

Northern Leopard Frog (*Rana pipiens*): A Technical Conservation Assessment



**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

January 16, 2007

Brian E. Smith, Ph.D.¹ and Douglas A. Keinath²

¹Dept. of Biology, Black Hills State University, 1200 University Street Unit 9044, Spearfish, SD 57799-9044

²Wyoming Natural Diversity Database, University of Wyoming, 1000 East University Ave., Dept. 3381, Laramie, WY 82071

Peer Review Administered by
[Society for Conservation Biology](#)

Smith, B.E. and D.A. Keinath. (2007, January 16). Northern Leopard Frog (*Rana pipiens*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: <http://www.fs.fed.us/r2/projects/scp/assessments/northernleopardfrog.pdf> [date of access].

ACKNOWLEDGMENTS

The authors would like to acknowledge the anonymous reviewers and Charles Painter of the New Mexico Department of Game and Fish for reviews that markedly improved this manuscript.

AUTHORS' BIOGRAPHIES

Dr. Brian Smith is an associate professor in biology at Black Hills State University. His areas of research expertise include herpetology, biostatistics, and landscape ecology. He has conducted herpetological research in the Philippines, Peru, Guam, Costa Rica, Guatemala, and the Caribbean. He has also worked on the herpetofauna of Louisiana, Texas, New Mexico, and Arizona, and he spent four years working in the Department of Herpetology at the Dallas Zoo. For the last 10 years, he has been working on reptiles and amphibians in the Badlands and Black Hills of western South Dakota and in the Bear Lodge Mountains in northeastern Wyoming. Dr. Smith received his B.S. from Washington State University in 1980, his M.S. from Louisiana State University in 1983, and his Ph.D. from the University of Texas at Arlington in 1996.

Doug Keinath is the Senior Zoologist for the Wyoming Natural Diversity Database, a research unit of the University of Wyoming and a member of the Natural Heritage Network. He has been researching Wyoming's wildlife for the past nine years and has 11 years experience in conducting technical and policy analyses for resource management professionals. His broader scope of research focuses on bat and small mammal ecology, survey, and monitoring at the population and landscape scales, and more recently on the spatially explicit predictive distribution modeling of sensitive elements (i.e., animals, plants, communities) of the Rocky Mountain West. Mr. Keinath earned a B.S. in Interdisciplinary Engineering (1993; *magna cum laude*) and a B.S. in Natural Resource Management (1993; with Distinction) from the University of Michigan. In 2000, he earned a M.S. in Wildlife Biology from the University of Wyoming.

COVER PHOTO CREDIT

Northern leopard frogs (*Rana pipiens*). Photograph by Suzanne L. Collins, The Center for North American Herpetology. Used with permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE NORTHERN LEOPARD FROG

The northern leopard frog (*Rana pipiens*) is a widespread species that has experienced significant declines across most of its range, while remaining abundant in some areas. In the Rocky Mountain region, Colorado and Montana legally protect the species. Northern leopard frogs have been lost from wide areas of Montana, but they remain abundant in some parts of the region, such as the Black Hills. The species' status in other parts of the region is unclear. The reasons for this regional variability are under debate. Factors that have been invoked to explain northern leopard frog population declines include habitat destruction, diseases, chemical contamination, acidification of water, increased ultraviolet light due to loss of the ozone layer, introduced predators, overcollecting, climatic changes, and general environmental degradation. However, no one cause has emerged as the primary factor behind population declines. Instead, it is likely that multiple factors are involved and that they vary from site to site.

Because northern leopard frog populations in some parts of the Rocky Mountain region are experiencing declines and are exposed to all of the above threats, the USDA Forest Service (USFS) Rocky Mountain Region (Region 2) has listed the northern leopard frog as a sensitive species. Habitat degradation and elimination are ongoing threats throughout the region, affecting the national forests directly and indirectly. Habitat is degraded in the national forests through the impacts of grazing, recreation, road construction, facilities construction, logging, and hydrologic alteration caused by development of water resources. The rapid population growth of the Rocky Mountain region, in many areas from 20 to 30 percent annually, leads to a variety of negative effects on the species. National Forest System lands are not immune, as urbanized lands encroach on these lands, subdivisions are built on private inholdings, and human commensals (such as dogs or cats) spread out from urban/suburban interfaces. Increased pressure may be placed on the national forests of Region 2 by the expanding population living near these forests as they use the forests in increasing numbers.

We have identified introduced predaceous fish as a major problem for the northern leopard frog. Many studies show the decline or elimination of frogs after the introduction of predaceous fish for recreation, and we are aware of many sites, some far from access routes, in which predaceous fish have been introduced. Not only are these fish introduced by various government agencies, but also by the general public. Also of concern is the establishment of non-native populations of bullfrogs (*Rana catesbeiana*) that may displace native frog species. Reduction of these threats is essential and can be approached at landscape scales only through interagency cooperation and public education.

Intertwined with the problems of habitat degradation, recreational fishing, and the establishment of non-native predators is the potential for the introduction of serious diseases to populations of northern leopard frogs. The fungal disease chytridiomycosis is now well known to be causing frog population declines in many parts of the world. Many studies are ongoing to determine the seriousness of this threat to native frogs, but it is undeniable that the disease can cause major mortality events. In addition, ranavirus, a virus peculiar to ranid frogs like the northern leopard frog, is known to be 100 percent lethal. Chytridiomycosis may be introduced to ponds by the commonly introduced bullfrog.

Malformations have been found in northern leopard frogs in parts of their range. Although these do not kill frogs outright, affected frogs tend to die early and do not reproduce, probably because they are unable to carry out normal functions of feeding and moving from place to place. It is unknown exactly what causes malformations, and multiple agents could be involved.

Other potential factors in frog declines are probably associated with habitat degradation caused by humans, but they are even less easily controlled. Such factors are chemical contamination, acidification of water (either acid rain or runoff from mines and ore processing sites), increased penetration of ultraviolet light with loss of the ozone layer, and general climatic changes, possibly due to global warming. Especially noticeable are the effects of drought, which is common in the Rocky Mountain west. Drought increases pressure on wetlands as sources of water become depleted, and remaining water sources are more heavily visited by wildlife of all sorts, especially by introduced grazers like cattle. Little can be done about some of these problems, but minimizing their effects become important management objectives.

The northern leopard frog is at great risk of decline across its range and that is true in the Rocky Mountain region. Numerous northern leopard frog populations have been lost across the region, and the potential for continued loss is very real. The USFS can play a major role in mitigating losses across large areas of the Rocky Mountain west by reducing habitat loss, fragmentation, and degradation on National Forest System lands through creative management of logging, grazing, road construction, water development projects, and other land uses on the national forests. Creative management solutions should be explored with state wildlife agencies to minimize landscape-scale effects on leopard frogs, such as ways to limit the impacts of introduced predaceous fish on leopard frogs and other amphibians. Such efforts can have secondary positive benefits; in the case of reducing the impacts of predaceous fish, a simultaneous reduction in the spread of lethal diseases into ponds may be achieved.

Management to benefit northern leopard frog populations revolve around several issues. Cattle grazing probably affects this species adversely, and we suggest that suitable ponds (i.e., smaller, semi-permanent ponds with emergent vegetation such as *Typha* spp.) be fenced off from cattle. We also suggest minimal intrusion within a buffer zone of perhaps 200 m around these ponds, although the needed size of buffer zones for maintenance of amphibian populations is poorly understood. Northern leopard frogs disperse along creeks and small riparian areas, and degradation of these waterways is inimical to successful dispersal in the species. Natural and exotic diseases can be introduced through a variety of vectors, including introduced animals and the muddy boots of anglers; movement of these vectors should be minimized to the extent possible. Northern leopard frogs have no defense against introduced predaceous fish, and frog populations can decline and go locally extinct in the presence of such fish. Deliberate and accidental introduction of exotic fish should be minimized to the extent possible. Amphibians of all sorts can be killed on roadways, and roadways can fragment habitat and alter frog dispersal patterns. Road construction also causes siltation, which can smother and kill frog eggs. Runoff from roads can carry oil and other automotive pollutants into waterways, adversely affecting frog populations. Roads should be constructed with an eye towards maintenance of potential dispersal pathways and reduction of pollutants to receiving waterways. Because amphibians can absorb all manner of pollutants, use of pesticides and fertilizers near ponds and linked waterways should be avoided.

The northern leopard frog is one of the best known anurans, but many knowledge gaps remain in Region 2. Habitat fragmentation could be occurring at a damaging level, but this issue has not been studied in any populations of northern leopard frogs. Development could be putting pressure on northern leopard frogs, as it has many species, but the effects of such growth on northern leopard frogs are unknown in Region 2. Development and road building fragments habitat, disrupting dispersal patterns, but the magnitude of the problem is unknown. Anurans utilize pond habitat for reproduction and upland habitat for foraging, but the required size of buffer zones around ponds suitable to conserve populations has not been studied in anurans. Movement patterns of northern leopard frogs are not understood, especially as regards dispersing juveniles. Sources of mortality and their relative importance at various life stages have not been studied in Region 2. Sources of pollutants and their discharge into ponds suitable for reproduction are poorly known. It is not known how extensive the effects of introduced predaceous fish are on mortality of northern leopard frogs in Region 2.

The northern leopard frog is likely to be an important indicator of water quality in ponds in which it occurs. This species is a vital link in trophic structure, and tadpoles can have significant effects as primary consumers of algae in ponds. The northern leopard frog eats many species of insects, although how much it controls pest species is unknown. In turn, many species depend on the northern leopard frog for food. Consequently, it is imperative that this species be managed to maintain a vital link in aquatic ecosystems across the region.

TABLE OF CONTENTS

ACKNOWLEDGMENTS	2
AUTHORS' BIOGRAPHIES	2
COVER PHOTO CREDIT	2
SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE NORTHERN LEOPARD FROG	3
LIST OF TABLES AND FIGURES	7
INTRODUCTION	8
Goal	8
Scope, Uncertainty, and Limitations	8
Peer Review and Web Publication	8
MANAGEMENT STATUS AND NATURAL HISTORY	8
Management Status	8
Federal designations	8
State wildlife agency designations	9
Natural Heritage Program ranks	9
Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies	9
Biology and Ecology	10
Description and systematics	10
Distribution and abundance	11
Population trend	11
Activity and movement patterns	15
Habitat	17
Breeding habitat and tadpole habitat	17
Subadult habitat	18
Adult upland habitat	18
Adult overwintering habitat	18
Food and feeding habits	19
Breeding biology	19
Population demography	21
Community ecology	23
Natural predators	23
Introduced predators	24
Competitors	25
Parasites and disease	25
Envirogram	26
CONSERVATION	29
Conservation Status and Threats	29
Trends	29
Distribution trend	29
Abundance trends	29
Causes of trends	29
Extrinsic threats	30
Intrinsic vulnerability	36
Conservation and Management of the Northern Leopard Frog in Region 2	37
Implications and conservation elements	37
Protection of known and potential breeding sites	38
Control of introduced predaceous fish	38
Protection of overwintering sites	39
Control of introduced infectious diseases	39
Water quality	39
Protection of migratory and dispersal pathways	39
Road-related mortality	39
Control of other factors	39

Tools and practices	40
Considerations for inventory and monitoring	40
Instituting an inventory and monitoring program in Region 2	43
Population and habitat management	46
Information Needs	47
Survey and monitoring	47
Mapping of habitat	47
Characterization of habitat	48
Overwintering habitat	48
Studies of movements	48
Disease, pollution, and limb malformations	48
Effect of introduced predaceous fish	48
Grazing effects	49
Timber removal	49
Effect of roadways	50
Genetic studies	50
Prescribed fire and fire suppression	50
REFERENCES	51

EDITOR: Gary Patton, USDA Forest Service, Rocky Mountain Region

LIST OF TABLES AND FIGURES

Tables:

Table 1. Historic and current abundance and population trends for the northern leopard frog across its range in North America.....	14
--	----

Figures:

Figure 1. Photograph of adult northern leopard frogs.....	10
Figure 2. Probable historic North American range of the northern leopard frog.....	12
Figure 3. Predictive distribution map for the northern leopard frog in the five states of USDA Forest Service Rocky Mountain Region.	13
Figure 4a. Envirogram for larval northern leopard frogs.....	27
Figure 4b. Envirogram for post-metamorphosis northern leopard frogs.	28

INTRODUCTION

Goal

This conservation assessment of the northern leopard frog (*Rana pipiens*) was produced in support of the Species Conservation Project, undertaken by the USDA Forest Service (USFS) Rocky Mountain Region (Region 2). The northern leopard frog was selected for a conservation assessment because USFS Region 2 classifies it as a sensitive species due to observed declines in abundance and distribution across its range in the Rocky Mountain region. This assessment addresses the biology, ecology, and conservation of the northern leopard frog throughout its range in Region 2. Our goal is to provide a current summary of published information and expert interpretation of this information that can be used to develop conservation strategies and management plans.

The northern leopard frog is, or was, one of the most visible and abundant amphibians, occurring in small ponds throughout much of the northern United States and southern Canada. In some places, however, it is now almost completely eliminated. Because dozens of other species also frequent the ponds in which northern leopard frogs breed, conservation of these ponds will have consequences that will reverberate throughout the animal and plant kingdoms. These small ponds are typically ignored by management plans and are often not covered by protective legislation such as the Clean Water Act. It is critical that loss of these wetlands be minimized.

Scope, Uncertainty, and Limitations

The northern leopard frog is one of the best known frogs in North America, and we have attempted to compile the most relevant primary literature on the species. However, the literature is voluminous. We used over 260 citations in this report, and there are still hundreds of other references available in the literature. Where extensive reviews are available for specific topics, we have relied primarily on these reviews for sources, occasionally referring back to the original citations. In most cases, this was not possible, so we extensively cite primary research articles. We have concentrated on literature from the Rocky Mountains but have made liberal use of studies from throughout the range of the northern leopard frog, on the assumption that the biology of the frog should be similar across its range. Even though the species is well known, there are still extensive gaps in our knowledge. These gaps are

mentioned throughout the document but are discussed in detail in the *Information Needs* section.

In this assessment, the strength of evidence from research is noted, and alternative explanations of observational data and expert inference are provided when appropriate. Peer-reviewed literature represents the strongest set of data and is therefore used preferentially to draw conclusions regarding the northern leopard frog. Hypotheses and inferences are noted with appropriate qualifications, and when there is little or no research to support specific ideas, expert opinion was sought.

Peer Review and Web Publication

To make the information in this assessment accessible more rapidly than publication as a book or report, to facilitate its use by USFS personnel, other agencies, and the public, and to make updates and revisions more efficient, this document will be published on the World Wide Web site (<http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml>) of USFS Region 2. A link to this publication also will be available on the web site of the Wyoming Natural Diversity Database (WYNDD, University of Wyoming; <http://uwadmnweb.uwyo.edu/WYNDD>).

In keeping with the standards of scientific publication, assessments developed for the Species Conservation Project have been externally peer reviewed prior to their release on the Web. Under the editorial guidance of Gary Patton (USFS Region 2), this assessment was submitted to scientific peer review, administered by the Society for Conservation Biology, who engaged two recognized experts on this or related taxa to provide critical input on the manuscript.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Federal designations

The northern leopard frog is not listed as threatened or endangered under the Endangered Species Act of 1973. It is listed as a sensitive species by the Northern (Region 1) and Rocky Mountain (Region 2) regions of the USFS (USDA Forest Service 1994, 1999, 2003, 2005), and by the Bureau of Land Management (BLM) state offices in Wyoming (Bureau of Land Management 2001) and Colorado (Bureau of Land

Management 2000). There are no BLM offices in South Dakota, Nebraska, or Kansas, so the BLM does not rank this species in those states.

State wildlife agency designations

The northern leopard frog has no special status (i.e., threatened or endangered) in most states where it occurs, including those in Region 2. However, several states near the periphery of its range do accord the species special status. Northern leopard frogs are considered to be of special concern in Idaho, Colorado, Indiana, and Connecticut, while Montana considers it endangered on the western side of the Continental Divide and of special concern to the east. It is protected in Oregon and classified as endangered in Washington. Despite acknowledging a substantial decline in abundance, the Wyoming Game and Fish Department ranks the northern leopard frog as NSS4 (common with stable habitat) in its Comprehensive Wildlife Conservation Strategy (Wyoming Game and Fish Department 2005), which does not afford it special protection.

Natural Heritage Program ranks

The Natural Heritage Program considers the northern leopard frog to be globally secure (G5). Interestingly, the state heritage programs in Nebraska and South Dakota consider this species to be secure (S5) while the state heritage programs in Colorado and Wyoming consider it vulnerable (S3). This illustrates a common perception that the species is relatively secure across its range in the Great Plains but is relatively rare in the Rocky Mountains. The northern leopard frog does not occur in Kansas.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

We are not aware of any other regulatory mechanisms, management plans, or conservation strategies pertaining specifically to the northern leopard frog. As part of an unpublished report, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; 2000) discussed some aspects of northern leopard frog management, but did not focus explicitly on management. COSEWIC (2000) indicated that it was necessary for upland foraging habitat to be adjacent to breeding ponds to manage the northern leopard frog but did not describe the characteristics of upland foraging habitat. COSEWIC (2000) also

pointed out problems associated with introduced predators, overcollecting, and disease, which we discuss in our conservation assessment. Maxell (2000) covers some aspects of the management of the northern leopard frog as part of a more general publication on the management of the 14 species of amphibians found on the national forests of Montana.

Many states have non-game regulations that prohibit unauthorized destruction of native, non-game wildlife, and all Region 2 states consider the northern leopard frog a native, non-game species. However, this protection generally takes the form of non-binding guidance on conservation needs and/or is limited to prohibitions of direct impact (e.g., poaching, poisoning) and does little to address the major threats discussed elsewhere in this assessment (e.g., habitat alteration). In addition, many states allow exceptions to prohibitions of direct impact, such as the legal take of amphibians for use as fish bait. For example, in South Dakota, the holder of a general fishing license can take 15 leopard frogs per day for personal use, with a possession limit of 30, and holders of a commercial bait dealers license can take more (see <http://legis.state.sd.us/statutes/index.aspx> for pertinent statutes). Moreover, given other duties of state wildlife law enforcement officials, which generally focus on game animals, it is the experience of the authors that prohibitions on direct take of amphibians (much less degradation of their habitat) are not tracked, and infringements are rarely prosecuted. Until the scope of such policies is expanded to include protection of suitable habitat and concurrently demonstrate a fiscally feasible and legally defensible mode of enforcing this protection, they will remain largely ineffective tools for conserving amphibians.

The Black Hills National Forest Land and Resource Management Plan, as amended, (USDA Forest Service 2006), specifically added an objective to protect some of the smaller ponds on the Forest. Objective 240 seeks to protect aquatic, shoreline, and upland vegetation around ponds or water catchments containing leopard frogs. Although the Plan contains no standards specific to those small ponds or springs occupied by leopard frogs, Standard 3104 says: "Do not develop springs or seeps as water facilities where sensitive species or species of local concern exist unless development mitigates an existing risk." Because the northern leopard frog is a sensitive species in USFS Region 2, it gains some protection on the Forest from this standard.

Biology and Ecology

Description and systematics

The northern leopard frog is a ranid frog of moderate size (5.1 to 9.0 cm snout-vent length), with brown or green background color, and two or three irregular rows of dark spots on the dorsum (**Figure 1**; Conant and Collins 1991). It is also characterized by conspicuous dorsolateral ridges bordering the spots at the edge of the dorsum. Males have swollen thumbs on their forefeet, paired vocal pouches at the sides behind the head, which are visible when vocalizing, and they are usually smaller than females in body size. Two other phenotypes occur in Minnesota and adjacent states (Conant and Collins 1991), but they should not be encountered within the Rocky Mountain region. A figure of the tadpole of the northern leopard frog is found in Conant and Collins (1991; see figure 119, p. 353). Tadpoles of most frogs are difficult to identify without

a dissecting microscope and expert advice. Tadpoles are brown, olive, or gray above and white below. The vent is located on the lower right side of the midline of the body near the tail fin. Leopard frog tadpoles can reach total snout-vent lengths of 3.4 inches (87 mm).

Pace (1974) includes a synonymy of names applied to the leopard frog complex, including *Rana pipiens*. The name *R. pipiens* was first applied by Schreber in 1782, based on a leopard frog sent to him from New York (Schreber 1782, cited in Pace 1974). Using biochemical techniques, Hillis et al. (1983) resolved the phylogeny of the Alpha and Beta groups of the *R. pipiens* complex. *Rana pipiens*, along with *R. blairi*, *R. sphenoccephala*, and *R. berlandieri*, falls within the Beta division. The Alpha division contains *R. palustris*, *R. capito*, and *R. areolata*. Hillis (1988) further reviewed the literature and provided range maps of all North American leopard frogs referred to the *R. pipiens* complex, including the northern leopard



Figure 1. Photograph of adult northern leopard frogs; used by permission of Suzanne L. Collins, The Center for North American Herpetology.

frog. Dunlap and Platz (1981) discussed areas of hybridization deduced through calling variation in the upper Midwest. Lynch (1978) discussed the distribution of the northern leopard frog and the Plains leopard frog (*R. blairi*) and zones of sympatry of the two species in Nebraska. Dunlap and Kruse (1976) discussed the distribution of the “northern” (*R. pipiens*) and “western” (*R. blairi*) “morphotypes” (now known as two distinct species) in the northern and central Plains states. From the discussion of Dunlap and Kruse (1976), it is clear that a zone of hybridization between *R. pipiens* and *R. blairi* may exist in Region 2 from south-central South Dakota to northeastern Nebraska. It is possible that frogs from central South Dakota and central Nebraska (i.e., Fort Pierre National Grassland, Samuel R. McKelvie National Forest, and the eastern portion of the Nebraska National Forest) could be hybrids of the two species. All other leopard frogs studied by Dunlap and Kruse (1976) from Region 2 are clearly assigned to *R. pipiens* or *R. blairi*.

Distribution and abundance

The northern leopard frog is a species of cooler climates, with a range that encompasses most of the northern states of the United States and stretches far north into Canada (**Figure 2**). The northern extent of this species’ range in Canada and Alaska is not well understood (Russell and Bauer 1993, Fournier 1997, Maunder 1997). Fournier (1997) concludes that northern leopard frogs are rare in the Northwest Territories, and Russell and Bauer (1993) point out that in Alberta its range north of 55 °N latitude is poorly known. Canadian populations are discussed in Green (1997) and Bishop and Pettit (1992). The species ranges southward only in the western United States, including areas of Region 2 (**Figure 3**), where they have been found up to 3,355 m in the mountains of southern Colorado (Hammerson 1999) and to 2,700 m in the mountains of Wyoming (Baxter and Stone 1985). **Table 1** lists the states and provinces in which the northern leopard frog is found, historical abundance (if known), present abundance (if known), and the population trend (where known). Localized extinctions of this species have occurred in many areas across its range, while it has been introduced to a variety of other areas. For instance, populations in Newfoundland and on Vancouver Island, British Columbia were introduced (Buckle 1971, Green and Campbell 1984), and California populations may have been introduced (Bury and Luckenbach 1976, Jennings and Hayes 1984).

Population trend

The northern leopard frog was formerly abundant across its range, but it has since suffered wide-ranging population declines. McAlpine (New Brunswick; 1997), Mierzwa (Illinois; 1998), and Orr et al. (Ohio; 1998) were the only three reports we were able to find in the peer-reviewed literature that did not claim declines in northern leopard frog populations.

In the western United States, the species has undergone major declines, suffering extinctions in some areas (Rorabaugh 2005). Clarkson and Rorabaugh (1989) surveyed 13 of the 28 historical localities known in Arizona and found that the species was absent from all of these sites. However, they did find a population at a previously unreported locality in the White Mountains. The northern leopard frog is now absent from its historic range in California, except for a few small populations in northeastern California (Stebbins and Cohen 1995). Leonard et al. (1999) visited 27 historical collecting localities in eastern Washington and found populations at only three of them.

The northern leopard frog is now locally extinct west of the Continental Divide in Montana except for two population centers, one near Kalispell and one near Eureka (Maxell 2000). It is also largely absent from central Montana, where it was found at only nine of 47 historical sites in the mid-1990’s (Maxell 2000), and it is declining in some parts of eastern Montana (Reichel 1996). Although northern leopard frogs may still be common in some parts of Wyoming (Baxter and Stone 1985, Stebbins and Cohen 1995), the species has apparently been extirpated in the Targhee National Forest of western Wyoming and adjacent Idaho (Koch and Peterson 1995), and severely reduced in numbers in the Laramie area (Baxter and Stone 1985). Northern leopard frogs have become scarce at many sites in Colorado (Hammerson 1999). Corn and Fogleman (1984) documented extinctions at nine high elevation sites in Colorado, and this species has also gone extinct or become severely reduced at low elevation sites in the state (Hammerson 1982, Cousineau and Rogers 1991). The northern leopard frog was formerly common throughout the central Great Plains but has declined there as well (Stebbins and Cohen 1995).

In the upper Midwest, northern leopard frogs are generally thought to be less abundant than in the past (Lannoo 1998a provides recent estimates of their

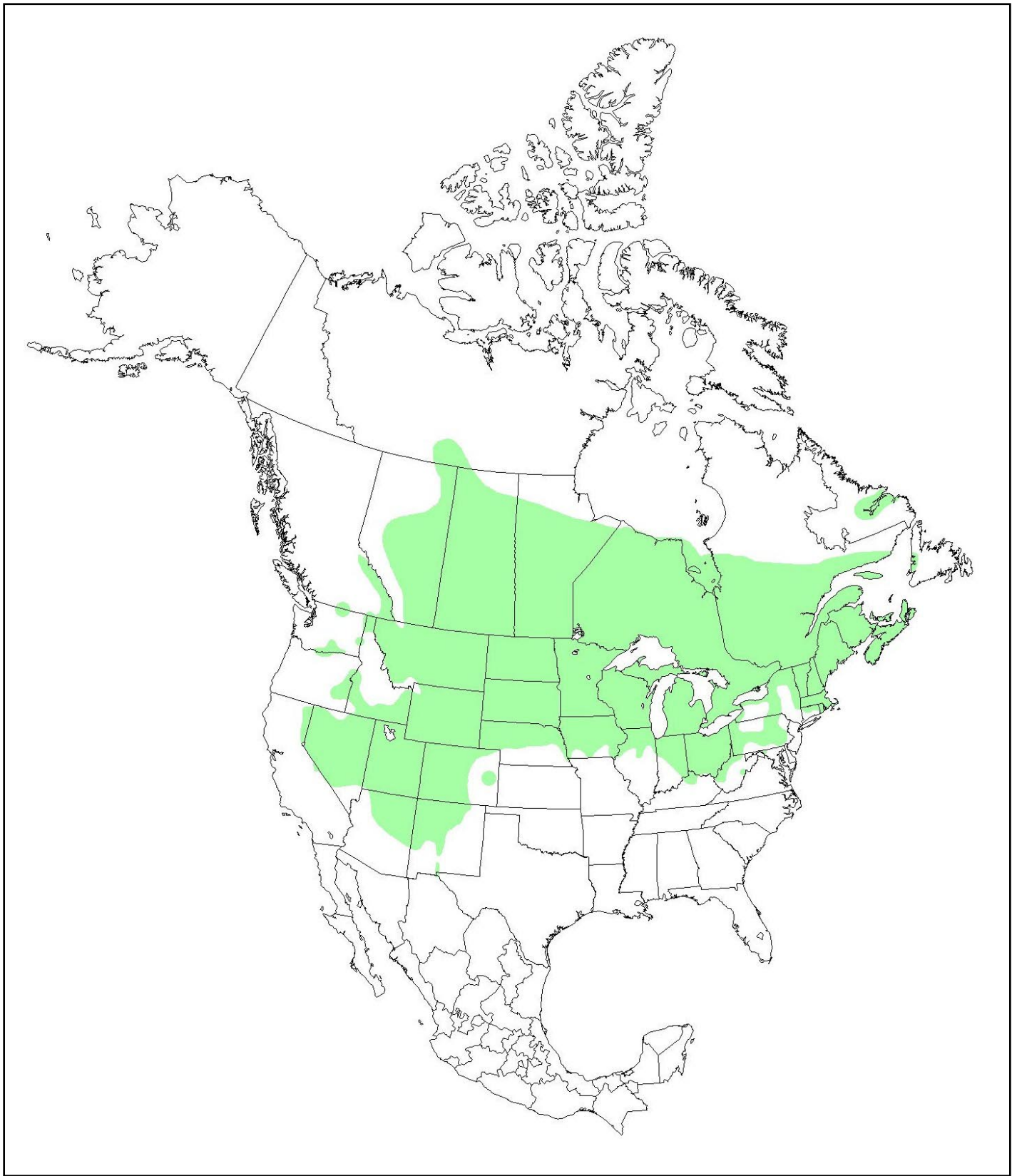


Figure 2. Probable historic North American range of the northern leopard frog, as synthesized from Stebbins (2003), Hillis (1988), and Conant and Collins (1991).

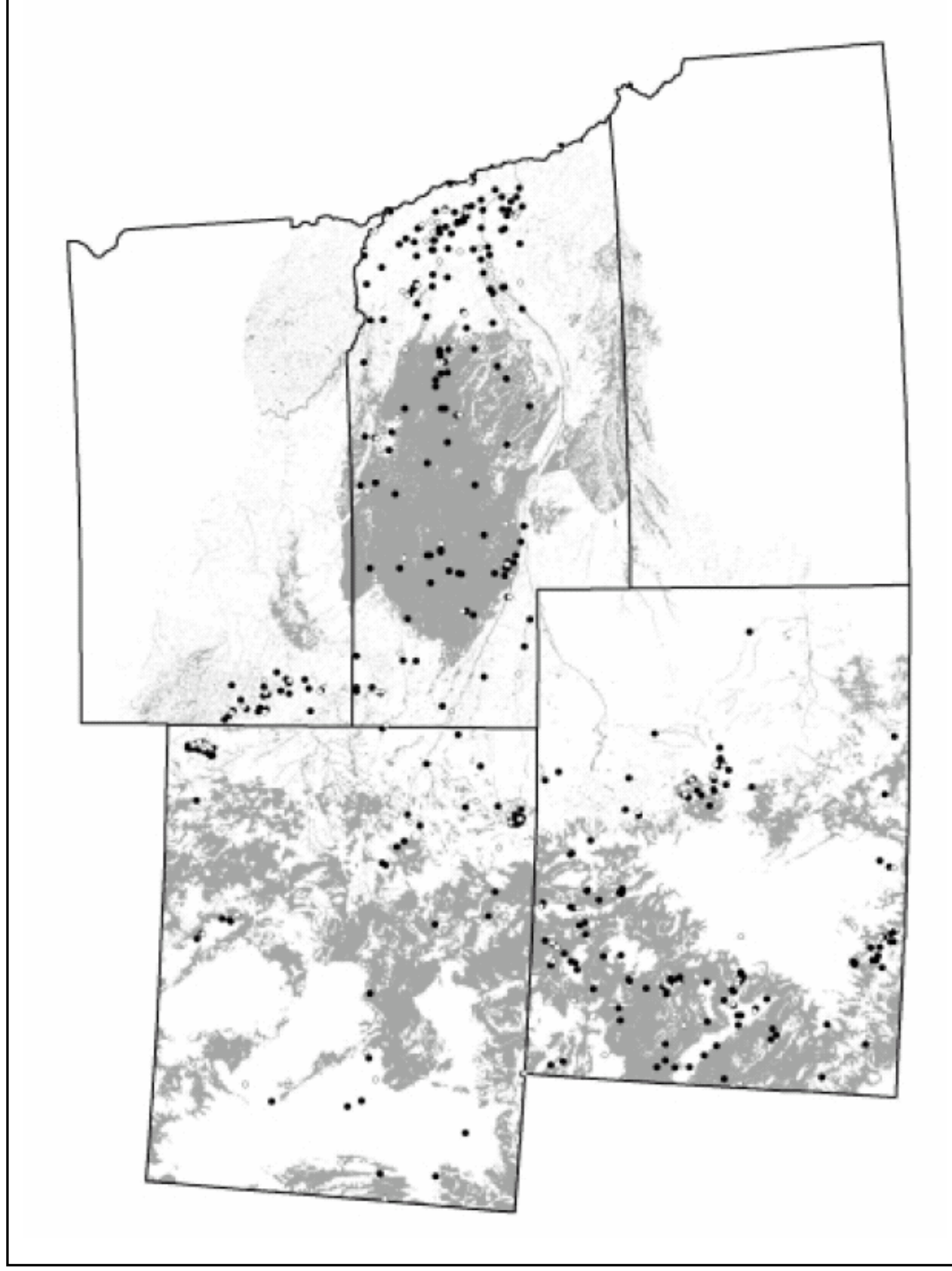


Figure 3. Predictive distribution map for the northern leopard frog in the five states of the Rocky Mountain Region of the USDA Forest Service (Beauvais et al. 2004). Gray areas show the ecological systems that (1) encompass the land cover types associated with the species, as selected by Gap Analysis teams within each state, and (2) are within the suitable biophysical envelope for the species. Solid circles are the points of known occurrence of the taxon that were used to model the biophysical envelope; open circles are points of known occurrence that were withheld from the modeling process and used for independent validation of the model.

Table 1. Historic and current abundance and population trends for the northern leopard frog across its range in North America. See **footnotes** for references.

State or Province	Historical Abundance	Present Abundance	Population Trend
Alberta	Unknown ¹	Uncommon ^{1,2,3}	Declining ^{1,2,3}
Arizona	Uncommon ⁴	Uncommon ⁴	Declining ⁴
British Columbia	Unknown	Unknown	Unknown
California	Extralimital? ^{5,6}	Uncommon ³	Declining ³
Colorado	Unknown	Uncommon ^{7,8,9}	Declining ^{7,8,9,10}
Connecticut	Unknown	Unknown	Unknown
Idaho	Unknown	Uncommon ¹¹	Declining ¹¹
Illinois	Unknown	Common ¹²	Stable ¹²
Indiana	Common ¹³	Uncommon ^{13,14}	Declining ^{13,14}
Iowa	Common ¹⁵	Uncommon ¹⁵	Declining ¹⁵
Kentucky	Unknown	Unknown	Unknown
Maine	Unknown	Unknown	Unknown
Manitoba	Unknown	Unknown	Unknown
Massachusetts	Unknown	Unknown	Unknown
Michigan	Uncommon ¹⁶	Unknown	Declining ¹⁶
Minnesota	Common ¹⁷	Common ¹⁷	Declining ¹⁷
Montana	Unknown	Uncommon ^{18,19}	Declining ^{18,19}
Nebraska	Unknown	Unknown	Unknown
Nevada	Unknown	Unknown	Unknown
New Brunswick	Unknown	Common ²⁰	Stable ²⁰
New Hampshire	Unknown	Unknown	Unknown
New Mexico	Unknown	Unknown	Declining ³⁷
New York	Unknown	Unknown	Unknown
Newfoundland	Extralimital ^{21,22}	Unknown	Unknown
North Dakota	Unknown	Unknown	Unknown
Northwest Territories	Unknown	Uncommon ²³	Unknown
Nova Scotia	Unknown	Unknown	Unknown
Ohio	Unknown	Common ²⁴	Stable ²⁴
Ontario	Unknown	Unknown	Unknown
Pennsylvania	Unknown	Unknown	Unknown
Quebec	Unknown	Unknown	Unknown
Saskatchewan	Unknown	Unknown ²⁵	Unknown ²⁵
South Dakota	Unknown ²⁶	Common ^{26,27,28,29,30}	Unknown ²⁶
Utah	Unknown	Unknown	Unknown
Vermont	Unknown	Unknown	Unknown
Washington	Uncommon ³¹	Uncommon ³¹	Declining ³¹
West Virginia	Unknown	Unknown	Unknown
Wisconsin	Common ³²	Common ³²	Declining ^{32,33,34,35}
Wyoming	Unknown	Unknown	Declining ^{3,11,36}

If no reference is given, the data are unknown for the various provinces and states that are listed.

References: 1 = Russell and Bauer (1993); 2 = Roberts (1992); 3 = Stebbins and Cohen (1995); 4 = Clarkson and Rorabaugh (1989); 5 = Bury and Luckenbach (1976); 6 = Jennings and Hayes (1994); 7 = Hammerson (1999); 8 = Hammerson (1982); 9 = Cousineau and Rogers (1991); 10 = Corn and Fogleman (1984); 11 = Koch and Peterson (1995); 12 = Mierzwa (1998); 13 = Minton (1998); 14 = Brodman and Kilmurry (1998); 15 = Lannoo (1994); 16 = Collins and Wilbur (1979); 17 = Moriarty (1998); 18 = Werner et al. (2004); 19 = Reichel (1996); 20 = McAlpine (1997); 21 = Buckle (1971); 22 = Green and Campbell (1984); 23 = Fournier (1997); 24 = Orr et al. (1998); 25 = Didiuk (1997); 26 = B. Smith, personal observation; 27 = Peterson (1974); 28, 29, 30 = Smith et al. (1996a, b; 1998); 31 = Leonard et al. (1999); 32 = Mossman (1998); 33, 34 = Hine et al. (1975, 1981); 35 = Dhuey and Hay (2000); 36 = Baxter and Stone (1985); 37 = C.W. Painter unpublished data 2006.

abundance in this region). Moriarty (1998) found them to be widespread across Minnesota but much less common than historical records indicated. Hine et al. (1975, 1981) documented a decline of northern leopard frogs in Wisconsin in the 1970's, and Mossman et al. (1998) reported a further decline from 1984 to 1995 although they were still common in the state. Casper (1998) reported that some investigators believed they saw a partial rebound after 1985, but Dhuey and Hay (2000) reported northern leopard frogs to be rare. Collins and Wilbur (1979) noted that this species had become rare on their study site near Ann Arbor, Michigan, during the previous 20 years. Orr et al. (1998) found them still abundant in northeastern Ohio, but Davis et al. (1998) considered them rare or extinct in Hamilton County, in southwestern Ohio. Mierzwa (1998) found them to be common in northeastern Illinois while Brodman and Kilmurry (1998) reported them to be rare or uncommon at their study sites in northwestern Indiana. Hemesath (1998) was unable to determine whether there had been further declines in Indiana based on calling survey data, but Minton (1998), writing from a perspective of 45 years of collecting in that state, concluded that northern leopard frog populations have declined markedly since 1948. Lannoo et al. (1994) wrote that northern leopard frog populations had probably declined across Iowa by two to three orders of magnitude over historical levels.

In Canada, Orchard (1992) reports that the species has suffered declines in British Columbia, and apparently they are now extirpated or rare throughout much of Alberta (Roberts 1992, Russell and Bauer 1993, Stebbins and Cohen 1995). While northern leopard frogs are found in Saskatchewan, data are insufficient to assess abundance or population trends (Didiuk 1997). They remain common in New Brunswick (McAlpine 1997).

Population declines may not have occurred everywhere. Data showing that declines are not occurring may not be as "interesting" as data showing that declines are occurring, so such information may not be published. Generally speaking, it is thought that eastern populations are in somewhat better condition than western populations. While northern leopard frogs have clearly declined broadly throughout the western United States and Canada, they still are common in some areas of eastern Canada and the upper Midwestern United States.

Activity and movement patterns

Northern leopard frog movement patterns have been studied by Bovbjerg and Bovbjerg (1964), Bovbjerg (1965), Dole (1965a, 1965b, 1967, 1968), Merrell (1970, 1977), and Seburn et al. (1997). Seasonal movement patterns consist of spring movement from overwintering sites to breeding ponds (Dole 1967, Merrell 1970, 1977), adult dispersal from breeding ponds into upland foraging habitat during the summer (Dole 1965a, 1965b, 1968), natal dispersal from breeding ponds (Bovbjerg and Bovbjerg 1964, Bovbjerg 1965, Seburn et al. 1997), and fall migration to overwintering sites (Merrell 1970, 1977).

In the spring, frogs in Minnesota moved from overwintering sites in deep water of larger lakes to the shore, but they would not leave the lakeshore until temperatures were above 10 °C (Merrell 1970). Sexually mature frogs migrated from overwintering sites to breeding ponds, sometimes under extremely dry conditions and during daylight, even becoming dusty while doing so (Merrell 1970). In contrast, subadult frogs stayed near the larger lakes (Merrell 1970). This appears unusual given the fact that many larger ponds have longer seasonal hydroperiods and may, therefore, have predaceous fish that prey on subadult frogs (Semlitsch 2000a).

Dole (1965b) and Merrell (1977) both agreed that northern leopard frogs utilized home ranges in the summer, but Fitch (1958) concluded that they did not have home ranges at his study site in Kansas. Dole (1965b) found that home range sizes varied from 68 to 503 m² and varied in size with habitat type, sex, and life stage (i.e., subadult or adult). He also found that northern leopard frogs tended to make several types of short-distance movements within their home range and used resting sites (called "forms") to which individuals returned on a regular basis. In this study, 33 frogs that were trailed for five days or longer moved straight-line distances of 7 to 53 m. He measured long-distance movements (>100 m in one night) in the species in response to nocturnal summer rains, but the reasons for these movements remained unknown. Merrell (1977) was in general agreement with these observations. As temperatures rose and vegetation dried out, Merrell (1970) noted that frogs tended to move closer to water.

In Minnesota, tadpoles metamorphosed into subadult frogs in July (Merrell 1970, 1977), after which young frogs stayed close to breeding ponds until their tails had been fully resorbed (Merrell 1977). Dole (1965a) agreed that small frogs were closely tied to water. Following this period of breeding pond fidelity, mass migrations to larger lakes occurred and sometimes would result in mass mortality events along roadways (Bovbjerg and Bovbjerg 1964, Bovbjerg 1965, Merrell 1977).

Seburn et al. (1997) also studied dispersal of young frogs, marking 938 metamorphs at a source pond in southern Alberta and recapturing 104 at various sites away from the source pond. These young frogs dispersed up and down streams and across land; some were found at ponds as far as 4.0 km from source ponds, with no aquatic connections between the two. On average, however, they dispersed twice as far up and down streams as across land. Frogs reached dispersal ponds within 1 km of the source pond within three weeks; they reached more distant ponds within six weeks.

The issue of faithfulness to natal areas and breeding sites has not been specifically studied in northern leopard frogs, but it appears that they are probably not territorial (Wells 1977) and may exhibit breeding site fidelity (Livo 1981). Merrell (1970) noted that genetic drift appeared low in northern leopard frog populations, suggesting that this species might not show a high degree of philopatry to natal sites (genetic drift is greater in small and highly philopatric populations). Although many researchers assume that amphibians return to their natal ponds to breed (Semlitsch and Bodie 1998), these types of movements have not been studied in the northern leopard frog. Eighteen percent of over 5,000 wood frogs (*Rana sylvatica*) dispersed to new ponds to breed in one study (Berven and Grudzien 1990), and 27 percent of Fowler's toads (*Bufo fowleri*) dispersed to new ponds to breed in another study (Breden 1987). At a study site in Germany, where several ponds were spaced very closely, between 80 and 98 percent of three species of ranids and one bufonid returned to their natal ponds to breed (Kneitz 1998, cited in Pough et al. 2001).

In fall, frogs migrated to overwintering sites in lakes, streams, and rivers (Merrell 1970, Emery et al. 1972, Cunjak 1986, Ultsch et al. 2000). Fall migration of northern leopard frogs in Minnesota usually occurred at night from mid-September through October, but this appeared to end by late October (Merrell 1970). At the overwintering area in the fall, disturbance of frogs caused them to swim directly into deep water, in

contrast to their summer behavior in which they tended to return to shore (Merrell 1970). Frogs hibernated on lake bottoms, often under debris, and they tended to congregate near areas of high oxygen concentration such as the bottom of spillways (Merrell 1970). They may also excavate shallow pits on the bottom of sandy ponds as overwintering sites (Emery et al. 1972).

Anecdotal information is available on how far northern leopard frogs can move. Merrell (1970) marked 107 frogs (their age was not noted) and released them in "favorable" habitat, returning a day later to find that only one frog had moved (0.40 km). Seburn et al. (1997) recorded subadult movements up to 2.1 km while Dole (1971) recorded maximum subadult movements of 5.2 km. These are estimated straight-line movements, and undoubtedly, the reported distances underestimate the full extent of distance traveled by these individuals.

Semlitsch (2000a) pointed out that to develop a successful management strategy for amphibians, it will be important to understand their movement patterns and the spatial distribution and size of ponds and migration corridors. For example, Semlitsch and Bodie (1998) and Semlitsch (2000b) convincingly showed that elimination of wetlands less than 5 ha in size could prevent some species from reaching and colonizing new ponds, depending on the movement patterns of species and the spatial distribution of wetlands suitable for reproduction by these species. Semlitsch (1998) measured the dispersal distances of several southeastern salamanders and determined that core habitat for salamanders consisted of the wetlands habitat in which they bred and a surrounding upland area to which they dispersed following breeding. The upland habitat was described by Semlitsch (1998) as "buffer" habitat but is more appropriately considered "core" habitat, as it is necessary for the survival of local populations (Semlitsch personal communication 2001). Semlitsch (1998) found that an upland area that included up to 164 m of upland habitat around a pond would contain roughly 95 percent of salamanders of six species studied. Based on what we know of northern leopard frog movements, an area containing 95 percent of a population of these frogs would probably be much larger.

Northern leopard frogs are similar to the salamanders that Semlitsch (1998) reviewed in that the frogs also use wetland habitat for breeding and spend considerable amounts of time away from the pond after the breeding season, feeding in upland habitat (personal observations). It is not known, however, how large of an upland area should surround each breeding site to

manage a population of northern leopard frogs nor what types of routes frogs use to migrate between breeding ponds or to disperse from the natal area as subadults. Given the importance of identifying movement corridors to management strategies, the general lack of knowledge of movement patterns and home range use among northern leopard frogs is a serious impediment to managing the species.

Habitat

Northern leopard frogs require a broad range of habitats in close proximity due to their complicated life histories. Merrell and Rodell (1968) categorized three major habitat types: winter habitat (overwintering in lakes, streams, and ponds), summer habitat (feeding by adults in upland areas), and tadpole habitat (up to three months spent as tadpoles in shallow breeding ponds). To understand the types of habitats used by northern leopard frogs, the habitat they use during various stages of their life history must be categorized, including habitat used by tadpoles, subadults, and adults, and any sexual differences in habitat usage. Their complicated movement patterns during the year must also be considered and include habitat used for reproduction, natal dispersal, summer feeding ranges, fall migrations, and overwintering. It should also be recognized that the relevant literature that characterizes northern leopard frog habitat comes from populations scattered across North America. Consequently, it is likely that differences in habitat use by northern leopard frogs exist regionally, and within Region 2.

Breeding habitat and tadpole habitat

In an extensive study of the life history of the northern leopard frog in Minnesota, Merrell (1977) found that northern leopard frogs bred in mid-sized ponds that were 30 to 60 m in diameter, from 1.5 to 2.0 m in depth, and dried “periodically every few years”. Merrell (1968) further characterized breeding ponds as sites that did not support fish populations, were not connected with other bodies of water, and dried up during droughts. Collins and Wilbur (1979) similarly found that northern leopard frogs bred only in ponds that were permanent, dried completely in exceptionally dry years, or dried only by the very end of the summer. In this study, the presence of fish did not affect breeding, but subadults were found only at sites that were fishless, which coincidentally were either semi-permanent ponds or ponds that dried by the end of the summer. Semlitsch (2000a) discussed the importance of mid-sized ponds to reproductive success (i.e., egg laying, egg hatching, and successful metamorphosis) in many species of

amphibians. According to Semlitsch (2000a), the most important ponds for amphibians were semi-permanent to seasonal palustrine habitats that tended to last from 30 days to one year. Werner and Glennemeier (1999) also found that northern leopard frogs required breeding ponds with an open canopy.

Various studies of northern leopard frog breeding habitats have been conducted in the Rocky Mountain region. In northern Colorado and in Wyoming, Corn and Livo (1989) found that northern leopard frogs bred and successfully hatched in a gravel pit, stock ponds, and beaver ponds. Hammerson (1999) noted that the northern leopard frogs bred in shallow, quiet areas of permanent bodies of water, in beaver ponds, and in seasonally flooded areas adjacent to or contiguous with permanent pools or streams in Colorado.

Unpublished field notes on northern leopard frogs in the Black Hills made by one author of this assessment (Smith) generally agree with the studies of Merrell (1968, 1977), Collins and Wilbur (1979), Corn and Livo (1989), and Hammerson (1999). He has found northern leopard frogs breeding in stock ponds and semi-permanent ponds, in the margin of larger lakes, and in beaver ponds. When streams were used for reproduction, eggs were deposited in backwaters out of the main flow. While he found northern leopard frogs breeding in habitat with introduced predaceous fish in the Black Hills, tadpoles and metamorphs were seldom found in such habitats. In addition, he did not find breeding adults, tadpoles, or metamorphs in springs in the Black Hills, which probably stay too cold throughout the summer for normal development of the tadpoles.

We apply the classification system of Cowardin et al. (1979) to what we consider the “most typical” kind of breeding site used by northern leopard frogs in the Rocky Mountain region. These are palustrine sites with an unconsolidated bottom, and they usually have a pond margin with extensive growth of cattails (*Typha* spp.). Cowardin et al. (1979) consider the following four features to be characteristic of palustrine systems:

- ❖ size under 8 ha
- ❖ no wave-formed or bedrock shoreline
- ❖ water depth typically less than 2 m at the deepest part of the pond
- ❖ very low salinity.

Palustrine systems with an unconsolidated bottom generally have a mud bottom (often composed of bentonite in parts of the Black Hills and Wyoming) and vegetative cover less than 30 percent. The cattail margin is typical of these ponds in the Rocky Mountain Region and probably indicates some degree of permanency of the pond; however, some of these sites may dry completely by late fall.

The lead author's experience in the Black Hills indicates that breeding ponds there are of roughly the size determined by Semlitsch (2000b) (slightly smaller than 5.0 ha) to be highly productive for amphibian abundance and diversity in the southeastern United States. These ponds should not be connected to larger bodies of water to preclude accidental introduction of predaceous fish. Although these types of ponds may be the most common ponds in the landscape, they may also be the most in danger of elimination and the least protected by law and management guidelines (Semlitsch and Bodie 1998, Semlitsch 2000b). As noted earlier in this document, the amended Black Hills National Forest Land and Resource Management Plan (USDA Forest Service 2006) does include an objective that specifically seeks to protect those small ponds supporting leopard frogs. However, most conservation and land management plans of which we are aware do not.

Tadpoles need bodies of water with no overhead canopy and that are free of introduced predaceous fish (Kruse and Francis 1977, Hecnar and M'Closkey 1997a, Werner and Glennemeier 1999). These bodies of water should be reasonably shallow so that the sun can heat them to temperatures suitable for rapid development, especially at higher elevations, where the growing season may be short. However, the ponds should not be too shallow because they would dry too rapidly for tadpoles to complete their 58 to 105 day larval period (Hammerson 1999).

Subadult habitat

In various locations across their range, subadult frogs, after completing their larval period, migrate across land to suitable feeding sites at larger lakes (see Activity and movement patterns section). The habitat through which successful dispersal occurs is not known completely. Bartelt (1998) documented the deaths of thousands of western toad metamorphs (*Bufo boreas*) in Idaho following the trampling by sheep of tall grasses in which the metamorphs were living. He attributed many of the deaths to trampling but believed that survivors may have died from desiccation following the loss of

the relatively humid microclimate that existed beneath the tall grass. The destination habitat for subadults is other ponds and suitable foraging habitat around those ponds. Seburn et al. (1997) have shown that juvenile northern leopard frogs disperse farther and more rapidly along streams than they do over land.

Adult upland habitat

Conant and Collins (1991) point out that the northern leopard frog is one of the more terrestrial of the ranid frogs, using a considerable amount of upland habitat around breeding ponds. Following reproduction, adult northern leopard frogs move into upland habitat in which they may feed for the summer. In a study by Merrell (1970), northern leopard frogs tended to frequent grassy meadows in the summer when grass was from "several inches to a foot" (i.e., up to 30 cm) in height. USFS biologists working in the Black Hills have commented that they have found northern leopard frogs a considerable distance from water in wet meadows or grasslands (Martinez personal communication 1998). Many citations mention movements by this species of up to 3.0 km from water, and Dole (1971) notes that subadults move up to 5.2 km away from natal ponds.

Frog movements among habitats and pond spacing are two of the most important factors to consider in management of northern leopard frogs, as both factors are likely to affect population density in this species greatly, as Semlitsch (2000a) has noted for other amphibians. The pattern of spacing of suitable breeding sites across the landscape and upland movements made by northern leopard frogs are probably both very important in colonization or recolonization of ponds and the maintenance of healthy metapopulations. In the Rocky Mountain Region, meadows, wetlands, and riparian areas are probably important connecting habitats due to relatively humid microclimates compared to surrounding habitats (see Seburn et al. 1997 for data from other parts of their range).

Adult overwintering habitat

In the fall, subadult and adult frogs migrate to overwintering sites. Little is known of potential overwintering sites for northern leopard frogs in Region 2; however, winter habitat in the Rocky Mountain region is expected to be similar to that throughout the species' range. We suspect they use the bottoms of flowing streams and ponds (and possibly springs) that are large enough that they do not freeze solid in winter. However, there could be local adaptations of importance. For example, the Black Hills historically had no large

bodies of water, such as lakes (Froiland 1990), and northern leopard frogs may have used streams and possibly other habitat types in which to overwinter. Interestingly, Oscar Martinez of the USFS (personal communication 1997) found a leopard frog under snow in a wet meadow that had flowing water. It is unlikely that they would overwinter in recently created lakes for two reasons: first, these lakes may not have been used historically for overwintering, and second, these lakes have introduced predaceous fish such as brown trout (*Salmo trutta*) and northern pike (*Esox lucius*).

Overwinter mortality may be important for northern leopard frogs, as it is for other ranid frogs (Bradford 1983). Especially important may be oxygen depletion at overwintering sites (Merrell and Rodell 1968, Bradford 1983), which may account for the habit of frogs to overwinter at inflow areas where oxygen saturation of water is relatively high (Oldfield and Moriarty 1994). It may also be why they overwinter in streams, where oxygen saturation is typically higher than in lakes or ponds. This further underscores the potential importance of permanently flowing streams, springs, and wet meadows as overwintering sites in the Rocky Mountain region.

For example, Bradford (1983) noted that anoxia was one source of mortality for overwintering mountain yellow-legged frogs (*Rana muscosa*) in California and Nevada. Bradford (1983) observed that anoxia was more severe in shallow (less than 4 m) lakes or ponds and that nearly all adult frogs died in these bodies of water in some winters. Repeated winterkill has been observed in ponds in northern Indiana (Manion and Cory 1952), and Ultsch et al. (2000) observed winterkill in a river in Vermont. Northern leopard frogs remain capable of movement throughout the winter, but they are usually very sluggish (Emery et al. 1972, Cunjak 1986).

Predation by introduced fish in streams and larger ponds is another modern, and at times substantial, source of mortality for the northern leopard frog. Within the Rocky Mountain region, introduced fish include brown trout, brook trout (*Salvelinus fontinalis*), and rainbow trout (*Oncorhynchus gairdneri*). Brook trout are smaller, insectivorous trout that probably do not eat frogs the size of northern leopard frogs. Cunjak (1986) reported no leopard frogs in the stomach contents of more than 100 brook trout he examined from his study site. However, splake (a non-fertile hybrid of lake trout [*Salvelinus namaycush*] and brook trout) have been reported to eat northern leopard frogs in the winter (Emery et al. 1972). Brown trout are more piscivorous

and may well eat adult northern leopard frogs. Ice anglers in North Dakota have reported northern leopard frogs in the stomachs of northern pike caught during mid-winter (unpublished data), and pike are intentionally introduced by anglers to some waters.

Food and feeding habits

Most of what is known about the food habits of tadpoles, subadults, and adult northern leopard frogs is anecdotal. Merrell (1977) considered northern leopard frog tadpoles to be generalist herbivores, but he also noted that they sometimes scavenged dead animals including conspecifics. Franz (1971) found that northern leopard frog tadpoles mostly ate various species of free-floating green algae and blue-green algae. Hendricks (1973) examined gut contents in tadpoles of the Rio Grande leopard frog (*Rana berlandieri*, formerly known as *R. pipiens*), which is closely related to the northern leopard frog. He described this species as a filter feeder that primarily ate free-floating algae. Merrell (1963) discussed raising tadpoles on boiled lettuce, corn meal, and tropical fish food.

Northern leopard frogs become carnivorous at metamorphosis (Merrell 1977), and are opportunistic insectivores with a propensity to snap at anything that moves and is small enough to be swallowed, including smaller northern leopard frogs (Drake 1914, Linzey 1967, Merrell 1977, Miller 1978). In dissecting 209 adult northern leopard frogs, Drake (1914) found that they primarily ate "insects" (this category was not broken down any further), spiders, mollusks, crustaceans, and various other arthropods. Whitaker (1961) also found that they primarily ate insects, mostly coleopterans (beetles) and orthopterans (grasshoppers), but also dipterans (flies and associated groups), hemipterans (true bugs), and hymenopterans (wasps and their allies). Linzey (1967), in a study of 463 northern leopard frog specimens, found that nearly one quarter of food items were beetles. Breckenridge (1944) reported such unusual food items in the stomachs of northern leopard frogs as a small garter snake, ruby-throated hummingbirds, and a yellow warbler.

Breeding biology

The reproductive biology of northern leopard frogs has been studied in Michigan (Collins and Wilbur 1979), Minnesota (Merrell 1965, 1968, 1970, 1977), Colorado and Wyoming (Corn and Livo 1989), and in the laboratory (Noble and Aronson 1942, Aronson and Noble 1945, McClelland and Wilczynski 1989).

Hammerson (1999) gave an excellent summary of breeding phenology for populations at various elevations in Colorado.

As soon as males leave overwintering sites, they travel to breeding ponds and call in shallow water of suitable pond sites (Merrell 1965, 1968, 1970, 1977, Oldfield and Moriarty 1994, Hammerson 1999). Like many pond-breeding frogs, male northern leopard frogs attract females by breeding calls from specific locations within a breeding pond, with several males typically calling together to form a breeding chorus. Females come to males and breed at the calling sites. After breeding, females immediately leave the ponds while males stay in the chorus continuing to call (Merrell 1977), resulting in a preponderance of males at breeding ponds (Merrell 1977).

Merrell (1977) stated that northern leopard frogs tended to call while floating in water, but Noble and Aronson (1942) found that they also called from land if particularly excited. Dunlap and Platz (1981) found little variation in calls from Wisconsin to Idaho. Noble and Aronson (1942) described the mating call as a quavering sound pronounced phonetically as “ir-a-a-a---a-a-h”, lasting about three seconds, with the call starting softly and growing louder as the vocal sacs inflate (Pace 1974 pointed out that male northern leopard frogs do not have external vocal sacs, but have well-developed internal vocal sacs). Wright and Wright (1949) described the call as a long, low guttural note lasting three or more seconds followed by three to six short notes each a second or less in length. Davidson (1996) provided a recording of northern leopard frogs calling in the Rocky Mountains.

Pace (1974) gave the most extensive description of the call of the northern leopard frog and provided sonograms of the various components of the call. She divided the call into three components, including a long many-pulsed trill, a series of short trills, and a series of pulses that usually terminated calls. Typically, male frogs gave calls that consisted of several of these sounds, usually commencing with the longer trills, unless they were in the middle of a larger chorus. They usually followed these longer trills with the shorter trills, ending the typical call with a series of a few pulses. To the typical observer, this call sounds like a kind of lower frequency trill that may descend in frequency and end with what sounds like a few short grunts (personal observations of the lead author). Pace (1974) found that male frogs were stimulated to call by playbacks of the longer trills, and isolated males gave calls that consisted of a longer series of the longer trills. She concluded that

the long, slow, trilled call functioned as a long-range call that attracted females, and the shorter, rapid trills were short-range calls that helped females to find the calling male at close distances. Finally, the calls typically were terminated by some short terminal sounds that were used to maintain separation amongst males in choruses (the third part of a typical call).

Northern leopard frogs give one other type of call, known as a release call. Male northern leopard frogs will clasp virtually anything with the general size and shape of a female frog and have been found clasping floating beer cans, females of other *Rana* species, a female American toad (*Bufo americanus*), a dead female northern leopard frog, and a bowfin (*Amia calva*) (Merrell 1977). It is therefore not surprising that the other vocalizing males will give a release call when clasped by other males (Merrell 1977, McClelland and Wilczynski 1989). Females also give the release call if not in mating readiness (McClelland and Wilczynski 1989). McClelland and Wilczynski (1989) printed a sonogram of the release call.

As described by Wright and Wright (1949), choruses in the eastern United States (near Ithaca, New York) were conspicuous while an individual call was very quiet. However, various workers have found choruses to vary in volume. Bishop et al. (1997) described breeding choruses of northern leopard frogs as “low volume,” and Peterson (1974) noted a “faintly vocalizing” chorus at Stockade Lake in the Black Hills. The lead author has consistently found it difficult to hear breeding choruses in the Black Hills, where calling can be nearly indiscernible over other night-time sounds, and calls are often sporadic.

Specific sites used for calling and breeding within ponds were described by Merrell (1977) as being the warmest part of the pond, typically in water of 40 cm depth or less in an unshaded location with maximum exposure to sunlight. Corn and Livo (1989) noted that two to three days of air temperatures of 15 to 20 °C were needed to initiate calling activity at their study sites in northern Colorado and southern Wyoming at elevations of 1,555 to 2,520 m. Merrell (1977) found that daytime air temperatures were usually greater than 20 °C when calling began. Merrell (1977) believed that differences in temperature within ponds typically resulted in the use of one spot 1 to 2 m in diameter to lay eggs even when most breeding ponds in his study area were 30 to 60 m in diameter. Corn and Livo (1989) also recorded precipitation but noted that calling and breeding at their sites apparently corresponded more with temperature than with precipitation.

Northern leopard frogs show geographic variation in the timing of reproduction and egg-laying that is probably determined by various environmental cues. The timing of courtship and breeding likely occurs sooner in southern populations and at lower elevations. At lower elevations in Colorado, northern leopard frogs began breeding in March, but at higher elevations, they often did not start breeding until April or May (Hammerson 1999). Corn and Livo (1989) found that calling in Colorado and Wyoming started anywhere from mid-March to early to late May, depending on elevation. At these sites, eggs were laid within two to three days following the onset of chorusing (Corn and Livo 1989). In the San Luis Valley of Colorado at elevations of 2,285 m, Hammerson (1999) reported that calling extending into late June. High elevation populations studied in northern Colorado began breeding in May (Corn and Livo 1989). In the Black Hills, the timing of reproduction is uncertain, but calling has been heard in April at mid-elevation (ca. 1,500 m) ponds (personal observations of the lead author), and has been recorded in May and June by Smith et al. (1998). In Minnesota, northern leopard frogs bred from mid-March to mid-May depending on the weather, but usually in April (Merrell 1977).

The number of eggs laid in a clutch varies widely, even within a population. Linzey and Wright (1947) estimated a clutch of 3,500 to 6,500 eggs for northern leopard frogs. Merrell (1965) reported from 2,000 to more than 5,000 eggs in some Minnesota clutches. Hupf (1977) counted from 1,000 to 7,000 eggs in an unreported number of preserved females from Nebraska. Corn and Livo (1989) counted from 645 to 6272 eggs in clutches at their study ponds, with a mean of 3,045 eggs per clutch. They also reported three distinct size classes of clutches, suggesting a rough correspondence to three different size classes of females at their study sites. Hatching success at six ponds in Colorado ranged between 70 and 99 percent (Corn and Livo 1989).

Eggs are deposited as single large round masses 5 to 13 cm in diameter, and they are black in color. Egg masses were attached to emergent vegetation such as sedges (*Carex* spp.) or rushes (*Scirpus* spp.) in Colorado and Wyoming (Corn and Livo 1989). Hammerson (1999) stated that egg masses were attached to vegetation just below the surface in warm, shallow water from 7 to 25 cm deep. Merrell (1977) noted that egg masses were attached to vegetation "a few cm" below the water surface; mean water depth of 39 oviposition sites was 12.9 cm (standard deviation = 3.3 cm). In Minnesota, females left egg masses in the area in which males had been calling, and were placed in water less than 40 cm

in depth that was exposed to the sun (Merrell 1977). The temperature of egg masses was typically 2 to 3 °C higher than the water temperature adjacent to the egg masses (Merrell 1970). Merrell (1977) suggested that the dark pigmentation of the embryos caused them to act like black bodies, implying that it was adaptive for females to lay their eggs in locations that would receive a substantial amount of solar radiation. It may also help embryos to avoid freezing during short periods of cold springtime weather (Merrell 1977). Warm temperatures also speed development in amphibian eggs and larvae (Duellman and Trueb 1986). Wright and Wright (1949) reported that egg masses were flattened spheres, 75 to 150 mm by 5 to 75 mm in dimension.

Hatching time and time to metamorphosis varies geographically and altitudinally, probably dependent on environmental variables, especially temperature. Hine et al. (1981) reported that hatching occurred in 5 to 9 days when temperatures were at or above 10 °C, while Wright (1914) reported that eggs hatched in 13 to 20 days near Ithaca, New York. Wright and Wright (1949) reported that tadpoles usually transformed in 60 to 80 days. In contrast, Corn (1981) found that the larval period ranged from 58 to 105 days, but his study ended before tadpoles were fully transformed. The 105-day larval period was reported at the highest elevation sites (Corn 1981), suggesting a relationship between developmental time and elevation, which may ultimately be due to differences in temperature regime. Corn (1981) observed egg laying in late May and early June at elevations of 2,035 to 2,365 m in Larimer County, Colorado (northern Colorado) with metamorphosis from mid-July through mid-September. In various high elevation sites in Colorado, Hammerson (1999) reported metamorphosis throughout August. Mosimann and Rabb (1952) collected newly metamorphosed tadpoles July 26, 1950, in Liberty County, in north-central Montana. The lead author has observed large numbers of tadpoles in some ponds in the Black Hills in July, but has not taken detailed notes on their development. Ryan (1953) noted that northern leopard frogs metamorphosed in the Ithaca area from June 30 to August 15, with most individuals metamorphosing in the first half of July. Wright and Wright (1949) also reported that most individuals metamorphosed in July in the Ithaca area. Like all ranid frogs, there is no parental care in this species.

Population demography

Data on age to maturity, age at first reproduction, and age at death are incomplete, and very little is known about age-specific survival rates. Therefore, northern

leopard frog demography does not merit formal analysis in a population demographic model (e.g., Caswell 2000), as the results from such a model would be inaccurate and potentially misleading. The spatially and temporally disparate information that is currently available is presented in the following paragraphs.

In a population that Ryan (1953) studied near Ithaca, New York, female northern leopard frogs did not become sexually mature until at least their first year following metamorphosis, and most were probably not sexually mature until their second year. Similarly, Leclair and Castanet (1987) reported that males in Quebec populations reached sexual maturity at two years of age. Force (1933) estimated that northern leopard frogs attained reproductive maturity at three years of age in northern Michigan. Likewise, Baxter (1952) reported that females did not achieve sexual maturity until late in the second year in frogs from the vicinity of Laramie, Wyoming (2,200 m), with eggs laid in the third year following metamorphosis. At elevations of 2,600 m, he found that female frogs did not attain sexual maturity until late in the third year, with eggs being laid in the fourth year following metamorphosis.

Although Flower (1936) reported that a captive leopard frog lived for five years and 11 months, Leclair and Castanet (1987) found few frogs older than four to five years. It is probably reasonable to assume from these data that most northern leopard frogs living in the wild seldom reach their sixth year. It is also reasonable to conclude that female northern leopard frogs may breed two or three times during their lives, and certainly no more than four times in any part of Region 2. This agrees in general with the conclusions of Corn and Livo (1989) in southern Wyoming and northern Colorado, who wrote that the three classes of clutch sizes occurring at their study sites corresponded to three age classes of frogs.

There appears to be no other information on growth rates, age at sexual maturity, or age at death in any natural populations of the northern leopard frog. Corn and Livo (1989) recorded an average of 3,045 eggs per clutch (range 645 to 6,272 eggs), which may mean that females produce some 9,000 eggs during their lifetime, assuming three reproductive bouts during three consecutive years. Hatching success seems high, from 70 to 99 percent at the sites studied by Corn and Livo (1989) and around 95 percent at sites studied by Hine et al. (1981). There are no studies of survival rates of northern leopard frogs to sexual maturity, but it is likely that mortality is significant after hatching.

There also are no studies of survivorship at any other life stage in northern leopard frogs. Merrell (1977), however, has provided some interesting insights from work done near Minneapolis/St. Paul, Minnesota. He counted 173 egg masses at eight adjacent breeding ponds. At 2,000 to 5,000 eggs per mass (determined from studies of Merrell 1965), Merrell (1977) calculated that the number of eggs at his study sites ranged from 346,000 to 865,000. Capture/mark/release data obtained in July prior to dispersal of the young metamorphs indicated that approximately 20,000 metamorphs existed in the area. This study would indicate a mortality rate of at least 94 percent and possibly as high as 97 percent in the tadpole stage. Merrell (1977) used a Lincoln – Peterson index to derive this estimate, which is probably an inappropriate estimator for an open population such as the one under study (Krebs 1999), but the mortality rates he calculated appear reasonable. Another study found a ratio of newly metamorphosed frogs to sexually mature adult frogs somewhere between 15:1 and 20:1 (Merrell 1969). This would indicate a mortality rate of 93 to 95 percent from the metamorph stage to sexually mature frogs, corroborating Merrell (1977). Although these numbers should all be considered approximate due to the techniques used, they still indicate a mortality rate that probably exceeds 90 percent in young age classes (i.e., from tadpole to metamorph and from metamorph to the adult stage).

Various estimates of population density of northern leopard frogs exist. Merrell (1968) found populations of 124 to 1,568 individuals at six breeding ponds in Minnesota. Although the exact sizes of these ponds were not given, he stated that they were “about 50 to 100 feet in diameter” (i.e., 0.019 to 0.075 ha each). Hine et al. (1981) found two to 76 frogs at six ponds in Wisconsin that were from 0.02 to 32 ha in size; they claimed that this represented a serious decline in northern leopard frog populations in the upper Midwest. Merrell (1977) estimated that there were about 20,000 newly metamorphosed frogs in a 15 ha study area in Minnesota in a sample of about 25,000 frogs of all ages.

Estimates of mortality rates derived from the data of Merrell (1977) show rather clearly that northern leopard frogs are probably typical r-selected species with a type III survivorship curve and probably experience large fluctuations in population dynamics from year to year (Begon et al. 1996). This is typical of many amphibians, making it difficult to identify population trends (Pechmann et al. 1991, Pechmann and Wilbur 1994). Species that are r-selected can recover from low

population densities due to high potential growth rates, but they can also go locally extinct if affected by severe mortality pressures at times when population densities are low (Begon et al. 1996).

Community ecology

Several studies have been conducted on northern leopard frogs and their role in amphibian communities (DeBenedictis 1974, Smith-Gill and Gill 1978, Woodward 1982, 1983, McAlpine and Dilworth 1989, Hecnar and M'Closkey 1998, Relyea and Werner 2000, Relyea 2001a, 2001b). These studies can be divided into those of tadpoles (DeBenedictis 1974, Smith-Gill and Gill 1978, Woodward 1982, 1983, Relyea and Werner 2000, Relyea 2001a, 2001b) and adults (McAlpine and Dilworth 1989, Hecnar and M'Closkey 1998). They can be further divided into studies on competition (DeBenedictis 1974, Smith-Gill and Gill 1978, Woodward 1982, McAlpine and Dilworth 1989), predation (Woodward 1983, Relyea and Werner 2000, Relyea 2001a, 2001b), and general ecology (McAlpine and Dilworth 1989, Hecnar and M'Closkey 1998). There is a growing body of literature on the parasites and diseases of ranid frogs in general and a variety of studies on other aspects of ranid frog ecology.

Although no studies examining tadpole densities or their role in structuring the community have been completed in Region 2, northern leopard frog tadpoles can clearly dominate in some semi-permanent Rocky Mountain ponds during the spring and early summer (personal observations of the lead author). Woodward (1982, 1983) found that temporary pond breeders were often superior competitors to permanent pond breeders, and that some temporary pond breeders ate tadpoles of permanent pond breeders (Woodward 1982). For example, Mexican spadefoot (*Spea multiplicata*) ate the tadpoles of northern leopard frogs (Woodward 1982). Plains spadefoot (*S. bombifrons*) occurs in Region 2 and breeds in temporary ponds, but it has not been found above 1,400 m in the Black Hills area (Smith unpublished data). Since northern leopard frogs do not breed in the temporary ponds in which the Plains spadefoot breeds (unpublished data), they probably do not interact in the wild in Region 2. Although they are at a competitive disadvantage to temporary pond breeders, Woodward (1983) found that northern leopard frog tadpoles are better able to avoid predation because they tend not to move very much, as compared to tadpoles of temporary pond breeders. He also found that there are more tadpole predators in permanent ponds, thus explaining why northern leopard frogs might have evolved this important behavioral trait.

Alford (1999) pointed out that high densities of tadpoles of various species may be the primary consumers in some ecosystems and are known to reduce the standing crop and change the species composition of algae. For example, Lamberti et al. (1992) found that tailed frog (*Ascaphus truei*) tadpoles at a density of five tadpoles per square meter could reduce periphyton biomass by 98 percent and chlorophyll a by 82 percent in streams in Washington. Some ponds in parts of Region 2 have very high northern leopard frog tadpole densities that probably significantly affect algal biomass (Smith, personal observations).

Two studies examined interspecific relationships of northern leopard frogs and how they affected the distribution of adult frogs in Canada. McAlpine and Dilworth (1989) investigated competition and microhabitat of various anurans in New Brunswick, and Hecnar and M'Closkey (1998) examined species richness patterns of various frogs in Ontario. McAlpine and Dilworth (1989) found that the diets of green frogs (*Rana clamitans*) and northern leopard frogs overlapped significantly. However, these two species, which are similar in size, appeared to occupy different niches based on microhabitat characteristics. In terrestrial habitats, northern leopard frogs tended to be found in areas of denser vegetation and farther from shore than green frogs when the two co-occurred in ponds. Both showed up in the diet of bullfrogs (*R. catesbeiana*). Whether these patterns of microhabitat use by northern leopard frogs are similar in Region 2 is unknown. They also found that vegetation structure and composition affected the patterns of species richness that they observed, with increased amphibian richness in woodland areas. Hecnar and M'Closkey (1998) underscore the effect of predatory fish on amphibian presence; it was one of the most significant factors structuring the amphibian community across much of southwestern Ontario.

Natural predators

A variety of predators eat northern leopard frogs at all life stages. Merrell (1977) reported that most mortality occurred in the tadpole stage and was largely caused by predators, although overwintering mortality was important to subadults (i.e., recently metamorphosed tadpoles). He also noted that various early authors recorded the following as predators of tadpoles: waterfowl, garter snakes (*Thamnophis* spp.), water snakes (*Nerodia* spp.), newts (unknown species), fishes, leeches, and aquatic insects, including diving beetle larvae and adults (Dytiscidae), dragonfly larvae (Libellulidae and probably other families), caddisfly

larvae (Phryganeidae), backswimmers (*Notonecta* spp.), and giant water bugs (*Belostoma* spp.). Spiders (Lycosidae and Pisauridae) may also eat tadpoles (Merrell 1977). More recently, Woodward (1983) identified the following important northern leopard frog predators in his predation experiments: checkered garter snakes (*T. marci*), tiger salamander (*Ambystoma tigrinum*) larvae, belostomatids (diving beetles), aeshnid (dragonfly) larvae, corydalid (dobsonfly) larvae, and notonectids (backswimmers). It is probable that all of these predators are also found in Region 2, but the garter snake species may differ (*T. elegans*, *T. radix*, and *T. sirtalis* are found in Region 2).

Tiger salamander adults and larvae are known to feed on frog tadpoles (Petranka 1998), and in experimental interactions, they have eliminated frog tadpoles completely (Morin 1983). In the Black Hills, the breeding period of the tiger salamander overlaps with that of the northern leopard frog, and they sometimes breed in similar ponds (Smith unpublished observations). Paedomorphic tiger salamanders occur across much of Region 2 (Petranka 1998), and we suspect that they readily eat northern leopard frog eggs and tadpoles. Hammerson (1999) noted that pied-billed grebes (*Podilymbus podiceps*) and tiger salamanders preyed on northern leopard frog tadpoles in Colorado.

In a series of studies, Relyea and Werner (2000) and Relyea (2001a, b) examined morphological and behavioral plasticity in response to predation threats on tadpoles of a number of amphibian species, including the tadpoles of northern leopard frogs. Increases in tail depth should result in better swimming speed of tadpoles (Wassersug and Hoff 1985, McCollum and Leimberger 1997). Relyea and Werner (2000) found that northern leopard frog tadpoles were marginally smaller with deeper tailfins and more robust tail musculature when reared in the presence of dragonfly (*Anax* spp.) larvae, a known predator on frog larvae, but the difference was not significant. Relyea (2001a, b) found that responses to predators were complex and varied according to predator and anuran species. In the presence of dragonfly larvae and mudminnows (*Umbra* spp.), northern leopard frog larvae became less active, but their activity levels did not change in the presence of eastern newts (*Notophthalmus viridescens*) or giant water beetles (*Dytiscus* spp.) (Relyea 2001a). Relyea (2001b) explained why these behavioral differences probably occurred; eastern newts and giant water beetles were relatively inefficient predators on northern leopard frog tadpoles, while mudminnows and dragonfly larvae had high capture efficiencies. Relyea (2001a) also found that northern leopard frog tadpoles changed morphology

in the presence of mudminnow species, developing smaller bodies with deeper tail fins, a result that was not found to be significant when they were reared with dragonfly larvae (Relyea and Werner 2000). This result was not obtained when tadpoles were reared with any of the other predators. When taken together, Relyea and Werner (2000) and Relyea (2001a, b) showed that the responses of anurans to predators were complex, with changes in morphology and behavior depending on the predators to which they were exposed. Most importantly as regards the natural history of northern leopard frogs, these studies showed that predation is probably a significant factor structuring various aspects of the natural history of anuran tadpoles.

Most authors have combined discussions of predation on subadults with that on adults. Dole (1965b, 1968) hypothesized that snakes were major predators of subadult and adult northern leopard frogs. Hammerson (1999) reported that recently metamorphosed frogs were preyed upon by great blue herons (*Ardea herodias*), burrowing owls (*Athene cunicularia*), northern water snakes (*Nerodia sipedon*), and western terrestrial garter snakes (*Thamnophis elegans*). According to Merrell (1977), the most common predators on adult and subadult northern leopard frogs were garter snakes (*Thamnophis* spp.). He claimed that northern leopard frogs supported large populations of garter snakes. Leeches also fed on northern leopard frogs, leaving them debilitated and presumably more likely to die (Merrell 1977). Merrell (1977) also reported that various predators such as fishes, snakes, turtles, amphibians, birds, and mammals all fed on adult northern leopard frogs. The lead author has observed garter snakes feeding on northern leopard frogs in the Black Hills (unpublished observations).

Introduced predators

Introduced predators have the capacity to overwhelm northern leopard frog populations since the frogs have not co-evolved with such predators. Bullfrogs are well known to cause the elimination of populations of ranid frogs, especially in the western United States, where bullfrogs have been widely introduced (Stebbins and Cohen 1995). Although northern leopard frogs and bullfrogs co-occur naturally in parts of their range, in areas where bullfrogs and northern leopard frogs are not sympatric and in which bullfrogs have been introduced, northern leopard frogs have declined (Hammerson 1982, 1999). Consequently, the establishment of non-native populations of bullfrogs should be treated as a major management problem for the persistence of native frog populations.

Because northern leopard frogs probably have no natural defense against introduced predaceous fish, the widespread establishment of these non-native species is a serious issue, probably causing significant declines in Region 2. Hecnar and M'Closkey (1997b) showed that introduced predaceous fish reduced the abundance and diversity of frog communities in Canada, including those in ponds that contained northern leopard frogs. Bovbjerg (1965) reported that the introduction of truckloads of young fish by the Iowa Conservation Commission completely exterminated a population of northern leopard frog tadpoles at his study site following stocking of the slough under study. Introduced fish also eat overwintering northern leopard frogs, which are extremely vulnerable to predation (Emery et al. 1972). Brönmark and Edenhamn (1994) showed that introduced predaceous fish reduced the abundance of tree frogs (*Hyla arborea*). In the Black Hills, the lead author has observed that some ponds with breeding colonies of chorus frogs (*Pseudacris triseriata*) and northern leopard frogs that also contained predaceous fish had no successful metamorphs later in the active season.

Introduced predaceous fish known to occur in parts of Region 2 include rainbow trout, brown trout, brook trout, northern pike, largemouth bass (*Micropterus salmoides*), green sunfish (*Lepomis cyanellus*), and rock bass (*Ambloplites rupestris*). The various trout species will all eat tadpoles (Smith et al. 1998) and probably also eat frog eggs. Northern pike will eat hibernating adult frogs (Smith, unpublished data), and bass and sunfish will probably eat eggs and tadpoles. Kruse and Francis (1977) found that largemouth bass, green sunfish, and black bullhead (*Ameiurus melas*) all ate northern leopard frogs. Bluegill sunfish (*L. macrochirus*) will also eat northern leopard frogs (Relyea 2001b).

Competitors

In amphibian assemblages, the most obvious stage at which competition could occur is the larval period. Tadpoles of other amphibian species may have similar diets to those of northern leopard frogs, and so they may compete with each other for limited resources in typically confined breeding ponds. Interactions during this life stage have been emphasized in studies of amphibian competition. Relationships of adult northern leopard frogs with competitors, such as generalist insectivores of similar size, have not been studied.

Larval amphibians have provided an excellent system in which to study competition within a closely related group of competitors (Wilbur 1997).

DeBenedictis (1974) and Smith-Gill and Gill (1978) studied competition between northern leopard frogs and wood frogs, which breed slightly earlier in the spring than northern leopard frogs but frequently in the same types of ponds. DeBenedictis (1974) conducted a field study while the study of Smith-Gill and Gill (1978) was a laboratory study designed to examine some of the predictions of competition as determined by the Lotka-Volterra competition equations. The tadpoles of these two species have a high degree of temporal overlap in most parts of the range of the northern leopard frog, and they co-occur in the Rocky Mountains in northern Colorado and northern and southern Wyoming (Stebbins 2003). DeBenedictis (1974) found that the intensity of competition depended on the amount of food, predation, and density of the two species, and in some situations, competition did not occur at all. Smith-Gill and Gill (1978) also found complex density effects and discussed these with relation to the Lotka-Volterra competition equations.

In much of Region 2, northern leopard frogs co-occur with tiger salamanders and may breed in the same ponds. These two species may compete as larvae, but no studies of competition between these species have been done. As previously discussed, however, the tiger salamander is known to prey on northern leopard frog tadpoles (Morin 1983, Woodward 1983, Petranka 1998, Hammerson 1999).

Parasites and disease

Three basic types of diseases have been identified in amphibians: viruses, fungal infections, and bacterial infections (Carey et al. 1999). Of these three, Carey et al. (1999) and Daszak et al. (1999) wrote that only viruses and fungal infections have been implicated in mass mortality events. However, the bacterial diseases collectively called "red leg" have been reported to cause mass mortality events by Faeh et al. (1998). The term "red leg" may refer to the symptomology of a variety of different bacteria (Faeh et al. 1998) but is frequently associated with *Aeromonas hydrophila*, a bacterium blamed for the disappearance of boreal toads at several sites in Colorado (Carey 1993). However, Carey et al. (1999) stated that they believed that bacterial infections were largely secondary to fungal and viral infections.

Specific types of iridoviruses known as ranaviruses can infect ranid frogs (Cunningham et al. 1996, Daszak et al. 1999), and some amphibian declines have been blamed on these viruses (Jancovich et al. 1997, Daszak et al. 1999). Daszak et al. (1999) reported that ranaviruses were extremely lethal, with 100

percent mortality in exposed ranid tadpoles. Tadpoles are most susceptible to these viruses, but all life stages can acquire the disease (Daszak et al. 1999). Infected metamorphs die without apparent signs of infection, and infected adults show no overt signs but may display a general weakness (Daszak et al. 1999). Secondary bacterial infections are common during ranavirus infection. Introductions of bullfrogs have probably spread ranaviruses around the country (Daszak et al. 1999). In South Dakota, tiger salamanders are often introduced as fish bait, and this species has an iridovirus of its own (Daszak et al. 1999) and may be a potential transmission vector to ranid frogs.

Although a link between ranaviral infections and amphibian declines is suspected, it is less clear than the link between chytridiomycosis and amphibian declines (Daszak et al. 1999). Chytridiomycosis, a disease of anurans caused by a chytrid fungus (*Batrachochytrium dendrobatidis*), has recently been blamed for frog declines around the world (Berger et al. 1998, Morell 1999, Daszak et al. 1999, 2000), and it has been found in northern leopard frogs (Carey et al. 1999). The extent of this disease and mortality rates in northern leopard frogs are unknown. Chytridiomycosis was first blamed for amphibian declines in Australia in 1998, but it probably emerged separately on two continents at around the same time (Berger et al. 1998) and has been found in frogs collected as far back as 1978 (Milius 2000). Although the exact mode of transmission of this disease is unknown, field herpetologists routinely disinfect field gear used at multiple wetland sites. It is possible that the disease could be transmitted by any person, including anglers. The signs of chytridiomycosis are loss of the righting reflex, lethargy, and abnormal posture (Daszak et al. 1999).

Carey et al. (1999) discussed hypotheses that could explain the apparent recent increases in the susceptibility of amphibians to infectious disease. They suggested that these pathogens can be introduced to frog habitats by fish stocking, introduction of non-native amphibians (e.g., commercially obtained bullfrogs or tiger salamanders that are dumped into areas far from their collection sites), wind-blown insects, the activity of birds or other animals, by workers monitoring amphibian ponds, or by anglers or other tourists.

Like many amphibians, northern leopard frogs collected in the wild probably have a high parasite load. There have been various field investigations of the parasites of this species, including Prudhoe and Bray (1982), Baker (1987), and McAlpine and Burt

(1998). Goldberg et al. (2001) discussed the helminths of northern leopard frogs from North Dakota and South Dakota, and Dyer (1991) reviewed records of parasites found in northern leopard frogs. Fried et al. (1997) found that some parasites are particularly lethal to northern leopard frog tadpoles. Of particular interest are trematode parasites in the genus *Ribeiroia*, which have emerged as a potential cause of limb abnormalities in Pacific treefrogs (*Pseudacris regilla*) (Sessions and Ruth 1990, Johnson et al. 1999) and western toads (Johnson et al. 2001). It is not known if any of these parasites cause population declines in northern leopard frogs.

Envirogram

Andrewartha and Birch (1984) outline a “Theory of Environment” that seeks to organize the ecology of a species into a coherent and logically connected web of factors that influence its ability to survive and reproduce. The heart of this endeavor is the envirogram, which orders these factors in a hierarchical dendrogram. The main stem of this dendrogram is comprised of a “centrum” of components that act directly on the species under consideration. From this centrum are branches that “trace pathways from distal causes in the web to proximate causes in the centrum.”

We have developed an envirogram for the northern leopard frog (**Figure 4a** and **Figure 4b**). It is a useful heuristic tool to conceptualize how various factors might affect the northern leopard frog. It is largely a hypothetical effort that may depend on the authors, their objectives, and their knowledge. As Andrewartha and Birch (1984) clearly state, “the detail of the structure scarcely matters; it is bound to vary as each operator pieces the story together in his own way.” More importantly, they state the following:

If here and there we seem to have been too preoccupied with the attempt to place a component of environment in its proper category, we would not want to give the impression that classification is an end in itself. The model should work better if we can be consistent in identifying the components of the environment, but the chief aim remains to present a general model of how the environment works, hoping that it might point to the most effective questions to be asked at each stage of an investigation.

With this in mind, the attached envirogram should be viewed as our attempt to model the

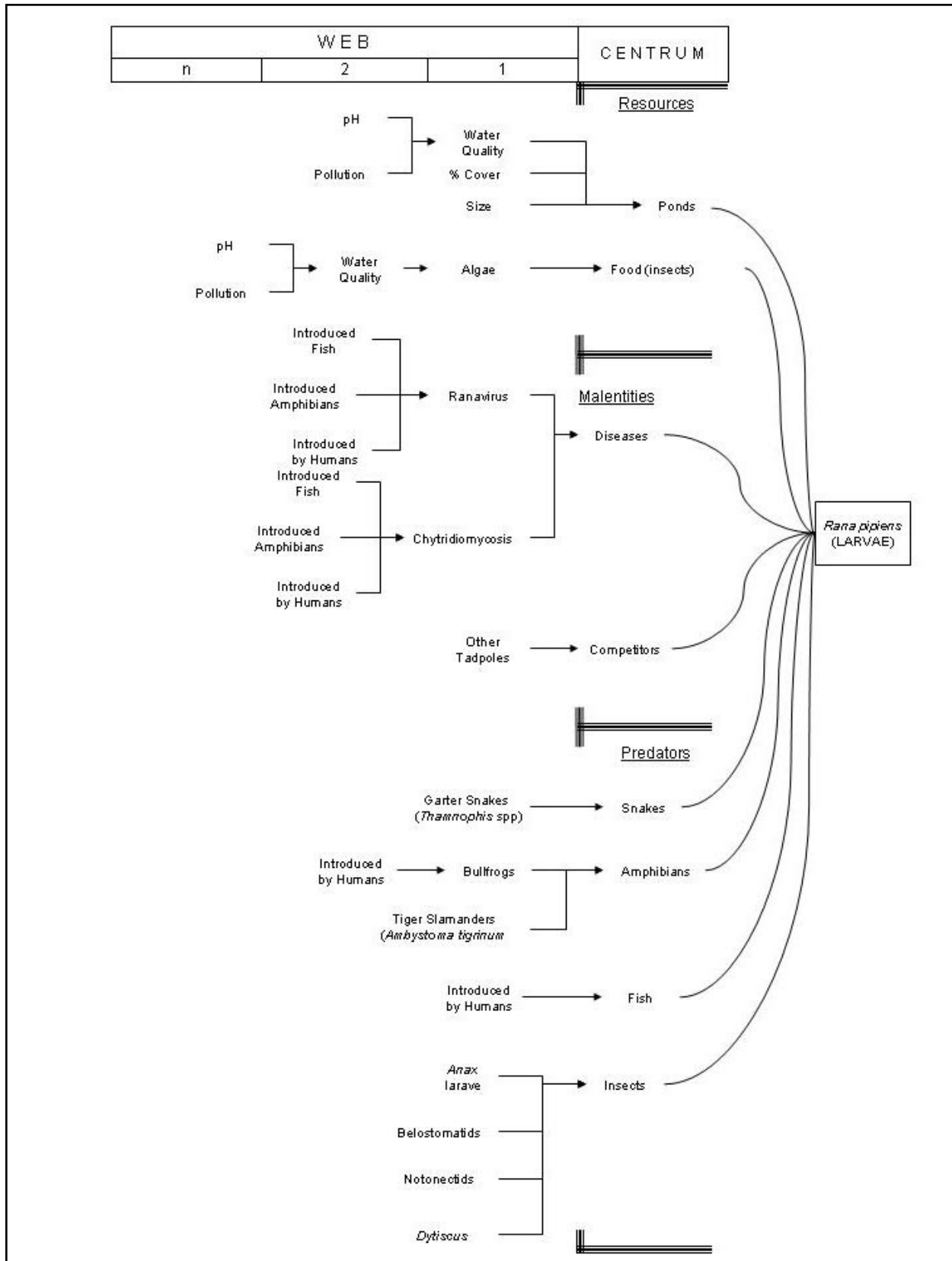


Figure 4a. Envirogram for larval northern leopard frogs.

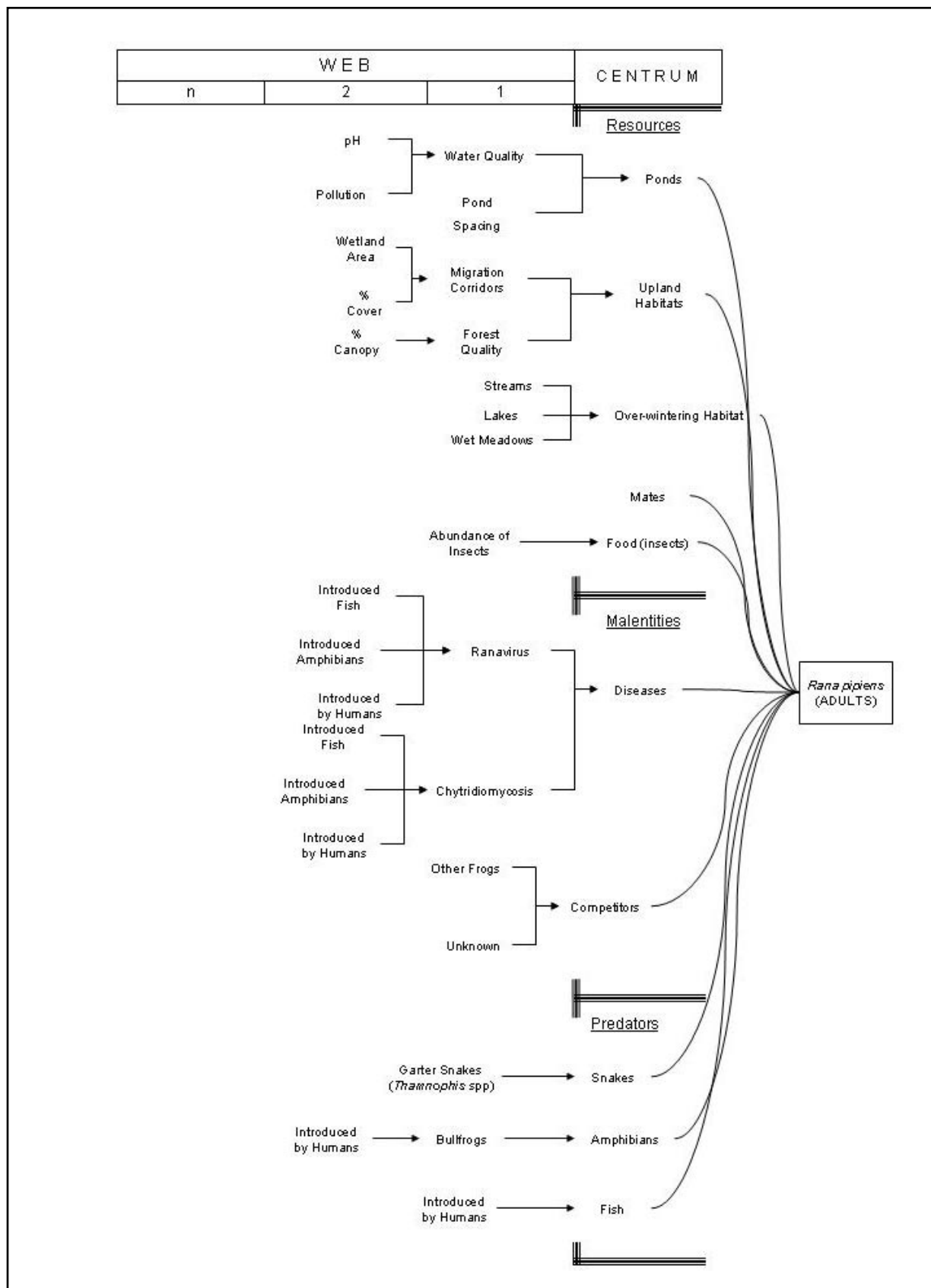


Figure 4b. Envirogram for post-metamorphosis northern leopard frogs.

environment of the northern leopard frog. It highlights some key links for future study, but by no means does it define this environment.

CONSERVATION

Conservation Status and Threats

Trends

Distribution trend

Rorabaugh (2005) is the most recent summary of distributional and abundance patterns of the northern leopard frog. Overall, the range of the northern leopard frog has contracted in recent time, especially in the western two-thirds of the United States, where there have been widespread extinctions (Rorabaugh 2005). Localized extinctions have occurred in Colorado (Hammerson 1982, Corn and Fogleman 1984, Cousineau and Rogers 1991), Montana (Maxell 2000), Idaho (Koch and Peterson 1995), eastern Washington (Leonard et al. 1999), California (Stebbins and Cohen 1995), and Arizona (Clarkson and Rorabaugh 1989).

Most relevant to conservation of the species in Region 2 are range contractions in Colorado, Wyoming, Nebraska, and South Dakota. Northern leopard frogs are considered “vulnerable” by the Natural Heritage Programs in Colorado and Wyoming, the two states in Region 2 dominated by the Rocky Mountains. Although it is a common perception that population extinctions have occurred primarily at high elevation sites, we have found studies showing extinctions not only at high elevations (Koch and Peterson 1995, Corn and Fogleman 1984) but also at low elevations (Hammerson 1982, Cousineau and Rogers 1991, Reichel 1996, Nelson 1999). Conversely, Smith et al. (2004) found no extinctions at seven national parks in the northern Great Plains or at several localities in the Black Hills of South Dakota (Smith et al. 2005).

Abundance trends

Many studies have demonstrated range contractions in the northern leopard frog, but very few have studied abundance trends (Rorabaugh 2005). However, in the western United States the species appears to have undergone major population declines or has become locally extinct. In Region 2, northern leopard frogs are now severely reduced in the Laramie Basin of southern Wyoming, but they may still be common in other parts of the state (Baxter and Stone 1985, Stebbins and Cohen 1995). They have also

become scarce at many sites in Colorado (Hammerson 1999). The species was formerly common throughout the central Great Plains states, but it has declined there as well (Stebbins and Cohen 1995). Still, Smith et al. (2004) found them to be common at national parks in western North Dakota, western South Dakota, eastern Wyoming, and western Nebraska, and they remain the most abundant amphibian in the Black Hills of South Dakota (Smith et al. 2005). Nevertheless, although they are apparently still common in parts of the northern Plains states (Smith et al. 2004, 2005), we believe that the species is in general decline across the western two-thirds of the United States (Rorabaugh 2005).

We presume that further declines in abundance can be predicted from the U.S. census data presented earlier. Most of the western United States is growing rapidly, and the Rocky Mountain States are no exception. Census data reveal annual growth rates of 5 to 15 percent for many towns and cities in the region from 1990 to 2000, ranging to as high as 95 percent. Population growth of this nature will lead to further habitat loss, habitat fragmentation, and pressure on national forests by all types of users. We predict that the abundance of northern leopard frogs will continue to trend down.

Causes of trends

There is no way to know exactly what has caused declines and extinctions in Region 2 because there are no synthetic studies on declines and extinctions across any large part of the range of the northern leopard frog. In fact, there is much disagreement about what has caused amphibian declines in general (Stebbins and Cohen 1995). We have discussed a number of factors so far, but the ones listed below appear to be of most importance in the Rocky Mountain Region.

Habitat loss and fragmentation in the Rocky Mountain region are caused by a variety of land uses, including urbanization and the growth of suburbs, logging, and building of roads and trails. Any kind of habitat fragmentation in any locality, including construction in relatively pristine areas, can result in loss of important habitat. For example, many streams and lakes in national forests are used for fishing, and this often results in heavy use of sites near or in wetlands, and construction of shelters, picnic areas, recreational beaches, campsites, restrooms, walkways, and other structures. Because wetlands are popular areas for recreation, a variety of wetlands are being converted from wetlands suitable for northern leopard frogs to other uses. An example of the pressure

being put on amphibian habitats is a site under study by the lead author, Cook Lake in the Bear Lodge Mountains of Wyoming. Although currently visited by recreationalists, it has remained relatively pristine. Now, however, it is being developed, with the addition of more restrooms, campsites, and canoe launching points. A concrete walkway is being constructed around the lake, removing much of the emergent vegetation around the lake that would be used by frogs. Although we think of national forests as natural areas used for recreation, wetlands are negatively affected through their use by boaters, swimmers, anglers, hunters, and other types of users, and by construction of facilities for these visitors.

Because of the popularity of fishing in the Rocky Mountains and other mountainous areas of the western United States, fish stocking is widely practiced and is likely having a tremendous impact on amphibian populations. Stocking often occurs in ponds and lakes that were naturally fishless, especially those in high mountain environments. Some of these waters are likely critical to successful frog reproduction, and stocking of non-native species in these locations is particularly harmful. Non-native predaceous fish are even introduced by helicopter into very remote lakes in some wilderness areas in the western mountains (Peterson personal communication 2003), many of which are only lightly visited by anglers and in which predaceous fish did not naturally exist. Given the detrimental effect that introduced predaceous fish have on native amphibian populations, federal and state agencies should review their current stocking practices to consider the implications for native amphibian assemblages.

Introduction of diseases (e.g., chytridiomycosis and ranavirus) is a concern. Such diseases can be lethal to local populations and are probably transmitted through a number of vectors, including humans (e.g., on clothing, boots, waders), but it is not known precisely how they move from population to population. Common practices in the Rocky Mountain Region that might result in the introduction of disease are the extensive introductions of predaceous fish for sport anglers and the use of bait, which is frequently dumped into ponds and lakes following fishing. In addition, diseases can be transported on muddy boots of anglers if they have been in aquatic habitats containing frogs of any species. Many species of animals (e.g., bullfrogs) use ponds similar to the ponds that northern leopard frogs inhabit (Rumble et al. 2004), and they could transport diseases on their bodies as they move from pond to pond.

Extrinsic threats

There are a number of potential threats to the continued viability of northern leopard frogs in the Rocky Mountain region. Although it is difficult to say which of these is most important, we believe that risk factors threatening northern leopard frogs in Region 2 fall into three main categories: 1) landscape-scale processes that threaten the viability of populations, 2) direct threats of mortality from various non-indigenous biotic agents, and 3) water quality issues.

Landscape scale changes such as loss and fragmentation of breeding habitat, disruption of migratory pathways, and loss or alteration of overwintering sites, may have caused range-wide declines in northern leopard frogs. However, we lack the kind of detailed data necessary to document these changes over the last 100 to 200 years of European settlement in the western United States, and particularly in Region 2. In one case, Parrish et al. (1996) documented changes in the physiography of the Black Hills over approximately 100 years. Using the best historical data available to them, these authors determined that one of the most noticeable changes was a loss of wetlands and a general loss of soil moisture.

Parrish et al. (1996) also determined that fire suppression has allowed ponderosa pine (*Pinus ponderosa*) to increase in density and to expand in areal extent. The excess of pine has caused the Black Hills to become drier by increasing evapotranspiration across the region. Increased evapotranspiration results in loss of water from the soil, generally drying the soil. In addition, they found that the near extirpation of beaver (*Castor canadensis*) greatly reduced the number of beaver dams, allowing water to run more quickly out of the Black Hills while reducing the number of wetlands. Beaver ponds can be one of the richest habitats for northern leopard frogs because the frogs use the beaver ponds and associated wetland complexes for breeding. The moist, dense vegetation of upland habitats around these complexes is often ideal for foraging.

Finally, Parrish et al. (1996) found that stream margins in the Black Hills were largely denuded of vegetation during the 20th century as property owners cleared vegetation for road construction. Grazing of livestock may also be an important factor, but it was not addressed by Parrish et al. (1996). Livestock can have significant impacts on wetland and riparian vegetation and aquatic communities, including damage

to streamside vegetation, increased sedimentation as a consequence of resulting erosion, and more rapid movement of water through stream systems where riparian vegetation is no longer present to stem water flow. The effects are a further reduction of water resources available to amphibians and a loss of effective habitat.

Human development of wild lands has been shown to affect amphibian populations negatively at the regional scale (e.g., Hecnar and McCloskey 1996). Lehtinen et al. (1999) showed that habitat fragmentation from development activities lowered amphibian species richness at 21 glacial lakes in Minnesota, where the northern leopard frog was the most abundant anuran. These authors found that amphibian species richness at ponds declined with distance from other ponds and with increased road density, both common results of urbanization. They also found that species richness declined as urban land use increased at all spatial scales, implying that increasing levels of urbanization should lead to decreased species richness, no matter the scale at which development takes place. They recommended that land management plans address landscape changes caused by urbanization and attempt to minimize such changes.

Increasing development of formerly “wild” private and public land is probable in virtually all parts of the Rocky Mountain region. Census figures compiled from 1990 to 2000 show that the population of most states in Region 2 grew between 8 and 9 percent, with Colorado growing at a rate of 30 percent. The Denver area was the fourth fastest-growing large metropolitan area in the western United States, and even smaller towns and counties have grown rapidly (e.g., from 1990 to 2000 Cheyenne grew 12 percent, Rapid City grew 13 percent, and Laramie County grew 9 percent). These figures suggest that loss of wild land has probably been extensive throughout the Rocky Mountain region and is likely to continue into the foreseeable future. It is likely that urbanization will have negative effects in the Rocky Mountain region, as found by Lehtinen et al. (1999) in Minnesota. Further, human growth on nearby private land can have off-site impacts on national forests, because such growth puts additional pressure on the national forests as recreational demands commensurately increase, with potentially detrimental impacts to local herpetofauna (e.g., Garber and Burger 1995). Consequently, we believe that habitat on national forests is becoming increasingly important to amphibians (and wildlife in general) and that forest managers must consider this when developing management strategies.

To accommodate the increased traffic associated with population growth, more roads are built or expanded throughout the region. Backcountry roads and trails are created for logging access and for off-road vehicles and mountain bikes on public lands. Roads affect amphibian populations most obviously by eliminating or altering migration and dispersal corridors, but also directly through road mortality or simply by damaging habitat. Herpetologists are well aware of road-related mortality, as they frequently use roads to survey their target organisms (Shaffer and Juterbock 1994). Large migrations, some consisting of thousands of individuals, cross many roads. Koch and Peterson (1995) describe such a situation for the tiger salamander. Semlitsch (1998) noted that roads placed too close to wetlands are known to reduce populations of salamanders. The lead author has found countless dead herpetofauna of all kinds on roads over a 30-year career.

The effects of introduced organisms on amphibians are extensively documented, and a review of this literature is beyond the scope of this assessment. In the case of the northern leopard frog, the effects of introduced predaceous fish and bullfrogs have already been discussed. Also relevant is the impact of diseases. Chytridiomycosis has recently been recognized as a threat to the persistence of amphibian populations and is causing population declines in many frog species. Ranavirus can cause population declines in ranid frogs, but it is probably not an introduced disease. Many organisms visit frog ponds, ungulates and other mammals, waterfowl, fishes, various species of insects, and doubtless others (Rumble et al. 2004), and they could move these diseases around the landscape, as could humans, although no evidence for this exists.

The complex life cycle of amphibians and the permeability of their skin make them especially susceptible to ecotoxicological agents (Cooke 1981, Duellman and Trueb 1986, Bishop 1992, Hall and Henry 1992). Consequently, there has been great interest in their response to such agents. Power et al. (1989), Pauli et al. (2000), and Sparling et al. (2000a) have all summarized the voluminous literature on the ecotoxicology of amphibians. There has been extensive work on the effects of water quality on northern leopard frogs as well. The database of Pauli et al. (2000) is particularly useful since it is searchable using a variety of parameters including species, contaminant, author, and study type (i.e., field study, lab study, and other types). A literature search of Pauli et al. (2000) for studies on this species returned 412 citations, and a comprehensive summary of this literature is beyond

the scope of this report. However, review articles by Harfenist et al. (1989), Diana and Beasley (1998), and Sparling et al. (2000a) provide a useful summary of existing ecotoxicological data on amphibians.

Diana and Beasley (1998) offered a concise review of toxicant studies in amphibians, including brief summaries of studies on polychlorinated biphenyls, benzene, phenol, crankcase oil, mercury, cadmium, lead, hydrogen ions (acidification), aluminum, nitrate fertilizers, trichlopyr, triazine herbicides, phenoxy herbicides, dipyridyl herbicides, glyphosate (found and tested in Roundup®), pyrethroids, cholinesterase-inhibiting insecticides, carbamate insecticides, organophosphorus insecticides, organochlorine insecticides, and rotenone. They pointed out that, collectively, the amount of toxicants dumped into the environment constituted an enormous amount of chemical pollution and likely contributed to amphibian declines around the world. Breeding ponds used by northern leopard frogs tend to collect all manner of toxicants from runoff water, and so they are doubtless exposed to these agents at all points in their life cycle.

It is impossible to discuss meaningfully the relationship between water quality issues and northern leopard frogs anywhere in Region 2 without relevant background data on water quality. Unfortunately, Region 2 is a large, heterogenous region spanning a wide range of elevations, topographic types, habitats, urban and industrial development patterns, and ecotoxicological impacts. Much water quality information is collected and reported by local, state, and federal agencies in unpublished reports. It is not possible to summarize the types of toxicants to which this species may be exposed without writing an extensive review of water quality throughout the region, which is beyond the scope of this assessment. However, we can more generally summarize the ecotoxicological hazards to which northern leopard frogs may be exposed. The toxic inputs discussed below are those that appear to be of most concern within Region 2, but not all are a concern in every locality. Twelve main factors contribute to poor water quality in wetland habitats frequented by northern leopard frogs:

- 1) **Pesticides:** As noted by Sparling et al. (2000b), this is one of the most studied classes of ecotoxicological agents. Throughout Region 2, various pesticides are used, the most common being 2, 4-D Amine, Escort®, Plateau®, and Roundup®. Unfortunately, pesticide use is one of the more difficult inputs to study, and typically, it is necessary to

contact county extension agents throughout a region to get a sense of the types of pesticides most commonly used and the pattern in which they are used. Fortunately, many of the commonly used pesticides have short half-lives, usually from one week to 30 days. If used judiciously, they may be more or less safe, but this depends on individual applicators. No region-wide statistics exist on the extent of the use of pesticides, and it is beyond the scope of this assessment to compile such data. Below we discuss specific pesticides that have been used and studied in various parts of North America.

Berrill and co-workers (Berrill et al. 1993, 1994, 1997) studied various pesticides commonly used in agriculture and silviculture in Canada. Berrill et al. (1993) found that the pyrethroid insecticides permethrin and fenvalerate did not kill frog eggs or tadpoles that were exposed to low levels of these insecticides. However, they caused delayed growth of tadpoles and abnormal behavior, such as twisting rather than darting away after being prodded by investigators. Both of these results indicated that higher mortality could occur in tadpoles exposed to these chemicals or hatched from eggs exposed to these chemicals. The effects of the insecticides varied at different temperatures and lessened with decreased dosages. However, the researchers pointed out that concentrations used in their study were considered low. Both of these insecticides are commonly used in the United States as well as Canada.

Berrill et al. (1994) studied herbicides used to manage coniferous forests in Canada. They exposed northern leopard frog embryos and tadpoles to low levels of the insecticide fenitrothion and the herbicides triclopyr and hexazinone. At the levels used in these experiments, none of these pesticides affected hatching success or subsequent behavior in tadpoles that were exposed. However, newly hatched tadpoles were very sensitive to the concentrations used in this study, (2.4 to 4.8 ppm triclopyr and 4.0 to 8.0 ppm fenitrothion) exhibiting paralysis or death. Berrill et al. (1997) exposed northern leopard frogs to low levels of the insecticides permethrin, fenvalerate, and fenitrothion and the herbicides hexazinone, triclopyr, glyphosate, bromoxynil, triallate, and trifluralin, which are used in the management of coniferous forests and croplands in Canada. Embryos were unaffected by the

exposures, but newly hatched tadpoles were paralyzed or killed. Most importantly, the authors concluded that amphibian tadpoles are generally similar to freshwater fish in their vulnerability to various pesticides.

Other studies have looked at the exposure of northern leopard frogs to pesticides in the field. Ouellet et al. (1997) sampled northern leopard frogs in farm ponds and non-farm ponds in the St. Lawrence River Valley of Québec, Canada, and they found a large number of instances of a variety of hind limb deformity in frogs from farmland habitats. They blamed pesticides for these deformities but established no causal link. Leonard et al. (1999) blamed the loss of leopard frog populations in Washington partially on water quality issues stemming from the use of DDT. They noted that large amounts of pesticides had been found in waters throughout their Columbia River Plateau study area and pointed out the recent results of Berrill et al. (1997) on the effects of low levels of pesticides on larval stages of amphibians. Their conclusions, however, were largely conjectural.

It has been shown that atrazine affects wildlife at ecologically relevant doses (Hayes et al. 2002). Its half-life is approximately five to six years. Hayes et al. (2002) found that it created hermaphroditic *Xenopus laevis* (African clawed frogs, a common experimental frog) and emasculated male frogs. Although Atrazine use is being phased out by order of the U.S. Environmental Protection Agency, it has been commonly used in the northern Great Plains and was found in 80 to 90 percent of the row-crop acreage in the region in the 1980's (Grue et al. 1986). Impacts of many pesticides used in Region 2 are probably greatest at lower elevations, since fewer crops are grown at higher elevations.

2) **Fertilizers:** Only one study (Hecnar 1995) has looked at the effects of fertilizers on northern leopard frogs. In this study, northern leopard frog tadpoles were exposed to chronic and acute doses of ammonium nitrate fertilizer. In acute tests, tadpoles suffered severe weight loss, and an LC50 of 22.6 mg per l was calculated. In chronic tests, tadpoles not only lost weight, but also died, even at fairly low dosages of 10 mg per l. The northern leopard frog was the most severely affected of the species tested, which included American

toads, boreal chorus frogs, and green frogs. Hecnar (1995) pointed out that the differential mortality of the species tested would likely cause shifts in species composition in free-living communities of amphibians. As the boreal chorus frog is common in most of Region 2, it is possible that such community shifts could be seen in the region, but such data do not exist. While fertilizer effects may not be important in much of the national forests of Region 2, runoff from croplands, lawns, and golf courses could affect National Forest System lands in some areas.

- 3) **Mining/metals:** Mining has been practiced in parts of Region 2 for at least 150 years. Although this activity has become less important and less destructive in recent years, residue from abandoned mining sites continues to adversely affect many drainages in the primary mineral belts. Mining causes acidification of water and leads to metals-laden effluent from mines and smelter sites (including surrounding soils) into receiving waters. Some authors have found devastating effects of mining on local herpetofauna, long after mines have closed (Porter and Hakanson 1976). Porter and Hakanson (1976) found that an entire drainage in Colorado was devoid of amphibian life due to runoff from mining residue almost 80 years after mining had ceased. Linder and Grillitsch (2000) reviewed the effects of metals on amphibians. Acidification of water is another potential effect of mining and smelting on amphibians, and this is discussed below.
- 4) **pH/acidification:** Acidification has been studied intensively in frogs due to the potential for acid rain to cause amphibian declines (see symposium in the Journal of Herpetology, volume 26, number 4, December 1992). Mine waste drainage also causes acidification of waters receiving runoff (Diana and Beasley 1998). Schlichter (1981), Freda and Dunson (1985), Corn and Vertucci (1992), Freda and Taylor (1992), and Long et al. (1995) have all studied the effects of low pH or acid rain in northern leopard frogs. Northern leopard frog eggs cannot develop normally at pH 5.8 or lower (Schlichter 1981), and tadpoles were amongst the most sensitive to low pH of all species tested so far, with an LC50 pH of 4.06 (Freda and Taylor 1992). Northern leopard

frog sperm also shows decreased motility at lower pH, with 50 percent of normal motility at pH 5.5 and maximum motility at pH above 6.5 (Schlichter 1981). Northern leopard frogs also show chronic effects of decreased pH, with increasing mortality over time when exposed to low pH waters (Freda and Dunson 1985). Low pH also acts synergistically with higher levels of UV-B that might result from loss of the ozone layer, resulting in higher mortality in amphibians (Long et al. 1995).

Acidification of water in Region 2 can result from acid rain or mining. As Porter and Hakanson (1976) have shown, acidification can be extreme in localized cases due to point sources, such as old mines and mine and smelter waste piles; in these situations, the water is highly lethal. However, Corn and Vertucci (1992) studied non-point sources of acid rain from upwind power plants. They found that declines of northern leopard frogs across the Rocky Mountains of Colorado and Wyoming were, in general, probably not due to acidification of ponds, since the ponds were not acidic enough to affect northern leopard frogs. Although acidification from acid rain across the Rocky Mountain Region may not be significant enough to cause wide-ranging declines (Corn and Vertucci 1992), point sources of acidification can be a significant source of mortality for this species (Porter and Hakanson 1976).

- 5) **Motorized transportation:** Roads can cause substantial direct mortality from road-kill events (Bovbjerg and Bovbjerg 1964, Bovbjerg 1965, Merrell 1977, and Ashley and Robinson 1996), but they can also have indirect impacts. For example, motor oil washes off roads during rain and snowmelt, and when suspended in water, it can kill local populations of amphibians (Sparling 2000). Similarly, sedimentation and toxic runoff from roads can negatively affect amphibians in nearby ponds (Welsh and Ollivier 1998, Trombulak and Frissell 2000). There are a large number of roads in Region 2, both paved and unpaved, that can result in both direct mortality from road-kill events and indirect mortality and morbidity from pollution of nearby ponds. New road construction should be minimized, and old logging roads should be closed when they serve no useful purpose.

- 6) **Lumberyards:** The production of treated lumber uses various chemicals, and lumberyards are common throughout Region 2. Coal tar creosote, used in treating lumber, is a well-known carcinogen (Holme et al. 1999). The agents of primary concern from lumberyards are polycyclic aromatic hydrocarbons (PAHs). Sparling (2000) stated that PAHs can kill amphibians, but there are no detailed studies of this class of pollutants on amphibians in the field or laboratory.

- 7) **Cattle grazing:** Cattle produce considerable amounts of waste products that run into waterways. Cattle feedlots produce inordinate amounts of waste that may run off into amphibian breeding ponds. Grazing by cattle has also been reported to affect water quality (Buckhouse and Gifford 1976), water chemistry (Jefferies and Klopatek 1987), and water temperature (Van Velson 1979). The changes are subtle over time (Elmore and Beschta 1987), but they profoundly alter aquatic ecosystems (Kauffman and Krueger 1984). High levels of cattle grazing activity in and around frog breeding ponds lead to substantial increases in the levels of nitrates and fecal coliform bacteria in these ponds. Two tadpoles collected in a heavily polluted pond used by cattle in Lawrence County, South Dakota, had deformed mouthparts and irritated skin (Smith unpublished data 1998). Reaser (2000) found that cattle grazing influenced the decline of the Columbia spotted frog (*Rana luteiventris*) at a study site in Nevada. Ross et al. (1999) recommended that cattle be fenced out of sensitive wetlands in Nevada to conserve these frogs. No one, however, has investigated the specific agents causing amphibian declines in grazed areas. We recommend studies of the effects of cattle on northern leopard frog tadpoles in breeding ponds in Region 2. Excluding cattle from key breeding ponds used by this species, upstream drainages, and the surrounding upland habitat could mitigate impacts. Water for cattle could be routed to metal stock tanks downstream from such ponds.

- 8) **Sedimentation:** Sedimentation can also run into waterways due to erosion from a variety of sources. Road cuts are sources

of sedimentation; cattle are known to cause erosion by trampling and overgrazing streamside vegetation and slopes; and logging can increase erosion. Recent large fires throughout Region 2 could also contribute to sediment load in nearby waterways. Sedimentation can cover eggs in water and probably inhibits gas exchange by eggs.

- 9) **Rotenone:** This chemical is commonly used in fisheries management and can negatively affect northern leopard frogs (Hamilton 1941). Hamilton found that northern leopard frog tadpoles could not survive levels of rotenone typically used to sample fish. Metamorphs survived for 24 hours after exposure to rotenone, but Hamilton gave no further details about morbidity or mortality in metamorphs following the initial 24 hours of exposure. However, he concluded that rotenone had substantially the same effect on tadpoles (or other organisms that use gills to breathe) as on fish; the chemical was lethal to most of these organisms. Rotenone should not be used in waterways used by northern leopard frogs during the breeding season.

- 10) **Polychlorinated biphenyls (PCBs):** Sparling (2000) has summarized the large amount of literature on PCBs and their effects on amphibians. Phaneuf et al. (1995) studied PCB contamination in northern leopard frogs in Canada following a fire; although concentrations of PCBs were elevated in frogs in the area, researchers were not able to assess mortality of the frogs by PCBs released by the fire. In Wisconsin, high concentrations of PCB 126 caused significant mortality of northern leopard frog tadpoles in the laboratory (Jofre et al. 2000), but these authors found that there was no effect at concentrations of PCB 126 found in the wild. Large manufacturing processes that utilize PCBs could affect northern leopard frogs, depending on the concentration of PCBs in effluent reaching receiving waters, but no data exist.

- 11) **Arsenic:** Birge and Just (1973, cited in Linder and Grillitsch 2000) found that high level of sodium arsenite were lethal to northern leopard frog tadpoles. Arsenic was used in fertilizers in the early 1900's and is a byproduct of the production of sulfuric acid.

Production in most nations, including the United States, ceased around the turn of the 20th century. Arsenic still can be a significant pollutant in some parts of the United States (Aurilio et al. 1995), but we are not aware of studies conducted in Region 2. Williamson and Carter (2001) reported that arsenic occurs naturally in some streams in the Black Hills and that levels of this chemical can occasionally be very high in these streams.

- 12) **Other contamination leading to limb malformations:** This section would not be complete without a discussion of limb malformations, known from forty states and four Canadian provinces (Northern Prairie Wildlife Research Center 1997). The most famous recent reports were those from Minnesota, which virtually all concerned metamorphic northern leopard frogs (Helgen et al. 1998). These frogs usually do not survive long because locomotion and basic behavior is seriously compromised by these gross malformations (Merrell 1969). Helgen et al. (1998) featured several photographs of the affected frogs, most of which had multiple hind limbs or missing hind limbs, although some front limbs were also affected. Helgen et al. (1998) assumed that the cause must be a teratogen or possibly a chemical that disrupts normal endocrine function. The Minnesota Pollution Control Agency sampled the water in which these frogs were found to search for possible causes, including pesticides, heavy metals, or PCBs, but Helgen et al. (1998) did not report these results. Encysted parasites have also been implicated as a possible cause of some limb malformations (incidents of multiple legs) in amphibians (Sessions and Ruth 1990, Johnson et al. 1999, Sessions et al. 1999). However, Meteyer et al. (2000) suggested that limb malformations in frogs probably have several causes. Limb malformations are not a new phenomenon; Merrell (1969) reported a high frequency of malformations in metamorphic northern leopard frogs collected at a site in Minnesota in 1965. Hoppe (2000) also discussed various historical reports of limb malformations. Northern leopard frogs with limb malformations should be reported to the Northern Prairie Wildlife Research Center, which collects such

reports from around North America (<http://www.npwrc.usgs.gov/narcam>).

These water quality issues have the potential to affect amphibians seriously, and northern leopard frogs appear to be somewhat more sensitive to many of these agents than most amphibians that have been tested. As Sparling et al. (2000b) noted, overall input of these agents into aquatic systems is considerable and is probably partially responsible for the decline of amphibians worldwide. Because Region 2 is large and heterogenous, there is no way to assess the potential impact of any of these agents on northern leopard frogs region-wide without extensive study. The most important local considerations are likely to be pollution from cattle, input of pesticides into streams and breeding ponds, mining and smelting and associated pollutants, and runoff from roadways (including sedimentation). Almost none of these have been extensively investigated in Region 2, except for acid rain. Most importantly, they have not been investigated in small ponds of standing water where northern leopard frogs breed. Typically, local, state, and federal studies are conducted on running water, large lakes, or aquifers, where human health concerns are more immediate. Further studies on water quality in Region 2 would be useful, but these studies should concentrate on breeding ponds rather than on streams and other waterways, as has been the case in the past. Finally, we would recommend consulting the database of Pauli et al. (2000) on specific pesticides that are being used by applicators in Region 2 or when new treatments are planned. Similarly, this database can be consulted for the effects of specific chemicals. Pauli et al. (2000) provided literature for all chemicals that had been investigated in amphibians as of the publication date of this database.

Loss of beaver and the resultant loss of wetlands (Parrish et al. 1996) has widely reduced available breeding habitat for northern leopard frogs. Beaver were nearly extirpated in many parts of Region 2. Although they have rebounded in some areas, their abundance remains well below historic levels in most of the Rocky Mountain region. Redoubled efforts to reintroduce beaver and to protect beaver habitat would also benefit the northern leopard frog.

Other activities that can have unexpected, though more localized, effects on northern leopard frogs, include noise and bright lights. Nash et al. (1970) showed that northern leopard frogs remained immobile when exposed to generalized noise, probably interrupting feeding and breeding behavior, and increasing susceptibility to road mortality. This effect

would be of importance in any area of intense human activity, particularly in areas near construction or logging operations, and at some recreational facilities. Buchanan (1993) found that bright light blinds frogs for a few minutes to hours.

Recent concern over the loss of the ozone layer has prompted investigations of the effects of increasing levels of ultraviolet light on limb deformities in northern leopard frogs (Ankley et al. 1998, 2000). Elevated levels of ultraviolet light can cause hind limb malformations in the laboratory (Ankley et al. 1998) and in the field (Ankley et al. 2000), but the significance of these results for northern leopard frog populations in natural situations remains unclear. Crump et al. (1999) found that incident light levels had no significant effect on this species in the field.

Intrinsic vulnerability

The northern leopard frog may be intrinsically vulnerable to disturbance factors for a number of reasons:

- 1. Use of small ponds for reproduction.**

Northern leopard frogs use small (usually less than 5 ha) ponds in which to breed (Merrell 1968, 1977, Collins and Wilbur 1978, Corn and Livo 1989, Hammerson 1999). Ponds of this size are often not protected by law (Semlitsch 2000b) and typically are not addressed in management plans. It is imperative that management plans take into consideration the distribution of small ponds across the landscape and protection of these ponds to foster healthy populations of northern leopard frogs.

- 2. Need for fishless ponds in which to breed.**

In much of their range, northern leopard frogs selectively breed in small, fishless ponds, and the introduction of predatory fish to such ponds is a well-known threat to this species. Yet federal and state agencies introduce such fish throughout the range of the northern leopard frog. Because the USFS is mandated to provide for multiple uses of national forests as part of its mission and due to recreational demands of the public, it is unlikely that fish introductions can be entirely halted. In addition, accidental or intentional introductions of predatory fish by the public will probably be difficult to prevent. However, it may be possible to reduce the

overall effects of such introductions by limiting them in time and space. For example, some watersheds could be managed for native wildlife such as amphibians while others are managed for recreation. In addition, a public information campaign to inform the public of the harm of accidental or intentional introduction of predatory fish into fishless ponds might help to reduce the frequency of these introductions.

3. **Use of upland habitats for summertime foraging.** Northern leopard frogs use moist upland habitats surrounding breeding ponds for summertime foraging. Although Semlitsch (1998) has determined the size of upland habitat around ponds that is used by salamander populations, such work has not been done on northern leopard frogs. This is a critical information need. Semlitsch (1998) found that an upland area of up to 164 m surrounding each breeding pond might be sufficient to protect 95 percent of the adult population of salamanders of various species that use a pond for reproduction in the spring.
4. **Highly permeable skin.** The skin of freshwater amphibians is highly permeable (Duellman and Trueb 1986). Consequently, toxins can be readily absorbed through the skin and incorporated into the body of amphibians, including northern leopard frogs. Since northern leopard frogs serve as prey items for many species, the accumulation of toxins in their body tissues can have repercussions throughout the food web. In this sense, northern leopard frogs might serve as a key indicator species in ecosystems in which they occur. It is possible that population size and health of northern leopard frogs might indicate overall ecosystem health. However, there appears to be little work on the presence of toxins in northern leopard frogs in the wild. This also is a key information need.
5. **Susceptibility to introduced diseases.** Northern leopard frogs are susceptible to various diseases. Chytridiomycosis is an emerging disease and, as such, may not be considered an intrinsic threat. Ranavirus, however, has probably always been a threat to northern leopard frog populations (Jancovich et al. 1997, Carey et al. 1999, Daszak et al.

1999). Ranavirus can become an extrinsic threat through the deliberate introduction of non-native predatory fish into watersheds in which frogs breed, accidental or intentional introductions of predatory fish and fish bait (e.g., salamanders, which can also be infected by iridoviruses; Jancovich et al. 1997), and human travel among breeding ponds.

6. **Necessity of overland migration routes between seasonal habitats and to reach and colonize new ponds.** Northern leopard frogs move across the landscape for many reasons, including dispersal of metamorphs (Dole 1971, Merrell 1977), summer movements associated with feeding (Dole 1965b, 1967, Merrell 1977), and migrations to and from overwintering sites (Dole 1967, Merrell 1977). The routes followed probably include wet meadows, tall grass, and riparian corridors. These corridors can be affected by habitat degradation from a variety of causes. For instance, deMaynadier and Hunter (1998) found that ranid species that frequently are found in water were less affected by clearcutting than were the more terrestrial ranids, such as wood frogs, and some salamanders. Skelly et al. (1999) showed that there was high turnover of northern leopard frog populations in a metapopulation in Michigan, likely due to the disruption of migratory pathways.

Conservation and Management of the Northern Leopard Frog in Region 2

Implications and conservation elements

The following factors, in rough order of priority, should be considered when trying to conserve northern leopard frogs in Region 2:

- ❖ protection of known and potential breeding sites
- ❖ control of introduced predaceous fish and bullfrogs
- ❖ protection of overwintering sites
- ❖ control of introduced infectious diseases
- ❖ monitoring and protection of water quality

- ❖ protection of migratory and dispersal pathways
- ❖ control of road-related mortality
- ❖ other factors.

Prioritization is an uncertain enterprise since risk factors will vary from site to site and are incompletely known in many cases. Therefore, this ordering should be taken as a tentative and general prioritization. In some ways, these risks are presented as much in order of ease of avoidance of risk as they are in order of clear and present danger to northern leopard frog populations in Region 2. Beyond the first two items, which are of nearly equal importance, the order of the list is highly speculative. What is not speculative, however, is the fact that all these factors have affected northern leopard frogs at certain study sites throughout North America.

Protection of known and potential breeding sites

Semlitsch and Bodie (1998) and Semlitsch (2000b) noted that breeding ponds that produced the highest density and biodiversity of amphibians are not protected by current federal law. Nor do management plans for most national forests in Region 2 provide protection of waters appropriate for the reproduction of large numbers of northern leopard frogs. While streams, springs, and large lakes are protected, what is needed by northern leopard frogs are the smaller (less than 5 ha) seasonal and semi-permanent ponds (Semlitsch and Bodie 1998, Semlitsch 2000b).

Upland areas surrounding these ponds are used throughout the summer as foraging habitat and must also be protected (Semlitsch 1998, 2000a). For data on the use of upland habitat by northern leopard frogs, see publications by Dole and Merrell cited in this assessment. Although Semlitsch (1998) refers to upland habitat as a “buffer zone,” it is more appropriately referred to as “core habitat area” (Semlitsch personal communication 2001) and should be protected as such. Dole (1965a, 1965b) showed that northern leopard frogs typically used a home range of about 68 to 503 m², but his work does not provide guidance for how much upland core area should be protected to conserve an entire population because some of the population will have home ranges farther from the breeding pond than other members of the population.

Studies of Semlitsch (1998) on pond-breeding salamanders could be used as a start to protect upland core area for northern leopard frogs. Semlitsch (1998)

reported that core upland habitat extending 164 m in all directions from each breeding pond is needed to conserve 95 percent of the adult breeding population of various pond-breeding salamanders foraging in the upland habitat following the breeding season. However, this core area is highly species-specific. The larger salamanders that Semlitsch (1998) studied are similar in mass to northern leopard frogs and use upland core areas of 150 to 200 m surrounding breeding ponds. This might be taken as a general indication of the amount of upland core area that northern leopard frogs need, pending the availability of data specific to this species.

Control of introduced predaceous fish

Introduced non-native predaceous fish have been clearly implicated in the decline of some frogs (Bovbjerg 1965, Brönmark and Edenhamn 1994, Hecnar and M'Closkey 1997b), and ongoing fisheries management by various agencies maintains populations of these fish throughout Region 2. It is difficult to resolve the conflict between sport fishing management priorities and the need to protect populations of northern leopard frogs and other amphibians. Some of the ponds discussed in this report are not suitable for introduced predaceous fish and are therefore excellent sites in which to promote the growth of vigorous populations of northern leopard frogs. However, many ponds are connected to waterways with introduced predaceous fish, and many ponds that are not connected to such waterways have these fish. Only with communication and cooperation among agencies involved in management of non-native fish species might it be possible to resolve conflicts between management for sport fishing and northern leopard frogs.

Because introduced predaceous fish often do well in habitats not extensively used by northern leopard frogs, such as streams and lakes (but see Protection of overwintering sites section), it might in some places be possible to separate areas for fish propagation from habitats used by northern leopard frogs. However, a major impediment to management of ponds for northern leopard frogs in Region 2 is the predilection of the public to introduce predaceous fish to any body of water that may be suitable for their propagation (and also to ponds that are not suitable). One author (Smith) has found predaceous fish in many ponds on National Forest System lands in the Black Hills. It is difficult, and may be impossible, to guard against these intentional introductions. If fish are found, they might be safely removed using electroshock or rotenone, but only when northern leopard frogs are not in the pond at the same time. If frogs use ponds for breeding

and overwintering, it would be difficult or impossible to use either technique without damaging the frog population. In addition, ponds without frogs but with fish may become good frog habitat if fish were to be removed. Therefore, timing for removal of predatory fish is critical. *In any regard, all involved agencies must realize that management for the maintenance of introduced predaceous fish for anglers and management for the conservation of the northern leopard frog are mutually exclusive management objectives at the scale of individual ponds.* Collaborative and innovative solutions must be found and researched.

Protection of overwintering sites

Since overwintering mortality can be high at times in ranid frogs (Bradford 1983), it is important that overwintering sites in Region 2 be identified and protected. Northern leopard frogs use lakes, larger ponds, and streams in which to overwinter (Merrell 1977, Cunjak 1986), but identification of specific sites requires underwater work during the winter. Unfortunately, no work has been done in this region. Without such specific investigations, further management actions to protect overwintering habitats are compromised. It is important to note that many of these sites are also heavily used by introduced non-native predaceous fish.

Control of introduced infectious diseases

Modes of transmission of infectious diseases are not known. Carey et al. (1999) noted that introduced exotics might spread disease, and tiger salamanders are known to harbor iridoviruses (Daszak et al. 1999). It has been inferred that diseases can travel on any animal agent, including humans, from pond to pond. It is therefore assumed that limitation of travel by humans from pond to pond is desirable, but impractical. Limiting the introductions of fish and bait into breeding ponds is also desirable, but also impractical in its entirety. Animals as vectors need more research to determine their roles in the spread of diseases.

Water quality

Water quality has major effects on amphibians, as we have discussed. Ponds, especially those known to have breeding or overwintering populations of frogs, should be monitored for the quality of their water, particularly those close to sources of pollutants, those where herbicides and pesticides may be used to control exotic plants and other noxious organisms, those near

construction sites or logging activities, and those near roadways and ponds near recreation sites.

Protection of migratory and dispersal pathways

Dole (1965b, 1967, 1971) and Merrell (1977) found that leopard frogs use many routes and habitats for migration and dispersal, including wet meadows, tall grass, and riparian corridors. Habitat destruction and road construction interrupt these pathways, and it is likely that grazing and logging do so as well. We suggest that these movement corridors be afforded protection, but there are no detailed studies that examine the management of such areas. It will be necessary to understand the landscape (i.e., where ponds are placed, where riparian corridors are located and how these relate to ponds, and where wet meadows and tall grass are located) to manage migratory pathways. Also needed is basic knowledge of how frogs move among suitable breeding ponds.

Road-related mortality

In addition to fragmentation of the landscape, roads result in amphibian mortality. It has been known for some time that roads cause extensive mortality of juvenile northern leopard frogs (Bovbjerg and Bovbjerg 1964, 1965, Merrell 1977). Recently Ashley and Robinson (1996) found that young-of-the-year northern leopard frogs were disproportionately represented among dead herpetofauna on roads at their study site in Ontario. Carr and Fahrig (2001) found that traffic density within a 1.5 km radius of frog breeding ponds was negatively associated with the abundance of northern leopard frogs, suggesting that the viability of populations can be affected by road mortality. Road-associated factors such as sedimentation and runoff of toxic compounds can also affect aquatic communities near roads (Welsh and Ollivier 1998, Trombulak and Frissell 2000).

Control of other factors

Other activities can have unexpected effects on northern leopard frogs, such as the immobility response as a result of generalized noise (Nash et al. 1970) and temporary blinding by bright lights (Buchanan 1993). Controlling for these factors (and potentially many others) may be impractical, but they should be considered in land management and work planning. For instance, the effect of bright lights should be carefully considered where important breeding sites are located near lighted facilities, such as campgrounds, work areas, or offices.

Tools and practices

Considerations for inventory and monitoring

In this section, we provide some guidance on designing and implementing inventory and monitoring plans at district, forest, and regional scales. Most important is determining specific localities where northern leopard frogs are found within Region 2 by conducting basic inventories. A large-scale inventory of the northern leopard frog across Region 2 has never been undertaken, and monitoring of the species cannot start without an inventory. Inventory can be simple, such as determination of the presence or absence of breeding choruses across a landscape. It can be sophisticated as well, such as determining the effective population sizes at sites where frogs are found. We doubt that sophisticated inventories can be undertaken in a region as large as that of Region 2 due to funding limitations, but relatively simple presence/absence data can be acquired with minimal expense and would be highly valuable. Depending on the techniques, some information on relative abundance can also be gathered. Regardless, precise location data should be entered into a Geographical Information Systems database, and these data should be maintained and updated on a regular basis so managers always have access to the most recent information. We will expound further on developing a monitoring plan at the close of this section.

Heyer et al. (1994) compiled existing techniques for surveying and monitoring amphibians. They and their contributors also discussed associated issues such as standardization and quantification, research design including data management and planning of studies, estimation of population size, and data analysis. Of the survey and monitoring techniques discussed in Heyer et al. (1994), the following techniques could be useful in surveying and monitoring northern leopard frogs in Region 2:

1. acoustic monitoring, i.e., call surveys (Berrill et al. 1992, Peterson and Dorcas 1994, Zimmerman 1994, Bishop et al. 1997, Bonin et al. 1997, Lepage et al. 1997, Johnson 1998, Mossman et al. 1998)
2. drift fences and pitfall traps (Corn 1994, Dodd and Scott 1994, Smith et al. 1996a, 1996b)
3. various quadrat sampling techniques (Jaeger 1994a, 1994b, Jaeger and Inger 1994)
4. cover boards (Fellers and Drost 1994, Bonin and Bachand 1997, Davis 1997)
5. visual encounter surveys (Crump and Scott 1994, Smith et al. 1996a, 1996b, 1998).
6. Various marking techniques can be used in conjunction with these survey methods to mark and track amphibians in the field (Dole 1972, Green 1992, Ashton 1994, Heyer 1994, Richards et al. 1994, Madison 1997, Madison and Farrand 1997, Semlitsch 1998).

Probably the simplest, least expensive, and most commonly used practice to survey amphibian populations is the call survey (Berrill et al. 1992, Peterson and Dorcas 1994, Zimmerman 1994, Bishop et al. 1997, Bonin et al. 1997, Lepage et al. 1997, Johnson 1998, Mossman et al. 1998). Call surveys may be set up a number of ways, including traveling along transects randomized by habitat, at locations specified along a roadway (itself a kind of transect), and other methods. In the Black Hills, the lead author has typically carried out call surveys by first surveying during daytime hours for ponds in which northern leopard frogs may occur. Investigators then visit potential breeding ponds at night to listen for breeding choruses of frogs. Size of the chorus is then estimated by auditory means: 1) a few individuals calling sporadically, but calls widely spaced in time; 2) several individuals calling but investigator is usually able to discern individual calls; and 3) a full chorus. Usually, ponds are visited at least three times during the breeding season to verify whether the pond is being used as a chorus site. The longest lasting and most successful set of yearly call surveys has been the volunteer call survey ongoing in Wisconsin since 1981 (Mossman et al. 1998).

Depending on the species, call surveys can be an excellent way to survey and monitor frogs, but not all anurans are easily surveyed by this method. The calls of some frog species vary in volume geographically. For example, Bishop et al. (1997) noted that northern leopard frogs have low volume calls that may be hard to hear, and Smith et al. (1996b) have pointed out that northern leopard frogs call sporadically and at very low volume in the Black Hills region. Consequently, they have cautioned against the use of call surveys to survey or inventory the species in the Black Hills. Bonin et al. (1997) have also advised against the use of the technique to quantitatively assess the extent of frog declines over several years. Auditory techniques, such

as audio strip transects (Zimmerman 1994), breeding site surveys (Scott and Woodward 1994), automated data loggers (Peterson and Dorcas 1994), or basic acoustic monitoring (Rand and Drewry 1994), should be evaluated for their efficacy in Region 2 before using them as monitoring tools. We recommend daytime visual searches later in the active season (May through October, depending on weather and elevation) to find northern leopard frogs until other monitoring tools have proved their effectiveness.

Herpetologists for many years have used simple visual searches in suitable habitat to find amphibians. This is frequently the most productive way to search for amphibians and, if properly quantified, is a suitable technique to survey and monitor many species (Crump and Scott 1994). Proper quantification of search effort involves recording the amount of time spent actively searching, not including time spent traveling, stopping to take photos, etc. Crump and Scott (1994) called the technique a visual encounter search. Investigators simply approach a survey area and walk around the area searching for the species of interest, possibly flipping suitable cover objects. After a pre-determined period of time, the search is halted and results (number of specimens encountered) are recorded. The lead author has used this technique in all of the survey work he has conducted, and it has worked well to find all species (Smith et al. 1996a, 1996b, 1998). These researchers typically worked in three or four person crews and conducted two person-hour searches at each survey site. (Search time was derived by multiplying the crew size by the time searched [e.g., a three person crew searching for 40 minutes is equal to 2 person-hours; a four person crew searching for 30 minutes is equal to 2 person-hours].)

The lead author has also used visual encounter searches to find subadults, adults, and metamorphs after the breeding season and to search for developing tadpoles using dipnets swept through shoreline vegetation. However, this method results in presence/absence data only. Sometimes tadpoles are obvious using this technique, but sometimes they cannot be found at sites where metamorphs are found later in the season. During the breeding season, the lead author has found that northern leopard frogs are cryptic and hard to locate either by sight or by sound. The tadpoles may also be hard to find because they are hiding in dense cover. The lead author found it difficult to attain accurate counts of northern leopard frogs because they can be present in large numbers (e.g., hundreds of tadpoles or metamorphs) or are otherwise hard to count (e.g., several individuals jump and escape simultaneously).

Unless precise numbers are required, he usually records northern leopard frogs as “present” or “absent” at study sites and provides only a rough indication of abundance. Given that failure to see frogs during a single survey is not proof of absence, we recommend surveying a site at least three times, preferably including at least one visit during breeding and after suspected metamorphosis of tadpoles, before recording northern leopard frog absence. Crump and Scott (1994) covered the assumptions and limitations of the visual encounter technique and provided a sample data sheet.

Another survey method useful in monitoring northern leopard frogs is egg mass survey (Corn and Livo 1989, Werner et al. 1999, Crouch and Paton 2000). In this type of survey, investigators visit ponds that are suspected to have breeding populations of northern leopard frogs to search for egg masses. As described in the **Breeding Biology** section, eggs are laid in clumps on submerged vegetation slightly below the water surface and may be found by trained investigators. Since a single female lays each clump, simply counting all egg masses found in a pond gives an estimate of the number of females using the pond for reproduction. If a 1:1 sex ratio is assumed, the total breeding population size can be estimated. However, it is important to recognize that not all females are likely to breed during a given year, the sex ratio may not be 1:1, and there will be an undetermined number of sexually immature individuals in the population. In addition, egg mass surveys require training because it is often difficult for non-specialists to identify northern leopard frog eggs.

Drift fences and pitfall traps can be installed and periodically monitored to assess the abundance of amphibians at a study site (Corn 1994). Drift fences can also be installed at breeding sites, completely encircling the site and trapping every individual entering or leaving the site (Dodd and Scott 1994). Drift fences are long fences made of sheet metal and placed flush to the ground such that amphibians cannot climb over or burrow under the fence. Pitfall or funnel traps are placed along the fence to trap amphibians moving along the fence. In our experience, it can be difficult to train non-herpetologists to install drift fences properly, and we recommend that a herpetologist be consulted and survey teams be properly trained if drift fences are to be used. We believe that the primary use of drift fences would be for studies of northern leopard frog breeding ponds or studies of movement in the species, not as a routine method of survey. Drift fences can be costly, both in terms of materials and construction effort, but once installed they can be cheaply and easily operated.

Upland habitats can be quantitatively sampled using quadrat sampling (Jaeger and Inger 1994), transect sampling (Jaeger 1994a), and patch sampling (Jaeger 1994b). Each of these techniques relies on sampling various sizes and shapes of plots to determine how many amphibians occur per unit area of sampled habitat. Of all the techniques discussed, these are the only techniques that can provide information on the number of animals per unit of habitat.

Patch sampling (Jaeger 1994b) refers to the sampling of patches where frogs are more likely to occur, which in the case of northern leopard frogs should be habitat near breeding ponds, along streams, or in riparian corridors. One general drawback to patch sampling is that the habitat is not randomly sampled because habitats that investigators think lack frogs are not sampled. However, as long as the data are not presented as being a random sample of all possible habitats, patch sampling is an appropriate tool to survey amphibians.

Patch sampling can be combined with quadrat or transect sampling. During the breeding season, northern leopard frogs are concentrated at ponds, but following breeding they are dispersed in upland habitat and may be more difficult to locate (although it may still be expected that frogs will be found near ponds, streams, or riparian areas). Therefore, areas near ponds, streams, and in riparian strips can be selected as patches in which to search for northern leopard frogs following the breeding season. To systematically sample these areas, researchers might restrict searches to areas immediately adjacent to ponds (for example, the 200 m area as discussed under Intrinsic vulnerability, along streams, and in riparian corridors. They can then conduct quadrat or transect samples (quadrats are square plots while transects are long strip-like plots; some researchers make little distinction between the two) in these patches to assess the numbers of adult frogs using these habitats. These combined techniques could result in an assessment of frog density around breeding ponds, along streams, and in riparian corridors following the breeding season.

Cover boards are objects such as plywood boards that are placed in the environment to take advantage of the fact that many amphibians take refuge under such objects (Fellers and Drost 1994). They can be placed in various arrays as a method of quantitatively surveying amphibians. The technique has proven useful to monitor salamander populations (Bonin and Bachand 1997, Davis 1997), but there are differences in how species use cover boards and the types of cover boards favored

by different species (Bonin and Bachand 1997, Davis 1997). Construction techniques and suggested arrays can be found in Bonin and Bachand (1997) and Davis (1997). Cost would be minimal following initial testing and construction of cover boards. Unlike drift fences, cover boards could be left in place unmonitored for long periods of time since specimens can leave or use cover boards at will and are not trapped in pitfalls or funnel traps that cause rapid desiccation and must be checked frequently. However, it should be noted that use of cover boards as a sampling technique has not been validated for use with northern leopard frogs; they are probably best used for salamanders and snakes.

Any technique that allows the hand capture of specimens can be used in conjunction with marking techniques as part of a larger study on breeding or movement patterns. Amphibians can be marked and tracked using a variety of devices including thread bobbins (Heyer 1994), radiotransmitters (Richards et al. 1994), radioactive tags (Ashton 1994), toe clipping (Green 1992), and passive integrated transponder (PIT) tags (Painter personal communication 2000). Thread bobbins have been used to track northern leopard frogs (Dole 1972). The device is a spool of thread attached to a harness that is tied around the body of the frog just ahead of the hind legs. It can be used to track frogs over distances of up to 50 m (Heyer 1994). The technique is somewhat time-consuming, but it is inexpensive and can provide basic information on the movements of northern leopard frogs in the field (Dole 1972). There are occasional harmful effects of the harness as the frogs can become entangled in the string or the harness can irritate the frog (Dole 1972).

Radiotracking has been used on larger animals for a number of years, but with miniaturization of transmitters, it has recently (within the last ten years) been successfully used on amphibians in the field, including ranid frogs (Rathbun and Murphey 1996, Lamoureux and Madison 1999, Mathews and Pope 1999, Bull 2000, Bull and Hayes 2001) and northern leopard frogs in particular (Waye 2001). The technique is time-consuming and expensive, requires detailed training of investigators, and may require invasive surgery to install transmitters. However, it is the best way available to obtain detailed information on the movement of animals in the field.

Radioactive tags have also been used to monitor amphibian movements in the field (Ashton 1994) and have been used in salamanders for several years (Semlitsch 1998). Radioactive tags are particularly useful for small organisms that cannot be tracked using

radio-transmitters. The tags can be detected from up to 5 m by scintillation counters (Semlitsch 1998), so they can be used to find specific locations of frogs where a restricted movement area is expected. Although this technique is available, there are concerns over handling of the tags, health effects on frogs with implanted tags, and environmental effects that may argue against studies using radioactive tags.

Toe clipping has long been used to mark various animals in the field and is best used in conjunction with recapture surveys to roughly track northern leopard frogs over time. Green (1992) outlines a basic pattern for numbering frogs using toe clipping. When effectively used in conjunction with other sampling techniques, toe clipping can be used to monitor the movements of individuals and to derive a mark-recapture estimate of population density using a number of open population estimators given in Krebs (1999). Deriving a mark-recapture estimate of population size at most ponds would probably require marking and recapturing large numbers of northern leopard frogs. Since toe clipping is invasive, it should not be used unless it is part of a determined effort to monitor frog movements or to derive population estimates. Toe clipping, when done in conjunction with basic sampling, is simple and inexpensive to implement.

Passive integrated transponder (PIT) tags can be used to mark individuals as well. These are small glass rods, usually no more than 10 mm in length, that are inserted under the skin. A device reads uniquely coded numbers from the tags when waved over the marked individuals. Such tags have been used for several years to mark Jemez Mountain salamanders (*Plethodon neomexicanus*), a slim and small salamander with a snout-vent length of only 4.7 to 7.2 cm (Painter personal communication 2000). They would probably work for marking northern leopard frogs as well, again as part of a detailed movement or population study. Pit tags and the reader are somewhat expensive to purchase, but they are much less expensive than radio-transmitters and do not have the safety issues associated with radioactive tags. Pit tags can be inserted subcutaneously on the dorsal surface and have been used successfully on boreal toads (Wahl personal communication 2006).

Individual northern leopard frogs may be identifiable through unique markings. Robert Newman, of the University of North Dakota, has identified a number of wood frogs through computer analysis of photographs of unique patterns on their back (personal communication 1997). The spotted pattern across the back of northern leopard frogs might serve to identify

individuals should an intensive study of population sizes or movements be undertaken at certain sites. The technique is time consuming and management of the individual records could be difficult. Attempting to discern one frog from another using specific markings could be prove difficult or impossible. We are not aware of anyone that has attempted such a study in northern leopard frogs.

Aquatic funnel trapping is a technique that can be used to detect the presence of northern leopard frog tadpoles in breeding ponds. Various types of funnel traps are described in Adams et al. (1997). These traps are placed in ponds, where tadpoles swim into them and are captured. The traps are checked on a frequent basis, and tadpoles are identified and released. The materials used are not expensive (minnow traps and even two-liter plastic soda bottles can be used for the purpose), but they need to be checked daily or every few days during the tadpole growing season. Additional training is necessary for this technique, because non-specialists often find it difficult to differentiate the various tadpoles found in Region 2.

Instituting an inventory and monitoring program in Region 2

Standard references that discuss planning and inventory, inventory techniques, monitoring protocols, data management, and data analysis for herpetofauna are Heyer et al. (1994), Olson et al. (1997), and Lips et al. (2001). Olson et al. (1997) also provide a number of very readable papers on inventories, surveys, and monitoring that should be consulted by managers interested in instituting an inventory and monitoring program. Developing a monitoring protocol can be a complicated process requiring the services of specialists in statistics, sampling theory, and herpetofauna. However, the lead author has experience in inventory and survey of northern leopard frogs for federal, state, and local agencies in North Dakota, South Dakota, Wyoming, and Nebraska, and based on this experience, we tentatively propose the following basic inventory and monitoring guidelines for the region. We strongly suggest that managers starting such a program consult with a professional herpetologist prior to initiating development of an inventory and monitoring program.

- 1) **Sampling design:** Arguments about sampling design and theory are legion at professional herpetological meetings (Smith personal experience). Professional statisticians often disagree about the best sampling design, and there is by no consensus in the herpetological

community. One approach would be to hire a statistician specializing in sampling theory to devise a sampling strategy. This would be the best method to develop a sophisticated monitoring strategy, but sampling methods change on a routine basis and many agency biologists become frustrated at being told that their sampling design is out of date every few years.

We believe that agency biologists most often want information on population distribution and trends in their administrative areas and the types of habitat used by the species. Our approach would be to consult a professional herpetologist who can suggest appropriate habitat to monitor and who can spend some time in the field with agency biologists visiting wetlands. We suggest that agencies monitor only sites that were known to have populations of frogs at the start of the monitoring effort. Although it is of interest to know the number of occupied versus unoccupied breeding sites in an inventory effort, we believe that trends in abundance would most easily and efficiently be tracked by starting the monitoring program with several sites that have frogs. If frogs go extinct at one of these sites during the monitoring period, the site should continue to be monitored for potential recolonization.

It is not necessarily clear what types of water bodies northern leopard frogs will be occupy. The lead author has found them in temporary muddy water holes, degraded wetlands, relatively pristine small ponds with emergent vegetation (possibly their preferred habitat), and at lake margins with emergent vegetation. If funding is sufficient, a season of work by a trained herpetological crew would be of great help to find suitable monitoring sites. At the very least, a professional herpetologist should be consulted at this stage.

By identifying sites where northern leopard frogs occur, agencies can monitor these sites for signs of decline through time. More sophisticated studies, or simple experience over time if funding is lacking, might help agency biologists to create new habitat or to conserve appropriate habitat for the species.

- 2) **Historical surveys:** The best way to start a monitoring plan would be to uncover historical records of occurrence within a jurisdictional area, as it is instructive to

compare historical data to current data. The historic survey uses locality data from sources such as museum collections, natural heritage databases, or observational databases that some agencies maintain. Museum records with voucher specimens are the best source of information, but observational records can be suitable depending on the qualifications of the observer. These historical sites of occurrence should first be investigated to determine whether the species is still present at these sites.

Historically occupied localities are revisited to determine presence or absence of the target species and to examine general trends in distribution. Although presence/absence data lack statistical precision, the results are illustrative nonetheless. Other workers (Rorabaugh 2005) have used historic surveys to describe trends in distribution over time, as have we in this assessment. Simple hand capture or auditory surveys would suffice to determine presence or absence of the species at these sites, but we caution that several surveys may have to be conducted at a historical site before the species can be declared absent. If new surveys at several historical sites do not turn up new records, there is reason to be concerned that frogs may be in decline in the region.

- 3a) **Basic technique 1:** Techniques used to start a monitoring program can be very simple. Smith et al. (1996a, 1996b, 2004) found that northern leopard frogs could be inventoried using auditory surveys, but this required a trained ear, excellent hearing, and patience. Many workers conduct auditory surveys for three minutes at each site. However, the lead author has found that northern leopard frogs are very cryptic in chorusing behavior in much of eastern Wyoming, North Dakota, western South Dakota, and western Nebraska, and they may not call for long periods of time (Smith et al. 1996b, 2004). C. R. Peterson (personal communication 2001) has found the same to be true in western Wyoming and eastern Idaho. If auditory surveys are used, we suggest that trained observers visit several breeding ponds a night during the spring breeding season (April to July, depending on elevation and weather), listening for about three minutes at each site. If a breeding chorus is confirmed, the site does not necessarily need to be visited

again that breeding season. However, lack of calling does not necessarily indicate the absence of frogs, and we believe that each site should be visited at least three times before concluding that there are no northern leopard frogs at the site. Auditory surveys cannot be used to determine successful reproduction. All that can be determined is that a breeding chorus was found at specific sites during the breeding season.

3b) **Basic technique 2:** In the lead author's experience, northern leopard frogs are more easily detected later in the active season (June to October, depending on weather and elevation), when subadults and adults may be found at the edges of wetlands basking in the sun. They are then easily observed with simple visual searches. Once again, a single observation at a site is sufficient to score presence of the species at the site, while sites must be visited at least three times without positive identifications for frogs to be considered absent. However, visual surveys can be timed (Crump and Scott 1994) and observations turned into encounter rates that can then be used in simple statistical analyses of abundance through time. To standardize the sampling protocol in his studies, the lead author has typically used 2 person-hour searches (e.g., four investigators working for 30 minutes, three for 40 minutes, or two for one hour), except at very small ponds that can be completely searched in less time. This technique is easier to conduct and has fewer errors of omission (i.e., if frogs are present at a site they are more likely to be found on a visual search than on an auditory survey).

4) **Sampling of tadpoles:** Tadpoles can be sampled in various ways, including dipnets and various aquatic traps, but we discourage the use of this technique for routine survey work by non-herpetologists for several reasons. First, the lead author has had difficulty collecting tadpoles using dipnets in the thick emergent vegetation in which they occur. Second, tadpoles are difficult to identify, and it is likely that misidentifications will compromise the data. Third, when using dipnets to sample tadpoles, diseases could easily be transferred from pond to pond if dipnets are not properly disinfected (see item 6 below).

5) **Geographical Information Systems (GIS):** All data should be entered into the GIS database for each jurisdictional area to track locality data more closely. Various authors (Hayek and McDiarmid 1994, Juterbock et al. 1994, Fellers 1997) discuss the use of GIS in herpetofaunal studies, but GIS is a universal system used for many applications. Most USFS districts or national forests have GIS experts that can assist in compiling data into a format that can easily be traded among researchers and used by managers.

6) **Number of sampling sites:** There is no consensus on the number of sites that should be monitored across a region to examine trends in abundance, and there is no standard used among studies, herpetological or otherwise. However, Hayek and Buzas (1997) determined from theoretical considerations that a sample size of 20 should be adequate to infer biologically meaningful results from most biological data sets. We tentatively suggest that a minimum of 20 ponds be monitored, depending on the size of the area to be monitored. However, we should also note that any statistical textbook (e.g., Sokal and Rohlf 1994, Zar 1998) will point out that sample sizes should be as high as reasonable. Many factors will influence the number of ponds to be monitored, including size of the management area, number of suitable wetlands, funding, personnel, and possibly other factors. Somewhat reassuringly, Hayek and Buzas (1997) also found that sample sizes of less than 20 might be adequate in some cases. However, we strongly recommend that at least 20 ponds be monitored for a meaningful monitoring effort.

7) **Disinfection of sampling gear:** Our preferred technique, simple visual surveys, typically requires walking around a pond. Observers are much less likely to be working in and out of the water on such a survey than they would on surveys that require use of waders or dipnets. This should reduce the chance of transmission of disease from pond to pond, but we also recommend disinfection of field boots. As a standard protocol for amphibian survey and monitoring, investigators should sterilize boots and other gear between survey sites with a solution of 10 percent standard household bleach (1:10 by volume) by

completely soaking the gear in this solution for at least 10 seconds, then rinsing it with distilled water and allowing it to dry in the sun prior to use. This technique, commonly used in veterinary clinics to prevent the transmission of virulent disease, should minimize the chance of introducing diseases to disease-free ponds. A current and detailed discussion of standard operating procedures for disinfecting field gear can be found online through the Declining Amphibian Population Task Force (<http://www.open.ac.uk/daptf/>).

Population and habitat management

Few papers have addressed management of amphibians, fewer still have looked at ranid frog management, and none have done so specifically for northern leopard frogs. Semlitsch (2000a) is the most extensive review of the amphibian management literature available, and deMaynadier and Hunter (1995) have reviewed forest management practices and their affect on amphibians in North America. However, Lannoo (1998b) provided the most succinct summation of a potentially successful strategy for conservation of frog populations in North America. Modified for northern leopard frogs in Region 2, his advice might be to provide a series of seasonal or semi-permanent ponds that are connected by upland migration and dispersal corridors plus habitat for terrestrial life history stages (the upland core areas advocated by Semlitsch 1998, 2000a).

To summarize briefly the findings of deMaynadier and Hunter (1995), we conclude that several standard forestry practices can adversely affect populations of amphibians in general, and probably have some effect on northern leopard frogs. First, most amphibians do not use habitat in recently clear-cut areas, and there is a general association of stand age and abundance, with frogs more common in older stands. However, microhabitat variables such as herbaceous cover, downed wood, and litter depth appear to be more important than broad-scale stand features. Amphibians better tolerate habitats that provide a variety of near-ground cover because these habitats provide a broad range of microclimates that allow effective behavioral thermoregulation and avoidance of desiccation. Therefore, timbering operations that strive to minimize understory disturbance are probably better for conserving amphibian populations than other types of forestry practices. Also, scattering this type of disturbance around the landscape is probably beneficial; i.e., smaller clear-cut areas interspersed

among areas that have not been cut or have been cut using less intrusive treatments is better than large areas of clear-cutting. Secondly, several amphibian species use riparian corridors as migration pathways, and we expect that the wider they are and the more connected northern leopard frog breeding ponds are to these riparian zones, the better off populations of northern leopard frogs will be. Third, roadways can isolate populations or reduce their size, sometimes even if these roadways are low or no-use roadways. This might be less of a problem for the northern leopard frog because they are known to migrate long distances under less than ideal conditions. However, heavily used roads may result in substantial mortality of migrating frogs. Finally, the few data that exist on prescribed burning have shown that amphibians can tolerate prescribed burning rather well. We emphasize that there are few data to date, and these conclusions are largely based on types of amphibians other than ranid frogs and remain to be tested in ranid frogs.

Semlitsch (2000a) has provided a wider-ranging review of various management practices that is less focused on specific types of forestry practices. He identifies several threats to local and regional amphibian populations including habitat destruction and alteration, global climate change, chemical contamination, diseases, invasive species, and commercial exploitation. Among this group, we have already discussed the threats that pertain to Region 2 populations of northern leopard frogs, namely habitat destruction, chemical contamination, diseases, and especially, invasive species (introduced predaceous fish). Yet to be discussed in this report is the importance of local population dynamics and metapopulation dynamics as emphasized by Semlitsch (2000a).

Like many species, pond-breeding amphibian populations are connected across the landscape, with each pond serving as a population, and all populations of all ponds existing as one, or several, metapopulations. Each pond may be more or less isolated, depending on how far each is from other ponds, the predilection of frogs to migrate from pond to pond, the tendency of young to disperse from natal ponds, the risks associated with inter-pond migration, and the philopatry of subadult and adult frogs. Without detailed studies of the genetics and movement patterns of frogs at given sites, it is difficult to know whether there is a high degree of within-population genetic variability (i.e., most genetic variability is found within a population or pond), or a high degree of among-population genetic variability (i.e., most genetic variability is found among ponds). In the former case, conservation of one or a

few breeding ponds and surrounding upland habitat conserves most of the genetic variability within the metapopulation. In the latter case, more ponds must be conserved to maintain a high degree of genetic diversity within the metapopulation. In either case, the safest way to conserve high genetic diversity is to maintain as many ponds and their surrounding upland core area as possible, with numerous inter-pond migration and dispersal corridors. This reduces the chance of the whole population becoming extinct due to an unforeseen stochastic event and facilitates recolonization of local extirpations by dispersers from neighboring ponds.

Captive propagation and reintroduction in herpetological conservation have a mixed history. Sexton et al. (1998) documented a recent success; they reported that reintroduced wood frogs began expanding into formerly occupied habitat at sites in Missouri. However, a recent reintroduction of boreal toads into Rocky Mountain National Park was a failure (Muths et al. 2001). Dodd and Seigel (1991) document many such failures from the herpetological literature.

Since 1999, a project has been underway to reintroduce northern leopard frogs into some areas of Alberta (Fisher 1999, Kendell 2001, 2002). Young frogs were raised from egg masses collected at various localities (Kendell 2001) and were released into the wild in spring of the following year. Of 6,692 tadpoles successfully hatched from four egg masses, 1,477 young frogs were released at three release sites in the spring of next year. None of these frogs was observed during later surveys at the release sites. Kendell (2002) reported that approximately 4,500 young frogs had been released during the three years of the project. Of these, 13 were recaptured at the release sites, and calling activity was recorded for the first time in the third year of the project. Kendell (2002) predicted eventual success of the project, based on the fact that calling activity was recorded during 2001 and many of the released frogs were not yet sexually mature.

Although work in Alberta has shown that a reintroduction program can be successful, a tremendous amount of effort has obviously been expended in this research. For example, about 21,000 tadpoles were reared in 2001 in a predator-free enclosure, and this resulted in only 13 subadult or adult frogs being collected in 2001 (Kendell 2002). Each of the thousands of small frogs that were released were marked to determine survival (Kendell 2001, 2002), and a field laboratory was maintained to raise the frogs (Kendell 2001, 2002). While none of the authors of these various

reports has reported the cost of this project, one could imagine that it is considerable. While the effort is worthwhile if it serves to restore northern leopard frogs to areas in which they are now extinct, the expense is obviously considerable compared with protecting known populations of frogs, and the outcome is never assured. Therefore, protection of existing populations is the prudent course of action.

Information Needs

Survey and monitoring

It is not clear how many surveys of northern leopard frogs have been undertaken throughout Region 2. It is critical that baseline data are obtained to assess the abundance of northern leopard frogs throughout Region 2 and that population trends are tracked. Many of the information needs identified in this report cannot be completed before basic surveys have been conducted. Heyer et al. (1994), Olson et al. (1997), and suggestions in this report can be used to institute a survey program throughout Region 2.

Mapping of habitat

Northern leopard frog habitat has not been mapped throughout Region 2. Northern leopard frogs likely need seasonal and semi-permanent ponds that are probably less than 5 ha in size (e.g., Semlitsch and Bodie 1998, Semlitsch 1998, 2000a, 2000b). The lead author has used National Wetlands Inventory maps on parts of the Black Hills National Forest to locate potential northern leopard frog breeding habitat, but he has found them to be frequently inaccurate, both because dense forests found throughout the Black Hills hamper visibility in aerial photographs, and because many ponds dry out over the years. This is probably likely throughout Region 2. There appears to be no substitute for ground surveys of appropriate northern leopard frog breeding habitat. When found, these ponds need to be located using GPS and then downloaded into an appropriate GIS system to find these ponds in the future and to track presence and absence of northern leopard frogs at these sites over time. Mapping of northern leopard frog sites should be relatively quick and inexpensive with the appropriate equipment and software. As Oscar Martinez has demonstrated on parts of the Spearfish-Nemo District in the Black Hills National Forest, when these ponds are located and protected, the result is large and growing populations of the northern leopard frog over time (personal observations).

Characterization of habitat

Unfortunately, although we have good studies of the natural history of the northern leopard frog to guide mapping efforts (Merrell 1977), the habitat of the species has not been carefully characterized in a quantitative sense (but see Beauregard and Leclair 1988) and has not been studied in much of Region 2. A good herpetologist can guide a mapping team to “good” northern leopard frog habitat, but the mapping team may not easily find such habitats without special training. Quantitative characterization of ponds used by northern leopard frogs should be relatively easy, and some work has already been done (Smith et al. 1998). Upland habitat and migration corridors that northern leopard frogs use extensively will probably be more difficult to find than breeding habitat, but they should also be easy to characterize once found. Unfortunately, mapping needs to be completed and habitat models need to be developed to guide conservation efforts. These types of data are needed to develop any habitat management plan (as envisioned by Semlitsch 2000a) for the northern leopard frog in Region 2.

Overwintering habitat

Studies of overwintering sites can be difficult to undertake. Cunjak (1986) relied on SCUBA techniques to study frogs overwintering in streams in Ontario while Merrell (1977) relied on simple but careful visual observations early in the spring and late in the fall to report on frogs entering and leaving overwintering sites. Currently we know very little about where northern leopard frogs may overwinter in Region 2.

Radio-tracking in late fall could show where frogs go to overwinter and the migratory pathways they take to reach these sites. Such a study would be expensive, but the data obtained would be invaluable and difficult to obtain in any other manner. Otherwise, we would recommend observing frogs at appropriate times of the year or checking potential overwintering sites, such as springs, wet meadows, lakes, and streams, in the winter. Investigating potential overwintering sites in the winter would obviously present numerous logistical difficulties. Northern leopard frogs are also difficult to observe in mid-winter as they become covered in debris on the bottom of lakes and streams (Cunjak 1986, Grier personal communication 1998). This aspect of northern leopard frog natural history may well be the most challenging to investigate.

Studies of movements

Movement studies are probably the most time-intensive and difficult field studies to conduct on amphibians. They would, however, give us detailed information on how adults and subadults use the habitat, information that may be difficult to obtain any other way. They would also address two critical questions: 1) how much upland habitat is needed to conserve 95 percent of the northern leopard frog population at a particular breeding pond (i.e., how much core upland habitat needs to be protected around each pond) and 2) what habitat features are used for migration by subadult and adult northern leopard frogs (i.e., how do we protect migration corridors used by frogs). As a side benefit, movement studies conducted over numerous years would give information on the basic demography of populations. Another benefit to movement studies is that they could be combined with studies of other issues in northern leopard frog conservation, including timber practices, burning, the effects of roads, mining, and overwintering, and in fact movement studies are critical in studies of most of these potential conservation issues.

Disease, pollution, and limb malformations

Any potential disease outbreaks should be carefully noted and investigated. Determination of the presence of disease would have to be made by a qualified wildlife disease specialist. Investigators whose works are cited in the Parasites and disease section should be alerted and consulted. Any large kills of northern leopard frogs should be reported as these could represent death by disease or by chemicals. Pesticides used in Region 2 should be investigated, especially if large amounts will be used to combat disease or insect outbreaks. Kills of northern leopard frogs could result from overuse of pesticides or accidental (or intentional) pesticide spills. Any limb malformations observed in Region 2 should be reported to the biologist responsible for the affected district, to the lead author, to the various state game departments, and especially to the limb malformations website maintained by the Northern Prairie Wildlife Research Center (Northern Prairie Wildlife Research Center 1997).

Effect of introduced predaceous fish

Sport fishing is a large industry throughout Region 2, and it is unlikely to diminish in importance. It can be

assumed that management agencies will continue to manage for the presence of sport fish that are predators on all life stages of the northern leopard frog. The industry depends on predaceous fish that have been introduced throughout Region 2. Therefore, it can be assumed that northern leopard frogs have not evolved a natural defense against these predators and that some of their life history strategies put them into the same habitats occupied by these predators. All life stages are probably vulnerable, but there may be certain life stages that are more subject to predation than are others. Some unanswered questions include:

- ❖ Are eggs and tadpoles more vulnerable than subadult and adult frogs to predation by introduced predaceous fish?
- ❖ What types of introduced fish are most likely to eat which life history stages?
- ❖ Are frogs likely to suffer predation during the overwintering period?
- ❖ Do frogs overwinter in habitats that introduced predaceous fish also use?
- ❖ Is predation by introduced predaceous fish ameliorated in certain types of habitats, and can introduced fish be kept out of these habitats?

Given the likelihood that management objectives for northern leopard frogs will continue to clash with management objectives for sport fishing, it is imperative that management agencies come up with innovative and collaborative means of managing for these two conflicting objectives.

Some of these studies could be rather simple; for example, breeding ponds can be sampled for predaceous fish and monitored to determine the likelihood of successful frog metamorphosis at these ponds. One would expect decreased or no metamorphosis at breeding ponds with predaceous fish. Another simple study would be to examine the stomach contents of predaceous fish captured in winter by ice anglers. Anecdotal evidence from North Dakota showed that stomachs of pike caught in winter contained many northern leopard frogs (unpublished data). Other studies could be much more difficult. Determining effective means to isolate frogs from introduced fishes could be one of the biggest challenges in deriving a management plan for the northern leopard frog.

Grazing effects

Cattle can easily affect all life stages of leopard frogs. They can affect breeding ponds through erosion of pond margins or by direct effects. Erosion leads to siltation, which can cover eggs with silt and impede respiration through membrane surfaces. Cattle can affect tadpoles in breeding ponds through the toxic buildup of nitrogen from manure accumulation in and around the ponds. This problem could be addressed by comparing tadpoles from ponds that are fenced from cattle to those that remain unfenced. Post-mortem of two diseased tadpoles collected at one pond open to cattle in 1998 showed that the tadpoles had deformed mouthparts and skin irritation consistent with exposure to an aquatic irritant (Smith et al. 1998).

The effects of cattle on upland frog habitat would be more difficult to study, but might be accomplished with a controlled study of ponds where fences were set at different circumferences from each pond. Mark-recapture techniques can be used to determine if the protection of a core upland habitat area results in a higher density of northern leopard frogs at a site. Such a study would serve several purposes as it should tell us something about the size of core upland areas needed to foster large and healthy northern leopard frog populations. These core sizes can be applied broadly across the forest to manage timber harvest and other practices that could adversely affect frog populations.

Grazing effects on migration corridors in Region 2 would be much less clear. It would appear that streamside vegetation and riparian corridors should be protected as northern leopard frog migration routes. However, the only controlled studies possible would be to allow cattle to invade such corridors between ponds to try to determine the effects on northern leopard frog populations. However, the results of such a study might be difficult to interpret. A more direct study of streamside and riparian corridors would be to simply mark and follow frogs in these corridors or to survey for frogs in these corridors during appropriate times of the year.

Timber removal

As has been shown by deMaynadier and Hunter (1995) in their review of forest management practices and their effect on amphibian populations, timber removal practices have significant effects on amphibian populations. As part of studies on other aspects of northern leopard frog biology in Region 2, study sites

could be picked such that some sites are located in or nearby areas under different types of forest removal practices to investigate the effects of these practices on northern leopard frogs. Such a study would be long-term and therefore somewhat costly but would represent value added to any ongoing studies while costing relatively little additional funding to implement.

Effect of roadways

The results of Wyman (1991) demonstrated that roadways can cause heavy mortality in some amphibian populations. However, the results of deMaynadier and Hunter (1995) showed that this is not necessarily the case depending on the road type. There is almost certainly a considerable amount of both paved and unpaved roads throughout Region 2. An objective of management throughout Region 2 should be to reduce the number and extent of these roads. It would seem logical to combine movement studies with a study of the effect of roadways by picking a few breeding ponds near different types of roads as study sites. If done in combination with a broader study on the movement of northern leopard frogs, a study on road effects would simply represent value added to a current study and would not cost anything beyond funds spent on the broader movement study.

Genetic studies

It would be relatively easy to collect frogs from several sites across the forest, sample small pieces of tissue (this should not increase mortality or morbidity

of the frogs as very small amounts of tissue are needed), and subject them to genetic analysis. However, the genetic data needed are very fine-grained and require considerable expertise and funding to obtain. Such data would be invaluable and could tell us the extent of philopatry at specific ponds, the extent of genetic connectedness of each pond, and whether there is high within- or among-site genetic variation in northern leopard frogs in Region 2. These data can be used to guide management strategies by telling us something about which ponds need conservation attention (for example, which ponds serve as sources for colonization) and the extent and direction of movement of frogs from pond to pond.

Prescribed fire and fire suppression

It would be interesting to investigate the effects of fire on northern leopard frog populations. This could be done either opportunistically; for example, by tracking frog populations within recently burned areas, or through studies that specifically address the effects of a prescribed fire regime on northern leopard frog populations. In the latter case, studies on some other aspect of northern leopard frog biology, such as movements, could be modified by placing study sites within areas under prescribed burn regimes and in areas in which fire is suppressed. The study sites in both study areas could then be compared. Again, such a study would represent value added to an ongoing study while costing relatively little additional funding to implement.

REFERENCES

- Adams, M.J., K.O. Richter, and W.P. Leonard. 1997. Surveying and monitoring amphibians using aquatic funnel traps. Pages 47-54 in D.H. Olson, W.P. Leonard, and R.B. Bury, editors. Sampling Amphibians in Lentic Habitats: Methods and Approaches for the Pacific Northwest. Northwest Fauna No. 4. 134 pp.
- Alford, R.A. 1999. Resource use, competition, and predation. Pages 240-278 in R.W. McDiarmid and R. Altig, editors. Tadpoles: The Biology of Anuran Larvae. The University of Chicago Press, Chicago, IL. 444 pp.
- Andrewartha, H.G. and L.C. Birch. 1984. The Ecological Web. University of Chicago Press, Chicago, IL.
- Ankley, G.T., J.E. Tietge, D.L. DeFoe, K.M. Jensen, G.W. Holcombe, E.J. Durham, and S.A. Diamond. 1998. Effects of ultraviolet light and methoprene on survival and development of *Rana pipiens*. Environmental Toxicology and Chemistry 17:2530-2542.
- Ankley, G.T., J.E. Tietge, G.W. Holcombe, D.L. DeFoe, S.A. Diamond, K.M. Jensen, and S.J. Degitz. 2000. Effects of laboratory ultraviolet radiation and natural sunlight on survival and development of *Rana pipiens*. Canadian Journal of Zoology 78:1092-1100.
- Aronson, L.R. and G.K. Noble. 1945. The sexual behavior of Anura. 2. Neural mechanisms controlling mating in the male leopard frog, *Rana pipiens*. Bulletin of the American Museum of Natural History 86:83-140.
- Ashley, E.P. and J.T. Robinson. 1996. Road mortality of amphibians, reptiles, and other wildlife on the Long Point Causeway, Lake Erie, Ontario. Canadian Field-Naturalist 110:403-412.
- Ashton, R.E., Jr. 1994. Tracking with radioactive tags. Pages 158-166 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Aubry, K.B., L.L. C. Jones, and P.A. Hall. 1988. Use of woody debris by plethodontid salamanders in Douglas-fir forests in Washington. Pages 32-37 in R.C. Szaro, K.E. Severson, and D.R. Patton, editors. Management of Amphibians, Reptiles, and Mammals in North America. USDA Forest Service General Technical Report. RM-166. 458 pp.
- Aurilio, A.C., J.L. Durant, H.F. Hemond, and M.L. Knox. 1995. Sources and distribution of arsenic in the Aberjona watershed, eastern Massachusetts. Water, Air, and Soil Pollution 81:265-282.
- Baker, M.R. 1987. Synopsis of the Nematoda parasitic in amphibians and reptiles. Memorial University of Newfoundland, Miscellaneous Publications in Biology 11:1-325.
- Bartelt, P.E. 1998. *Bufo boreas* mortality. Herpetological Review 29:96.
- Baxter, G.T. 1952. Notes on growth and the reproductive cycle of the leopard frog, *Rana pipiens* Schreber, in southern Wyoming. Journal of the Colorado-Wyoming Academy of Science 4:91.
- Baxter, G.T. and M.D. Stone. 1985. Amphibians and Reptiles of Wyoming. Second edition. Wyoming Game and Fish Department. 137 pp.
- Beauregard, N. and R. Leclair, Jr. 1988. Multivariate analysis of the summer habitat structure of *Rana pipiens* Schreber, in Lac Saint Pierre (Québec, Canada). Pages 129-143 in R.C. Szaro, K.E. Severson, and D.R. Patton, editors. Management of Amphibians, Reptiles and Small Mammals in North America. USDA Forest Service General Technical Report RM-166. 458 pp.
- Beauvais, G.B., R. Thurston, and D.A. Keinath. 2003. Predictive range maps for 15 species of management concern in the Rocky Mountain Region of the USDA Forest Service. Wyoming Natural Diversity Database, Laramie, WY.
- Begon, M., J.L. Harper, and C.R. Townsend. 1996. Ecology: Individuals, Populations, and Communities. Third edition. Blackwell Science Ltd., Editorial Offices, Osney Mead, Oxford, London. 1068 pp.

- Berger, L., R. Speare, P. Daszak, D.E. Green, A.A. Cunningham, C.L. Gogging, R. Slocombe, M.A. Ragan, A.D. Hyatt, K.R. McDonald, H.B. Hines, K.R. Lips, G. Marantelli, and H. Parkes. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences* 95:9031-9036.
- Berrill, M., S. Bertram, and B. Pauli. 1997. Effects of pesticides on amphibian embryos and larvae. Pages 233-245 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- Berrill, M., S. Bertram, D. Brigham, and V. Campbell. 1992. A comparison of three methods of monitoring frog populations. Pages 87-93 in C.A. Bishop and K.E. Pettit, editors. *Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy*. Occasional Paper Number 76, Canadian Wildlife Service, Ottawa, ON, Canada. 120 pp.
- Berrill, M., S. Bertram, L. McGillivray, M. Kolohon, and B. Pauli. 1994. Effects of low concentrations of forest-use pesticides on frog embryos and tadpoles. *Environmental Toxicology and Chemistry* 13:657-664.
- Berrill, M., S. Bertram, A. Wilson, S. Louis, D. Brigham, and C. Stromberg. 1993. Lethal and sublethal impacts of pyrethroid insecticides on amphibian embryos and tadpoles. *Environmental Toxicology and Chemistry* 12:525-539.
- Berven, K.A. and T.A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic structure. *Evolution* 44:2047-2056.
- Bishop, C.A. 1992. The effects of pesticides on amphibians and the implications for determining the causes of declines in amphibian populations. *In*: C.A. Bishop and K.E. Pettit, editors. *Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy*. Ottawa, Ontario, Canadian Wildlife Service. Occasional Paper Number 76.
- Bishop, C.A. and K.E. Pettit. 1992. *Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy*. Canadian Wildlife Service, Occasional Paper No. 76.
- Bishop, C.A., K.E. Pettit, M.E. Gartshore, and D.A. MacLeod. 1997. Extensive monitoring of anuran populations using call counts and road transects in Ontario (1992 to 1993). Pages 149-160 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- Bonin, J. and Y. Bachand. 1997. The use of artificial covers to survey terrestrial salamanders in Québec. Pages 175-179 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- Bonin, J., M. Ouellet, J. Rodrigue, J.L. DesGranges, F. Gagné, T.F. Sharbel, and L.A. Lowcock. 1997. Measuring the health of frogs in agricultural habitats subjected to pesticides. Pages 246-257 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- Bovbjerg, R.V. 1965. Experimental studies on the dispersal of the frog, *Rana pipiens*. *Proceedings of the Iowa Academy of Science* 72:412-418.
- Bovbjerg, R.V. and A.M. Bovbjerg. 1964. Summer emigrations of the frog *Rana pipiens* in northwestern Iowa. *Proceedings of the Iowa Academy of Science* 71:511-518.
- Bradford, D.F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. *Ecology* 64:1171-1183.
- Breckenridge, W.J. 1944. *Reptiles and Amphibians of Minnesota*. University of Minnesota Press, Minneapolis, MN. xiii + 202 pp.
- Breden, F. 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*. *Copeia* 1987:386-395.

- Brodman, R. and M. Kilmurry. 1998. Status of amphibians in northwestern Indiana. Pages 125-136 in M.J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, IA. 507 pp.
- Brönmark, C. and P. Edenhamn. 1994. Does the presence of fish affect the distribution of tree frogs (*Hyla arborea*)? Conservation Biology 8:841-845.
- Buchanan, B. 1993. Effects of enhanced lighting on the behavior of nocturnal frogs. Animal Behaviour 45:893-899.
- Buckhouse, J.C. and G.F. Gifford. 1976. Water quality implications of cattle grazing on a semi-arid watershed in southeastern Utah. Journal of Range Management 29:109-113.
- Buckle, J. 1971. A recent introduction of frogs to Newfoundland. Canadian Field-Naturalist 85:72-74.
- Bull, E.L. 2000. Comparison of two radio transmitter attachments on Columbia spotted frogs (*Rana luteiventris*). Herpetological Review 31:26-28.
- Bull, E.L. and M.P. Hayes. 2001. Post-breeding season movements of Columbia spotted frogs (*Rana luteiventris*) in northeastern Oregon. Western North American Naturalist 61:119-123.
- Bureau of Land Management. 2000. Information Bulletin No. CO-2000-014: Colorado BLM state director's sensitive species list. Bureau of Land Management, Colorado State Office, Lakewood, CO.
- Bureau of Land Management. 2001. Instruction Memorandum No. WY-2001-040, Sensitive Species Policy and List. Bureau of Land Management, Wyoming State Office, Cheyenne, WY. Available online at: <http://www.wy.blm.gov/wildlife/02species.pdf>.
- Bury, R.B. and P.S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: Relation of the herpetofauna to stand age and moisture. Pages 11-22 in R.C. Szaro, K.E. Severson, and D.R. Patton. Management of Amphibians, Reptiles, and Small Mammals in North America. USDA Forest Service General Technical Report. RM-166. 458 pp.
- Bury, R.B. and R.A. Luckenbach. 1976. Introduced amphibians and reptiles in California. Biological Conservation 10:1-14.
- Carey, C. 1993. Hypothesis concerning the causes of the disappearance of boreal toads from the mountains of Colorado. Conservation Biology 7:355-362.
- Carey, C., N. Cohen, and L. Rollins-Smith. 1999. Amphibian declines: An immunological perspective. Developmental and Comparative Immunology 23:459-472.
- Carr, L.W. and L. Fahrig. 2001. Effect of road traffic on two amphibian species of differing vagility. Biological Conservation 15:1071-1078.
- Casper, G.S. 1998. Review of the status of Wisconsin amphibians. Pages 199-205 in M.J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, IA. 507 pp.
- Caswell, H. 2000. Matrix Population Models: Construction, Analysis, and Interpretation. Second edition. Sinauer Associates, Sunderland, MA.
- Clarkson, R.W. and J.C. Rorabaugh. 1989. Status of leopard frogs (*Rana pipiens* complex: Ranidae) in Arizona and southeastern California. Southwestern Naturalist 34:531-538.
- Collier, A., J.B. Keiper, and L.P. Orr. 1998. The invertebrate prey of the northern leopard frog, *Rana pipiens*, in a northeastern Ohio population. Ohio Journal of Science 98:39-41.
- Collins, J.P. and H.M. Wilbur. 1979. Breeding habits and habitats of the amphibians of the Edwin S. George Reserve, Michigan, with notes on the local distribution of fishes. Occasional Papers of the Museum of Zoology, University of Michigan. No. 686:1-34.
- Conant, R. and J.T. Collins. 1991 A Field Guide to Reptiles and Amphibians: Eastern and Central North America. Third edition. Houghton Mifflin Company, Boston, MA. 450 pp.
- Cooke, A.S. 1981. Tadpoles as indicators of harmful levels of pollution in the field. Environmental Pollution Series A 25:123-133.

- Corn, P.S. 1981. Field evidence for a relationship between color and developmental rate in the northern leopard frog (*Rana pipiens*). *Herpetologica* 37:155-160.
- Corn, P.S. 1994. What we know and don't know about amphibians declines in the west. Pages 59-67 in: W. Covington and L.F. DeBano, editors. Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management. General Technical Report RM-247. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.
- Corn, P.S. and J.C. Fogleman. 1984. Extinction of montane populations of the northern leopard frog (*Rana pipiens*) in Colorado. *Journal of Herpetology* 18:147-152.
- Corn, P.S. and L.J. Livo. 1989. Leopard frog and wood frog reproduction in Colorado and Wyoming. *Northwestern Naturalist* 70:1-9.
- Corn, P.S. and F.A. Vertucci. 1992. Descriptive risk assessment of the effects of acidic deposition on Rocky Mountain amphibians. *Journal of Herpetology* 26:361-369.
- COSEWIC. 2000. COSEWIC assessment and update status report on the northern leopard frog *Rana pipiens* (Southern Mountain and Prairie populations) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Canada. vi + 40 pp.
- Cousineau, M. and K. Rogers. 1991. Observations on sympatric *Rana pipiens*, *R. blairi*, and their hybrids in eastern Colorado. *Journal of Herpetology* 25:114-116.
- Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. Classification of Wetlands and Deepwater Habitats of the United States. U.S. Government Printing Office, Washington, D.C. 103 pp.
- Crouch, W.B. and P.W.C. Paton. 2000. Using egg-mass counts to monitor wood frog populations. *Wildlife Society Bulletin* 28:895-901.
- Crump, M.L. and N.J. Scott, Jr. 1994. Visual encounter surveys. Pages 84-92 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayak, and M. Foster, editors. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Crump, D., M. Berrill, D. Coulson, D. Lean, L. McGillivray, and A. Smith. 1999. Sensitivity of amphibian embryos, tadpoles, and larvae to enhanced UV-B radiation in natural pond conditions. *Canadian Journal of Zoology* 77: 1956-1966.
- Crump, M.L., F.R. Hensley, and K.L. Clark. 1992. Apparent decline of the golden toad: Underground or extinct? *Copeia* 1992:413-420.
- Cunjak, R.A. 1986. Winter habitat of northern leopard frogs, *Rana pipiens*, in a southern Ontario stream. *Canadian Journal of Zoology* 64:255-257.
- Cunningham A.A., T.E.S. Langton, P.M. Bennett, J.F. Lewin, S.E.N. Drury, R.E. Gough, and S.K. MacGregor. 1996. Pathological and microbiological findings from incidents of unusual mortality of the common frog (*Rana temporaria*). *Philosophical Transactions of the Royal Society of London* 351:1539-57.
- Daszak, P., L. Berger, A.A. Cunningham, A.D. Hyatt, D.E. Green, and R. Speare. 1999. Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases* 5:735-748.
- Daszak, P., A.A. Cunningham, and A.D. Hyatt. 2000. Emerging infectious diseases of wildlife: Threats to biodiversity and human health. *Science* 287:443-449.
- Davidson, C. 1996. Frog and toad calls of the Rocky Mountains: Vanishing voices. Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, NY.
- Davis, J.G., P.J. Krusling, and J.W. Ferner. 1998. Status of Amphibians in Minnesota. Status and Conservation of Midwestern Amphibians. Pages 166-168 in M.J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, IA. 507 pp.

- Davis, T.M. 1997. Non-disruptive monitoring of terrestrial salamanders with artificial cover objects on southern Vancouver Island, British Columbia. Pages 161-174 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Herpetological Conservation, Number One. Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- DeBenedictis, P.A. 1974. Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: An experimental field study. *Ecological Monographs* 44:129-151.
- deMaynadier, P.G. and M.L. Hunter, Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12:340-352.
- Dhuey, B. and R. Hay. 2000. Frog and toad survey. Pages 140-147 in 1999 Wildlife Survey Summary Report. Wisconsin Department of Natural Resources, Madison, WI.
- Dial, N.A. and C.A.B. Dial. 1987. Lethal effects of diquat and paraquat on developing frog embryos and 15-day-old tadpoles, *Rana pipiens*. *Bulletin of Environmental Contamination and Toxicology* 38:1006-1011.
- Diana, S.G. and V.R. Beasley. 1998. Amphibian toxicology. Pages 266-277 in M.J. Lannoo, editor. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Didiuk, A. 1997. Status of amphibians in Saskatchewan. Pages 110-116 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- Diller, L.V. and R.L. Wallace. 1994. Distribution and habitat of *Plethodon elongatus* on managed young growth forests in north coastal California. *Journal of Herpetology* 28:310-318.
- Dodd, C.K., Jr. and D.E. Scott. 1994. Drift fences encircling breeding sites. Pages 125-141 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Dodd, C.K., Jr. and R.A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? *Herpetologica* 47:336-350.
- Dole, J.W. 1965a. Spatial relations in natural populations of the leopard frog, *Rana pipiens* Schreber, in northern Michigan. *American Midland Naturalist* 74:464-478.
- Dole, J.W. 1965b. Summer movement of adult leopard frogs, *Rana pipiens* Schreber, in northern Michigan. *Ecology* 46:236-255.
- Dole, J.W. 1967. Spring movements of leopard frogs, *Rana pipiens* Schreber, in northern Michigan. *American Midland Naturalist* 78:167-181.
- Dole, J.W. 1968. Homing in leopard frogs, *Rana pipiens*. *Ecology* 49:386-399.
- Dole, J.W. 1971. Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. *Copeia* 1971:221-228.
- Dole, J.W. 1972. The role of olfaction and audition in the orientation of leopard frogs, *Rana pipiens*. *Herpetologica* 28:258-260.
- Drake, C.J. 1914. The food of *Rana pipiens*. *The Ohio Naturalist* 14:257-269.
- Duellman, W.E. and L. Trueb. 1986. *Biology of Amphibians*. McGraw-Hill, Inc. New York, NY. 670 pp.
- Dunlap, D.G. and K.C. Kruse. 1976. Frogs of the *Rana pipiens* complex in the northern and central plains states. *Southwestern Naturalist* 20:559-571.
- Dunlap, D.G. and J.E. Platz. 1981. Geographic variation of protein and call in *Rana pipiens* from the northcentral United States. *Copeia* 1981:876-879.
- Dyer, W.G. 1991. Helminth parasites of amphibians from Illinois and adjacent Midwestern states. *Transactions of the Illinois State Academy of Science* 84:125-143.
- Elmore, W. and R.L. Beschta. 1987. Riparian areas: Perceptions in management. *Rangelands* 9:260-265.

- Emery, A.R., A.H. Berst, and K. Kodaira. 1972. Under-ice observations of wintering sites of leopard frogs. *Copeia* 1972:123-126.
- Faeh, S.A., D.K. Nichols, and V.R. Beasley. 1998. Infectious diseases of amphibians. Pages 259-265 in M.J. Lannoo, editor. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Fellers, G.M. 1997. Design of amphibian surveys. Pages 23-34 in D.H. Olson, W.P. Leonard, and R.B. Bury, editors. *Sampling Amphibians in Lentic Habitats: Methods and Approaches for the Pacific Northwest*. Northwest Fauna Number 4. Society for Northwestern Vertebrate Biology, Olympia, WA. 134 pp.
- Fellers, G.M. and C.A. Drost. 1994. Sampling with artificial cover. Pages 146-150 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Fisher, C. 1999. Feasibility of northern leopard frog translocations in Alberta: A review of physiological, ecological, methodological requirements for successful repatriations and results from field investigations. Alberta Environment, Fisheries, and Wildlife Management Division, Edmonton, AB, Canada. Unpublished report. 30 pp.
- Fitch, H.S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. University of Kansas Publications, Museum of Natural History 11:63-326.
- Flower, S.S. 1936. Further notes on the duration of life in animals II: Amphibia. *Proceedings of Zoological Society of London*: 369-394.
- Force, E.R. 1933. The age of the attainment of sexual maturity of the leopard frog *Rana pipiens* (Schreber) in northern Michigan. *Copeia* 1933:128-131.
- Forman, R.T.T., D. Sperling, J.A. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale, L. Fahrig, R. France, C.R. Goldman, K. Heanue, J.A. Jones, F.J. Swanson, T. Turrentine, and T.C. Winter. 2003. *Road Ecology: Science and Solutions*. Island Press, Washington, D.C. 481 pp.
- Fournier, M.A. 1997. Amphibians in the Northwest Territories. Pages 100-106 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- Franz, R. 1971. Notes on the distribution and ecology of the herpetofauna of northwestern Montana. *Bulletin of the Maryland Herpetological Society* 7:1-10.
- Freda, J. and W.A. Dunson. 1985. Field and laboratory studies of ion balance and growth rates of ranid tadpoles chronically exposed to low pH. *Copeia* 1985:415-423.
- Freda, J. and D.H. Taylor. 1992. Behavioral response of amphibian larvae to acidic water. *Journal of Herpetology* 26: 429-433.
- Fried, B., P.L. Pane, and A. Reddy. 1997. Experimental infection of *Rana pipiens* tadpoles with *Echinostoma trivolvis* cercariae. *Parasitology Research* 83:666-669.
- Froiland, S.G. 1990. *Natural History of the Black Hills and Badlands*. The Center for Western Studies, Augustana College, Sioux Falls, SD. 225 pp.
- Garber, S.D. and J. Burger. A 20-year study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 5:1151-1162.
- Goldberg, S.R., C.R. Bursey, R.G. McKinnell, and I.S. Tan. 2001. Helminths of northern leopard frogs, *Rana pipiens* (Ranidae), from North Dakota and South Dakota. *Western North American Naturalist* 61:248-251.
- Grant, B.W., K.L. Brown, G.W. Ferguson, and J.W. Gibbons. 1994. Changes in amphibian biodiversity associated with 25 years of pine forest regeneration: Implications for biodiversity management. Pages 355-367 in S.K. Majumdar, F.J. Brenner, J.E. Lovich, J.F. Schalles, and E.W. Miller, editors. *Biological Diversity: Problems and Challenges*. Pennsylvania Academy of Science, Philadelphia, PA.

- Green, D.M. 1992. Fowler's toads (*Bufo woodhousei fowleri*) at Long Point, Ontario: Changing abundance and implications for conservation. Pages 37-43 in C.A. Bishop and K.E. Pettit, editors. Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Paper Number 76, Canadian Wildlife Service. 120 pp.
- Green, D.M. 1997. Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation, No. 1, Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- Green, D.M. and R.W. Campbell. 1984. The Amphibians of British Columbia. Royal British Columbia Museum, Handbook 45.
- Grier, J.W. 1998. Personal communication. Department of Biological Sciences, 218 Stevens Hall, North Dakota State University, Fargo, ND 58105-5517. E-mail: james.grier@ndsu.edu
- Grue, C.E., L.R. DeWeese, P. Mineau, G.A. Swanson, J.R. Foster, P.M. Arnold, J.N. Huckins, P.J. Sheehan, W.K. Marshall, and A.P. Ludden. 1986. Potential impacts of agricultural chemicals on waterfowl and other wildlife inhabiting prairie wetlands: An evaluation of research needs and approaches. Transactions of the Northern American Wildlife Natural Resources Conference 51:357-383.
- Hall, R.J. and P.F.P. Henry. 1992. Review. Assessing effects of pesticides on amphibians and reptiles: Status and needs. Herpetology Journal 2:65-71.
- Hamilton, H.L. 1941. The biological action of rotenone on fresh water animals. Proceedings of the Iowa Academy of Science 48:467-479.
- Hammerson, G.A. 1982. Bullfrog eliminating leopard frogs in Colorado? Herpetological Review 13:115-116.
- Hammerson, G.A. 1999. Amphibians and Reptiles in Colorado. Second edition. University Press of Colorado and Colorado Division of Wildlife, Niwot, CO. 484 pp.
- Hayek, L.A.C. and M.A. Buzas. 1997. Surveying Natural Populations. Columbia University Press, NY. 563 pp.
- Hayek, L.A.C. and R.W. McDiarmid. 1994. GIS and remote sensing techniques. Pages 166-171 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayak, and M. Foster, editors. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Hayes, T.B., A. Collins, M. Lee, M. Mendoza, M. Noriega, A.A. Stewart, and A. Vonk. 2002. Hermaphroditic, demasculinized frogs after exposure to the herbicide atrazine at low ecologically relevant doses. Proceedings of the National Academy of Sciences 99:5476-5480.
- Hecnar, S.J. 1995. Acute and chronic toxicity of ammonium nitrate fertilizer to amphibians from southern Ontario. Environmental Toxicology and Chemistry 14:2131-2137.
- Hecnar, S.J. and R.T. M'Closkey. 1996. Regional dynamics and the status amphibians. Ecology 77:2091-2097.
- Hecnar, S.J. and R.T. M'Closkey. 1997a. The effects of predatory fish on amphibian species richness and distribution. Biological Conservation 79:123-131.
- Hecnar, S.J. and R.T. M'Closkey. 1997b. Changes in the composition of a ranid frog community following bullfrog extinction. American Midland Naturalist 137:145-150.
- Hecnar, S.J. and R.T. M'Closkey. 1998. Species richness patterns of amphibians in southwestern Ontario ponds. Journal of Biogeography 25:763-772.
- Helgen, J., R.G. McKinnell, and M.C. Gernes. 1998. Investigation of malformed northern leopard frogs in Minnesota. Pages 288-297 in M.J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, IA. 507 pp.
- Hemesath, L.M. 1998. Iowa's Frog and Toad Survey, 1991-1994. Pages 206-216 in M.J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, IA. 507 pp.
- Hendricks, F.S. 1973. Intestinal contents of *Rana pipiens* Schreber (Ranidae) larvae. Southwestern Naturalist 18:99-101.

- Heyer, W.R. 1994. Thread bobbins. Pages 153-155 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Heyer, W.R., M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster. 1994. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Hillis, D.M. 1988. Systematics of the *Rana pipiens* complex: Puzzle and paradigm. *Annual Review of Ecology and Systematics* 19:39-63.
- Hillis, D.M., J.S. Frost, and D.A. Wright. 1983. Phylogeny and biogeography of the *Rana pipiens* complex: A biochemical evaluation. *Systematic Zoology* 32:132-143.
- Hine, R.L., B.L. Les, and B.F. Hellmich. 1981. Leopard frog populations and mortality in Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin No. 122:1-139.
- Hine, R.L., B.L. Les, B.F. Hellmich, and R.C. Vogt. 1975. Preliminary report on leopard frog (*Rana pipiens*) populations in Wisconsin. Wisconsin Department of Natural Resources Research Report No. 81:1-31.
- Holme, J.A., M. Refsnes, and E. Dybing. 1999. Possible carcinogenic risk associated with the production and use of creosote-treated wood. *Tidsskrift for den Norske Laegeforening* 119:2664-2666.
- Hoppe, D.M. 2000. History of Minnesota frog abnormalities: Do recent findings represent a new phenomenon? *Journal of the Iowa Academy of Science* 107:86-89.
- Hupf, T.H. 1977. Natural histories of two species of leopard frogs, *Rana blairi* and *Rana pipiens*, in a zone of sympatry in northeastern Nebraska. Unpublished M. S. thesis, University of Nebraska, Lincoln, NE. 125 pp.
- Jaeger, R.G. 1994a. Transect sampling. Pages 103-107 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Jaeger, R.G. 1994b. Patch sampling. Pages 107-109 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Jaeger, R.G. and R.F. Inger. 1994. Quadrat sampling. Pages 97-102 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Jancovich, J.K., E.W. Davidson, J.F. Morado, B.L. Jacobs, and J.P. Collins. 1997. Isolation of a lethal virus from the endangered tiger salamander *Ambystoma tigrinum stebbinsi*. *Diseases of Aquatic Organisms* 31:161-167.
- Jefferies, D.L. and J.M. Klopatek. 1987. Effects of grazing on the vegetation of the blackbrush association. *Journal of Range Management* 40:390-392.
- Jennings, M.R. and M.P. Hayes. 1994. Amphibian and reptile species of special concern in California. Unpublished report submitted to the California Department of Fish and Game. 255 pp.
- Jofre, M.B., M.L. Rosenshield, and W.H. Karasov. 2000. Effects of PCB 126 and ammonia, alone and in combination, on green frog (*Rana clamitans*) and leopard frog (*Rana pipiens*) hatching success, development, and metamorphosis. *Journal of the Iowa Academy of Science* 107:113-122.
- Johnson, P.T.J., K.B. Lunde, and A.R. Blaustein. 2001. *Ribeiroia ondatrae* (Trematoda: Digenea) infection induces severe limb malformations in western toads (*Bufo boreas*). *Canadian Journal of Zoology* 79:370.
- Johnson, P.T.J., K.B. Lunde, E.G. Ritchie, and A.E. Launer. 1999. The effect of trematode infection on amphibian limb development and survivorship. *Science* 284:802-804.
- Johnson, T.R. 1998. Missouri toad and frog calling survey: The first year. Pages 357-359 in M.J. Lannoo, editor. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.

- Juterbock, J.E., S.S. Sweet, and R.W. McDiarmid. 1994. Manual GIS application for habitat specialists. Pages 171-175 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayak, and M. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Kaplan, H.M. and S.S. Glaczinski. 1965. Hematological effects of organophosphate insecticides in the frog (*Rana pipiens*). *Life Sciences* 4:1213-1219.
- Kauffman, J. and W.C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications: A review. *Journal of Range Management* 37:430-437.
- Kendell, K. 2001. Northern leopard frog reintroduction: Raven River – Year 2 (2000). Alberta Sustainable Resource Development, Fish and Wildlife Service, Alberta Species at Risk Report No. 13, Edmonton, AB, Canada. 43 pp.
- Kendell, K. 2002. Northern leopard frog reintroduction: Year 3 (2001). Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Report No. 42, Edmonton, AB, Canada. 45 pp.
- Koch, E.D. and C.R. Peterson. 1995. *Amphibians and Reptiles of Yellowstone and Grand Teton National Parks*. University of Utah Press, Salt Lake City, UT. 188 pp.
- Krebs, C.J. 1999. *Ecological Methodology*. Second edition. Benjamin Cummings, Menlo Park, CA. 620 pp.
- Kruse, K.C. and M.G. Francis. 1977. A predation deterrent in larvae of the bullfrog, *Rana catesbeiana*. *American Fisheries Society Transactions* 106:248-252.
- Lamberti, G.A., S.V. Gregory, C.P. Hawkins, R.C. Wildman, L.R. Ashkenas, and D.M. Denicola. 1992. Plant-herbivore interactions in streams near Mt. St. Helens. *Freshwater Biology* 27:237-247.
- Lamoureux, V.S. and D.M. Madison. 1999. Overwintering habitats of radio-implanted green frogs, *Rana clamitans*. *Journal of Herpetology* 33:430-435.
- Lang, R.E. and P.A. Simmons. 2001. “Boomburbs”: The emergence of large, fast-growing suburban cities in the United States. *Fannie Mae Foundation Census Note* 06. 14 pp.
- Lannoo, M.J. 1998a. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Lannoo, M.J. 1998b. Amphibian conservation and wetland management in the upper midwest: A catch-22 for the cricket frog? Pages 330-339 in M.J. Lannoo, editor. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Lannoo, M.J., K. Lang, T. Waltz, and G.S. Phillips. 1994. An altered amphibian assemblage: Dickinson County, Iowa, 70 years after Frank Blanchard’s survey. *American Midland Naturalist* 131:311-319.
- Leclair, R., Jr. and J. Castanet. 1987. A skeletochronological assessment of age and growth in the frog *Rana pipiens* Schreber (Amphibia, Anura) from southwestern Quebec. *Copeia* 1987:361-369.
- Lehtinen, R.M., S.M. Galatowitsch, and J.R. Tester. 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. *Wetlands* 19:1-12.
- Leonard, W.P., K.R. McAllister, and R.C. Friesz. 1999. Survey and assessment of northern leopard frog (*Rana pipiens*) populations in Washington State. *Northwestern Naturalist* 80:51-60.
- Lepage, M., R. Courtois, C. Daigle, and S. Matte. 1997. Surveying calling anurans in Québec using volunteers. Pages 128-140 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Herpetological Conservation Number One. Society for the Study of Amphibians and Reptiles, St. Louis, MO. 338 pp.
- Linder, G. and B. Grillitsch. 2000. Ecotoxicology of metals. Pages 325-459 in D.W. Sparling, G. Linder, and C.A. Bishop, editors. *Ecotoxicology of Amphibians and Reptiles*. SETAC Press, Pensacola, FL. 877 pp.
- Linzey, D.W. 1967. Food of the leopard frog, *Rana pipiens pipiens*, in central New York. *Herpetologica* 23:11-17.

- Linzey, D.W. and A.H. Wright. 1947. A synoptic key to the salientian eggs of the United States. *American Midland Naturalist* 37:179-222.
- Lips, K.R., J.K. Reaser, B.E. Young, and R. Ibáñez. 2001. Amphibian Monitoring in Latin America: A Protocol Manual. Society for the Study of Amphibians and Reptiles Herpetological Circular Number 30:1-115.
- Long, L.E., L.S. Saylor, and M.E. Soule. 1995. A pH/UV-B synergism in amphibians. *Conservation Biology* 9:1301-1303.
- Lynch, J.D. 1978. The distribution of leopard frogs (*Rana blairi* and *Rana pipiens*) (Amphibia, Anura, Ranidae) in Nebraska. *Journal of Herpetology* 12:157-162.
- Madison, D.M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31:542-552.
- Madison, D.M. and L. Farrand. 1997. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. *Copeia* 1998:402-410.
- Manion, J.J. and L. Cory. 1952. Winter kill of *Rana pipiens* in shallow ponds. *Herpetologica* 8:32.
- Martinez, O. 1997. Personal communications while on the Black Hills National Forest. Current contact information: Medicine Bow-Routt National Forest, Yampa Ranger District, Yampa, CO. E-mail: omartinez@fs.fed.us.
- Martinez, O. 1998. Personal communications while on the Black Hills National Forest. Current contact information: Medicine Bow-Routt National Forest, Yampa Ranger District, Yampa, CO. E-mail: omartinez@fs.fed.us.
- Mathews, K.R. and K.L. Pope. 1999. A telemetric study of the movement patterns and habitat use of *Rana muscosa*, the mountain yellow-legged frog, in a high-elevation basin in Kings Canyon National Park, California. *Journal of Herpetology* 33:615-624.
- Maunder, J.E. 1997. Amphibians of Newfoundland and Labrador: Status changes since 1983. Pages 93-99 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*, Society for the Study of Amphibians and Reptiles, St. Louis, MO.
- Maxell, B.A. 2000. Management of Montana's amphibians: A review of factors that may present a risk to population viability and accounts on the identification, distribution, taxonomy, habitat use, natural history, and the status and conservation of individual species. Report to USFS Region 1, Order Number 43-0343-0-0224. University of Montana, Wildlife Biology Program. Missoula, MT. 161 pp.
- McAlpine, D.F. 1997. Historical evidence does not suggest New Brunswick amphibians have declined. Pages 117-127 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Society for the Study of Amphibians and Reptiles, St. Louis, MO.
- McAlpine, D.F. and M.D.B. Burt. 1998. Helminths of bullfrogs, *Rana catesbeiana*, green frogs, *R. clamitans*, and leopard frogs, *R. pipiens*, in New Brunswick. *Canadian Field Naturalist* 112:50-68.
- McAlpine, D.F. and T.G. Dilworth. 1989. Microhabitat and prey size among three species of *Rana* (Anura: Ranidae) sympatric in eastern Canada. *Canadian Journal of Zoology* 67:2244-2252.
- McClelland, B.E. and W. Wilczynski. 1989. Release call characteristics of male and female *Rana pipiens*. *Copeia* 1989:1045-1049.
- McCollum, S.A. and J.D. Leimberger. 1997. Predator-induced morphological changes in an amphibian: Predation by dragonflies affects tadpole shape and color. *Oecologia* 109:615-621.
- McLeod, R. and J.E. Gates. 1998. Response of herpetofaunal communities to forest cutting and burning at Chesapeake Farms, Maryland. *American Midland Naturalist* 139:164-177.
- Mennell, L. 1997. Amphibians in southwestern Yukon and northwestern British Columbia. Pages 107-109 in D.M. Green, editor. *Amphibians in Decline: Canadian Studies of a Global Problem*. Society for the Study of Amphibians and Reptiles, St. Louis, MO.
- Merrell, D.J. 1963. Rearing tadpoles of the leopard frog, *Rana pipiens*. *Turtlex News* 41:263-265.

- Merrell, D.J. 1965. The distribution of the dominant Burnsi gene in the leopard frog, *Rana pipiens*. *Evolution* 19: 69-85.
- Merrell, D.J. 1968. A comparison of the estimated size and the “effective size” of breeding populations of the leopard frog, *Rana pipiens*. *Evolution* 22:274-283.
- Merrell, D.J. 1969. Natural selection in a leopard frog population. *Journal of the Minnesota Academy of Science* 35: 86-89.
- Merrell, D.J. 1970. Migration and gene dispersal in *Rana pipiens*. *American Zoologist* 10:47-52.
- Merrell, D.J. 1977. Life history of the leopard frog, *Rana pipiens*, in Minnesota. *Bell Museum of Natural History Occasional Papers No. 15*:1-23.
- Merrell, D.J. and C.F. Rodell. 1968. Seasonal selection in the leopard frog, *Rana pipiens*. *Evolution* 22:284-288.
- Meteyer, C.U., I.K. Loeffler, J.F. Fallon, K.A. Converse, E. Green, J.C. Helgen, S. Kersten, R. Levey, L. Eaton-Poole, and J.G. Burkhardt. 2000. Hind limb malformations in free-living northern leopard frogs (*Rana pipiens*) from Maine, Minnesota, and Vermont suggest multiple etiologies. *Teratology* 62:151-171.
- Mierzwa, K.S. 1998. Biogeography of Midwestern Amphibians. Pages 24-30 in M.J. Lannoo, editor. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Milius, S. 2000. New frog-killing disease may not be so new. *Science News* 157:133.
- Miller, J.D. 1978. Observations on the diets of *Rana pretiosa*, *Rana pipiens*, and *Bufo boreas* from western Montana. *Northwest Science* 52:243-249.
- Minton, S.A. 1998. Observations on Indiana amphibian populations: A Forty-five-year overview. Pages 217-220 in M.J. Lannoo, editor. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Morell, V. 1999. Are pathogens felling frogs? *Science* 284:728-731.
- Moriarty, J.J. 1998. Status of Amphibians in Minnesota. Pages 166-168 in Lannoo, M. J., ed. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecological Monographs* 53: 119-138.
- Mosimann, J.E. and G.B. Rabb. 1952. The herpetology of Tiber Reservoir Area, Montana. *Copeia* 1952:23-27.
- Mossman, M.J., L.M. Hartman, R. Hay, J.R. Sauer, and B.J. Dhuey. 1998. Monitoring long-term trends in Wisconsin frog and toad populations. Pages 169-198 in M.J. Lannoo, editor. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Mushinsky, H.R. 1985. Fire and the Florida sandhill herpetofaunal community: With special attention to responses of *Cnemidophorus sexlineatus*. *Herpetologica* 41:333-342.
- Muths, E., T.L. Johnson, and P.S. Corn. 2001. Experimental repatriation of boreal toad (*Bufo boreas*) eggs, metamorphs, and adults in Rocky Mountain National Park. *Southwestern Naturalist* 46:106-112.
- Nash, R.F., G.G. Gallup, Jr., and M.K. McClure. 1970. The immobility reaction in leopard frogs (*Rana pipiens*) as a function of noise-induced fear. *Psychonomic Science* 21:155-156.
- Nelson, J.K. 1999. Monitoring frog and toad populations using vocalization surveys at Rocky Flats Environmental Technology Site, Colorado. *Journal of the Colorado-Wyoming Academy of Sciences* 31:11.
- Newman, R.A. 1997. Personal communication. University of North Dakota, Department of Biology, Grand Forks, ND. E-mail: robert.newman@und.nodak.edu.
- Noble, G.K. and L.R. Aronson. 1942. The sexual behavior of Anura: The normal mating pattern of *Rana pipiens*. *Bulletin of the American Museum of Natural History* 80:127-142.

- Northern Prairie Wildlife Research Center. 1997. North American Reporting Center for Amphibian Malformations. Jamestown, North Dakota: North Prairie Wildlife Research Center Home Page. Available online at: <http://frogweb.nbii.gov/narcam/> (Version 12, April 2001).
- Oldfield, B. and J.J. Moriarty. 1994. Amphibians and Reptiles Native to Minnesota. University of Minnesota Press, Minneapolis, MN. 237 pp.
- Olson, D.H., W.P. Leonard, and R.B. Bury, editors. 1997. Sampling Amphibians in Lentic Habitats: Methods and Approaches for the Pacific Northwest. Northwest Fauna Number 4. Society for Northwestern Vertebrate Biology, Olympia, WA. 134 pp.
- Orchard, S.A. 1992. Amphibian population declines in British Columbia. Pages 10-13 in C.A. Bishop and K.E. Pettit, editors. Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Papers of the Canadian Wildlife Service No. 76. 120 pp.
- Orr, L., J. Neumann, E. Vogt, and A. Collier. 1998. Status of northern leopard frogs, pickerel frogs and wood frogs, in Illinois. Pages 83-90 in M.J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, IA. 507 pp.
- Ouellet, M., J. Bonin, J. Rodrigue, J.-L. DesGranges, and S. Lair. 1997. Hindlimb deformities (ectromelia, ectrodactyly) in free-living anurans from agricultural habitats. *Journal of Wildlife Diseases* 33:95-104.
- Pace, A.E. 1974. Systematic and biological studies of the leopard frogs (*Rana pipiens* Complex) of the United States. Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 148:1-140.
- Painter, C.W. 2000. Personal communication. New Mexico Department of Game and Fish, Santa Fe, NM. E-mail: charles.painter@state.nm.us.
- Parrish, J.B., D.J. Herman, and D.J. Reyher. 1996. A Century of Change in Black Hills Forest and Riparian Ecosystems. USDA Forest Service Agricultural Experiment Station, South Dakota State University. No. B722. 20 pp.
- Pauli, B.D., J.A. Perrault, and S.L. Money. 2000. RATL: a database of reptile and amphibian toxicology literature. Technical Report Series No. 357E. Canadian Wildlife Service, Headquarters, Hull, PQ, Canada.
- Pechmann, J.H.K. and H.M. Wilbur. 1994. Putting declining amphibian populations in perspective: Natural fluctuations and human impacts. *Herpetologica* 50:65-84.
- Pechmann, J.H.K., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt, and J.W. Gibbons. 1991. Declining amphibian populations: The problem of separating human impacts from natural fluctuations. *Science* 253:892-895.
- Peterson, C.R. 1974. A Preliminary Report on the Amphibians and Reptiles of the Black Hills of South Dakota and Wyoming. Unpublished M.S. Thesis, University of Illinois at Urbana-Champaign, IL. 59 pp.
- Peterson, C.R. 2001. Personal communications. Department of Biological Sciences, Idaho State University, Pocatello, ID. E-mail: petechar@isu.edu.
- Peterson, C.R. 2003. Personal communications. Department of Biological Sciences, Idaho State University, Pocatello, ID. E-mail: petechar@isu.edu.
- Peterson, C.R. and M.E. Dorcas. 1994. Automated data acquisition. Pages 47-57 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C. 587 pp.
- Petranka, J.W., M.P. Brannon, M.E. Hopey, and C.K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecology and Management* 67:135-147.
- Petranka, J.W., M.E. Eldridge, and K.E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. *Conservation Biology* 7:363-370.

- Phaneuf, D., J.L. DesGranges, N. Plante, and J. Rodrigue. 1995. Contamination of local wildlife following a fire at a polychlorinated biphenyls warehouse in St. Basile le Grand, Quebec, Canada. *Archives of Environmental Contamination and Toxicology* 28:145-153.
- Porter, K.R. and D.E. Hakanson. 1976. Toxicity of mine drainage to embryonic and larval boreal toads (*Bufo boreas*). *Copeia* 1976:327-331.
- Pough, F.H., R.M. Andrews, J.E. Cadle, M.L. Crump, A.H. Savitzky, and K.D. Wells. 2001. *Herpetology*. Second edition. Prentice Hall, Upper Saddle River, NJ. 612 pp.
- Pounds, J.A. and M.L. Crump. 1994. Amphibian declines and climate disturbance: The case of the golden toad and the harlequin frog. *Conservation Biology* 8:72-75.
- Power T., K.L. Clark, A. Harfenist, and D.B. Peakall. 1989. A review and evaluation of the amphibian toxicological literature. Technical Report No. 61, Canadian Wildlife Service, Headquarters, Ottawa, ON, Canada.
- Prudhoe, S. and R.A. Bray. 1982. *Platyhelminth Parasites of the Amphibia*. Oxford University Press, Oxford, United Kingdom. 217 pp.
- Ramotnik, C.A. and N.J. Scott, Jr. 1988. Habitat requirements of New Mexico's endangered salamanders. Pages 54-63 in R.C. Szaro, K.E. Severson, and D.R. Patton, editors. *Management of Amphibians, Reptiles, and Mammals in North America*. USDA Forest Service General Technical Report RM-166. 458 pp.
- Rand, A.S. and G.E. Drewry. 1994. Acoustic monitoring at fixed sites. Pages 150-153 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Rathbun, G.B. and T.G. Murphey. 1996. Evaluation of a radio-belt for ranid frogs. *Herpetological Review* 27:187-189.
- Raymond, L.R. and L.M. Hardy. 1991. Effects of a clearcut on a population of the mole salamander, *Ambystoma talpoideum*, in an adjacent unaltered forest. *Journal of Herpetology* 25:509-512.
- Reaser, J.K. 2000. Demographic analysis of the Columbia spotted frog (*Rana luteiventris*): Case study in spatiotemporal variation. *Canadian Journal of Zoology* 78:1158-1167.
- Reichel, J.D. 1996. Status of amphibians and reptiles in eastern Montana. *Intermountain Journal of Sciences* 2:57.
- Relyea, R.A. 2001a. Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* 82:523-540.
- Relyea, R.A. 2001b. The relationship between predation risk and antipredator responses in larval anurans. *Ecology* 82:541-554.
- Relyea, R.A. and E.E. Werner. 2000. Morphological plasticity in four larval anurans distributed along an environmental gradient. *Copeia* 2000:178-190.
- Resetar, A.R. 1998. Locating historical information on amphibian populations. Pages 379-384 in M.J. Lannoo, editor. *Status and Conservation of Midwestern Amphibians*. University of Iowa Press, Iowa City, IA. 507 pp.
- Richards, C.M. 1958. The inhibition of growth in crowded *Rana pipiens* tadpoles. *Physiological Zoology* 31:138-151.
- Richards, S.J., U. Sinsch, and R.A. Alford. 1994. Radio tracking. Pages 155-158 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Roberts, W.E. 1992. Declines in amphibian populations in Alberta. Pages 14-16 in C.A. Bishop and K.E. Pettit, editors. *Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy*. Occasional Papers of the Canadian Wildlife Service No. 76. 120 pp.
- Rome, L.C., E.D. Stevens, and H.B. John-Alder. 1992. The influence of temperature and thermal acclimation on physiological function. Pages 183-205 in M.E. Feder and W.W. Burggren, editors. *Environmental Physiology of the Amphibians*. University of Chicago Press, Chicago, IL.

- Rorabaugh, J.C. 2005. *Rana pipiens*. Pages 570-580 in M. Lannoo, editor. Amphibian Declines: The Conservation Status of North American Species. University of California Press, Berkeley, CA.
- Ross, D.A., J.K. Reaser, P. Kleeman, and D.L. Drake. 1999. *Rana luteiventris* mortality and site fidelity. Herpetological Review 30:163.
- Rumble, M.A., D. Willis, and B.E. Smith. 2004. Wildlife of created palustrine wetlands. Pages 216-239 in M.C. McKinstry, W.A. Hubert, and S.H. Anderson, editors. Wetlands and Riparian Areas of the Intermountain West. University of Texas Press, Austin, TX.
- Russell, A.P. and A.M. Bauer. 1993. The Amphibians and Reptiles of Alberta. University of Alberta Press, Edmonton, AB, Canada. 264 pp.
- Russell, K.R., D.H. Van Lear, and D.C. Guynn, Jr. 1999. Prescribed fire effects on herpetofauna: Review and Management implications. Wildlife Society Bulletin 27:374-384.
- Ryan, R.A. 1953. Growth rates of some ranids under natural conditions. Copeia 1953:73-80.
- Schlichter, L.C. 1981. Low pH affects the fertilization and development of *Rana pipiens* eggs. Canadian Journal of Zoology 59:1693-1699.
- Scott, N.J., Jr. and B.D. Woodward. 1994. Surveys at breeding sites. Pages 118-125 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Seburn, C.N.L., D.C. Seburn, and C.A. Paszkowski. 1997. Northern leopard frog (*Rana pipiens*) dispersal in relation to habitat. Pages 64-72 in D.M. Green, editor. Amphibians in Decline: Canadian Studies of a Global Problem. Society for the Study of Amphibians and Reptiles, Herpetological Conservation Number One. St. Louis, MO. 338 pp.
- Semlitsch, R.D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12:1113-1119.
- Semlitsch, R.D. 2000a. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615-631.
- Semlitsch, R.D. 2000b. Size does matter: The value of small isolated wetlands. National Wetlands Newsletter, January-February 2000:5-13.
- Semlitsch, R.D. 2001. Personal communication. University of Missouri—Columbia. 212 Tucker Hall, Division of Biological Sciences, University of Missouri, Columbia, MO 65211. E-mail: SemlitschR@Missouri.edu.
- Semlitsch, R.D. and J.R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129-1133.
- Sessions, S.K. and S.B. Ruth. 1990. Explanation for naturally occurring supernumerary limbs in amphibians. Journal of Experimental Zoology 254:38-457.
- Sessions, S.K., R.A. Franssen, and V.L. Horner. 1999. Morphological clues from multilegged frogs: Are retinoids to blame? Science 284:800-802.
- Sexton, O.J., C.A. Phillips, T.J. Bergman, E.B. Wattenberg, and R.E. Preston. 1998. Abandon not hope: Status of repatriated populations of spotted salamanders and wood frogs at the Tyson Research Center, St. Louis County, Missouri. Pages 340-344 in M.J. Lannoo, editor. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, IA. 507 pp.
- Shaffer, H.B. and J.E. Juterbock. 1994. Night driving. Pages 163-166 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C. 364 pp.
- Skelly, D.K., E.E. Werner, and S.A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80:2326-2337.

- Smith, B.E., S.K. Ashton, and R.E. Baum. 1998. Herpetofaunal surveys on the Spearfish-Nemo District, Black Hills National Forest: Preliminary report and recommendations, 1998. Unpublished report submitted to the USDA Forest Service, Black Hills National Forest, Spearfish-Nemo District. 27 pp.
- Smith, B.E., D.M. Browning, E. Taylor, R.S. Ferguson, and K. Yturalde. 1996b. Herpetofaunal surveys of the Fall River Ranger District, USDA Forest Service, southwestern South Dakota and Badlands National Park. USGS/Biological Resources Division. Northern Prairie Science Center. 27 pp.
- Smith, B.E., L.R. Cottingham, C.R. Peterson, and M.J. Goode. 2005. A herpetofaunal inventory of the Black Hills, summer 2004. Final report submitted to the South Dakota Game, Fish, and Parks Department, Pierre, SD. 64 pp.
- Smith, B.E., J.J. Kolbe, and R.S. Ferguson. 1996a. A herpetological survey of Wind Cave National Park, South Dakota. USGS/Biological Resources Division. Northern Prairie Science Center. 66 pp.
- Smith, B.E., J.L. Massie, and B.G. Blake. 2004. Inventory of reptiles and amphibians at seven national park service units in the northern Great Plains 2002-2003. Final report submitted to the Northern Great Plains Inventory and Monitoring Coordinator, Mount Rushmore National Park, Keystone, SD. 48 pp.
- Smith-Gill, S.J. and D.E. Gill. 1978. Curvilinearities in the competition equations: An experiment with ranid tadpoles. *American Naturalist* 112:557-570.
- Sokal, R.R. and F.J. Rohlf. 1994. Biometry. Third edition. W.H. Freeman, New York, NY. 880 pp.
- Sparling, D.W. 2000. Ecotoxicology of organic contaminants to amphibians. Pages 461-494 *in* D.W. Sparling, G. Linder, and C.A. Bishop, editors. *Ecotoxicology of Amphibians and Reptiles*. SETAC Press, Pensacola, FL. 877 pp.
- Sparling, D.W., G. Linder, and C.A. Bishop, editors. 2000a. *Ecotoxicology of Amphibians and Reptiles*. SETAC Press, Pensacola, FL. 877 pp.
- Stebbins, R.C. 2003. *A Field Guide to Western Reptiles and Amphibians*. Third edition. Houghton Mifflin Company, Boston, MA. 533 pp.
- Stebbins, R.C. and N.W. Cohen. 1995. *A Natural History of Amphibians*. Princeton University Press, Princeton, NJ. 316 pp.
- Trombulak, S.C. and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18-30.
- USDA Forest Service. 1994. FSM 5670 R2 Supplement No. 2600-94-2; Region 2 Sensitive Species List. USDA Forest Service, Rocky Mountain Region, Denver, CO.
- USDA Forest Service. 1997. Black Hills National Forest Plan of Land and Resource Management. Black Hills National Forest, Custer, SD. Available online at: <http://www.fs.fed.us/r2/blackhills/projects/planning/97Revision/fp/index.shtml>
- USDA Forest Service. 1999. Northern Region Sensitive Species List. USDA Forest Service, Northern Region, Missoula, MT. Available online at: http://www.fs.fed.us/r1/tes_index.html.
- USDA Forest Service. 2003. Species Conservation Project: Region 2 Regional Forester's Sensitive Species. USDA Forest Service, Rocky Mountain Region, Golden, CO. Available online at: <http://www.fs.fed.us/r2/projects/scp/sensitivespecies/index.shtml>.
- USDA Forest Service. 2005. Threatened, endangered, and sensitive plants and animals. Chapter 2670 *in* Forest Service Manual: wildlife, fish, and sensitive plant habitat management, R2 Supplement 2600-2005-1, Exhibit 01, Regional Forester's Sensitive Species. USDA Forest Service, Rocky Mountain Region, Denver, CO.
- USDA Forest Service. 2006. Black Hills National Forest Land and Resource Management Plan, 1997 Revision, Phase II Amendment. USDA Forest Service, Rocky Mountain Region, Black Hills National Forest, Custer, South Dakota. March 2006.

- Ultsch, G.R., T.E. Graham, and C.E. Crocker. 2000. An aggregation of overwintering leopard frogs, *Rana pipiens*, and common map turtles, *Graptemys geographica*, in northern Vermont. *Canadian Field-Naturalist* 114:314-315.
- Van Velsion, R. 1979. Effects of livestock grazing upon rainbow trout in Otter Creek, Nebraska. Pages 53-55 in O.B. Cope, editor. *Proceedings of the Forum – Grazing and Riparian/Stream Ecosystems*. Trout Unlimited, Denver, CO.
- Wassersug, R.J. and K. Hoff. 1985. Kinematics of swimming in anuran larvae. *Journal of Experimental Biology* 119: 1-30.
- Waye, H.L. 2001. Teflon tubing as radio transmitter belt material for northern leopard frogs (*Rana pipiens*). *Herpetological Review* 32:88-89.
- Wells, K.D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour* 25:666-693.
- Wells, K.D. 1978. Territoriality in the green frog (*Rana clamitans*): Vocalizations and agonistic behaviour. *Animal Behaviour* 26:1051-1063.
- Welsh, H.H., Jr. and A.J. Lind. 1995. Habitat correlates of the Del Norte salamander, *Plethodon elongatus*, in northwestern California. *Journal of Herpetology* 29:198-210.
- Welsh, H.H., Jr. and L.M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: A case study from California's redwoods. *Ecological Applications* 8:1118-1132.
- Werner, E.E. and K.S. Glennemeier. 1999. Influence of forest canopy cover on breeding pond distributions of several amphibian species. *Copeia* 1999:1-12.
- Werner, J.K., B.A. Maxell, P. Hendricks, and D.L. Flath. 2004. *Amphibians and Reptiles of Montana*. Mountain Press Publishing Company, Missoula, MT. 262 pp.
- Werner, J.K., J. Weaselhead, and T. Plummer. 1999. The accuracy of estimating eggs in anuran egg masses using weight or volume measurements. *Herpetological Review* 30:30-31.
- Whitaker, J.O., Jr. 1961. Habitat and food of mousetrapped young *Rana pipiens* and *Rana clamitans*. *Herpetologica* 17:174-179.
- Wilbur, H.M. 1997. Experimental ecology of food webs: Complex systems in temporary ponds. *Ecology* 78:2279-2302.
- Williamson, J.E. and J.M. Carter. 2001. Water-quality characteristics in the Black Hills area, South Dakota. *Water-Resources Investigations Report* 01-4194. 196 pp.
- Woodward, B.D. 1982. Tadpole competition in a desert anuran community. *Oecologia* 54:96-100.
- Woodward, B.D. 1983. Predator-prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. *Ecology* 64:1549-1555.
- Wright, A.H. 1914. *North American Anura: Life-histories of the Anura of Ithaca, New York*. Carnegie Institution, Washington, Publication 197:1-98.
- Wright, A.H. and A.A. Wright. 1949. *Handbook of Frogs and Toads*. Comstock Publishing. Ithaca, NY. 640 pp.
- Wyman, R.L., editor. 1991. *Global Climate Change and Life on Earth*. Chapman and Hall, New York, NY. Available online at: <http://gf.state.wy.us/wildlife/CompConvStrategy/index.asp>.
- Zar, J.H. 1998. *Biostatistical Analysis*. Fourth edition. Prentice Hall, Upper Saddle River, NJ. 929 pp.
- Zimmerman, B. 1994. Audio strip transects. Pages 92-97 in W.R. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, editors. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C. 364 pp.

The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD). To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, S.W., Washington, DC 20250-9410, or call (800) 795-3272 (voice) or (202) 720-6382 (TDD). USDA is an equal opportunity provider and employer.