

The worldwide decline in amphibian populations was first recognized in the 1970's (Vitt et al. 1990), but did not receive significant attention from the conservation community until the early 1990's (Blaustein and Wake 1995, Halliday 2002). Amphibian declines have been attributed to numerous causes including disease, exotic species, chemical pollution, global climate change, increased exposure to UVB radiation, and most importantly habitat loss and degradation (Blaustein and Wake 1995, Adler 2002, Blaustein and Kiesecker 2002, Halliday 2002, Crawford and Semlitsch 2006, Blaustein and Bancroft 2007). Unique evolutionary characteristics of amphibians make them relatively vulnerable to a host of environmental stressors (Behler and King 1979, Blaustein and Wake 1995, deMaynadier and Hunter 1995, Conant and Collins 1998, Petranka 1998, Welsh and Droege 2001, Blaustein and Bancroft 2007). For example, most amphibians require an aquatic and terrestrial phase to complete their life cycles (Blaustein and Wake 1995, Blaustein and Bancroft 2007), a dependency that increases the number of potential environmental stressors by which amphibian populations may be impacted. Amphibians, especially some salamander species, use their skin for respiration (Behler and King 1979, deMaynadier and Hunter 1995, Conant and Collins 1998, Petranka 1998, Blaustein and Bancroft 2007). In fact, members of the family Plethodontidae have no lungs and depend solely on air exchange through their skin (Behler and King 1979, deMaynadier and Hunter 1995, Conant and Collins 1998, Petranka 1998, Blaustein and Bancroft 2007). The skin of a salamander must be thin and moist to effectively respire, a characteristic that makes this group susceptible to absorption of environmental pollutants (Blaustein and Wake 1995, Blaustein and Bancroft 2007). Amphibian eggs also lack a hard outer shell that also allows ready adsorption of pollutants (Blaustein and Bancroft 2007). As ectotherms, amphibians are exposed to greater amounts of UVB radiation that can cause mutations (Blaustein and Bancroft 2007). Finally, many juvenile amphibian species are herbivorous, but as they metamorph into adults they become carnivorous (Blaustein and Wake 1995), a life history attribute that inherently exposes them to pollutants from both aspects of the food web spectrum (Welsh and Droege 2001, Blaustein and Bancroft 2007).

Factors primarily responsible for amphibian habitat loss include wetland destruction due to human development, logging, and conversion to grazing land (Blaustein and Wake 1995). Because some salamanders use biotic or abiotic habitat cues to determine suitable habitat areas (Phillips 1986, McGregor and Teska 1989, Deutschlander et al 2000, Rittenhouse et al 2004), habitat degradation could affect salamanders even if it does not directly destroy important habitat features. Abiotic factors that may remain after habitat destruction and influence salamander behavior include the earth’s magnetic field and olfaction cues that affect orientation and movement of the eastern newt (Phillips 1986, Deutschlander et al 2000) and spotted salamander (McGregor and Teska 1989, Rittenhouse et al 2004), respectively. Because these cues remain after habitat destruction, the salamanders will still try to navigate through unsuitable habitat (Phillips 1986, McGregor and Teska 1989, Deutschlander et al 2000, Rittenhouse et al 2004). Salamander movements through unsuitable altered habitats can often result in death (Rothermel 2004).

While habitat loss is cited as the single most important factor driving the current loss of biodiversity (Blaustein and Wake 1990, Phillips 1990, Wyman 1990, Pechman et al 1991, Blaustein et. al 1994) no single factor appears to be the sole cause of the observed worldwide decline in amphibian species (Blaustein and Bancroft 2007). In national parks, undisturbed rural areas, and conservation lands, amphibian populations are declining despite the presence of intact habitat (Sjogren 1991, Halliday 2002, Blaustein and Bancroft 2007). It is likely that amphibian declines are the result of several factors working synergistically to stress amphibians to the point of decline or extinction (Blaustein and Kiesecker 2002). Moreover, because there are multiple stressors which are regionally variable, a single management solution to ameliorate this decline is not realistic (Blaustein and Kiesecker 2002, Blaustein and Johnson 2003a, Blaustein and Johnson 2003b, Blaustein and Bancroft 2007).

Other factors known to impact amphibian populations include disease, exotic species, and pollutants. Diseases such as the parasitic flatworm *Ribeiroia ondatrae* is responsible for most amphibian malformations in North America (Blaustein and Johnson 2003a, Blaustein and Johnson 2003b), and infectious pathogens such as the fungus *Batarachochytrium dendrobatidis* (chytridiomycosis), has caused mass mortality events in amphibians (Halliday 2002, Rachowicz et al. 2005). Exotic species such as the introduced American bullfrog (*Rana catesbeiana*) in California have outcompeted and preyed upon native amphibian species, which has led to significant population declines (Blaustein and Wake 1995, Halliday 2002). Introduced fish in ecosystems that were naturally devoid of fish have had devastating effects on amphibian populations by preying upon their eggs, tadpoles, and even adults (Blaustein and Wake 1995, Halliday

2002). Alteration and fragmentation of habitat by invasive species may also hinder amphibian re-colonization events. For example, mountain yellow-legged frogs (*Rana muscosa*) were prohibited from re-colonization of high elevation sites, in Kings Canyon National Park, California due to connecting streams being inhabited by introduced fish that prey upon *R. muscosa* larvae (Bradford 1991).

The thin membranous skin of amphibians make them susceptible to chemical pollutants including acid rain, fungicides, herbicides, insecticides and industrial chemicals (Blaustein and Wake 1995). Such pollutants can affect reproduction and development (Bridges and Semlitsch 2000, Blaustein and Johnson 2003a). Herbicides used to increase reforestation success and long-term timber yields (Wagner et al 2004) have become an integral part of modern forestry practices. Herbicide use, which results in higher crop yields, also reduces the amount of land needed for these activities (Wagner 2004). Studies suggest that herbicides used in forestry pose negligible damage to wildlife, and if ingested, are rapidly eliminated from animal systems (Tatum 2004). However, insecticides which are also used to prevent pest outbreaks in eastern forests can have negative impacts on amphibians (Relyea 2008). Pesticide concentrations acceptable for drinking water by the United States Environmental Protection Agency can result in 99% mortality of some amphibian species (Relyea 2008). Furthermore, a mixture of several pesticides, as often experienced in nature, can have larger impacts on amphibian mortality than each pesticide would otherwise have alone (Relyea 2008).

The exothermic nature of amphibians increases their exposure to UVB radiation. The effects of UVB radiation may have been compounded by the shrinking ozone layer. As large amounts of radiation penetrate the earth’s surface, amphibian eggs die, and invertebrate prey populations decline (Blaustein and Wake 1995). UVB radiation can cause mutations and cell death (Blaustein and Bancroft 2007) as well as slow growth rates, impair immune systems, and induce various types of sub lethal damage at the individual level (Tevini 1993). Exposure to UV radiation has also been linked with the disease chytridiomycosis (Blaustein and Wake 1995, Blaustein and Bancroft 2007), providing more evidence that multiple factors are causing amphibian population declines. However, UVB rays have minimal impact on forest dwelling amphibians because sunlight often does not reach the forest floor where many amphibians live (Halliday 2002). Nonetheless, timber harvest activities that create large canopy gaps may expose forest dwelling amphibians to increased UVB radiation.

Salamander Life Histories

Salamanders have radiated to fill many niches, and thus their habitats include deep permanent water sources, ephemeral streams and ponds, and upland forests (Petranka 1998). Species that may be found in proximity to ephemeral streams in eastern Kentucky include the eastern newt (*Notophthalmus viridescens),* spotted salamander *(Ambystoma maculatum)* and marbled salamander (A. *opacum)* which are typically associated with vernal pools and adjacent uplands (Petranka 1998, Colburn 2004). Additionally several species of lungless salamanders (family Plethodontidae) may also occur in ephemeral streams as members of this family are among the most common salamanders found in headwater streams of the Southern Appalachian Mountains (Behler and King 1979, Conant and Collins 1998, Petranka 1998). Within Plethodontidae there are two subfamilies, Desmognathine, and Plethodontinae; Desmognathine contains the genus *Desmognathus*, and others, Plethodontinae contains three tribes, the Hemidactyliini which have aquatic larvae and include the genera *Eurycea*, *Gyrinophilus*, *Hemidactylium*, *Pseudotriton* and several others, the Plethodontini which lack aquatic larvae and include the genera *Aneides* and the *Plethodon* and the Bolitoglossini which lack aquatic larvae and are mostly found in the western United States (Petranka 1998). The species from family Plethodontidae found in eastern Kentucky include *Aneides aeneus* (green salamander), *Desmognathus fuscus* (northern dusky salamander), *Desmognathus monticola* (seal salamander), *Desmognathus ochrophaeus* (Allegheny dusky salamander), *Desmognathus welteri* (Black Mountain salamander), *Eurycea longicauda* (long-tailed salamander), *Eurycea cirrigera* (southern two-line), *Gyrinophilus porphyriticus* (Kentucky spring salamander), *Hemidactylium scutatum* (four-toed salamander), *Plethodon glutinosus* (northern slimy salamander), *Plethodon kentucki* (Cumberland Plateau salamander), *Plethodon richmondi* (ravine salamander), *Pseudotrito ruber* (red salamander), and *Pseudotriton montanus* (midland mud salamander)

Biphasic Life Histories

Some of the salamander species that may inhabit ephemeral streams in eastern Kentucky have biphasic life histories. Adults of such species inhabit uplands habitats throughout much of the year, but return to aquatic environments seasonally to breed (Conant and Collins 1998, Petranka 1998). These include Eastern newts, spotted salamander, marbled salamander, northern dusky, seal, Allegheny dusky, black mountain, long-tailed, southern two-lined, Kentucky spring, and four-toed salamanders. Of these, the genus *Eurycea* is a general, common example. Northern two-lined salamander (*E. bislineata)* is relatively abundant throughout its range, but is sensitive to intensive timbering, land clearing, stream pollutants, siltation, and low soil pH (Wyman and

Jancola 1992, Petranka 1998). The *Eurycea (*especially *E. bislineata)* are generally found from sea level to 2000 m (Petranka 1998). Adults of this genus use rocks and logs along small streams and seeps as cover, but can also be found on the forest floor far from sources of running water (Petranka 1998). *E. bislineata* adults lay eggs under submerged debris in running water (Petranka 1998) and rarely in lakes (Bahret 1996). They share these breeding streams with other salamander species and fish (Petranka 1998). The larvae live in slow moving pools and are benthic feeders, (Petranka 1998) primarily consuming chironomid larvae, copepods, fly pupae, and stonefly nymphs (Caldwell and Houtcooper 1973, Petranka 1984). As the larvae grow, their prey size increases, and includes isopods, amphipods, chironomid larvae, and zooplankton, and if available hatchling salamanders (Petranka 1984). Larvae take from 1 to 3 years to metamorph, the latter being further north in the species range (Wilder 1924, Duellman and Wood 1954, Hudson 1955, Bruce 1982, 1985, Stewert 1968). Metamorphosis usually occurs between April and July (Petranka 1998). In the southern Appalachians the length of the larval period depends on stream size where larvae overwinter. The larval phase is usually 1 year in ephemeral streams and 1 to 2 years in permanent streams (Voss 1993).

Blue-ridge two-line salamander (*E.b. wilderae*) takes 3-4 years to mature (Bruce 1988). Both juveniles and adults live along stream margins and the surrounding forests, and adults may undergo yearly migrations to and from breeding streams (Petranka 1998). While breeding in May, *E.bislineata* make nightly forays to and from streams to feed (MacCulloch and Bider 1975). Post breeding adults migrate up hill, away from streams in June and sometimes travel over 100m (MacCulloch and Bider 1975). Another migration occurs in post metamorphic juveniles in August; however, these individuals stay fairly close to streams (MacCulloch and Bider 1975). In October, adults migrate back to the stream (MacCulloch and Bider 1975), and during cold weather individuals retreat underground 8-82 cm (Ashton and Ashton 1978). Adults feed year round on food items including beetles, spiders, sowbugs, mayflies, dipterans, annelids, stonefly nymphs, and thrips (Hamilton 1932).

Fish can have large impacts on the survival of larval salamanders (Efford and Mathais 1969, Heyer et al. 1975, Petranka 1983, Sih et al. 1988). As such, salamanders have developed several defenses against fish, the most important being parental water source selection of fishless water bodies (Behler and King 1979, Conant and Collins 1998, Petranka 1998). In contrast, two-lined salamanders (*E. bislineata*) breed in permanent streams, frequently encounter fish, and are considered palatable to fish, but shows strong signs of reduced mobility and hiding when chemical cues from fish are present in the water (Kats et al. 1988). Other biphasic species defenses include reduced mobility (Woodward 1983), cryptic coloration (Wasserburg 1971), chemical repellents (Voris and Bacon 1966, Brodie et al 1978), shifts in diel activity patterns (Taylor 1983), use of chemical cues to detect predatory fish (Petranka et al. 1987), and un-palatability (Kats et al. 1988).

Terrestrial Breeding Life Histories

Other salamanders that may inhabit ephemeral streams in eastern Kentucky have terrestrial breeding life histories. Such species require moist upland environments throughout they year and do not require aquatic environments during the breeding season (Conant and Collins 1998, Petranka 1998). Species with terrestrial breeding life histories that may inhabit ephemeral streams in eastern Kentucky include green, northern slimy, Cumberland-plateau, ravine, red, midland mud. Large plethodons, especially the slimy salamander (*Plethodon glutinosus)* are common inhabitants of eastern deciduous forests below 1500 m elevation (Petranka 1998). Even though these salamanders do not require streams to breed, they still require moist habitat. *P. glutinosus* can be found in bottomland hardwoods, swamp forests, and wet pinewoods in the southeastern coastal plains (Petranka 1998). They are frequently found in caves, under rocks and logs or on the forest floor at night (Noble and Marshall 1929, Wells and Gordon 1958, Peck 1974, Petranka 1998).

P. glutinosus breeding season varies greatly depending on geographic location, anywhere from February thru August in Florida (Highton 1956), to September thru October in northern populations in New York (Bishop 1941, Highton 1962). In Kentucky, and the middle of the species range, females lay eggs from late spring to early summer (Bush 1959, Highton 1962). Eggs are usually deposited on the ceilings of natural cavities, and often guarded by the female (Petranka 1998). Most nests are presumed to be in underground refugia, as few above ground nests have been discovered (Petranka 1998). Embryonic development lasts 2-3 months before hatching (Highton 1956).

Most *P. glutinosus* females become sexually mature at 2 years of age and ova-deposit the following year (Petranka 1998). Males sometimes mature in their first year and mate the next year (Petranka 1998). Growth rates vary greatly with latitude and environmental conditions (Petranka 1998). Adults are active on the surface year-round except during droughts and periods of extreme heat or cold (Petranka 1998). Adults move greater distances than juveniles with a maximum distance of 92 m recorded between captures, but most move < 9 m (Petranka 1998). Adults also aggressively defend their territories (Thurow 1976, Marshall et al 2004) and in optimal habitat in Pennsylvania and Maryland, they can be found in densities of 0.52-0.81 salamanders/ m^2 (Petranka 1998).

P. glutinosus forage at night on the forest floor during wet periods (Petranka 1998). Populations of P.*glutinosus* in the southern Appalachians are most active during the first few hours of dark (Gordon et al 1962). This species is a generalist predator that consumes a variety of prey species including springtails (Collembola), leaf hoppers, cicadas, scale insects planthoppers and aphids (Homoptera), true bugs (hemipterans), butterflies and moths (Lepidoptera) , flies (Diptera), ants (Hymenoptera), daddy-long-legs, pseudoscorpians and spiders (Arachnida), beetles (Coleoptera), millipedes (Diplopoda), earthworms (Annalida), snails and slugs (Gastropoda) and centipedes (Chilopoda) Surcafe 1913, Hamiliton 1932, Pope 1950). They may also cannibalize smaller salamanders of other species (Powers 1973, Powers and Tietjen 1974, Pertanka 1998).

Most eastern Kentucky salamanders are lungless and thus require moist environments (Behler and King 1979, Conant and Collins 1998, Petranka 1998). Optimal salamander habitats in southern Appalachia are mesic cove forests or streambeds with dry ridge tops and low-elevation forests with poor sandy soil (Petranka et al 1993). From a microhabitat perspective, salamanders require cover items such as rocks and logs for protection from predators and as foraging sites (Behler and King 1979, Jaeger 1980, Jaeger et al 1995, Conant and Collins 1998, Petranka 1998, Davis 2002, Cummer and Painter 2007). However, some salamander species also require specific habitat associations. For example, four-toed salamanders (*Hemidactylium scutatum*) require hollows in Sphagnum above standing water for their nests (Colburn 2004). Green salamanders (*Aneides aeneus*) are frequently found in cliff faces < 1340 m elevation (Petranka 1998) that are comprised of sandstone, granite and schist and contain deep shaded crevices that are moist but not dripping wet (Netting and Richmond 1932, Gordon and Smith 1949, Schwartz 1954, Bruce 1968, Mount 1975). Therefore, in forests where salamander diversity and abundance is a conservation goal, managers should maintain appropriate microhabitat conditions in both upland and riparian communities.

Salamander Community Dynamics

Salamander community composition and structuring may be determined by competition among salamander species (Thurow 1976, Jaeger and Forester 1993, Mathis et al 1995, Grover 1998, Houze and Chandler 2002). For instance, *Plethodontid* salamanders often defend a central cover object from conspecifics and other salamander species (Thurow 1976, Jaeger and Forester 1993, Mathis et al 1995, Grover 1998), and thus behaviorally limit local salamander population densities. Territoriality was also observed by Houze and Chandler (2002) who found no more than 1 salamander under 30 cm x 30 cm coverboards and by Thurow (1974) between large and small Plethodons although small Plethodons showed less aggression than larger ones. Differences in use of rock and wood cover objects can partially be explained by species present in a given area; with more terrestrial species favoring wood objects (Southerland 1986a). Jaeger et al (2001) found more male-female pairs and less same sex pairs under the same cover board than that expected by chance, thus suggesting that cover objects were providing habitat for breeding pairs, and were foci of territoriality between males. Cover objects may also affect the success of foraging in small Plethodons (Grover 1998). Collectively, these findings suggest that the availability of cover objects and moisture levels could regulate salamander densities but vary by species and age (Grover 1998).

Seal salamanders regularly used bank and forest floor habitats and exclusion from either resulted in poor survival (Sutherland 1986b). Conspecifics and equal size congeners decreased the growth and reduced survival of seal salamanders (Sutherland 1986b). Predation from black belly salamanders (*Desmognathus quadramaculatus*) reduced juvenal survival and altered habitat selection in seal salamanders (Sutherland 1986b). Sutherland (1986b) also states that intermediate species, especially seal salamanders, are limited by the availability of stream bank cover objects.

Other factors that may influence salamander community structure and composition include food (Jaeger 1972), burrow availability (Jaeger 1974), predation (Hairston 1986, Southerland 1986a, 1986b), and intra-specific dominance. For instance the *Desmognathus* species assemblages are arranged such that the larger species inhabit the stream itself with progressively smaller species inhabiting drier areas further from the stream (Hairston 1949, Organ 1961, Hairston 1980). Grover (1996, 2000) observed that larger salamander species were found closer to, and in streams, while smaller species inhabited peripheral areas outside the stream, due to their ability to rehydrate faster. Several salamander species were also found further from streams when the larger aquatic species black belly salamander (*Desmognathus quadramaculatus*) was present than when it was absent (Grover 2000). Survivorship has also been found to increase in more terrestrial species, than in aquatic ones, with a larger proportion of individuals reaching sexual maturity, and a lower number of eggs produced per female (Organ 1961)

Impacts of Timber Management on Salamander Communities

Many studies have investigated the effects of silvicultural treatments on herpetofauna (Rudolph and Dickson 1990, Raymond and Hardy 1991, DeGraaf and Yamasaki 1992, Petranka et al 1993, Petranka et al 1994, Ash 1995, Dupuis et al 1995, deMaynadier and Hunter 1995, Ash 1997, deMaynadier and Hunter 1998, Moseley et al 2003, Fortino et al 2004). Silvicultural treatments such as individual tree removal, clear cutting, and prescribed burning can have direct and indirect effects on amphibian communities (Raymond and Hardy 1991, Petranka et al. 1993, Ash 1995, 1997, DeMaynadier and Hunter 1998, Russell et al. 1999, Moseley et al. 2003, Becker et al. 2007, Reichenbach and Sattler 2007, Fonseca et al. 2008, Becker et al. 2010). For example, removal of coarse woody debris, increased soil compaction, altered above and below ground hydrology, increased organic and inorganic runoff, altered stream flow rate, and reduced leaf litter depth and moisture content can result from timber management practices (Patric 1978, Hornbeck et al. 1993, Ash 1995, Ash 1997, Rothermel and Luhring 2005).

Few generalizations can be made regarding the effect of specific silvicultural treatments on amphibian communities due to regional environmental differences. For example, habitat use by riparian amphibian species varies greatly by elevation, stream type, and adjacent land use (Petranka and Smith 2005). The presence of aquatic and terrestrial breeding salamanders differed depending on elevational changes in southern Appalachia (Petranka and Smith 2005). Specifically, terrestrial breeding salamanders were more common at higher elevations than at lower elevations, and stream breeding salamanders were more common at lower elevations than at higher elevations (Petranka and Smith 2005).

Most studies that examined amphibian response to forest management have evaluated the effects of clear cutting on amphibian diversity and abundance (Raymond and Hardy 1991, Petranka et al 1993, Ash 1995, Blaustein and Wake 1995, Ash 1997, Reichenbach and Sattler 2007). Clear cutting is a timber harvest method that removes all trees from an area in a single harvest (Bolen and Robinson 2003, Kimmins 2004). Clear cutting removes the forest canopy which increases light penetration and water temperature, and decreases humidity, soil moisture, and litter cover (Raymond and Hardy 1991, Fortino et al 2004, Riechenbach and Sattler 2007). Clear cutting has been linked to high levels of salamander mortality (Petranka et al 1993, Blaustein and Wake 1995).

The majority of studies that examined the effects of silvicultural treatments on salamanders have reported population declines, although a few detected no change in population sizes (DeGraaf and Yamasaki 1992, Petranka et al 1993, 1994, Dupuis et al 1995, deMaynadier and Hunter 1998, Reichenbach and Sattler 2007). For example, recent clear cuts resulted in a decline in the number of adult salamanders returning to breeding habitat (Raymond and Hardy 1991). A review of 18 independent studies reported that salamander and anuran abundances were 4.3 and 1.7 times higher on un-harvested (control) than on clear cut stands (deMaynadier and Hunter 1995). In southern Appalachia, amphibian species abundances on clear cuts were half of that observed on un-harvested control plots in high-elevation stands, and one third of that observed on un-harvested control plots in mid-elevation stands (Petranka et al. 1993, 1994). Several studies have reported lower salamander species abundances on clear cuts, but results have not been statistically significant (Bury 1983, Enge and Marion 1986, Paris et al 1988, Corn and Bury 1991, deMaynadier and Hunter 1995). The reason for declining salamander populations after clear cutting is unclear (deMaynadier and Hunter 1995). It is uncertain how many salamanders die, emigrate off site, or retreat to underground refuges after clear cutting (deMaynadier and Hunter 1995). The number of individuals that emigrate off site would vary greatly depending on the size of the clear cut as well as the distance to favorable habitat (Reichenbach and Sattler 2007). In one study, 41% of the salamanders moved to more favorable habitat after clear cutting (Reichenbach and Sattler 2007).

Several studies have investigated the amount of time it takes post-timber harvest for salamander populations to recover to levels similar to those of mature forest (Petranka et al 1992, Ash 1997). However, such studies are difficult to conduct because salamander abundance is not linked to forest age, but rather to microhabitat characteristics such as coarse woody debris (Aubry et al 1988, Bury and Corn 1988, Ramotnik and Scott 1988, Raphael 1988, Welsh and Lind 1991, Petranka et al 1994), litter depth and type (Heatwole 1962, Pough et al 1987, DeGraaf and Rudis 1990, Corn and Bury 1991), soil pH (Wyman and Hawksley-Lescault 1987, Wymann 1988, Wyman and Jancola 1992) and shrub abundance (Pough et al. 1987, Raphael 1988, Corn and Bury 1991, Welsh and Lind 1995). These microhabitat characteristics do not necessarily follow the same trends as forest age (Spies et al 1988, Welsh 1990, Hansen et al 1991, Welsh 1993, Petranka 1994). Petranka (1994) found that clear cuts < 5 years old and forest stands > 120 years old had the highest amounts of coarse woody debris, although mean log diameter and number of logs in advanced decay, increased with stand age.

Best Management Practices for Riparian Zones

In recent decades, BMPs have been developed to promote long-term sustainable timber harvest and protect against soil erosion and water quality degradation (Stringer 2001). Buffers or forested riparian strips, also called streamside management zones (SMZs) are often important components of BMP guidelines developed for Appalachian forests (Stringer 2001, Fortino et al 2004). Stream buffers are designed to enhance ecosystem functions, and protect aquatic species such as fish and mussels, as well as maintain water quality (Petranka and Smith 2005). Riparian buffers also protect core habitat for semi-aquatic species such as salamanders by retaining some or all of the pre-cut vegetation (Fortino et al. 2004). Little is known regarding the effects of variation in riparian buffer widths on herpetofaunal communities (Rudolph and Dickson 1990) and buffer effectiveness in maintaining functional ecosystems (Fortino et al 2004). Nearly 50% of all amphibians captured in Texas pine plantations were in riparian buffers 50 m to 95 m wide, whereas only 13% of all captures were in 25 m wide buffers (Rudolph and Dickson 1990). They attributed differences in capture rates to variation in microhabitats (Rudolph and Dickson 1990). Wide buffers had open under-story and thick leaf litter, while thin buffers had dense graminoids and thin leaf litter cover, as well as higher incident light and lower humidity (Rudolph and Dickson 1990).

Petranka and Smith (2005) also observed spatial segregation of species with regard to distance from streams or moisture gradients. Due to this segregation, buffer strips that cover the entire moisture gradient are especially important. Buffer strips not only benefited terrestrial salamander species but other aquatic species as well including fish, mussels, and invertebrate communities (Newbold et al. 1980, noel et al. 1986, Wesche et al. 1987, Rudolph and Dickson 1990, McComb et al. 1993, Darveau et al. 1995, Spackman and Hughes 1995, Hodges and Krementz 1996, Collier and Smith 1998, Semlitsch 1998, Rask et al. 1998, Young et al.1999, Bodie 2001, Darveau et al. 2001, Petranka and Smith 2005).

Prescribed Burning

The effect of prescribed fire on herpetofauna has also been studied (Russell et al. 1999, Moseley et al. 2003). Although fire inhibits hardwood species succession in pine forests (Moseley et al. 2003), and may be detrimental to woodland salamander species (Bennett et al. 1980, Ford et al. 1999), fire maintained communities are important to some herpetofaunal species (Means and Campbell 1981, Mushinsky 1985), and provide a means of maintaining habitat diversity (Moseley et al 2003). There is no evidence that fires directly harm herpetofauna (Russell et al. 1999). However, indirect effects may positively or negatively affect many herpetofaunal species (Russell et al. 1999). Kirkland et al. (1996) found significantly more amphibians in a recently burned stand than in adjacent control stands, but could not specifically link the difference to fire. Appropriate season or frequency of burns may be important (Russell et al. 1999). Winter burns did not affect coarse woody debris volumes, which may have allowed for similar salamander abundance, diversity and richness between burned and unburned stands (Moseley et al. 2003). Burning, however, did affect litter depth and canopy height, with both being greater in unburned areas, and percent bare ground cover, which was greater in burned areas (Moseley et al. 2003). Ash (1995, 1997) found that decreased litter depth and moisture reduced salamander abundance; additionally Moseley et al. (2003) found that salamander abundance was negatively correlated with percent bare ground. Most studies have examined the effect of fire on fire-maintained ecosystems, and inferences cannot be as readily applied to other regions (Russell et al. 1999).

Review of Herpetofauna Capture and Survey Methods

Many survey methods have been developed to sample or monitor herpetofauna including time and area constraint searches, cover boards, pitfall traps, drift fencing, and land transects (Burton and Likens 1975, Bennett et al. 1980, Wyman and Hawksley-Lescuault 1987, Jaeger et al. 2001, McDade and Maguire 2005, Crawford and Semlitsch 2006, Perkins and Hunter 2006). The effectiveness of each method varies depending on study location, target species, precipitation amounts, and temperature. However, no survey technique can adequately assess all herpetofauna species; therefore, some are specifically designed to catch individual species or groups (e.g. terrestrial salamanders, frogs or snakes). A study in the Pacific Northwest found that pitfall traps were the best method to capture terrestrial salamanders, while cover boards were very ineffective (McDade and Maguire 2005). However, studies from the eastern United States have had great success using cover boards to capture terrestrial salamanders (Harpole and Haas 1999, Monti et al. 2000, Jaeger et al. 2001).

Each survey method has associated costs and benefits, and due to varying effectiveness, many studies incorporate more than one method. Ground searches, transects, and hand searches all have potential for human-generated biases (Houze and Chandler 2002), and vary in effectiveness depending on survey period, species surveyed, and the experience of the searcher (McDade and Maguire 2005). Time and area constraint searches may also have observer-based biases but can be used to document species not likely to be encountered via other sampling methods (Corn and Bury 1990).

Searching under rocks in streams is especially important for sampling aquatic amphibians. Additionally, arboreal or other microhabitat specialists may not be detected using other methods, but could be surveyed with area and time constraint searches.

Pitfall traps, holes dug in the ground in to which animals fall and cannot escape, can be left open 24 hours a day and can catch species that are nocturnal, crepuscular or diurnal. They are also useful because they contain the captured animals until the trap is checked (Enge 2005). Problems associated with pitfall traps include not adequately sample all species because many species are active only in water or primarily underground. Pitfall traps also become more time efficient the longer they are used, due to the great effort required to install them (McDade and Maguire 2005). Other negative aspects associated with pitfall traps include the capture of non targets and deaths due to dehydration, drowning, or predation.

Cover boards used to survey salamanders are usually small (<1 m^2) and made of wood to retain moisture (Monti et al. 2000, Houze and Chandler 2002, Marsh and Goicochea 2003). Cover boards are effective for sampling forest salamanders in the eastern United States because they simulate natural coarse woody debris (CWD) and have very low impact on the forest floor (Houze and Chandler 2002, McDade and Maguire 2005). Cover boards are preferred over searching coarse woody debris, because the latter requires extensive, irreversible, disturbance of habitat (Houze and Chandler 2002). Cover boards are simply lifted off the forest floor and then replaced after individuals have been identified and recorded (Jung et al. 2000, Hyde and Simmons 2001). However, cover boards need to effectively trap moisture to remain attractive to amphibians (McDade and Maguire 2005). Marsh and Goicochea (2003) used boards of white oak, while non-treated plywood boards and cedar boards have been used in other studies (Monti et al. 2000, Houze and Chandler 2002).

McDade and Maguire (2005) suggested the following procedures to improve cover board effectiveness for sampling salamander communities: (1) use seasoned or slightly decayed cover boards; (2) check boards during or immediately following suitable weather conditions (i.e. rain); (3) use cover board materials that retain moisture; (4) place boards directly on the ground without spacer sticks to inhibit desiccation of cover boards; and (5) place litter over boards to help maintain moisture levels. Cover boards can effectively detect most salamander species present under natural coarse woody debris, although at lower, more variable rates (Houze and Chandler 2002). Temperature under cover boards was likely the most influential variable affecting salamander presence, especially in late summer (Houze and Chandler 2002). This could be due to the cover board thickness or other physical attributes compared to natural cover objects, allowing for different air and water flow under the objects (Houze and Chandler 2002). Cover boards were biased towards finding adults, whereas all age classes were found under natural coarse woody debris (Marsh and Goicochea 2003).

The objective of this study is to determine the use of ephemeral stream by salamander communities. The relationships between salamander species and habitat variables will be used to determine better SMZ guidelines. These same characteristics will also be useful for repairing damaged habitats and preserving vulnerable areas in ephemeral streams in order to help maintain these salamander communities from decline and extinction.

Chapter 3

STUDY AREA

This study was conducted on The University of Kentucky's Robinson Forest, located in Breathitt, Perry, and Knott Counties in southeastern Kentucky. Robinson Forest is a 4000 ha relatively intact second growth experimental forest. Elevations in Robinson Forest ranged from 243 m (800 feet) to 487 m (1600 feet) (Overstreet 1984). Public access to the forest was restricted and at the time of the study human disturbances to the forest were minimal. Some perennial streams had been modified with weirs for hydrological monitoring and a network of single lane, dirt roads with a mostly intact canopy above was present. The predominant forest community was characterized as mixed-mesophytic characterized by 30 co-dominant canopy tree species including American beech (*Fagus grandifolia*), yellow-popular (*Liriodendron tulipifera*), basswood (*Tilia spp*.), sugar maple (*Acer saccharum*), northern red oak (*Quercus rubra*), white oak (*Quercus alba*), eastern hemlock (*Tsuga canadensis*), and yellow buckeye (*Aesculus octandra*) (Braun 1950). Understory species included eastern redbud (*Cercis canadensis*), flowering dogwood (*Cornus florida*), spicebush (*Lindera benzoin*), and pawpaw (*Asimina triloba*). Ridge tops, southwest facing slopes and areas with rocky shallow soils were characterized by oak-hickory (*Quercus-Carya*) and oak-pine (*Quercus-Pinus*) communities (Overstreet 1984).

Eastern Kentucky's climate is temperate-humid-continental with warm summers and cool winters (Overstreet 1984). From 1972-1998 multiple precipitation collectors in Robinson forest measured the average annual rain fall to be 117.5 cm. The average high temperature is 29°C (84°F) in July, with the average low temperature of -3°C (26°F) in January (U.S. Climate Data 2009).

I chose to study 12 random ephemeral stream segments in 7 watersheds located within the Clemons Fork area (Figure 1). These watersheds ranged from 25-60 ha. The ephemeral stream segments I surveyed spanned approximately the same elevational range (305 m – 378 m) (Table 1), and had bank slopes over 15°. Streams were identified as ephemeral based on water flow data (C. Barton, University of Kentucky). The length of each stream segment ranged from 325 m to 493 m (800 to 1617 feet). Aspects for each stream segment varied and are shown in Table 1.

Seventeen salamander species that could have potentially been captured in ephemeral streams and surrounding uplands in eastern Kentucky are *Ambystoma maculatum* (spotted salamander), *Ambystoma opacum* (marbled salamander), *Aneides aeneus* (green salamander), *Desmognathus fuscus* (northern dusky salamander), *Desmognathus monticola* (seal salamander), *Desmognathus ochrophaeus* (Allegheny mountain dusky salamander), *Desmognathus welteri* (black mountain salamander), *Eurycea longicauda* (long-tailed salamander), *Eurycea cirrigera* (southern two-line), *Gyrinophilus porphyriticus* (Kentucky spring salamander), *Hemidactylium scutatum* (four-toed salamander), *Notophthalmus viridescens* (eastern or red spotted newt), *Plethodon glutinosus* (northern slimy salamander), *Plethodon kentucki* (Cumberland Plateau salamander), *Plethodon richmondi* (ravine salamander), *Pseudotriton ruber* (red salamander), and *Pseudotriton montanus* (midland mud salamander) (Behler and King 1979, Conant and Collins 1998, Petranka 1998, McGregor 2001).

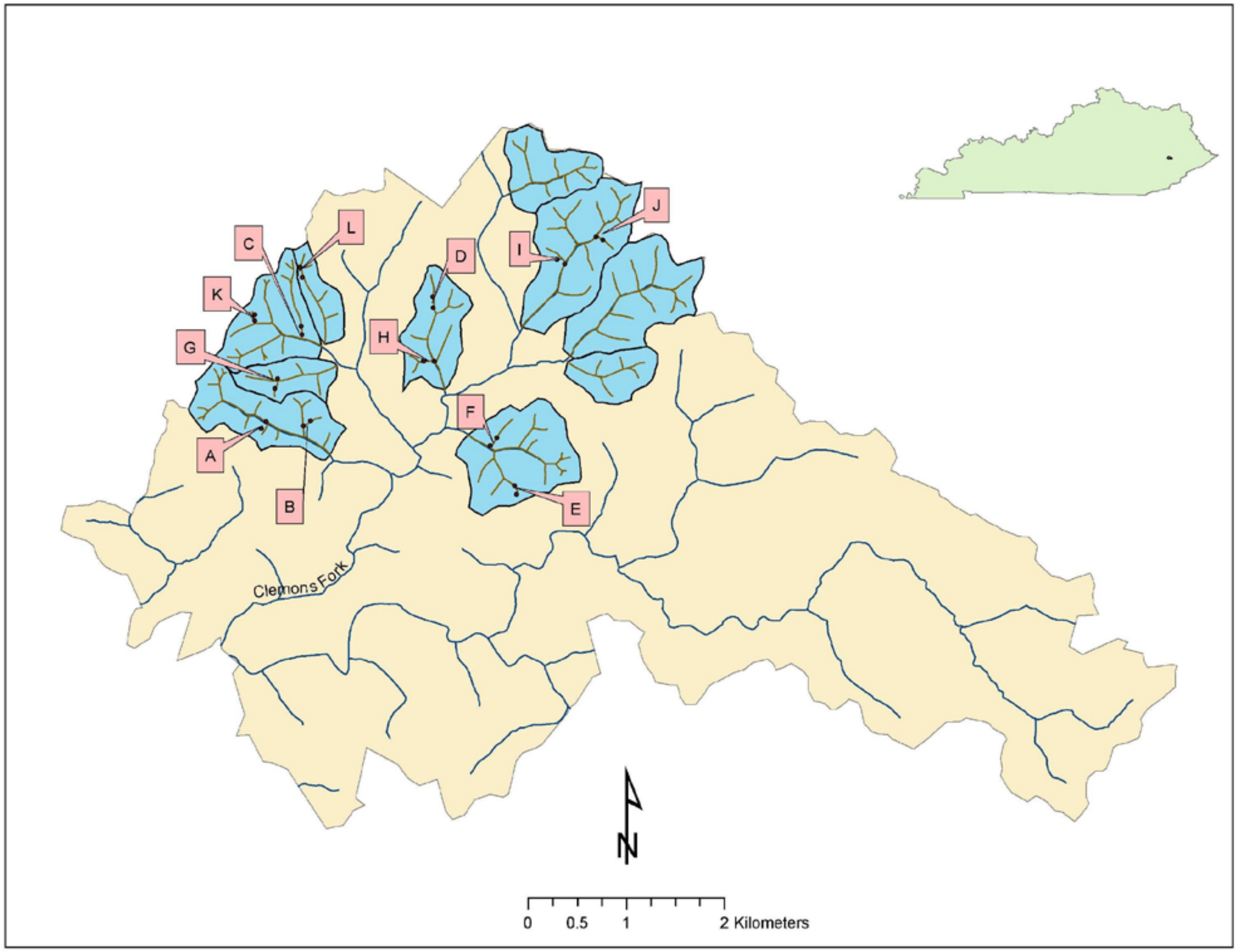

Figure 1: Map of Robinson Forest, Clemons Fork, Breathitt County, Kentucky. Twelve experimental ephemeral streams are located in 7 smaller watersheds. The large outline is Robinson forest's main block, while the smaller shaded outlines are the individual watersheds. The top and bottom locations of the 12 experimental ephemeral streams are marked with black dots with each ephemeral stream section labeled A though L.

Table 1: Data for the experimental ephemeral streams in Robinson forest, Breathitt County, Kentucky. Streams were named A through L, and had aspects and elevations (measured by GPS) shown in the table.

Stream ID	Watershed	Aspect	Length (m)	Downstream Elevation (m)	Upstream elevation (m)
A	Little Millseat	North East	366	329	360
B	Little Millseat	South West	340	317	347
C	Shelly Rock West	South West	325	323	329
D	Booker	South West	345	347	366
E	Falling Rock	North West	325	341	378
F	Falling Rock	South West	460	323	329
G	Shelly Rock South	North	395	341	366
H	Booker	East	382	305	317
I	Wet Fork	South East	493	341	378
J	Wet Fork	North West	417	341	378
K	Shelly Rock West	South	363	354	378
L	Shelly Rock North	South	427	366	378

Chapter 4

METHODS

Trap Arrays

Each ephemeral stream segment, a 325 m to 460 m stretch of stream, I surveyed had one salamander sampling array which consisted of four parts (Figure 2): 1) 3 arms of 15.24 m (50 feet) of drift fencing with 4 pitfall traps, 2) 20 cover boards, 3) one 5 m section of hand-searched stream, and 4) ten 50 cm^2 square searches of leaf litter. Cover boards were 60 cm X 60 cm sheets of 1.5 cm thick plywood, similar to those used in other studies (Marsh and Goicochea 2003, Houze and Chandler 2002) were placed within 5m of the stream edge depending on the terrain. New cover boards were placed in the field in July 2005; however by the time this project was initiated cover boards had aged for approximately 2 years. Cover boards were individually numbered and arranged in a staggered pattern so that 10 were located on each side of the stream (Figure 2).

In addition to cover boards, each sampling location had one drift fence and pitfall array. The pitfall arrays were established in 2005 and consisted of three arm segments of fencing arranged in a ‘Y’ shape (Figure 2). Drift fences were made with a sturdy landscaping fabric, which was stapled over wooden stakes that had been hammered in to the ground for support. The fencing was similar to that used to sample amphibians in steep head ravines in Florida (Enge 2005). The pitfall traps consisted of four, 13.3 L (3.5 gallon) buckets buried flush to the ground. One bucket was located at the end of each of the three drift fence arms and one was located at the center where the three arms intersected. Each arm was 15.2 m (50 feet) in length, except for the right arm (looking at

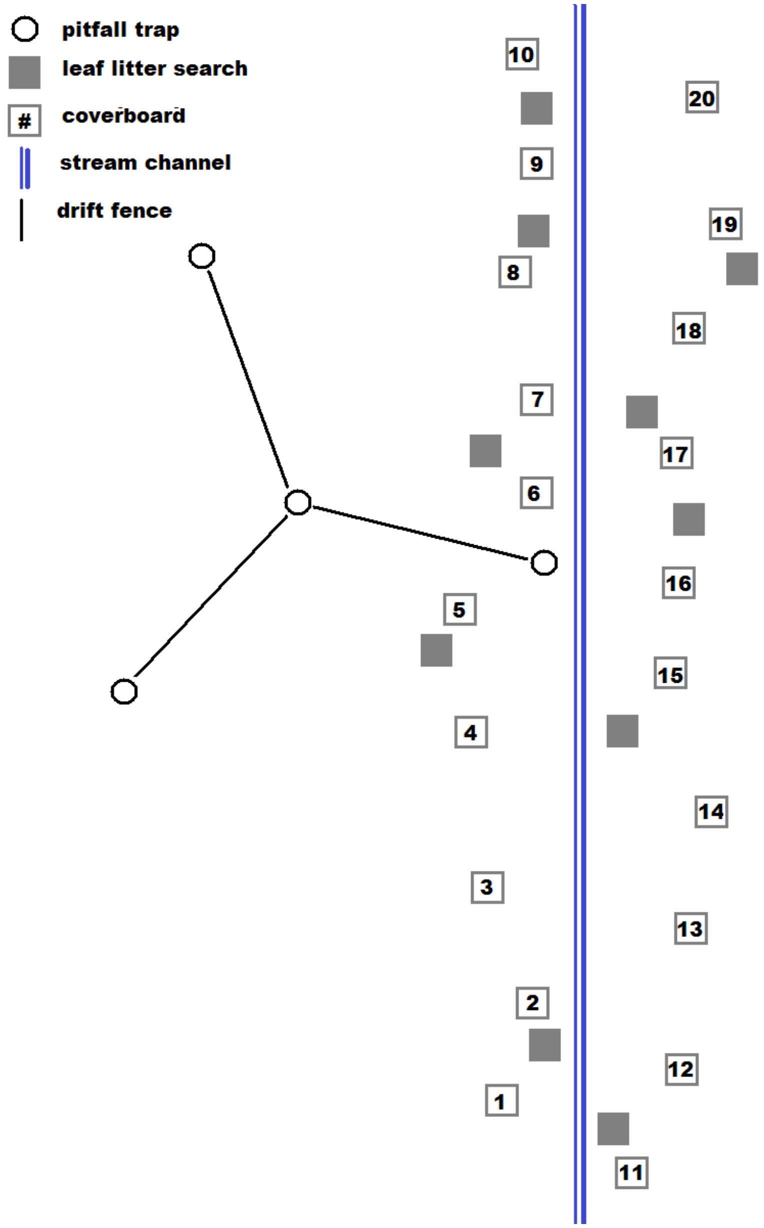

Figure 2: Illustration of salamander trap arrays at ephemeral stream sections, Clemons Fork watershed, Breathitt County, Kentucky. Cover boards are numbered and varied in distance from the stream based on local topography. The random litter searches were performed between any of the cover boards, 5 on each side. The 5 m stream search was performed at a random location in areas of rock cover, along the channel.

the array from the stream channel) in stream “I” which was 6.1 m (20 feet) because it would have crossed another ephemeral stream if it had been the full length.

Each 5 m section of hand-searched stream was located adjacent to the cover board arrays (Figure 2). These sections were searched by looking under each rock and other potential cover located throughout the 5 m long stream segment. When the stream flow was below the main channel, only rocks and other debris in the main channel were searched. If the stream was above the main channel every rock that was in contact with or under the water was searched. The 10 random leaf litter searches (5 on each side of the stream) were each 50 cm^2. I removed the litter one layer at a time until bare dirt was exposed.

All salamander identifications were made in the field using McGuire’s (2004) dichotomous key, and recorded to the species level except when *Desmognathus* escaped before species identification could be determined. In such cases I recorded these individuals as *Desmognathus* spp.

I sampled ephemeral streams monthly from March 2007 to May 2008 (except May 2007, December 2007, January 2008, and February 2008). Each sampling bout lasted 4-14 continuous days and, if possible was timed with a rain event to maximize catch potential (Enge 2005). Pitfall traps were checked every day of each sampling bout. Cover boards, stream searches and leaf litter searches were performed on the same day for the same stream segment. Each set (cover boards, stream searches, and leaf litter searches) was checked two to three times per sampling bout, with the maximum number of days between checks based on the sampling bout length (Marsh and Goicochea 2003). Marsh and Goicochea (2003) found that cover boards checked daily contained significantly fewer salamanders compared to boards checked weekly, although they found no difference in salamander abundance between boards checked weekly and boards checked every three weeks (Houze and Chandler 2002). I performed this sampling protocol to minimize human-generated damage (erosion) to the habitat while still adequately sampling each stream segment. Salamander capture rates have also been linked to amount and timing of precipitation events (Enge 2005, Reichenbach and Sattler 2007). However, I checked all the streams within 2 to 3 days of each other to try to eliminate or reduce any bias precipitation events would have introduced.

Habitat Sampling

I sampled habitat characteristics at all 12 ephemeral stream segments in May 2008. Habitat data were collected along four transects that were perpendicular to each stream segment (Figure 3). I also sampled coarse woody debris along a 15 m transect that ran parallel to the stream (Figure 3) between the 2 middle habitat sampling sites on a randomly selected side. Transects were evenly spaced along each stream segment, and depending on the length of each stream segment were between 21 m and 37 m apart.

I sampled habitat characteristics at three plots along each transect. Two of these plots were 1 m^2 and characterized stream bank habitat. The third plot characterized stream channel habitat and was 5 m in length and the width of the stream channel. For each transect, one 1 m^2 stream bank plot was located 1 m from the stream edge and the other 1 m^2 plot was located on the opposite side of the stream 5 m from the stream edge. Aspect was recorded for each stream segment. Within each 1 m^2 stream bank plot, I measured soil pH, percent ground shaded by plant cover $\leq$ 2 m in height, ground cover (soil, rocks, moss, and leaf litter, measured as percent cover in the 1 m^2bank plot).

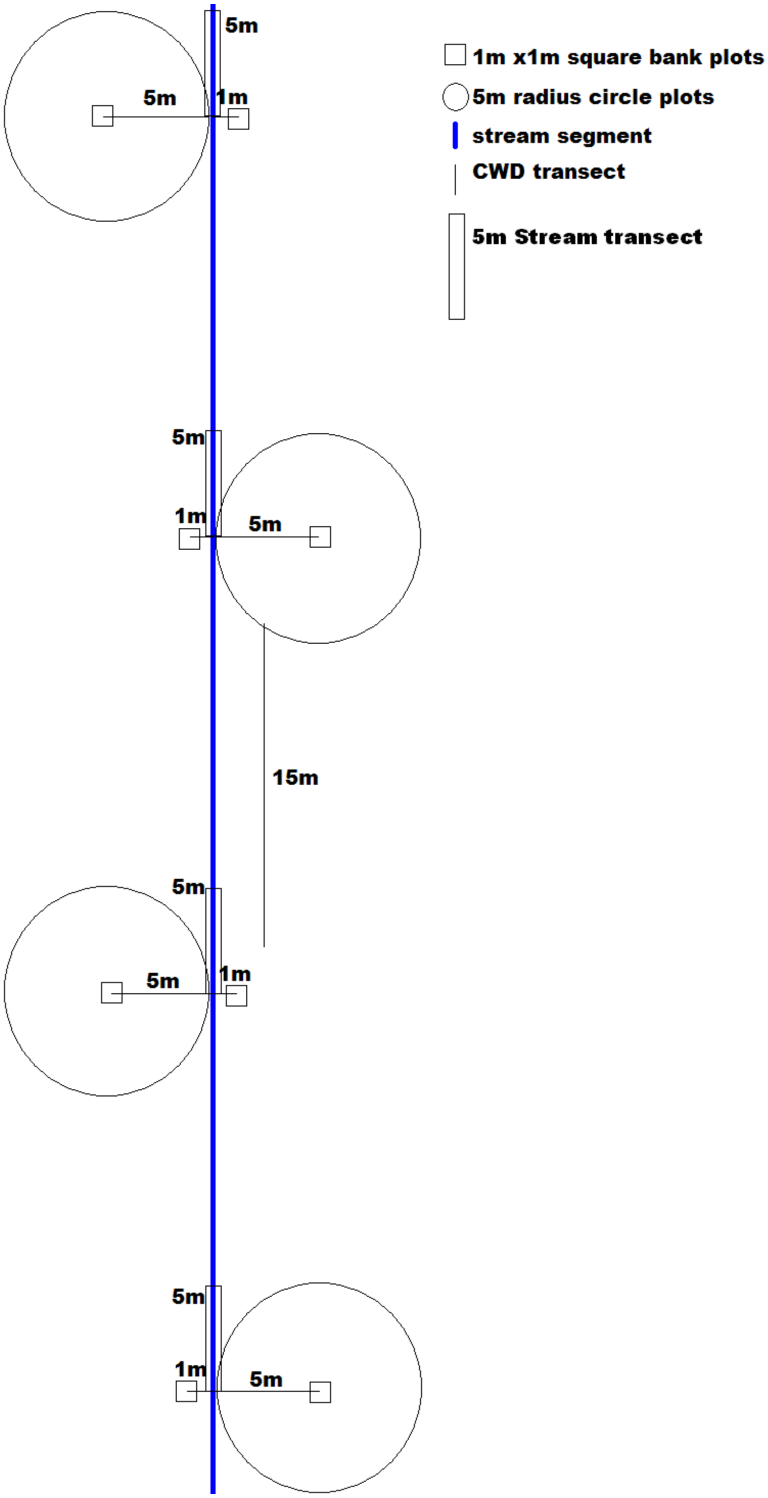

Figure 3: Salamander habitat sampling array at each of 12 ephemeral stream segments, Clemons Fork watershed, Breathitt County, Kentucky.

I also measured understory features in four 5 m radius circular plots that were centered on the 1 m^2 stream bank plots located 5 m from the stream edge (Figure 3). Within each 5 m-radius plot, I recorded the number of stems of woody species between 0.05 m and 3 m tall. From the center of each 5 m diameter circular plot, percent canopy cover was measured using an ocular tube.

For each stream channel plot, I recorded stream channel width, number and decay class of coarse woody debris, density of small (0.03 m-1 m) and large rocks (>1 m) and leaf litter depth. A list of all the habitat variable names, descriptions, and abbreviations are provided in Table 2.

Data Analysis

Salamander species diversity (H') and evenness (J') for each stream segment were determined using Shannon's index (Shannon 1948, Heyer et al. 1994, Zar 1999). Shannon's diversity index values were then transformed by the formula $e^{H'}$ (Jost 2006) in order to allow for direct comparison. A Jaccard's similarity matrix was created to compare salamander communities of each stream segment (Glowacinski and Jarvinen 1975). The formula used to create a Jaccard's matrix was:

$$QJ= 100c/ (a+b+c)$$

Where, a = number of species present only in community A, b= number of species present only in community B, and c= number of species present in communities A and B (Glowacinski and Jarvinen 1975).

I transformed all habitat percentage data using arcsine transformation (arcsin (sqrt(x/100)) + (180/π) (Zar 1999). The Beers transformation was used to convert aspect (Beers et al. 1966). Coarse woody debris decay class data was scaled using a log

Table 2: All habitat variables with abbreviations and descriptions of each variable. Habitat variables were measured in Robinson Forest Kentucky, in the spring of 2007.

Variable name	Abbreviation	Description
Aspect	ASPE	Average aspect of the entire stream segment
Canopy cover percentage	APCC	Average of the 8 bank plots canopy coverage
Aerage channel width	ASCW	Average of the 4 stream plots stream channel widths in meters
Average bank slope	ABSP	Percentage slope at the 8 bank plots
Avg leaf litter depth in stream	ALLS	Average of the 4 stream plots depth of leaf litter depths with 5 measurements per plot.
Avg decay class in stream	ADCS	Average of all the CWD objects class of decay, 0-6
Number CWD objects in stream	NCWS	Number of all the CWD objects in all of the 4 stream plots (20 m total)
Small rock density	SMDS	Density of rocks size 0.02-1m in size based on the 5m long stream segments and the width of each stream channel
Large rock density	LRDS	Density of rocks size >1m in size based on the 5m long stream segments and the width of each stream channel
Understory stem count under 3m	USS3	Number of stems of trees under 3m tall but still identifiable as a tree from the 8 bank plots.
Average basal area	ABAS	Average of the 8 bank plots basal areas
Average soil pH	ASPH	Average pH of the soil from 8 bank plots per stream segment
Percent ground cover	PGCB	Percentage of the 8 bank plots 1m2 that was shaded by plants <3m tall
Percent leaf litter	PLLB	Percentage of the 8 bank plots 1m2 that was covered by leaf litter
Percent moss	PMOS	Percentage of the 8 bank plots 1m2 that was covered by moss
Percent soil	PSOI	Percentage of the 8 bank plots 1m2 that was bare soil
Percent rock cover	PROC	Percentage of the 8 bank plots 1m2 that was covered by rocks
Area downed woody debris on bank	ACWB	Total area (meter2) of CWD on the bank with in the 15m transect on Each stream bank
Average decay class on bank	ADCB	Average decay class of all the CWD objects from the 15m transect on the bank
Area of CWD in stream	CWDS	Area of CWD objects in the 4 stream plots

transformation ($X' = \log(X+1)$) (Zar 1999). Salamander abundance data were converted to Hellinger data using the formula:

$$Y'_{ij}=\sqrt{(Y_{ij}/Y_{i+})}$$

where Y'_{ij}= Hellinger transformed abundance value, Y_{ij} =species abundance table, $_i$=sites (rows), $_j$=species (columns), and Y_{i+}= row sums (Legendre and Gallagher 2001). The Hellinger transformation allows the use of Euclidean-based ordination methods such as principle components analysis (PCA) and redundancy analysis (RDA), without having to deal with the problems associated with Euclidean distance (Legendre and Gallagher 2001).

I calculated Pearson's product moment correlation coefficients to screen habitat variables for potential multicollinearity (Program R 2.8.1, R development Core Team 2008). Pairs of variables with a Pearson's coefficient > 0.6 were considered highly correlated. To address the problem of highly correlated variables, I standardized correlated variables to have a mean of zero and a unit variance. I then transformed them into orthogonal composite variables using principle components analysis (PCA; Legendre and Gallagher 2001, Smith and Grossman 2003, Reichenbach and Sattler 2007). Only PCs with standard deviations above 1.0 were retained because those variables explained greater variation than any of the original variables used to make the RDA (Manly 2004). I also calculated Pearsons's correlation coefficient for any new composite variables and the previously uncorrelated variables to confirm that none of the remaining variables were correlated.

I used RDA forward stepwise function to compare the Hellinger-transformed salamander abundance data to the reduced set of habitat variables (Braak and Smilauer

1998). The RDA consisted of a Chi-square transformed data matrix, subjected to un-weighted linear regression on constraining variables (R Development Core Team 2008). Then, the fitted values were submitted to correspondence analysis performed via un-weighted singular value decomposition (R Development Core Team 2008). I included the variable with the lowest p-value (strongest variable) based on a permutation test at each step (Program R 2.8.1, package vegan, R Development Core Team 2008). I continued to add variables until the p-value for the strongest variable exceeded 0.1. Overall significance of the final RDA model was also established by a permutation based on a pseudo F-value (Braak and Smilauer 1998).

Linear regression models were used to compare salamander diversity to habitat variables. Data were checked to ensure that normality was maintained. Program R was used to create linear regression models with up to two habitat variables per model. Models were limited to two variables in order to maintain at least 6 (of the 12) samples per explanatory variables in the model. Akaike's Information Criterion values corrected for small sample size (AICc) were calculated for each model. Models were ranked according to their AICc values, with the best model indicated by the lowest AICc value (Burnham and Anderson 2002). Models within 2 AICc (Δ AICc ≤ 2) of the "best" model were considered competing with the best model and were also included as informative (Burnham and Anderson 2002). The Δ AICc values were then used to calculate model likelihood given the data:

$$\exp\left(-\frac{1}{2}\Delta_i\right).$$

The likelihoods for all the competing models were then used to calculate Akaike weights for use in mode averaging:

$$w_i = \exp\left(-\frac{1}{2}\Delta_i\right) \Big/ \sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_r\right).$$

Final regression coefficients values were based on averaging competing models (Burnham and Anderson 2002). The model was considered as important if the importance value was greater than 0.4

Chapter 5

RESULTS

From March 2007 to May 2008, a total of 780 salamanders belonging to at least 10 species (Table 3) were detected during 10,460 trap nights (Table 4). The average number of salamanders caught per trap night was 0.07 and ranged from 0.02 (n = 17) to 0.15 (n = 127) among individual streams (Table 4). Number of salamanders detected per stream throughout the entire study period ranged from 17 to 127, with an average of 65 salamanders per stream (Table 3). Salamander species captured included: slimy (n = 364), ravine (n = 158), eastern newts (n = 89), two-line (n = 45), seal (n = 43), northern red (n = 31), *Desmognathus spp*. (n = 20), unknown (n = 16), Allegheny mountain dusky (n = 6), northern dusky (n = 4), four-toe (n = 2) and green (n = 1).

Detections per month, standardized by trap nights per month, varied from 0.04 to 0.14 salamanders, and averaged 0.89 salamanders per night for the entire study area (Table 5, Figure 4). For all salamanders caught (n = 780), pitfall traps captured 119 (15.3), cover boards captured 506 (64.9%), stream searches detected 94 (12.1%), and 61 (7.8%) were found in leaf litter searches (Table 6). Trap type effectiveness varied depending on salamander species. Slimy salamanders had the greatest disparity with 95% caught under coverboards and 0% observed during stream searches (Table 6).

Trends in nightly salamander capture rates varied from month to month (Table 7). The number of salamanders captured averaged by trap nights was greatest during spring (April and May) and fall (September and October). Nightly capture rates were lowest during summer (August) and winter (November and March) (Figure 4). Trends in monthly capture rates varied by species (Figure 4). For example, ravine salamanders

Table 3: Salamander capture totals for twelve ephemeral stream segments (A –L) located in the Clemons Fork Watershed, Breathitt County, Kentucky, March 2007-May 2008.

		Ephemeral Stream Segments												
Common Name	Species	A	B	C	D	E	F	G	H	I	J	K	L	Total
Two-line	*Eurycea cirrigera*	5	1	18	2	0	4	1	6	6	2	0	0	45
Eastern Newt	*Notophthalmus viridescens*	9	5	9	11	1	5	12	2	8	3	19	5	89
Ravine	*Plethodon richmondi*	13	11	14	9	8	22	25	13	15	18	4	6	158
Slimy	*Plethodon glutinosus*	45	24	59	11	16	78	20	70	13	20	7	1	364
Northern Red	*Pseudotrition rubber*	0	0	3	3	2	4	5	5	4	2	1	2	31
Four-toe	*Hemidactylium scutatum*	0	0	0	0	0	0	0	0	0	1	1	0	2
Green	*Aneides aeneus*	0	0	0	0	0	0	1	0	0	0	0	0	1
Seal	*Desmognathus monticola*	2	1	6	5	9	8	3	4	2	1	2	0	43
Northern Dusky	*Desmognathus fuscus*	0	0	2	1	0	0	0	0	0	0	1	0	4
Allegheny Mountain Dusky	*Desmognathus ochrophaeus*	1	0	0	0	0	1	2	2	0	0	0	1	7
Unknown Desmognathus	Desmognathus spp.	0	0	9	1	7	2	0	0	0	1	0	0	20
Unknown	Unknown	0	0	3	1	2	3	0	4	1	0	0	2	16
	Total	75	42	123	44	45	127	69	106	49	48	35	17	780

Table 4: Capture rates of salamanders in ephemeral streams located in the Clemons Fork Watershed, Breathitt County, Kentucky, March 2007 – May 2008.

Stream ID	Trap Nights (n)	Salamanders captured (n)	Salamanders per Trap Night (n)
A	865	75	0.09
B	865	42	0.05
C	873	123	0.14
D	873	44	0.05
E	873	45	0.05
F	873	127	0.15
G	873	69	0.08
H	873	106	0.12
I	873	49	0.06
J	873	48	0.05
K	873	35	0.04
L	873	17	0.02
TOTAL	10460	780	0.075
Average			0.075

Table 5: Monthly salamander capture data, Clemons Fork watershed, Breathitt County, Kentucky. Captures occurred from March 2007 until May 2008. Standardized values are per trap night.

	Slimy	Ravine	Two-line	Northern Red	Eastern Newt	Seal	*Desmognathus*	Total
March 2007								
Total (standardized)	6 (0.012)	21 (0.041)	4 (0.01)	1 (0.00)	0 (0)	0 (0)	0 (0)	33 (0.064)
Trap Nights	516	516	516	516	516	516	516	516
Pitfall	0	1	3	0	0	0	0	4
Cover Board	6	13	0	0	0	0	0	19
Stream Search	0	0	1	1	0	0	0	2
Leaf Litter	0	7	0	0	0	0	0	7
April 2007								
Total (standardized)	11 (0.010)	27 (0.024)	2 (0.002)	3 (0.003)	6 (0.005)	4 (0.004)	0 (0)	56 (0.050)
Trap Nights	1112	1112	1112	1112	1112	1112	1112	1112
Pitfall	0	6	0	3	6	2	0	17
Cover Board	10	15	1	0	0	1	0	27
Stream Search	0	0	1	0	0	1	0	2
Leaf Litter	1	6	0	0	0	0	0	7
June 2007								
Total (standardized)	51 (0.052)	0 (0)	4 (0.004)	3 (0.003)	10 (0.010)	7 (0.007)	0 (0)	79 (0.080)
Trap Nights	984	984	984	984	984	984	984	984
Pitfall	1	0	0	3	7	0	0	11
Cover Board	46	0	3	0	2	0	0	51
Stream Search	0	0	0	0	0	7	0	7
Leaf litter	4	0	1	0	1	0	0	6
July 2007								
Total (Standardized)	16 (0.017)	0 (0)	6 (0.006)	6 (0.006)	14 (0.015)	7 (0.007)	0 (0)	54 (0.058)
Trap Nights	936	936	936	936	936	936	936	936
Pitfall	0	0	1	5	6	0	0	12
Cover Board	15	0	5	1	6	0	0	27
Stream Search	0	0	0	0	2	7	0	9
Leaf Litter	1	0	0	0	0	0	0	1
August 2007								
Total (standardized)	3 (0.006)	0 (0)	5 (0.010)	2 (0.004)	11 (0.021)	0 (0)	0 (0)	21 (0.041)
Trap Nights	516	516	516	516	516	516	516	516
Pitfall	0	0	1	2	7	0	0	10
Cover Board	1	0	4	0	4	0	0	9
Stream Search	0	0	0	0	0	0	0	0
Leaf Litter	2	0	0	0	0	0	0	2

Table 5: continued

	Slimy	Ravine	Two-line	Northern Red	Eastern Newt	Seal	*Desmognathus*	Total
September 2007								
Total (standardized)	56 (0.060)	1 (0.001)	7 (0.007)	2 (0.002)	7 (0.007)	0 (0)	0 (0)	76 (0.081)
Trap Nights	936	936	936	936	936	936	936	936
Pitfall	0	0	1	0	0	0	0	1
Cover Board	54	1	6	1	6	0	0	68
Stream Search	0	0	0	0	1	0	0	1
Leaf Litter	2	0	0	1	0	0	0	3
October 2007								
Total (standardized)	39 (0.042)	3 (0.003)	5 (0.005)	2 (0.002)	11 (0.012)	0 (0)	3 (0.003)	65 (0.069)
Trap Nights	936	936	936	936	936	936	936	936
Pitfall	0	0	0	1	7	0	0	8
Cover Board	39	2	3	0	2	0	0	46
Stream Search	0	0	2	0	2	0	3	7
Leaf Litter	0	1	0	1	0	0	0	2
November 2007								
Total (standardized)	16 (0.016)	16 (0.016)	3 (0.003)	0 (0)	4 (0.004)	1 (0.001)	4 (0.004)	44 (0.043)
Trap Nights	1032	1032	1032	1032	1032	1032	1032	1032
Pitfall	0	2	1	0	3	0	0	6
Cover Board	16	10	2	0	0	0	0	28
Stream Search	0	1	0	0	1	1	4	7
Leaf Litter	0	3	0	0	0	0	0	3
March 2008								
Total (Standardized)	16 (0.018)	27 (0.003)	3 (0.003)	1 (0.001)	1 (0.001)	4 (0.004)	2 (0.002)	54 (0.06)
Trap Nights	900	900	900	900	900	900	900	900
Pitfall	0	1	2	0	1	0	0	4
Cover Board	16	21	0	0	0	0	0	37
Stream Search	0	0	1	0	0	4	2	7
Leaf Litter	0	5	0	1	0	0	0	6
April 2008								
Total (standardized)	91 (0.069)	51 (0.039)	3 (0.002)	1 (0.001)	16 (0.012)	12 (0.009)	14 (0.011)	189 (0.143)
Trap Nights	1320	1320	1320	1320	1320	1320	1320	1320
Pitfall	3	7	1	0	12	3	1	27
Cover Board	85	29	1	0	4	2	5	126
Stream Search	0	4	0	1	0	7	8	20
Leaf Litter	3	11	1	0	0	0	0	15

Table 5: continued

	Slimy	Ravine	Two-line	Northern Red	Eastern Newt	Seal	*Desmognathus*	Total
May 2008								
Total (standardized)	59 (0.046)	12 (0.009)	3 (0.002)	10 (0.008)	9 (0.007)	8 (0.006)	8 (0.006)	109 (0.086)
Trap Nights	1272	1272	1272	1272	1272	1272	1272	1272
Pitfall	0	1	0	9	8	0	0	18
Cover Board	59	5	2	0	1	0	1	68
Stream Search	0	0	0	1	0	8	7	16
Leaf Litter	0	6	1	0	0	0	0	7
Totals								
Total (standardized)	364 (0.035)	158 (0.015)	45 (0.004)	31 (0.003)	89 (0.009)	43 (0.004)	31 (0.003)	780 (0.075)
Trap Nights	10460	10460	10460	10460	10460	10460	10460	10460
Pitfall	4	18	10	23	57	5	1	117
Cover Board	347	96	27	2	25	3	6	500
Stream Search	0	5	5	3	6	35	24	54
Leaf Litter	13	39	3	3	1	0	0	59

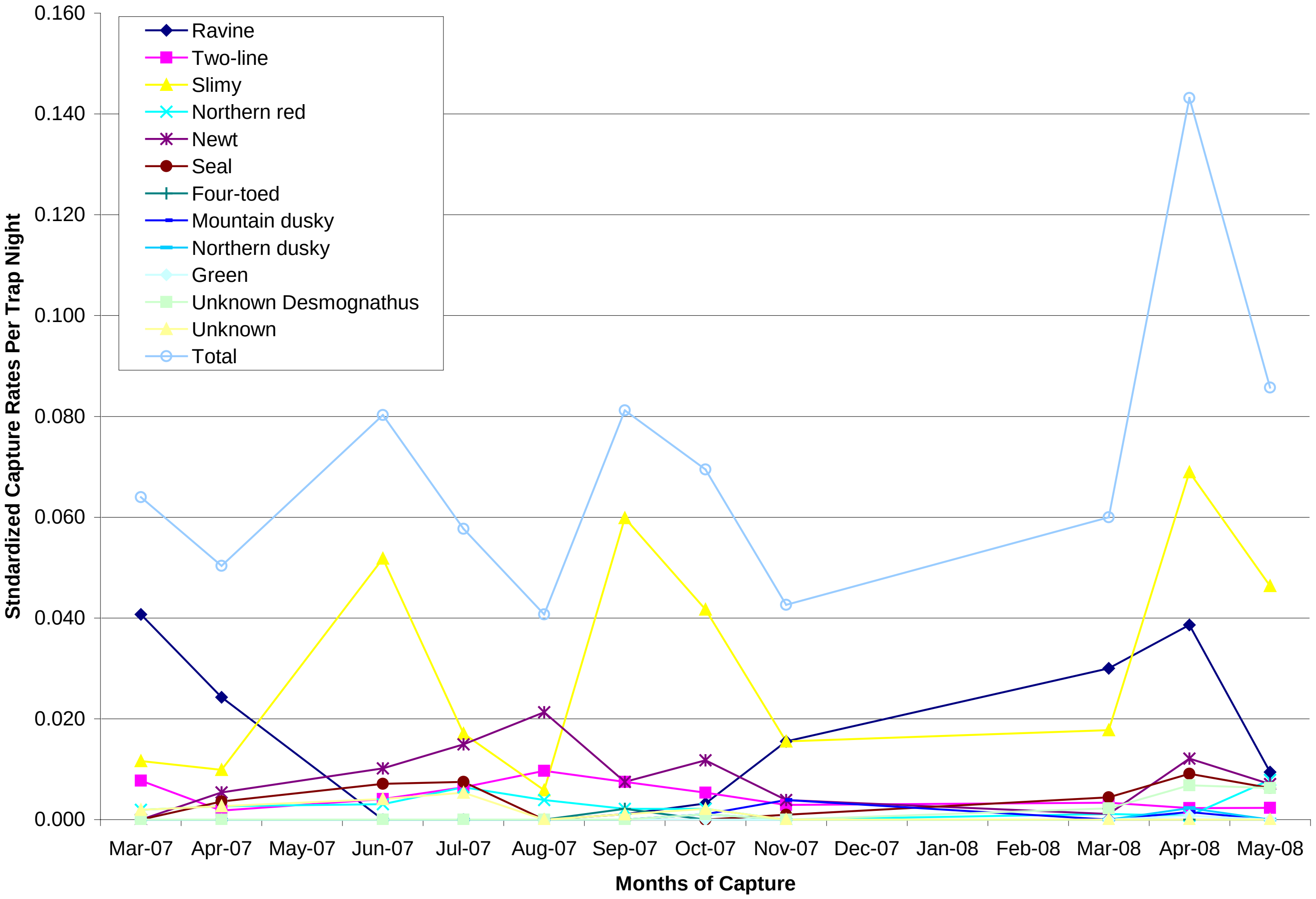

Figure 4: Salamander capture rates at Clemons Fork watershed, Breathitt County, Kentucky from March 2007 thru May 2008. Capture rates were standardized by number of trap nights for each month.

Table 6: Trap effectiveness for the 6 salamander species with ≥ 30 captures. Trap arrays included 20 coverboards, 4 pitfall traps, 10 leaf litter searches, and 5 m of stream searches, and were placed in 12 ephemeral streams in Robinson forest, Clemons fork, Breathitt County, Kentucky. Trapping occurred between March 2007 and May 2008.

Salamander Species	Pitfall (%)	Pitfall (n)	Coverboard (%)	Coverboard (n)	Stream Search (%)	Stream Search (n)	Leaf Litter (%)	Leaf Litter (n)
Slimy	1.1	4	95.3	347	0.0	0	3.6	13
Ravine	11.4	18	60.8	96	3.2	5	24.7	39
Two-line	22.2	10	60.0	27	11.1	5	6.7	3
Northern Red	74.2	23	6.5	2	9.7	3	9.7	3
Eastern Newt	64.0	57	28.1	25	6.7	6	1.1	1
Seal	11.6	5	7.0	3	81.4	35	0.0	0
Total	16.0	117	68.5	500	7.4	54	8.1	59

Table 7: Amount of salamanders captured per month standardized by number of trap nights. Salamanders were trapped from March 2007 to May 2008, in Robinson Forest, Breathitt County, Kentucky.

Salamander species	Mar-07	Apr-07	Jun-07	Jul-07	Aug-07	Sep-07	Oct-07	Nov-07	Mar-08	Apr-08	May-08
Ravine	0.041	0.024	0.000	0.000	0.000	0.001	0.003	0.016	0.030	0.039	0.009
Two-line	0.008	0.002	0.004	0.006	0.010	0.007	0.005	0.003	0.003	0.002	0.002
Slimy	0.012	0.010	0.052	0.017	0.006	0.060	0.042	0.016	0.018	0.069	0.046
Northern red	0.002	0.003	0.003	0.006	0.004	0.002	0.002	0.000	0.001	0.001	0.008
Newt	0.000	0.005	0.010	0.015	0.021	0.007	0.012	0.004	0.001	0.012	0.007
Seal	0.000	0.004	0.007	0.007	0.000	0.000	0.000	0.001	0.004	0.009	0.006
Four-toed	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000
Mountain dusky	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.000	0.002	0.000
Northern dusky	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.002	0.000
Green	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000
Unknown *Desmognathus*	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.002	0.007	0.006
Unknown	0.002	0.003	0.004	0.005	0.000	0.001	0.002	0.000	0.000	0.000	0.000
Total	0.064	0.050	0.080	0.058	0.041	0.081	0.069	0.043	0.060	0.143	0.086

were common (n=90) during spring sampling (April and May), were not observed during the summer months (June thru September), and were detected (n=20) again during fall sampling (September, October, November). *Desmognathus* spp. was only detected during fall (n=7) and spring (n=24), where as eastern newts were observed more often during summer (n=35) and spring (n=32) surveys than any other months (n=22).

Diversity ($e^{H'}$) and evenness (J') for individual streams ranged from a min $e^{H'}$ = 3.00 (stream B), and *J'*= 0.59 (stream H) to a max $e^{H'}$= 6.36 (stream D), and *J'*= 0.87 and averaged $e^{H'}$= 4.45 and *J'*= 0.73 (stream L) (Table 8). The Jaccard's matrix revealed that two pairs of streams (D and C, and H and F) had 100% similarity in salamander species compositions, while two streams (L and B) had only 42% similarity of salamander species (Table 9). Average similarity among all 12 streams was 60.43%.

All salamander species and habitat variables (Tables 10 and 11) were included in the RDA stepwise analysis. Ten habitat variables that were highly correlated ($r > 0.60$) were combined to form three PCA variables (Table 12). The three PCA variables were included in the analysis instead of the correlated habitat variables. Only the first component was retained for all three PCA composite variables based on the standard deviation for each (Table 12).

The RDA forward stepwise analysis included two habitat variables in the final model: Coarse woody debris area in stream (P=0.016, pseudo-F= 3.74) and PCA2-stream variables (P= 0.022, pseudo-F= 3.37) (Figure 5). The variable stream characteristics consisted of 3 habitat variables representing a contrast between average decay class in stream and two other variables average channel width and number of CWD objects in stream (Table 12). The RDA variables accounted for 47% of the total variation

Table 8: Shannon’s diversity (H’) and evenness (J’) values of salamander communities in twelve (A-L) ephemeral streams located in the Clemons Fork Watershed, Breathitt County, Kentucky, March 2007 to May 2008. $E^{H'}$ value is a standardized value of diversity that allows for direct comparison (Joust 2006).

Stream ID	J’	H’	$e^{H'}$
A	0.67	1.20	3.32
B	0.68	1.10	3.00
C	0.76	1.66	5.26
D	0.84	1.85	6.36
E	0.85	1.65	5.21
F	0.60	1.31	3.71
G	0.76	1.58	4.85
H	0.59	1.24	3.46
I	0.86	1.68	5.37
J	0.68	1.41	4.10
K	0.62	1.37	3.94
L	0.87	1.56	4.76
Mean	0.73	1.47	4.45

Table 9: Jaccard's comparative matrix of salamanders communities in twelve (A-L) ephemeral streams located in the Clemons Fork Watershed, Breathitt County, Kentucky, March 2007 to May 2008. Values are % of similarity between stream segments.

Stream ID	A	B	C	D	E	F	G	H	I	J	K	L
A	-	83.33	62.50	62.50	57.14	85.71	75.00	85.71	71.43	62.50	50.00	57.14
B	-	-	71.43	71.43	66.67	71.43	62.50	71.43	83.33	71.43	50.00	42.86
C	-	-	-	100	71.43	75.00	66.67	75.00	85.71	75.00	75.00	50.00
D	-	-	-	-	71.43	75.00	66.67	75.00	85.71	75.00	75.00	50.00
E	-	-	-	-	-	71.43	62.50	71.43	83.33	71.43	71.43	66.67
F	-	-	-	-	-	-	87.50	100	85.71	75.00	55.56	71.43
G	-	-	-	-	-	-	-	87.50	75.00	66.67	50.00	62.50
H	-	-	-	-	-	-	-	-	85.71	75.00	55.56	71.43
I	-	-	-	-	-	-	-	-	-	85.71	62.50	57.14
J	-	-	-	-	-	-	-	-	-	-	75.00	50.00
K	-	-	-	-	-	-	-	-	-	-	-	50.00
L	-	-	-	-	-	-	-	-	-	-	-	-

Table 10: Bank habitat variables, measured in May 2008, from 12 ephemeral streams (A-L) in Robinson Forest, Breathitt County, Kentucky.

Stream ID	ASPE (beers transformation)	APCC (%)	ABSP (%)	USS3 (n)	ABAS (m2/ ha	ASPH (pH)	PGCB (%)	PLLB (%)	PMOS (%)	PSOI (%)	PROC (%)	ACWB (m2)	ADCB*
A	2.00	88	41.38	52.75	23.75	4.81	46.88	91.38	0.50	2.13	2.88	2.40	4.00
B	0.40	68	67.63	29.50	20.63	4.11	12.75	72.75	8.38	14.13	0.38	0.00	0.00
C	0.00	56	51.17	41.00	25.00	4.37	20.13	88.88	5.00	3.13	1.50	6.14	3.11
D	0.00	76	58.50	35.75	28.13	4.61	20.63	76.00	0.63	11.88	3.75	1.38	3.00
E	1.98	87	74.25	37.75	28.13	4.47	13.13	78.13	8.50	3.38	6.25	14.60	3.00
F	0.40	88	49.88	17.75	33.75	3.95	4.25	83.75	1.25	9.75	1.50	8.70	3.63
G	1.67	86	61.63	27.00	16.25	4.73	35.25	91.88	0.25	2.88	0.00	22.40	3.67
H	1.53	71	49.50	41.75	20.63	4.33	32.00	89.00	0.00	4.13	1.00	12.50	0.00
I	0.55	84	47.88	15.50	30.00	4.38	14.00	81.00	0.00	4.00	10.00	0.58	2.67
J	0.62	84	83.13	28.50	23.75	4.12	14.50	79.75	0.00	7.75	6.25	1.38	2.75
K	0.00	53	47.25	84.50	21.88	4.17	24.75	82.50	0.38	12.38	2.25	19.40	2.67
L	0.00	70	60.75	75.50	20.00	4.15	28.88	78.88	2.75	5.00	10.00	7.80	3.50
Mean	0.76	75.92	57.74	40.60	24.32	4.35	22.26	82.82	2.30	6.71	3.81	8.11	2.67
STD ERROR	0.23	3.58	3.58	6.11	1.43	0.08	3.43	1.80	0.93	1.23	1.02	2.21	0.38
95% CI lower	0.53	72.34	54.17	34.49	22.90	4.27	18.83	81.02	1.37	5.48	2.79	5.90	2.29
95% CI upper	1.00	79.50	61.32	46.72	25.75	4.43	25.69	84.63	3.23	7.94	4.83	10.31	3.05

* Coarse woody debris decay class ranged from 1 - 5. 1=:Intact, recently down 2=:intact wood with loose bark 3=: Bark beginning to slough off and decayed sapwood 4=:loss of most bark and decayed heartwood 5=:hummocks of wood chunks and organic material (Maser et al. 1979)

ASPE = aspect (beers Transformation), APCC = canopy cover percentage, ABSP = average bank slope (degrees), USS3 = understory stem count under 3m, ABAS = average basal area, ASPH = average soil pH, PGCB = percent ground cover, PLLB = percent leaf litter, PMOS = percent moss, PSOI = percent soil, PROC = percent rock, ACWB = area coarse woody debris on bank (m^2), ADCB = average decay class of coarse woody debris on bank.

Table 11: Stream channel habitat variables, measured in 12 ephemeral streams (A-L) in Robinson Forest, Breathitt County, Kentucky May 2008.

Stream ID	ASCW (m)	ALLS (cm)	ADCS*	CWDS (m^2)	NCWS (n per 20m)	SMDS (per m^2)	LRDS (per m^2)
A	2.35	5.75	2.67	1.14	3.00	2.00	0.06
B	1.59	19.00	3.00	2.23	5.00	0.57	0.19
C	2.73	0.00	3.31	7.53	13.00	3.74	0.00
D	1.58	3.95	2.83	12.54	12.00	4.00	0.41
E	1.08	7.70	4.00	1.20	1.00	1.35	0.00
F	2.98	3.90	2.50	11.24	6.00	3.95	0.13
G	1.09	4.25	3.29	10.83	7.00	2.53	0.09
H	3.98	0.95	1.91	10.17	16.00	1.97	0.00
I	2.90	5.85	3.00	11.32	10.00	1.41	0.53
J	1.72	10.90	2.33	3.12	12.00	1.43	0.03
K	0.85	9.90	3.50	7.43	2.00	1.82	0.00
L	1.55	13.40	3.00	32.25	7.00	2.10	0.03
Mean	2.03	7.13	2.94	9.25	7.83	2.24	0.12
STD ERROR	0.27	1.57	0.16	2.42	1.38	0.32	0.05
95% CI lower	1.76	5.56	2.78	6.83	6.46	1.92	0.07
95% CI upper	2.30	8.70	3.11	11.67	9.21	2.56	0.17

*Coarse woody debris decay class ranged from 1 - 5. 1=: Intact, recently down 2=: intact wood with loose bark 3=: Back beginning to slough off and decayed sapwood 4=:loss of most bark and decayed heartwood 5=: hummocks of wood chunks and organic material (Maser et al. 1979)

ASCW = average channel width (m), ALLS = average leaf litter depth in stream (cm), ADCS = average decay class of coarse woody debris in stream, CWDS =area of CWD objects in stream (m^2), NCWS = Number of CWD objects in stream, SMDS = small rock (0.03m-1m) density in stream (per m^2), LRDS = large rock (>1m) density in stream (per m^2)

Table 12: Principal component analyses variables used in analyses of salamander-habitat relationships. Variables were measured in May 2008 in Robinson Forest, Breathitt County, Kentucky. Variable abbreviations stand for the following: APCC = average canopy cover percentage, ASPE = Aspect of stream segment, ASCW = average chanel width, ADCS = average decay class of CWD in stream, NCWS = number of CWD objects in stream, ALLS = average leaf litter depth in stream, PGCB = percent ground cover, PLLB = percent leaf litter, PSOI = percent soil, ASPH = average soil pH.

PCA 1- Light characteristics		PC1	PC2
	Standard deviations:	1.272101	0.617866
	Proportion of Variance	0.809	0.191
	Cumulative Proportion	0.809	1
Variables	APCC	-0.70711	0.707107
	ASPE	-0.70711	-0.70711

PCA 2- Stream characteristics		PC1	PC2	PC3
	Standard deviations:	1.51676	0.63545	0.54373
	Proportion of Variance	0.767	0.135	0.0985
	Cumulative Proportion	0.767	0.901	1
Variables	ASCW	-0.58366	0.444459	0.679557
	ADCS	0.587214	-0.34698	0.731289
	NCWS	-0.56082	-0.82587	0.058473

PCA 3-Ground characteristics		PC1	PC2	PC3	PC4	PC5
	Standard deviations:	1.77408	0.952293	0.666323	0.629567	0.324714
	Proportion of Variance	0.63	0.181	0.0888	0.0793	0.0211
	Cumulative Proportion	0.63	0.811	0.8996	0.9789	1
Variables	ALLS	0.386471	0.688318	-0.33619	-0.2766	0.432809
	PGCB	-0.42607	0.595358	-0.24262	0.363099	-0.52279
	PLLB	-0.49547	-0.21537	-0.49067	0.316409	0.606013
	PSOI	0.469496	0.078019	0.238136	0.829071	0.171521
	ASPH	-0.45077	0.345391	0.728449	-0.06462	0.377755

in the salamander abundance data set. The first RDA axis (RDA axis 1) described 82% of the variability in the species-environment interaction (38.5% over all), while the second RDA axis (RDA axis 2) described 18% of the variability in the species-environment interaction (8.5% overall). RDA axis 1 was the most informative axis because it explained approximately 4 times more variation between habitat features and salamander abundances than RDA axis 2.

Based on the RDA bi-plot, area of coarse woody debris in streams was positively associated with the index of relative abundances of northern red, and mountain dusky salamanders. Components of the stream characteristic variable, stream channel width and number of coarse woody debris, were positively associated with the index of relative abundance of two-line salamanders. Decay class of coarse woody debris in streams was negatively associated with the index of relative abundance in two-line salamanders. A positive association between the area of coarse woody debris in stream with the index of relative abundance of eastern newts. Stream channel width and number of coarse woody debris were positively associated with the index of relative abundance of slimy salamanders. Decay class of coarse woody debris in stream, and area of coarse woody debris in stream were negatively associated with the index of relative abundance in slimy salamanders. Stream channel width and number of coarse woody debris objects in stream was negatively associated with the index of relative abundance of eastern newts. Decay class of coarse woody debris in the stream was positively associated with the index of relative abundance of eastern newts. Decay class of coarse woody debris in the stream was positively associated with the index of relative abundance of seal salamander along the weaker RDA 2 axis. Stream channel width, number of coarse woody debris objects

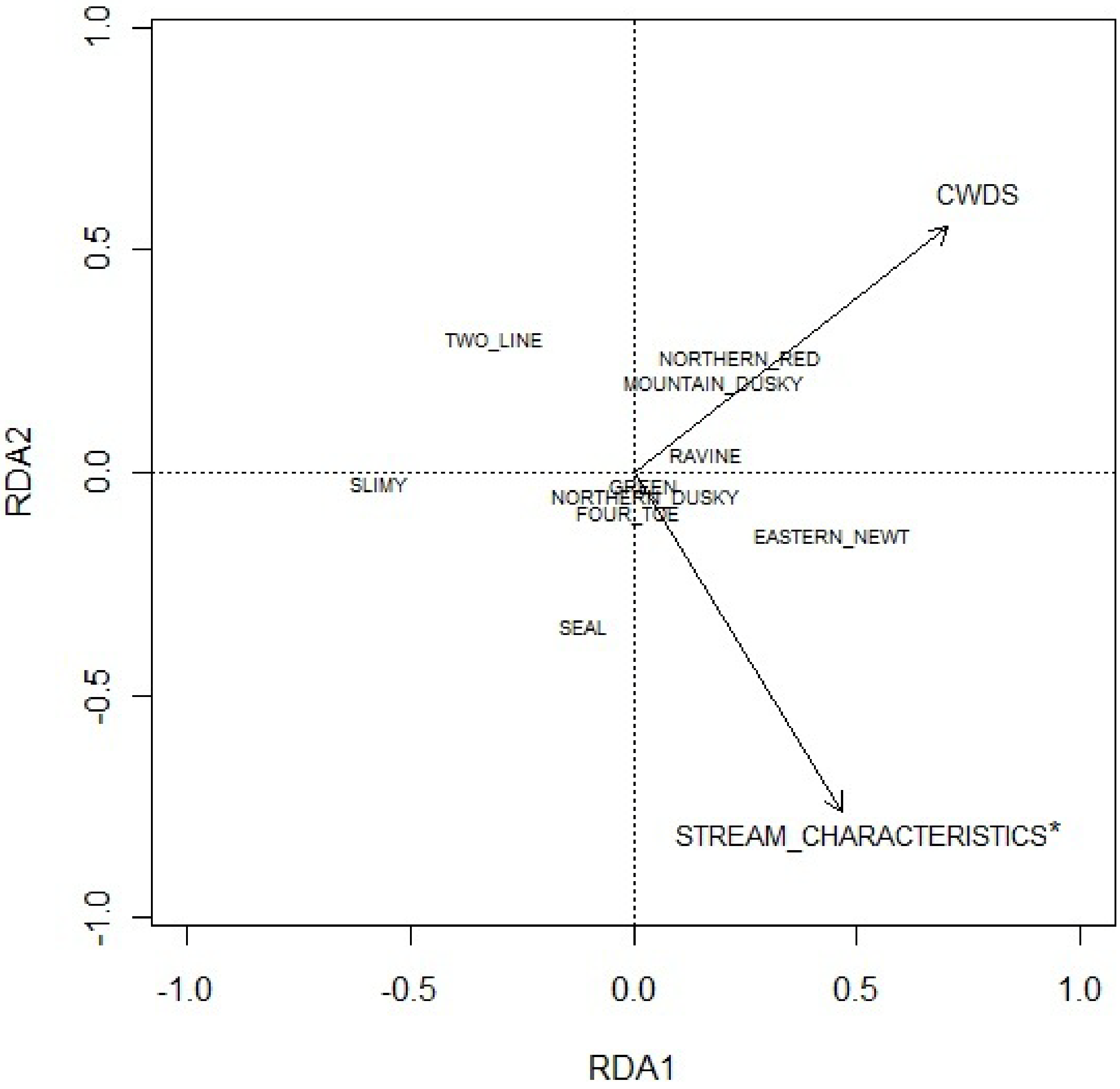

Figure 5: Redundancy analysis bi-plot showing the relationships among two habitat variables (CWDS = area of coarse woody debris in stream; PCA 2 – Stream characteristics), and 10 salamander species, Clemons Fork watershed, Breathitt County, Kentucky. RDA axis 1 accounts for 82% of the variation and RDA axis 2 accounts for 18% of the variation.

*PCA2- Stream characteristics is a composite variable consisting of 3 components: negatively: stream channel width and number of coarse woody debris. Positively: average decay class of coarse woody debris in stream.

in stream, and area of coarse woody debris in stream were negatively associated with the index of relative abundance of seal salamanders along the weaker RDA 2 axis. The species green, northern dusky and four-toe salamanders had a low number of total captures (< 30; Table 3) and did not show a strong response to either of these variables. Ravine salamanders also lacked a strong response, but had much higher capture numbers (158; Table 3).

The comparison of the salamander diversity ($e^{H'}$) for each stream to 12 habitat variables resulted in 7 competing models within 2 AICc values of the "best" model (Table 13). The seven competing models included 4 variables whose coefficients were then averaged and standard errors given: average decay class of coarse woody debris on bank (0.190 ± 0.272), large rock density in stream (0.192 ± 0.267), small rock density in stream (0.194 ± 0.276), and percent rock cover on bank (0.130 ± 0.214). Two of the four variables had importance values > 0.40; large rock density in stream (0.436) and small rock density in stream (0.406), while the other two variables did not; average decay class of coarse woody debris (0.384), and percent rock cover on bank (0.277).

Table 13: The seven competing models (within 2 AICc units of the lowest) from the regression analysis comprised of 1 variable and 2 variables that were tested for significance.

Variable 1	Variable 2	AICc	adjsted r^2	Model Weights	delta AICc
LRDS	ADCB	35.97	0.31	0.211	0.00
SMDS	PROC	36.17	0.30	0.191	0.20
ADCB		36.37	0.17	0.173	0.40
LRDS		37.05	0.12	0.123	1.08
SMDS		37.22	0.11	0.113	1.25
SMDS	LRDS	37.43	0.22	0.102	1.46
PROC		37.76	0.07	0.086	1.79

LRDS: = large rock density in stream
SRDS: = small rock density in stream
PROC: = percent rock cover on bank
ABCD: = average CWD decay class on bank

Chapter 6

DISCUSSION

My analyses revealed that the ephemeral streams surveyed in southeastern Kentucky supported a diverse salamander community that included 10 species detected over the entire study period. The distribution of salamander species varied considerably between different stream microhabitats (stream channel vs. stream bank) and among streams. Some salamander species in my study were caught almost exclusively in stream channels (i.e., seal 81.4%) or on banks (i.e., slimy 100%). This observation suggests that some salamander species may have been restricted to specific microhabitats in ephemeral streams similar to other studies conducted in headwater regions (DeGraaf and Rudis 1990, Grover 2000, Grant et al. 2005). Additionally, Shannon's diversity indices revealed that some streams were more than twice as diverse as others (6.36 vs. 3.01) (Joust 2006) (Table 4). Salamander community similarities also varied considerably among the 12 streams whereby similarity values ranged between 45 and 100%.

A comparison of my results with those from a recent study (Secrist et al 2004) that surveyed salamanders in areas adjacent to perennial streams in Robinson Forest provides evidence of the importance of ephemeral streams for certain salamanders species inhabiting this natural area. The most apparent differences in salamander abundances between ephemeral and perennial stream habitats involved slimy salamanders, two-line salamanders and northern dusky salamanders. Ephemeral streams supported greater proportions of slimy (46% vs. 19%) and two-line salamanders (5.7% vs. 0%) and fewer northern dusky salamanders (0.5% vs. 27%) than perennial streams. The natural history of slimy and two-line salamanders compared to northern dusky salamanders supports these findings. The slimy salamander occurs in moist forests and two-line salamander can be found from streamside habitats to moist forests far from streams, whereas the northern dusky is considered aquatic to semi-aquatic and largely restricted to the stream channel (Petranka 1998). Nonetheless, northern dusky salamander populations in perennial streams may be negatively impacted by activities that degrade ephemeral streams as this species is easily eliminated by siltation and pollution (Mitchell et al 2006).

Habitat Effects on Species Diversity

All seven competing models from my regression analysis incorporated cover object variables such as small rock density, large rock density, percent cover of rocks on bank, and decay class of CWD on bank (Table 13). However, only large rock density and small rock density were found to be significant predictors of salamander diversity. Ephemeral streams with higher salamander diversity had greater densities of large and small rocks in the stream channel. Stream channels averaged 1 ± 1.44 large rock (> 1 m) for approximately every 8 m^2 and small rocks (0.03m-1m) averaged 2.24 ± 1.11 for every m^2 of stream channel (Table 14). Therefore, ephemeral streams with 1 to 3 large rocks per 8 m^2 of stream and 2 to 4 small rocks per m^2 should support high salamander diversity. The importance of cover object availability to salamander populations inhabiting ephemeral streams may be critical due to the large variability in moisture throughout the year. Additionally, juvenile and larval amphibians use cover objects extensively to avoid predation (Mitchell et al 2006). Other studies have found rock cover to be significant predictor of salamander species diversity and abundance (Southerland 1986c, Ford et al. 2002). Grant et al. (2005) found *Desmognathus* spp. abundance was

Table 14: Minimum recommended amounts of habitat variables found to influence salamander species diversity or individual salamander species abundance in ephemeral streams in Robinson Forest Kentucky.

Variable	Recommended Range
Area of CWD in stream	9-17 m^2 per 20m of stream
Number of CWD in stream	4-8 pieces per 20m of stream
Decay class of CWD in stream	Mid decay (class 3)
Stream channel width	1-3 m wide
Large rock density (>1m)	1-3 rocks per $8m^2$
Small rock density (0.02m – 1m)	2-4 rocks per m^2

correlated with rock cover, but detected no correlation between salamander species richness and rock cover. Black belly salamander (*D. quadramaculatus*) abundance in North Carolina was positively correlated with rock cover in first order streams (Davic and Orr 1987). Additionally, cover density may have been the primary habitat feature that limited other salamander populations in forested streams of western North Carolina (Davic and Orr 1987). Seal salamander abundance in headwater streams of Virginia was positively correlated with rock cover (Grover 2000). Moore et al. (2001) observed Allegheny Mountain dusky (*D. ocrophoaeus*), and redback (*Plethodon cincerus*) abundances to be greater under rocks and coarse woody debris compared to under leaf litter. In the same study, redback salamanders found under rocks weighed more than those found under coarse woody debris or leaf litter (Moore et al. 2001).

Behavioral factors that are known to influence salamander occurrence and abundance such as interspecific interactions were not quantified during my study, but likely influenced my results. For example, several studies have found that salamander community composition is spatially arranged throughout the stream based on the presence/absence of certain species; larger more dominant salamander species inhabit optimal habitat in the stream channel where there is ample cover, whereas smaller, less aggressive species are found on the periphery of streams in apparently less optimal habitat (Hairston 1949, 1980, 1986, Organ 1961, Keen 1982, Carr and Taylor 1985, Roudebush and Taylor 1987, Southerland 1986a, Southerland 1986b, Grover 2000). Cover objects have been shown to be focal points of interspecific competition among salamanders (Mathis 1989, 1990, Smith and Pough 1994). Some salamander species such as some *Desmognathus*, *Plethodon*, and *Eurycea* sp. select specific types of cover objects based on their size and location relative to stream channel in Virginia (Grover 2000). In Virginia, more terrestrial salamander species such as *P. glutinosus* and *P. cinereus* used thick, narrow cover objects (i.e. logs) and larger species, *D. monticola*, used wide cover objects (i.e. rocks) (Grover 2000).

In my study, the RDA analysis showed northern red salamander, eastern newt, and Allegheny Mountain dusky salamander were positively correlated with the number of coarse woody debris objects in streams. These species may out-compete smaller or less adapted salamander species and limit population sizes as was shown in different salamander communities elsewhere (Hairston 1949, 1986, Grover 1996). I found that area of coarse woody debris in the stream was positively correlated with northern red salamanders (primarily caught in pitfall traps near the stream) and negatively correlated with slimy salamanders (caught under coverboards on the bank), which suggests that the larger northern red species may out compete the smaller slimy salamander species in streams and limited them to the dryer bank areas. Stream management zones with more rock should have sufficient cover to support less dominant species because more rock cover objects could provide enough range in size or placement relative to the stream channel that larger more aggressive species can inhabit preferred cover objects (high quality), while the availability of additional cover objects will support populations of the smaller less dominant species.

Research specifically designed to examine this resource partitioning hypothesis would need to be conducted to adequately evaluate whether my observation is the result of competition or some other environmental or physiological factor. Because several of the most significant variables in my analyses were associated with cover objects, it stands to reason that such competitive interactions over cover objects may have influenced the salamander species distribution I observed when a gradient of optimal to marginal habitat was available. This pattern suggests that the availability of cover objects, especially coarse woody debris and rocks, was an important factor driving the distribution of several salamander species in my study, particularly northern red, eastern newt, slimy, and two-line salamanders. As such, land managers interested in maintaining or restoring diverse salamander communities in ephemeral streams should create SMZs to better protect the integrity of stream channel and bank microhabitat. Additionally, partial harvests in SMZ's that leave slash in and adjacent to ephemeral streams may benefit salamander communities, so long as care is taken to maintain other aspects of stream integrity and canopy closure.

Habitat Effects on Individual Species Abundances

Individual species abundances also differed among the 12 ephemeral streams despite the fact that all stream segments were located at similar elevations within the same type and age forest (80-100 years). Although aspect differed among stream segments, it did not have an effect on these abundances. This finding suggests that individual salamander species abundances in ephemeral streams may be influenced by microhabitat characteristics similar to what has been reported in higher order streams (Conant and Collins 1998, Petranka 1998, Moore et al 2001, Greenberg 2001, Grover and Wilbur 2002, Davic and Welsh Jr. 2004, Rundio and Olson 2007). Based on my RDA analysis, the habitat variables that appeared to be most important to individual salamander species abundances were area of coarse woody debris in the stream and PCA-

2 stream variables (stream channel width, decay class of coarse woody debris, and the area of coarse woody debris).

Area of coarse woody debris in the stream channel varied greatly among the streams I surveyed (Table 11) with a mean of 9.25 m^2 ± 8.39 per 20 meter of stream length. Therefore, ephemeral streams having between 9 and 17 m^2 of coarse woody debris per 20 m segment should be adequate to support abundances of individual species similar to those observed in my study (Table 3). The stream channel width averaged 2.03 m ± 0.95 m, the decay class of coarse woody debris, and number of coarse woody debris objects averaged 2.94 ± 0.56, and 7.83 ± 4.76 per 20 m of stream, respectively. Thus, forested ephemeral streams between 1 m to 3 m wide with approximately 4-8 moderately decayed (classes 2-4 in Table 11) coarse woody debris objects per 20m of stream channel should support populations similar to what was observed during my study (Table 3).

The amount and condition (i.e., decay class) of cover objects are two factors that are known to effect salamander distributions and abundances elsewhere (Corn and Bury 1991, Raphael 1988, Welsh and Droeg 2001). Several studies have quantified the effects of varying amounts of coarse woody debris on salamander communities (McComb et al 1993, Grover 1998, 2000, Moore et al 2001, Grover and Wilbur 2002). A study of upland forest seep habitat found that redback salamander and juvenile slimy salamander abundances were higher in areas with greater amounts of cover objects (Grover 1998, Grover and Wilbur 2002). In Oregon rough-skin newts (*Taricha granulosa*) were positively correlated with length of coarse woody debris and with the number of stumps (McComb et al 1993).

In my study, slimy salamanders were found almost exclusively under cover boards on the stream bank, and none were found in the stream. In agreement with this observation, the RDA bi-plot revealed that this species had the strongest negative association with variables that characterized the stream channel (area, number, and decay class of coarse woody debris in stream and stream channel width). Negative associations between slimy salamander abundance and coarse woody debris in the stream channel differ from their published positive associations of bank coarse woody debris (Grover 1998, Petranka 1998). It is also possible that coarse woody debris in the stream was correlated with another variable I did not measure, but which had a direct influence on slimy salamander abundance. This species is considered widespread and stable throughout its range, including Kentucky with records from 85 counties (Kentucky Fish and Wildlife 2010, Petranka 1998)

I captured seal salamanders most often (Table 6) within stream channels. The RDA revealed that the seal salamander was associated with streams that were wider and had greater amounts of coarse woody debris. This observation is not surprising as the seal salamander was the most aquatic of the species observed in my study and their association with coarse woody debris agrees with the species' life history (Petranka 1998). This species is considered widespread and stable throughout its range, including Kentucky with records from 29 counties (Kentucky Fish and Wildlife 2010, Petranka 1998).

The two-line salamander requires streams to reproduce, but adults can also be found away from streams during the non-breeding season (Petranka 1998). Nonetheless, this species is restricted to small streams, seeps, and springs that traverse intact forest cover (Mitchell et al 2006). Hence, two-line salamander occurrence within ephemeral streams in eastern Kentucky is likely influenced by the availability of intact forests. A large proportion (60%) of two-line salamanders I caught was found under cover boards, but several were also detected via pitfall traps (22%), leaf litter searches (7%), and stream searches (11%). The RDA analysis revealed that the two-line salamander was negatively associated with several stream channel variables (area, number, and decay class of coarse woody debris in stream and stream channel width). This species is considered widespread and stable throughout its range including Kentucky, with records from 86 counties (Kentucky Fish and Wildlife 2010, Petranka 1998).

The northern red salamander occurs on land or near headwater streams (Petranka 1998). Adults use stream habitats to breed and to over-winter, but spend summer in relatively dry habitats further from streams (Petranka 1998). The RDA analysis revealed that this species was positively associated with the stream channel variables along the RDA1 axis. Thus, this species' association with stream channel variables is not surprising. This species' ability to use drier habitats away from streams during the non-breeding season allows the species to benefit from the numerous ephemeral streams in eastern Kentucky. The northern red salamander is considered widespread and stable throughout its range including Kentucky, with records from 41 counties (Kentucky Fish and Wildlife 2010, Petranka 1998).

The eastern newt (Family Salamandridae), the only non-plethontid in my study, breeds in more permanent, lentic habitats, but has a terrestrial immature phase (red eft stage), which is the primary dispersal phase during which it spends several years on land (Petranka 1998). In contrast to plethodontids, eastern newts which have lungs, have the ability to spend significant lengths of time on land, and thus would not be expected to have as close of a relationship with ephemeral streams compared to plethodontids (Behler and King 1979, Conant and Collins 1998, Petranka 1998). On the other hand, similar diet and hunting methods (invertebrates in the leaf litter) may result in Eastern newts being associated with ephemeral streams more than expected given its more terrestrial life history. This species was neutrally associated with the stream channel variables in the RDA. Secrist et al (2004) reported that eastern newt was the most widespread and abundant amphibian detected across bottomland, upland, interior, and edge habitat in Robinson Forest. This species is considered widespread and stable throughout its range including Kentucky, with records from 71 counties (Kentucky Fish and Wildlife 2010, Petranka 1998).

Ravine salamander was prevalent throughout my study area, and the RDA revealed that its abundance was not found to have any relationship, with the habitat variables I measured. This observation agrees with published observations in that ravine salamanders are upland species often found in rock habitat, talus slopes, and mesic hardwood forests with rocky substrates (Petranka 1998). The ravine salamander was also one of the most abundant and widespread species observed in a previous amphibian study in Robinson Forest (Secrist et al. 2004). This species is considered widespread and stable throughout its range including Kentucky, with records from 46 counties (Kentucky Fish and Wildlife 2010, Petranka 1998).

Conclusions

My study has revealed that the availability of coarse woody debris and rocks are important influences on salamander diversity and relative abundance in ephemeral streams that occur in intact mature forest systems. The importance of cover objects to salamanders in forested systems has long been recognized (Heatwole 1962). Cover objects are used by riparian salamanders as refugia during the day and throughout periods of dry weather (Heatwole 1962). In addition to reducing the risk of desiccation, cover objects are important to salamanders because they provide protection from predators, foraging areas, and brooding chambers (Behler and King 1979, Conant and Collins 1998, Petranka 1998). As suggested by Grover (2000), availability of cover objects could regulate salamander population densities. For these reasons, the availability of cover objects may limit salamander abundance and diversity in ephemeral streams that traverse harvested timber stands. However, cover object availability may not be as important as habitat features such as canopy cover. For instance, if canopy cover is removed (even partially) within the SMZ, no matter how many cover objects are present, the habitat may simply not be suitable for salamander habitation.

Several habitat features that are known to influence salamander populations and community structure elsewhere including litter depth, hardwood understory, percent cover of understory vegetation, canopy cover, soil pH, and slope (Pough et al. 1987, Wyman and Hawksley-Lescuault 1987, Paris et al. 1988, Raphael 1988, DeGraaf and Rudis 1990, Gibbs 1998, Petranka and Murry 2001) were not identified as being important in my study. Perhaps these habitat features simply did not vary enough among the 12 streams to account for observed differences in salamander abundances and diversity. For example, canopy cover and soil pH were consistent across all 12 streams in my study (Table 10 and 11). Moreover, the values for these habitat features all fell within the tolerance range of forest dwelling salamanders (Wyman and Hawksley-

Lescuault 1987, Petranka 1998, Greenberg 2001, Rudio and Olson 2007). For example, canopy cover ranged from 55% to 88%. Also, soil pHs in my study area were between 3.6 and 5. Wyman and Hawksley-Lescuault (1987) found that salamanders preferred pHs of 7 with a pH between 2.5 and 3 being lethal. Therefore, if the range of pH for the streams I surveyed had extended beyond this threshold (i.e. below pH 3), my analyses may have revealed soil pH to be more important to salamander community composition.

Ephemeral streams may also be important habitats for green salamanders and four-toe salamanders which I did not expect to observe in the ephemeral streams I surveyed. Both species have very specific habitat requirements that were patchily distributed throughout my study area. Green salamanders require cliff faces that are not too wet or too dry, with some evidence that they are weakly arboreal (Bishop 1928) and sometimes found beneath loose bark of fallen trees (Bishop 1928, Welter and Barbour 1940, Fowler 1947, Gordon 1952). Four-toed salamanders require *Sphagnum* hollows over or near pools of water, or sluggish streams for breeding, which are rarely associated with ephemeral streams (Petranka 1998). Even within high quality habitats these two species are relatively rare or disjunct throughout their entire ranges (Petranka 1998), which increase the importance of my observation of their use of ephemeral streams. While I only detected 1 green salamander and 2 four-toed salamanders, my observations indicate that these species do use ephemeral streams that contain appropriate microhabitat elements.

The fact that the green and four-toed salamanders are associated with habitat features not normally found in ephemeral streams may also indicate that ephemeral streams may also be important to salamander ecology by providing dispersal corridors l throughout the forests. These corridors may be very important in the long-term persistence of many of these species. Additionally, intact ephemeral streams may promote salamander re-colonization of watersheds after logging has occurred and appropriate habitat conditions restored.

My study has shown that ephemeral streams provide habitat for several salamander species. Thus, the creation of guidelines for minimizing human disturbances in and around ephemeral streams should be a priority. Protection measures should be included in SMZ regulations in order to preserve these areas. These guidelines should include preserving/ enhancing residual cover objects, both rock and coarse woody debris in the ephemeral streams and bank areas protecting the minimum amount needed for diverse salamander communities (Table 14).

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Effects of timber harvest on amphibian populations: Understanding mechanisms from forest experiments

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Effects of Timber Harvest on Amphibian Populations: Understanding Mechanisms from Forest Experiments

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Harvesting timber is a common form of land use that has the potential to cause declines in amphibian populations. It is essential to understand the behavior and fate of individuals and the resulting consequences for vital rates (birth, death, immigration, emigration) under different forest management conditions. We report on experimental studies conducted in three regions of the United States to identify mechanisms of responses by pond-breeding amphibians to timber harvest treatments. Our studies demonstrate that life stages related to oviposition and larval performance in the aquatic stage are sometimes affected positively by clearcutting, whereas effects on juvenile and adult terrestrial stages are mostly negative. Partial harvest treatments produced both positive and weaker negative responses than clearcut treatments. Mitigating the detrimental effects of canopy removal, higher surface temperature, and loss of soil-litter moisture in terrestrial habitats surrounding breeding ponds is critical to maintaining viable amphibian populations in managed forested landscapes.

Keywords: amphibian, clearcut, forest management, land use, vital rate

The extraction of natural resources, such as timber, is strongly associated with the loss and modification of forested habitat in most regions of the world (Putz et al. 2008). Deforestation may be long term (e.g., DeFries 2002, Biggs et al. 2008, Putz et al. 2008) or part of a sustainable forest management system (e.g., Hunter 1999). There is general agreement that timber harvest in temperate regions can have numerous negative effects on species richness and abundance of forest-dependent species, including amphibians (e.g., Bury 1983, Petranka et al. 1994, deMaynadier and Hunter 1995, Grialou et al. 2000, Ross et al. 2000, DeGraaf and Yamasaki 2002, Knapp et al. 2003). Yet, few data exist for species with differing life histories (Ross et al. 2000), and there are conflicting views concerning the mechanisms of population decline across regions, especially among lungless woodland salamanders (e.g., Ash and Bruce 1994, Ash 1997, Petranka 1999). This lack of data is of great concern because recent estimates indicate that 1896 species of amphibians worldwide, about one-third, are currently threatened with extinction (Stuart et al. 2004), and 89% of all threatened species are affected by habitat loss (Young et al. 2004). Despite recognition of habitat loss and alteration as major contributors to amphibian declines, the effects of structural habitat change have not been well studied for amphibians (Gardner et al. 2007, deMaynadier and Houlahan 2008).

We initiated a collaborative research project with a primary goal of understanding the mechanisms by which timber harvest affects pond-breeding amphibian populations. Although past studies of timber harvest effects have focused on species richness or abundance or both (reviewed in deMaynadier and Hunter 1995, Gardner et al. 2007), we believe that the response of individual amphibians to timber harvest and the subsequent effects on population demography are critical to understanding the effects of timber harvest on these animals (Armstrong 2005, Todd and Rothermel 2006). Studies of effects on vital rates (birth, death, immigration, emigration) are essential in mitigating population declines or losses. Understanding the mechanisms of decline from timber harvest may also

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yield insights on declines from other types of land use. Specifically, clearcutting is a form of canopy loss that shares several, but certainly not all, features of agricultural, industrial, and urban development. Understanding mechanisms may help land managers to mitigate some of the most detrimental practices to protect particular species of interest.

We focused on amphibians for several reasons. First, because most amphibian species possess a complex life cycle (distinct aquatic larval and terrestrial juvenile-adult phases), the loss or alteration of either aquatic or terrestrial habitats by timber extraction can negatively affect their vital rates. Further, although aquatic habitats are necessary for reproduction, juveniles and adults of most species spend the majority of their lives in terrestrial environments (Semlitsch 1998, Semlitsch and Bodie 2003). They possess small home ranges and have relatively limited dispersal capacity, compared with mammals or birds. Also, limited physiological mechanisms to prevent water loss necessitate the use of relatively cool, moist forested habitats, in conjunction with the use of underground refuges or coarse woody debris (CWD) to maintain high moisture levels. Thus, we assume that removal of the forest canopy or CWD would expose amphibians to warmer and drier microclimate conditions (Ash 1995, Harpole and Haas 1999) that could eventually lead to lower survival (Todd and Rothermel 2006) or higher evacuation of habitats (Semlitsch et al. 2008). Thus, amphibians can be useful bioindicators of environmental change because they are sensitive to habitat alteration associated with timber extraction (Welsh and Droege 2001), they play a major role in forest food webs as both predators of invertebrates and prey of larger vertebrates (Davic and Welsh 2004), and they make up a significant portion of animal biomass available to other trophic levels (Gibbons et al. 2006, Peterman et al. 2008).

In this article, we summarize our published results on the effects of timber harvest treatments on pond-breeding amphibian populations during the first four years following experimental harvests. Our synthesis includes comparisons of (a) forest management treatments, (b) three regions of the United States, (c) nine species, (d) life history stages, and (e) multiple response variables affecting both behavioral and demographic traits. Our approach to understanding timber harvest effects was a collaborative effort that allowed simultaneous and standardized experimental studies across regions to generate results that were comparable and had strong management implications for pond-breeding amphibians.

Experimental and regional approaches

Although it is unlikely that we can assign precise differences to given factors, identifying similarities in responses across such a wide region would produce robust implications for forest management. Previous studies conducted in different regions and years and on various species demonstrate that responses, especially abundance, differ greatly but are often confounded with many other factors, thereby introducing ambiguity in understanding declines. We selected widely separated sites in Maine, Missouri, and South Carolina to incorporate large differences in climate, amphibian species diversity, forest type, and topography (figure 1).

In the New England Province physiographic region, arrays were located in the Dwight B. Demeritt Forest and the Penobscot Experimental Forest near Orono, Maine. These study sites consisted of mature (at least 60 years old) mixed-deciduous and coniferous stands (Patrick et al. 2006). We established each of the arrays around a central breeding pond that was approximately 10 meters (m) in diameter (area 80 m^2) and 0.5 to 0.75 m deep, and constructed by mechanically enlarging existing pools from December 2003 to March 2004. Species used for experimental studies included the spotted salamander (*Ambystoma maculatum*), northern leopard frog (*Rana pipiens*), and wood frog (*Rana sylvatica*).

On the upper Ozark Plateau physiographic region, we located arrays within the Daniel Boone Conservation Area (1424.5 hectares [ha]) in Warren County, Missouri. We situated arrays in mature (80 to 100 years old) second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with varying amounts of sugar maple (*Acer saccharum*) in the understory (Semlitsch et al. 2008). Each array was centered on a small breeding pond (high-water area 160 to 330 m^2). These ponds, originally built for other wildlife, are between 27 and 47 years old and have naturally colonized breeding populations of up to 14 species of amphibians (Hocking et al. 2008). Species used for experimental studies included the spotted salamander, American toad (*Bufo americanus*), gray treefrog (*Hyla versicolor*), and wood frog.

In the upper Coastal Plain physiographic region of the southeastern United States, we located arrays on the US Department of Energy's Savannah River Site in Barnwell County, South Carolina. These areas are second-growth forests composed predominantly of mature (> 30 years old) loblolly pine (*Pinus taeda*; Rothermel and Luhring 2005). Each array was centered on a natural, isolated, seasonal depression wetland (high-water area 1100 to 1300 m^2) identified as a "Carolina bay" (Sharitz 2003). Species used for experimental studies included the marbled salamander (*Ambystoma opacum*), mole salamander (*Ambystoma talpoideum*), and southern toad (*Bufo terrestris*).

We established four replicate experimental forest arrays in each region (12 total). Replicates in each region were spaced 0.3 to 3.0 kilometers apart. Each array was centered on an amphibian breeding pond and consisted of a circle of mature forest divided into four quadrants, each containing a different treatment (figure 1). The size of the experimental arrays encompassed 95% of the estimated core terrestrial habitat needed by breeding populations of six species of salamanders, including species we studied (Semlitsch 1998).

To delineate the treatments around each pond, a circular area with a radius of 164 m from the pond edge was divided into four equal quadrants (approximately 2.1 ha each in Maine and Missouri; about 4.0 ha in South Carolina; figure 2). In each array, the control treatment (unmanipulated quadrant) was randomly assigned to one quadrant, two clearcut treatments were randomly assigned to the two adjacent quadrants, and

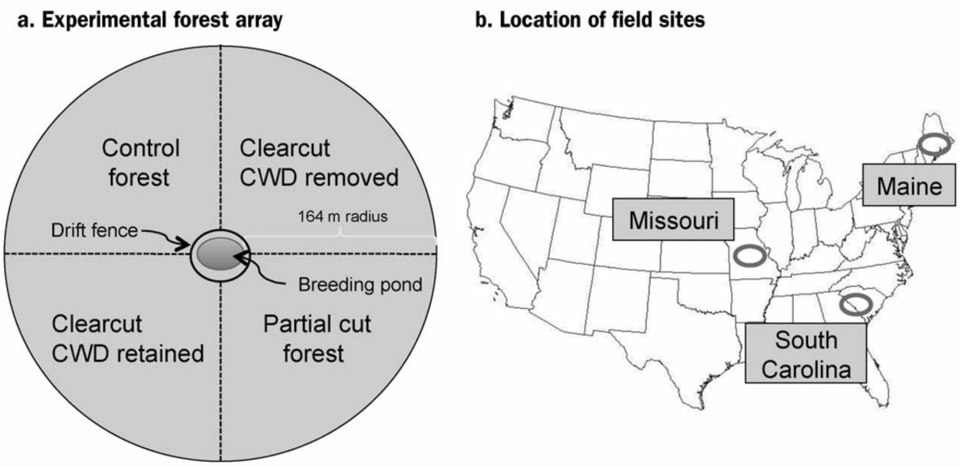

Figure 1. Illustration of (a) the four forest management treatments centered on an amphibian breeding pond and (b) the three LEAP (Land-use Effects on Amphibian Populations) regions. Abbreviation: CWD, coarse woody debris.

the partial treatment was fixed to the quadrant opposite the control (figure 2). We designed one clearcut treatment to test the potential for retaining CWD to mitigate the negative effects of clearcutting on amphibians (clearcut retained). Coarse woody debris benefits amphibians by providing moisture-retaining refugia (e.g., Herbeck and Larsen 1999, McKenny et al. 2006). The second clearcut treatment retained little to no CWD (clearcut removed) and was representative of whole-tree harvest, the practice followed in industrial timber management in the southeastern United States, which is analogous to the clearing of forests for agricultural, urban, or industrial development. The partial-cut treatment was designed to simulate regional management that either thinned forests of unmarketable trees (Missouri) or reduced canopy closure by select harvests of some marketable trees (Maine and South Carolina). The partial-cut treatments across all regions resulted in canopy reduction of

Figure 2. Representative pictures from the Land-use Effects on Amphibian Populations (LEAP). (a) Aerial photograph of the four forest management treatments centered on an amphibian breeding pond in Maine's LEAP Gilman site; (b) a spotted salamander; (c) a leopard frog; and (d) a log skidder used in Missouri.

about 50% to 60%. Treatments were applied in Maine from November 2003 to April 2004, in Missouri from March 2004 to January 2005, and in South Carolina from February to March 2004.

A range of experiments was conducted in replicate arrays that included large-scale comparisons among treatment quadrants (2 to 4 ha each) using drift fence and pitfall trap captures and radiotelemetry of free-ranging individuals across timescales of seasons and years. Other experiments were conducted across timescales of seasons, weeks, or days and at small scales using terrestrial enclosures (3 × 3 m pen or a cage 15 centimeters in diameter) and aquatic mesocosms (1000-liter cattle tank or 200-liter wading pool) within treatment quadrants.

We included only response variables found to be statistically significant in the source study and those testing two or more of the four timber harvest treatments from our design (see the appendix at *http://hdl.handle.net/10355/1365*). Although other responses have been tested and some were found to be statistically nonsignificant, our purpose was to highlight those effects that have been shown to clearly contribute to demographic responses in amphibians. To standardize response variables, we calculated relative effect size (percentage) for each variable by subtracting the mean value of each treatment by the mean value of the control, dividing the result by the mean value of the control, and then multiplying by 100. The resulting value was then assigned a positive or negative sign depending on whether the effect would be expected to have beneficial (i.e., positive) or harmful (i.e., negative) consequences for population growth.

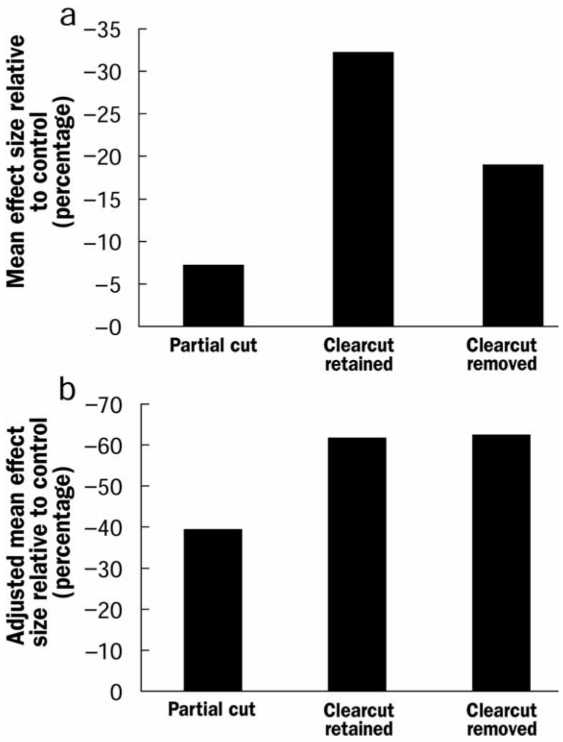

Figure 3. Overview of the (a) mean effect size of all amphibian responses for each forest management treatment relative to the unharvested control, and (b) adjusted mean effect size to determine where the greatest negative effects occur (removing positive effects).

Forest treatment effects on amphibians

Our studies generated 33 statistically significant effects of timber harvest treatments on a broad range of pond-breeding amphibian responses, some positive and some negative (see the appendix; *http://hdl.handle.net/10355/1365*). The average net effect of timber harvest treatments relative to the control for all 33 responses was negative (figure 3a, 3b). The partial harvest treatment had the smallest effect size (–7.2%), followed by the clearcut-removed (–18.9%) and clearcut-retained (–32.2%) treatments. If we adjust the overall effect size to determine where negative effects are greatest by removing all positive responses, the partial harvest treatment still has the smallest effect size (–37.3%) followed by the clearcut-retained (–61.8%) and the clearcut-removed (–62.4%) treatments.

When positive and negative effects are examined separately, the positive effects in clearcut treatments were mostly associated with reproductive behavior at experimental breeding ponds or with aquatic larval growth and development (figure 4). For example, gray treefrogs had much greater male calling activity and

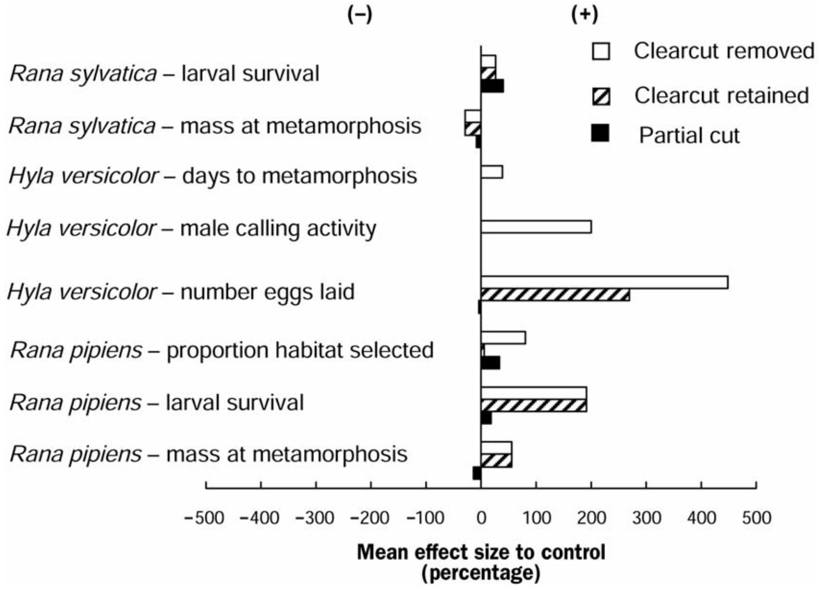

Figure 4. Overview of the mean effect sizes for each larval aquatic or reproductive behavioral response variables (see appendix at **http://hdl.handle.net/10355/1365** *for the source and details of each response variable).*

oviposition by females in experimental ponds in clearcuts relative to ponds in partial or control forests. Similarly, northern leopard frogs had greater tadpole survival, and gray treefrog tadpoles had faster development, in clearcut experimental ponds relative to ponds in control forests. The exception was the wood frog, which had smaller mass at metamorphosis in all treatments, especially clearcuts, compared with controls (figure 4). Some terrestrial responses (27%, 7 of 26) were also positive, but only in the partial harvest treatments (figure 5) and never in clearcuts. For example, habitat use and juvenile survival for wood frogs was positive in the partial harvest relative to control treatments. Furthermore, emigration and immigration of southern toads, water loss for mole salamanders, and adult survival for marbled salamanders and spotted salamanders were all positive in the partial harvest relative to control treatments (figure 5). Among the various traits measured, the negative effects of clearcut treatments were most prevalent for behavioral traits (e.g., migration, capture rate, distance moved, relocations) and the vital rate of survival (juvenile and adult), and had the greatest effect (–112%) on the physiological trait of water loss (figure 5).

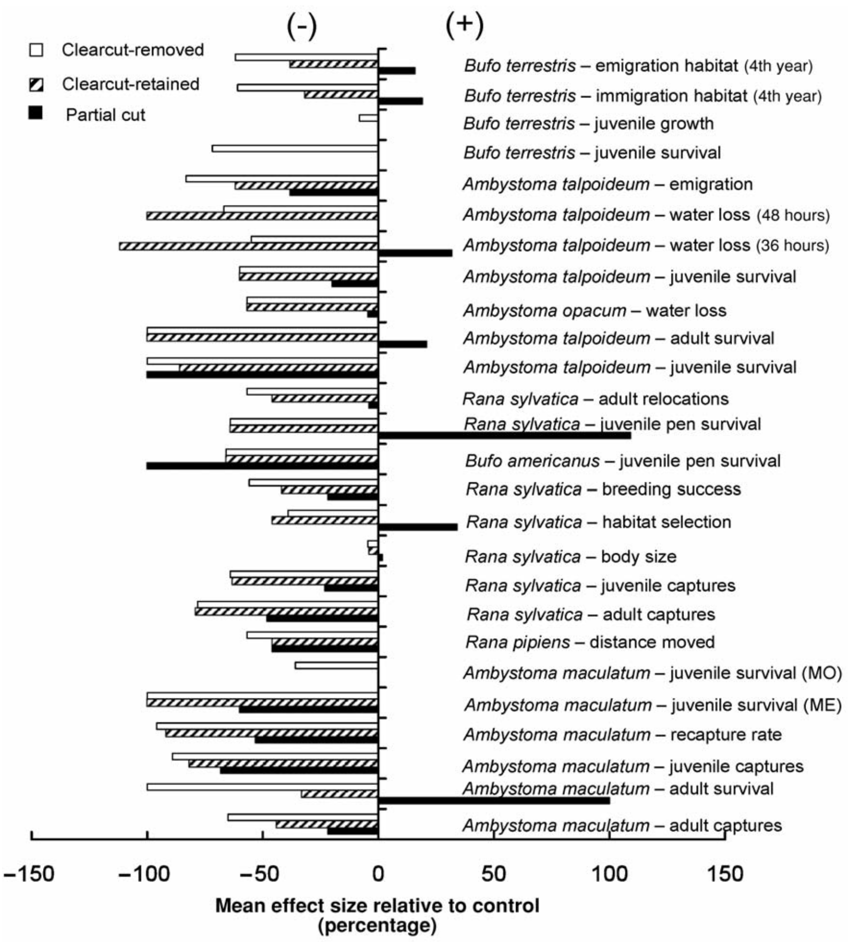

Figure 5. Overview of the mean effect sizes for each juvenile or adult terrestrial response variable (see appendix at **http://hdl.handle.net/10355/1365** *for the source and details of each response variable).*

Regional effects appeared to be strongest in South Carolina, with effect sizes increasing sharply between the control and both clearcut treatments, from –69% in clearcut-retained to –127% in the clearcut-removed treatments. Maine displayed intermediate effects, from –50% to –63%. Missouri showed the smallest effects, from 19% to –50% across treatments, most likely because the gray treefrog was not a primary study species in the other regions, and gray treefrogs displayed significant benefits from using clearcut treatments for reproduction and larval performance. Seven of the nine species we studied displayed similar and negative effects of harvest treatments, especially clearcuts (figure 5).

Ecological consequences and mechanisms

Our research has demonstrated strong and consistent effects of timber harvest on pond-breeding amphibians across three regions, nine species, and a broad range of physiological, behavioral, and demographic responses. Because of the coordination and standardization of our study, our results allow strong inferences about mechanisms to be made across multiple regions of the eastern United States for many pond-breeding species. Focusing on the mechanisms of decline using experimental approaches at several scales avoids potential problems with detection probability and pseudoreplication that can limit inferences resulting from studies of abundance or occupancy alone (reviewed by Kroll 2009). Further, our results help clarify ambiguities of previous studies by showing that when species are exposed to the same treatments, they differ in their responses to timber harvest—some species show positive breeding and larval performance while effects on juvenile and adult terrestrial stages of most species were largely negative.

The most consistent negative effects occurred in both of our clearcut treatments, which was not surprising given that clearcutting alters the fundamental structure of forests by removing the canopy and exposing the forest floor to more sunlight and wind, leading to a warmer, drier surface microclimate (Keenan and Kimmins 1993, Chen et al. 1999, Zheng et al. 2000), eventually reducing leaf litter (Hughes and Fahey 1994, Ash 1995) and food resources (Seastedt and Crossley 1981). In some regions, clearcutting may also result in soil compaction and disturbance to the soil profile during the course of timber extraction and postharvest site preparations, such as burning. We documented lethal surface soil temperatures at our clearcut sites—more than 40 degrees Celsius (°C) in Missouri (Harper 2007) and more than 43°C in South

Carolina (Todd and Andrews 2008). Lethal temperatures were documented previously in a study of spotted salamanders in New York (Pough et al. 1987). We also showed that such microhabitat conditions lead to rapid water loss and high mortality in small-scale caging studies (Rothermel and Luhring 2005, Rittenhouse et al. 2008, Todd et al. 2008) and most likely provide the direct mechanism for reduced abundance demonstrated in many previous studies.

Behavioral studies show that both juvenile and adult amphibians often avoid entering clearcuts when given a choice (Rittenhouse and Semlitsch 2006, Patrick et al. 2008, Todd et al. 2009; but see Graeter et al. 2008). Using smaller-scale mechanistic studies, we found that retention of CWD helped reduce water loss and increase the survival of juveniles over short periods, especially in slash piles (Rittenhouse et al. 2008). Studying net movement between adjacent control and clearcut treatment quadrants after clearcutting, we also found that CWD retention significantly reduced evacuation of salamanders from clearcuts (Semlitsch et al. 2008). Although this indicates that CWD has a positive short-term effect for amphibians, the two clearcut treatments in Missouri were much more similar to each other in effect size than to the partial treatments, suggesting that leaving CWD for amphibians may increase the probability of successful movement through clearcuts or enhance survival just after metamorphosis, but that does not preclude deleterious effects over the longer term. Moseley and colleagues (2004) found that mole salamanders increased their use of CWD only when there was very little pine litter on the ground, and that salamanders in litter removal treatments had higher activity levels. They concluded that CWD may be important for mole salamanders only immediately after harvesting, when there is little litter or ground cover. More field research is needed to document how species respond to different sizes or decay classes of CWD, determine whether different volumes of retained CWD and species have response thresholds (Ross et al. 2000, McKenny et al. 2006), and determine whether some species, such as the ambystomatid mole salamanders, may be using small-mammal burrows adjacent to CWD instead of using CWD directly (deMaynadier and Houlahan 2008).

We observed movements of amphibians through clearcuts in every region. However, the willingness to travel through clearcuts differed by region and species or stage. In Maine, both juvenile and adult amphibians traveled through clearcuts, and individuals settled for short periods (Patrick et al. 2006, 2008). In Missouri, adults traveled through clearcuts, but virtually no metamorphs traveled successfully through clearcuts. In Missouri, we generally saw more evacuation and avoidance behavior by adults (Rittenhouse and Semlitsch 2006, 2009, Semlitsch et al. 2008). In South Carolina, none of the three species studied showed strong behavioral avoidance of the clearcut quadrants (Graeter et al. 2008): Southern toads preferred clearcuts, southern leopard frogs initially selected clearcuts but ultimately preferred forested treatments, and marbled salamanders selected treatments randomly. Todd and colleagues (2008) found that many adult amphibians (especially toads) migrate through clearcuts but that salamanders tended to avoid them, especially during postbreeding emigration. Overall, we found that long-term use of clearcuts or the inability to evacuate clearcuts resulted in increased mortality in all regions. Thus, strong negative effects of long-term use of clearcuts occurred despite avoidance by some species and despite widely ranging climatic conditions across our three study regions.

Our enclosure survival studies show strong negative effects, but also that the natural heterogeneity of habitats can produce variation in survival rates equal to or greater than those observed in the clearcut treatments in some regions (Harper 2007). In Missouri, for example, we found that juveniles constrained by cages in control quadrants on south-facing slopes with thin soil had lower survival than juveniles constrained in clearcuts on north-facing slopes. Further, radiotelemetry monitoring revealed that temporal variation in habitat quality also affected amphibian habitat choice across large-scale arrays (Patrick et al. 2008), and survival rates (Rittenhouse et al. 2009). In dry years, individuals suffered higher mortality, but they were more likely to use relatively shady and cool sites that were less common and more isolated. Thus, retaining CWD and limiting the amount of timber harvest on high-quality north-slope habitats may provide refuges for amphibians within a landscape that supports timber harvest.

Effects of the partial-harvest treatment were less consistent, but 7 out of 26 responses of juvenile or adult traits were positive (figure 5). The positive effects may have been caused by the enhanced productivity of the herbaceous or shrub vegetation on the forest floor (Zheng et al. 2000). We suggest that the herbaceous-shrub layer may have created a favorable microclimate usually missing from the closed, dense canopy of mature forests, or it may have enhanced the production of invertebrate food resources. In support of this idea, Ross and colleagues (2000) found a strong rise in the percentage of ground cover (< 1-m high) when tree basal area in Pennsylvania forest stands was reduced. But, they also found that abundance levels of 12 species of salamanders (including four pond-breeding species) dropped at tree basal areas below 15 to 20 m^2 per ha (or approximately 50% to 60% canopy cover; deMaynadier and Houlahan 2008). Thus, small increases in light levels reaching the forest floor and creating a favorable microclimate may partially ameliorate the negative effects of selectively removing trees. Still, the remaining negative effects of partial-tree harvest were presumably attributable to some of the same changes in microclimate and soil compaction that characterize clearcuts, albeit to a lesser degree. Our results are also consistent with another experimental study done in Virginia showing that three partial harvest treatments also had significantly reduced terrestrial salamander abundance (Harpole and Haas 1999). However, other studies have concluded that partial harvest of timber, including select harvest, has little or no effect on amphibians (e.g., Pough et al. 1987, Grialou et al. 2000, Ross et al. 2000, McKenny et al. 2006).

We found that timber-harvest effects were consistent across a wide range of demographic and behavioral variables measured across all three regions of the United States. Mechanistically, exposure of amphibians to high temperatures and low moisture in the terrestrial environment amplifies water loss, one of the most critical problems facing amphibians (see Jorgensen 1997). The largest effect size we measured in a single treatment was for water loss in the South Carolina clearcut treatment for mole salamanders (Rothermel and Luhring 2005). Summertime air temperatures in South Carolina are higher than in the other regions (Maine and Missouri), and soil moisture may also be substantially reduced during summer months because the extremely sandy, well-drained Coastal Plain soils do not retain moisture between rainfalls. Further, because all the basic needs of amphibians (e.g., food, shelter) usually require movement overland, every aspect of their lives in the terrestrial environment is affected by water loss. Water loss was rapid in clearcut treatments and on ridgetops in forest controls—anywhere there was greater exposure to sunlight or wind—and this led to increased mortality unless individuals burrowed underground, used CWD, or emigrated to moist ravines (e.g., Missouri) or forested wetlands (e.g., Maine). Individuals usually moved during rain events in Missouri or South Carolina, but in Maine, surface moisture appeared less limiting. As a direct result of water loss limiting amphibian activity, growth rate and survival were reduced whenever the terrestrial microhabitat was warm and dry, most dramatically in the clearcuts (Todd and Rothermel 2006) and to a lesser extent in the partial treatment. We would expect the same reductions in survival to occur with other forms of land use (e.g., agriculture, powerline rights-of-way, road-effect zone) that lower the quality of the microclimate for movement, foraging, and growth, as happens with clearcutting (e.g., Semlitsch et al. 2007).

We did find that two of nine species benefited from clearcuts, but only for reproduction and larval development in aquatic habitats within clearcuts. The gray treefrog is probably representative of an early successional or edge species that prefers habitat that is periodically disturbed and has an open canopy, at least for reproduction. During the nonbreeding season and for overwintering, adults clearly prefer forested habitats (Johnson et al. 2007, 2008). We hypothesize that treefrogs select pools in clearcut treatments over forested treatments for mating and oviposition (Hocking and Semlitsch 2007) because they evolved to breed in new ponds created by uprooted trees within forested habitats (Putz 1983, Ulanova 2000), or in new pools created by other disturbances. These uprooted trees leave holes in the ground that fill with water (Ulanova 2000) and are initially free of predators and competitors; they also receive more sunlight, which increases the water temperature and periphyton productivity, to the benefit of herbivorous tadpoles (Skelly et al. 2005). In Maine, northern leopard frogs also benefited from enhanced larval development in clearcuts (Blomquist and Hunter 2009). Thus, we predict that other species requiring early successional or open habitats for reproduction (e.g., chorus frogs, narrow-mouthed toads, spadefoot toads) would benefit from the presence of breeding pools in clearcuts (e.g., use of skidder ruts; Cromer et al. 2002). Hossack and Corn (2007) reported that disturbance created by wildfire can also benefit some pond-breeding amphibians, especially if fire creates or mimics early successional habitats. This does not mean that all stages of these species would benefit from clearcut or early successional habitat. These stage-specific and carryover effects need to be studied more thoroughly. In some cases we know that adults of species such as the gray treefrog require forested habitat at other times, and will not venture far into clearcuts (< 50 m; Hocking and Semlitsch 2007). Thus, the larval aquatic stage presumably benefits from the presence of pools in small clearcuts, but juvenile and adult treefrogs must find suitable forested habitat nearby (Johnson et al. 2007, 2008). Hossack and Corn (2007) found that toads (*Bufo boreas*) increased the use of wetlands up to two to three years after wildfires, and suggested that this species was adapted to disturbance created by fire. However, some species, such as the wood frog in Maine, benefited little from breeding pools in clearcuts; these most likely represent species with a strongly forest-dependent life history (Blomquist and Hunter 2009). Knowing the life history requirements of species at all stages is therefore critical for predicting timber-harvest effects or disturbance effects in general. Finally, it is important to note that the presumed benefits of clearcutting to early life stages may not enhance population persistence if timber harvest causes a reduction in postmetamorphic survival (Biek et al. 2002, Taylor et al. 2006, Harper et al. 2008).

Although our study did not differentiate among all possible mechanisms of decline in abundance after harvest, we have strong support for two hypotheses explaining declines. The mortality hypothesis assumes that abundance in clearcuts declines as a result of mortality from lack of refuge or food, from desiccation, and from an inability to evacuate. We found that a large portion of the population dies if they stay in clearcut areas, especially small juveniles (Rothermel and Luhring 2005, Todd and Rothermel 2006, Harper 2007, Patrick et al. 2008, Todd et al. 2008). The evacuation hypothesis assumes that individuals leave clearcuts in response to increasing temperature and reduced moisture and food, and select more suitable habitat in nearby forests. We have found that a portion of the breeding population in Missouri evacuates from clearcuts into neighboring forest habitats, especially adult spotted and ringed (*Ambystoma annulatum*) salamanders (8.7% to 35.0%; Semlitsch et al. 2008).

A third hypothesis, the retreat hypothesis, assumes that individuals remain in the clearcuts but move to more suitable underground habitat where individuals survive for limited periods on minimal resources and energy stores, reduce activity, and reemerge as forest succession proceeds. We did not find out in our study, however, whether any of the individuals remaining in clearcut plots retreated underground for some period, as hypothesized for the more fossorial species of woodland salamanders (genus *Plethodon*; Petranka et al.

1994), nor do we know the long-term fate of individuals that evacuate clearcuts (Reichenbach and Sattler 2007).

Implications for amphibian conservation and timber harvest

One goal of this synthesis is to articulate some generalities about timber harvest effects on pond-breeding amphibians, specifically, mechanisms that could result in population decline. Current evidence indicates that the negative effects of clearcutting are pervasive and more or less consistent across regions as diverse as the northeastern, midwestern, and southeastern United States. Clearcutting is directly implicated in the loss of suitable habitat and in the reduction of population size through mechanisms such as reduced terrestrial survival or evacuation by resident amphibians. Consequently, we propose that these effects may extend through much of eastern North America. Moreover, because studies in other regions of North America that address the effects of forest loss on amphibians have demonstrated declines in abundance and richness (e.g., Dupuis et al. 1995, Adams and Bury 2002, Karraker and Welsh 2006, Olson et al. 2007; but see Kroll 2009), it is likely that our research on mechanisms are more broadly applicable to other regions and species not explicitly included in our experiments.

We encourage forest management that enhances the conservation of sensitive species and has a goal of long-term sustainability. Habitat management guidelines for amphibians are available and can be incorporated into harvest operations (Calhoun and deMaynadier 2004, deMaynadier and Houlahan 2008, PARC [*www.parcplace.org/habitat_management_guide.html*]). In general, harvest operations should consider zones of protection around breeding ponds and the adjacent upland habitats to conserve local populations and enhance connectivity at the landscape level (deMaynadier and Houlahan 2008). Clearcutting or timber harvests that remove more than 40% to 50% of the canopy should be minimized or eliminated in areas in which amphibian diversity or abundance is known to be high, or in which sensitive species of conservation concern are known to occur (e.g., in the southeastern United States, flatwoods salamander, *Ambystoma cingulatum*). Additionally, the locations of timber removal should consider topographical features known to promote amphibian persistence (e.g., ravines, north-facing slopes, and uplands within a radius of 150 m from breeding ponds; Semlitsch and Bodie 2003).

The size of clearcut plots is also important. Our clearcut treatment sites were relatively small (approximately 2.1 ha each in Maine and Missouri, and approximately 4.0 ha in South Carolina), but even at this size it was not certain whether all individuals, especially juveniles, could readily escape to adjacent forests. McKenny and colleagues (2006) found little reduction in abundance of terrestrial *Plethodon* salamanders in treatments using small (0.05 ha) group harvests. However, Renken and colleagues (2004) found significant reductions in the abundance of several species of amphibians within 5-ha clearcut plots in the Ozark hills of Missouri. It is realistic to assume that clearcuts larger than 2 to 4 ha and representative of industrial timber management in the southeastern United States or boreal Canada would have stronger negative effects on amphibian abundance and longer recovery times for populations. It has also been noted that small clearcuts surrounded by large areas of high-quality habitat rather than low-quality habitat (habitat with human development, agriculture, grazing, or high road density, e.g.) allow better connectivity to source habitats, minimize nest parasites and edge predators, and promote diversity of birds (Faaborg 2002). We agree that landscape composition is critical when considering timber-harvest options for amphibians, primarily to ensure complementation of aquatic breeding and adult terrestrial habitats, connectivity to source habitats essential for recolonization, and suitable forested habitat for evacuation from clearcuts (Semlitsch et al. 2008).

On the basis of our findings for the partial treatment, and those of others using selection-harvest methods (summarized by deMaynadier and Houlahan 2008), removal of a portion of the canopy (50% or less) appears to minimize negative effects on amphibian populations. Also, because many trees remain in selection-harvest plots, it is likely that microclimates recover more quickly than in large clearcuts, and thereby longer-term effects are minimized (Ash 1997). However, we acknowledge that more total area is disturbed (by roads and skidder trails) when using selection-harvest relative to the same amount of timber extracted from a clearcut. This results in a potential trade-off between small, intense disturbances versus large, diffuse disturbances. Further, because the effects of partial harvest treatments in our study were more similar to those in the control treatment than to the clearcut treatments, some species that benefit from some open canopy or early-successional habitat for reproduction may be reduced or excluded (e.g., chorus frogs, toads). These early-successional species would most likely benefit from more group-selection cuts that open small patches of forest (Skelly et al. 2005) while avoiding some of the negative effects of larger clearcuts. It also appears that partially thinned forests support a greater abundance of small snakes than do unharvested control forests or clearcuts (Todd and Andrews 2008), reinforcing the benefits of selection-harvest methods beyond amphibians alone.

Because amphibians often reside on or in the soil, future research might use field experiments to investigate the effects of soil compaction during logging, and the effects of other postharvest site preparation methods (e.g., burning, herbicide application, plowing) as well as their seasonal timing and potential alternatives. As we mentioned, experiments to determine thresholds for the volume and density of retained CWD and the percentage of forest canopy removal will also be critical for understanding mitigation of timber harvest and the limit of sustainable harvest. To fully understand the recovery of amphibian populations, we hope that future studies will link successional changes in vegetation structure to microclimate, food resources, and vital rates. As we have shown, coordinated studies explicitly designed to focus on the mechanisms of decline will be most useful in understanding how to reverse declines and conserve amphibian biodiversity.

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Effects of timber harvesting on pond-breeding amphibian persistence: Testing the evacuation hypothesis

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EFFECTS OF TIMBER HARVESTING ON POND-BREEDING AMPHIBIAN PERSISTENCE: TESTING THE EVACUATION HYPOTHESIS

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Abstract. Numerous studies have documented the decline of amphibians following timber harvest. However, direct evidence concerning the mechanisms of population decline is lacking and hinders attempts to develop conservation or recovery plans and solutions for forest species. We summarized the mechanisms by which abundance of amphibians may initially decline following timber harvest into three testable hypotheses: (1) mortality, (2) retreat, and (3) evacuation. Here, we tested the evacuation hypothesis within a large-scale, replicated experiment. We used drift fences with pitfall traps to capture pond-breeding amphibians moving out of experimental clearcut quadrants and into control quadrants at four replicate arrays located within the Daniel Boone Conservation Area on the upper Ozark Plateau in Warren County, Missouri, USA. During the preharvest year of 2004, only 51.6% of the 312 individuals captured were moving out of pre-clearcut quadrants, and movement did not differ from random. In contrast, during both postharvest years of 2005 and 2006, the number of captures along the quadrant edge increased, and a higher proportion of individuals (59.9% and 56.6%, respectively, by year) were moving out of clearcut quadrants than entering. Salamanders moved out of clearcuts in large percentages (*Ambystoma annulatum,* 78.2% in 2005, 78.2% in 2006; *A. maculatum,* 64.0% in 2005, 57.1% in 2006). Frogs and toads also moved out of clearcut quadrants, but in lower percentages (*Bufo americanus,* 59.6% in 2005, 53.3% in 2006; *Rana clamitans,* 52.7% in 2006). Salamanders moved out of clearcuts with low-wood treatments more than out of clearcuts with high-wood treatments. Movement of salamanders out of clearcuts was independent of sex. Estimated movement out of clearcuts represented between 8.7% and 35.0% of the total breeding adults captured for two species of salamanders. Although we recognize that some portion of the amphibian population may retreat underground for short periods and others may not survive the effects of timber harvest, these data are the first direct evidence showing that individuals are capable of leaving clearcuts and shifting habitat use.

Key words: Ambystoma *spp.; anuran; clearcut; evacuation hypothesis; forest management; frogs; mortality; salamanders.*

Introduction

In many parts of the world, the loss of habitat associated with the extraction of natural resources, such as timber, is a major threat to animal populations. Despite a general agreement among biologists about the negative effects of timber harvest on amphibian abundance (e.g., Bury 1983, Noss 1989, Petranka et al. 1994, de Maynadier and Hunter 1995, Grialou et al. 2000, Knapp et al. 2003), there are scant data and even some conflicting views concerning the mechanisms of population decline, especially among lungless woodland salamanders (e.g., Ash and Bruce 1994, Ash 1997, Petranka 1999). A summary of mechanisms across studies indicates three general hypotheses: (1) mortality hypothesis, which assumes that abundance in clearcuts declines due to mortality from lack of food or refuge from desiccation and an inability to evacuate; (2) retreat hypothesis, which assumes that individuals remain in the clearcuts but move to more suitable underground habitat where individuals survive for limited periods on minimal resources and energy stores, perhaps reduce activity, and re-emerge as vegetative recovery proceeds; and (3) evacuation hypothesis, which assumes that

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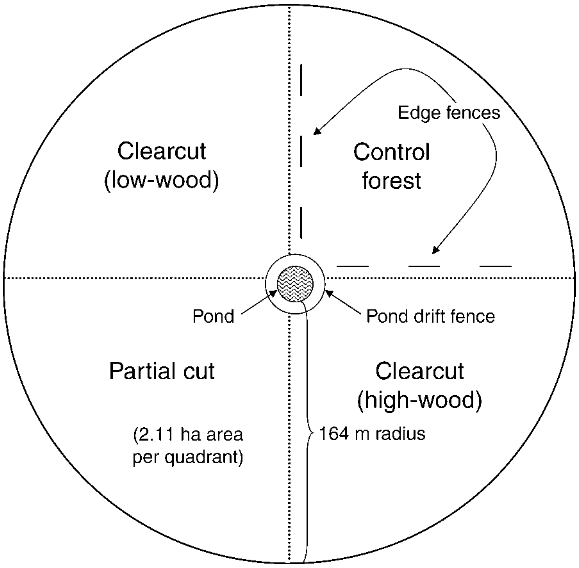

FIG. 1. A schematic diagram of the experimental forest treatments, central breeding pond, and edge fences used to sample amphibians.

individuals leave clearcuts in response to increasing temperature, reduced moisture and food, and select more suitable habitat nearby.

We currently have some direct support for the mortality hypothesis for several pond-breeding amphibians. Experimental studies have shown that when amphibians are confined to enclosures in clearcuts they exhibit higher desiccation rates and lower survival than those confined to closed canopy forest (Rothermel and Semlitsch 2006, Todd and Rothermel 2006; E. B. Harper and R. D. Semlitsch, *unpublished manuscript*; T. A. G. Rittenhouse, E. B. Harper, L. R. Rehard, and R. D. Semlitsch, *unpublished manuscript*). However, enclosure studies cannot determine if amphibians would choose to remain in these unsuitable habitats or would evacuate clearcuts to reduce the risk of desiccation and mortality. Distinguishing among mechanisms of decline is important because in the case of mortality, individuals are permanently lost and the population declines. Yet, if the retreat or evacuation hypotheses are important, individuals may only be temporarily absent from the habitat as reflected by low abundance, but could return, and the population may not decline permanently. Thus, distinguishing among the mechanisms of decline is required to affect solutions for reversing declines and the recovery of amphibian populations, especially those already threatened or endangered. Amphibians are the most threatened vertebrate taxa globally, with one-third, or 1896 species, currently threatened with extinction (Stuart et al. 2004).

We acknowledge that the three hypotheses are likely not mutually exclusive. Declines in abundance of amphibians may be due to a combination of factors, depending on habitat alteration type, time to habitat recovery, and species of concern. Here, we present a large-scale, replicated experiment designed to monitor the movement of pond-breeding amphibians out of clearcuts to test the evacuation hypothesis. We use the term “evacuation” because it is not known whether individuals are dispersing to new populations, dispersing and subsequently suffering mortality, or emigrating and will eventually return. Providing a rigorous test of the evacuation hypothesis at this time is crucial to direct current mechanistic studies of population declines to help understand how alternative timber extraction practices or the scale of management might ameliorate detrimental effects on amphibian populations and to balance resource extraction with the urgent need for conservation of biodiversity.

METHODS

Our experiment was conducted as a part of the National Science Foundation (NSF) Collaborative Project “Land-use Effects on Amphibian Populations” (LEAP) underway at the University of Missouri to test amphibian responses to forest management treatments. Four replicate arrays were located within the Daniel Boone Conservation Area (1424.5 ha) on the upper Ozark Plateau in Warren County, Missouri, USA. The arrays were spaced 0.38–1.35 km apart and situated in mature (80–100 years old), second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with varying amounts of sugar maple (*Acer saccharum*) in the understory. Each array was centered on a natural breeding pond and selected from ~40 ponds in the conservation area to meet our criteria of being >300 m apart and similar in size (high water area 160–330 m^2). These ponds were originally built for other wildlife (e.g., turkey and deer), are between 27 and 47 years old, and have naturally colonized breeding populations of up to 16 species of amphibians (D. J. Hocking, T. A. G. Rittenhouse, B. Rothermel, J. Johnson, C. A. Conner, E. B. Harper, and R. D. Semlitsch, *unpublished manuscript*).

Four forestry treatments were applied at each array and consisted of a clearcut with high levels of coarse down wood (high-wood), a clearcut with less coarse down wood (low-wood), a partial-canopy removal, and a control forest (Fig. 1). The two clearcut treatments were designed to test the potential for retaining more wood to mitigate negative effects of clear-cutting on amphibians. Coarse down wood has the potential to benefit amphibians by providing moisture-retaining refugia (e.g., Herbeck and Larsen 1999). In the clearcuts, all marketable timber >25 cm diameter at breast height (dbh) was removed for sale. The clearcuts with the high wood had the remaining trees (<25 cm dbh) felled and left on the ground. In the clearcuts with low wood, the remaining trees (<25 cm dbh) were girdled and left standing to reduce the down wood on the ground. The partial-cut treatment was thinned by girdling or felling poor quality trees and undesirable species (primarily

Acer saccharum) to a basal area of 13.8 m^2/ha that was ~60% of the stocking level. This type of partial-cut treatment is a common part of timber stand improvement in central Missouri. However, we did not address movement patterns in or out of the partial harvest quadrants in this study.

To delineate the treatments around each pond, a circular area with a radius of 164 m from a pond was divided into four equal quadrants (~2.11 ha each). A radius of 164 m was used because it is proposed to encompass 95% of the core terrestrial habitat needed by breeding populations of six species of salamanders in the area (Semlitsch 1998). The control treatment was randomly assigned to one quadrant, the two clearcut treatments were randomly assigned to the two quadrants adjacent to the control, and the partial treatment was fixed in the quadrant opposite the control (Fig. 1). All experimental forest treatments were harvested between March 2004 and January 2005.

We completely encircled the central breeding ponds at the four arrays with a drift fence and pitfall traps during October–December 2003. This drift fence enabled us to census the breeding population of each species each year. The drift fence was constructed of aluminum flashing buried ~30 cm into the ground and extending 60 cm above ground (Gibbons and Semlitsch 1982). Pitfall traps consisted of plastic plant pots (23 cm diameter, 24 cm deep) buried such that the top is flush with the ground and against the fence. Traps were paired along each side of the fence every 3.0 m. A wooden board was held 4 cm above each trap to reduce predation and a moist sponge was placed in the bottom of each trap to reduce desiccation.

To test whether amphibians were moving out of clearcut quadrants into controls after harvesting, we installed six additional drift fences (each 15.4 m long) between control and clearcut quadrants at each array (hereafter called "edge fences"; Fig. 1) to capture individuals moving laterally in the terrestrial habitat (i.e., perpendicular to expected migrations to and from the breeding pond). We placed drift fences 1–2 m within the control treatment quadrant parallel to clearcut edges on each side of the control (total of 46.2 m or 28.2% of the total length of each side; Fig. 1). Throughout each year (2004, 2005, 2006; February–November), pitfall traps at pond and edge fences were checked every 1–3 days, depending on amphibian activity and rainfall. At all arrays we recorded date, species, sex, age class, and direction of movement for all individuals captured in our traps and released them on the opposite side of the fence, the presumed direction of travel.

We used total number of adults captured exiting the complete pond fences to approximate breeding population sizes of select species and to assess what portion of the total captures might be leaving clearcuts. To assess movement out of clearcuts, we first tested captures using pre-harvest data from edge fences in 2004 against the random expected ratio of 50% in and 50% out of the clearcut quadrants. The spring and early-summer migration period of 2004 had above average rainfall (49.7 cm) compared to the 20-year mean (44.3 cm) and was reflected in high captures of breeding adults in drift fences at all ponds. Thus, we considered the 2004 edge data to be robust and reflect the typical "control" condition for lateral movement between experimental quadrants prior to timber harvest. Under these conditions, our data showed subtle biases in capture probabilities in one direction at edge fences that was due to variation in landscape features (i.e., slope) that channel movements consistently from year to year (based on decades of drift fence studies; R. D. Semlitsch, *personal observation*), but have no relationship to our randomly assigned forest treatments. Even when we tested post-harvest data each year using the random expected ratio of 50:50, the overall amphibian and salamander movement was still significantly biased out of clearcuts. However, we used the preharvest data from edge fences in 2004 to more accurately establish expected values (proportion of total captures) for all amphibians moving laterally in and out of clearcut quadrants. We totaled amphibian captures at edge fences during post-harvest years (2005 and 2006) in and out of clearcuts for each array to test against expected captures determined from observed 2004 ratios. Total amphibian captures (primarily four species) at edge fences for each year were then tested using log-likelihood *G* tests (Zar 1974). Dependence of drift fences along edges or within arrays, and high variance in captures precluded using variance analysis. Additional *G* tests were conducted separately for anurans and salamanders, postharvest years, coarse woody debris (CWD) treatments, sex, and by individual species where sample sizes were adequate to address species differences in responses: adult *Ambystoma annulatum* (ringed salamander; see Plate 1), adult *Ambystoma maculatum* (spotted salamander), adult and juvenile *Bufo americanus* (American toad), and juvenile *Rana clamitans* (green frog).

RESULTS

A total of 1661 individuals representing primarily four species of amphibians were captured in edge fences during the three years of our study (Table 1). During the preharvest year of 2004, only 51.6% of the 312 individuals captured were moving out of clearcut quadrants, and movement did not differ from that expected at random. Salamanders were captured more frequently than anurans, and salamanders moved into clearcut quadrants (*Ambystoma annulatum* 62%, *A. maculatum* 52.1%) and anurans moved out of clearcut quadrants prior to cutting (*Bufo americanus* 67.6%, *Rana clamitans* 64.9%; Table 1). However, only the combined total of anurans and *B. americanus* alone differed from random movement (Table 1).

In contrast, during both postharvest years of 2005 and 2006, more individuals (n = 736 and n = 613,

TABLE 1. Total amphibian captures from four replicate study arrays at the Daniel Boone Conservation Area, Missouri, USA.

	2004 (preharvest)		2005 (1 yr postharvest)		2006 (2 yr postharvest)	
Taxon	In : out	*P*†	In : out	*P*‡	In : out	*P*‡
Total amphibians	151:161	0.571	295:441	<0.001	266:347	0.013
Salamanders	124:112	0.435	107:243	<0.001	90:151	<0.001
Ambystoma annulatum	31:19	0.090	39:140	<0.001	17:61	<0.001
Ambystoma maculatum	75:69	0.617	40:71	<0.001	51:68	0.044
Anurans	27:49	0.012	188:198	<0.001	176:196	<0.001
Bufo americanus	12:25	0.033	38:56	0.010	43:49	0.003
Rana clamitans	13:24	0.071	148:138	<0.001	130:145	<0.001

Note: Cumulative numbers of individuals moving into and out of clear-cut quadrants are shown for each species or group of amphibians for each year of the study.

† *P* values generated from a χ^2 ratio using an expected ratio of 1:1, in : out.

‡ *P* values generated from an adjusted χ^2 ratio using observed amphibian movements in and out of clearcuts for each array tested against expected captures determined from observed 2004 ratios.

respectively) were captured at edge fences, and a higher percentage of individuals (59.9% and 56.6%, respectively) were moving out of clearcut quadrants. When we analyzed the capture data by species, salamanders were now moving out of clearcuts in highly significant percentages (*A. annulatum,* 78.2% in 2005, 78.2% in 2006; *A. maculatum,* 64.0% in 2005, 57.1% in 2006; Table 1). Anurans were also moving out of clearcut quadrants (*B. americanus,* 59.6% in 2005, 53.3% in 2006; *Rana clamitans,* 52.7% in 2006; Table 1), but not in as high percentages as salamanders. In only one case, *Rana clamitans* were moving into clearcuts in higher percentages (51.7% in 2005; Table 1).

We also detected a significant year effect ($\chi^2 = 11.2$, $P = 0.0008$), with more individuals and higher percentages moving out of clearcuts in 2005 ($n = 736$, 59.9%) than in 2006 ($n = 613$, 56.6%) for all species, but especially for salamanders (Table 1). When we tested the two species of salamanders that were most abundant, combining 2005 and 2006 data, a higher portion of individuals moved out of low-wood treatments and a lower portion moved out of high-wood treatments than would be expected at random ($\chi^2 = 61.0$, $P < 0.0001$). The percentage of individuals moving out of clearcuts was independent of sex ($\chi^2 = 2.11$, $P = 0.146$). When we used the total number of captured breeding adults to approximate minimum population size for the two primary species of salamanders and to estimate what percentage of individuals were leaving the two clearcut quadrants, we found that between 10.6% and 35.0% of *A. annulatum* and 8.7% and 30.0% of *A. maculatum* were leaving clearcuts each year (Table 2).

DISCUSSION

We report experimental evidence to support the hypothesis that evacuation plays a role in the initial decline in abundance of pond-breeding amphibians in terrestrial habitats following clearcut timber harvest at our sites in Missouri. We found that salamanders responded strongly by leaving clearcuts, but anurans demonstrated a weak or reverse response, that movement out of clearcuts was greater during the first postharvest year than the second year, and that the presence of a higher amount of coarse down wood reduces evacuation. Although we recognize that some amphibians may retreat underground for short periods and others may die as a result of the clearcut harvest, especially small juveniles (e.g., Rothermel and Semlitsch 2006, Todd and Rothermel 2006), our data are the first experimental evidence showing that individuals of some species actually leave altered habitats and move into more suitable habitat.

We suggest that the high temperatures associated with removal of the overstory canopy (Geiger 1971, Keenan and Kimmins 1993, Chen et al. 1999) contribute to a net

TABLE 2. Total captures of breeding adults of two species of salamanders (*Ambystoma annulatum* and *A. maculatum*) totaled over four ponds for each year.

	Breeding year		
Species	2004	2005	2006
A. annulatum	4072	4200	2941
Number in clearcuts†	1784	1827	1474
Net number leaving‡		101	44
Adjusted min. percentage leaving§		19.6	10.6
Adjusted max. percentage leaving‖		35.0	18.9
A. maculatum	2722	1695	2492
Number in clearcuts†	1416	848	1246
Net number leaving‡		31	17
Adjusted min. percentage leaving§		16.8	8.7
Adjusted max. percentage leaving‖		30.0	15.6

Note: In postharvest years, the captures in clearcuts, net number of individuals captured leaving clearcuts, and the adjusted minimum and maximum percentage leaving clearcuts are shown.

† Based on total captures exiting ponds into the two clearcut quadrants at each pond.

‡ Based on captured individuals moving in and out of clearcuts presented in Table 1.

§ Adjusted to account for lateral movements and potential captures at drift fences encompassing 28.2% of each edge only between control and clearcut quadrants.

‖ Adjusted to account for lateral movements and potential captures at drift fences encompassing 15.8% of all possible clearcut edges along forest habitat.

PLATE 1. The ringed salamander (*Ambystoma annulatum*) is an endemic species of the Ozark Plateau, Warren County, Missouri, USA. Individuals of this species inhabit oak–hickory forests and breed in fishless ponds in autumn. Photo credit: D. J. Hocking.

movement of amphibians out of clearcut habitats and into nearby forested control habitats. For example, E. B. Harper and R. D. Semlitsch (*unpublished manuscript*) have shown that survival of juvenile woodfrogs and toads in terrestrial pens in the same experimental forest arrays is most closely negatively associated with maximum substrate temperature. Substrate temperatures under the leaf litter during the hottest months of the year reached high levels in clearcut quadrants (mean maximum = 46.3° + 1.58°C [mean + SE] in low down wood and 47.2° + 1.49°C high down wood) relative to control quadrants (33.87° + 0.76°C; E. B. Harper and R. D. Semlitsch, *unpublished manuscript*: Table 2) and likely exceeded the maximum critical limits for any amphibians (maximum recorded amphibian body temperatures 36°–41°C; Hutchison and Dupre 1992). Because the presence of high amounts of down wood reduced the proportion of salamanders leaving clearcuts at our sites in Missouri, we argue that down wood enhanced moisture and moderated temperature levels in slash piles following clearcutting and improved amphibian habitat as suggested in other studies (e.g., Herbeck and Larsen 1999). In support, T. A. G. Rittenhouse, E. B. Harper, L. R. Rehard, and R. D. Semlitsch (*unpublished manuscript*) showed that piles of slash left after clearcut harvest ameliorated the effects of water loss and reduced desiccation mortality relative to open areas on clearcuts in three species of frogs in Missouri.

We found that salamanders had a stronger evacuation response to clearcutting than anurans. Although speculative, we propose several likely reasons. Salamanders as a whole are more forest-associated than many anurans, especially our dominant frog species *R. clamitans*. Salamanders may be more sensitive to canopy removal, have a lower threshold to changes in temperature, moisture or both, and are able to respond behaviorally by leaving clearcuts. We have previously shown that adult *A. maculatum* can detect grassland–forest edges during breeding migrations, reverse direction, and avoid entering unsuitable grassland habitats (Rittenhouse and Semlitsch 2006). In fact, part of the trend we observed for both salamanders between pre- and post-cut years (Table 1) indicates more total captures at edge fences, but somewhat lower numbers of individuals entering clearcuts (i.e., avoidance), which helped increase the proportion of individuals leaving clearcuts, especially for *A. maculatum* (Table 1). Second, salamanders may have survived in greater numbers both during and following timber harvest. Mole salamanders of the family Ambystomatidae use small-mammal burrows some distance underground as refugia (Madison 1997, Faccio 2003). They may have been able to retreat underground, protected from mechanical disturbance, and wait for suitable weather conditions to evacuate clearcuts. Further, the restriction of surface movement to the cool and wet months of early spring or late fall at our sites (D. J. Hocking, T. A. G. Rittenhouse, B. Rothermel, J. Johnson, C. A. Conner, E. B. Harper, and R. D. Semlitsch, *unpublished manuscript*) could have minimized exposure to dry and hot conditions experienced during summer in clearcuts and presumably reduced their risk of mortality. Other than toads, frogs may not burrow or use underground refuges such as rodent burrows as readily as salamanders. Post-breeding migrations of many anurans occur after salamanders (D. J. Hocking, T. A. G. Rittenhouse, B. Rothermel, J. Johnson, C. A. Conner, E. B. Harper, and R. D. Semlitsch, *unpublished manuscript*) when temperatures are higher and drier, possibly making evacuation risky and resulting in higher mortality than salamanders. Wood frogs (*R. sylvatica*) are an exception among the anurans in our study; they are strongly forest associated and migrate very early in spring along with spotted salamanders. Thus, our two most abundant anurans (American toads and green frogs) may have been more susceptible to mortality from clear-cutting than the salamanders and, subsequently, this may explain their lower numbers, especially leaving. Third, the lack of any large net movement out of clearcuts by anurans may indicate that the primary species at our study site (adult *B. americanus* and juvenile *R. clamitans*) are habitat generalists and are able to utilize clearcut habitat as well as closed canopy habitat.

Variation in the response of these species has important implications for studies failing to consider such life history requirements while trying to develop effective conservation and management plans. For example, the weak evacuation response by *R. clamitans* to clearcutting is likely the opposite to what we would expect for wood frogs, which are infrequently captured in our arrays but have been found to be strongly forest associated and sensitive to the loss of forest canopy in other studies (*R. sylvatica*; Gibbs 1998, Skelly et al. 2002, Regosin et al. 2003). Thus, we caution that any management recommendation based on responses of one species of frog (*R. clamitans*) to clearcutting would have potentially devastating effects on efforts to protect another (*R. sylvatica*), even within the same family.

We also found that more amphibians moved out of clearcuts the first year following timber harvest (2005, $n = 736$) than in the second year (2006, $n = 613$). One possible explanation is that 2005 was drier (total precipitation = 34.9 cm) during February–June than in 2006 (38.6 cm) and below the 20-year average (44.3 cm; M. O. Hermann, *available online*).[2] Less rainfall at this time may have allowed the new clearcuts to dry more rapidly and to a greater extent, thereby creating a stronger cue to evacuate in 2005 than in 2006. Additionally, succession via the increasing density of herbaceous ground vegetation (e.g., blackberry thicket, grasses) and oak regeneration in our clearcuts occurred at a rapid rate in the first two years (*unpublished habitat data*). Effects of succession in the second year may have begun to ameliorate canopy removal by providing cover in the form of herbaceous vegetation and more suitable microhabitat needed to protect amphibians from heat and desiccation (Seebacher and Alford 2002). A desiccation experiment conducted at our sites in a variety of microhabitats using three species of anurans showed a significant year effect with greater water loss and mortality in 2005 than in 2006 (T. A. G. Rittenhouse, E. B. Harper, L. R. Rehard, and R. D. Semlitsch, *unpublished manuscript*). This experiment indicated that 2005 was a more environmentally stressful year than 2006, but still does not allow us to separate rainfall from succession effects. Finally, we cannot eliminate the possibility that the reduced number of amphibians moving out of clearcuts in the second year postharvest (2006) might also reflect a reduced number of remaining individuals. With each individual leaving or dying in clearcut quadrants, fewer remain. The evacuation in 2005 for even abundant species like salamanders, using the minimum estimate just along lateral edges of quadrants, can reduce abundance by large increments (Table 2). We assume that even abundant species could be reduced substantially, at minimum rates of evacuation of 8–10%, especially if evacuation continues for a number of years.

Our results in Missouri provide support for the evacuation hypothesis. Most amphibian studies reporting declines in abundance due to clear-cutting, especially on lungless woodland salamanders of the family Plethodontidae (e.g., Petranka et al. 1993, Ash 1997, Herbeck and Larsen 1999) have assumed mortality is the primary mechanism. We have shown that some species, especially mole salamanders, display a significant evacuation response and may reduce their short-term exposure and mortality on clearcuts by shifting to more suitable habitats. The novelty of our finding is that these individuals, if they survive, may eventually serve to recolonize the clearcut after succession produces suitable habitat. We are well aware, however, that our study focused on migratory species having greater vagility than the more sedentary plethodontids and that the size of our clearcuts and distance to suitable forest habitats was relatively short (~2.11-ha quadrants; 82-m mean dispersal distance from the center of our clearcuts). Woodland salamanders are known to have substantially reduced vagility, so our results may not be applicable (but see Marsh et al. 2004). It is also unknown whether individuals at our sites that move to adjacent forest habitats might displace resident populations, saturate the habitat, and subsequently reduce per capita resources to the extent that all individuals then suffer negative and long-term effects of density dependence on survival or other demographic parameters. Significant effects of density dependence in the terrestrial environment have only recently been revealed for two species of amphibians with strong effects on growth and survival (Harper and Semlitsch 2007). So, although we have documented a shift in habitat use that appears beneficial, long-term consequences are unknown.

Our results strengthen recommendations to manage and harvest timber in small plots to allow forest-dependent, pond-breeding amphibians to shift habitat to increase survival and increase the potential for subsequent recolonization after succession. Our results also show that evacuation of pond-breeding salamanders is reduced by the presence of high amounts of down wood and strengthens management recommendations to retain down wood on clearcuts, especially in the first few years, while plots are undergoing rapid succession. Further, our results indicate that species that are habitat generalists such as green frogs may not suffer strong effects from clear-cutting. More research is needed to

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[2] ⟨www.wunderground.com⟩

follow the fate of individuals shifting habitats, the succession of forests and subsequent changes in microclimate essential to amphibians, recolonization processes, and to determine the amount of time needed for species populations to recover to preharvest levels.

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Quasi-extinction risk and population targets for the Eastern, migratory population of monarch butterflies (*Danaus plexippus*)

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The Eastern, migratory population of monarch butterflies (*Danaus plexippus*), an iconic North American insect, has declined by ~80% over the last decade. The monarch's multi-generational migration between overwintering grounds in central Mexico and the summer breeding grounds in the northern U.S. and southern Canada is celebrated in all three countries and creates shared management responsibilities across North America. Here we present a novel Bayesian multivariate auto-regressive state-space model to assess quasi-extinction risk and aid in the establishment of a target population size for monarch conservation planning. We find that, given a range of plausible quasi-extinction thresholds, the population has a substantial probability of quasi-extinction, from 11–57% over 20 years, although uncertainty in these estimates is large. Exceptionally high population stochasticity, declining numbers, and a small current population size act in concert to drive this risk. An approximately 5-fold increase of the monarch population size (relative to the winter of 2014–15) is necessary to halve the current risk of quasi-extinction across all thresholds considered. Conserving the monarch migration thus requires active management to reverse population declines, and the establishment of an ambitious target population size goal to buffer against future environmentally driven variability.

Monarchs are a charismatic species with high levels of public interest in their status and conservation[1,2]. In 2014, due to concern over the lowest overwintering population size since recordkeeping began in 1994, the U.S. Fish and Wildlife Service was petitioned to list the Eastern, migratory subpopulation (hereafter "population") of monarchs as a threatened species under the Endangered Species Act[3] and has subsequently initiated a status review to determine whether listing is warranted. More recently, the White House announced a strategic goal of increasing the Eastern population of the monarch butterfly to 225 million butterflies occupying an area of approximately 6 hectares in the overwintering grounds in Mexico by 2020[4].

Given the cultural significance of monarch butterflies and difficulty of addressing the causes of their decline, it is important to establish the extent of their vulnerability and identify the population size needed to reduce the risk of quasi-extinction to an acceptable level. Population viability analysis is a key input to decisions about whether or not to list a species as threatened or endangered and an important step in the process of conservation planning. Here we present a novel Bayesian multivariate auto-regressive state-space model to assess quasi-extinction risk. We do not attempt to specify an acceptable level of risk, but present a range of results bracketing the level likely to be adopted by decision makers. Throughout this paper we refer to "quasi-extinction" as the loss of a viable migratory population of monarchs in eastern North America.

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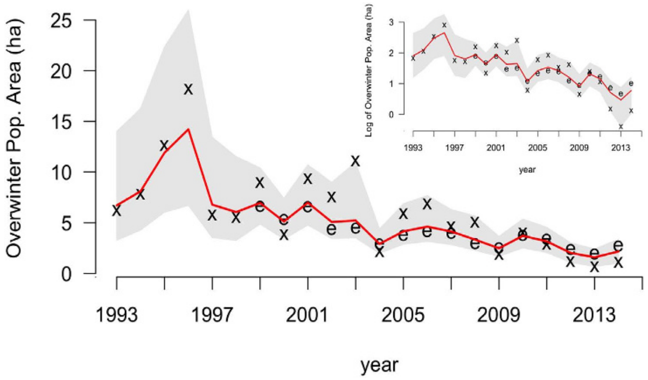

Figure 1. Model estimated annual over wintering population size (median of posterior estimates; red line) with 95% credible intervals (gray shaded area). The **x** symbols define overwintering habitat area data from Mexico, while the **e** symbols represent observations of annual egg production in the Midwest scaled to match the magnitude of the overwintering data (Extended Data Table 1). The inset depicts the data and model results on a log-scale.

The size of the monarch overwintering population has followed a general downward trend, with the lowest populations recorded in the last three censuses[5] (Fig. 1). The cause of the recent decline has been predominantly attributed to the loss of breeding habitat, primarily in the U.S.[6,7]. Monarchs lay eggs on many species of milkweed (*Asclepias* spp.) that developing larvae require for food. Declines in milkweed abundance are well documented and highly correlated with the adoption of herbicide-tolerant genetically modified corn and soybeans[6], which now constitute 89% and 94% of these crops, respectively, in the U.S.[8]. Other threats, summarized by Shahani *et al.*[9], include habitat loss in the wintering sites, climate change, insecticides (including neonicotinoids and others), mowing regimes, invasive species, and disease incidence.

We created a multivariate first-order auto-regressive state-space model[10,11] to generate population parameter estimates for use in quasi-extinction risk forcasting. We fit the model using both area (ha) of forest occupied by overwintering colonies (1993–2014)[5] and total annual egg production in the Midwest (1999–2014)[6]. Our modeling approach permitted us to separate measurement error and process noise (population stochasticity due to biological and environmental variability) in these data and subsequently generate probabilistic quasi-extinction risk estimates for the population.

In the context of population viability analysis, estimates of process noise can dramatically influence extinction risk, as environmental variability can cause populations to stochastically hit quasi-extinction thresholds well before a deterministic decline would indicate; this is particularly true for small populations[12]. Measurement (observation) error at the overwintering sites is substantial, originating primarily from the difficulty in measuring the density of monarchs at each colony. Published density estimates vary widely, ranging from 6.9–60.9 million monarchs per hectare in the overwintering areas[13,14]. Similarly, we expect measurement error associated with egg production in the Midwest to be considerable, and independent from measurement error associated with the overwintering population. Our modeling approach thus separately estimates process noise and both measurement errors, and affords the ability to generate quasi-extinction probabilities based on probabilistic estimates of (1) process error (independent of measurement errors), (2) estimated overwintering population size in the last census year (winter 2014/2015), and (3) the growth rate of the population. Importantly, because these estimates are probabilistic, we were able to translate uncertainty in these parameter estimates into probabilistic estimates of quasi-extinction risk over specific time horizons.

Results

Model results indicate that the monarch population declined by 84% from a population maximum of 13.90 ha (6.92 – 25.61; hereafter, median and 95% credible interval; CI) in the winter of 1996–97, to 2.20 ha (1.00–3.14 CI) in 2014–15 (the most recent survey year; Fig. 1). Over the modeled timeframe (1993–2014), the estimated annual rate of growth (λ) was 0.94 (0.69–1.3 CI), with 66% of the posterior distribution falling below $\lambda = 1$ (Fig. 2). In other words, based on the data and uninformative priors, there is a 66% chance the average annual growth rate underlying the stochastic trajectory of the population is below 1.

Our model estimated process noise (standard deviation) at 0.49 (0.28–0.80 CI), overwintering habitat area measurement error at 0.44 (0.21–0.67 CI), and egg production measurement error at 0.04 (0.001–0.41 CI). The variability in true population size ultimately drives quasi-extinction probability over short periods of time[15]. Our estimate of process noise is considerably higher than the range of values reported in the literature[16], although to date no synthetic study has attempted to generate a range of plausible process noise values for insects in general or lepidopterans in particular. The apparent high process noise identified by our model reflects the fact that the population is subject to stochastic environmental events such as extreme temperatures or winter storms[14,17]; indeed, the susceptibility of insect populations to environmental stochasticity is widely accepted as the main driver of high variability in population size[17]. Additionally, the fact that monarchs undergo multiple generations between successive survey periods likely contributes to the high process noise in the time-series.

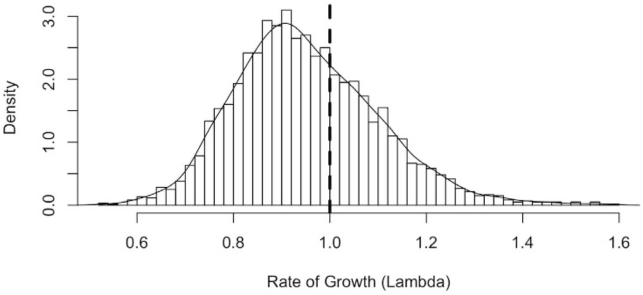

Figure 2. Posterior likelihood distribution for the estimated annual rate of growth in the monarch population. The vertical dashed line identifies the rate of growth that would result in no growth or decline from year to year (Lambda = 1). Lambda values >1 result in population growth, while values <1 result in decline.

Time horizon	Quasi-extinction Threshold			
	0.01 ha	**0.05 ha**	**0.15 ha**	**0.25 ha**
10 years	**0.03** (0.00–0.34)	**0.13** (0.01–0.62)	**0.30** (0.04–0.81)	**0.42** (0.07–0.88)
20 years	**0.16** (0.01–0.83)	**0.34** (0.01–0.93)	**0.52** (0.06–0.98)	**0.62** (0.09–0.98)

Table 1. Quasi-extinction risk (median probabilities with 95% credible intervals) over 10 & 20 years for a range of quasi-extinction thresholds, based on the current population growth rate (Lambda) of 0.94.

Quasi-extinction Threshold	Starting Population Size									
	1 ha	**2 ha**	**3 ha**	**4 ha**	**5 ha**	**6 ha**	**7 ha**	**8 ha**	**9 ha**	**10 ha**
10-Year Projection										
0.01	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.05	0.13	0.06	0.04	0.03	0.02	0.02	0.01	0.01	0.01	0.01
0.15	0.30	0.18	0.13	0.10	0.08	0.06	0.06	0.04	0.04	0.04
0.25	0.42	0.26	0.19	0.15	0.13	0.11	0.09	0.08	0.07	0.06
20-Year Projection										
0.01	0.11	0.07	0.05	0.04	0.03	0.03	0.03	0.02	0.02	0.02
0.05	0.28	0.19	0.14	0.13	0.10	0.10	0.09	0.08	0.07	0.07
0.15	0.46	0.34	0.28	0.24	0.20	0.19	0.17	0.16	0.14	0.14
0.25	0.57	0.43	0.34	0.30	0.27	0.25	0.23	0.22	0.20	0.18

Table 2. Quasi-extinction risk (median probabilities) over 10 and 20 years given different starting population sizes and quasi-extinction thresholds and based on a population growth rate of 1.0. For reference, the most recent winter population size was measured at 1.13 ha.

We used the model to estimate the probability of quasi-extinction over 10- and 20-year periods based on a range of quasi-extinction thresholds from 0.01–0.25 ha (see methods). Starting with the winter 2014/2015 estimated population level and using the average growth rate over the period of record, our model predicts the probability of quasi-extinction to be 3–42% over 10 years and 16–62% over 20 years (Table 1; Extended Data Figs 1 and 2). We also generated estimates of quasi-extinction risk over 10 or 20 years based on different starting population sizes, and under an assumed population growth rate of 1.0 (Table 2). We performed this latter latter exercise in order to assess quasi-extinction risk associated with different population size management targets. Scenario specific risk assessments assume that population size targets are met in the initial year, and that management actions have successfully mitigated declining trends in the population.

Discussion

While monarchs are currently under consideration for listing as threatened under the Endangered Species Act (ESA), there is no existing convention for defining threatened or endangered status under the ESA based on a quantitative extinction risk analysis. Given that the annual cycle of the monarch population spans Mexico, the United States, and Canada, it is worth placing our quasi-extinction risk results in the context of international standards for species conservation status. The International Union for the Conservation of Nature (IUCN) Redlist criteria provides a set of conservation classifications ranging from Least Concern to Critically Endangered[18]. Using the median values of our quasi-extinction risk analysis, monarchs would be classified as Endangered according to the IUCN for all but the lowest extinction threshold, given that quasi-extinction risk over 20 years is greater than 20% regardless of the quasi-extinction threshold considered (Table 1).

Our finding of a high probability of quasi-extinction over the next two decades stands in stark contrast to the only other published monarch extinction risk estimate. Flockhart *et al.*[7] used a spatially structured, stochastic and density-dependent periodic projection matrix model to estimate the cumulative probability of quasi-extinction (<1000 individuals) over the next century, which they reported to be ~5%. The difference between our quasi-extinction risk estimates is principally attributable to the quasi-extinction thresholds used, the incorporation of uncertainty in parameter estimation, and the way in which process noise was incorporated into forecasts. The quasi-extinction threshold of 1000 individuals used by Flockhart *et al.*[7] is likely too optimistic. Based on an assumed density of 40 million monarchs/ha in overwintering habitat[13,14], 1000 monarchs would occupy just 0.25 square meters of forest. We believe it is unrealistic to expect population functions to remain intact at such a reduced abundance for a species that clusters in winter for thermal regulation, needs to find mates during northward migration across the entire eastern part of North America, and is susceptible to extreme weather[14,19]. Simple population models with relatively few estimated demographic parameters, such as ours, generally yield more accurate estimates of future population states[15,20]. While our model does not account for density dependence, our estimates of quasi-extinction risk are likely robust, given that the population is in decline and has fluctuated widely[21].

Our modeling exercise uses overwintering habitat area as a proxy of the population size of monarchs. However, the specific conversion between habitat area and the number of monarchs is uncertain. Previous studies[13,14,22] attempting to estimate the density of monarchs per ha in overwintering grounds have generated disparate estimates, although arguably the best estimates of density with uncertainty come from Calvert[13] who used multiple census techniques to arrive at an estimated uncertainty interval of 6.9–60.9 million monarchs ha^{-1}. If we assume this interval represents a normally distributed 95% confidence interval, the error associated with the estimate is approximately 0.23 SD (after converting the interval to log ha by assuming a fixed monarch density of 40 million monarchs/ha). This is approximately half the estimate of measurement error associated with the log of overwintering habitat area occupied that we derived from our modeling exercise (0.44 SD). This difference is not surprising, however, given that the measurement error term in our model essentially represents both 1) the ability to accurately estimate the true number of ha occupied by monarchs, and 2) uncertainty in the number of monarchs per ha, which undoubtedly varies by year. In contrast, the estimate from Calvert[13] represents only the latter uncertainty (# of monarchs ha^{-1}) for a single year.

The selection of a target population size is a key step in conservation planning and requires wildlife managers to determine a level of risk that they are willing to accept. We calculated the risk of quasi-extinction over 10 and 20 years for starting population sizes ranging from 1–10 ha (Table 2). If attained, the near-term (2020) population target of 6 ha adopted by the White House will reduce the risk of quasi-extinction over 10–20 years by more than 50% for all thresholds considered. For all but the highest quasi-extinction threshold of 0.25 ha, reaching this goal would be sufficient to transition the population from Endangered to a lower-threat category under the IUCN criteria.

Our target population exercise indicates a high level of quasi-extinction risk over relatively short time windows, even when assuming large starting population sizes, which highlights the peril that monarchs currently face. Given the population's present low numbers, poor reproductive success by monarchs in future breeding seasons due to weather conditions and reduced breeding habitat, followed by catastrophic mortality while overwintering in Mexico, could bring the monarch migration to the brink of extinction. Stabilizing the growth rate of the population and meeting the 2020 target population goal will substantially decrease extinction risk due to stochastic environmental processes. The documented decline in available breeding habitat[6,7] is likely a major driver of the monarch population decline and suggests that efforts to recover the population towards the 2020 goal should focus on the creation and restoration of habitat.

Methods

Data. We used two different time series depicting dynamics of the Eastern, migratory population of monarch butterflies. First we used the log of the total extent (ha) of overwintering forest area occupied in Mexico per year from 1993–2014 measured by the World Wildlife Federation- Mexico and the Monarch Butterfly Biosphere Reserve (MBBR)[5]. Second, we used the log of the estimated total amount of egg production in the Midwest per year from 1999–2012[6] and extended this through 2014 for the current analysis (Extended Data Table 1). The egg production per year was based on the average estimated eggs per milkweed stem for that year multiplied by the number of available milkweed stems on the landscape in that year. Eggs per stem estimates come from weekly monitoring data reported to the Monarch Larva Monitoring Project (MLMP - http://www.mlmp.org) from citizen scientists throughout the monarch range. We used the eggs per stem value from the week of peak egg production as an index for the production estimation. The number of available milkweed stems was based on estimates of the density of milkweeds in different habitats based on surveys[23,24] and the area on the landscape occupied by those habitats using U.S. Department of Agriculture (USDA) databases[25] and a function describing the decline of milkweeds in agricultural fields[6].

Estimating Population Parameters. We developed a multivariate first-order auto-regressive state-space model[10–12] to generate monarch population parameter estimates for quasi-extinction risk forecasting. We chose a Bayesian modeling approach because the resulting parameter posterior distributions provide a complete characterization of parameter uncertainty that can be seamlessly propagated through to our quasi-extinction risk analysis. In so doing, we can account for uncertainty in quasi-extinction risk due to uncertainty in the parameters controlling population change. Moreover, the hierarchical nature of state-space modeling is easily handled through Bayesian estimation.

The log-scale population modeling framework takes the following form:

$$x_t = x_{t-1} + \bar{u} + w_t, \text{ where } w_t \sim N(0, q)$$

$$m_t = x_t + v_t, \text{ where } v_t \sim N(0, q^*p)$$

$$e_t = x_t + a + f_t, \text{ where } f_t \sim N(0, r)$$

In the above set of equations, x represents the state process (estimated log of the true size of the overwintering population in Mexico) across all years t for which we have data. The state process evolves from one year to the next according to a mean population growth rate, $\overline{u}$, and associated random yearly deviates to growth, w_t, which we assumed to be normally distributed with a mean of 0 and a standard deviation q (process noise). The exception to this is that we must directly estimate the population state in the first year (1993) using an uninformative uniform prior, since there is no prior year to evolve from. Note that $e^{\overline{u}} = \lambda$, the average annual (non-logged) population growth rate, where λ values of <1 result in population decline, while values of >1 results in population growth.

Values of m_t are the log of yearly estimates of Mexican overwintering habitat occupied, which we assumed to deviate from the state x_t by v_t. Values of v_t follow a normal distribution with a mean of 0 and a standard deviation of q^*p (measurement error), where q is the process noise and p is a proportion parameter. We used this parameterization based on the assumption that process noise in the time series is greater than the measurement error associated with the Mexican overwintering data. This assumption is based on a consensus among the authors that measurement error is exceeded by variation in population sizes caused by demographic and environmental variation, and because process noise is typically the predominant form of variability in time series' of wild populations[26]. As such, measurement error in m is defined to be a proportion (p) of process noise q.

Similarly, the log of annual estimates of Midwestern egg production, e_t, are assumed to deviate from the state x_t by a, a scaling parameter[11] that shifts the egg production index to the same scale as the overwintering habitat index , and f_t, where values of f are assumed to be normally distributed with a mean of 0 and a standard deviation of r (measurement error). Note that, in the context of the linear modeling framework outlined above, the parameter a is essentially an intercept term.

We fit our model using R[27] and JAGS[28] (Just Another Gibbs Sampler), and assessed convergence by examining parameter trace-plots and calculating Gelman-Rubin diagnostics using the CODA[29] package in R. Parameter estimates are provided in Extended Data Tables 1 and 2.

For the purposes of quasi-extinction risk forecasting, we report the following posterior estimates after removing variation caused by measurement error:

- x_{2014}, the estimate of the true size of the Mexican overwintering population during the winter of 2014–15,
- $\overline{u}$, the monarch population growth rate, and
- q, the process noise associated with the monarch population.

The process noise, q, represents year-to-year variability in the population after accounting for overall trend through time ($\bar{u}$, the mean growth rate in log space) and after removing variation caused by measurement error. Note that using these model estimates, we can simulate the population forward in time from its estimated current size (x_{2014}).

Calculating Quasi-extinction Risk. Because each posterior draw from the Bayesian state-space model represents a complete set of likely parameter values, we can use all the posterior draw sets to generate annual probabilistic quasi-extinction risk estimates that account for both uncertainty in population parameters and uncertainty due to the stochastic population process (random yearly growth or decline due to process noise). For each posterior draw i, we simulate the population 20 years into the future 1000 times, starting at x_{2014_i}, using the growth rate $\overline{u}_i$ and process noise q_i. For each of i simulation sets, we subsequently calculated the percent of runs that fall below a given quasi-extinction threshold (described below). Because we carried out this exercise for each i posterior draw, we can subsequently generate median and 95% credible interval estimates of quasi-extinction risk that account for population parameter uncertainty. Using a model run with a burn in of 4e5 iterations, and a sample window 10e5 iterations (3 separate chains) thinned by 600, our model achieved satisfactory convergence based on both visual inspection of trace plots and Gelman and Rubin diagnostics[30]; the Potential Scale Reduction Factors for all parameters were below 1.05.

The quasi-extinction threshold, or population size at which extinction of the Eastern monarch migration becomes inevitable, is unknown. We do know that monarch ecology exhibits at least two characteristics that suggest the likelihood of a strong Allee[26] effect and therefore the existence of an extinction threshold: tightly clustered overwintering colonies convey important microclimate advantages that diminish as colony size decreases[19,31] and the increased efficiency of locating mates in overwinter aggregations[32–34]. Diminishing colony size can therefore result in higher winter mortality rates and lower fecundity in the spring, which can cause the population growth rate to drop below replacement.

Regarding the size of winter aggregations specifically, expert opinion among the monarch biologist authors of this manuscript (Taylor, Oberhauser, Pleasants) favored an extinction threshold of no less than 0.05 ha, with most favoring a threshold closer to 0.25 ha. For reference, the smallest observed size of a Mexican overwintering colony is 0.01 ha[5], and the minimum number of colonies that has been observed in Mexico in any given year is 7[5]. To be sure that we have captured the real quasi-extinction threshold, we opted to consider a range of values from 0.01 ha (1 viable colony, equivalent to approximately 1 occupied tree) to 0.25 ha. Our lowest (most optimistic) quasi-extinction threshold is therefore equivalent to the smallest observed colony size on record, which permits the loss of all but one core colony and the associated redundancy of multiple colonies before quasi-extinction occurs. The presence of multiple colonies provides a buffer against extinction during winter storms because of their variable storm severity within the overwintering region[14]. Our least optimistic estimate of the threshold suggests that quasi-extinction could occur well before the population declines to a single core colony at the minimum observed size. These values are intended to bookend the plausible range of the extinction threshold based on the best available information.

A mechanistic approach to estimating suitable threshold values was presented by Wells *et al.*[33], who developed a model of monarch butterfly mating in California overwinter clusters that demonstrated a relationship between mating success and overwintering density. They found that reproductive success was highest for aggregations over 250,000 individuals. As aggregation size dropped below 250,000, reproductive success started to decline, and the rate of decline increased substantially below 50,000. They further noted that stable overwintering aggregations in California normally fall within this range (50,000–250,000), but acknowledge that they did not account for predation, which is a significant factor at Mexican overwintering sites and would likely require shifting this range higher. In addition, this model does not account for the population-level benefits of having multiple colonies.

The number of individuals present in overwintering colony areas is strongly dependent upon the density of monarchs per hectare. There are five published estimates of monarch overwintering densities, ranging from 6.9–60.9 million monarchs per hectare[13,14]. At the low end of this range, a quasi-extinction threshold of 0.05 ha would yield ~345,000 individuals, which may be just small enough to impact mating success according to the Wells *et al.*[33] model, once higher Mexican predation rates are accounted for. A threshold of 0.01 ha yields just 69,000 individuals at the lowest density and ~324,000 at the average density, which is more firmly in the realm of reduced mating success according to the Wells *et al.*[33] model.

Estimating a target population size. We ran the quasi-extinction risk simulation across a range of initial starting population sizes and thresholds to develop associated quasi-extinction risks for each combination of values. The quasi-extinction risk simulation was run at initial population sizes ranging from 1 ha–10 ha, in 1 ha increments. We ran these simulations for quasi-extinction thresholds of 0.01, 0.05, 0.15, and 0.25 ha over 10 and 20 years. Because the intent of this exercise was to inform the selection of a recovery goal based on population sizes that confer protection against quasi-extinction risk, we conducted our simulation exercise under the assumption that population declines have been halted and the annual growth rate (λ) of the population is 1. All quasi-extinction events in our simulations are thus exclusively a function of process noise.

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Author Contributions

B.X.S. developed the modeling concepts and methods, analyzed the data, developed a synthesis of results, and led manuscript writing and preparation. D.J.S. and J.E.D. helped develop the concepts behind the manuscript, and guide analysis and interpretation in the context of species management. W.E.T., L.L.H. and R.W. provided assistance with interpreting analytic results. J.M.P., K.S.O. and O.R.T. guided the development of realistic model parameterization based on monarch biology expertise. All authors helped write the manuscript.

Additional Information

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ECOLOGY OF *GLAUCOMYS SABRINUS*: HABITAT, DEMOGRAPHY, AND COMMUNITY RELATIONS

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A common arboreal rodent of boreal and montane coniferous forests, the northern flying squirrel (*Glaucomys sabrinus*) has several life-history traits typical of K-selected species. Density varies among forest types, with core areas of use centering on food patches. Density is largely limited by food, and to a lesser extent, suitable natal dens, but also is influenced by potential competitors and predators. Local abundance of *G. sabrinus* frequently is correlated with density of large trees and snags, shrub and canopy cover, prevalence of old-forest features (e.g., coarse woody debris), and abundance of hypogeous mycorrhizal fungi (truffles). Diet varies seasonally and among habitats, but truffles (spring and autumn) and lichens (winter) are most often reported. In some parts of its geographic range, *G. sabrinus* has a more diverse diet and lower reliance on truffles in forests with a depauperate arboreal small mammal community. *G. sabrinus* is a keystone species in the Pacific Northwest, because its diet facilitates an obligate mutualistic relationship between mycorrhizal fungi and some trees and shrubs and because it is essential prey for mesocarnivores and avian predators. *G. sabrinus* achieves its highest densities in old growth, but also occurs in secondary forests. Disturbance that reduces structural complexity, canopy cover, or the availability of large, decadent trees typically results in smaller populations through effects on food, den sites, or risk of predation. The fundamental niche of *G. sabrinus* may be broader than suggested by early research in the Pacific Northwest. Sustaining viable and well-distributed populations in heavily modified landscapes will depend on the capability of remaining forest habitat to sustain breeding populations without immigration, or functional connectivity among fragmented populations such that viable metapopulations will persist. Future research should focus on identifying habitat conditions that sustain breeding populations in modified habitats and determining whether *G. sabrinus* can migrate freely through a matrix of unsuitable habitat.

Key words: demography, *Glaucomys sabrinus*, habitat relations, home range, interspecific interactions, limiting factors, movements, northern flying squirrel, persistence, population dynamics

The northern flying squirrel (*Glaucomys sabrinus*) is a common arboreal rodent of boreal and montane coniferous forests. Its geographic range (Arbogast 2007:843, figure 2) extends to southern portions of the Appalachian Mountains in the east and the Rocky Mountain and Sierra Nevada Ranges in western North America and includes the San Bernardino Mountains of southern California (Hall 1981; Wells-Gosling and Heaney 1984). This species is active year-round, in air temperatures as low as −26°C (Mowrey and Zasada 1984); is primarily nocturnal, especially in more southern latitudes; and typically has 2 peaks of daily activity (Weigl and Osgood 1974; but see Wilson et al., in press), but adjusts timing and duration of activity according to the onset of darkness and air temperature (Cotton and Parker 2000a). *G. sabrinus* has several life-history traits typical of K-selected species (sensu MacArthur and Wilson 1967): it inhabits late-seral habitat, it is relatively long-lived (≥7 years—Villa et al. 1999), it has delayed development and age at 1st reproduction, it is a seasonal breeder with small litters (average 2 or 3 young) after a relatively long (37- to 42-day) gestation (Wells-Gosling and Heaney 1984), and it undergoes density-dependent population growth (Fryxell et al. 1998; Lehmkuhl et al. 2006). Females seem to invest substantial energy (during gestation and lactation) in each offspring, presumably to produce larger young with greater competitive ability (MacArthur and Wilson 1967).

Glaucomys sabrinus is considered a keystone species in the Pacific Northwest because it is an important link in the food chain and dynamics of coniferous forests. It is important prey for several predators (Forsman et al. 1984; Rosenberg et al. 2003; Wilson and Carey 1996) and facilitates an obligate symbiotic relationship between mycorrhizal fungi and domi-

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TABLE 1.—Densities of northern flying squirrels (*Glaucomys sabrinus*) among forested habitats of western North America (adapted from Smith et al. 2003).

Forest type	Age and disturbance history	Season	Densities (number/ha) $\bar{X}$	Range	Source
Douglas-fir	Young growth, clear-cut	Spring	1.1	0.7–1.6	Carey et al. 1992
Douglas-fir	Young growth, clear-cut	Autumn	0.5	0.3–0.7	Carey et al. 1992
Douglas-fir	Young growth, clear-cut	Autumn	1.9	1.1–2.5	Rosenberg and Anthony 1992
Douglas-fir	Old growth, natural	Spring	1.8	1.1–2.2	Carey et al. 1992
Douglas-fir	Old growth, natural	Autumn	1.9	1.8–2.2	Carey et al. 1992
Douglas-fir	Old growth, natural	Autumn	2.3	1.4–3.3	Rosenberg and Anthony 1992
Douglas-fir	Old growth, natural	Annual	1.0	0.5–1.8	Witt 1992
Douglas-fir	Second growth, clear-cut	Annual	0.1	0–0.2	Witt 1992
Western hemlock–Sitka spruce	Young growth, clear-cut	Autumn	0.2	NA[a]	Carey et al. 1992
Western hemlock–Sitka spruce	Old growth, natural	Autumn	0.5	NA	Carey et al. 1992
Western hemlock–Sitka spruce	Old growth, natural	Spring	1.8	1.6–2.0	Smith and Nichols 2003
Western hemlock–Sitka spruce	Old growth, natural	Autumn	3.2	2.2–4.0	Smith and Nichols 2003
Mixed conifer	Old growth, natural	Spring	1.7	0.9–3.2	Carey et al. 1992
White fir–red fir	Mature, fire replacement	Summer	2.3	2.2–2.4	Waters and Zabel 1995
White fir–red fir	Old growth, natural	Summer	3.3	2.8–3.5	Waters and Zabel 1995
White fir–red fir	Old growth, shelterwood cut	Summer	0.4	0.2–0.6	Waters and Zabel 1995
Ponderosa pine	Second growth, selective harvest	Autumn	1.2	0.9–1.6	Lehmkuhl et al. 2006
Mixed conifer	Young growth, selective harvest	Autumn	1.8	1.4–2.2	Lehmkuhl et al. 2006
Mixed conifer	Mature, natural	Autumn	2.3	1.9–2.6	Lehmkuhl et al. 2006

[a] NA = not available.

nant tree species (Maser and Maser 1988). *G. sabrinus* feeds on sporocarps of hypogeous fungi and deposits fecal pellets with fungal spores and nitrogen-fixing bacteria across the forest floor (Caldwell et al. 2005). The spores germinate and establish new colonies or contribute new genetic material to existing colonies. The mycorrhizae facilitate the tree's ability to absorb water and nutrients. Whether *G. sabrinus* plays a similar role in other forest biomes across its range is uncertain, but Smith et al. (2005) suggest that its habitat relations and specialized mycophagous diet in the Pacific Northwest may be attributable (at least in part) to the diverse ecological community of arboreal rodents (Carey 1989, 1991, 1995, 1996; Verts and Carraway 1998).

Glaucomys sabrinus was the focus of considerable research during the past 2 decades, especially in the Pacific Northwest where it is recognized as an essential prey species throughout much of the range of the spotted owl (*Strix occidentalis*—Carey et al. 1992; Forsman et al. 2001) and because of its keystone role in western coniferous forests (Maser et al. 1986; Maser and Maser 1988). In the southern and central Appalachians, federal listing of 2 subspecies renewed and increased interests in the demography and habitat relations of several isolated endemic populations (Payne et al. 1989; Weigl et al. 1999). A fundamental issue underlying much of the research during this period has been whether the habitat of *G. sabrinus* is an emergent property of old-growth forest (Carey 2000; Carey et al. 1999). With few exceptions (Rosenberg and Anthony 1992), the findings of several studies suggest that optimal conditions for *G. sabrinus* occur in mature or old-growth forests (e.g., Carey 1995), which led to its prominence as an indicator species (Smith et al. 2005). However, recent retrospective or manipulative experiments (e.g., Ransome and Sullivan 2003) have produced evidence that challenges any generalization that *G. sabrinus* relies on old-growth forest.

The purpose of this paper is to develop a conceptual ecological model of factors that shape the local and regional distribution of *G. sabrinus* throughout its geographic range, based on a summary of information from the scientific literature. Specific objectives include linking demography to habitat (at multiple spatial scales) and community relations to identify factors (particularly land-use patterns) that may be limiting distribution and abundance. A preponderance of evidence is used to evaluate multiple hypotheses regarding the role of cumulative disturbance, forest structure, specific resources, or interspecific interactions in limiting abundance, and whether factors constraining local populations vary across forest communities.

HABITAT

Influence on distribution.—*Glaucomys sabrinus* occupies a broad range of habitats, mostly coniferous forests (Smith et al. 2003), but it can occur in deciduous forests and is common in mixed forests including spruce (*Picea*)–northern hardwood and other mixed-coniferous–hardwood forest types (Ford et al. 2004; Holloway 2006; Holloway and Malcolm 2006; Payne et al. 1989; Weigl 1978; Weigl et al. 1999). *G. sabrinus* apparently shows little preference for coniferous or hardwood forest types in the Appalachians (Weigl 1978), suggesting that factors other than habitat selection might play a role in determining distribution in portions of its range. Population density varies across portions of its range (Wells-Gosling and Heaney 1984) and among forest types within a region (Smith et al. 2003). In the Pacific Northwest, population density in mature or old-growth forests may vary among sites by an order of magnitude (Table 1). Interestingly, both the lowest (0.5/ha) and highest (4.0/ha) mean densities recorded in the region were in coastal temperate rain forests (Smith et al. 2003; Smith and

Nichols 2003). There are few estimates of density for populations in the eastern portion of its range (Bowman et al. 2005).

Regional and landscape scales.—The contemporary distribution of *G. sabrinus* may be largely determined by factors associated with regional land-use and recent climate change, particularly at the southern limit of its geographic range. In the southern and central Appalachians, the distribution of *G. sabrinus* is naturally disjunct (Payne et al. 1989), with the species occurring as relict populations among islands of montane coniferous forests that were restricted to higher elevations after glacial retreat because of post-Pleistocene climatic shifts. Boreal-type relict forests are among the rarest in the eastern United States (Hackett and Pagels 2003; Schuler et al. 2002). However, post–European settlement land use has dramatically altered landscape and stand-level composition of forests in the region. Forests dominated by red spruce (*Picea rubens*) have been reduced by 90% (Ford et al. 2004), and Appalachian montane coniferous forest communities of red spruce, eastern hemlock (*Tsuga canadensis*), and Fraser fir (*Abies fraseri*) are considered among the most threatened forested ecosystems in the United States (Schuler et al. 2002). Extensive logging followed by widespread fires changed the overstory composition and destroyed much of the humus layer and coarse woody debris in the understory, which reduced habitat quality for hypogeal fungi or altered the composition of local fungal communities (Loeb et al. 2000). Thus, human-caused disturbances have degraded coniferous forests and facilitated expansion of oak (*Quercus*) and hickory (*Carya*) forest communities to higher elevations (Odom et al. 2001; Payne et al. 1989; Weigl 2007; Weigl et al. 1999). Although ecotones between coniferous and hardwood forests are considered optimal habitat for both subspecies of *G. sabrinus* in the Appalachians (Payne et al. 1989; Weigl et al. 1999), continued disturbance and global warming likely will replace conifer-dominated stands with hardwood forest communities and further reduce, fragment, and isolate populations of *G. sabrinus* (Payne et al. 1989; Weigl 2007).

Similarly, post–European settlement land use converted the Great Lakes region from landscapes of largely ‘‘frontier’’ forests to mostly nonforest landcover or different forest communities (Cole et al. 1998; Frelich 1995), with the greatest changes occurring in a reduction of white pine (*Pinus strobus*) and red pine (*P. resinosa*—Leadbitter et al. 2002). Ordinarily, modified landscapes return to native forest types through ecological succession, but climate change may retard or interrupt ecological processes that reestablish forest communities after disturbance (Flannigan et al. 1998; Hennon and Shaw 1997). One significant consequence to *G. sabrinus* has been the fragmentation of populations amid an agricultural matrix (Bowman et al. 2005). In addition, climate change apparently has facilitated the expansion northward (or to higher elevations) of hardwood forest communities typical of more southern latitudes (or lower elevations), with potential negative impacts to federally listed populations of *G. sabrinus* in the region (Ford et al. 2004; Holloway 2006; Menzel et al. 2006a; Payne et al. 1989).

In western North America, habitat of *G. sabrinus* also has undergone substantial modification, but for shorter periods and over smaller portions of its range. Type, intensity, and frequency of broad-scale disturbances that western forests experience (e.g., fire, logging, and windthrow) changed dramatically after European settlement (Dale et al. 2001; Nowacki and Kramer 1998). Consequences of climate warming to ecological succession or patterns of forest cover might not seem as apparent as in eastern North America, but the projected redistribution of climate space because of global warming is substantial, with subboreal and montane climate regions in British Columbia, for example, rapidly disappearing (Hamann and Wang 2006). Furthermore, history has shown that interactions between disturbance and climate change can accelerate changes in landcover and forest communities (Ford et al. 2004; Odom et al. 2001; Payne et al. 1989) that could possibly limit the distribution of *G. sabrinus* in the region. Although broad-scale replacement of coniferous forest types from climatic shifts likely is not imminent, a continued warming trend could significantly affect forest composition and structure (Hamann and Wang 2006; Hennon and Shaw 1997), shift forests toward more xeric types with significant consequences for fungal and understory plant communities (Lehmkuhl et al. 2004; Meyer and North 2005), or change the pattern of natural disturbance across an entire biome (Flannigan et al. 1998), with profound repercussions for the distribution of *G. sabrinus* in western North America, particularly in the southern extent of its range (Meyer and North 2005).

Broad-scale changes in native forest vegetation directly and indirectly influence the distribution of *G. sabrinus* (Menzel et al. 2006a). Across landscapes in eastern North America, the probability of occurrence of *G. sabrinus* is positively correlated with the density of large spruce (*Picea*) and northern hardwood trees and amount of downed woody debris (Holloway 2006). In this region, density of *G. sabrinus* is inversely correlated with the density of the southern flying squirrel (*G. volans*—Bowman et al. 2005; Weigl et al. 1999) and distance to coniferous forest (Menzel et al. 2006a; Odom et al. 2001) or to mixed-spruce–hardwood forests (Menzel et al. 2006a). Furthermore, the extent to which forested landscapes are fragmented influences the northward range expansion and distribution of *G. volans* (Bowman et al. 2005). In the more southeastern portion of its range, *G. sabrinus* has $\geq$0.9 probability of occurrence in forested landscapes where the relative importance value of conifer overstory (especially red spruce) is $\geq$50 (maximum score of 90—Ford et al. 2004). A similar relationship between spruce forests and the distribution of *G. sabrinus* was reported for central Ontario (Holloway 2006; Holloway and Malcolm 2006). Hypogeous fungi are an essential resource associated with coniferous forests (Loeb et al. 2000) and decayed standing and coarse woody debris (Carey et al. 1999, 2002; Clarkson and Mills 1994; Colgan et al. 1999; Gomez et al. 2003; Lehmkuhl et al. 2004, 2006; North et al. 1997; Pyare and Longland 2001a, 2002; Smith et al. 2000, 2002; Waters et al. 1997, 2000). Furthermore, in mixed-hardwood–conifer forest or at the ecotone of hardwood and coniferous forests *G. sabrinus* uses dreys (i.e., external leaf nests) almost exclusively in conifers (Menzel et al. 2004; Mowrey and Zasada 1984; Stihler et al. 1987). Dreys are especially important where *G. sabrinus* is sympatric with *G. volans* and competition for cavities can be intense (Hackett and Pagels 2003; Holloway 2006; Holloway and Malcolm 2006; Muul 1968; Weigl 1978, 2007).

Thus, landscapes where hardwood forest communities (especially hard mast–producing species) are increasing (through land-use or climate change) will probably experience declining populations of *G. sabrinus*, not because hardwood forests are unsuitable, but because oak and hickory forests are ideal habitat for *G. volans* (Payne et al. 1989), an aggressive competitor (Muul 1968; Weigl 1978, 2007) and vector of a pathological nematode (Pauli et al. 2004; Weigl et al. 1999). In recent years, the range of *G. volans* has expanded northward (Bowman et al. 2005; Holloway 2006) and to higher elevations in more southern latitudes (Odom et al. 2001; Weigl et al. 1999), with concomitant declines in populations of *G. sabrinus* (Holloway 2006; Weigl et al. 1999). As more landscapes in the southeastern portion of the range of *G. sabrinus* experience change in land cover or a shift in forest composition, a greater proportion of regional populations will become fragmented and isolated (Payne et al. 1989). At more northern latitudes, climate warming could facilitate migration of boreal forest northward but it is unclear to what extent *G. sabrinus* could shift its range to higher latitudes.

The response of populations of *G. sabrinus* to habitat fragmentation has not been widely studied, but evidence from central Ontario suggests that populations of *G. sabrinus* can occur in forest fragments within an agricultural matrix (Bayne and Hobson 1998; Bowman et al. 2005; Côté and Ferron 2001). In heavily modified landscapes of the Olympic Peninsula, *G. sabrinus* was captured in only 3 of 20 old-growth fragments (ranging from $\approx$3 to 60 ha) that were $<$40 ha in size and within 2.5 km of old-growth rain forest (Lomolino and Perrault 2001). Further study revealed that the distribution and size of high-quality habitat fragments determines the genetic diversity of source populations and the likelihood of empty suitable patches becoming recolonized (Wilson 2003). In southeastern Alaska, Smith and Person (2007) used simulations of a birth–death process model developed from empirical estimates of demographic parameters (Smith and Nichols 2003; Villa et al. 1999) to examine the persistence of populations of *G. sabrinus* in hypothetical old-growth reserves isolated in managed landscapes. Based on the results of their population model, the estimated probability that populations of *G. sabrinus* can persist in small ($<$100-ha), high-quality habitat patches for 25 years without migration was $\leq$0.90 in rain forest of southeastern Alaska. According to model predictions (which have not been rigorously tested), the minimum area of primary habitat to confidently ($P \approx 0.90$) sustain populations for at least 100 years without migration was estimated to be about 5,000 ha (Smith and Person 2007). The persistence of populations of *G. sabrinus* in heavily managed landscapes likely depends on the ability of individuals to move freely through the matrix (Smith and Person 2007; Taylor et al. 1993; Wilson 2003), taking advantage of the spatial arrangement of landscape elements and any available suitable habitat (Selonen and Hanski 2006).

The most effective means of achieving functional connectivity remains unclear, but Wilson (2003) proposed focusing on the spatial and temporal scale of heterogeneity in the matrix (stand age, rotation, and juxtaposition) rather than relying on narrow corridors. This view requires understanding how individuals respond to disturbance at different scales (Desrochers et al. 2003; Reunanen et al. 2000). With the Siberian flying squirrel (*Pteromys volans*), fine-scale fragmentation poses a greater risk to landscape connectivity than comparable habitat reduction occurring in a coarser pattern (Reunanen et al. 2000). Furthermore, landscape character has little effect on decisions of young squirrels to remain philopatric or to become short- or long-distance dispersers (Selonen and Hanski 2003). The home ranges of flying squirrels (*Glaucomys* and *Pteromys*) in fragmented habitat typically are larger (Menzel et al. 2006b; Selonen and Hanski 2003) than those of individuals in continuous forests, consequences of which are a greater association with and more frequent movements along forest edges and a higher risk to predation (Desrochers et al. 2003; Wilson 2003; Wilson and Carey 1996). Still, maintaining physical connectivity between optimal breeding habitats is deemed essential for the persistence of *P. volans* in managed boreal forests of Finland (Reunanen et al. 2000). Despite the ability of juveniles to move long distances in modified landscapes or opportunities in the short term for migration between populations (Selonen and Hanski 2003, 2004), cumulative disturbances that fragment populations into isolated patches, if unchecked, can ultimately lead to the extirpation of flying squirrels from an entire region (Hokkanen et al. 1982; Reunanen et al. 2000).

Correlates of occupancy, density, and habitat use.—*Glaucomys sabrinus* is more abundant in mature or old forest than in 2nd-growth forests (Carey 1989, 1995; Lehmkuhl et al. 2006; Waters and Zabel 1995; Witt 1992; but see Rosenberg and Anthony 1992). Furthermore, Carey et al. (1999) reported that variation in population density of *G. sabrinus* across regions in the Pacific Northwest could not be explained by individual habitat features; rather, habitat of *G. sabrinus* was multifactorial. The abundance of *G. sabrinus* among stands varied directly with multivariate factors such as "decadence," which was positively correlated with density of large snags and fallen tree cover, or "crown class diversification," which was directly correlated with conifers $>$50 cm in diameter at breast height, herbaceous cover, midstory cover, and foliage height diversity (Carey et al. 1999). Consequently, habitat of *G. sabrinus* in the Pacific Northwest became viewed as an emergent property of old-growth forest (Carey et al. 1999), and the northern flying squirrel became an indicator species for ecosystem management (Carey 2000).

More recently, Smith et al. (2005) concluded that the habitat of *G. sabrinus* in southeastern Alaska was not multifactorial because individual habitat variables were more effective in explaining variation in population density and individual captures than were multivariate factors. Across unmanaged rain-forest habitats, 77% of the variation in population density was explained by the volume of decayed downed wood on the forest floor, whereas 65% of the variation was attributable to the density of large-diameter (≥74-cm) trees (Fig. 1; Smith et al. 2004). In fact, numerous studies conducted across the range of *G. sabrinus* have established a direct relationship between population density and several individual features typical of mature or old forest, including large-diameter trees (Gomez et al. 2005; Holloway 2006; Lehmkuhl et al. 2006; Smith et al. 2004), large snags (Carey 1995; Carey et al. 1999; Holloway and Malcolm 2006; Smith et al. 2004), coarse woody debris, particularly decayed downed logs (Carey et al. 1999; Smith et al. 2004), and measures of truffle abundance (Fig. 2; Gomez et al. 2005; Lehmkuhl et al. 2006; Waters and Zabel 1995). Not surprisingly, retaining "legacy" (e.g., snags or coarse woody debris) in logged stands reduces the disparity in population density between mature and 2nd-growth forests (Carey 1995; Rosenberg and Anthony 1992).

Many of the features that explain variation in abundance among landscapes and across stands also are significant predictors of capture sites or microhabitat use (Carey et al. 1999; Payne et al. 1989; Smith et al. 2004). However, evidence from multiple studies suggests that resource selection by *G. sabrinus* can be scale dependent (Carey et al. 1999; Holloway and Malcolm 2006; Smith et al. 2004). Within drier forest types, microhabitat use is inversely related to distance from streams (Meyer et al. 2005a, 2007); in mesic forests, which typically support higher population densities than xeric forests (Lehmkuhl et al. 2006; Smith et al. 2003), microhabitat use is not as biased toward riparian areas (Carey et al. 1999; Smith et al. 2003). And in rain forest, the odds of capturing *G. sabrinus* are either unaffected by or inversely related to the amount of surface water (Smith et al. 2004). Similarly, in more-productive (greater basal area) stands of old-growth rain forest, large trees are uniformly abundant and large-tree density, a significant correlate of population density, explained little variation in microhabitat use (Smith et al. 2004). But in less-productive rain forest with much lower (order of magnitude) densities and clumped distributions interspersed among sparsely forested muskegs, large trees had the greatest ecological impact (17-fold) in increasing the odds of capturing *G. sabrinus* (Smith et al. 2004). Carey et al. (1999) and Meyer et al. (2007) reported similar patterns for populations of *G. sabrinus* in the Pacific Northwest and in the Sierra Nevada, respectively. Still, in portions of its range where essential resources are less abundant, *G. sabrinus* may depend on suitable conditions occurring uniformly across multiple spatial scales. In the Appalachians, Payne et al. (1989) reported not only that stands with red spruce were likely to be occupied by *G. sabrinus*, but that all capture sites had red spruce in the overstory.

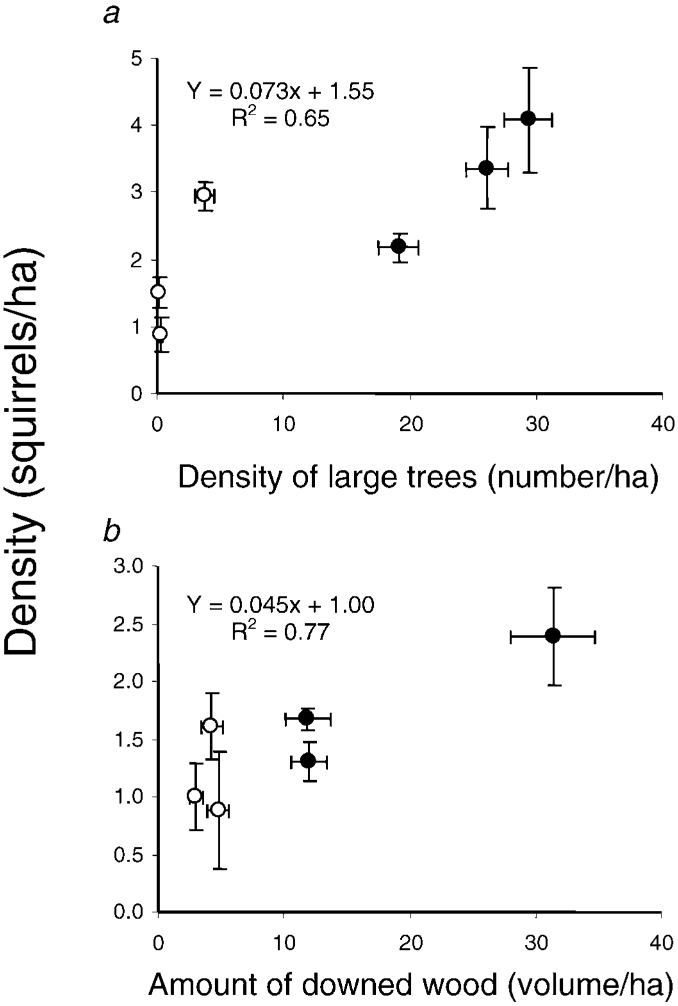

FIG. 1.—Relationship between a) autumn density of *Glaucomys sabrinus* and density of large (>74-cm)-diameter trees and b) spring population density and abundance of downed wood in decay class III (i.e., bark sloughing or absent, heartwood mostly sound, and large branches longer than log diameter present). Decay class based on Sollins (1982). Data points constitute average values ($\bar{X} \pm SE$) for upland old-growth (●) and peatland–mixed-conifer (○) habitats. Standard error bars denote variation in both the predictor (x) and response (y) variables. (Adapted from Smith et al. 2004.)

Nest site selection.—Types and attributes of nests vary geographically, likely reflecting differences in climatic conditions (Bakker and Hastings 2002; Mowrey and Zasada 1984) and energetic demands (Stapp 1992). *G. sabrinus* typically uses 2 types of nests: external leaf nests (dreys) constructed on branches and boles, or nests in cavities (Cowan 1936). Witches' broom, a branch deformity caused by dwarf mistletoe (*Arceuthobium*) or spruce rust (*Chrysomyxa arctostaphyli*) infection, is commonly used as an external nesting substrate (Bakker and Hastings 2002; Cotton and Parker 2000b; Gerrow 1996; Mowrey and Zasada 1984). Also, use of subterranean structures (Bakker and Hastings 2002; Gerrow 1996; Hackett and Pagels 2003) may be more prevalent than previously recognized (Hackett and Pagels 2003). Carey et al. (1997) suggested that this behavior may be more common among females seeking solitary nests in circumstances where cavities may be limited (e.g., young secondary forests). However, Hackett and Pagels (2003) reported that only males used below-ground nests, which did not differ between old and 2nd-growth forests. Within a population, the number of nest trees regularly used by individual *G. sabrinus* can vary from 1 to as many as 11 (Mowrey and Zasada 1984) but the mean number used per month (range 2.3–4.8) is similar between males and females, and differences throughout the range of this species

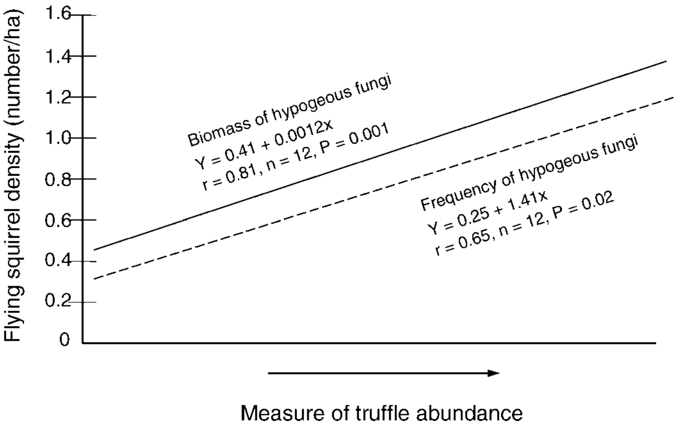

FIG. 2.—Relationship of population density of *Glaucomys sabrinus* with 2 measures of truffle abundance, biomass (solid curve) and frequency (dashed curve), among 12 stands in the northern Oregon Coast Range. (Adapted from Gomez et al. 2005.)

are relatively minor (Carey et al. 1997; Cotton and Parker 2000b; Hackett and Pagels 2003; Menzel et al. 2004; Meyer et al. 2005a; Weigl et al. 1999). Some individuals show strong fidelity to 1 or 2 nests, whereas others have a more uniform utilization distribution (Hackett and Pagels 2003). Number of consecutive nights at a nest (range 1–16) can vary substantially (Mowery and Zasada 1984); however, the majority of individuals remain ≥ 2 days in the same den (Carey et al. 1997; Cotton and Parker 2000b) and mean values ranged from 4.2 to 9.8 days (Hackett and Pagels 2003; Menzel et al. 2004).

The propensity to use cavities varies considerably among (Fig. 3a) and within (Fig. 3b) regions, and seems to be influenced largely by factors that affect the suitability of nest sites (Cotton and Parker 2000b; Hackett and Pagels 2003; Meyer et al. 2005a) or the availability of suitable nesting structures (Carey et al. 1997; Lehmkuhl et al. 2006). In Alaska's coastal rain forests, *G. sabrinus* mostly uses cavities (Bakker and Hastings 2002) but in interior boreal forests external nests are used 3 times more often than cavities (Mowrey and Zasada 1984:353). Within southeastern Alaska, use of external nests (Fig. 3b) can vary from as much as 27% (Bakker and Hastings 2002) to virtually zero (S. Pyare and W. P. Smith, in litt.). Similarly, relatively few external nests were used in the southern Appalachian (Weigl and Osgood 1974) and Sierra Nevada ranges (Wilson et al., in press) and during winter in subboreal forests of British Columbia (Cotton and Parker 2000b). In young forests, however, opportunities to nest in cavities likely are limited in many regions. In the eastern Cascades, the proportion of external nests in mistletoe was higher (and number of cavities lower) in young mixed-conifer stands than in mature forests (Lehmkuhl et al. 2006). Across the range of *G. sabrinus*, cavities typically represent <60% of nests (Fig. 3a; Carey et al. 1997; Gerrow 1996; Hackett and Pagels 2003; Lehmkuhl et al. 2006; Menzel et al. 2004; Rosenberg et al. 1996; Weigl et al. 1999; Wilson and Carey 1996).

Macro- and microhabitat characteristics of den sites vary depending on type of nests, ecological community, and land use or management history (Carey et al. 1997; Cotton and Parker 2000b; Hackett and Pagels 2003; Menzel et al. 2004; Weigl and Osgood 1974). In the central Appalachians, nests were located within 100 m of the ecotone between pure conifer and mixed northern hardwood–conifer stands (Menzel et al. 2004). *G. sabrinus* invariably selected hardwoods, mostly beech (*Fagus*), birch (*Betula*), or maple (*Acer*), as nest trees in the southern Appalachians (Weigl and Osgood 1974) and as cavity trees in central Ontario (Holloway and Malcolm 2007). However, leaf nests are almost exclusively found in conifers (Holloway and Malcolm 2007; Weigl et al. 1999), high in the canopy (Stihler et al. 1987). Elevation, tree height, nest height, and mean diameter at breast height of overstory trees were all greater at leaf nest sites than at cavity sites in the central Appalachians (Menzel et al. 2004). Large hardwood snags are a common nesting structure in eastern forests (Gerrow 1996; Hackett and Pagels 2003; Holloway and Malcolm 2006, 2007), which likely is related to their higher decay rates and the

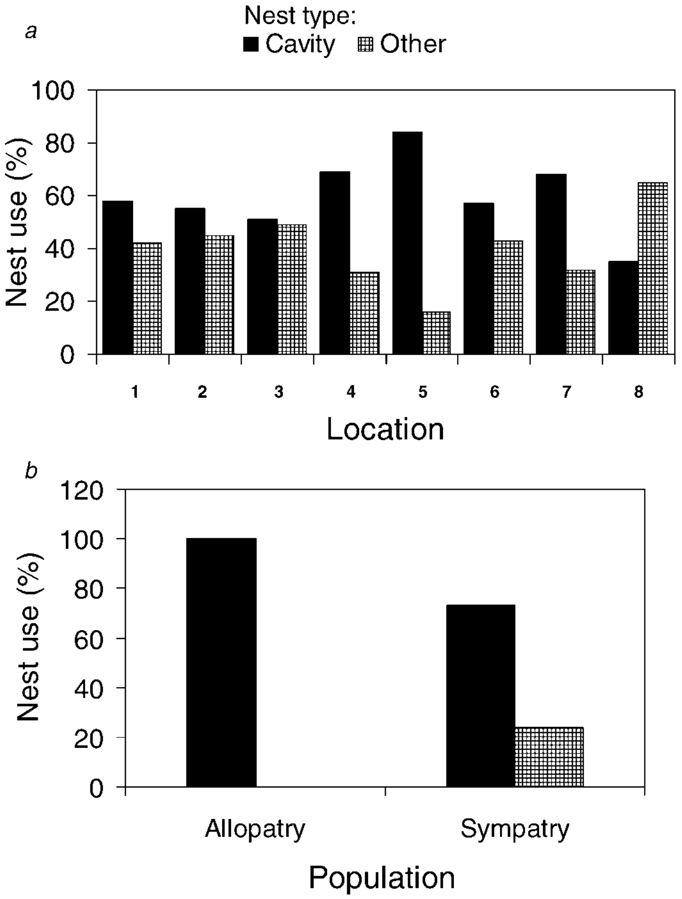

FIG. 3.—Relative use of cavities and external nests (= other) by *Glaucomys sabrinus* a) among various locations in its geographic range: 1 = New Brunswick, Canada (Gerrow 1996); 2 = Cascade Range, Oregon (Rosenberg et al. 1996); 3 = Puget Trough, Washington (Carey et al. 1997); 4 = central Appalachians, United States (Menzel et al. 2004); 5 = interior British Columbia, Canada (Cotton and Parker 2000b); 6 = southern Appalachians, United States (Weigl et al. 1999); 7 = Ontario, Canada (Holloway 2006); 8 = interior Alaska (Mowrey and Zasada 1984); and b) in allopatry (Prince of Wales Island, southeastern Alaska) and in sympatry with *Tamiasciurus hudsonicus* (Mitkof Island, southeastern Alaska).

preferences of primary excavators (Holloway 2006). Nest sites in eastern forests often occur on cooler, more mesic sites such as in spruce stands (Holloway and Malcolm 2007; Menzel et al. 2004; Weigl and Osgood 1974), on northern slopes (Menzel et al. 2004; Payne et al. 1989; but see Hackett and Pagels 2003), in "coves" (Payne et al. 1989), or in areas with large amounts of downed wood (Hackett and Pagels 2003), all of which are favorable conditions for higher decay rates and fungal growth (Loeb et al. 2000). Selection for mesic to wet conditions (Cotton and Parker 2000b) or riparian areas (Meyer et al. 2005a, 2007) also occurs in western coniferous forests. In xeric forests, truffle abundance, biomass, and species composition are highest in riparian areas (Meyer and North 2005).

In western forests, live conifers are the primary structure used for internal and external nests (Carey et al. 1997; Cotton and Parker 2000b; Mowery and Zasada 1984; Wilson et al., in press). This in part might be related to the limited availability of snags of sufficient size because of management history (Bakker and Hastings 2002; Carey et al. 1997; Cotton and Parker 2000b; Lehmkuhl et al. 2006; Meyer et al. 2005a) or growth and decay rates (Mowrey and Zasada 1984). One notable exception is in rain forests of southeastern Alaska, where a snag was more than 3 times more likely than a live tree to be a den (Bakker and Hastings 2002). *G. sabrinus* also used more snags than live trees in Alberta (McDonald 1995) and it uses more snags (relative to availability) in the Sierra Nevada (Meyer et al. 2005a). In southeastern Alaska, the more frequent (60%) use (as well as preference) of snags over live trees (Bakker and Hastings 2002) likely is related to availability; the mean density of large (>50-cm) snags in old-growth spruce–hemlock rain forests (18.0/ha, *SE* = 2.1—W. P. Smith, in litt.) is among the highest recorded in western coniferous forests (Carey et al. 1997).

Nevertheless, there are circumstances of *G. sabrinus* preferring cavities in live trees over snags (Carey et al. 1997; Cotton and Parker 2000b). Furthermore, Carey et al. (1997) suggested that live trees might be more suitable as nesting structures because the dense canopy overhead provides protection from weather, hiding cover and structural complexity for predator avoidance, and because live trees persist longer than snags. In southeastern Alaska, nest sites were characterized by features highly correlated with the presence of cavities (snags, conks, and bole entries), external nesting structures (witches' broom), or large-diameter trees (Bakker and Hastings 2002). In fact, regardless of region or forest type, *G. sabrinus* selects den trees (live and snags) that are older, larger, and taller than what is randomly available throughout the stand (Bakker and Hastings 2002; Cotton and Parker 2000b; Menzel et al. 2004; Wilson et al., in press). Larger live trees and snags likely provide more suitable cavities, greater thermal insulation, reduced predation risk, and greater biomass of arboreal forage lichens (Meyer et al. 2005a).

The benefits of cavities over external nests remain uncertain (Carey et al. 1997). Cavities ostensibly provide better protection from inclement weather (Carey et al. 1997; Maser et al. 1981; Menzel et al. 2004) and are more predator-proof (Carey and Sanderson 1981). Because cavities are more resistant to wind and precipitation, they are thought to be thermally superior to stick nests (Carey and Sanderson 1981). Bakker and Hastings (2002) reported that *G. sabrinus* in southeastern Alaska selected features associated with more-weatherproof cavities. And in interior British Columbia during winter, *G. sabrinus* mostly used cavities (Cotton and Parker 2000b). However, in interior Alaska *G. sabrinus* on average used external nests ($\bar{X} = 6.4$) more frequently than cavities ($\bar{X} = 2.1$). Moreover, when air temperature drops abruptly, solitary individuals often move from cavity nests to aggregations in witches' broom (Mowrey and Zasada 1984). Thus, in forests where tree diameters (and presumably nest chambers) are too small to accommodate cohabitation, perhaps the benefits of reduced energy expenditure from aggregations (Stapp et al. 1991) are greater than what might be expected from differences between external nests and cavities in thermal properties. Den trees in boreal forest of interior Alaska had diameters that averaged <33 cm in diameter at breast height (Mowrey and Zasada 1984). In forests where larger (>50 cm in diameter at breast height) trees are available, *G. sabrinus* seems to use primarily cavities (Bakker and Hastings 2002; Carey et al. 1997; Gerrow 1996; Weigl and Osgood 1974), especially during winter (Cotton and Parker 2000b; Maser et al. 1981), and group denning (2–4 squirrels/den) commonly occurs throughout the year (Carey et al. 1997). Nonetheless, in coastal regions where annual precipitation is relatively high and mostly rainfall, *G. sabrinus* uses primarily cavities year-round (Bakker and Hastings 2002; Carey et al. 1997; W. P. Smith and S. Pyare, in litt.) presumably to reduce risk to hypothermia, which seems to be the primary cause of mortality of individuals exposed to wet ambient conditions (W. P. Smith and S. Pyare, in litt.). Thus, heavy precipitation may render exposed outside nests uninhabitable, particularly during winter (Cowan 1936).

Alternatively, cavities may provide better protection from predators, which may explain why females almost exclusively use cavities (or nest boxes) for natal dens when they are available (Carey et al. 1997; Holloway 2006; Ransome and Sullivan 2004). Or, *G. sabrinus* may select den sites because of benefits unrelated directly to the attributes of trees or nest types. Vernes et al. (2004) reported that *G. sabrinus* selected den sites that were near red squirrel (*Tamiasciurus hudsonicus*) middens, and Currah et al. (2000) suggested that the winter overlap in diet between these 2 species was due to *G. sabrinus* raiding the middens of *T. hudsonicus*. Core areas of use in eastern forests were centered on food patches (hypogeous fungi) or foraging areas rather than dens (Holloway 2006; Menzel et al. 2006b), and *G sabrinus* may select den sites according to the availability of nearby food resources (Hackett and Pagels 2003; Menzel et al. 2004; Payne at al. 1989; Weigl et al. 1999). Also, proximity to a permanent water source is a significant correlate of nest sites in both western coniferous forests (Meyer et al. 2005a) and Appalachian mixed hardwood–coniferous forests (Hackett and Pagels 2003).

Spatial ecology.—Average daily movements determined from successive locations from mark–recapture studies (Ransome and Sullivan 2003; Smith et al. 2003) and from radiotelemetry (Martin and Anthony 1999) typically are <100 m and rarely differ between sexes or among habitats. Mean maximum distance moved can be highly variable among individuals (range 20–240 m—Vernes et al. 2004) and occasionally males (153.4, *SE* = 27.7 m) and females (105.6, *SE* = 53.5 m) will differ (Holloway 2006). In forests of the northern Sierra Nevada, females moved greater distances than males while foraging, although movements were similar across 4 activity periods and distance from the nearest nest tree was similar between sexes (Wilson et al., in press). However, mean maximum distance moved is surprisingly similar across a wide range of habitats regardless of sex, with means varying from 60 to 150 m (Smith et al. 2003).

Distance moved between dens also is highly variable (Cotton and Parker 2000b; Hackett and Pagels 2003) and can be as great as 1 km (Carey et al. 1997). In western forests, both Carey et al. (1997) and Meyer et al. (2005a) reported that mean distance between successive nest sites was smaller for females (range 68–107 m) than for males (range 114–212 m). The combined (male + female) means for populations in the central Appalachians (164 m—Hackett and Pagels 2003) and British Columbia (163 m—Cotton and Parker 2000b) were similar. Movements, home-range size, and use of space appear to be influenced mostly by availability of food resources (Holloway 2006; Menzel et al. 2006b; Smith et al. 2003), primarily the distribution of truffles (Gomez et al. 2005; Pyare and Longland 2002). Captures are higher at sites where truffles are more abundant (Pyare and Longland 2002) and female movements on average (mean maximum distance moved) decline as truffle abundance increases across sites (Gomez et al. 2005). The larger home ranges and a 10-fold difference between core nest area and home-range size in northern Sierra Nevada suggest that *G. sabrinus* must forage over larger areas (Wilson et al., in press). Forays by males can exceed 1.5 km (Weigl et al. 1999), and daily movements of several kilometers have been recorded for males during the breeding season and for juveniles while dispersing (W. P. Smith, in litt.).

The mean (± *SE*) size of core nest areas (area enclosed by an animal's nest trees—Cotton and Parker 2000b) ranges from 0.9 ± 0.29 ha to 2.7 ± 0.62 ha, with males having larger (2.2 compared to 0.9 ha—Meyer et al. 2005a) and more variable (range = 0.9–8.6 ha—Cotton and Parker 2000b) nest areas than females. Home-range (including forage areas) size varies with habitat quality (based on population density, survival, and recruitment), with the home ranges of individuals occupying poorer habitat averaging 85% larger than individuals in higher-quality habitat (Lehmkuhl et al. 2006). The largest home range (59.8 ha) recorded for this species was recorded in the highly fragmented and degraded habitat of the central Appalachians (Menzel et al. 2006b). Mean sizes of home ranges of males (3.7–59.8 ha) typically are larger than those of females (3.4–15.3 ha), but home-range size also is influenced by season (Weigl et al. 1999) and forest type (Holloway 2006; Lehmkuhl et al. 2006; Menzel et al. 2006b; Smith et al. 2003). Typically, home ranges of females are <5 ha (e.g., Martin and Anthony 1999); home ranges of males usually are <10 ha, except in winter when they can be much larger (Menzel et al. 2006b). Mean core area (50% kernel utilization contour—Holloway 2006) in central Ontario was similar between females (1.6 ha) and males (2.6 ha) and comparable in size to core nest areas reported in other portions of the range of this species, suggesting that the disparity in home-range size that occasionally occurs between sexes is related to movements associated with foraging (Gomez et al. 2005; Holloway 2006; Pyare and Longland 2002) or breeding (W. P. Smith, in litt.).

Foraging ecology.—Although *G. sabrinus* inhabits conifer forests throughout its range, conifer seeds are not a major food item (Smith et al. 2003). Rather, *G. sabrinus* is primarily mycophagous and consumes a wide variety of fungi (Maser et al. 1986), especially hypogeous, mycorrhizal fungi (truffles), particularly during snow-free periods (Hall 1991; Pyare et al. 2002). Furthermore, *G. sabrinus* prefers truffles over other food items in feeding trials (Zabel and Waters 1997) and uses truffles relatively more often than would be expected from availability across the forest (Cazares et al. 1999; Lehmkuhl et al. 2004). Arboreal lichens also are a common (≤49% in central Appalachians) food (Hall 1991; McKeever 1960; Mitchell 2001; Pyare et al. 2002), particularly during winter, but not everywhere (Currah et al. 2000). Diet composition and diversity vary depending on forest type (Holloway 2006; Lehmkuhl et al. 2004; Pyare et al. 2002; Weigl 2007; Weigl et al. 1999), ecological community (Carey et al. 1999; Holloway 2006; Maser and Maser 1988; Weigl 1978), and season (Cazares et al. 1999; Currah et al. 2000; McKeever 1960; Mitchell 2001; Rosentreter et al. 1997; Vernes et al. 2004).

The fundamental food niche of *G. sabrinus* seems quite broad and its diet can include a wide range of plant and animal items (Smith et al. 2003) that change with availability (Mitchell 2001; Pyare et al. 2002; Weigl et al. 1999). In any region, however, the diet or other niche dimensions of *G. sabrinus* can be narrow or highly specialized (Carey 1991, 1996) and differ substantially from other portions of its range (Fig. 4). Individuals in southeastern Alaska consumed truffles less frequently, consumed fewer genera of truffles, and consumed vascular vegetation, lichens, and mushrooms more frequently than did *G. sabrinus* in other geographic areas (Pyare et al. 2002). Moreover, regional variation and diversity of its diet likely have been underestimated because microscopic examination of fecal pellets does not adequately characterize thoroughly digested food items, such as fruits, nuts, seeds, and vegetation (Hall 1991; Thysell et al. 1997). *G. sabrinus* seems to rely on fungi, largely truffles, in western coniferous forests (Cazares et al. 1999; Currah et al. 2000; Meyer and North 2005; Rosentreter et al. 1997), especially in the Pacific Northwest (Carey 1995; Carey et al. 1999; Hall 1991; Maser et al. 1985, 1986; Lehmkuhl et al. 2004; Thysell et al. 1997; Waters et al. 2000). This species depends less on truffles in the eastern portion of its range (Holloway 2006; Mitchell 2001; Vernes et al. 2004), or where plant understories are more diverse (Loeb et al. 2000; Weigl 2007; Weigl et al. 1999) or small mammal communities are less diverse (Pyare et al. 2002). However, factors that determine the diet of local populations remain unknown.

Although much has been learned about the diet of *G. sabrinus*, little is known about its foraging behavior and ecology (Pyare and Longland 2001a); specifically, interrelationships among habitat structure, food resources, and use of space remain poorly understood (Pyare and Longland 2002). Indirect evidence suggests that *G. sabrinus* spends considerable time in search of and digging for truffle fruiting bodies (sporocarps), which typically occur 5–15 cm below the surface of the forest floor. Furthermore, the distribution of truffles within forests is patchy because suitable habitat is patchy (Smith et al. 2000). Truffles are less abundant in xeric forest types (Lehmkuhl et al. 2004), where fungal communities may be concentrated in riparian areas (Meyer and North 2005). In the southern Appalachians, truffles are more abundant at higher elevations or on northerly aspects, where spruce (*Picea*)–fir (*Abies*) or mixed spruce–fir–hardwood forests predominate (Loeb et al. 2000). Truffles (and most fungi) favor cool, mesic to wet microenvironments with relatively large amounts of decayed logs or coarse woody debris across the forest floor (Amaranthus et al. 1994; Carey et al. 1999; Lehmkuhl et al. 2004; Smith et al. 2000; Waters et al. 1997). For that reason, fungal communities purportedly achieve their greatest abundance (total biomass) and highest diversity in old growth, as compared to younger, managed forests (North et al. 1997). Furthermore, a greater percentage of unique taxa occur in old growth than in younger, managed Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest (Smith et al. 2002). However, abundance, species composition, and species richness of fungal communities (especially the prevalence of truffles) vary seasonally, which likely contributes to the temporal variability of diets of *G. sabrinus* (Mitchell 2001; North et al. 1997; Vernes et al. 2004). Still, the consistency with which *G. sabrinus* consumes truffles throughout its range year-round indicates that hypogeous fungi are a vital food resource (Currah et al. 2000; North et al. 1997; Rosentreter et al. 1997; Vernes et al. 2004).

Furthermore, movements (Gomez et al. 2005; Menzel et al. 2006b) and patterns of habitat use at multiple spatial scales (Ford et al. 2004; Meyer et al. 2005a; Pyare and Longland 2002) suggest that *G. sabrinus* tracks short-term temporal and spatial dynamics of truffle fruiting bodies (sporocarps), and perhaps other food resources. Indirect evidence comes from observations that captures of *G. sabrinus* are predicted by habitat conditions (e.g., coarse woody debris) typical of abundant fungal communities (Carey et al. 1999; Meyer et al. 2007). In at least 1 study, however, captures of *G. sabrinus* were unrelated to habitat correlates of abundant fungal communities (Pyare and Longland 2002). Rather, individuals were captured more often where there was direct evidence (i.e., animal diggings or sampled plots) of sporocarps in the immediate vicinity of understory cover. Truffles are an ephemeral food resource, and at any time not all favorable habitats will have fruiting bodies available (Fogel 1976). Nonetheless, flying squirrels choose to forage in microhabitats with abundant understory cover (Pyare and Longland 2002; Rosenberg and Anthony 1992; Smith et al. 2005), presumably to reduce predation risk or to opportunistically feed on other food items (Smith et al. 2005).

The mechanisms that underlie truffle detection remain unclear, but recent field study and laboratory experiments suggest that there may be 3 interacting elements: cognitive mapping or ability to recall locations of food patches, olfactory capability that facilitates detecting hypogeous fungi with specific chemical signatures, and microhabitat features (coarse woody debris) that serve as fine-scale cues for locating sporocarps (Pyare and Longland 2001a, 2002). Feeding trials demonstrated that *G. sabrinus* spends the vast majority of time searching sites where truffles are buried. Also, time allocated to a treatment condition was consistently higher at sites where a decayed log was present (truffle + log) than at sites with truffles alone. And detection rate (truffles/min) was significantly higher at truffle + log treatment sites than at sites with just buried truffles. Furthermore, chemical analysis revealed that truffles used in the feeding trials possessed highly volatile compounds capable of attracting mammals (Pyare and Longland 2001a). The capacity to memorize or recall locations has not been demonstrated conclusively; however, several lines of indirect evidence suggest that *G. sabrinus* has some cognitive mapping ability, including fine-scale patterns of habitat use (Pyare and Longland 2002) and the capacity to consistently relocate other key resources (e.g., den sites—Mowrey and Zasada 1984). Nevertheless, the expected benefits of timely visits to fungal-rich microhabitats are quite high, because >80% of locations with fruiting bodies in one year have sporocarps present at about the same time (±2 weeks) in following years (Pyare and Longland 2001a). That *G. sabrinus* uses decayed logs as a microhabitat cue for locating sporocarps is not surprising given the ecological association between

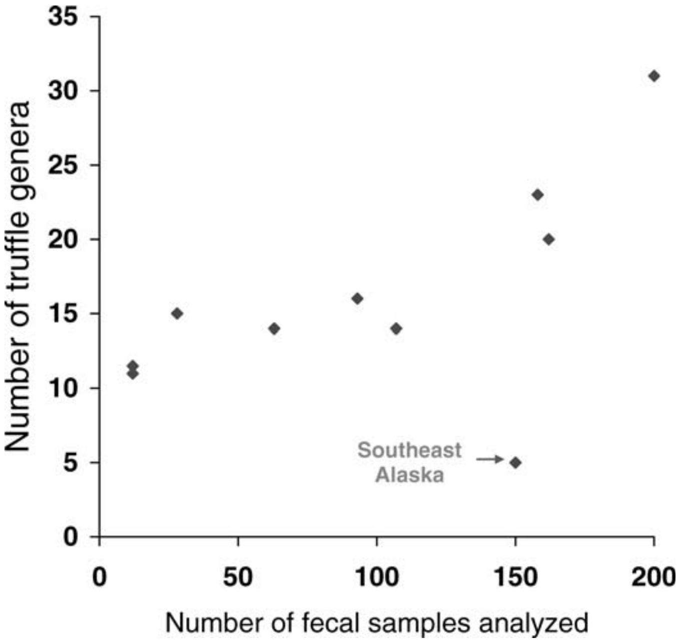

FIG. 4.—Comparison of truffle diversity in diet (number of truffle genera detected in fecal samples) of *Glaucomys sabrinus* in southeastern Alaska with other populations in western North America. The correlation coefficient (*r*) excluding data from southeastern Alaska is 0.90. Data are from Carey et al. (1999), Cazares et al. (1999), Colgan et al. (1997), Hall (1991), Maser et al. (1985, 1986), Pyare and Longland (2001b), Pyare et al. (2002), and Rosentreter et al. 1997. (Adapted from Pyare et al. 2002.)

TABLE 2.—Sex ratio (males/females) and recruitment (number of young per adult female) in populations of *Glaucomys sabrinus*.

Forest type	Sex ratio	Percentage females reproductive	Recruitment[a]	Source
Douglas-fir (2nd growth)	1.0	0.90	0.72[b]	Villa et al. 1999.
Conifer−northern hardwood	1.4	0.83	1.4	Reynolds et al. 1999
Conifer−northern hardwood	1.2	0.59[b]	0.33[b]	Weigl et al. 1999
Aspen−black spruce	1.2	NA[c]	1.30[b]	Davis 1963
Peatland−mixed conifer	1.7	0.75	0.41[b]	Smith and Nichols 2003
Sitka spruce−western hemlock	1.1	0.75	0.50[b]	Smith and Nichols 2003
Fir (old)	1.0	NA	0.97[b]	Waters and Zabel 1995
Fir (young)	1.2	NA	0.84[b]	Waters and Zabel 1995
Douglas-fir (old growth)	0.9[b]	NA	0.40[b]	Rosenberg and Anthony 1992
Douglas-fir (2nd growth)	0.6[b]	NA	0.33[b]	Rosenberg and Anthony 1992
Ponderosa pine	1.1	NA	0.28	Lehmkuhl et al. 2006
Mixed conifer (young)	1.0	NA	0.35	Lehmkuhl et al. 2006
Mixed conifer (old)	1.0	NA	0.37	Lehmkuhl et al. 2006
Western hemlock (young)	1.0	0.29	1.62[b]	Carey 1995
Western hemlock (old)	0.8	0.31	0.62[b]	Carey 1995

[a] Ratio of juveniles to adults in the autumn population (includes births and immigration).
[b] Estimated from data in source.
[c] NA = not available.

fungal-rich communities and coarse woody debris (Amaranthus et al. 1994; Carey et al. 1999, 2002; Smith et al. 2000).

POPULATION AND COMMUNITY DYNAMICS

Population attributes.—Much of what is known about populations of *G. sabrinus* comes from the upper Pacific coast (Carey 1995; Carey et al. 1999; Lehmkuhl et al. 2006; Ransome and Sullivan 2003; Smith and Nichols 2003; Villa et al. 1999; Waters and Zabel 1995) and the Appalachians (Reynolds et al. 1999; Weigl et al. 1999). *G. sabrinus* typically produces 1 litter/year, typically in late spring–early summer (Cowan 1936; Well-Gosling and Heaney 1984). Litter size averaged 2.5 ± 0.82 *SE* in the Appalachians (Reynolds et al. 1999) and 2.3 ± 0.19 in the Pacific Northwest (Villa et al. 1999), where younger females gave birth to smaller litters ($\bar{X} = 1.6 \pm 0.24$) than older females ($\bar{X} = 2.9 \pm 0.29$). Sex ratios usually do not depart from unity (Table 2), but Smith and Nichols (2003) recorded male-biased ratios in old-growth peatland–mixed-conifer rain forest of southeastern Alaska and Rosenberg and Anthony (1992) reported female-biased sex ratios in 2nd-growth Douglas-fir forest of western Oregon. Although *G. sabrinus* undergoes density-dependent population growth (Fryxell et al. 1998; Lehmkuhl et al. 2006), populations can fluctuate widely among years (Fig. 5). Furthermore, there is evidence of autocorrelation between population densities (4-year lag), indicative of periodic population dynamics (Fryxell et al. 1998). Little is known about dispersal (Smith et al. 2003; Wells-Gosling and Heaney 1984). In heavily managed landscapes of southeastern Alaska, many juveniles remain near their apparent natal area through the winter and into the following spring, whereas some move straight-line distances of several hundred meters during autumn (W. P. Smith and S. Pyare, in litt.). Adult males in breeding condition will make daily long-distance ($\geq$2-km) movements during spring, presumably in search of estrous females. In unmanaged landscapes, juveniles have the ability in early autumn of moving several kilometers per day; in intensively managed landscapes, straight-line movements of juveniles (based on radiotelemetry) from putative natal areas were $<$2 km (W. P. Smith and S. Pyare, in litt.).

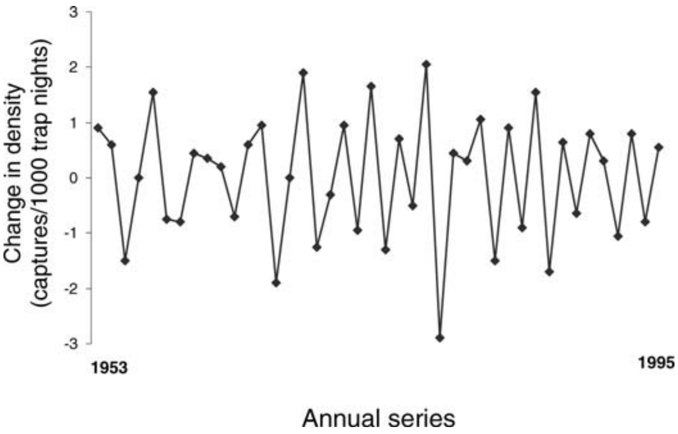

FIG. 5.—Annual changes in population density of *Glaucomys sabrinus* as indexed by live captures per 1,000 trap nights in Algonquin Park, Ontario, Canada, between 1952 and 1995 (Fryxell et al. 1998). (No captures were recorded in 1952.)

The population density of *G. sabrinus* is not a reliable indicator of habitat quality. Smith and Nichols (2003) concluded that peatland–mixed-conifer forests likely sustain populations of *G. sabrinus* because densities were comparable to those in old-growth forests in the Pacific Northwest (Table 1). In addition, select population attributes in peatland–mixed conifer were generally similar to those in Sitka spruce–western hemlock forest, the primary habitat of this species in southeastern Alaska (Figs. 6a and 6b; Smith and Nichols 2003). However, when demographic variability was explicitly considered in simulations of a simple birth–death population model (Smith and Person 2007), the majority of per capita

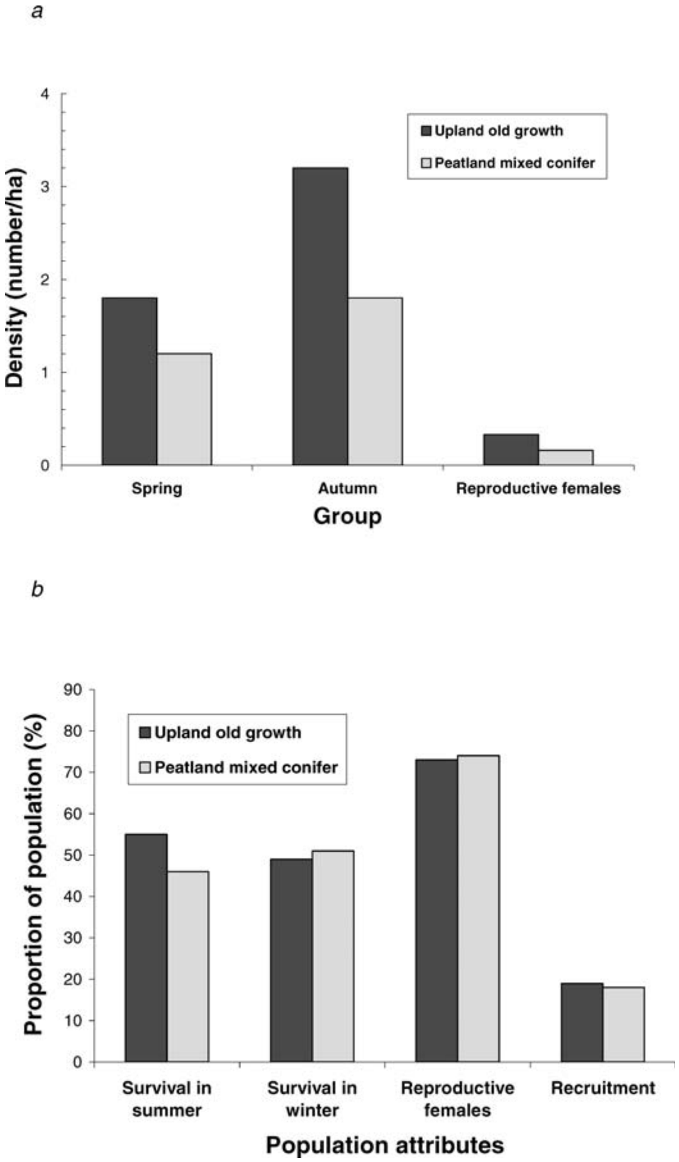

FIG. 6.—a) Spring and autumn population density and density of reproductive females × 10 and b) winter and summer survival, percentage reproductive females, and recruitment of *Glaucomys sabrinus* in old-growth Sitka spruce—western hemlock (upland old growth) and peatland–mixed-conifer forests in southeastern Alaska between 1998 and 2000.

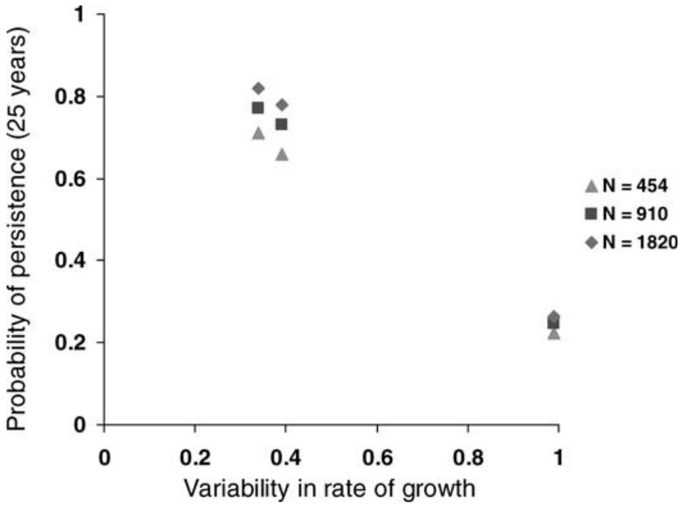

FIG. 7.—Probability of persistence (without immigration) for a period of 25 years of populations of *Glaucomys sabrinus* in fragments of old-growth Sitka spruce–western hemlock forests for 3 population sizes (*N*) relative to demographic variability (*v*) or total population size (adapted from Smith and Person 2007).

population growth values (*r*) were <0, suggesting that in some years peatland–mixed conifer was a sink (sensu Pulliam 1988). Lehmkuhl et al. (2006) reported similar findings for ponderosa pine (*Pinus ponderosa*) forest of the eastern Cascades, which had population densities of *G. sabrinus* comparable to that reported for some old-growth forests of western Oregon and Washington (Table 1), but which had finite rates of growth (λ) that were <1. Furthermore, according to simulations of a population model based strictly on demographic parameters, the probability of *G. sabrinus* persisting (without immigration) in fragments of primary habitat is much more sensitive to demographic variability than to population size (Fig. 7). The modeled effect of demographic variability on population viability increases disproportionally as the time horizon increases (Smith and Person 2007).

Dispersal.—The state of knowledge regarding dispersal of *G. sabrinus* includes mostly information about flying squirrel anatomy (Scheibe et al. 2007), or about habitat and landscape structure and how they influence locomotor ability or performance (Scheibe et al. 2006, 2007; Vernes 2001). There are a few accounts of *G. sabrinus* moving several kilometers over relatively short time periods, but little is known about long-distance movements (Weigl et al. 1999). In the Pacific Northwest, adult males evidently move great lengths in search of mates (Wilson 2003). However, large clear-cuts and dense, young 2nd-growth stands are barriers to *G. sabrinus* undergoing natal dispersal or searching for females for at least 20–35 years after harvest (Wilson 2003). Ongoing studies in southeastern Alaska (on cost of transport, behavior, and movement capability) have documented daily movements of several kilometers for males during the breeding season and for juveniles while dispersing from putative natal areas (W. P. Smith, in litt.). Movement rates through recent (<5-year-old) clear-cuts (≈10 m/min) averaged an order of magnitude lower than in old-growth forest, which was 2 times higher than in young, 2nd-growth stands (W. P. Smith and S. Pyare, in litt.). In the southern Appalachians, typical movement rates ranged from 1,080 to 1,440 m/h for males and 1,008 m/h for females (Weigl et al. 1999).

Most of what is known regarding flying squirrel dispersal comes from studies of *P. volans*, which is somewhat more arboreal than *G. sabrinus*. Unlike *G. sabrinus*, which spends considerable time foraging on the forest floor (Pyare and Longland 2001a, 2002), *P. volans* obtains its essential resources in the forest canopy (Reunanen et al. 2000). It rarely visits the forest floor, only running along the ground for short distances when canopy gaps exceed its gliding capability (Selonen and Hanski 2003). Still, *P. volans* is capable of dispersing long distances in fragmented landscapes (Selonen and Hanski 2004). It uses woodland strips for interpatch movements, but also uses the matrix with trees and is able to cross narrow, treeless gaps (Selonen and Hanski 2003). Individual behavioral differences suggest decisions to disperse short or long distances occur before the onset of dispersal. Surprisingly, long-distance dispersers explored the area around their natal site less than short-distance dispersers; exploration by philopatric individuals was similar to dispersers (Selonen and Hanski 2006).

Community relations.—Throughout its range, *G. sabrinus* performs an essential ecological function within forest communities (Caldwell et al. 2005), most notably in the Pacific Northwest (Maser and Maser 1988). The extent to which this facultative role is unique within a community depends on the assortment of ectomycorrhizal fungi the squirrel consumes and the small mammal assemblage (Pyare and Longland 2001b). Interspecific variation among mycophagists in patterns of home range, habitat use, fungal consumption, vagility, and digestive physiology facilitate nonredundant dispersal of ectomycorrhizal fungi. Still, *G. sabrinus* consumes the greatest variety of ectomycorrhizal fungi and therefore has the greatest potential to influence forest community dynamics (Pyare and Longland 2001b). Furthermore, where ecological communities of arboreal and semiarboreal rodents are diverse, such as in the Pacific Northwest (Carey 1991; Verts and Carraway 1998), *G. sabrinus* is a highly specialized mycophagist and its population density and microhabitat use are correlated with structural features (e.g., coarse woody debris) typical of old forest and fungal-rich communities (Amaranthus et al. 1994; Carey et al. 1999; Smith et al. 2000; Waters et al. 1997). In contrast, southeastern Alaska has a depauperate small mammal fauna (Smith 2005), *G. sabrinus* has a less specialized diet (Pyare et al. 2002), and its habitat relations differ from those of populations in the Pacific Northwest (Smith et al. 2004, 2005). Similarly, Mitchell (2001) reported a more varied diet (compared to populations in the Pacific Northwest) for *G. sabrinus* in forest communities of the Appalachians, where the diversity of arboreal rodents is notably less than that in forest communities of the Pacific Northwest (Smith et al. 2003, 2004; Weigl et al. 1999). The extent to which fungal community diversity is directly linked to arboreal small mammal diversity remains unclear, but biological variation among mycophagists that facilitates nonredundant dispersal of fungal spores presumably promotes ecological opportunities for radiation among ectomycorrhizal fungi. Clearly, the number of truffle genera sampled by *G. sabrinus* in southeastern Alaska (5) was much less than that (32) recorded for populations in the Pacific Northwest (Fig. 4; Pyare et al. 2002). This apparent relationship between small mammal assemblages, ectomycorrhizal fungal communities, and diet and habitat use of *G. sabrinus* suggest a coevolved forest community structure that underpins the ecology of populations of *G. sabrinus* throughout its range.

Glaucomys sabrinus also is an essential link in the food chain of forest communities (Carey 2000). In the Pacific Northwest, it is the primary prey of the northern spotted owl (*Strix occidentalis caurina*—Carey et al. 1992; Forsman et al. 2001) and California spotted owl (*S. o. occidentalis*—Munton et al. 1998; Verner et al. 1992) and common prey of weasels (*Mustela*—Wilson and Carey 1996) and American marten (*Martes americana*—Bull 2000). In central Ontario, the population dynamics of American marten are closely linked to population density of *G. sabrinus* (Fryxell et al. 1999). *G. sabrinus* also is common prey of northern goshawks (*Accipiter gentilis*) during breeding in the Pacific Northwest (Reynolds and Meslow 1984), and there is little reason to doubt that it is a regular prey item of goshawks and other forest specialists elsewhere, especially across more northern latitudes where the daylight regime facilitates hunting throughout much of the day (e.g., Lewis 2001). The ecological community of small mammals and other vertebrate prey species likely influences the population dynamics of *G. sabrinus*, which can change with seasonal differences in predation pressure (Bull 2000) or have a stabilizing influence on predator populations that ultimately determines interannual variation in predation pressure (Fryxell et al. 1999). Abundant and diverse prey communities likely facilitate specialization by predators, as in the example of northern spotted owls in the Pacific Northwest (Carey et al. 1992; Forsman et al. 2001). Prey-rich forest communities likely have a greater diversity of mammalian or avian predators, which ostensibly reinforces food partitioning and prey specialization to reduce competition (Reynolds and Meslow 1984). Nevertheless, the persistence of viable and well-distributed populations of *G. sabrinus* has significant implications for fundamental ecological processes in many forest communities, which is why it was proposed as an indicator of ecosystem management in the Pacific Northwest (Carey 2000).

Direct interspecific competition has not been widely reported, but because of similarities in behavior and shared vital resources, *G. volans* potentially is a formidable competitor (Weigl 2007; Weigl et al. 1999). Although the ranges of *G. volans* and *G. sabrinus* overlap in eastern North America (Arbogast 1999, 2007:figure 2; Hall 1981), coexistence varies in time and space (Bowman et al. 2005) and the 2 species are rarely syntopic in the Appalachians (Weigl 2007; Weigl and Osgood 1974; Weigl et al. 1999). It is unlikely that habitat preferences completely explain their distributions (Weigl 1978, 2007; Payne et al. 1989). Some investigators suggest that *G. sabrinus* in the southern Appalachians might require both conifer and hardwood forest components (Payne et al. 1989; Weigl et al. 1999). There are multiple examples where *G. sabrinus* occupies hardwood forest when *G. volans* is absent (Bowman et al. 2005; Holloway 2006; Weigl 2007; Weigl et al. 1999). Furthermore, *G. volans* reputedly interferes with use of key resources by *G. sabrinus* in hardwood forests of the southern Appalachians (Muul 1968; Weigl 1978; Weigl et al. 1999). More importantly, habitat segregation is not uniform across the entire region of overlap; the probability of syntopy increases with increasing latitude (Bowman et al. 2005; Holloway 2006; Pagels et al. 1990). Still, there is evidence of competitive interactions at northern latitudes, because densities appear to be inversely related across the region of overlap (Bowman et al. 2005; Holloway 2006; Holloway and Malcolm 2006; Weigl 2007; Weigl et al. 1999).

The distributional patterns suggest it may be the presence of *G. volans* that determines the relative abundance of *G. sabrinus* (Bowman et al. 2005; Weigl et al. 1999). *G. sabrinus* seems more tolerant of cold temperatures than *G. volans* (Weigl et al. 1999), which likely explains the latter's reliance on cavities for nesting (Muul 1968; but see Holloway and Malcolm 2006), its propensity for aggregating to reduce winter energy expenditure (Stapp 1992), and its northern range limit (Bowman et al. 2005). But it likely is not cold temperature alone that defines the northern limit of *G. volans*, but rather, an energetic bottleneck that occurs as a result of periods of concurrent cold temperature and mast failure. This phenomenon appears to underpin a range boundary dynamic that also influences the local and regional abundance of *G. sabrinus* in Ontario (Bowman et al. 2005). In fact, it probably is one example of a broader-scale pattern precipitated by a warming trend that affects northern and elevational limits of *G. volans* at more southern latitudes, such as in the Appalachians (Payne et al. 1989; Weigl 2007; Weigl et al. 1999).

However, the distribution and relative abundance of *G. sabrinus* in the region of range overlap are only indirectly related to factors constraining the range of *G. volans*. Arguably, additional ecological factors must be responsible for the observed reciprocal relationship in density in Ontario (Bowman et al. 2005) and the exclusion of *G. sabrinus* from hardwood forests at more southern latitudes (Weigl 2007, Weigl et al. 1999). One proposed mechanism is through interference competition of essential resources (Weigl 2007). *G. volans* is more aggressive than *G. sabrinus* and likely prevents the latter from using cavities in hardwood forests through agonistic interactions (Muul 1968; Weigl 1978). Female *G. sabrinus* rely on cavities for natal dens (Carey et al. 1997), and the availability of suitable natal dens likely limits reproduction by females (Carey 2002; Ransome and Sullivan 2004; Smith et al. 2004). In southeastern Alaska, lower densities of populations and breeding females of *G. sabrinus* occurred in peatland–mixed-conifer forest (Smith and Nichols 2003), a habitat in which large tree and snag density and population growth were an order of magnitude lower than in its primary habitat (Smith et al. 2004).

Alternatively, *G. sabrinus* may be excluded from hardwood forests through parasite-mediated competition (Weigl 2007; Weigl et al. 1999). Furthermore, aggressive evictions of *G. sabrinus* by *G. volans* likely further reduce the availability of cavities by displacing *G. sabrinus* from cavities (Muul 1968; Weigl 2007; Weigl et al. 1999) that subsequently become unsuitable because of the risk of infection (Pauli et al. 2004). Nonetheless, a significant difference between congeners in their tolerance of infection could produce a pattern of increasing syntopy with increasing latitude because the parasitic nematode *Strongyloides robustus* has a low tolerance for cold (Weigl et al. 1999). At more northern latitudes, where coexistence occurs more often (Bowman et al. 2005; Holloway 2006), the frequency of infections with *S. robustus* in flying squirrels is lower, especially in *G. sabrinus* (Pauli et al. 2004). Overall, patterns of varying and reciprocal densities across landscapes of boreal forest (e.g., Bowman et al. 2005; Holloway 2006) likely are a result of interactions among energetic bottlenecks and range boundary dynamics of *G. volans*, which determines when and where sympatry occurs and ultimately the subsequent interspecific interactions that reduce survival or reproduction in *G. sabrinus*.

The potential for competition also exists with several other arboreal rodents, especially in the Pacific Northwest (Carey 1989, 1991, 1995). Yet, relatively little resource overlap occurs because species segregate according to forest type (Carey 1989) or microhabitat (Carey et al. 1999; Holloway and Malcolm 2006). In the southern Sierra Nevada (where small mammal communities are relatively depauperate), substantial dietary overlap of fungi occurs throughout the year between *G. sabrinus* and *Tamias speciosus*, the lodgepole chipmunk, particularly in frequently consumed taxa (Meyer et al. 2005b). The American red squirrel (*T. hudsonicus*), which overlaps much of the northern and eastern range of *G. sabrinus*, and Douglas's squirrel (*T. douglasii*), in the Pacific Northwest (Hall 1981), likely share resources with *G. sabrinus* (Maser and Maser 1988; Pyare and Longland 2001b; Smith et al. 2003). *T. douglasii*, in particular, uses fungi extensively (Maser and Maser 1988), and in the Sierra Nevada its consumption of hypogeous fungi is similar to that of *G. sabrinus* (Pyare and Longland 2001b). However, of the many studies that included both species (Carey 1989, 1995, 2001; Carey et al. 1999; Holloway 2006; Holloway and Malcolm 2006; Ransome and Sullivan 2002, 2003, 2004; Ransome et al. 2004) few reported evidence of competition between either species of *Tamiasciurus* and *G. sabrinus*. Carey (1995) recorded the greatest abundance of *G. sabrinus* where densities of *T. douglasii* were lowest, but abundance of *T. douglasii* might have been influenced also by the low density of the chipmunk *Tamias townsendii*, a species that specializes on conifer seeds and fungi (Carey 1995).

In southeastern Alaska, populations of *G. sabrinus* that were sympatric with *T. hudsonicus* (Mitkof Island) had lower spring and autumn population densities, fewer reproductive females, and lower recruitment than in similar habitat where red squirrels were absent (W. P. Smith, in litt.). The density of *G. sabrinus* explained 76% of the variation in density of *T. hudsonicus*, suggesting that the 2 species had similar habitat requirements. This conclusion is corroborated by observations in Ontario that the 2 species show a strong affinity for similar key habitat features (Holloway and Malcolm 2006). Although the underlying mechanism for patterns in southeastern Alaska remains unclear, the 2 species might compete for cavities, which *G. sabrinus* uses exclusively on Prince of Wales Island. On Mitkof Island, up to 27% of the dens used by *G. sabrinus* were external nests, which provide a poorer thermal microenvironment, especially in coastal rain forests (Bakker and Hastings 2002), and are probably less secure for females with young (Carey et al. 1997). Females of *G. sabrinus* prefer cavities as natal dens, which when limited can reduce the density of reproductive females (Smith et al. 2004) and population growth rate (Smith and Person 2007).

Limiting factors.—Carey (2002) suggested that 3 factors potentially limit populations of *G. sabrinus*: predation;

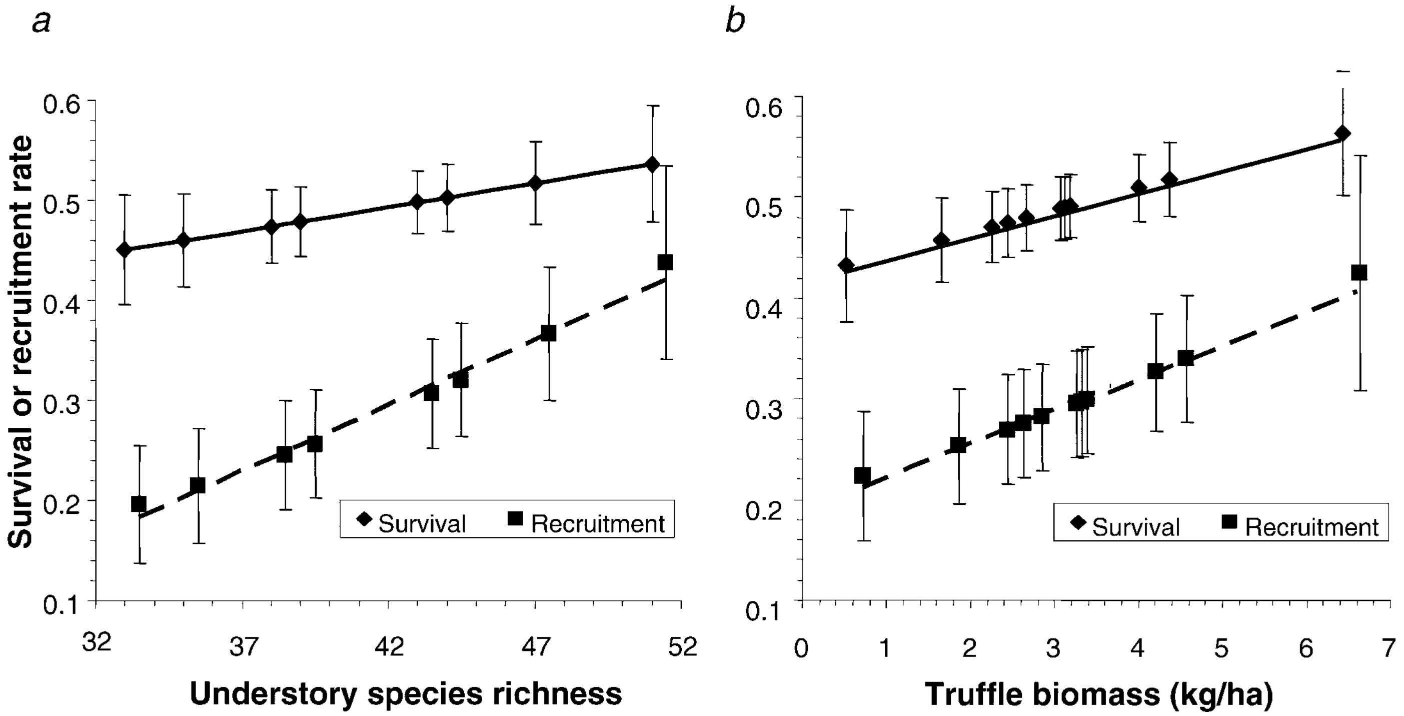

FIG. 8.—Survival and recruitment rates of populations of *Glaucomys sabrinus* relative to a) species richness of understory vegetation (Lehmkuhl et al. 2006) and b) truffle biomass (Lehmkuhl et al. 2006) in ponderosa pine and mixed conifer forests of the eastern Cascade Range, Washington.

availability of den sites, especially cavities; and diversity and abundance of mycorrhizal fungi sporocarps and other foods. Arguably, factors that limit local populations of *G. sabrinus* vary among regions and likely over time within regions, especially in portions of its range where broad-scale disturbance has dramatically altered forest habitats and landscapes (Bowman et al. 2005; Ford et al. 2004). Of the 3 hypotheses, predation appears to have the least empirical support, at least in terms of a being a pervasive ecological force limiting populations of *G. sabrinus*. Although *G. sabrinus* is important prey for several avian and mammalian predators (Carey et al. 1992; Forsman et al. 2001; Wilson and Carey 1996), and some predator populations are closely linked to squirrel population density (Fryxell et al. 1999), there are few examples of predators limiting populations of *G. sabrinus* (Carey et al. 1992).

As for cavities, most of the empirical support for dens as a limiting factor is indirect evidence—positive correlations between squirrel population density and large trees or large snags (Carey 1995; Gomez et al. 2005; Holloway 2006; Lehmkuhl et al. 2006; Smith et al. 2004). One experimental study suggested that nest boxes increase the carrying capacity of 2nd-growth forests (Witt 1991). However, more recent manipulative experiments indicate that populations of *G. sabrinus* probably are not generally limited by cavities (Carey 2002; Ransome and Sullivan 2004). Furthermore, a review of several studies across the range of *G. sabrinus* reveals that cavities are widely used, but drays and witches' broom also comprise a substantial proportion of nests (Fig. 3a). Still, there appear to be circumstances in which, either because of disturbance or other factors influencing ecological communities, the availability of cavities might become limiting. Examination of distributional and behavioral data from the southern Appalachians suggests that populations of *G. sabrinus* are excluded from hardwood forests as a result of direct competition with *G. volans* for cavities (Muul 1968; Weigl 1978; Weigl et al. 1999). Similarly, *G. sabrinus* in southeastern Alaska use external nests more often and are at lower populations densities in sympatry with *T. hudsonicus* than on islands where red squirrels are absent (Fig. 3b; W. Smith and S. Pyare, in litt.). Ransome and Sullivan (2004) reported that in populations limited by food, more females used nest boxes in stands with supplemental food than in stands supplemented only with nest boxes. Their explanation was that the additional food likely increased the number of reproductive females, which rely on cavities for natal dens. A similar pattern was reported for populations of *G. sabrinus* in southeastern Alaska, where density of reproductive females, population growth rates, and overall population density varied directly with large tree and snag availability (Smith et al. 2004; Smith and Person 2007).

Several lines of indirect evidence support availability of food resources as the primary factor limiting populations *G. sabrinus* across its range (Ransome and Sullivan 1997, 2004; but see Carey 2002). Not only is population density correlated with truffle abundance (Fig. 2), but survival is positively correlated with biomass of forage lichen (Lehmkuhl et al. 2006) and survival and recruitment are directly related both to truffle abundance and to understory species richness (Fig. 8), a measure of food availability (Lehmkuhl et al. 2006). Furthermore, many habitat features that explain population density or capture probability (e.g., decayed logs) are correlates of truffle abundance (Amaranthus et al. 1994; Carey et al. 1999, 2002; Smith et al. 2000). In fact, the lower habitat suitability of many 2nd-growth forests (Carey 1989, 1991; Carey et al. 1992; Ransome and Sullivan 1997) is likely related to the effects of clear-cut logging (Smith et al. 2002) or active management of 2nd-growth stands (Meyer et al. 2005c) on the abundance and diversity of fungal communities. In addition, truffle abundance and distribution influence movements of females (Gomez et al. 2005; Wilson et al., in press) and how individuals use space (Meyer and North 2005; Meyer et al. 2005a). Indeed, *G. sabrinus* tracks the location and timing of truffle sporocarps (Pyare and Longland 2002). Moreover, the size and location of core areas coincide with the availability of food resources (Gerrow 1996; Holloway 2006; Meyer et al. 2005a), and the magnitude of difference (10-fold) between core nest area and home-range size illustrates the significance of food resources in determining area requirements (Wilson et al., in press).

The experimental evidence in support of food limiting populations of *G. sabrinus* is sparse and ambiguous. Ransome and Sullivan (1997) reported population densities in food-supplemented stands that were twice as high as in untreated stands. Somewhat surprising, however, was the absence of a treatment effect on reproduction, adult body mass, recruitment, or adult survival. Perhaps season (summer compared to winter), or amount or type (natural compared to unfamiliar) of food was inappropriate to stimulate a measurable response among individuals (Ransome and Sullivan 1997). Alternatively, the marked increase in food resources attracted individuals residing outside the treated area, and thus the increase in population density was due to immigration rather than reproduction. Comparably high densities of *G. sabrinus* can be sustained in poorer quality (not necessarily food-limited) habitats through immigration (Lehmkuhl et al. 2006; Smith and Nichols 2003; Smith and Person 2007).

In a similar, more recent study, Ransome and Sullivan (2004) observed that the abundance, body mass, and recruitment of *G. sabrinus* did not differ between treated stands and controls. However, food supplementation markedly reduced trappability, which likely confounded efforts to detect a change in abundance. Nonetheless, survival was lower in controls than in stands that received additional food. Also, more females used nest boxes in treated stands than in controls, suggesting that more females became reproductive when food was supplemented.

The preponderance of evidence (albeit correlative) suggests that individual behavior and population demography are closely linked to food resources. However, factors limiting populations of *G. sabrinus* are complex and likely vary according to specific circumstances (Carey 2002). Indeed, there clearly are circumstances in which the availability of suitable natal dens can limit reproduction (Smith and Nichols 2003; Smith and Person 2007) or habitat distribution (Weigl 2007; Weigl et al. 1999). Thus, conservation strategies or restoration efforts that consider the full suite of ecological factors limiting fitness likely will be more robust in achieving a desirable outcome.

CONCLUSIONS

Despite significant loss and alteration of forests after European settlement, *G. sabrinus* occurs throughout most of its historical range in North America. Land use, fire, and climate shifts threaten the future of fragmented populations in the Appalachians. Northward expansion of *G. volans* in conjunction with climate warming has expanded the zone of sympatry with *G. sabrinus*, consequences of which remain uncertain. There remain portions of the range of *G. sabrinus*, such as in southern California, where little is known about its status and ecology.

An emerging ecological portrait of *G. sabrinus* differs from what was depicted from early studies in western North America. Although *G. sabrinus* often attains its highest population densities in pristine forest communities, it does not necessarily depend on old-growth forests to persist in forested landscapes. Rather, it flourishes in a wide variety of forest types and apparently can satisfy its life-history needs in deciduous forests and younger forests, depending on local conditions. However, further study is needed to determine whether younger forests can sustain viable populations. The extent to which local populations of *G. sabrinus* depend on select old-forest attributes likely is determined as much by the ecological community as by its autecological requirements. Direct evidence comes from populations of *G. sabrinus* in similar habitat, but vastly different ecological communities; forest structure and productivity appear similar, but habitat relations, population density, and demography differ and likely reflect interspecific interactions (predation and competition) that often are unique to local communities.

Habitat correlates of population density and microsite use also explain the spatial distribution of food resources, which likely limit populations of *G. sabrinus* through effects on home-range size, space use, reproduction by females, adult survival, and recruitment. Availability of suitable cavities limits the density of breeding females, which can limit populations in habitats where suitable den trees are less abundant (e.g., young growth). Much of the perception that *G. sabrinus* has a specialized diet stems from early studies in the Pacific Northwest where *G. sabrinus* relies heavily on truffles. However, evidence from portions of the range of this species indicates that it has the potential to be opportunistic, capable of eating a wide variety of food items with its local diet varying according to the diversity of ecological communities. In some portions of its range, *G. sabrinus* experiences less competition because of a depauperate indigenous vertebrate fauna or reduces competition by selecting habitats where it has exclusive use of select food resources. In highly diverse communities of arboreal rodents, *G. sabrinus* apparently has coevolved a specialized diet and mutualistic relationship that contributes directly to the availability of its future food resources. In summary, it appears the ecology of *G. sabrinus* is as varied as the forest communities in which it occurs.

However, the degree to which *G. sabrinus* can adapt to new circumstances is unclear; the wide variety of habitats, food, and other resources it can use suggest a relatively broad fundamental niche. Although regional differences in body size and morphology (and their potential effects on thermoregulation or other biological functions) are not trivial, there is no evidence to suggest that ecological variability across its range corresponds with genetic-based differences in environmental tolerances, physiology, or other biological attributes. An alternative explanation is that populations of *G. sabrinus* exhibiting varying degrees of specialization or sensitivity to perturbation represent examples where the fundamental niche of *G. sabrinus* has been modified by unique ecological circumstances of local forest communities.

As its forest habitats continue to be altered through disturbance or climatic shifts, the fate of local populations of *G. sabrinus* depends on its ability to sustain breeding populations in younger forests or forests that are undergoing shifts in plant and vertebrate species composition. The empirical evidence suggests that *G. sabrinus* likely has the ecological plasticity to adapt to changing conditions, but further study is needed, especially in regions where changes are occurring most rapidly. Indeed, further study is needed to identify regions of rapid transition. Limited empirical evidence (Bowman et al. 2005; Payne et al. 1989) indicates that priority be given to studying populations along the fringe of its geographic distribution, especially where knowledge is scarce (e.g., southern Sierra Nevada). Nevertheless, *G. sabrinus* cannot live in all forest habitats. In addition to the resources highlighted in this paper, there are essential elements of forest habitat that I did not consider, such as structural features of the overstory and midstory that facilitate gliding (see Scheibe et al. 2007). Because food resources frequently are clumped and ephemeral, relatively dense canopies, large tall trees, and open midstories are needed for individuals to move through their home range efficiently and safely (Scheibe et al. 2006; Vernes 2001). Furthermore, if climate change increases ambient temperatures and reduces precipitation, forest habitats in those regions (e.g., southern Sierra Nevada) likely will become less suitable and the presence of streams and mesic–wet microsites will become increasingly essential.

However, the most significant challenge is maintaining functional connectivity across landscapes. Many populations are fragmented and an increasing number of populations are becoming fragmented or more isolated throughout its range. Moreover, the relative importance of functional connectivity in sustaining viable and well-distributed populations of *G. sabrinus* increases as forests become increasingly altered, habitat suitability diminishes, and the uncertainty of persistence increases. Given the expected variability in population dynamics and the influence of demographic variability on intrinsic population growth rate, the presence of comparably high densities of breeding individuals does not ensure sustainability. Moreover, there is substantial uncertainty about the ability of *G. sabrinus* to disperse across managed habitats and the rate of dispersal required to sustain viable metapopulations of flying squirrels in fragmented landscapes. For this reason, I recommend that future studies of *G. sabrinus* focus on assessing metapopulation viability in fragmented landscapes, using demographic and genetic data from populations across an array of landscape configurations (i.e., size, composition, and spatial arrangement of habitat patches) to determine which landscapes have a high probability of sustaining populations of *G. sabrinus*.

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Special Feature Editor was Barbara H. Blake.

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Recovery Plan

FILE COPY

Spotfin Chub
(Hybopsis monacha)

Recovery Plan for

Spotfin Chub

Hybopsis monacha

Prepared by

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Atlanta, Georgia

September 1983

Approved: F. Eugene Hester
Deputy Director, U.S. Fish and Wildlife Service

Date: November 21, 1983

THIS IS THE COMPLETED SPOTFIN CHUB RECOVERY PLAN. IT HAS BEEN APPROVED BY THE U.S. FISH AND WILDLIFE SERVICE. IT DOES NOT NECESSARILY REPRESENT OFFICIAL POSITIONS OR APPROVALS OF COOPERATING AGENCIES, AND IT DOES NOT NECESSARILY REPRESENT THE VIEWS OF ALL INDIVIDUALS WHO PLAYED A KEY ROLE IN PREPARING THIS PLAN. THIS PLAN IS SUBJECT TO MODIFICATION AS DICTATED BY NEW FINDINGS AND CHANGES IN SPECIES STATUS AND COMPLETION OF TASKS DESCRIBED IN THE PLAN. GOALS AND OBJECTIVES WILL BE ATTAINED AND FUNDS EXPENDED CONTINGENT UPON APPROPRIATIONS, PRIORITIES, AND OTHER BUDGETARY CONSTRAINTS.

ACKNOWLEDGEMENTS SHOULD READ AS FOLLOWS:

U.S. Fish and Wildlife Service. 1983. Spotfin Chub Recovery Plan. U.S. Fish and Wildlife Service, Atlanta, Georgia. 46p.

ADDITIONAL COPIES MAY BE OBTAINED FROM:

U.S. Fish and Wildlife Reference Service
Unit j
3840 York Street
Denver, Colorado 80205
Telephone: 303/294-0917
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PART I

INTRODUCTION

The spotfin chub (Hybopsis monacha) is listed as Threatened (Federal Register September 9, 1977) throughout its present range in the Tennessee River drainage in the States of North Carolina, Tennessee, and Virginia. Once occurring widely in 12 tributary systems lying in 5 states, it now is extant in only 4 systems: Little Tennessee River, North Carolina; Duck and Emory Rivers, Tennessee; and North Fork of Holston River, Tennessee and Virginia.

Reasons for the reduction or extirpation of the initial spotfin populations from most of their former range were likely due to intermittent detriments or permanent destruction of their habitats such as: impoundments, channelization, pollution, turbidity or siltation, temperature change, possibly overcollecting, and interspecific competition as described by Jenkins and Burkhead (1982).

This small cyprinid (maximum standard length 92 mm) was first described by Cope (1868) from specimens collected the year before from the North Fork Holston River near Saltville, Smyth County, Virginia. Although the fish has been collected since that time in other Tennessee River tributaries, the species was not seriously studied until after 1970.

The spotfin chub was listed as a threatened species under the Federal Endangered Species Act and the notice was published in the September 9, 1977, Federal Register, Volume 42, No. 175, pages 45527 to 45529. Concurrently with that listing, Critical Habitat was also designated to include the following:

> North Carolina--Macon and Swain Counties: Little Tennessee River, main channel from backwaters of Fontana Lake upstream to the North Carolina-Georgia State line.
>
> Tennessee--Cumberland, Fentress, and Morgan Counties: Emory and Obed Rivers and Clear and Daddys Creeks in Morgan County; Clear Creek in Fentress County; Obed River upstream to U.S. Interstate Highway 127 in Cumberland County. Hawkins and Sullivan Counties; North Fork Holston River, main channel upstream from junction with South Fork Holston River to the Tennessee-Virginia State line.
>
> Virginia--Scott and Washington Counties: North Fork Holston River, main channel from the Virginia-Tennessee State line upstream through Scott and Washington Counties.

(The Buffalo River of the Duck system was not included as Critical Habitat because, at the time of Critical Habitat designation, the species was thought to have been extirpated there.)

Historical and Present Distribution

Once endemic to the Tennessee River drainage in Alabama, Georgia, North Carolina, Tennessee, and Virginia, the spotfin's range included upland-mountain habitats in 4 physiographic provinces encompassing 12 tributary systems (Figure 1): Blue Ridge (French Broad River and Little Tennessee River systems), Ridge and Valley (Clinch River, Powell River, North and South Forks of Holston River, and Chickamauga Creek systems), Cumberland Plateau (Emory River and Whites Creek systems), and Interior Low Plateau (Shoal Creek, Little Bear Creek, and Duck River systems).

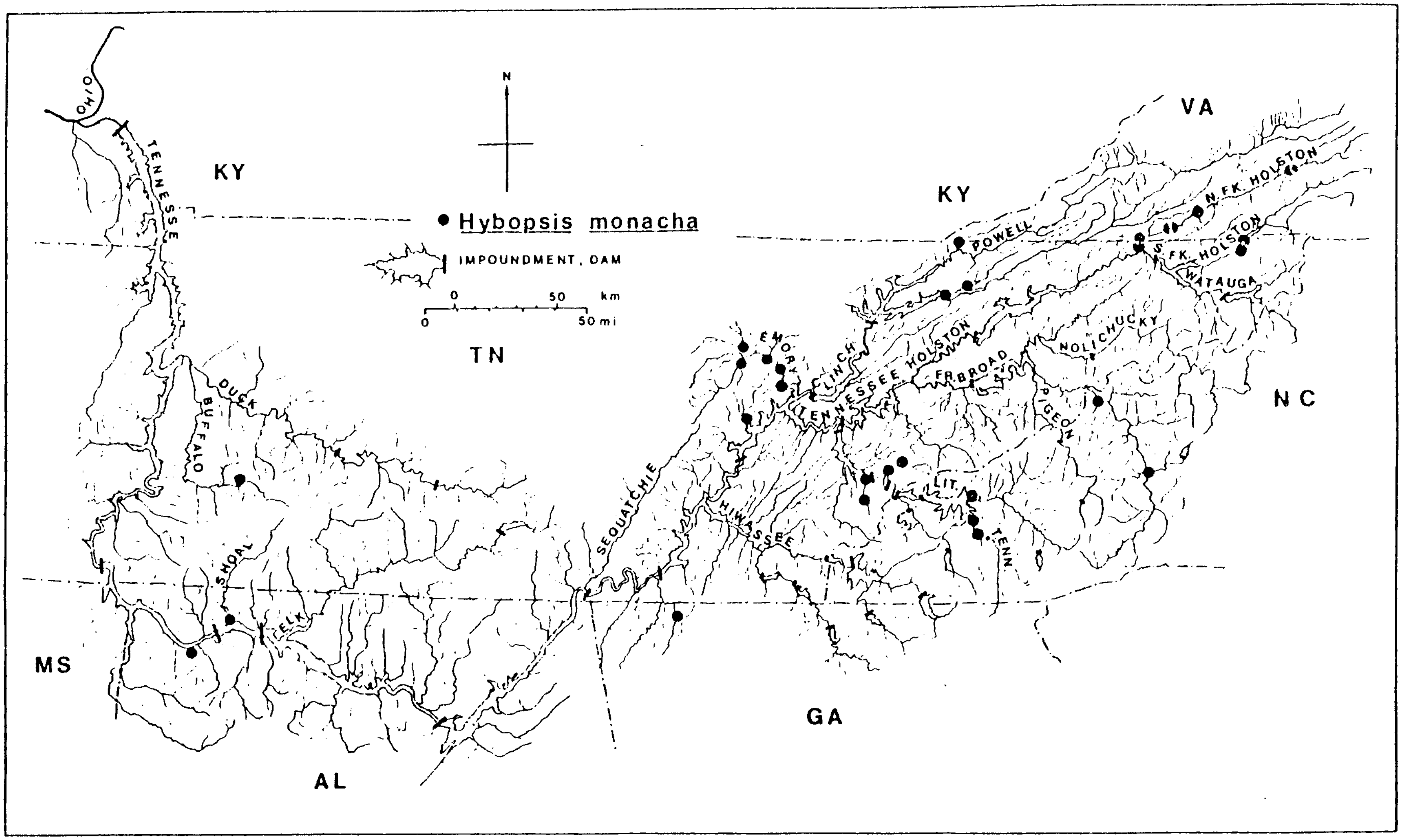

Figure 1
Distribution of Hybopsis monacha, showing all known extant and extirpated populations. Some dots cover more than one record locality. Records from three of four extant populations are shown in detail in Figs. 2-4. (Taken from Jenkins and Burkhead 1982).

Presently, it survives in some 166 total km of 4 isolated tributary systems: the Duck, Little Tennessee, Emory, and North Fork of Holston River systems.

Duck River System, Tennessee Even though the fish population of this large tributary system to the lower Tennessee River has been intensively sampled in recent years (1970-81), only four *H. monacha* specimens were located. These were collected in 1978 by N. H. Douglas (Douglas, personal communication as reported by Jenkins and Burkhead, 1982) in Buffalo River at the mouth of Grinders Creek, a small tributary to the Buffalo. During this period, Douglas collected some 50,000 fish by sampling annually at this single site. Several other collections have been made at this site, and elsewhere in the Buffalo. However, the only other *H. monacha* collection in this system was three specimens taken in middle Grinders Creek in 1937 by the Tennessee Valley Authority (TVA).

The Buffalo River still has moderately high species richness and its tributaries are typically clean, clear and contain varied substrate (Jenkins and Burkhead 1982). Isom and Yokley (1960) and Starnes et al. (1977) opined that the river is essentially pristine. Thus the apparent scarcity of *H. monacha* is a puzzle. Jenkins and Burkhead speculate that the species may be temperature limited by numerous high volume, cool springs in the Buffalo system.

Little Bear Creek System In 1937 during a preimpoundment survey of the lower section of this small northwestern Alabama stream, a single *H. monacha* was taken. The extreme lower section of Little Bear Creek in this area of the Tennessee River's southern bend region was inundated in 1938 by Pickwick

Reservoir. However, the capture site apparently was above the currently impounded portion; the creek probably has not been collected since 1937.

Shoal Creek System *H. monacha* was regarded as rare in 1884, when Gilbert (1891) recorded three specimens from lower Shoal Creek. The system has been sampled widely for the past 20 years (Wagers, 1974) without further records of *H. monacha*, and Ramsey (1976) regarded all Alabama populations as extirpated. At most, this species may have had only a marginal population in the western part of the Tennessee River bend area, which has been identified as a transitional area between lower and upper Tennessee faunas (Armstrong and Williams, 1971).

Chickamauga Creek System The first and only record of *H. monacha* in this system was taken in 1877 (Jordan and Brayton 1878) from South Chickamauga Creek at Ringgold, Georgia, where it was reported as abundant. The system was sparsely sampled before 1979, and has had a history of pollution, floods, and channelization. Apparently, the stream habitat has improved in the last few years, which is reflected by present ichthyofauna abundance and diversity including some rare or endangered species (Etnier, et al. 1981).

Citico Creek One specimen taken near the Creek's mouth and one from the middle section in 1940 are the only records of *H. monacha* from this creek. Regarding this population, Jenkins and Burkhead 1982 state "Only lower Citico may have provided preferred habitat, but because of longevity of good conditions and apparent current absence of *H. monacha* therein, we suspect the population was at least partly reliant on a hypothetical one in lower Little Tennessee River. Although the Little Tennessee River was freely flowing at the Citico Creek mouth until 1979, it was a cold tailwater since at least 1944."

Abrams Creek The species was reported in lower sections (up to approximately 12 km above the mouth) of the creek in 1937 and 1941 and was taken in the 1957 rotenone treatment of the creek. This reclamation (intended to benefit introduced trout) along with the impoundment of the lower creek, likely caused this extirpation of the species from these waters.

Upper Little Tennessee River (Figure 2) J. S. Gutsell surveyed the Tuckasegee River and tributaries as early as 1930. Hildebrand (1932) reported on Gutsell's collections which included six sites on the main river. C. L. Hubbs and/or TVA personnel sampled three sites (1937-40) and J. R. Bailey made three more collections in 1947. Only two specimens of H. monacha were recovered from this preimpoundment sampling of the Tuckasegee System. These were taken from Noland Creek mouth in 1940 by Hubbs. Most of this area was inundated by Fontana Dam in 1945. Three sites were rotenoned above Fontana by a North Carolina Wildlife Resources Commission (NCWRC) crew in 1961 (Messer and Ratledge, 1963) and 10 sites were cresoled by TVA personnel in 1968 (Anon., 1971) without any record of H. monacha. Above the impounded area this river has a history of pollution.

Concurrent with the above referenced sampling of the Tuckasegee River, the upper Little Tennessee was sampled without H. monacha being found. Subsequently, the species was collected by TVA personnel during 1975-76 by kick-seining at four sites on the mainstream below the town of Franklin,

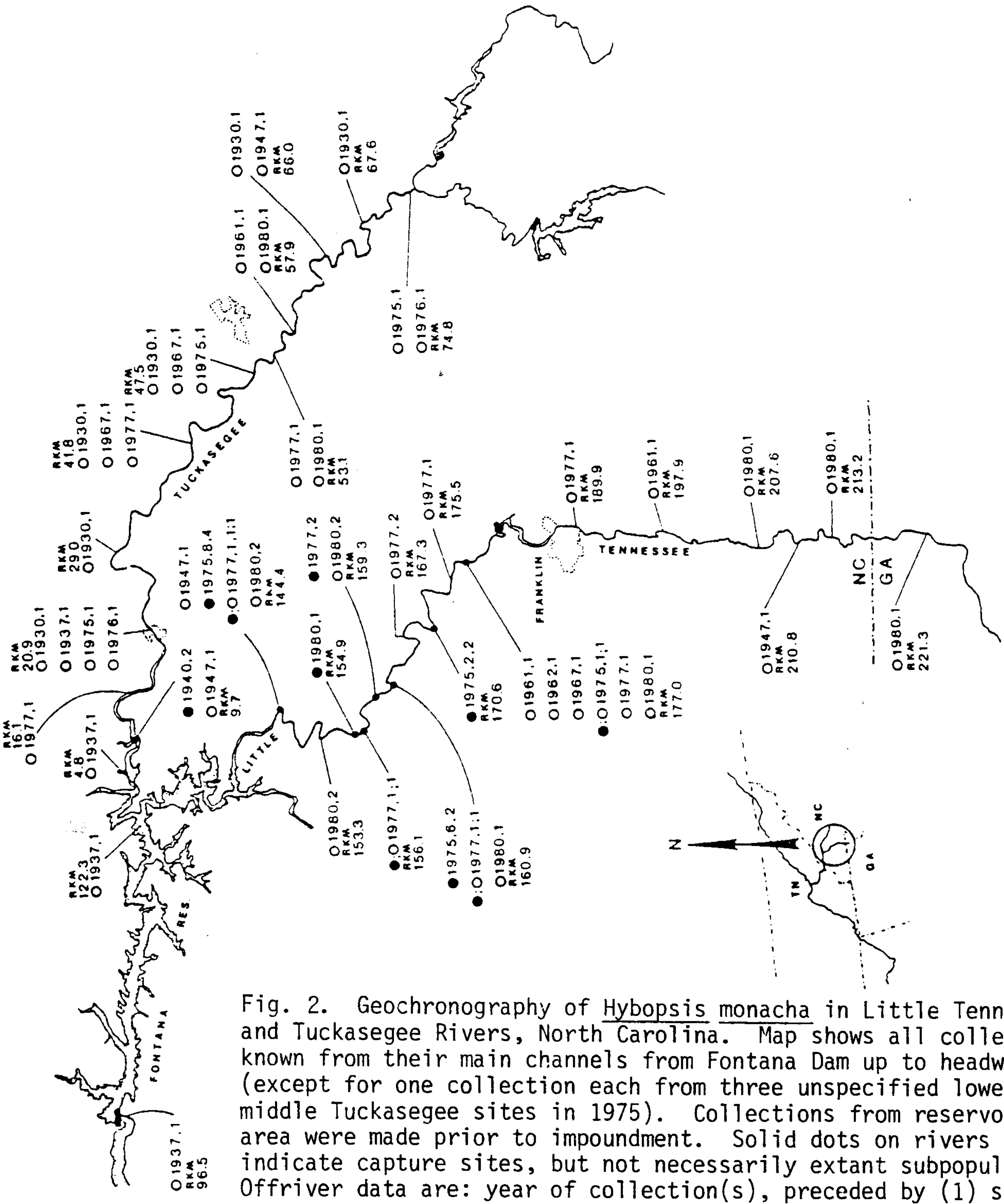

Fig. 2. Geochronography of Hybopsis monacha in Little Tennessee and Tuckasegee Rivers, North Carolina. Map shows all collections known from their main channels from Fontana Dam up to headwaters (except for one collection each from three unspecified lower and middle Tuckasegee sites in 1975). Collections from reservoir area were made prior to impoundment. Solid dots on rivers indicate capture sites, but not necessarily extant subpopulations. Offriver data are: year of collection(s), preceded by (1) solid dot if H. monacha taken, (2) open circle if not taken; following the year are: (3) number of specimens taken, if any (if specimens were taken more than once in a year, the number of specimens in each collection is given separately, hence indicating the number of collections yielding specimens), and lastly (4) the number of collections not yielding specimens (this number is separated by a semicolon from number of specimens). (Taken from Jenkins and Burkhead 1982).

North Carolina. During this same period similar sampling on the Tuckasegee and Cullasaja did not produce H. monacha. After the fish was located in the Little Tennessee area below Franklin in 1975, widespread and intensive sampling followed for the purpose of a status review. The range, defined by these surveys, spans approximately 32.3 km of the upper Little Tennessee from Fontana Reservoir to Franklin with H. monacha found at seven sites. Collectors or cooperators here (from 1975-80) included R. B. Eager (TVA) and D. A. Etnier, University of Tennessee; N. Burkhead, Roanoke College; and E. Crittenden, R. Smith, and H. D. Boles (USFWS).

French Broad River System Although there were two early records (Jordan, 1889) of H. monacha (three specimens) in the lower reaches of this system (Spring Creek, Swannanoa River) in North Carolina, the increase of general siltation, domestic and industrial pollution, along with population growth of smaller towns on the tributaries and of Brevard and Asheville on the mainstream, probably caused the extirpation of this population long before surveys were made by the state (Richardson et al. 1963).

Whites Creek System W. R. Taylor recorded seven spotfins caught under difficult seining conditions at 3 km above the Whites Creek arm embayment of Watts Bar Reservoir in 1959. A preimpoundment survey (rotenone) by TVA in 1941 at three sites failed to reveal H. monacha. Collections made by two TVA divers snorkeling above and below the record site in 1975, followed by three collections made in lower Whites Creek during 1981 by Crittenden (Crittenden, personal communication as reported by Jenkins and Burkhead 1982) did not reveal H. monacha.

Emory River System (Figure 3) The range of H. monacha in this system has been reduced in the lower reach by the Watts Bar impoundment (1942) and in the upper reaches mainly by silt or other detriments from coal mining (Anon., 1970; Riddle, 1975). This Cumberland Plateau system has been extensively surveyed since 1941. Seven preimpoundment collections from five sites were taken by TVA in 1941. In 1968 TVA used ichthyocides at 16 sites and Riddle in 1973-74 sampled by various methods.

The known H. monacha range, verified by sampling and/or on the basis of museum collections, extends from the mouth of White Creek on the Clear Creek tributary, and Lower Daddys Creek on the Obed tributary to the Emory River downstream to near the mouth of Crab Orchard Creek (Jenkins and Burkhead 1982). H. monacha specimens were identified as early as the collections made by TVA in 1941. Their abundance, noted in most of the combined sampling, was usually uncommon or rare in their recorded range.

Clinch River System A single specimen of H. monacha, taken in 1893 by Everman and Hildebrand and identified by Hubbs and Crowe (1956), was taken from the Clinch River in an area now inundated by Norris Reservoir. A small series was also taken in 1893 from lower Ball Creek near its confluence with Big Sycamore Creek, an area also later impounded by Norris Reservoir. Even though this species may have occupied the Clinch above the Norris Reservoir in early times, it was not found during extensive surveys after 1965 (Masnik 1974). Moreover, the history of continuous coal mining operations on the Virginia and Tennessee drainage into the upper Clinch and a major fish kill from an alkaline spill in 1967 (included 156 km of the stream above Norris Reservoir) on this river precluded the likelihood that H. monacha exists in

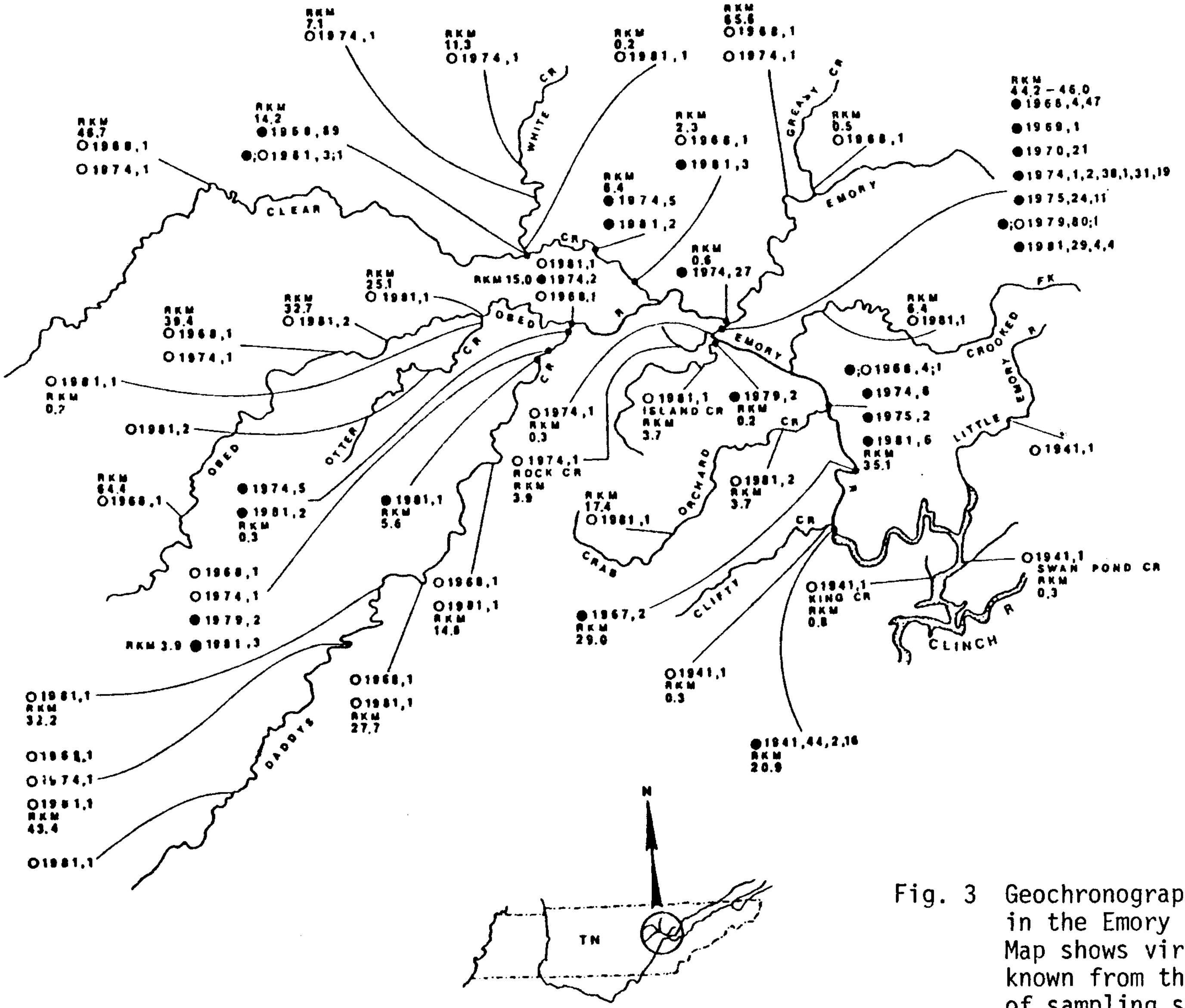

Fig. 3 Geochronography of Hybopsis monacha in the Emory River system, Tennessee. Map shows virtually all collections known from the system made by methods of sampling small fishes. Data format explained in Fig. 2. (Taken from Jenkins and Burkhead 1982.)

the upper drainage. The reduced water temperature in the fluvial drainage below Norris Reservoir, which is eventually impounded by Melton Hill Dam, forecloses any existence of this species further downstream.

Powell River System The spotfin distribution and collection history of the Powell system is similar to that of the upper Clinch. Everman and Hildebrand (1916) recorded three specimens from Indian Creek, Tennessee. This unimpounded tributary, its mouth, and the Powell itself were sampled extensively from 1964-81 with no further record of *H. monacha* (Taylor et al., 1971; Masnik, 1974; Starnes et al., 1977). As with the Clinch, there has been a history of coal mining pollution on the upper Powell River.

North Fork Holston River System (Figure 4) Sampling on the North Fork of the Holston River began as early as 1867 by Cope (1868), and through 1981 there had been 199 collections from 49 river sites. Of the above collections, from 1970-77, TVA had taken 67 collections from 22 stations by chemical treatment 1-4 times per year (Hill et al., 1975; Freeman, 1980). They also took four collections from one of the original stations (Click Island) in 1981 by a seine-snorkel method with some electrical field assistance. Burkhead and Jenkins (1982) also sampled during this latter period (1970-81) either by seine, shocker, or snorkeling.

Ranges of *H. monacha* were found in the following general river sections of the North Fork:

Lower North Fork Holston River Within the presently populated range of 72 km, from the mouth in Tennessee to western Washington County in Virginia, *H.*

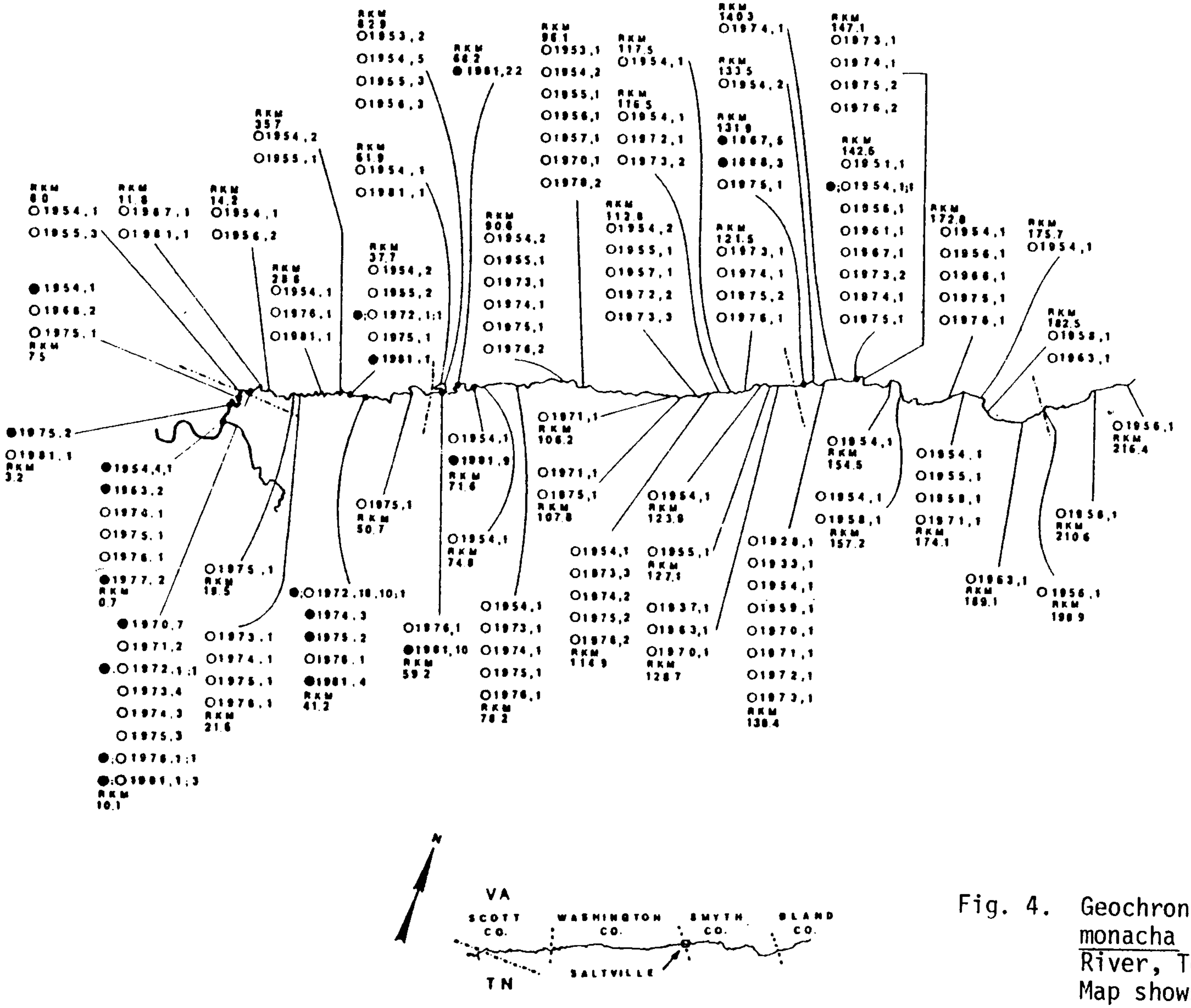

Fig. 4. Geochronography of *Hybopsis monacha* in North Fork Holston River, Tennessee and Virginia. Map shows virtually all known collections from the river. Data format explained in Fig. 2. (Taken from Jenkins and Burkhead 1982).

monacha was found at 6 of 14 sites, but was generally rare in numbers (Jenkins and Burkhead, 1982). Seven specimens were taken by Jenkins in 1970 by seining along Click Island (rkm 10.1), but further sampling at the same site in 1971, 1975, and 1981, yielded no more. Also, 13 rotenone collections by TVA (1971-76) in the same island area yielded only two H. monacha and five samples in 1981 yielded only one.

At the island off the mouth of Blue Springs Branch (rkm 41.2), 18 H. monacha were taken by seining May 16, 1972; 10 on June 4, 1972; but none on June 12, 1972 (Jenkins and Burkhead, 1982). Subsequent seining in 1974 and 1975 yielded 3 and 2, respectively, and chemical treatment of the island's left channel by TVA in 1976 yielded no H. monacha. Seining in 1981 yielded only two, which indicated a low reproduction rate or slow recruitment rate from other areas.

In a 13 km section of the river in western Washington County, Jenkins and Burkhead (1982) located H. monacha at three sites, with the greatest concentration at Hobbs Ford (rkm 68.2), an area of clean, small-medium gravel.

Some former H. monacha populations in the lower North Fork probably have either been extirpated by pollution moving downstream from Saltville or isolated in extant areas (possibly near tributary refugia), and are restricted from dispersion farther downstream by further pollution in the Kingsport area or by impoundment below Kingsport.

Upper North Fork Holston River Both Cope (1868) and Jordan (1889) reported *H. monacha* as "rare" or "scarce" in seining lengthy sections of the river in the Saltville area. Presumably this was before the onset of major pollution in that area. The fish was not found by Becker in 1928 or by TVA in 1933, but Patrick (1961) reported one specimen taken 7 km above Saltville in 1954. No others were reported in 44 collections made from 1954 through 1976.

South Fork Holston River In a preimpoundment survey by R. M. Bailey and TVA, 8 *H. monacha* specimens were collected from a 21 km section of the main channel of this river in Tennessee and 1 specimen was taken above the mouth of Jacob Creek, a tributary of this section. This population disappeared with the impoundment of South Holston Reservoir in 1950. No specimens were found during surveys made by Bailey and many others (1959-77) in the Virginia portion of this river. This population was apparently lost when South Holston Reservoir was completed (Jenkins and Burkhead, 1982). This area is also polluted (Anon., 1961; Higgins, 1978).

Description, Ecology, and Life History

Jenkins and Burkhead (1982) describe the spotfin chub as having a slightly compressed, elongated body ranging in standard length from about 20 mm early in the first year to about 85 mm in the third year of growth. Except for nuptial males, the color is a dusky green above the lateral line and silver on the lower sides bordered mid-dorsally and dorso-laterally by gold and green stripes. There are no blotches or speckling on the body, but the dorsal fin has a dark area posteriorly and a caudal fin spot is distinctive. The mouth is inferior with the upper lip expanded anteriad. Terminal small labial barbels are present. Pharyngeal teeth are 4-4. Scales are moderately small with those of the lateral line ranging from 52-66. The anal fin has 8 rays. Sexual dimorphism includes longer dorsal, anal, and pelvic fins in the males; the dorsal fin insertion is also more anterior in males. Nuptial males develop antrorse tubercules over most of the top of the head and the front and side of the snout. Also they develop a prominent metallic blue color above the lateral line and the fins bear white margins.

The spotfin chub seems to be a phyletic key species linking two large, complex groups of eastern American minnows--shiners (Notropis) and certain non-nestbuilding barbeled "chubs" (Hybopsis).

The species is an insectivore, feeding diurnally presumably by both sight and taste in benthic areas of slow to swift current over various substrates with little siltation. The streams may range from 15-60 m in width and, where occupied, 0.3-1.0 m in depth. Water temperature in their summer habitat usually reaches greater than 20° C, and submerged macrophytes are usually absent, occasionally common. The species has been observed associated with sand, gravel, rubble, boulder, and bedrock substrates (Jenkins and Burkhead, 1982).

Jenkins and Burkhead (1982) estimated the chubs spawning period (mid-May to late August) from capture dates of turberculate males and females with ripe ova. No observation of clearly reproductive behavior is known.

Reasons for Decline and Threats to Continued Existence

Jenkins and Burkhead (1982) have numerically coded the various impacts which have exterminated, reduced, or are now affecting the extant populations of *H. monacha*. They further identified spotfin-inhabited length of each stream section within each system and coded the type of impact within direct and indirect impact categories (Table 1). Jenkins and Burkhead (1982) referred to the decline of the spotifn chub as follows:

> "*Hybopsis monacha* survives in some 166 total km of four isolated tributary systems: one site in Buffalo River of the lower drainage; and in the upper drainage, one section each of Little Tennessee and North Fork Holston rivers, and essentially four streams of the Emory system (Table 6). Although current ranges identified within three systems (Little Tennessee excepted) may actually be somewhat greater, many subpopulations probably are discontinuous and no population is generally flourishing. Given the history of demise of *H. monacha*, and stresses affecting at least three of the remaining populations (Buffalo possibly excepted), their survival is remarkable and tenuity is suggested.
>
> "*Hybopsis monacha* is a victim of numerous impacts, generally at least two on each population (Table 1). For the 24 at least once inhabited stream sections (and inferred hypothetical downstream extension through formerly suitable habitat for some), the following anthropogenic stresses are invoked to have exterminated populations, followed by number of streams directly affected: silt or coal fine sedimentation 12; pollution 10; inundation by reservoir 10; temperature depression of dam tailwater 3; and channelization

Table 1. Length (km) of stream sections with extant populations (some discontinuous), and anthropogenic and natural limiting factors on all known populations of *Hybopsis monacha*. "Indirect" impacts are on stream sections receiving populated tributaries (some of the former also were or remain populated). Impacts: 1 impoundment, 2 cold tailwater, 3 channelization, 4 siltation and/or coal fine sedimentation, 5 pollution (inorganic and/or organic), 6 population renovation, 7 localized collecting, 8 natural cool temperature, 9 small stream size. Impact may not refer to all parts of occupied section. (Taken from Jenkins and Burkhead 1982).

			Impact:	
System	Stream	Length	Direct	Indirect
Duck	Buffalo	1	?8	-
	Grinders	-	?8, ?9	?8
Lit. Bear	Lit. Bear	-	?9	1
Shoal	Shoal	-	1	1
Chickamauga	S. Chickamauga	-	1,3,4,5	1
Lit. Tennessee	Citico	-	8,?9	1,2
	Abrams	-	1,6,8	1,2
	Tuckasegee	-	1,4,5,?8	1,4,5?8
	Lit. Tennessee	33	1,2,4,5,?8	-
French Broad	Spring	-	?5,?8,?9	4,5
	Swannanoa	-	4,5	4,5
Whites	Whites	-	1	1
Emory	Emory	25	1,4,5	1
	Island	0.2	?9	4,5
	Obed	15	4,5	4,5
	Clear	14	4,5	4,5
	Daddys	6	4,5	4,5
Clinch	Clinch	-	1,2,4,5	1
	Ball	-	?9	1
Powell	Indian	-	4	4
N. Fk. Holston	low. N. Fk. Holston	72	4,5,7	4,5
	up. N. Fk. Holston	-	4	4,5
S. Fk. Holston	S. Fk. Holston	-	1,2	4,5
	Jacob	-	1,?8,9	1

1. Most of these factors also affect master streams of tributaries, some of whose populations may have been at least partly dependent upon ingress of chubs from the former. Massive application of ichthyocide wiped out the entire Abrams Creek population. Localized seining in the North Fork Holston sharply depleted populations made vulnerable by enigmatic concentration at gravel areas. Natural factors such as cool maximum temperature and small stream size probably limited some populations. The latter two conditions tend to coincide, and when so, populations may have been truly marginal.

"The spotfin chub seems to be extinction prone. We could expect this of a large species when confined to a limited area, because of intrinsically low population density, and of predators at the top of food chains (Terborgh, 1974), but such clearly are unapplicable to H. monacha. Its competitive abilities, however, may be low. Except for one observation possibly more related to reproductive territoriality, its feeding activity seemed unaggressive and unopportunistic compared with several syntopic Notropis species, Hybopsis dissimilis, Nocomis micropogon and Phenacobius uranops. Spotfin chubs did not alter their benthic feeding to take drifting food stirred up from the substrate by observers; other fish did. Specimens cupped in a net and held in a bucket remained quiet on the bottom, contrasting with many shiners. However, such behaviors may be typical of many benthic insectivores such as H. monacha. Size and number of eggs are in the range of small cyprinids (Carlander, 1969), and the spawning period appears to be protracted. Fecundity may be much greater if it is a fractional spawner, and enhanced hatching success may attend crevice spawning, suggested in the Reproduction section. However, in North Fork Holston River self-recovery of the recruitment into depleted subpopulations were slight at best."

PART II

RECOVERY

A. Recovery Objectives:

The ultimate goal of this recovery plan is to restore viable populations* of spotfin chub (Hybopsis monacha) to a significant portion of its historic range and remove it from the Federal endangered species list. The spotfin chub shall be considered recovered when the following criteria are met, and no present or foreseeable threats exist which would cause it to become in danger of extinction throughout a significant portion of its range.

1. Through protection of existing populations and/or by introductions and/or discoveries of new populations there exist viable populations* in the Buffalo River System, Upper Little Tennessee River, Emory River System, and Lower North Fork Holston River of the following magnitudes.

   a. Buffalo River System, Tennessee: Species persists in the Buffalo River in the area of Grinders Creek and/or some other river section.

   b. Upper Little Tennessee River, North Carolina: The species occupies its preferred habitat throughout the approximately 32.5 km river reach from the head of Fontana Reservoir to near Franklin Dam. This can be measured by determining that the species exists at a minimum of 10 locations along this river reach.

c. Emory River System, Tennessee: The species occupies its preferred habitat in the Emory River from its confluence with the Obed River to Watts Bar Reservoir, in Clear Creek from its confluence with White Creek downstream to its confluence with the Obed River, and Daddy's Creek from rkm 5.6 downstream to its confluence with the Obed River. This can be measured by determining that the species exists at a minimum of eight locations in the Emory River section, five locations in the Clear Creek sections, and five locations in the Daddy's Creek section.

d. North Fork Holston River, Tennessee and Virginia: The species occupies its preferred habitat throughout the river reach from its mouth upstream 72 km. This can be measured by determining that the species exists at a minimum of 15 locations along this river reach.

2. Through introductions and/or discovery of two new populations there exist viable* populations in two other rivers.

*Viable populations - Population monitoring over a ten-year period (biannual samples) indicates that the species is reproducing (at least two year classes present each year sampled) and that the population is either stable or expanding.

B. Recovery Outline

Prime Objective: Recover the spotfin chub to the extent that it no longer requires Federal Endangered Species Act protection.

1. Preserve populations and presently used habitat of the spotfin chub.

    1.1 Continue to utilize existing legislation and regulations (Federal and state endangered species law, water quality requirements, stream alteration regulations, etc.) to protect the species and its habitat.

    1.2 Conduct population and habitat surveys.

        1.2.1 Determine species' present distribution and status.

        1.2.2 Characterize the habitat and ecological association and determine essential elements (biotic and abiotic factors) of the species' habitat for all life history stages.

        1.2.3 Determine the extent of the species' preferred habitat.

1.2.4 Present the above information in a manner which identifies specific areas in need of special attention.

1.3 Determine present and foreseeable threats to the spotfin chub and strive to minimize and/or eliminate the threats where necessary to meet the recovery objective.

1.3.1 Determine impacts on the species of the heavy sediment load carried by the upper Little Tennessee River.

1.3.2 Determine the impact of pollution from Saltville, Virginia, on the North Fork Holston River populations.

1.3.3 Investigate and inventory other factors negatively impacting the species and its environment.

1.3.4 Solicit information on proposed and planned projects that may impact the species.

1.3.5 Evaluate the potential threat to the species of overcollecting.

1.3.6 Determine measures that are needed to minimize and/or eliminate any adverse impacts and implement when necessary to meet the criteria outlined in the recovery objectives.

1.4 Solicit help in protecting the species and its essential habitat.

1.4.1 Inform local government officials and regional and local planners of our plans to attempt recovery and request their support.

1.4.2 Request local, state, and Federal agencies to utilize their authorities to protect the species and its river habitat.

1.4.3 Meet with local industry interests and try to elicit their support in implementing protective actions.

1.4.4 Meet with landowners adjacent to the species' population centers and inform them of the project and try to get their support in habitat protection measures.

1.4.5 Develop an educational program using such items as slide/tape shows, brochures, etc. Present this material to business groups, civic groups, Boy-Scouts, church organizations, etc.

1.5 Investigate the use of Scenic River Status and/or other designations to protect the species.

2. Determine the feasibility of reestablishing the species back into its historic range and introduce where feasible and necessary to meet recovery objectives.

2.1 Survey rivers within the species' historic range to determine the availability and location of suitable transplant sites. This can include areas for population expansion within rivers where the species presently exists.

2.2 Investigate and determine the best method of establishing new populations, i.e., introduction of adults, juveniles, artificially raised individuals, or other means or combinations.

2.3 Where needed to meet the recovery objectives, reestablish the species within historic range.

2.4 Implement the same protective measures for these introduced populations as outlined for established populations in numbers 1.3 through 1.5 above.

3. Conduct life history studies not covered under section 1.2.2 above, i.e., age and growth, reproductive biology, longevity, natural mortality factors, and population dynamics.

4. Investigate the necessity for habitat improvement and, if feasible and necessary to meet recovery, develop techniques and sites for habitat improvement and implement.

5. Develop and implement a program to monitor population levels and habitat conditions of presently established populations as well as introduced and expanding populations.

6. Assess overall success of recovery program and recommend action (delist, continued protection, implement new measures, other studies, etc.).

C. Narrative Outline

1. Preserve populations and presently used habitat of the spotfin chub. Reestablishment of the species back into its former range may be feasible; however, the protection of established populations and their essential habitat is the key to the survival of the species.

   1.1 Continue to utilize existing legislation and regulations (Federal and state endangered species law, water quality requirements, stream alteration regulations, etc.) to protect the species and its habitat. This species, although listed as threatened, could easily become an endangered species if presently known populations are not maintained.

1.2 Conduct population and habitat surveys.

1.2.1 Determine species' present distribution and status. Conduct population and habitat surveys where *H. monacha* is expected to have potential habitat or known extant "populations": Duck River system (Buffalo River); Little Tennessee River system (Upper Little Tennessee and Tuckasegee River); North Fork Holston River system (lower North Fork); Emory River system (Obed River, White Creek, Clear Creek, Daddy's Creek, Orchard Creek, Crooked Creek, and upper and lower Emory River areas). Also, survey lower Little Bear Creek, Colbert County, Alabama; this stream apparently has not been collected since *H. monacha* was found there in 1937.

Once distribution and status are known, the future emphasis of the recovery plan can be charted. If sufficient other populations are found, protection of habitat may be the prime management tool. However, if no other populations are encountered, introductions will be necessary.

1.2.2 Characterize the habitat and ecological association and determine essential elements (biotic and abiotic factors) of the species' habitat for all life history stages. To adequately protect potential habitat it should be characterized completely. Different workers specify different habitat characters with various substrates and feeding habits and other behavior. More information should be known of silt limitation, requirements of larval stage, and winter habitat, and spawning habitats.

1.2.3 Determine the extent of the species' preferred habitat. As knowledge on the preferred habitat is gathered, this information should be utilized to delineate specific habitat areas that need special attention within each stream.

1.2.4 Present the above information in a manner which identifies specific areas in need of special attention. The use of maps delineating areas of special concern will allow planners to avoid sensitive areas.

1.3 Determine present and foreseeable threats to the spotfin chub and strive to minimize and/or eliminate the threats where necessary to meet the recovery objective. Each river system inhabited by the species may be subject to certain environmental influences which threaten the species and its habitat. To minimize and/or eliminate these threats where needed to meet recovery, the threats must be identified; they must be correlated with species' specific habitat requirements gathered under 1.2.2; and measures must be taken to alleviate the problem areas.

1.3.1 Determine impacts on the species of the heavy sediment load carried by the upper Little Tennessee River. The mica fines and mobile fine sand emanating from farming and mining cause a major water and substrate quality problem in the upper Little Tennessee River. The extent of the impact on the species must be determined. The recovery of the species in the upper Little Tennessee River may not be possible without control of this problem.

1.3.2 Determine the impact of pollution from Saltville, Virginia, on North Fork Holston River populations. The State of Virginia is actively involved in an attempt to minimize this problem. If this problem is impacting recovery, FWS should actively support these efforts.

1.3.3 Investigate and inventory other factors negatively impacting the species and its environment. Threats to the species in each river must be assessed. Some threats such as gravel dredging and point source pollution may be fairly obvious to determine. However, other subtle factors may be adversely impacting the species.

1.3.4 Solicit information on proposed and planned projects that may impact the species. If the species is to be delisted, the Service must be assured that there are no proposed and/or planned projects that could likely jeopardize the continued existence of the species. Once all negative factors are assessed, those that would seriously affect the species will need to be minimized in order to effect recovery for the species.

1.3.5 Evaluate the potential threat to the species of overcollecting. If overcollecting is a threat, methods to control it should be implemented. However, such restrictions should not unduly interfere with legitimate and beneficial research that will aid in recovery of the species.

1.3.6 Determine measures that are needed to minimize and/or eliminate any adverse impacts and implement when necessary to meet the criteria outlined in the recovery objectives.

1.4 Solicit help in protecting the species and its essential habitat. Section 7 consultation under the Endangered Species

Act and Fish and Wildlife Coordination activities can assist in protecting the species, but these activities alone cannot recover the species. The assistance of other Federal agencies as well as state and local governments will be essential. Also, support of the local industrial and business community, as well as local people, will be needed to meet the goal of recovering the species. Without a commitment from the people in these river valleys who have an influence on habitat quality, the recovery effort will be doomed.

1.4.1 Inform local government officials and regional and local planners of our plans to attempt recovery and request their support.

1.4.2 Request local, state, and Federal agencies to utilize their authorities to protect the species and its river habitat.

1.4.3 Meet with local industry interests and try to elicit their support in implementing protective actions. Gaining cooperation from industries responsible for adverse impacts is an essential and most direct way to gain protective action for meeting recovery goals.

1.4.4 Meet with landowners adjacent to the species' population centers and inform them of the project and try to get their support in habitat protection measures. Private land owners may be unaware of adverse effects from their land use adjacent to species population centers; therefore, diplomacy may have to be substituted for authority to gain positive support of the recovery program and responsible protection.

1.4.5 Develop an educational program using such items as slide/tape shows, brochures, etc. Present this material to business groups, civic groups, Boy Scouts, church organizations, etc. Educational material outlining the goals of the recovery action with emphasis on the other benefits of maintaining and upgrading habitat quality will be extremely useful in informing the public of our actions.

1.5 Investigate the use of Scenic River Status and/or other designations to protect the species. Scenic River Status or other designations that recognize a particular river resource may be useful in protecting the river and thus aiding in the perpetuating of the species.

2. Determine the feasibility of reestablishing the species back into its historic range and introduce where feasible and necessary to

meet recovery objectives. Introductions may be necessary in order to increase the number of populations of spotfin chubs and thus increase the security of the species. In some cases, introductions will involve other streams outside its present range. However, introductions may also be useful to accelerate the expansion of the species within a stream presently inhabited by the species.

2.1 Survey rivers within the species' historic range to determine the availability and location of suitable transplant sites. This can include areas for population expansion within rivers where the species presently exists. The first step in the reintroduction of the species will be to locate suitable habitat for transplants. The information collected under Section 1.1.2 will be essential in locating these sites.

2.2 Investigate and determine the best method of establishing new populations, i.e., introduction of adults, juveniles, artificially raised individuals, or other means or combinations. Sufficient stock may not be available in the streams presently inhabited by the species to allow for enough chubs to be taken from these rivers to meet the needs for successful introductions. It may be necessary to artificially rear the species in a hatchery situation and use these individuals for stocking new rivers.

2.3 Where needed to meet the recovery objectives, reestablish the species within historic range where it is likely it will become established. If habitat is available, introductions are likely to succeed, and introductions are needed to meet the recovery objectives, the reestablishment of the species into other rivers within its historic range should proceed.

2.4 Implement the same protective measures for these introduced populations as outlined for established populations in numbers 1.3 through 1.5 above.

3. Conduct life history studies not covered under section 1.1.2 above, i.e., age and growth, reproductive biology, longevity, natural mortality factors, and population dynamics. Much of the information needed to manage the species will be available after completion of the tasks outlined in 1.1.2. However studies involving the fish's life history will likely be required to fully understand the response of the species to protective measures.

4. Investigate the necessity for habitat improvement and, if feasible and necessary to meet recovery, develop techniques and sites for habitat improvement and implement. Specific components of the chubs' habitat may be missing and these may limit the potential expansion and reintroduction of the species. Habitat improvement programs and activities may be helpful in alleviating these limiting factors.

5. Develop and implement a program to monitor population levels and habitat conditions of presently established populations as well as introduced and expanding populations. Once recovery actions are implemented, the response of the chub and its habitat must be monitored to assess any progress towards recovery. This will likely require an biannual census schedule.

6. Annually assess overall success of recovery program and recommend action (Changes in recovery objectives delist, continued protection, implement new measures, other studies, etc.). The recovery plan must be evaluated periodically to determine if it is on track and to recommend future actions. As more is learned about the species, the recovery objectives may need to be modified.

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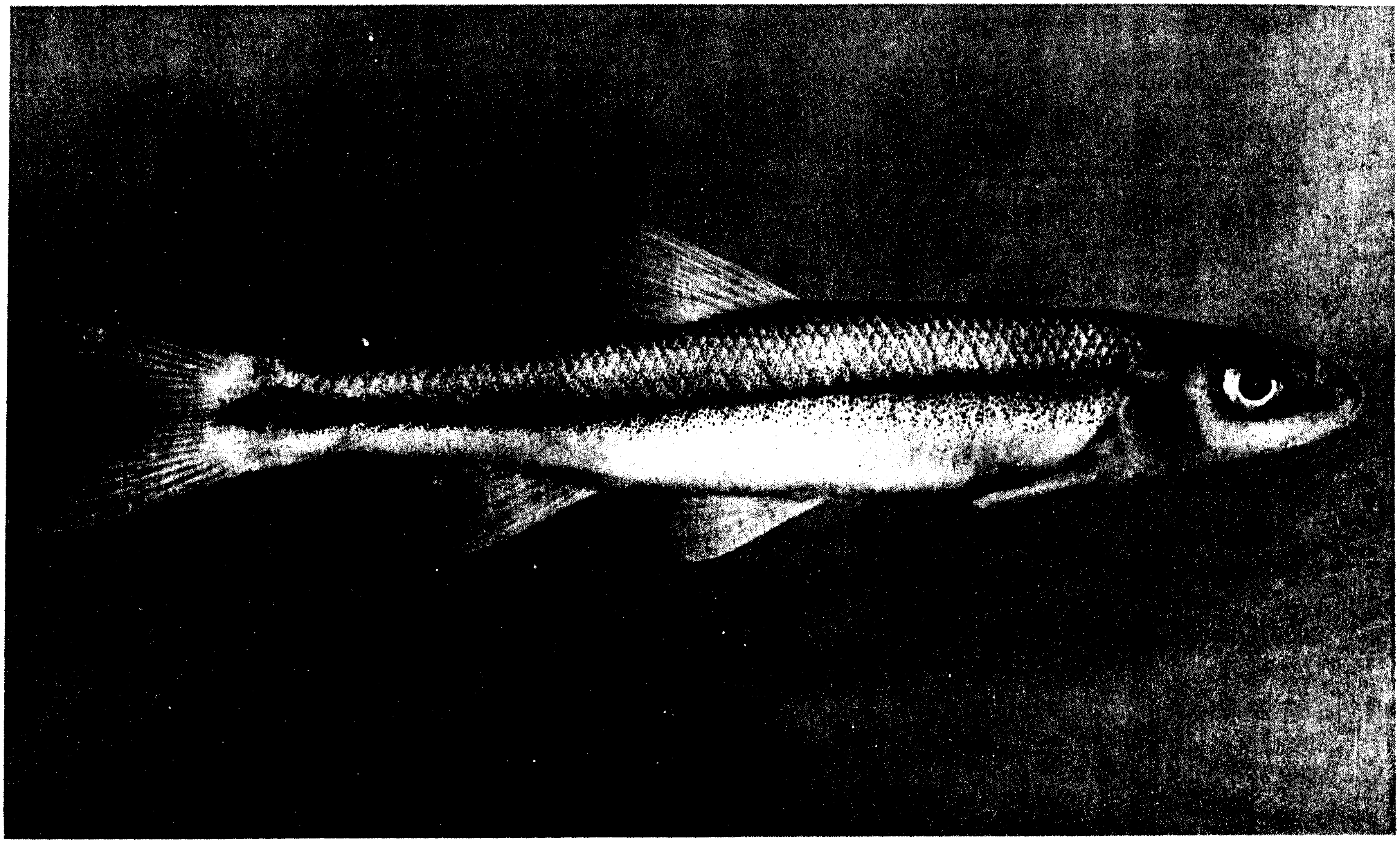

Spotfin Chub (<u>Hybopsis</u> <u>monacha</u>)

PART III.

IMPLEMENTATION SCHEDULE

Priorities within this section (Column 4) have been assigned according to the following:

Priority 1 - Those actions absolutely necessary to prevent extinction of the species.

Priority 2 - Those actions necessary to maintain the species' current population status.

Priority 3 - All other actions necessary to provide for full recovery of the species.

Spotfin Chub

Part III Implementation Schedule

1* General Category	Plan Task	Task Number	Priority	Task Duration	Responsible Agency FWS Region	Responsible Agency FWS Program	Responsible Agency Other 2*	Estimated Fiscal Year Costs FY 1	Estimated Fiscal Year Costs FY 2	Estimated Fiscal Year Costs FY 3	3* Comments/Notes
01-04	Continue to utilize existing legislation and regulations to protect species and habitat	1.1	2	continuous	4&5	SE&ES	Tennessee Valley Authority (TVA) Tn. Wildlife Resources Agcy. (TWRA) Va. Comm. of Game & Inland Fisheries (VCGIF) Tennessee Heritage Program (THP) NC Natural Heritage Program (NCNHP), NC Wildlife Resources Commission (NCWRC)	1,000	1,000	1,000	*1. See attachment: general categories for Implementation Schedules *2. Other agencies' responsibility would be of a cooperative nature or projects funded under a contract or grant program. In some cases contracts could be let to universities or private enterprises.
I1,I2	Determine species present distribution and status	1.2.1	3	1 yr.	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP& NCWRC	20,000	---	---	*3. Note: <u>ALL ESTIMATES ARE FOR FWS FUNDS ONLY</u>
R3,R8, R9,R10 R11	Characterize habitat and determine essential elements	1.2.2	3	2 yr	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP& NCWRC	---	10,000	---	
R3,02, M3	Determine the extent of preferred habitat and present information in a manner which identifies areas in need of species attention	1.2.3 & 1.2.4	3	1 yr	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP& NCWRC	---	---	5,000	
I12,I14	Determine present and foreseeable threats to species	1.3.1 1.3.2 1.3.3 1.3.4 & 1.3.5	3		4&5	SE&ES	TWRA,VCGIF TVA,THP,NCNHP& NCWRC	6,000	---	---	

Spotfin Chub

Part III Implementation Schedule

General Category	Plan Task	Task Number	Priority	Task Duration	Responsible Agency			Estimated Fiscal Year Costs			Comments/Notes
					FWS						
					Region	Program	Other	FY 1	FY 2	FY 3	
M3,M7	Determine measures needed to minimize threats and implement where needed to meet recovery	1.3.6	3	Unknown	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP, NCWRC & TN,VA& NC Nature Conservancy (TNC)	---	Unknown	---	
01,04	Solicit help in protecting species and essential habitat	1.4.1 1.4.2 1.4.3 1.4.4	3	Continuous	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP NCWRC&TNC	2,000	2,000	2,000	
01	Develop and utilize information and education programs (slide/tape shows, brochures, etc) for local distribution	1.4.5	3	1 yr for devel. continuous implementation	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP, NCWRC&TNC	5,000	1,000	1,000	
I13	Survey rivers within species' historic range to determine availability of suitable transplant sites	2.1	3	1 yr.	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP, NCWRC&TNC	---	5,000	---	
R13, R7	Determine best method of establishing new populations	2.2	3	2 yr.	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP& NCWRC	---	---	2,000	Task 2.1 - 2.3 may not be required if other populations are found in task 1.2.1
M2	Reestablish populations within historic range as needed to meet recovery	2.3	3	Unknown	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP& NCWRC	---	---	---	

Spotfin Chub

Part III Implementation Schedule

General Category	Plan Task	Task Number	Priority	Task Duration	Responsible Agency			Estimated Fiscal Year Costs			Comments/Notes
					FWS						
					Region	Program	Other	FY 1	FY 2	FY 3	
I12,I14 M3,M7	Implement same protective measures for these re-established populations as for known populations	2.4	3	Continuous	4&5	SE,ES	TWRA,VCGIF TVA,THP,NCNHP& NCWRC	---	---	---	
R8-R11	Conduct life history studies on a need-to know basis	3.	3	Unknown	4&5	SE	TWRA,VCGIF THP,TVA,NCNHP& NCWRC	---	Unknown	---	These studies will be developed and carried out where there is a specific need for data necessary to reach recovery
M3	Investigate the need for habitat improvement and implementation only where needed to meet recovery objective	4.	3	Unknown	4&5	SE	TWRA,VCGIF THP,TVA,NCNHP& NCWRC	---	Unknown	---	
I1,I2	Develop and implement a monitoring program	5.	3	Unknown	4&5	SE	TWRA,VCGIF THP,TVA,NCNHP& NCWRC	---	---	5,000	
04	Annual assessment of recovery program and modify where needed	6.	3	Continued	4&5	SE	TWRA,VCGIF TVA,THP,NCNHP, NCWRC&TNC	500	500	500	

GENERAL CATEGORIES FOR IMPLEMENTATION SCHEDULES *

Information Gathering - I or R (research)

1. Population status
2. Habitat status
3. Habitat requirements
4. Management techniques
5. Taxonomic studies
6. Demographic studies
7. Propagation
8. Migration
9. Predation
10. Competition
11. Disease
12. Environmental contaminant
13. Reintroduction
14. Other information

Management - M

1. Propagation
2. Reintroduction
3. Habitat maintenance and manipulation
4. Predator and competitor control
5. Depredation control
6. Disease control
7. Other management

Acquisition - A

1. Lease
2. Easement
3. Management agreement
4. Exchange
5. Withdrawal
6. Fee title
7. Other

Other - O

1. Information and education
2. Law enforcement
3. Regulations
4. Administration

* (Column 1) - Primarily for use by the U.S. Fish and Wildlife Service.

APPENDIX

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3-2011

The Forgotten Stage of Forest Succession: Early-Successional Ecosystems on Forest Sites

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The forgotten stage of forest succession: early-successional ecosystems on forest sites

Mark E Swanson[1]*, Jerry F Franklin[2], Robert L Beschta[3], Charles M Crisafulli[4], Dominick A DellaSala[5], Richard L Hutto[6], David B Lindenmaver[7], and Frederick J Swanson[8]

Early-successional forest ecosystems that develop after stand-replacing or partial disturbances are diverse in species, processes, and structure. Post-disturbance ecosystems are also often rich in biological legacies, including surviving organisms and organically derived structures, such as woody debris. These legacies and post-disturbance plant communities provide resources that attract and sustain high species diversity, including numerous early-successional obligates, such as certain woodpeckers and arthropods. Early succession is the only period when tree canopies do not dominate the forest site, and so this stage can be characterized by high productivity of plant species (including herbs and shrubs), complex food webs, large nutrient fluxes, and high structural and spatial complexity. Different disturbances contrast markedly in terms of biological legacies, and this will influence the resultant physical and biological conditions, thus affecting successional pathways. Management activities, such as post-disturbance logging and dense tree planting, can reduce the richness within and the duration of early-successional ecosystems. Where maintenance of biodiversity is an objective, the importance and value of these natural early-successional ecosystems are underappreciated.

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Severe natural disturbances - such as wildfires, windstorms, and insect epidemics - are characteristic of many forest ecosystems and can produce a "stand-replacement" event, by killing all or most of the dominant trees therein (Figure 1). Typically, limited biomass is actually consumed or removed in such events, but many trees and other organisms experience mortality, leaving behind important biological legacies (structures inherited from the pre-disturbance ecosystem; Franklin *et al.* 2000), including standing dead trees and downed boles (tree trunks; Franklin *et al.* 2000). Such legacies provide diverse physical/biological properties and suitable microclimatic conditions for many species. Thereafter, species-diverse plant communities develop because substantial amounts of previously limited resources (light, moisture, and nutrients) become available. These emerging plant communities create additional habitat complexity and provide various energetic resources for terrestrial and aquatic organisms.

In a nutshell:

- Naturally occurring, early-successional ecosystems on forest sites have distinctive characteristics, including high species diversity, as well as complex food webs and ecosystem processes
- This high species diversity is made up of survivors, opportunists, and habitat specialists that require the distinctive conditions present there
- Organic structures, such as live and dead trees, create habitat for surviving and colonizing organisms on many types of recently disturbed sites
- Traditional forestry activities (eg clearcutting or post-disturbance logging) reduce the species richness and key ecological processes associated with early-successional ecosystems; other activities, such as tree planting, can limit the duration (eg by plantation establishment) of this important successional stage

The ecological importance of early-successional forest ecosystems (ESFEs) has received little attention, except as a transitional phase, before resumption of tree dominance. In forestry, this period is often called the "cohort re-establishment" or "stand initiation" stage, with attention obviously focused on tree regeneration and the re-establishment of closed forest canopies (Franklin *et al.* 2002). Ecological studies have focused primarily on plant-community development and the needs of selected animal (mostly game) species, and not on the diverse ecological roles of ESFEs.

Here, we highlight important features of ESFEs, including their role in sustaining ecosystem processes and biodiversity, so that they may be appropriately considered by resource managers and scientists, and included within management/research programs dedicated to maintaining these functions, particularly at larger spatio-temporal scales. Most published examples focus on sites in western North America, but ESFEs are important elsewhere (Angelstam 1998; DeGraaf et *al.* 2003). We also discuss how traditional forestry practices, such as clearcutting, tree planting, and post-disturbance logging, can affect early-successional communities.

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Frontiers in Ecology and the Environment

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esa

Figure 1. *Stand-replacement disturbance events in forests create large areas free of tree dominance and rich in physical and biological resources, including legacies of the pre-disturbance ecosystem.*

Early-successional ecosystems on forest sites

Initial conditions after stand-replacing forest disturbances vary generically, depending on the type of disturbance; this includes the types of physical and biological legacies available. For example, aboveground vegetation may be limited immediately after the disturbance, as in the case of severe wildfires or volcanic eruptions. Conversely, intact understory communities may persist where forests have been blown down by severe windstorms. Spatial heterogeneity in conditions is characteristic, given that disturbances vary greatly in the amount of damage they cause (Turner *et al.* 1998). For instance, severe wildfires frequently include substantial areas of unburned as well as low to medium levels of mortality, creating variability in shade, litterfall, soil moisture, seed distribution, and other factors.

We define ESFEs as those ecosystems that occupy potentially forested sites in time and space between a stand-replacement disturbance and re-establishment of a closed forest canopy. These ecosystems undergo compositional and structural changes (succession) during their occupancy of a site. Changes begin immediately post-disturbance, as a result of the activities of surviving organisms (eg plants, animals, and fungi), including plant growth and seed production. Developmental processes are enriched by colonization of flora and fauna from outside the disturbed area. Successional change is often characterized by progressive dominance of annual and perennial herbs, shrubs, and trees, although all of these species are typically represented throughout the entire sequence of forest stand development (or sere; Halpern 1988).

The ESFE developmental stage ends with re-establishment of tree cover that is sufficiently dense to suppress and often eliminate many smaller shade-intolerant plants (Franklin *et al.* 2002). Consequently, the duration of ESFEs varies inversely with rapidity of tree regeneration and growth, which, in turn depend on such variables as tree propagule availability, conditions affecting seedling or sprout establishment, and site productivity. ESFE longevity after natural disturbances is therefore highly variable.

Development of a closed forest canopy may require a century or more in areas with limited seed sources, harsh environmental conditions, severe shrub competition (in some instances), or combinations thereof (Hemstrom and Franklin 1982). For example, tree canopy closure after wildfire in the Douglas fir region of western North America often requires several decades (Poage *et al.* 2009), but can occur much more rapidly when canopy seedbanks are abundant (eg Larson and Franklin 2005). Closed forest canopies may develop quickly in forests dominated by trees with strong sprouting ability (eg many angiosperms) or when windstorms "release" understories of shade-tolerant tree seedling banks by removing all or most of the overstory (Foster *et al.* 1997).

Attributes of early-successional ecosystems

After severe disturbances, forest sites are characterized by open, non-tree-dominated environments, but have high levels of structural complexity and spatial heterogeneity and retain legacy materials.

Environmental conditions

Removal of the overstory forest canopy during disturbances dramatically alters the site's microclimate, including light regimes. These changes lead to increased exposure to sunlight, more extreme temperatures (ground and air), higher wind velocities, and lower levels of relative humidity and moisture in litter and surface soil. Shifts in these environmental metrics favor some species, while creating suboptimal or intolerable conditions for others. For example, post-disturbance plant community composition, cover, and physiognomy are altered as shade-tolerant understory herbs are largely displaced by shade-intolerant and drought-tolerant species. New substrates deposited by floods or volcanic eruptions may lack nutrients, provide additional water-holding capacity, or have high albedo, all of which favor shifts in plant communities.

Survivors

Organisms (in a variety of forms) that survive severe disturbances are extremely important for repopulating and restoring ecosystem functions in the post-disturbance landscape. Even in severely disturbed areas, organisms may survive as individuals (mature or immature) or as reproductive structures (eg spores, seeds, rootstocks, and eggs), which become in situ propagule sources. For example, after the 1980 volcanic eruption of Mount Sr Helens (Washington State), most pre-eruption flora and many fauna (especially aquatic and burrowing terrestrial species) survived within the blast zone through several different mechanisms (Dale *et al. 2005).*

Surviving organisms are also often vital for the prompt re-establishment of important ecosystem functions, such as conservation of nutrients and stabilization of substrates. For instance, the important role of resprouting vegetation in curbing massive losses of nitrogen was demonstrated by experimentally clearcutting and applying herbicides in a watershed at Hubbard Brook Experimental Forest (Bormann and Likens 1979).

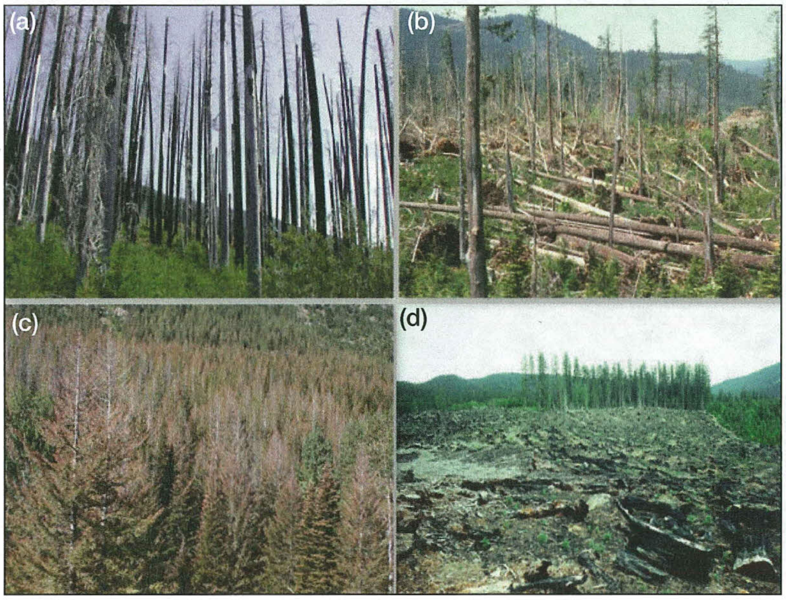

Figure 2. *Different types of disturbances produce different types of biological legacies, including living organisms and structures: (a) standing dead trees (snags) are dominant structural legacies after severe wildfires; (b) downed tree trunks and nearly intact understory communities are characteristic legacies after major windstorms; (c) standing dead trees are also dominant structural legacies after heavy insect infestations; and (d) clearcuts typically eliminate most aboveground structural legacies. Values for each metric are shown in Table 1 and are described in detail in the text.*

Structural complexity

The structural complexity of ESFEs depends initially on legacies, the general nature of which varies with the type of disturbance (Table 1; Figure 2); for example, snags and shrubs originating from belowground perennating (ie resprouting) parts or seeds are dominant legacies after wildfires, whereas downed boles and largely intact understories are typical post-disturbance characteristics of windstorms.

Woody legacies, such as snags and downed boles, play numerous roles in structuring and facilitating the development of the recovering ecosystem - providing habitat for survivors and colonists, moderating the physical environment, enriching aquatic systems in the disturbed area (Jones and Daniels 2008), and providing long-term sources of energy and nutrients (Harmon *et al. 1986).* Although subject to decomposition, these legacies can persist for many decades and sometimes even centuries.

Table 1. Different types of intense disturbances generate different types of biological legacies

	Disturbance				
Biological legacies	*Wildfire*	*Wind*	*Insect*	*Volcano*	*Clearcut*
Live trees	Infrequent	Variable	Variable (depends on stand composition)	Infrequent – confined to margins	Infrequent or absent
Snags	Abundant	Variable	Abundant	Abundant (spatially variable)	Infrequent or absent
Downed woody debris	Variable, but typically abundant	Abundant	Variable, but eventually abundant	Abundant (spatially variable)	Infrequent
Undisturbed understory	Infrequent	Abundant	Abundant	Infrequent – confined to disturbance margins	Infrequent
Spatial heterogeneity of recovery	High	Variable	High	High	Variable – usually low
Time in early-successional condition	Variable	Variable	Long	Variable – usually long	Variable – usually short

Figure 3. *Plant communities with well-developed shrub and perennial herb species are characteristic of early-successional communities on forest sites and provide diverse food resources. Twenty-five years after the Mount St Helens eruption in 1980, this community, which was within the blast zone, includes well-developed shrubs (eg* Sorbus *and* Vaccinium *spp), trees, and perennial herbs (eg* Epilobium angustifolium*).*

Structural complexity is further enhanced by the establishment and development of a variety of plant species, which often include perennial herbs and shrubs characteristic of open environments, as well as individual trees (Figure 3). The diversity of plant morphologies (maximum height, crown width, etc) increases structural richness, so that this associated flora contributes to both horizontal and vertical heterogeneity.

Spatial heterogeneity

Spatial heterogeneity is evident in early-successional ecosystems and has multiple causes: (1) natural variability in the geophysical template (topography and lithology) of the affected landscape; (2) variability in conditions in the pre-disturbance forest ecosystem; (3) variability in the intensity of the disturbance event; and (4) variability in rates and patterns of subsequent developmental processes in the ESFE. The first two sources relate to existing geophysical and biological patterns within the disturbed area. Land formations and patterns of geomorphic processes are certainly key geophysical elements (Swanson et *al.* 1988). The presence of surface water, such as streams and ponds, can be particularly influential in facilitating survival and re-establishment of biota.

Natural disturbances create heterogeneous environments at multiple spatial scales (Heinselmann 1973), because disturbances do not cause damage uniformly. Disturbances such as wildfires and windstorms are variable in intensity (eg "spotting", or initiation of new flame fronts by wind-thrown firebrands, during fire events). Alternatively, geographic variation in environmental conditions and topography (Swanson et *al.* 1988) influences the intensity of the disturbance and results in heterogeneity at multiple scales. Variability in the structure and composition of the pre-disturbance forest also creates spatial and temporal variability (Wardell-Johnson and Horowitz 1996). Some of these patterns may be transient, such as residual snowbanks protecting tree regeneration after the aforementioned Mount St Helens eruption (Dale et *al.* 2005).

Post-disturbance developmental processes also lead to spatial heterogeneity. For example, varying distances to sources of tree seed result in different rates and densities of tree re-establishment (Turner et *al.* 1998). Structural legacies can greatly influence the rates at which wind- or waterborne organic (including propagules) and inorganic materials are deposited. Finally, animal activity can strongly influence patterns of revegetation, as illustrated by the multiple effects that gophers (*Thomomys* spp) can have on post-disturbance landscapes (Crisafulli et *al.* 2005b) or the way ungulate browsing may impede tree regeneration (Hessl and Graumlich 2002).

■ Biological diversity

ESFEs in temperate forest seres show great diversity in the abundance of plant and animal species (Fontaine et *al.* 2009). Species composition may consist of a mix of forest survivors, opportunists, or ruderals (plants that grow on disturbed or poor-quality lands), and habitat specialists that co-exist in the resource-rich ESFE environment (Figure 3). Most forest understory flora can survive disturbances as established plants, perennating rootstocks, or seeds. In one study, in western North America, over 95% of understory species survived the combined disturbance of logging and burning of an old-growth Douglas-fir-western hemlock stand (Halpern 1988). Some important early-successional species (eg *Rubus* spp [blackberry; raspberry], *Ribes* spp [gooseberry], and *Ceanothus* spp [buckbrush]) may persist as long-lived seedbanks.

Opportunistic herbaceous species are often conspicuous dominants early in the development of ESFEs (Figure 4). Many of these weedy species (particularly annuals) decline quickly, although other opportunists will persist as part of the plant community until overtopped by slower growing shrubs or trees. Consequently, diverse plant communities of herbs, shrubs, and young trees emerge in ESFEs; this, combined with the structural legacies from the pre-disturbance ecosystem, often results in high levels of structural richness (Figure 3).

Many animals, including habitat specialists and species typically absent from the eventual tree-dominated com-

Figure 4. *Early-successional communities are often dominated by annual herbaceous species for the first few years after disturbance; these are quickly displaced by perennial herbaceous species and shrubs.*

munities, thrive under the conditions found in ESFEs. For some species, this is the only successional stage that can provide suitable foraging or nesting habitat. As an example, many butterflies and moths (Lepidoptera) found in forested regions depend on the high diversity and quality of plant forage in ESFEs (eg Miller and Hammond 2007), whereas jewel beetles (Coleoptera: Buprestideae) depend on abundant coarse woody debris. Also, a number of ground-dwelling beetle species occur as habitat specialists in early-successional communities (Heyborne *et* al. 2003).

Many vertebrates also respond positively to ESFEs, which may provide the only suitable habitat at a regional scale for some species. Ectothermic animals, such as reptiles (eg Rittenhouse *et* al. 2007), generally respond favorably to sunnier and drier conditions, colonizing early-successional habitat or increasing in abundance if present as survivors. Many amphibians also thrive in ESFEs, provided resources such as water bodies and key structures (eg logs) are available. The diversity and abundance of amphibians in the area affected by the 1980 Mount St Helens eruption is illustrative (Crisafulli *et* al. 2005a); eleven of 15 amphibian species survived the event, and some (eg western toad, *Bufo boreas)* have since had exceptional breeding success.

The broad array of birds using the abundant and varied food sources (eg fruits, nectar, herbivorous insects) and nesting habitat in ESFEs includes many raptors and neotropical migrants, often making bird diversity highest during the ESFE stage of succession (Klaus *et* al. in press). Some species are habitat specialists that directly utilize the legacy of recently killed trees; for instance, black-backed woodpeckers (Picoides *arcticus)* are almost completely restricted to early post-fire conditions (Hutto 2008). Mountain bluebirds *(Sialia currucoides)* and several other woodpecker species also favor structurally rich, early-successional habitats (Figure 5). Observed population declines of many avian species in eastern North America-which, in some cases, have proceeded to a point of conservation concern - are linked to conversion of early-successional habitat to closed forest (Litvaitis 1993).

Small mammal communities in ESFEs typically show high levels of diversity as well, including some obvious habitat specialists. The eastern chestnut mouse *(Pseudomys gracilicaudatus),* for example, inhabits early-successional environments in coastal eastern Australia for 2-5 years after a wildfire, and then declines dramatically until these environments are burned again (Fox 1990). Populations of mesopredators (medium-sized predators, such as raccoons *[Procyon lotor]* and fox species) benefit from the abundance of small vertebrate prey items characteristic of ESFEs. Likewise, some species of large mammals are well known to favor ESFEs (Nyberg and Janz 1990). Utilizing the diverse and luxuriant forage characteristically present in these ecosystems, ungulates, such as members of the Cervidae, in turn serve to benefit large predators (eg wolves *[Canis lupus])* as well as scavengers, making ESFEs important elements within those species' typically extensive home ranges. Omnivores, such as bears *(Ursus* spp), also rely on the diversity of food sources often present in ESFEs.

Food web diversity

ESFEs are exceptional in the diversity and complexity of food webs they support. Simply stated, a diverse plant community produces many food sources. Food resources for herbivores (grasses, shrubs, forbs) - as well as nectar, seeds, and shrub-borne fruit (eg produced by *Rubus* and *Vaccinium* spp [huckleberry]) - can reach high levels before site dominance by trees. In the temperate Northern Hemisphere, biologically important berry production is maximized in slowly reforesting ESFEs. Resource production in early-successional patches may even augment the richness of adjacent undisturbed forests, as in the case of fluxes of key prey species (Sakai and Noon 1997).

Aquatic biologists have, perhaps, best appreciated the greater complexity of food chains in early-successional versus closed forest environments (Bisson *et* al. 2003). In established forest stands, trees strongly dominate the physical and biological conditions in nearby small streams by controlling light and temperature, stabilizing channels, providing woody debris, and, importantly, offering allochthonous inputs (organic matter originating outside the aquatic ecosystem) - the primary energy and nutrient source for such ecosystems (Vannote *et* al. 1980).

Stand-replacement disturbances remove forest constraints on conditions and processes, and shift streams to an early-

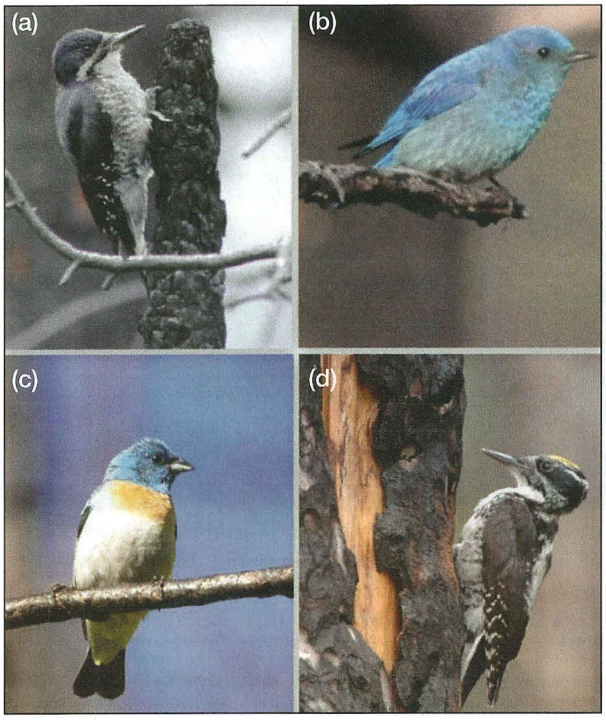

Figure 5. *Bird diversity is typically high in early-successional communities on forest sites and includes many habitat specialists: (a) black-backed woodpeckers (*Picoides arcticus*) are almost entirely restricted to early post-fire habitat; (b) mountain bluebirds (*Sialia currucoides*) favor early-successional ecosystems; (c) lazuli buntings (*Passerina amoena*) and (d) three-toed woodpeckers (*Picoides tridactylus*) have similar requirements.*

successional context (Minshall 2003; Figure 6). This greatly diversifies the rypes and timing of allochthonous inputs, as well as increases primary productiviry. Allochthonous inputs are shifted from primarily tree-derived litter (coniferous-based in many systems) to material from a range of flowering herbs, shrubs, and trees, as well as from conifers. Consequently, litter inputs are highly variable in qualiry (eg decomposability) and delivery time, as compared with litterfall contributed primarily by evergreen conifer species. Also, inputs to post-disturbance streams often include material with a high nitrogen content, such as litter from the early-successional genera *Alnus* and *Ceanothus* (Hibbs *et al.* 1994).

Greater algal production may increase the diversity and abundance of aquatic invertebrate populations, which, in turn, become prey for fish and other organisms. However, increases in sediment production associated with disturbances can negate some benefits to aquatic processes and organisms (Gregory *et al. 1987).*

■ Processes in ESFEs

Ecosystem processes in ESFEs can be more diverse than those in closed forest systems, where the primary productivity of trees is dominant and organic matter is processed primarily through detrital food webs. Development of more diverse, and perhaps more "balanced", trophic pathways is possible when a disturbance opens a previously closed forest canopy. The contrast is probably greatest in forests dominated by a single tree type, such as evergreen conifers, as opposed to more diverse forests, such as mixed evergreen associations.

Recharging nutrient pools

ESFEs provide major opportunities for recharge of nutrient pools, such as additions to the nitrogen pool by leguminous (eg *Lupinus)* and some non-leguminous early-successional (eg *Alnus* and *Ceanothus)* plant species. These genera are commonly absent from late-successional forests, but are well represented in ESFEs. Nitrogenous additions from these sources are particularly important where the disturbance - eg a wildfire - has volatilized a substantial amount of the existing nitrogen pool.

Mineralization rates of organic material are rypically accelerated (sometimes profoundly) after disturbances, as a result of warmer growing season temperatures. Diversified litter inputs in ESFEs, including a greater proportion of easily decomposed litter from herbs and deciduous shrubs, also result in more rapid mineralization. Finally, successional changes in the fungal and microbial communities can also hasten decomposition processes. As noted, these changes will be most profound in forest ecosystems dominated by a single species, including evergreen conifers or hard-leaved, evergreen hardwoods (such as the ash-type eucalypt forests of southeastern Australia).

In aquatic ecosystems that experience fire in adjacent forests, greater post-disturbance light and nutrient availability enhance primary productivity within the water body, causing shifts in food webs from the level of primary producers up through high-level consumers, such as fish (Spencer *et al. 2003).*

Modifying hydrologic and geomorphic regimes

Hydrologic regimes associated with ESFEs contrast greatly with those characterizing closed forest cover. For example, transpiration and interception are dramatically reduced and recover only gradually as forest canopies redevelop. Increases in normally low summer flows and annual water yields may occur immediately after a disturbance, as compared with levels in the dense young forests that may subsequently develop (Jones and Post 2004). The opposite may be true in systems where condensation of cloud or fog on tree crowns is an important component of the hydrologic cycle. ESFEs may also contribute to increased discharge peak runoff flows in hydrologic events of smaller magnitude (Harr 1986), but appear to have little effect on the magnitude of peak flows during large runoff events (Grant *et al.* 2008). From an ecological perspective, this may have a positive outcome, however, because floods restructure and rejuvenate many riparian communities (Gregory *et al.* 1991).

Rates and patterns of geomorphic processes, such as erosion and nutrient leaching losses, are also different between ESFEs and later successional stages. Tree death results in a loss of root strength that is critical for stabilizing soils and deeper rock layers on mountain slopes (Perry *et al.* 2008). Erosion and landslides may occur at higher rates in ESFEs, contributing to the variability of sediment budgets in watersheds (Reeves *et al.* 1995) and creating long-lasting substrates for ruderals. While enhancing erosion processes, ESFEs also provide materials and processes that counteract this effect, such as woody debris, which retain sediments and organic materials, and surviving vegetation, which stabilizes slopes and nutrient stores (eg Bormann and Likens 1979).

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Figure 6. *Streams within early-successional forest ecosystems contrast with forest-dominated reaches in many ecosystem attributes, including physical parameters (temperature and insolation), structure, plant and animal composition, and ecosystem processes, such as primary productivity.*

■ Land management implications

Incorporating ESFE attributes into forest policy and management is highly desirable, given the numerous advantages provided by these ecosystems. Many species and ecological processes are strongly favored by conditions that develop after stand-replacement disturbances. Rapid, artificially accelerated "recovery" of disturbed forest areas (eg via dense planting) to closed forest conditions has serious implications for many species. Clearly the term "recovery" has a different meaning for such early-successional specialists or obligates.

To fulfill their full ecological potential, ESFEs require their full complement of biological legacies (eg dead trees and logs) and sufficient time for early-successional vegetation to mature. Where land managers are interested in conservation of the biota and maintenance of ecological processes associated with such communities, forest policy and practices need to support the maintenance of structurally rich ESFEs in managed landscapes. Natural disturbance events will provide major opportunities for these ecosystems, and managers can build on those opportunities by avoiding actions that (1) eliminate biological legacies, (2) shorten the duration ofthe ESFEs, and (3) interfere with stand-development processes. Such activities include intensive post-disturbance logging, aggressive reforestation, and elimination of native plants with herbicides.

In particular, post-disturbance logging removes key structural legacies, and damages recolonizing vegetation, soils, and aquatic elements of disturbed areas (Foster and Orwig 2006; Lindenmayer *et al.* 2008). Where socioeconomic considerations necessitate post-disturbance logging, variable retention harvesting (retention of snags, logs, live trees, and other structures through harvest) can maintain structural complexity in logged areas (Eklund *et al.* 2009).

Prompt, dense reforestation can have negative consequences for biodiversity and processes associated with ESFEs, by dramatically shortening their duration. Such efforts reduce spatial and compositional variability characteristic of natural tree-regeneration processes, promote structural uniformity, and initiate intense competitive processes that eliminate elements of biodiversity that might otherwise persist. Artificial reforestation can also reduce genetic diversity by favoring dominance by fewer tree species/genotypes, and may make the system more prone to subsequent, high-severity disturbances (Thompson *et al.* 2007). The elimination of shrubs and broad-leaved trees through herbicide application can alter synergistic relationships, such as the belowground mycorrhizal processes provided by certain shrub species (eg *Arctostaphylos* spp).

Naturally regenerated ESFEs are likely to be better adapted to the present-day climate and may be more adaptable to future climate change. The diverse genotypes in naturally regenerated ESFEs are likely to provide greater resilience to environmental stresses than nursery-grown, planted trees of the same species. Given that climate change is also resulting in altered behavior of pests and pathogens (Dale *et al.* 2001), encouraging greater tree species diversity may also increase ecosystem resilience.

Clearcutting has been proposed as a technique to create ESFEs, but this can provide only highly abridged and simplified ESFE conditions. First, traditional clearcuts leave few biological legacies (eg Lindenmayer and McCarthy 2002), limiting habitat and biodiversity potential. Second, clearcuts are often quickly and densely reforested, and often involve the use of herbicides to limit competition with desired tree species. Clearcuts can provide some early-successional functionality (eg serving as nurseries or post-breeding habitat for many bird species in the southern US; Faaborg 2002), but this service is often truncated by prompt reforestation.

Management plans should provide for the maintenance of areas of naturally developing ESFEs as part of a diverse landscape. This should be in reasonable proportion to *historical* occurrences of different successional stages, as based on region-specific historical ecology. Major disturbance events provide managers with opportunities to incorporate a greater diversity of species and processes in forest landscapes and to enhance landscape heterogeneity. Some aspects of ESFEs can be incorporated into areas managed for production forestry as well, such as through variable retention harvest methods, the incorporation of natural tree regeneration, and extending the duration of herb/shrub communities in some portions of a stand by deliberately maintaining low tree stocking levels.

Finally, we suggest that adjustments in language are needed. Ecologists and managers often refer to "recovery" when discussing post-disturbance ecosystems, inferring that early seral conditions are undesirable and need to be restored to closed canopy conditions as quickly as possible. Emphasizing recovery as the management goal fails to acknowledge the essential ecological roles played by early-successional ecosystems on forest sites. It should also be considered that climate change and other factors may not permit "recovery" to pre-disturbance conditions.

• Conclusions

Twentieth-century forest management objectives were centered on wood production and, later, on conservation and development of late-successional forests. Rapid regeneration of dense timber stands was frequently seen as a way to address both of these divergent objectives. Recognizing the ecological value of early-successional ecosystems on forest sites extends the ecological concerns associated with old growth to another "rich" period in a forest sere. This represents an important development in the evolution of holistic management of forest ecosystems, whereby large landscapes are managed for diverse seral stages.

ESFEs provide a distinctive mix of physical, chemical, and biological conditions, are diverse in species and processes, and are poorly represented and undervalued in traditional forest management. Forest policy and practice must give serious attention to sustaining substantial areas of ESFEs and their biological legacies. Similarly, scientists need to initiate research on the structure, composition, and function of ESFEs in different regions and under different disturbance regimes, as well as on the historical extent of these systems, to serve as a reference for conservation planning.

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