KENTUCKY HEARTWOOD

Protecting the Beauty and Wellbeing of Kentucky's Native Forests

Dan Olsen, Forest Supervisor
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1700 Bypass Road
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April 15, 2019

RE: Forest Plan Amendment Environmental Assessment

Dear Supervisor Olsen,

Thank you for the opportunity to submit comments on the Draft Forest Plan Amendment Environmental Assessment (Draft EA). These comments are being submitted on behalf of both Kentucky Heartwood and the Kentucky Resources Council. We also thank you for taking the time to hold two public meetings, and for your willingness to extend the public comment period to accommodate review of supplemental materials.

As you are aware, Kentucky Heartwood has numerous and substantial concerns with the proposed amendment and the environmental analysis. Indiana and northern long-eared bat populations are crashing. Amending the plan to allow for increased impacts to these species, particularly during vulnerable times in their life cycle (i.e., spring staging, fall swarming, and when young are non-volant) is not something that we, nor our members, consider acceptable. We address our concerns and issues with the analysis in detail below.

1. Purpose and Need

Under "Need for the Proposal" (EA-3), you state:

> Since the 2004 Forest Plan was signed, there is new information specific to bat habitat management, there are additional Threatened and Endangered species and Designated Critical Habitat, and new USFWS documents regarding definitions and hibernacula for bats. These have combined to create circumstances where the Forest Plan's direction needs to be updated. There is also a need to change some standards from project level to the DBNF landscape level.

The Silviculture Report similarly states that:

> The project was developed to address changes in science applicable to the management of bat habitat, changes in the number of threatened and endangered species, and additional designations of critical habitat found on the Daniel Boone National Forest. (Report at 2)

From statements made by you and your staff during public forums, and elsewhere in the analysis documents, we understand that the intent of the Plan Amendment is actually to allow for a substantial increase in vegetation management (e.g., logging, prescribed fire, etc.) than has occurred since the Plan was adopted in 2004. However, the stated purpose and need, as presented in the Draft EA, must form the basis of the analysis and Decision. The weight of the analysis and decision, therefore, rests on 1) "new information specific to bat habitat management," and 2) "additional Threatened and Endangered species and Designated Critical Habitat." We are not addressing "new USFWS documents regarding definitions and hibernacula for bats," as these proposed change merely align terminology and categories with USWFS and will not lead to any actual changes in land management.

2. Lack of Baseline Information

The Draft EA and supporting documents fail to include essential baseline information to help inform the public and, ultimately, any decision to be made. For example, there is no information regarding actual timber harvest and vegetation management acres since adoption of the Forest Plan in 2004. How many acres have been logged, and using what prescriptions? And during what seasons? How many acres of timber harvest have occurred in areas covered by current Forest Plan Standards relating to Indiana bats? How many acres have been burned? During what seasons? The Draft EA and supporting documents instead rely on, and refer only to, acreages allowed by the Forest Plan. A valid description and analysis must compare anticipated changes and management goals to the *actual* completed actions carried out since 2004. The Forest Service's analysis fails to do this.

Additionally, we have not found any information in the Draft EA or supporting documents that provides the current status and trends of federally-listed bat populations on the DBNF, in Kentucky, or range-wide. Reviewing USFWS documents, it appears that the Kentucky population for Indiana bats dropped 18% from 2011 to 2017, with a loss of about 12,500 bats. This proposed Plan Amendment is predicated on updated bat management with current science. Any changes to the Forest Plan with respect to federally-listed bats is necessarily made within the context of sharply declining populations. But this is not adequately presented or analyzed.

3. Even-aged Management is Not Good for Indiana and Northern Long-eared Bats

The Draft EA does not adequately address how different types of forest management may negatively affect Indiana and northern long-eared bats. During the public meeting on March 26, 2019, a DBNF biologist made a general statement about how management (suggesting logging) can be good for bats. Another DBNF staff person made a comment suggesting that logging for "balanced age classes" (i.e., a roughly uniform distribution of different-aged, even-aged stands) was good for bats. But this is not the case. At least, it is much more complicated.

The BA states:

> Tree removal has the highest potential to impact roosting, foraging and commuting habitat especially where commercial harvest removes mature trees within large forested areas. **Large-scale tree removal may also cause fragmentation of commuting routes or the isolation of forest blocks, potentially resulting in increased energy expenditure for bats that must seek other foraging areas.** (BA at 74, emphasis added)

And:

> Murray and Kurta (2004) demonstrated the importance of wooded travel corridors for Indiana bats within their maternity habitat in Michigan; **they noted that bats did not fly over open fields but traveled along wooded corridors, even though use of these corridors increased commuting distance by over 55 percent**. (BA at 80, emphasis added)
>
> In a fragmented landscape, Indiana bats may have to fly across less suitable habitat. This could pose greater risk of predation (e.g., raptors). Indiana bats consistently follow tree-lined paths rather than cross large open areas. (BA at 81, emphasis added)

Even-aged management using low-retention shelterwood cuts (10-15 square foot per acre of basal area) is the preferred method of timber harvest across the DBNF. For example, of the 3,200 acres of proposed logging in the South Redbird Wildlife Habitat Enhancement Project, 2,600 acres are proposed for shelterwood harvest. Some of the blocks of forest proposed for logging are several hundred acres, where timber harvest would be in 40 acre regeneration patches separated by 330 ft., commercially thinned buffers. While bats are generally mobile (excepting for maternity colonies while young are non-volant), they do return each year to specific territories and roost trees. As the BA states:

> Although researchers have found it difficult to predict where maternity colonies may occur relative to forested habitat, researchers can reliably predict that once Indiana bats colonize maternity habitat, they will return to the same maternity areas annually (BA at 81)

Large-scale shelterwood logging in maternity areas would create large patches of unsuitable habitat for roosting and foraging for Indiana and northern long-eared bats. This sort of logging could result in lactating bats having to expend extra energy as they search the landscape for new suitable habitat while avoiding harvested areas. It is true that these areas of forest will grow back with time, but it will be decades (at least) before they provide suitable habitat for foraging or roosting. There is likely little difference for mature forest-dwelling bats (particularly *Myotis* species) between a 10 year-old shelterwood cut and a farm field. Flying over these areas, as stated in the BA, increases risk of predation and is largely avoided.

Contrary to information in the BA that demonstrates how even-aged timber management can negatively impact Indiana and northern long-eared bats, the BA provides an incorrect determination that large-scale logging projects would have an "Insignificant" effect on Indiana bats, and are "Not Likely to Adversely Affect the Species." The BA justifies this determination by stating:

> While the habitat may be altered to some degree, the conservation measures are intended to ensure that there is no significant loss of forested habitat or fragmentation that would result in measurable effects to Indiana bats. (BA at 82)

What "conservation measures" would those be? The proposed Plan Amendments remove nearly all binding conservation measures for Indiana and northern long-eared bats, and the preferred silvicultural methods used on the DBNF negatively impact these species.

We do, however, agree with statements in the BA that some types of forest management can be beneficial to Indiana and northern long-eared bats. For example, the BA states:

> Thinning harvest methods may remove roost trees, however thinning may also positively impact foraging and commuting habitat by reducing canopy and mid-story clutter to expand flyways for bats. (BA at 74)

And:

> In heavily forested landscapes, small cuts, thinning and uneven age management prescriptions can provide important habitat heterogeneity for bats and may increase use relative to adjacent undisturbed forest (Hayes and Loeb 2007). (BA at 90)

Midstory thinning, commercial thinning, and uneven-aged management approaches must be viewed differently and separately from even-aged timber management in terms of the effects on Indiana and northern long-eared bats. They simply are not comparable. And while these intermediate silvicultural approaches may have some indirect negative effects, unlike even-aged management they have the potential to enhance the suitability of habitat for Indiana and northern long-eared bats. Negative impacts may be justifiable in the short-term if they help toward recovery in the long-term. But specifics matter.

We point out here that Kentucky Heartwood suggested that uneven-aged silvicultural approaches be utilized in the South Redbird Wildlife Habitat Enhancement Project. These suggestions were made to the Forest Service during early "collaborative" meetings, emails with the District Silviculturalist, and in our formal comments. But these suggestions were completely rejected. The project instead relies almost solely on even-aged shelterwood cuts for commercial management (2,600 acres of shelterwood cuts and 600 acres of salvage logging). This is an instance (though not an exception) where the Forest Service could have opted for less impactful silvicultural approaches that assist in the development of structural complexity at the stand level – structural complexity that lends to high quality habitat for endangered bats – but instead chose to rely exclusively on silvicultural systems that remove a greater volume of timber.

4. Proposed, Endangered, Threatened, and Aquatic Critical Habitat Designation

The only rationale presented in the Need for Proposal for changing restrictions affecting timber harvest is for reducing impacts to proposed, endangered, and threatened aquatic species and aquatic critical habitats, which have increased in number since adoption of the Forest Plan. The Draft EA states:

> Since the Forest Plan was signed in 2004, eight newly listed threatened or endangered species have been identified on the Forest and thirty-nine newly designated Critical Habitat units have been listed under the Endangered Species Act (See tables in Appendix A). All but one of these is an aquatic species or has aquatic-related habitat that requires species specific avoidance and minimization measures. Best Management Practices have been included in past project planning to reduce the risk of adverse effects to listed aquatic species and Critical Habitats; however, risk could be further minimized by removing the restrictive seasonality treatment dates in the Forest Plan Standards. (EA-4)

Kentucky Heartwood has raised concerns about the impacts of logging to at-risk aquatic species and their habitats for years. Each and every time we raise these issues at the project level, the Forest Service responds, with no equivocation, that there will be no meaningful impacts to these species or their habitats. We agree that it is vital to reduce or eliminate damage to soils and sedimentation in streams incurred through logging. However, we find it appalling that after years of the Daniel Boone National Forest insisting that these impacts do not exist (at least in any substantive way), that you are now planning to drop significant protections for endangered bats under the premise that these impacts need to be reduced. If these impacts are significant enough to warrant this Forest Plan amendment, and put Indiana and northern long-eared bats at increased risk, then you must halt all active and pending timber sales until each project EA is revised and projects are amended.

We provide here selections from Environmental Assessments for approved timber projects from 2008 through 2017 that illustrate this point:

<u>Upper Rock Creek Vegetation Management Project (2008)</u>

3.1 Resources not affected by the Proposal

3.2.2 Soil and Water

> "Due to all of these reasons it would be very difficult to measure or detect a change in sedimentation at any given point in Rock Creek, and any increases in sedimentation could be considered undetectable." (EA 3-5)
>
> "This alternative would not affect water quality to the point where it would influence the designation of Rock Creek as a Wild and Scenic River or have an effect on the downstream karst system." (EA 3-5)

3.3 Biological Environment

3.3.3 Conservation Species

Affected Environment Aquatic

> "Prescribed fire would be implemented under Regional (R8) guidelines that protect the integrity of riparian areas and aquatic ecosystems. Special protective measures outlined in the FLRMP have been

incorporated within this project to minimize the potential for adverse impacts to the stream corridors and to ensure water quality protection. With incorporation of these protective measures, it is unlikely that this project would directly or indirectly effect aquatic conservation species." (EA 3-52)

"As the closest cutting units are at least 0.20 miles away (from Rock Creek) and Best Management Practices are incorporated in the design and layout of commercial and noncommercial thinnings, any sedimentation will likely be filtered out before it reaches the creek reducing the likelihood for adverse indirect effects."

3.3.4 Proposed, Endangered, Threatened, and Sensitive (PETS) Species

Blackside Dace

"No direct effects are expected since Blackside dace are aquatic"

"With regards to the commercial and noncommercial thinnings that are proposed, all of the sites are on upper slopes or ridge tops except for Stand 47. For all the sites there would be no direct affects (sic)."

"Sedimentation that does reach Rock Creek will do so during rain events and will have diminishing impacts over space and time making sediment generated through silvicultural practices and or prescribed fire, and its effects, very difficult to measure or detect." (EA 3-62)

Cumberland elktoe

"No direct effects are expected since the Cumberland elktoe is aquatic and all of the proposed actions are terrestrial… Indirect effects in the form of siltation could occur but can be lessened because of the manner in which the Forest Service applies prescribed fire."

"No direct effects are expected from the commercial and noncommercial thinnings because Cumberland elktoe is aquatic and all the sties for the proposed actions are terrestrial."

"Sedimentation that does reach Rock Creek will do so during rain events and will have diminishing impacts over space and time making sediment generated through silvicultural practices and or prescribed fire, and its effects, very difficult to measure or detect."

"These effects can be further reduced by implementing seasonal restrictions, operational restrictions, and clauses in timber sale contracts that will lessen the likelihood that Cumberland Elktoe would be impacted in any of its life stages. Such a negligible increase in sedimentation (4.1%) would not cause measureable effects and would thus be discountable." (EA 3-64, 3-65)

Cumberland Elktoe Designated Critical Habitat

"Most particulate matter that does enter the stream can be expected to be flushed out quickly. As for the ridgetop and upper slope commercial and noncommercial thinning sites, no direct affects (sic) to upper rock creek are expected as these sites are terrestrial."

"Indirect effects from sedimentation could occur as a result of the proposed actions. However, the likelihood of these affects (sic) is reduced through the application of best management practices; the distance between the project sites; and the amount of projects impolemented at any one time (year). In addition, stream sedimentation will be spread through time and space. That is, sediment produced as a result of the proposed action(s) will reach the stream only during rain events and will be difficult to measure or detect from that of the normal baseline. At the conclusion of the proposed actions, the water quality is expected to remain in the excellent category according to KBI standards and is within the acceptable range of the 2004 Forest Plan EIS. When affects cannot be meaningfully measured or detected they are considered discountable." (EA 3-68)

Spring Creek Vegetation Management Project (2015)

Hydrology and Soils Report for the Spring Creek Vegetation Management Project (Oct. 2010)

"There are several reasons why it is unlikely that changes in stream sedimentation of this magnitude will influence water quality in these drainages. As previously stated, for modeling purposes, the proposed actions were constrained to a single year to display the maximum possible effects that could occur. It is much more likely that activities will occur over a several year period which would reduce the total amount of sediment in the stream and any given time. Stream sedimentation will also be spread through time and space. Sediment will only reach the stream during rain events and there are approximately 25 of these events per year. In addition the proposed activities are spread throughout the watershed and as a result the sediment reaching the Red Bird River is staggered through time. Due to all of these reasons it will be very difficult to measure or detect and change in sedimentation at any given point in the Redbird River. It is also unlikely that groundwater will be affected." (Report at 9)

"There is no measurable change to the Watershed Condition Rank or the Species Sediment Load index listed in the Forest Plan (USDA Forest Service, 2004, FEIS, page 3-20) from this alternative and would still be in the excellent range." (Report at 11)

"Based on field work, water quality modeling, and best available science there would be no adverse effects to any of the hydrologic resources as a result of this undertaking if the provided recommendations are followed. The Spring Creek Vegetation Management project is consistent with Forest Plan direction for hydrologic resources, meets or exceeds Kentucky water quality regulations (401 KAR), and complies with the Clean Water Act." (Report at 12)

Spring Creek Environmental Assessment

Snuffbox mussel:

"The hydrology and soil analysis report indicates that implementing the proposed project would contribute to less than 1% sediment increase, and at this level, it is very difficult to measure or detect sedimentation changes (Walker 2010). The herbicide risk assessment indicates that site preparation using cut stump treatment with a triclopyr/imazapyr herbicide mixture diluted with water would produce negligible and discountable effects to aquatic species. Therefore, the proposed project would have negligible impacts on snuffbox." (EA-30)

Greenwood Vegetation Management Project (2017)

Greenwood Vegetation Management Soil & Water Report (Jan. 2017)

"Stream Sedimentation - Changes in stream sedimentation in the 6th level watersheds that contain treatment units from this alternative are shown in Table 5. The Proposed Action would produce between 26 and 539 tons/year of stream sedimentation in these watersheds. This represents a less than a 6 percent increase over current conditions. This increase in stream sedimentation can be attributed mainly to skid trails, landings, and temporary haul roads within the commercial harvest areas. Mechanically constructed fire lines may also be contributing to the sedimentation. This sedimentation would be greatest immediately after ground disturbing activities and would return to pre-disturbance levels in 3 years. The implementation of buffer strips and Best Management Practices (BMPs) as detailed in the Forest Plan would reduce the probability of sediment actually being delivered to the stream channels." (Report at 8)

"In the affected watersheds the cumulative percent stream sediment increases over current conditions are estimated to be between 1.0 and 6.1 percent (Table 3). These changes are often offset by other restoration projects in the watersheds (i.e., road and OHV trail closures). Based on these increases there is no measurable change to the Watershed Condition Rank or the Species Sediment Load index listed in the Forest Plan (USDA Forest Service, 2004, FEIS, page 3-20) from this alternative." (Report at 15)

Greenwood Vegetation Management Project Wildlife Resource Report (Updated May 2017)

(Regarding Blackside dace, Cumberland darter, and Cumberland arrow darter):

"With regards to the thinnings, mechanical site preparation/reforestation and upland vernal pools, all of the sites are on upper slopes or ridge tops. Best Management Practices (BMP) are incorporated in the design and layout to minimize indirect effects through sedimentation. Forest Plan standard DB-VEG-4 further protects the integrity of streams. Most sedimentation would be filtered out before it reaches aquatic habitat reducing the likelihood for adverse indirect effects.

It has been projected that between 26 and 539 tons of sediment generated from all projects could reach aquatic habitats. This is a less than 6 percent change over the current baseline (Walker 2016). Sedimentation that does reach inhabited streams will do so during rain events and will have diminishing impacts over space and time making sediment generated through the proposed actions very difficult to detect (Walker 2016)." (Report at 59)

"There would be no direct effects to aquatic macroinvertabrates as all of the proposed activities are terrestrial. Indirect effects could occur from all proposed activities as a result of sedimentation and/or a change in water chemistry. This is projected to be very minimal as it is predicted that there would be a less than six percent change in sediments and water chemistry (Walker 2016)." (Report at 73)

Greenwood project EA:

Soil and Water Resources:

"In a worst case scenario, less than a 6 percent increase in stream sedimentation over current conditions could occur for up to 3 years following implementation of this alternative. The worst case scenario assumes that the entire project would be implemented and completed within 1 calendar year, which is infeasible. This increase in sedimentation would be attributed mainly to skid trails, landings, and temporary haul roads within the commercial harvest areas. Mechanically constructed fire lines would also contribute to sedimentation. This sedimentation would be greatest immediately after ground disturbing activities and would return to pre-disturbance levels within 3 years. The implementation of design criteria, such as stream buffers, and BMPs would reduce the probability of sediment actually being delivered to the stream channels. Water quality changes would be small in magnitude and short-term in duration." (EA-38)

Wildlife Resources:

"Aquatic species identified for analysis were a macro-invertebrates assemblage, blackside dace, Cumberland darter and Cumberland arrow darter. The proposed action would only occur on terrestrial sites where no aquatics are present; however, aquatic fauna could be indirectly impacted by sedimentation as a result of implementing the proposed action. There could be indirect effects to these fishes if their habitat was affected by any of the practices associated with prescribed fire. Indirect effects are not expected because prescribed fires are typically backing fires that do not consume the duff layer, and they also burn poorly in riparian areas, reducing the likelihood of significant siltation. Mechanical fireline on erosive soils and fire line on steep terrain would be stabilized and reseeded at the completion of this project to further reduce sedimentation. Walker 2016 states that sedimentation is not expected to exceed 6% over the current baseline, which is within the limits of the Forest Plan. This increase would be spread out across the project area and would occur over a period of years. Therefore, specific impacts to aquatics would be low in intensity at any given time or location during project implementation. Design criteria would further reduce or eliminate these impacts rendering direct and indirect impacts to these species negligible." (EA-45)

Freeman Fork Oak Woodland Restoration Project (2014)

"There are several reasons why it is unlikely that changes in stream sedimentation of this magnitude would influence water quality in these drainages. As previously stated, for modeling purposes, the potential effects from proposed actions were constrained to a single year to display the maximum possible effects that could occur. It is much more likely that activities would occur over a several year period which would reduce the total amount of sediment in the stream at any given time. Stream sedimentation will also be spread through time and space. Sediment will only reach the stream during rain events and there are approximately 25 of these events per year. In addition the proposed activities are spread throughout the watershed and as a result the sediment reaching Beaver Creek and Cogur Fork are staggered through time. Due to all of these reasons it would be very difficult to measure or detect the change in sedimentation at any given point in the receiving streams. With surface water not being affected it is also unlikely that the connected groundwater resources would be affected." (EA 3-5)

(Regarding macro-invertebrates (MIS))

"There would be no direct effects to aquatic macro-invertebrates as all of the proposed activities are terrestrial. There could be indirect effects (sedimentation) from any of the ground disturbing activities or prescribed fire. These impacts have been considered and predicted in the *Hydrology and Soils Report for the Freeman Fork Oak Woodland Restoration Project* (Walker 2012). In Walker's report it is predicted that there would be a less than one percent increase in sedimentation over current conditions. The timeframe of the erosion model is bound by activities that occur three years prior and one year following the implementation of this proposed project." (EA 3-54)

(Regarding Blackside dace and Cumberland darter)

"With regards to the commercial thinnings that are proposed, none of the thinnings would occur in riparian corridors. Riparian corridors are excluded from timber harvest. There would be a buffer of 50 feet for intermittent streamcourses and 100 feet for perennial streamcourses, or the width of the 100 year floodplain, whichever is greater, established to protect streamcourses within riparian corridors. There would be no direct effects to the Blackside dace and Cumberland darter as there would be no skidding or landing in their habitat or the buffering riparian corridor. Design criteria are incorporated as part of the proposed action to protect water quality. The majority of any sedimentation would be filtered out before it reaches suitable habitat, reducing the likelihood for adverse indirect effects. Upland erosion and stream sediment values were determined by following the DBNF Aquatic Cumulative Effects Model (Walker, 2007). The model uses the Water Erosion Prediction Project (WEPP) developed by Elliott (2000). It was also based on erosion research by Dissmeyer and Stump (1978) and sediment delivery research by Roehl (1962). The model predicts that between 40 and 81 tons of sediment generated from all projects could reach aquatic habitats. This is a less than one percent increase in sediments over the current conditions from this project (indirect effect).

Sedimentation that does reach inhabitated streams would do so during rain events and would have diminishing impacts over space and time making sediment generated through the proposed actions very difficult to detect (Walker 2012)." (EA 3-75)

(Regarding Designated Critical Habitat)

"During commercial thinning operations, there would be no direct effects to designated critical habitat as there would be no skidding or landing in this habitat or the buffering riparian corridors. Temporary haul roads would be located on ridge tops. Skid trails would be located on ridge tops or benches using pre-existing roads where possible. No temporary haul roads or skid trails would be located in riparian corridors. Riparian corridors are excluded from timber harvest. There would be a buffer of 50 feet for intermittent streamcourses and 100 feet for perennial streamcourses, or the width of the 100 year floodplain, whichever is greater, established to protect streamcourses within riparian corridors. Design criteria are incorporated as part of the proposed action to protect water quality. The majority of any sedimentation would be filtered out by the riparian corridors before it reaches streamcourses, reducing the likelihood for adverse indirect effects to designated critical habitat." (EA 3-78)

"The likelihood of indirect effects from sedimentation is reduced through the application of design criteria, the distance between the proposed actions, and the amount of actions implemented at any one time (year). Any sedimentation produced as a result of the proposed action that does reach streams would do so during rain events and would have diminishing impacts over space and time making sediment generated through the proposed actions very difficult to detect from that of the normal baseline (Walker 2012)." (EA 3-79)

Group One Redbird River Project (2008)

"Aquatics Macro-invertebrate: Any effects on macroinvertebrates would primarily be indirect through changes in water quantity and quality (sedimentation and suspended particulate matter). Each sub-watershed that would contain a proposed ground disturbing action has been evaluated (See Appendix B). The largest projected increase in water yield would be 3.6% in Lower Jacks Creek. The yields for all others are projected at less than this. The highest projected rate of sedimentation would be for Little Double Creek and Lower Jacks Branch. The tons per decade found in Table B-2 represents only soil movement off-site. It does not represent the amount reaching an active stream channel. The amount of

> sediment actually reaching an active stream is very minor. Locally observed field conditions show that the effects of soil disturbance on water quality, even during and after storm events, is minor." (EA-48)
>
> "Snuffbox – This mussel is found in one known location downstream from the confluence of Sugar Creek and the Red Bird River. The effects of the project on water yield and sediment yield are projected to be minimal (see Section 4.2.2). Completing this project may impact individuals but is not likely to cause a trend toward federal listing or a loss of viability." (EA-57)
>
> "Table 27 summarizes the effects of stream sedimentation from the proposed actions. This alternative would produce 121.6 tons/year of stream sedimentation in the lower Red Bird River watershed. This represents a 9.5 percent increase over current conditions. This increase in stream sedimentation can be attributed mainly to skid trails, landings, and temporary haul roads within the commercial harvest areas. This sedimentation would be greatest immediately after harvest and will return to pre-harvest levels in 3 to 6 years. However, due to buffer strips and Best Management Practices (e.g. seeding, water bars, and skid road/temporary road closures) it is anticipated that there is less than a 50 percent probability that sediment will actually be delivered to the stream channels. It is unlikely that changes of this magnitude will influence water quality in the Red Bird River. Due to closures, it is also unlikely that user-developed OHV trails will increase as a result of this proposal." (EA-67)

5. Plan Amendment Would Increase, Not Decrease, Wet Weather Timber Harvesting

The Draft EA and supporting documents state that the proposed Plan Amendment would allow for a reduction in harmful impacts to soils and waters by shifting more timber harvesting activities to drier parts of the year. The Draft EA states:

> The Proposed Action seeks to balance the habitat of threatened and endangered species with watershed health and productivity. Adjusting tree felling dates will aid soil and water resource protection. The reduction of harvesting and other ground-disturbing activities in wet weather should decrease erosion and compaction, which should support healthier soils, less potential stream sedimentation, better aquatic habitat, healthier vegetation, and better habitat for the bats we are protecting. These changes to the Forest Plan will strengthen soil and water protection. (EA-18)

However, the proposal actually calls for a substantial *increase* in wet-weather logging over the status quo. This truth is obfuscated by the fact nowhere in the Draft EA or supporting documents is there information on how much timber harvesting has actually been taking place on the Daniel Boone, or at what times of year. The Draft EA states only that "The Proposed action will not increase vegetation management volume extracted identified in the 2004 Forest Plan" (EA-24). This, in itself, is a significant omission that needs to be corrected. Based on previously published data, we estimate that about 900 acres per year of timber harvest have been occurring on the Daniel Boone over the last decade, though your staff has said that it is actually less than this amount.

The Biological Assessment (BA) states:

> Tree removal activity could occur on approximately 5,500 acres annually and would occur during two timeframes. From April through October approximately 3,500 acres may be treated and the remaining 2,000 acres treated during November through March. (BA-71)

Because the Draft EA has failed to provide basic data on actual timber harvest acres and seasonality, we have to make some general calculations based on available data and reasonable assumptions. Based on the information in the BA (above), the Forest Service anticipates that approximately 36% of timber harvest could occur during the November through March wet season. Assuming that this seasonal proportionality is similar to the status quo, that would mean that less than 327 acres of timber harvest have been taking place each year during the November to

March wet season. Allowing for 2,000 acres to be harvested from November through March would constitute a roughly 600% *increase* in logging during the wet season.

At the recent public meeting, you stated that the Forest Service's general goal was to reach about 2,200 acres treated with timber harvest annually (not the 5,500 acres that would be allowable). Even at this lower level of timber harvest, there would still be an estimated 250% increase in logging during the wet season over the status quo.

Perhaps these numbers are off somewhat. We hope that you will provide clear and accurate data in a revised EA. But the fact remains that the Need for Proposal, and effects analysis, are based on the flawed (or misleading) statement that the proposed Plan Amendment will allow for a "reduction of harvesting and other ground-disturbing activities in wet weather," when, in fact, you are proposing a substantial increase in "harvesting and other ground-disturbing activities in wet weather."

In other words, we're looking at reducing protections for endangered bats while simultaneously proposing an *increase* in activities that you suggest are negatively impacting federally-listed aquatic species and their habitats. This is a problem.

6. Maternity colonies

We asked two related, important questions regarding maternity colonies in our scoping comments, and asked that they be addressed in the EA. They were not. Our questions were:

> 1) What are the current protocols for identifying maternity colonies or other active roosts? When during planning and harvest operations are surveys made, and by whom? What training is received by personnel to identify active roosts?
>
> 2) How often have maternity colonies been found in project areas? Following the identification of Indiana (and northern long-eared) bats, how did the Forest Service modify or delay specific projects and operations in order to comply with Forest Plan Standards? Please be specific.

The closest answer comes at EA-24:

> Specific summer bat survey information is limited across the Forest, therefore the Daniel Boone National Forest assumes presence across all forested habitat for several forest dwelling bat species. All forest-dwelling bats use forested habitat for daytime roosting and nighttime foraging from April through November.

At the public meeting held in Berea on March 26, 2019, we asked specifically what, if any, protocols were being used by the Forest Service to survey for Indiana bats. The response was that there are not any current protocols or survey efforts under way, but that something was being developed. However, current Plan Standard DB-WLF-9 says that the Forest Service should have been surveying for bat occupancy for felling that occurs from October 15 through March 31.

> DB-WLF-9. For non-vegetation management projects, currently suitable Indiana bat roost trees may be felled only from October 15 through March 31, if they are more than five miles from a significant bat caves (Indiana bat). If tree removal occurs at other times, the trees must be evaluated for current Indiana bat use, according to U.S. Fish and Wildlife Service protocol.

DB-WLF-10 has similar language, but for areas within 5 miles of significant bat caves. The Forest Service needs to address in detail whether and how these surveys have occurred.

The Draft EA also predicates the adequacy of a 150 ft. buffer around maternity colonies on the existence of surveys to identify roost trees:

> Known Indiana maternity roost trees and roosts documented during surveys or site specific project implementation will be protected with a 150-foot buffer year-round (DB-WLF-6). Any northern long-eared bat roost trees documented during surveys will be protected thru the Final 4(d) Rule. (EA-24)

Again, what surveys? If you have no protocol in operation for surveys, how will maternity roost trees and other roosts be protected?

The proposed Plan Amendment would reduce protections for maternity colonies – and therefore nonvolant pups – by reducing the buffer for logging from 2.5 miles to 150 feet. As discussed in the Draft EA and BA, "Many bats exhibit site fidelity and return to the same general areas each year" (EA-24). This is particularly true for maternity colonies.

> Many bats exhibit site fidelity and return to the same general areas each year. Indiana and northern long-eared bats are known to move between roost trees throughout the season (O'Keefe & Loeb 2017, Carter 2003, USDI-FWS 2007a, 2007b). The same can be said for other forest dwelling bat species. Known Indiana maternity roost trees and roosts documented during surveys or site specific project implementation will be protected with a 150-foot buffer year-round (DB-WLF-6). Any northern long-eared bat roost trees documented during surveys will be protected thru the Final 4(d) Rule. Known Indiana bat maternity habitat is considered 2.5 miles from known maternity roost tree or 5 miles from a juvenile or reproductive female captured between May 15 and August 15. The Proposed Action prohibits tree removal for new construction activities within maternity habitat during June and July without prior consultation with USFWS. Standard DB-WLF-5 ensures there will be no direct effects to non-volant pups in these project locations. (EA-24)

As discussed in the BA, bats will return to the same general area for maternity roosts each summer. Because suitable roost trees are temporary, bats will move among trees in a general area. The size of this "territory" is not clear from the literature, and not discussed in the Draft EA or BA. The purpose of the 2.5 mile buffer around maternity colonies is, ostensibly, to account for the fact that maternity colonies will not always be in the same previously identified tree, but will likely be in the same larger area.

And, as discussed in the BA, white nose syndrome has created new hurdles beyond mortality during winter hibernation. Bats that survive winter hibernation are severely depleted and may struggle during spring staging, migration to summer habitat, and successfully raising their young.

> These effects are compounded because most returning bats are coming from hibernacula infected with white-nose syndrome (WNS). Individuals surviving WNS have additional energetic demands. For example, WNS-affected bats have less fat reserves than non-WNS-affected bats when they emerge from hibernation (Reeder et al. 2012; Warnecke et al. 2012) and have wing damage (Reichard and Kunz 2009, Meteyer et al. 2009) that makes migration and foraging more challenging. Females that survive the migration to their summer habitat must partition energy resources between foraging, keeping warm, maintain a successful pregnancy, rearing pups, and healing their own bodies. (BA-75)

Given that the proposed Plan Amendment has been "developed to address changes in science applicable to the management of bat habitat," and that new science suggests new stressors from WNS, it is contrary to the purpose of the of the proposal to reduce, rather than increase, protections that support bats in establishing and maintaining maternity colonies.

The proposal does add the following:

> DB-WLF-5. Tree cutting is prohibited during June and July within known maternity habitat for new construction projects unless consultation with USFWS is conducted. Examples of new construction sites include new system roads, trails, recreation, and administrative sites that would result in permanent loss of habitat.

This proposed Standard is confusing, because it disallows tree cutting for “new construction,” which, presumably, would only affect a small number of trees and areas (probably no more than dozens of trees), but does allow for tree cutting during this period for logging projects, which would probably include the cutting of hundreds or thousands of trees. Disallowing the cutting a few trees for trail construction while allowing the cutting of thousands of trees for other timber management is arbitrary and capricious and not justified by any new science or reasonable rationale.

At the March 26, 2019 meeting it was stated that maternity colony buffers on the DBNF were based on previous surveys. It is possible, even probable, that the identified roost trees are no longer standing, and that the maternity colonies are utilizing other suitable trees in the general area. But the DBNF is not surveying for them. If the maternity colony buffer is dropped from 2.5 miles to 150 feet, and that 150 feet protects only formerly utilized or existing roost trees, then the maternity colony is not protected.

Absent mandatory, clearly defined, and rigorous surveys in new project areas, reducing maternity colony buffers from 2.5 miles to 150 feet essentially removes all protections for maternity colonies on the DBNF. This is not acceptable.

7. Spring Staging

As is discussed in the BA, the spring staging period for Indiana and northern long-eared bats is a critical juncture in their life cycle. At this time, bats are depleted of energy stores and must be able to forage and roost in their spring staging areas without hindrance. The BA also points out that white nose syndrome exacerbates the normal depleted state upon waking in the spring.

> These effects are compounded because most returning bats are coming from hibernacula infected with white-nose syndrome (WNS). Individuals surviving WNS have additional energetic demands. For example, WNS-affected bats have less fat reserves than non-WNS-affected bats when they emerge from hibernation (Reeder et al. 2012; Warnecke et al. 2012) and have wing damage (Reichard and Kunz 2009, Meteyer et al. 2009) that makes migration and foraging more challenging. Females that survive the migration to their summer habitat must partition energy resources between foraging, keeping warm, maintain a successful pregnancy, rearing pups, and healing their own bodies. (BA-75)

The proposal does not provide adequate protections for spring staging areas. The proposal would remove DB-WLF-11:

> Timber harvest will not occur on the DBNF within one mile of a known significant bat cave, or PETS bat staging cave (with the exception of the wooded grassland/shrubland habitat association), if this activity would result in more than 120 acres of forest less than 10 years of age on all ownerships (public and private)

And replace it with DB-WLF-8:

> DB-WLF-8. Timber harvest will not occur on the DBNF within one mile of a known P1, P2, P3, and Virginia big-eared bat hibernacula (with the exception of the wooded grassland/shrubland, woodland habitat association), if this activity would result in more than 120 acres of contiguous open forest less than 10 years of age on all ownerships (public and private) at the time of decision.

Foraging and roosting Indiana and northern long-eared bats use relatively mature forest. These conditions do not develop after 10 years. Generally, these are conditions that begin to emerge after >50 years on the DBNF (with true complex structure not occurring until >135 years). Even-aged forest of 15, 20, even 40 years of age will not provide suitable spring staging habitat for emerging Indiana and northern long-eared bats.

Furthermore, the new Standard changes the limit of no "more than 120 acres of forest less than 10 years of age" to no "more than 120 acres of *contiguous* open forest less than 10 years of age" (emphasis added). This is very problematic. The one mile radius from P1, P2, and P3 caves and Virginia big-eared bat hibernacula represents approximately 2,000 acres. Under the proposed Standard, most of that 2,000 acres could be logged, developed, or otherwise exist as unsuitable swarming habitat, and logging (including intensive, even-aged harvests) would still be consistent with DB-WLF-8. For example, DB-VEG-22 and DB-VEG-23 state:

> "The maximum size of a temporary opening created by even-aged or two-aged regeneration treatments is 40 acres" (DB-VEG-22)

And

> "Temporary openings created by even-aged or two-aged regeneration treatments will be separated from each other by a minimum of 330." (DB-VEG-23)

The document Public Meeting Map – March 26, 2019 (provided on the project page) shows a priority hibernacula in the South Redbird project area. That hibernacula has 436 acres of shelterwood logging proposed within the 1 mile buffer. That 1 mile buffer also includes 307 acres harvested since 1980 (under 40 years old), and about 40 acres of former strip mine land. Under the new Plan Amendment, 783 acres of the 2000 acre, 1-mile buffer around the maternity colony could be turned into unsuitable habitat. It's worth noting that this particular unit is also within a Critical Habitat unit for the Kentucky arrow darter.

In effect, under the newly proposed DB-WLF-8, all of any 2,000 acre spring swarming buffer could be logged without violating the Forest Plan because regeneration cuts would have thinned buffers, and therefore not be contiguous. The repercussions for endangered bats could be severe. DB-WLF-8 is simply not protective of endangered bats, and is essentially meaningless.

The Forest Service has not demonstrated that the proposed DB-WLF-8 is supported by existing science. The Standard should ensure a suitable acreage of forest representing high quality foraging and roosting habitat (forest > 50 years, mature canopies, complex structure, etc.) for forest dwelling bats during the especially vulnerable, post-hibernation period. We recommend that this Standard be changed to provide for a scientifically defensible total acreage of suitable staging and foraging habitat within the one mile radius around P1, P2, and P3 hibernacula. Even-aged logging for "balancing age classes" and future forests doesn't count as creating habitat for forest-dwelling bats just because it will grow up in the future.

8. Fall Swarming

The proposal would reduce the area protected from logging during the fall swarming season from 5 miles around priority hibernacula to ¼ mile. The existing Plan Standards state:

> DB-WLF-12. Within five miles of a significant Indiana bat hibernaculum, tree cutting is not to be conducted from September 1 through December 1.

And:

> 1.J-VEG-2. Do not permit tree-cutting activities from September 1 through December 1 within five miles of known significant Indiana bat hibernacula.

The above Standards are removed and replaced with:

> DB-WLF-7. Tree removal may not occur within ¼ mile of Hibernacula and Maternity Cave Prescription Area unless the purpose of the project is to protect or enhance microclimate of hibernacula, rare species, or rare communities.

We acknowledge and appreciate the restriction on logging within ¼ mile of Hibernacula and Maternity Cave Prescription Areas year-round. However, the BA states:

> Swarming 1 habitat is considered forested areas within 10 mile of P1-P2 hibernacula. Swarming 2 habitat is considered forested areas within 5 mile radius of P3-P4 hibernacula. (BA at 53)

The Forest Service has not demonstrated with any science that removing harvesting restrictions within 5 miles during the fall swarming season (when bats are mating) will not impact federally-listed bats.

9. Roost Trees

The Forest Service appears to be basing all changes to management for suitable roost trees on one study, O'keefe and Loeb, 2017. That study does recommend taking a landscape approach to roost tree management, as is stated at several points in the Draft EA and supporting documents. The main findings of the research were that, in the study area (which included the Cherokee National Forest in east Tennessee, the Nantahala National Forest in North Carolina, and Great Smoky Mountains National Park in TN and NC), Indiana bats preferentially used conifer (primarily shortleaf pine) snags. These findings suggest that there is considerably different roost tree selection behavior from the more Midwestern populations, which have been found to use live shellbark, shagbark, and red hickories, occasionally white oak, and a variety of dead hardwoods.

How these findings relate to roost tree selection in the DBNF is not clear. Our forests are intermediate in composition between the mountainous southern Appalachian forests in the study area and previously, more intensively studied Midwestern forests. Furthermore, the southern pine beetle has reduced the amount of available pine snag habitat in the DBNF (and pine is not terribly abundant in the Redbird District). The bottom line is that we really don't know what trees and sites are best suited to roosting Indiana and northern long-eared bats in the DBNF. However, the Draft EA does propose significant changes to management for roost trees, and does not back these changes up with studies or other data.

The proposal gets rid of most binding standards regarding the retention of roost trees and replaces them with the following, non-binding Guideline:

> DB-WLF-1. Ensure that Forest management maintains suitable roost trees across the entire forested landscape. Preference should be given in the following order: trees with a sheet of exfoliating bark, hickories (shagbark, shellbark, and red), and other live trees with cracks or crevices.

The Silviculture Resource Report similarly states:

> Under the Proposed Action the presence of snags and suitable roost trees would be analyzed across the landscape during site-specific project planning, and strategies would be assigned within stands to meet landscape-level habitat needs for threatened and endangered species. (Report at 7)

But the Draft EA and supporting documents do not discuss how snags and suitable roost trees would be "analyzed across the landscaping during site specific project planning" or what "strategies would be assigned within stands." Our experience has been that issues in the Forest Plan left to project- and site-specific surveys are not actually carried out adequately (or at all) during project planning and implementation. As you likely recall, this was a central issue in our comments and objection to the Greenwood Vegetation Management Project (relating to rare plants and rare community surveys).

We note here that the proposed amended definition for suitable roost trees for Indiana bats states that they "will have a dbh of 5 inches." The Silviculture Report also appears to rely on the presence of 5" dbh snags for meeting landscape-level habitat needs for Indiana bats.

> Recent Forest Service Forest Inventory and Analysis (FIA) data shows that on average there are ten snags per acre across the Forest (USFS FIA, 2018). In addition, FIA data for the Forest estimated over one-million trees over five inches in diameter dying annually (USFS FIA, 2018). This data shows that new snags are constantly being recruited by the annual mortality of live trees across the Forest. (Report at 4)

However, O'keefe and Loeb, 2017, which is cited as the scientific basis of many of the proposed changes to roost tree management, states:

> During harvests, retaining patches of large snags (≥35 cm dbh, with ≥12 snags/0.1 ha) and buffering such patches with live trees to protect them from wind throw may benefit Indiana bats in this area.

Thirty-five centimeters is 13.8 inches, not 5 inches.

10. Cave protections

The BA makes the claim that:

> "All DBNF caves and abandoned underground mines are closed thru regional closure order: FS-RO-08-01-2014; CFR 261.53(a), (b), and (d)." (BA at 52)

This statement is made more than once, and it suggests protections that do not exist. Caves and underground mines are indeed (and properly) under a closure order. However, they are not "closed" as there have been no additional barriers put in place, and many caves do not have signage telling people that there is a closure order in effect. Last year we were fortunate to join USFWS and DBNF staff during a winter bat surveys, and it was clear that one of the ungated caves we visited had been recently used recreationally. No signage regarding the closure was posted.

The effect of the statements and omissions is to imply that winter habitat for *Myotis* species, and year-round cave habitat for *Corynorhinus* species, are protected through administrative actions. Our observations are that they are not.

11. Stream Restoration

During the March 26, 2019, the issue of stream restoration was emphasized by DBNF staff, due to the difficulty in cutting trees for these projects given current Plan Standards. It seems a reasonable, rather simple alternative to create exemptions for the very limited amount of tree cutting associated with the very limited amount of stream restoration occurring on the DBNF. If stream restoration is indeed a major driver for this proposal, then the specifics of an exemption for this type of action should be considered and analyzed. Specifically, how much stream restoration work is occurring (or is anticipated to occur) on the DBNF? How many trees are typically cut (or are projected to be cut) for these projects? Certainly the number of trees to be cut for stream restoration annually would be several orders of magnitude fewer than the number of trees that would be cut to harvest timber on 2,200 to 5,500 acres, with very limited opportunity for incidental take. These actions need to be separated out in the proposal and analysis.

12. Restoration of Abandoned Mine Lands

The Soil and Water Report states that existing Plan Standards have been an impediment to the restoration of abandoned mine lands. To our understanding, restoration of abandoned mine lands typically includes ripping of compacted soils and planting of trees – not the cutting of forest and removal of potential roost trees. The Forest Service needs to explain how the existing Standards stymie restoration work on abandoned mine lands if this issue is to be used as a justification for eliminating or reducing forestwide protections for endangered bats. The Forest

Service must be specific about actions, acres of forest impacted, number of trees cut, etc. Similar to the issue of stream restoration, we suspect that a narrow exemption could be crafted for the very limited amount of abandoned mine restoration work happening that could result in take or otherwise negatively impact federally-listed bats.

13. Red Maple

The Silviculture Report states:

> Under the No Action Alternative, it is likely that in some stands it may be impossible to conduct treatments to move existing conditions towards desired future conditions due to the overabundance of undesirable species such as red maple that have characteristics of immediate roost trees, and must be retained due to existing Forest Plan Standards. It is also likely that the current Standards requiring retention of immediate roost trees may lead to losses in stand volume, decline in species diversity within Forest communities, future dominance by undesirable species such as red maple, and reduction in overall Forest health. (Report at 6)

And:

> The Proposed Action would allow land managers to focus snag retention and roost tree development across the landscape where they are most needed. Increased flexibility within site-specific project planning would ensure that snags and roost trees are maintained across the landscape where they are most needed (O'Keefe & Loeb 2017). This transition towards snag and roost tree management across the landscape would allow for overall increases in species diversity, and forest health due to the ability to be more flexible in forest stand prescriptions. It also allows for more holistic treatments that encourage the development of desirable species across the landscape, rather than encourage the development and retention of undesirable species such as red maple, that may be more vulnerable to decay, as we have observed in the No Action alternative. (Report at 7)

The issue of red maples was also raised by DBNF staff at the March 26, 2019. The issue is that existing Standards require that the Forest Service leave too many red maples in stands managed with midstory removal or commercial harvests, thus encouraging potential red maple dominance. The Forest Service could much more easily craft a narrow exemption to allow the removal of red maples. This would be a relatively simple change.

We look forward to continuing our dialogue over this proposal, and hope that you will ultimately make a Decision that supports our imperiled bat species.

Sincerely,

Jim Scheff

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Formulating an Expanding-Gap Regeneration System for *Quercus* Dominated Stands

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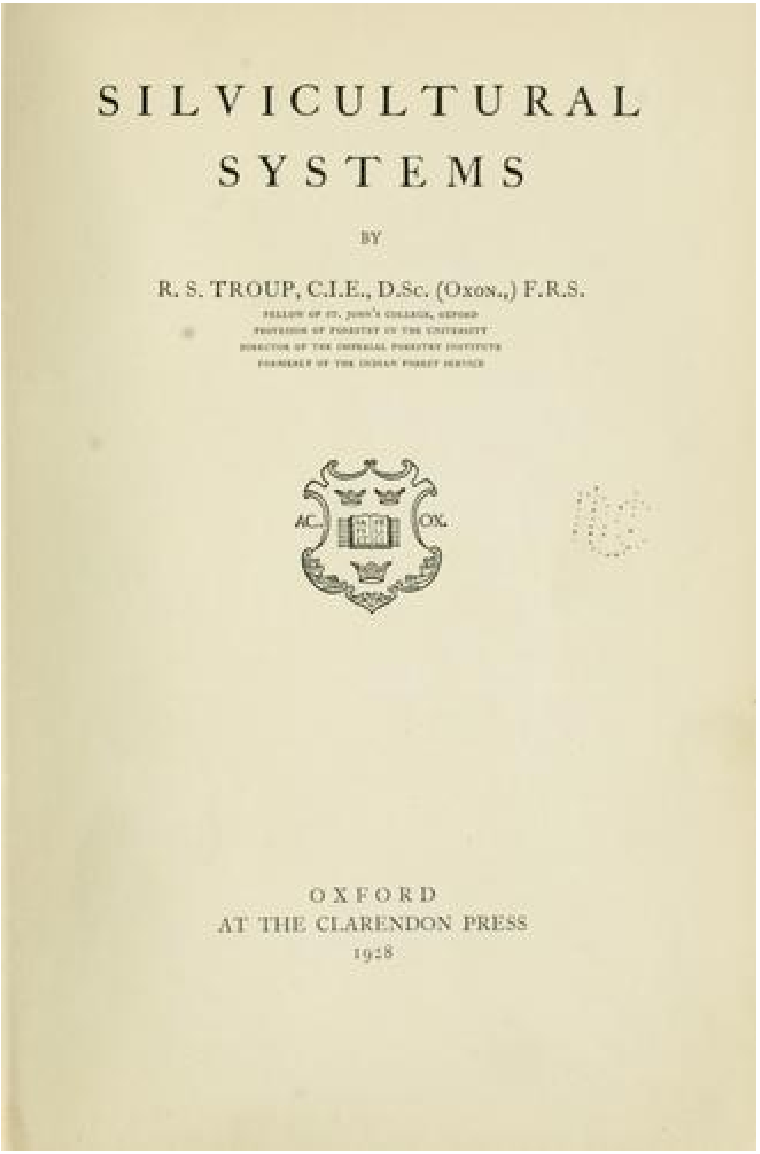
Presentation Outline

- What is an irregular shelterwood system?
- Rational for applying an irregular shelterwood system in *Quercus* stands
- “Proof of concept” study and future exploration

Historical Context



SILVICULTURAL
SYSTEMS

BY

R. S. TROUP, C.I.E., D.Sc. (Oxon.,) F.R.S.

OXFORD
AT THE CLARENDON PRESS
1928

Historical Context

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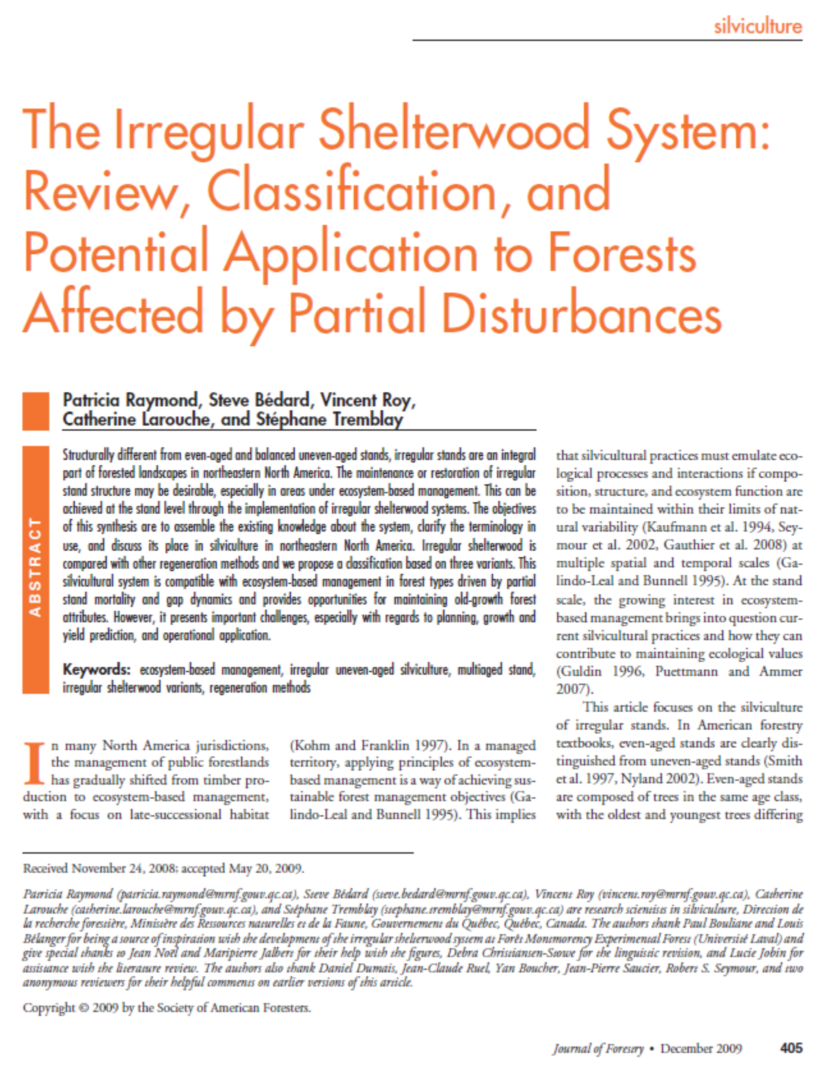

The Irregular Shelterwood System: Review, Classification, and Potential Application to Forests Affected by Partial Disturbances

Patricia Raymond, Steve Bédard, Vincent Roy, Catherine Larouche, and Stéphane Tremblay

ABSTRACT

Structurally different from even-aged and balanced uneven-aged stands, irregular stands are an integral part of forested landscapes in northeastern North America. The maintenance or restoration of irregular stand structure may be desirable, especially in areas under ecosystem-based management. This can be achieved at the stand level through the implementation of irregular shelterwood systems. The objectives of this synthesis are to assemble the existing knowledge about the system, clarify the terminology in use, and discuss its place in silviculture in northeastern North America. Irregular shelterwood is compared with other regeneration methods and we propose a classification based on three variants. This silvicultural system is compatible with ecosystem-based management in forest types driven by partial stand mortality and gap dynamics and provides opportunities for maintaining old-growth forest attributes. However, it presents important challenges, especially with regards to planning, growth and yield prediction, and operational application.

Keywords: ecosystem-based management, irregular uneven-aged silviculture, multiaged stand, irregular shelterwood variants, regeneration methods

In many North America jurisdictions, the management of public forestlands has gradually shifted from timber production to ecosystem-based management, with a focus on late-successional habitat (Kohm and Franklin 1997). In a managed territory, applying principles of ecosystem-based management is a way of achieving sustainable forest management objectives (Galindo-Leal and Bunnell 1995). This implies that silvicultural practices must emulate ecological processes and interactions if composition, structure, and ecosystem function are to be maintained within their limits of natural variability (Kaufmann et al. 1994, Seymour et al. 2002, Gauthier et al. 2008) at multiple spatial and temporal scales (Galindo-Leal and Bunnell 1995). At the stand scale, the growing interest in ecosystem-based management brings into question current silvicultural practices and how they can contribute to maintaining ecological values (Guldin 1996, Puettmann and Ammer 2007).

This article focuses on the silviculture of irregular stands. In American forestry textbooks, even-aged stands are clearly distinguished from uneven-aged stands (Smith et al. 1997, Nyland 2002). Even-aged stands are composed of trees in the same age class, with the oldest and youngest trees differing

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Irregular Shelterwood System Defined

Three general classifications:

- Expanding-gap irregular shelterwood
- Continuous cover irregular shelterwood
- Extended irregular shelterwood

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107(8):405-413.

Irregular Shelterwood System Defined

Expanding-gap irregular shelterwood -

“Aims to regenerate new cohorts in groups that are gradually enlarged until the stand is totally removed”

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107(8):405-413.

Irregular Shelterwood System Defined

Continuous cover irregular shelterwood –

“Sequence of cuttings is applied more freely in space and time, which permits maintenance of a multicohort structure and a continuous forest cover ”

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107(8):405-413.

Irregular Shelterwood System Defined

Extended Irregular Shelterwood –

“Aims to regenerate the whole stand while … two cohorts are maintained for at least 20% of the rotation length”

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. Journal of Forestry 107(8):405-413.

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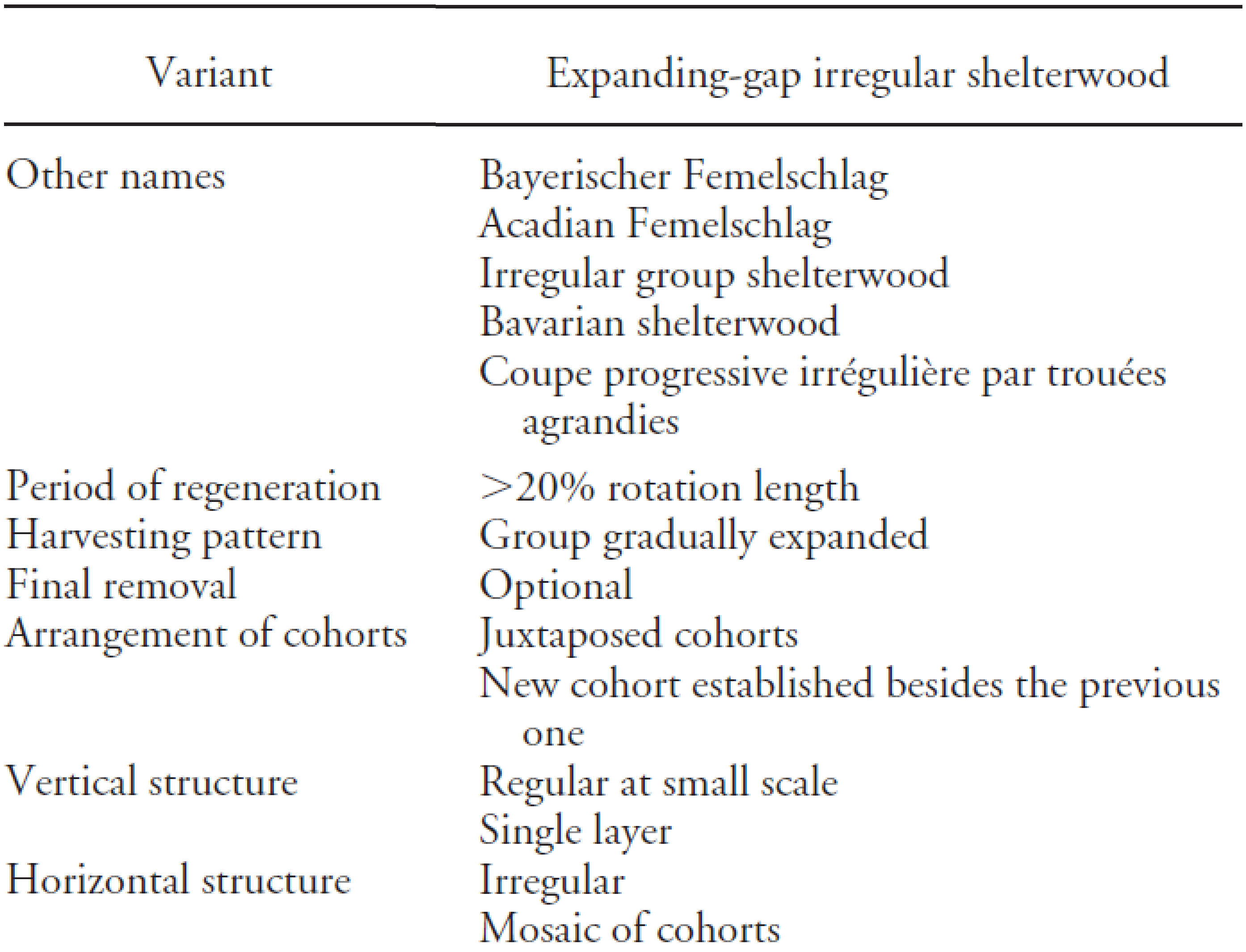
Expanding-gap irregular shelterwood



Variant	Expanding-gap irregular shelterwood
Other names	Bayerischer Femelschlag Acadian Femelschlag Irregular group shelterwood Bavarian shelterwood Coupe progressive irrégulière par trouées agrandies
Period of regeneration	>20% rotation length
Harvesting pattern	Group gradually expanded
Final removal	Optional
Arrangement of cohorts	Juxtaposed cohorts New cohort established besides the previous one
Vertical structure	Regular at small scale Single layer
Horizontal structure	Irregular Mosaic of cohorts

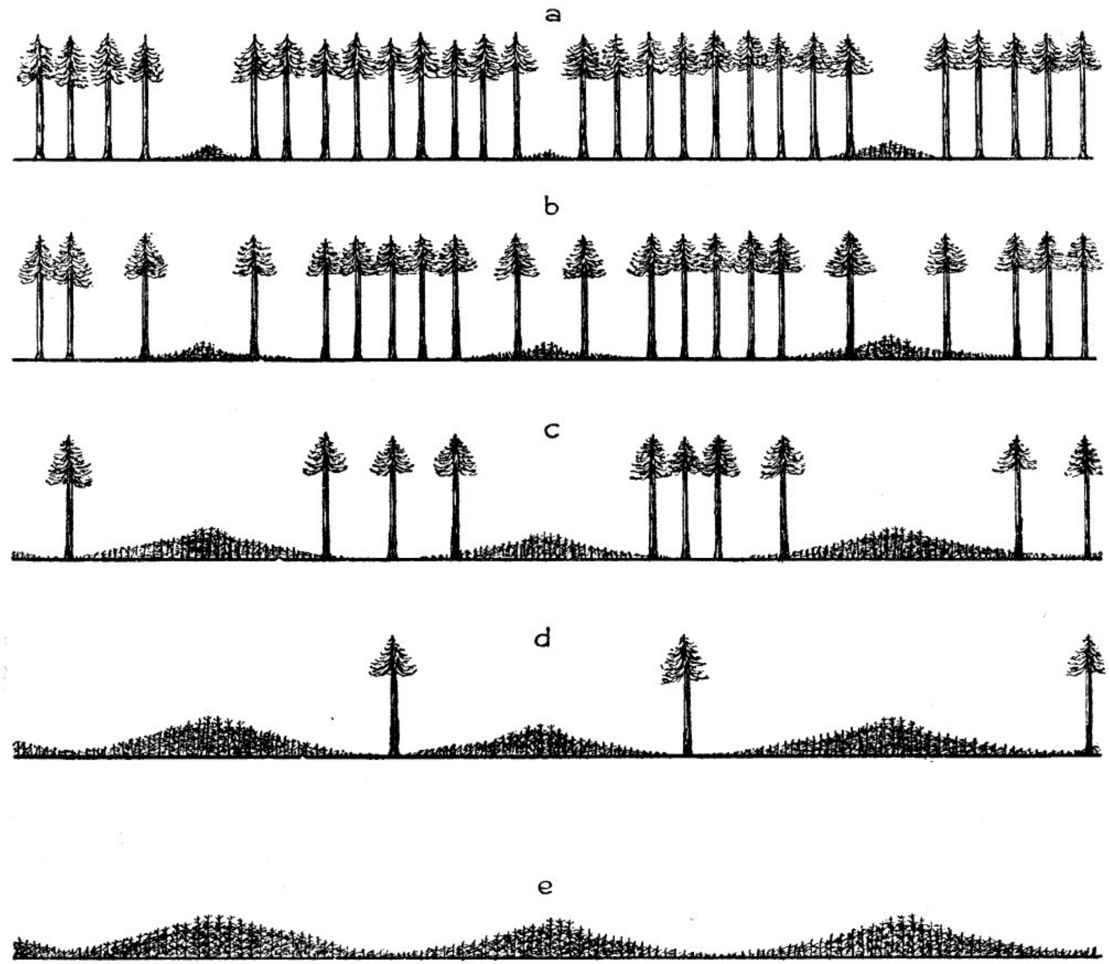
Irregular Shelterwoods and *Quercus* Forests

- *Femelschlag* systems are used throughout Europe
- While interest is gaining, no examples of expanding-gap irregular shelterwoods exist in North American oak forests
- Potential benefits of expanding-gap systems include:
  1. Structural complexity and continuous forest cover
  2. Multiple income flows over rotation
  3. Regeneration of diverse species groups, from shade intolerants in gap centers to intermediates and shade tolerants along gap edges

Research Goal

Our long-term goal is to develop an expanding-gap based silvicultural practices that address the oak regeneration problem present within the Central Hardwood Forest Region (CHFR)

Research Needed for System Development



Source: Troup 1928

Research Needed for System Development

Developing a expanding-gap regeneration system requires understanding of how the following factors influence spatial variation in resource gradients and regeneration dynamics:

- Gap size
- Edge effects
- Canopy structure in the forest matrix

Research Needed for System Development

Developing a expanding-gap regeneration system requires understanding of how the following factors influence spatial variation in resource gradients and regeneration dynamics:

- Gap size
- Edge effects
- Canopy structure in the forest matrix

This presentation integrates results from complementary research studies that together support the basis for applying expanding-gap regeneration systems in oak dominated stands

Research Studies

Gap Size

Lhotka (In Press) tested the effect of three gap sizes on oak recruitment 48 years following treatment

Edge Effects

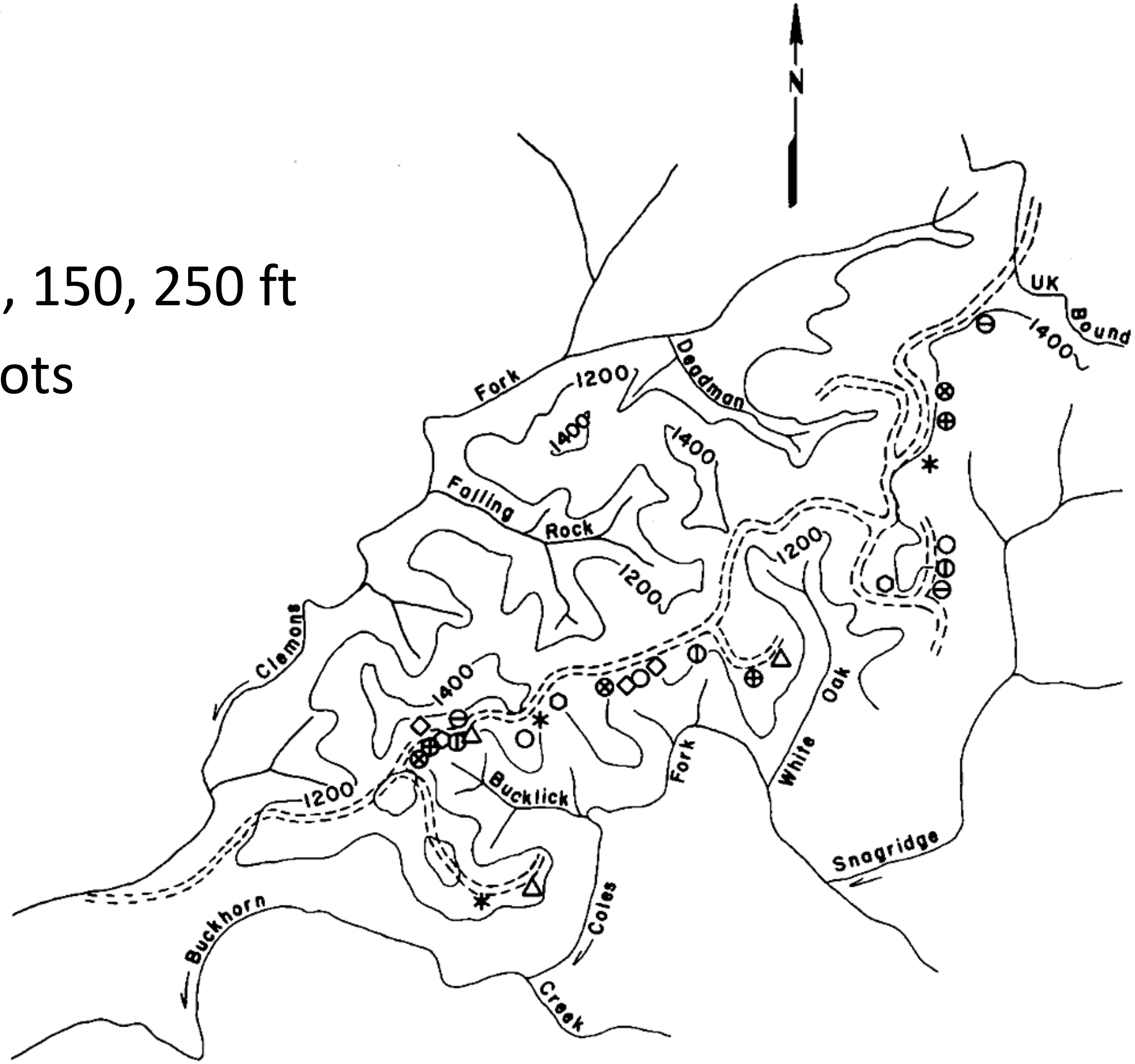
Lhotka and Stringer (In Review) characterized the relationship between distance from anthropogenically created edge and the height and density of oak reproduction

Midstory Removal

Parrott et al. (In Press) evaluated the effect of midstory removal on understory light availability and oak seedling survival and growth after 7 growing seasons

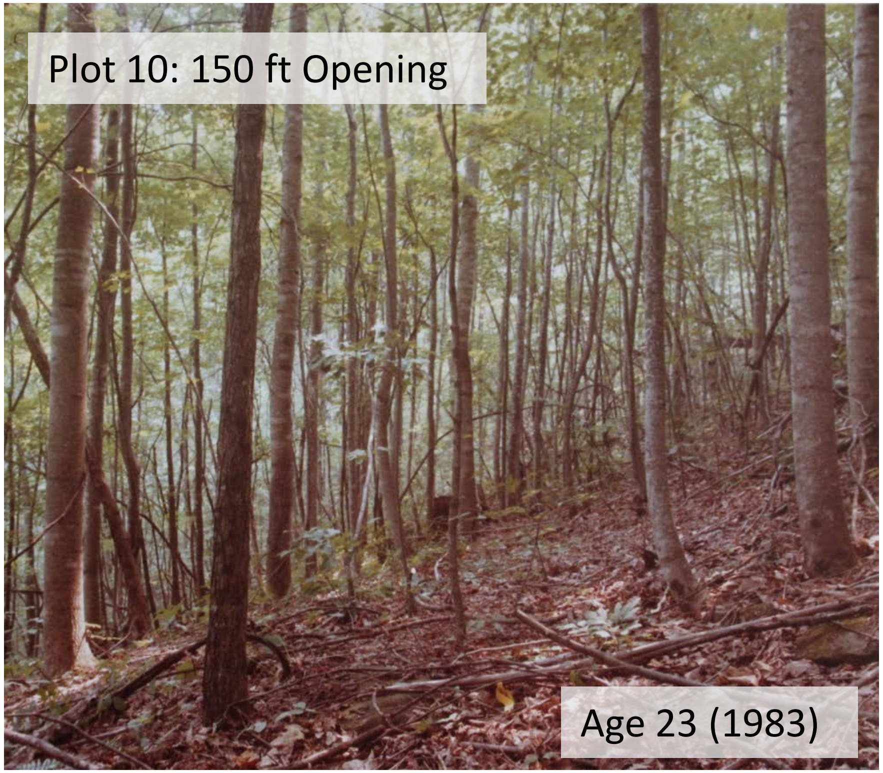
Robinson Forest Gap Size Study

- Established 1960
- Three gap sizes: 50, 150, 250 ft
- 27 experimental plots



Robinson Forest Gap Size Study

Hill and Muller (UK): 1981, 1985, 1987
USDA Forest Service: 1991


Plot 10: 150 ft Opening

Age 23 (1983)

Lhotka: 2008
*Thanks to Matt Strong


Plot 10: 150 ft Opening

Age 48 (2008)

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Robinson Forest Gap Size Study - Results

Stand Structure after 48 Years

Opening Size	BA $(m^2\ ha^{-1})$	Trees (ha^{-1})	QMD (cm)	Top Height (m)
50	12.2^{a*}	1008.2^{a}	12.2^{a}	19.8^{a}
150	21.1^{b}	953.7^{a}	17.0^{b}	26.6^{b}
250	21.6^{b}	719.1^{a}	19.7^{c}	28.6^{b}

*Means with similar letters are not statistically different ($\alpha = 0.05$)

Robinson Forest Gap Size Study - Results

Overstory Trees ha^{-1} by Treatment following 48 Years

Species Group	Opening Size		
	50 ft	150 ft	250 ft
Oak	27.4^{a*}	89.3^{b}	49.5^{b}
Maple	82.2^{a}	51.4^{a}	52.4^{a}
Yellow-poplar	0^{a}	39.3^{b}	50.4^{b}
Hickory	12.1^{a}	4.7^{a}	2.9^{a}
Other Commercial	6.1^{a}	2.7^{a}	4.9^{a}
Other	9.1^{a}	5.4^{a}	3.4^{a}

*Means within a species group that have similar letters are not statistically different ($\alpha = 0.05$)

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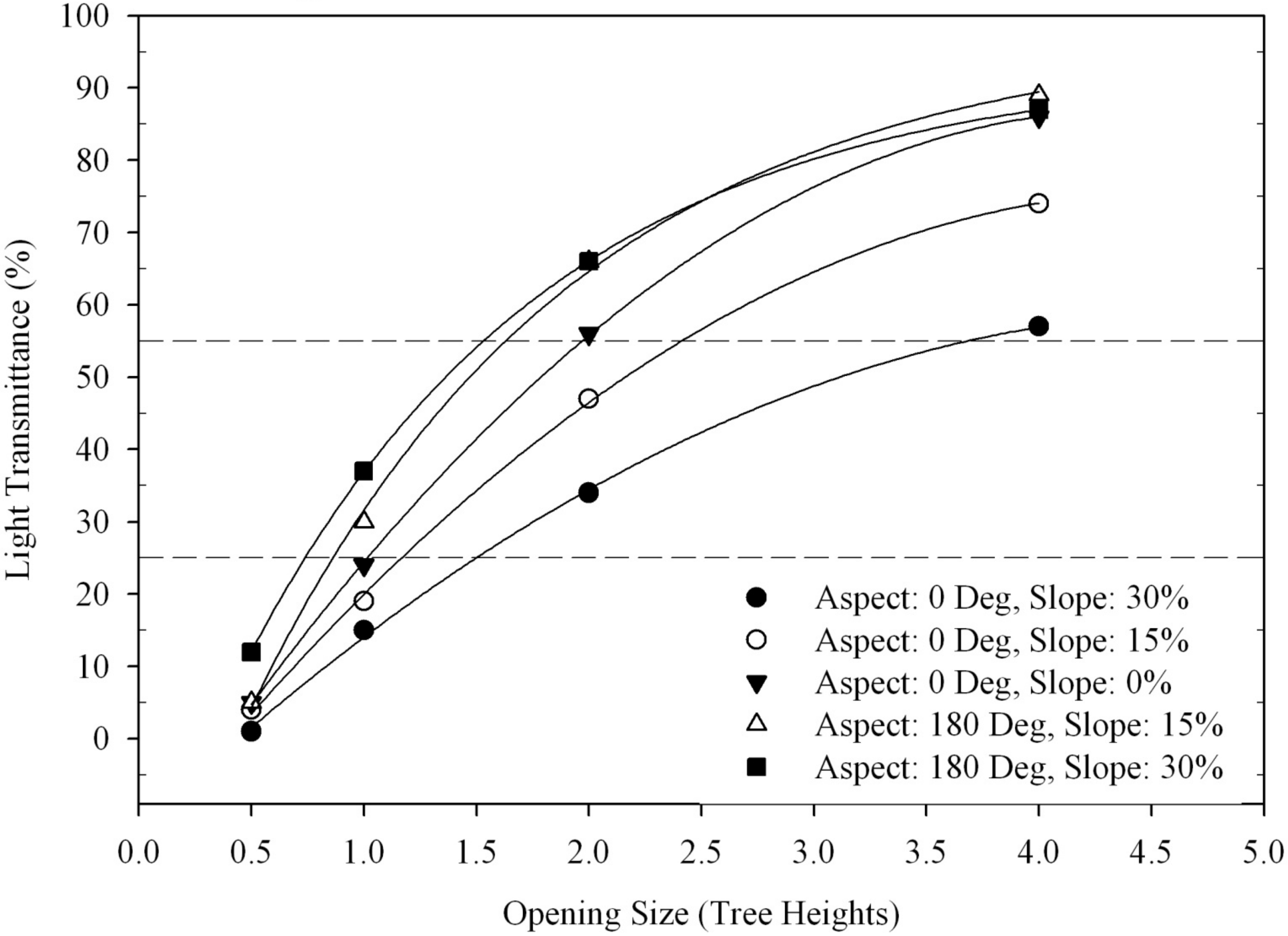
Robinson Forest Gap Size Study - Summary

Size of opening influenced structure and composition and apparent trends suggest:

- 50 ft opening favored maple
- Dominant and codominant oak density was “maximized” in 150 ft opening
- Yellow-poplar increased with larger opening sizes

Gap Size Study : Role of Light in Species Trends

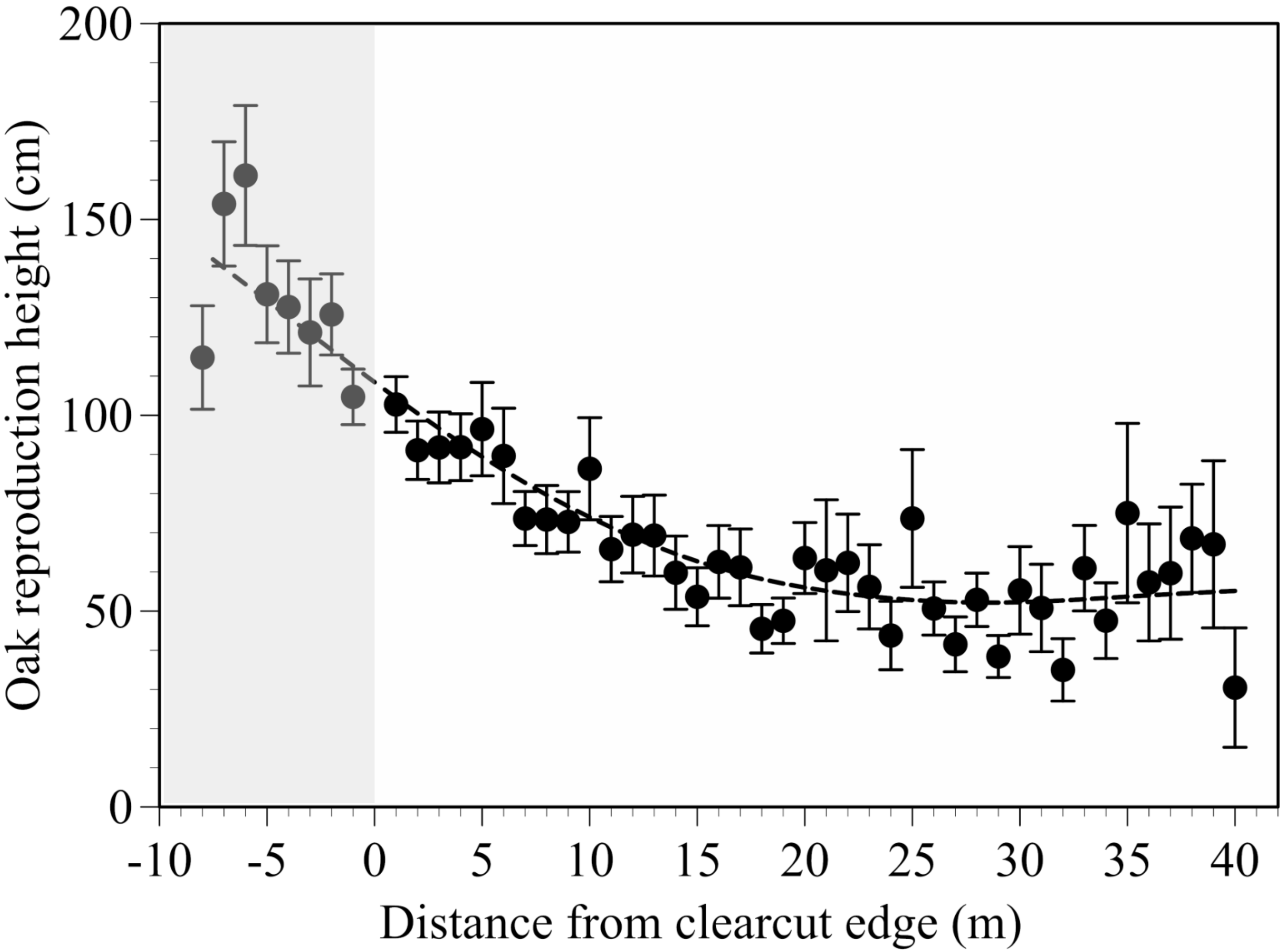
From: Fischer, B.C. 1981. Designing Forest Openings of the Group Selection Method.
SO-GTR-34. pp 274-277.



Berea Forest Edge Effects Study

- Initiated by Lhotka and Stringer in 2011
- Goal was to further understanding of how forest edge influences the development of advance reproduction along the gradient extending from a regeneration opening into adjacent, intact forest areas
- 48 m transects surround to 9-year-old clearcuts on Berea College Forest

Berea Forest Edge Effects Study – Seedling Heights



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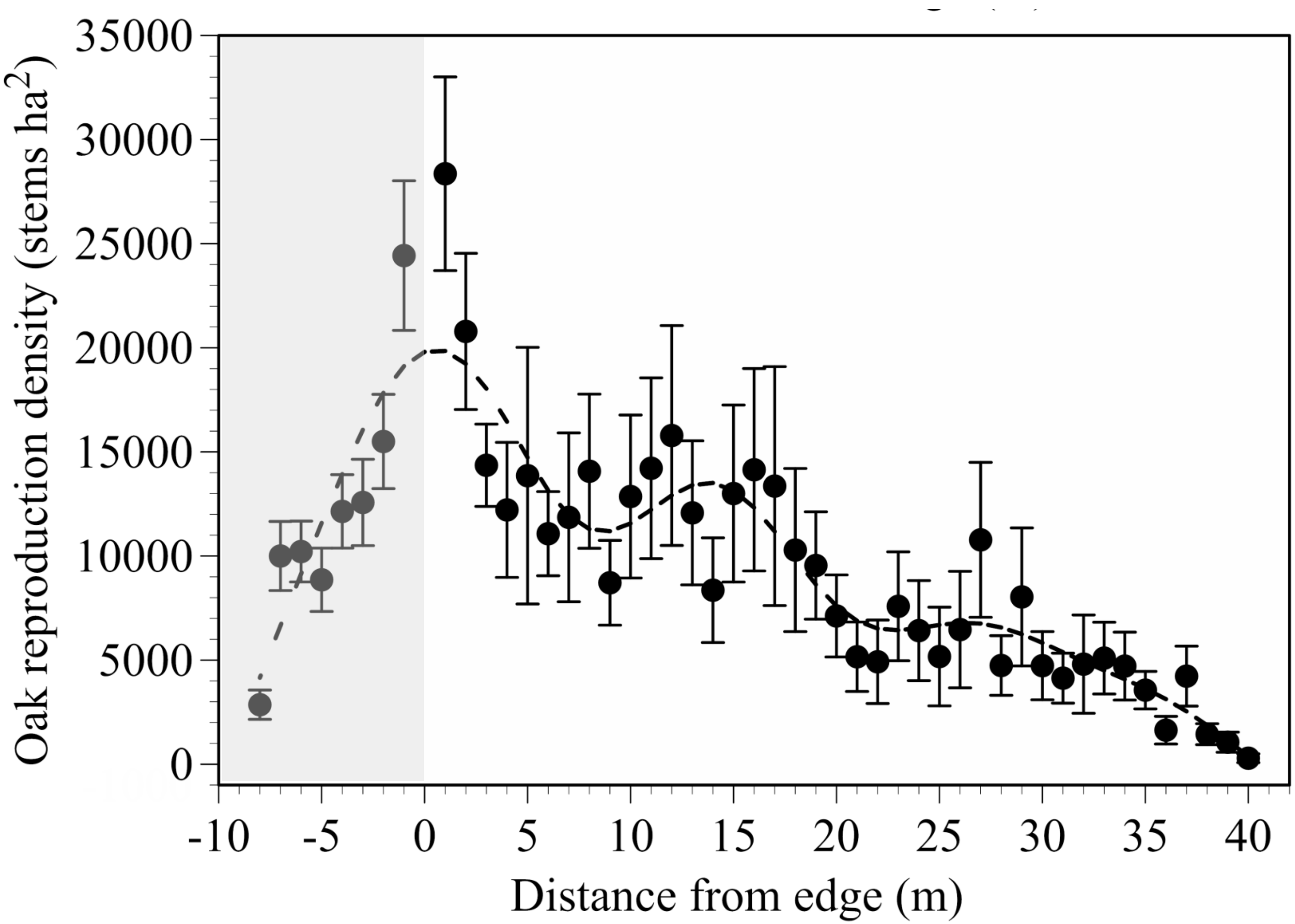
Berea Forest Edge Effects Study – Seedling Density



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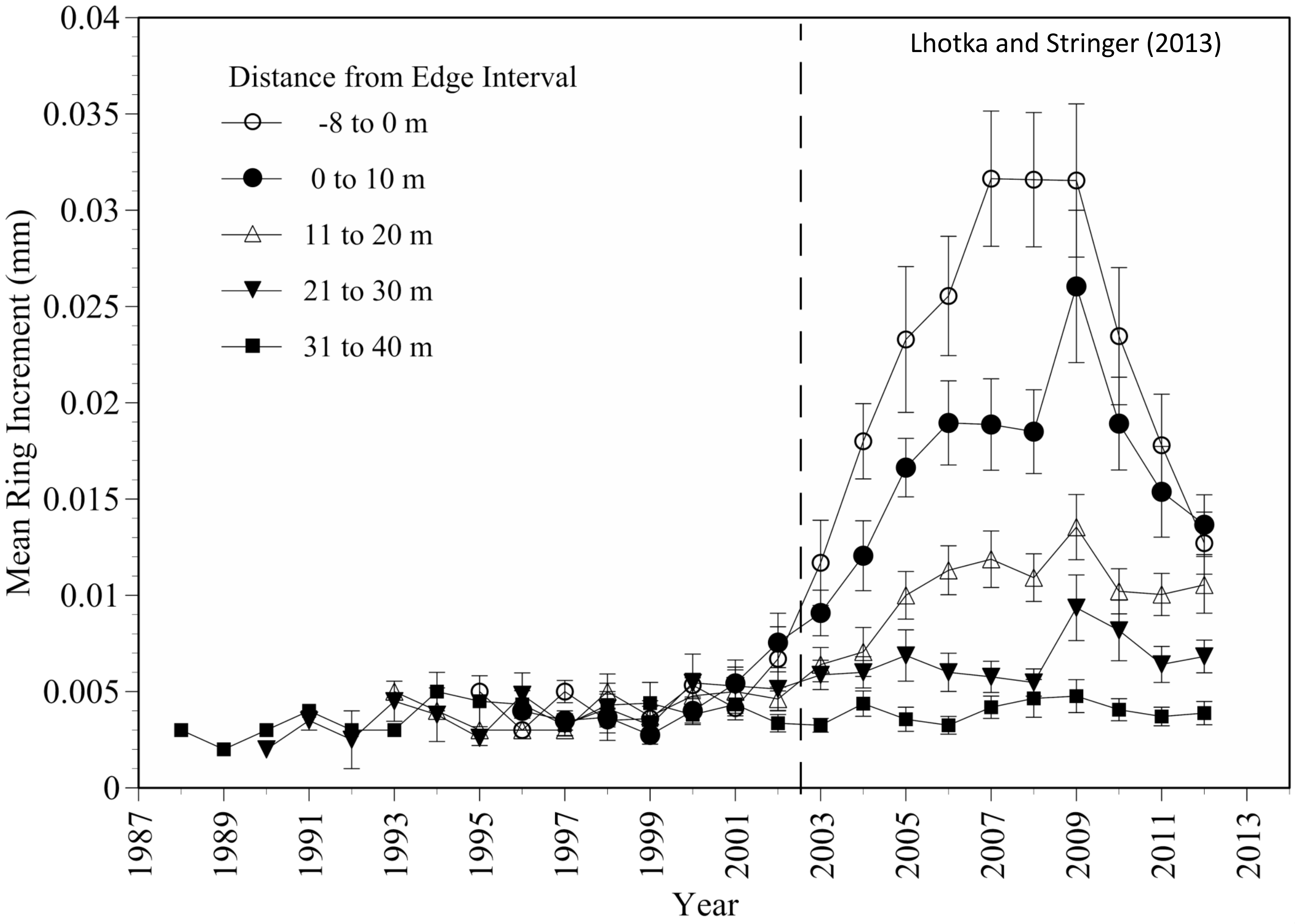
Edge Environment: Seedling Radial Growth



Berea Forest Edge Effects Study - Summary

Data indicate that environments associated with forest edges can increase the size and density of oak reproduction and that the edge influence may extend up to 20 m

Berea Midstory Removal Study

- Initiated by Dillaway and Stinger (2004)
- 4 sites, Berea College Forest
- Midstory removal treatment (20% basal area reduction)
- Natural advance reproduction and underplanted seedlings
- Monitored 7 years
- Understory microclimate characterized

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Berea Midstory Removal Study - Results

- Midstory removal increased understory light availability
  - Removal 10.3% full sunlight
  - Control 1.5% full sunlight

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Berea Midstory Removal Study – Results

Seven-year natural and underplanted seedling responses to midstory removal (Parrott et al. In Press)

	Natural Reproduction			Underplanted	
	Black Oak	White Oak	Red Maple	Black Oak	White Oak
Survival (%)					
Control	---	70.4*	80.6*	15.7*	46.0*
Midstory Treatment	---	85.9*	87.9*	45.8*	78.3*
Mean height (cm)					
Control	52.3	28.9 *	41.6 *	37.4	31.0 *
Midstory removal	77.1	45.3 *	69.8 *	51.4	46.3 *
Mean GLD (mm)					
Control	8.5	4.7 *	6.5 *	7.0 *	7.4 *
Midstory removal	13.0	7.8 *	10.1 *	9.9 *	9.1 *

Developing a expanding-gap regeneration system

Understanding factors that influence spatial variation in resource gradients and regeneration dynamics:

- Gap size
- Edge effects
- Canopy structure in the forest matrix

An Expanding-Gap Approach for Oak

What about gap size?

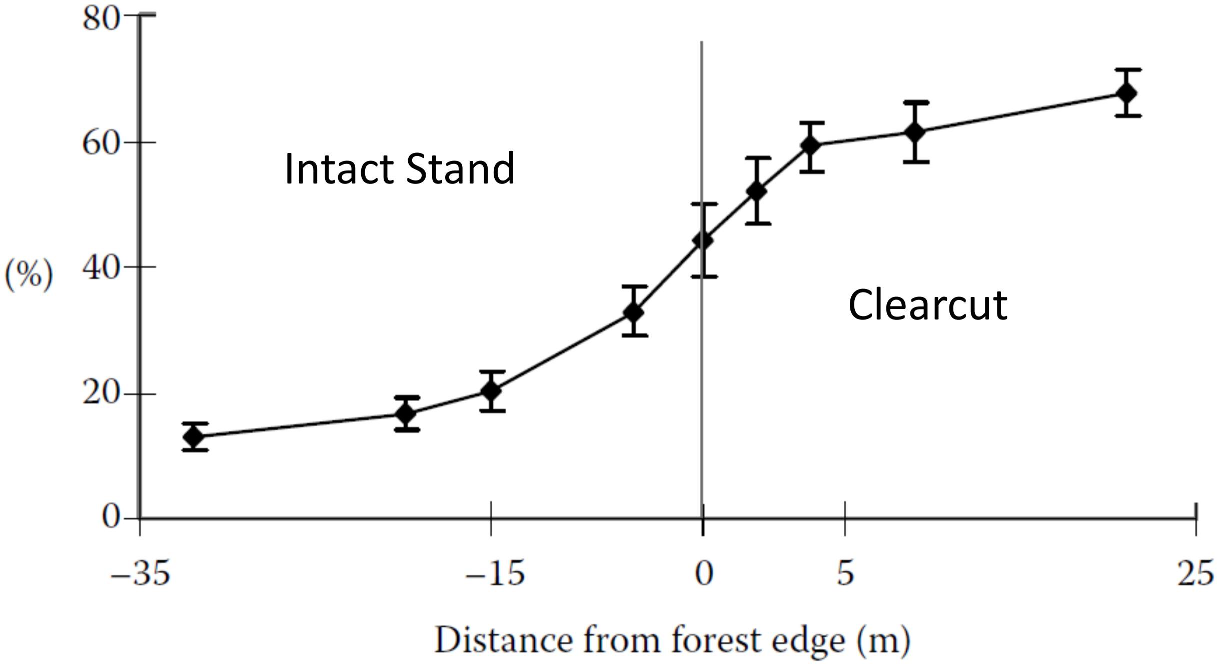
An Expanding-Gap Approach for Oak

What about gap size?

Research indicates that silvicultural gaps 1.5 to 2.5 times the dominant tree height can:

1. Improve oak recruitment within gaps
2. Create edge environments that may increase density and height of oak reproduction in the adjacent forest matrix

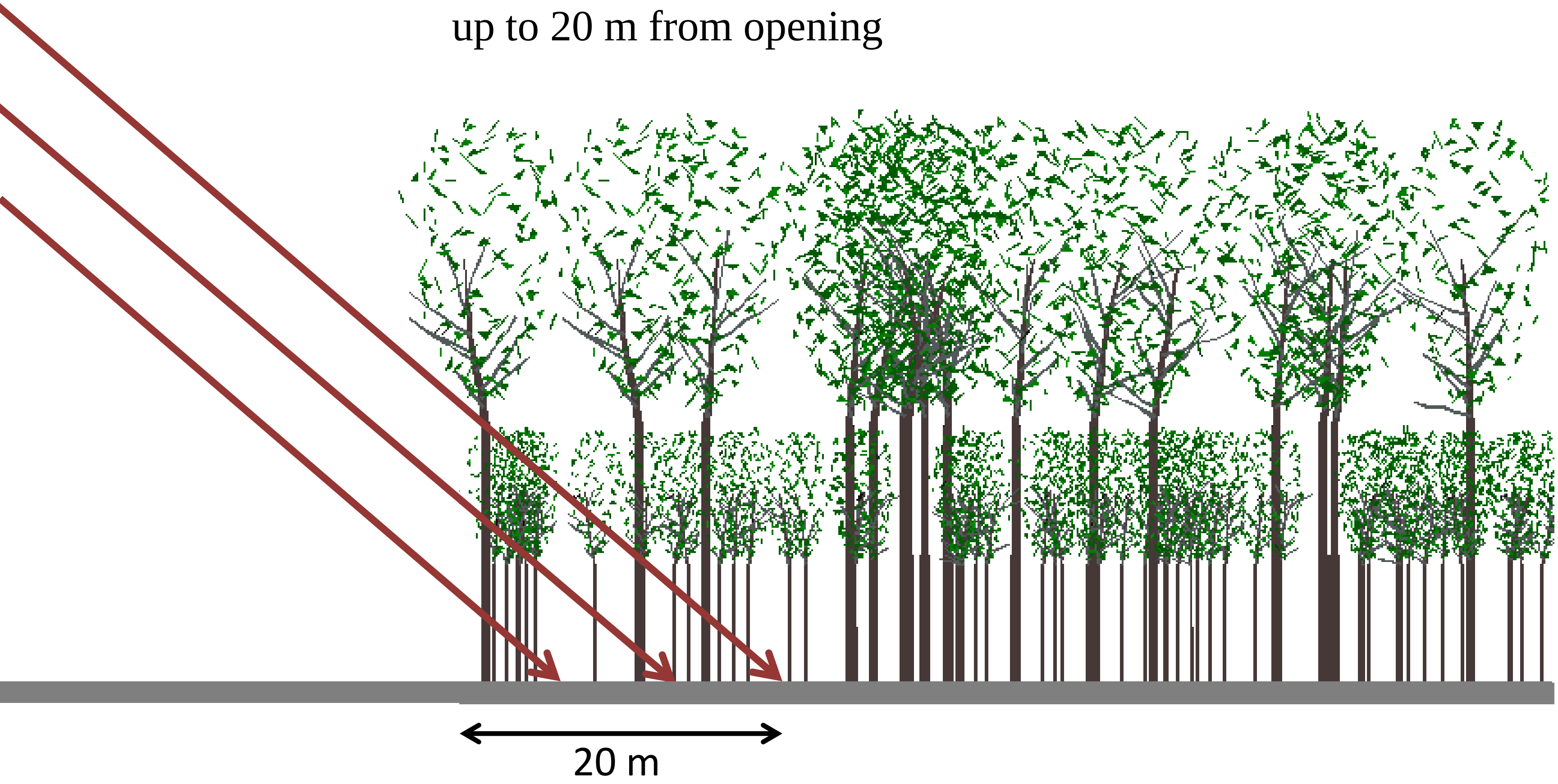
What about edge effects and forest structure in matrix?



Schmid, I., K. Klumpp, and M. Kazda. 2005. Light distribution within forest edges in relation to forest regeneration. Journal of Forest Science 51(1):1-5.

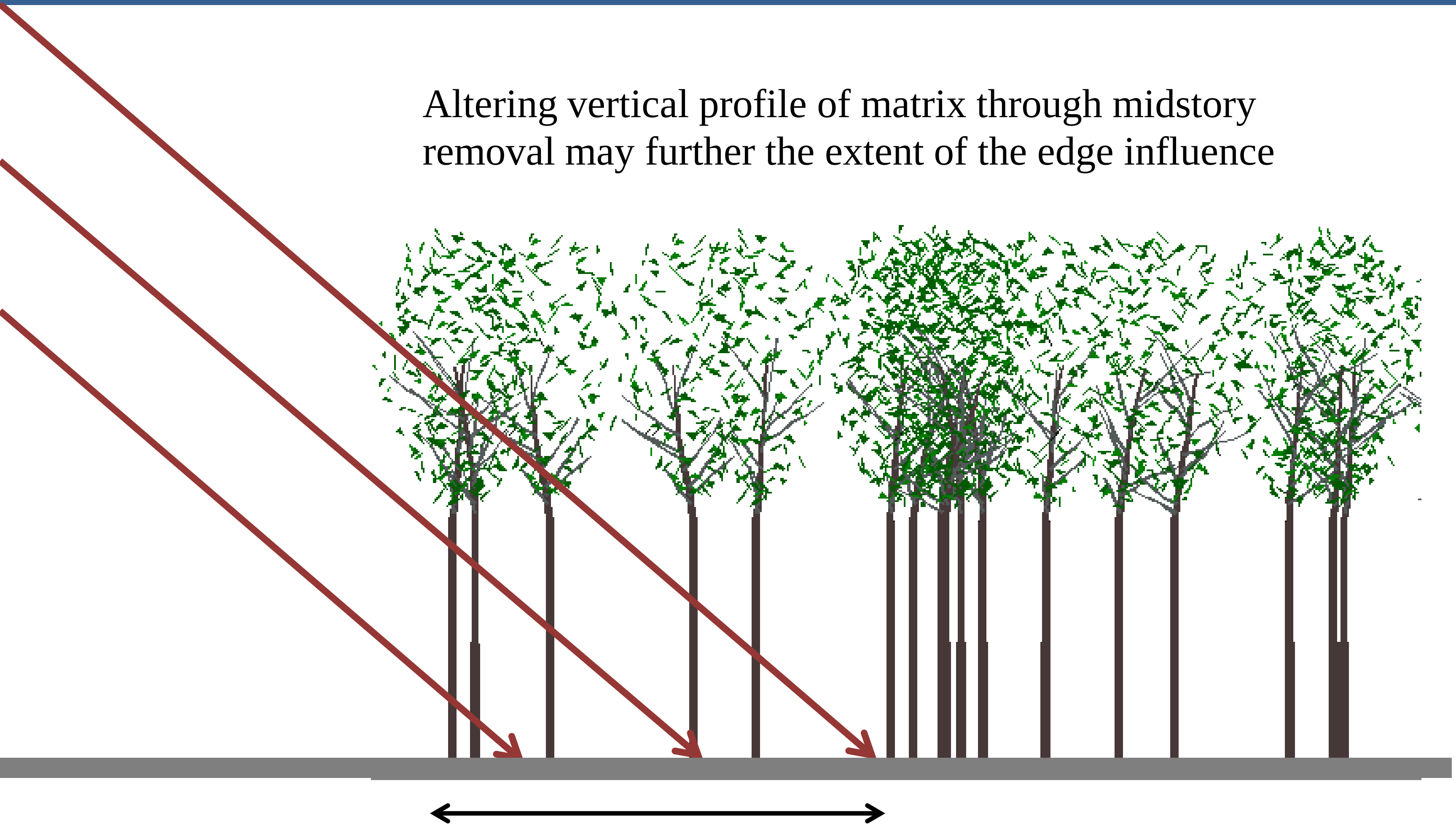
What about edge effects and forest structure in matrix?

Environmental effects of forest edges on oak may extend up to 20 m from opening



What about edge effects and forest structure in matrix?

Altering vertical profile of matrix through midstory removal may further the extent of the edge influence



Estimated to be 30 m

An Expanding-Gap Approach for Oak

What about edge effects and forest structure in matrix?

Removal of midstory canopies around silvicultural gaps may:

1. Improve oak survival and growth in areas to be released during subsequent gap expansions
2. Extend the enhancement effect of the edge environment on oak reproduction further in the forest matrix

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An Expanding-Gap Approach for Oak

An expanding-gap irregular shelterwood that uses intermediate gap sizes and midstory removal as a preparatory treatment around gaps may represent a novel silvicultural practice for increasing oak regeneration potential within the CHFR

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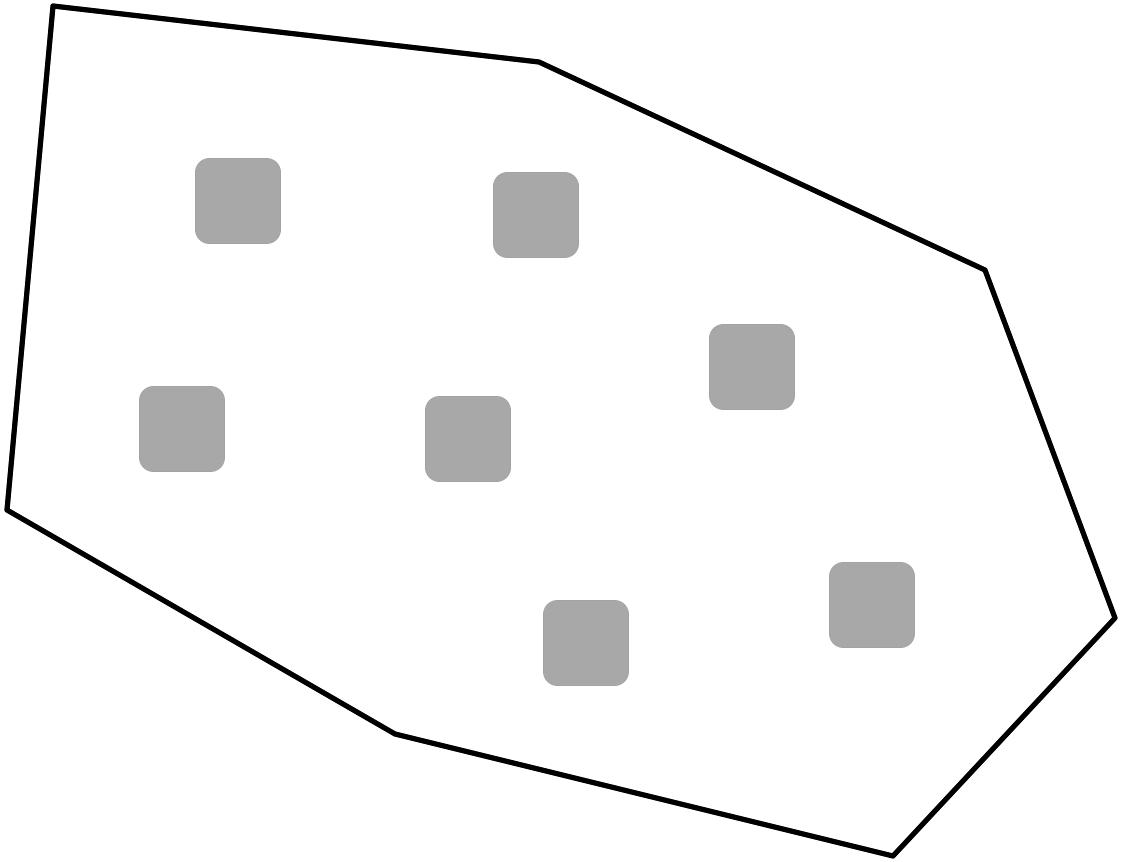
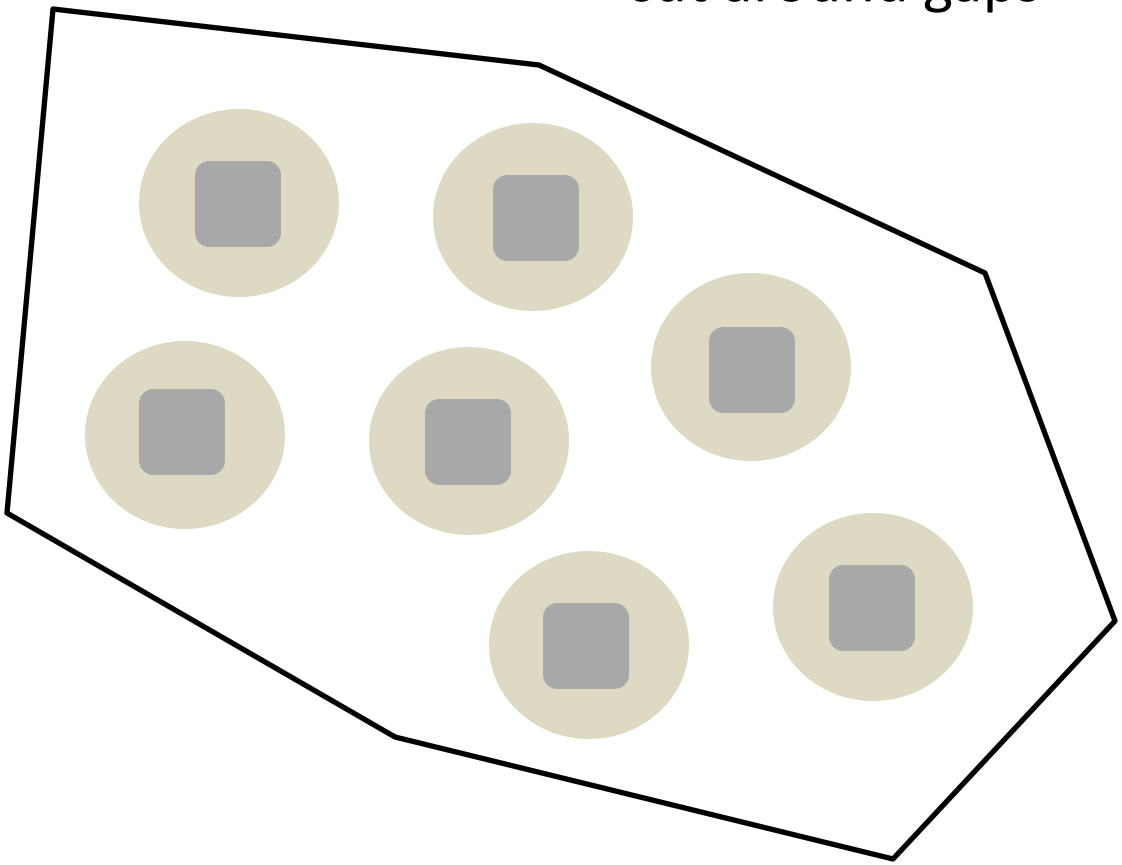
Expanding-Gap Irregular Shelterwood for Oak

Initial Gaps: 1.5 to 2.5 tree heights

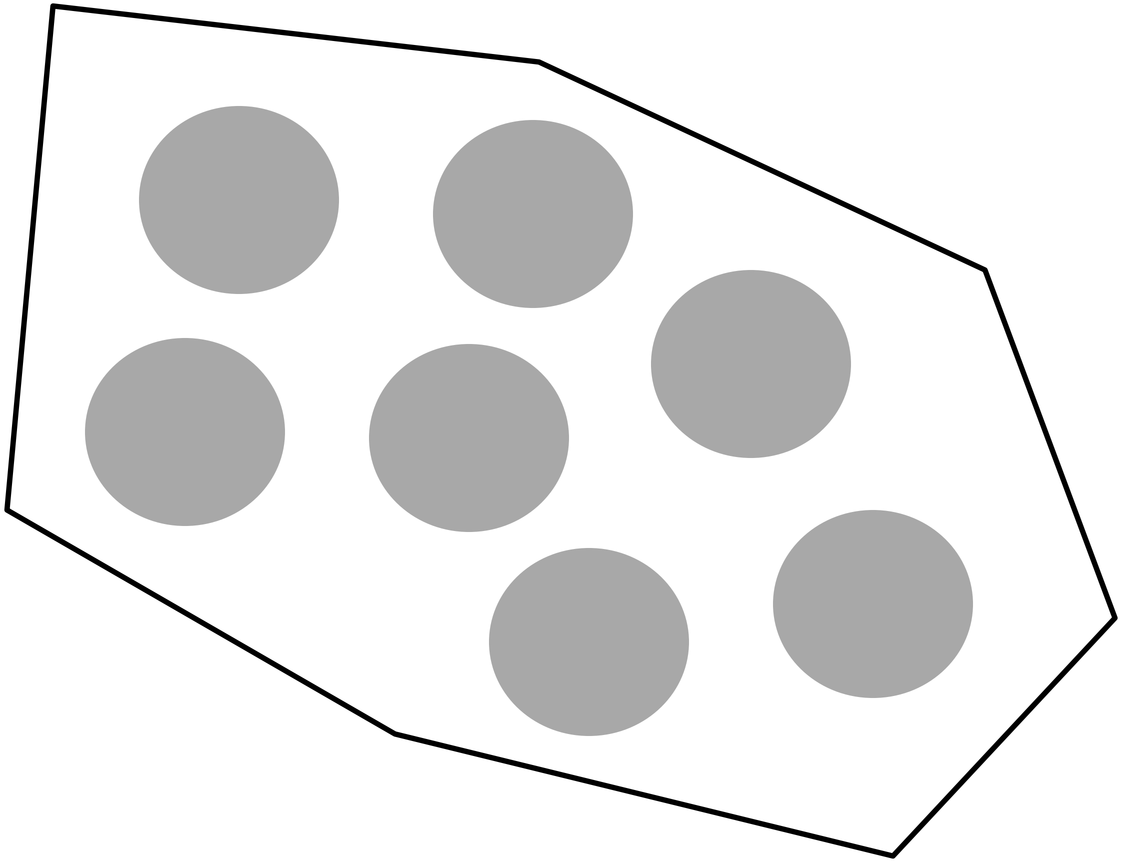


Expanding-Gap Irregular Shelterwood for Oak

Midstory removal as preparatory cut around gaps



Expanding-Gap Irregular Shelterwood for Oak



Subsequent gap expansion into midstory removal areas based upon oak reproduction development

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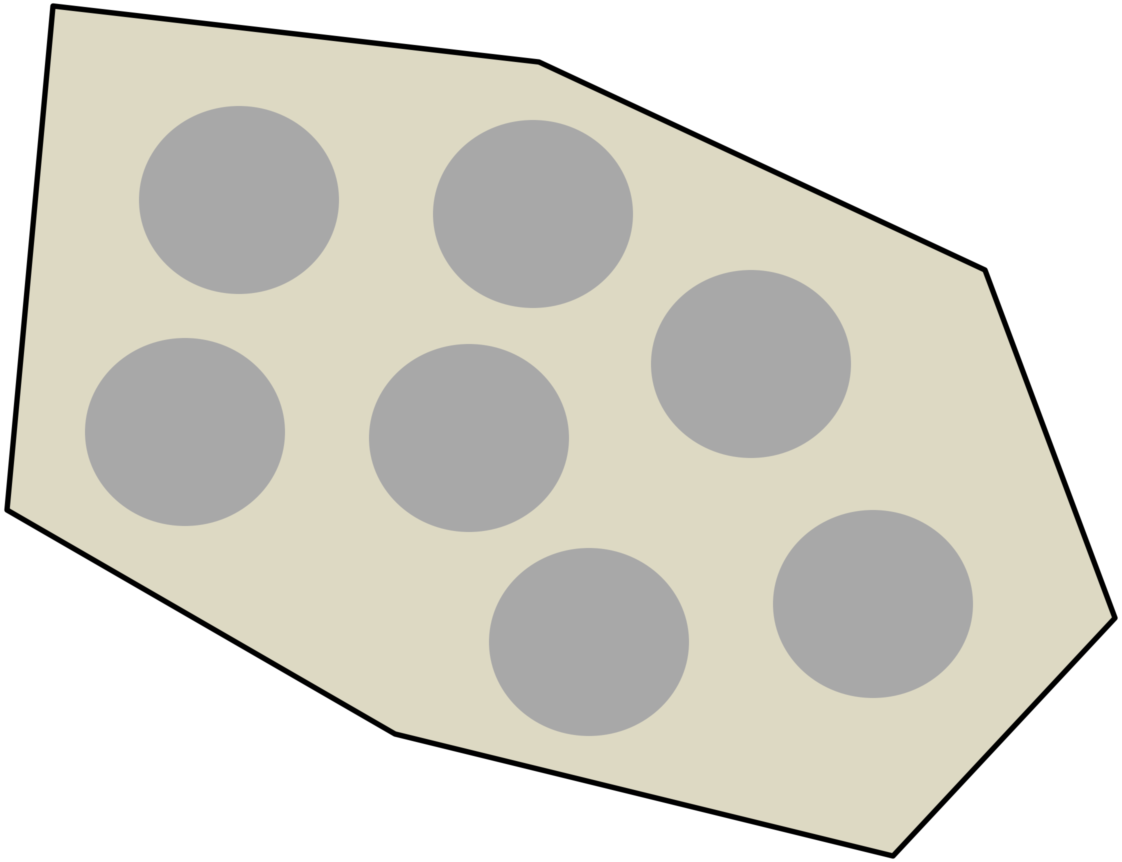
Expanding-Gap Irregular Shelterwood for Oak



Midstory removal following gap expansions

Berea Forest - Proof of Concept Study

- Expanding-gap Study
  - Lhotka, Stringer, Patterson
  - 12 replicated gaps
  - Two treatments
- Research foci:
  - Establishment and growth dynamics
  - Light transmittance modeling

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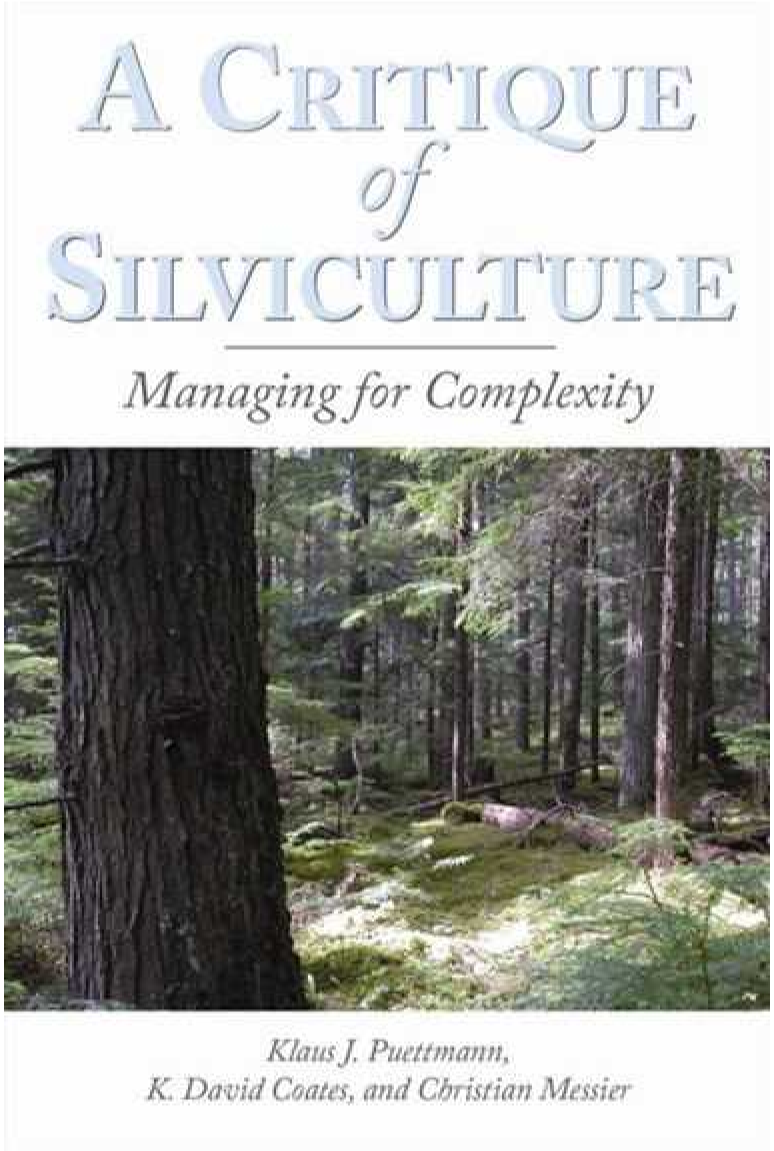
Future Extensions



A CRITIQUE
of
SILVICULTURE

Managing for Complexity

Klaus J. Puettmann,
K. David Coates, and Christian Messier

PRODUCTIVITY OF EARLY SUCCESSIONAL SHRUBLAND BIRDS IN CLEARCUTS AND GROUPCUTS IN AN EASTERN DECIDUOUS FOREST

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Abstract: Uneven-aged forest management has been advocated as a silvicultural practice because of concerns about the negative effects of even-aged management on birds that dwell in mature forests. Recent evidence, however, indicates that in the northeastern United States, bird species that inhabit early successional habitats may be experiencing more widespread declines than their mature-forest counterparts. We compared the effect of group selection, a widely used form of uneven-aged forest management, and clearcutting on nest survival rates of early successional shrubland birds in the White Mountains of New Hampshire. There was no difference in daily nest survival rate between clearcuts (0.990) and groupcuts (0.987) for 16 bird species combined ($n = 290$), and no difference in daily nest survival rate between clearcuts (0.993) and groupcuts (0.987) for chestnut-sided warblers (*Dendroica pensylvanica*), the only species for which enough nests were found for separate analysis ($n = 217$). There was no difference in daily nest survival rates of all species combined between edge (0.983) and interior areas (0.992) of clearcuts ($n = 204$), and no difference in daily nest survival rates of chestnut-sided warblers between edge (0.984) and interior (0.993) areas of groupcuts ($n = 156$). Thus, our results suggest that clearcuts and groupcuts provide similar habitat for species of early successional shrubland birds that inhabit both clearcuts and groupcuts. Recent studies, however, indicate that some bird species that use larger openings such as clearcuts do not occupy smaller openings created by group selection, which may limit the utility of group selection in managing habitat for early successional shrubland birds.

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Key words: birds, chestnut-sided warbler, clearcutting, *Dendroica pensylvanica*, even-aged management, group selection, reproductive success, selective cutting, silviculture, uneven-aged management.

The use of even-aged forest management, which includes clearcutting and shelterwood cutting, has been challenged nationwide, partially because of its effects on populations of mature forest-dwelling Neotropical migrant birds (Lansky 1992). However, even-aged management is an important source of early successional habitat required by many species of wildlife (DeGraaf et al. 1992), including early successional shrubland birds, which are experiencing more widespread population declines than their mature forest counterparts (Askins 1993). Thus, managers are confronted with a potential conflict between the maintenance of mature forest and the creation of early successional shrubland habitat (Hagan et al. 1997).

Public concerns about clearcutting have resulted in increased emphasis on uneven-aged silvicultural systems (Costello et al. 2000). Group selection is an uneven-aged silvicultural system in which timber is harvested in approximately 0.02–0.80-ha patches every 10–20 years, creating an uneven-aged structure within a stand (Leak et al. 1987). Group selection is gaining increasing popularity with forest managers because it retains a substantial proportion of the mature forest bird community (Chambers et al. 1999, Robinson and Robinson 1999, Costello et al. 2000) yet creates early successional habitat within the harvested areas similar in structure to that created by even-aged management (Leak et al. 1987). Thus, group selection could potentially represent a compromise between even-aged management, which is increasingly unpopular with the public, and single-tree selection, which does not usually provide adequate habitat for early successional shrubland habitat specialists (Annand and Thompson 1997, King and DeGraaf 2000).

Previous studies on bird habitat use in clearcut and selection harvests (Annand and Thompson 1997, Chambers et al. 1999, Robinson and Robinson 1999) have emphasized that information on the effect of these treatments on avian reproductive success is needed to accurately assess the impact of various silvicultural methods on the ecology of early successional bird species. This is especially important in the case of comparisons

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of the relative effect of management techniques that create large (clearcut) versus small (groupcut) patches, because birds in small patches of grassland (Johnson and Temple 1990, Winter and Faaborg 1999) and forest (Porneluzi et al. 1993, Hoover et al. 1995) habitat are known to experience higher nest predation rates relative to birds in larger patches. Lower reproductive success in smaller habitat patches may be due to increased edge-related nest predation (Andren and Angelstam 1988, Hoover et al. 1995). Thus, data on reproductive success is critical to accurately evaluate the relative suitability of patches of early successional shrubland habitat created by clearcutting versus group selection (Van Horne 1983).

We compared the reproductive success of shrubland-nesting bird species between patches of regenerating forest created by clearcutting and group selection to augment the findings of these earlier studies of bird distribution in clearcut and groupcut stands. Based on the results of other studies of the nesting ecology of passerine birds in large versus small habitat patches, we predicted that nest survival would be lower in small habitat patches, and that this pattern would be associated with lower nest survival near clearcut and groupcut edges.

METHODS

We conducted this study at 3 sites on the White Mountain National Forest in Caroll and Coos counties, New Hampshire: (44°03′ N, 71°15′ W). The White Mountain National Forest is 303,930 ha in extent and is 97% forested (U.S. Forest Service 1986: III-30). The forest in the study area consisted of beech–birch–maple subtype of northern hardwoods forest in the following size distribution: 87% mature forest, 5% poletimber and 8% regeneration–sapling stands (U.S. Forest Service 1986: III-30).

We established a clearcut plot and a groupcut plot at each of the 3 sites. Clearcut plots encompassed clearcuts 6, 9, and 10 ha, and groupcut plots each encompassed 10 or 11 groupcuts. Groupcuts averaged 0.39 ha (SE = 0.12) and ranged in size from 0.20–0.69 ha. Plots at 2 sites, Blue Mountain and Double Head, were established during 1994 in 5-year-old cuts, and plots at a third site, Black Brook, were established in 1995 in 4-year-old cuts. All plots were flagged in 50- × 50-m grids to facilitate nest location and monitoring.

We located nests by following birds carrying food or nesting material. We marked nests by placing a small piece of red vinyl tape 3–5 m from the nest, and we checked nests every 3 days to determine nest fate. If a nest was empty and visibly damaged before the predicted fledging date and we were unable to locate adults feeding fledglings, we considered it depredated. Conversely, if the nest contained nestlings up to the predicted date of fledging and we were able to find adults feeding young, the nest was classified as successful. We assigned the midpoint between the last nest check and the date the nest was found depredated as the date of predation (Mayfield 1975). We calculated nest survival using the Mayfield estimator (Mayfield 1975), and compared nest survival rates between clearcuts and groupcuts using contrasts following Sauer and Williams (1989). In addition, we compared nest survival rates between 0–10 m (hereafter "cut edge") and >10 m (hereafter "cut interior") from forest–clearcut and forest–groupcut borders. To account for possible species-specific differences in vulnerability in nest predation, we conducted the above analyses separately for all species for which we had sufficient samples, as well as for all species pooled.

RESULTS

We located 290 nests of 16 species during the study (Appendix 1). The chestnut-sided warbler was the only species for which enough nests were found for separate analyses ($n = 217$). The species for which we had the next largest sample was the American redstart ($n = 20$). Ninety-eight percent of nests were located 0.25–2 m above ground level in woody vegetation. The remaining 2% of nests were located directly on the ground.

Nest survival rates of all species combined, and for chestnut-sided warblers considered separately, did not differ between clearcuts and groupcuts in any year or at any site (Table 1). Nest survival rates of all species combined, and of chestnut-sided warblers considered separately, did not differ between cut edges and cut interiors in either clearcuts or groupcuts (Table 2).

DISCUSSION

Contrary to our predictions, nest survival rates did not differ between clearcuts and groupcuts, or between cut edges and interiors. We expected that nest survival rates would be lower in small patches because the proportion of a fragment consisting of edge is inversely proportional to fragment size, and elevated nest predation rates near edges have been implicated as an important factor in the reduced nesting success often observed in small fragments of mature forest (Andren and Angelstam 1988, Hoover et al.

Table 1. Daily nest survival rates (± SE) of 16 bird species combined, and of chestnut-sided warblers considered separately, compared between clearcuts and groupcuts on 6 plots on the White Mountain National Forest, New Hampshire, 1994–96.

	All species[a]				Chestnut-sided warbler			
	Clearcut	Groupcut	*P*	*n*	Clearcut	Groupcut	*P*	*n*
1994								
Blue Mountain	0.993 ± 0.004	0.995 ± 0.004	0.78	51	1.000 ± 0.000	0.996 ± 0.004	0.32	30
Double Head	0.990 ± 0.007	0.976 ± 0.009	0.22	3	0.984 ± 0.010	0.979 ± 0.008	0.72	26
1995								
Blue Mountain	0.982 ± 0.006	0.987 ± 0.009	0.63	44	0.991 ± 0.006	0.985 ± 0.011	0.62	28
Double Head	0.981 ± 0.010	0.981 ± 0.006	0.34	30	0.981 ± 0.010	0.995 ± 0.005	0.25	24
Black Brook	1.000 ± 0.003	0.990 ± 0.010	0.32	18	1.000 ± 0.000	0.987 ± 0.013	0.31	15
1996								
Blue Mountain	0.996 ± 0.003	0.980 ± 0.010	0.11	41	0.994 ± 0.004	0.978 ± 0.011	0.16	29
Double Head	0.987 ± 0.008	0.987 ± 0.007	0.96	32	0.981 ± 0.011	0.985 ± 0.009	0.76	26
Black Brook	0.994 ± 0.004	0.989 ± 0.006	0.45	41	0.997 ± 0.003	0.988 ± 0.006	0.19	39
All years and plots	0.990 ± 0.002	0.987 ± 0.003	0.34	290	0.993 ± 0.002	0.987 ± 0.003	0.10	217

[a] Species studied are listed in Appendix 1, with number of nests observed for each species.

1995). Nest predation is higher within mature forest near clearcut and groupcut borders (King et al. 1996, 1998*a*), which may be attributed to increased predator abundance within mature forest near clearcut borders (King et al. 1998*b*). It is possible that the marginally higher predation rates we observed on chestnut-sided warbler nests in groupcuts are the result of the marginally higher rates of nest predation near edges we observed; however, further study is required to determine whether these nonsignificant trends represent actual patterns in predation rates in clearcuts and groupcuts.

Overall, nest survival rates in our study were high compared to most studies of cup-nesting passerines (Martin 1992). High nest survival rates in clearcuts and groupcuts are probably due to high levels of nest concealment (Rudnicky and Hunter 1993) and low predator abundance (King et al. 1998*b*) in recently harvested areas. Annand and Thompson (1997), and Morse and Robinson (1999) reported substantially lower nest success rates for shrubland birds in regenerating clearcuts (18–51%, and <15% probability of a nest surviving to fledge ≥1 young; respectively) than we observed at our study sites (60–98.6% probability of a nest surviving to fledge ≥1 young). Nest predation rates (Robinson et al. 1995) and the composition of nest predator communities (Andren 1992) change with changes in regional forest cover, factors which may explain the differences between our results from New Hampshire (97% forested), and those of Annand and Thompson (1997) and Morse and Robinson (1999) at their sites in southeast Missouri (85% forested), and southern Illinois (53% forested), respectively.

There is an emerging consensus among conservationists that for forest management to most effectively conserve biodiversity, disturbances created during the course of forest practices should mimic, to the greatest extent possible, the frequency and scale of the natural disturbance

Table 2. Daily nest survival rates (± SE) of 16 bird species combined, and of chestnut-sided warblers considered separately, compared between edge (0–10 m from edge) and interior (>10 m from edge) areas within clearcuts and groupcuts on 6 plots on the White Mountain National Forest, New Hampshire, 1994–96.

All species				
	Cut edge	Cut interior	*P*	*n*
Clearcuts	0.981 ± 0.008	0.993 ± 0.002	0.13	118
Groupcuts	0.984 ± 0.006	0.989 ± 0.003	0.42	86
Combined	0.983 ± 0.005	0.992 ± 0.002	0.07	204
Chestnut-sided warblers				
	Cut edge	Cut interior	*P*	*n*
Clearcuts	0.989 ± 0.007	0.995 ± 0.002	0.37	83
Groupcuts	0.982 ± 0.006	0.990 ± 0.003	0.25	73
Combined	0.984 ± 0.005	0.993 ± 0.002	0.10	156

regimes in which the ecosystem evolved (Hansen et al. 1991). Approximately 1% of eastern hardwood and hardwood–conifer forests regenerate from natural death and windthrow (Runkle 1990), which would result in forest ≤ 10 years old covering 10% of the forest area. This figure is similar to the amount of forest cover in this age class (8%) on the White Mountain National Forest. Although Runkle (1982) reported that natural regeneration in eastern forests resulted mostly from the death of individual trees, Curtis (1943) reported that 22 storms of hurricane intensity occurred in New England forests over a period of 3 centuries, and surmised that the period of disturbance for any 1 locality was as little as 150 years. Similarly, Leak et al. (1994) report significant disturbances resulting from windthrow occurring every 30 years in New England hardwood–hemlock forests. Thus, it appears that both the small gaps created by group selection and the larger patches created by clearcutting have natural analogs in the White Mountains, and hence, both have a legitimate place in the silviculturalist's repertoire (DeGraaf and Miller 1996).

MANAGEMENT IMPLICATIONS

Our results indicate that the nesting success of early successional shrubland birds in clearcuts and groupcuts is similar; however, some species that are characteristic of large openings, such as those created by clearcutting, are absent from smaller habitat patches created by group selection. For example, Annand and Thompson (1997) reported that at their sites in Missouri, 3 species of early successional shrubland birds, the yellow-breasted chat (*Icteria virens*), prairie warbler (*Dendroica discolor*), and rufous-sided towhee (*Piplio eurythropthalmus*), were present in clearcuts 10.5–15.3 ha in size, yet absent from groupcuts of the same age 0.2–0.4 ha in size. Similarly, Robinson and Robinson (1999) reported that prairie warblers, blue-winged warblers (*Vermivora pinus*), and brown thrashers (*Toxostoma rufum*) were typical of the bird fauna of clearcuts at their sites in Illinois, yet were never detected in patches of regenerating forest 0.02–0.4 ha in size. Finally, Costello et al. (2000) detected alder flycatchers, indigo buntings, olive-sided flycatchers (*Contopus borealis*), eastern bluebirds (*Sialia sialis*), northern flickers (*Colaptes auratus*), rufous-sided towhees, song sparrows (*Melospiza melodia*), and tree swallows (*Tachycineta bicolor*) in clearcuts 8–12 ha in size in New Hampshire, but not in groupcuts of the same age 0.13–0.56 ha in size. Most of these area-sensitive species are considered species of special management concern in at least parts of their ranges (Peterson and Fichtel 1992, Hagan 1993, Smith et al. 1993, Thompson et al. 1993).

Conversely, some mature forest bird species, such as red-eyed vireos (Robinson and Robinson 1999, Costello et al. 2000), ovenbirds (*Seiurus aurocapillus*; Annand and Thompson 1997, Robinson and Robinson 1999) wood thrushes (Annand and Thompson 1997), and Swainson's thrushes (*Catharus ustulatus*; Chambers et al. 1999), are less abundant in stands managed by group selection than unmanaged stands. Gaps created by group selection displace the territories of many species of forest birds away from the harvest areas (Germaine et al. 1997), and appear to restrict within-stand movements of some forest birds (Desrochers and Hannon 1997). Finally, nest predation is higher in mature forest adjacent to groupcut edges (King et al. 1998*a*), and because group selection creates more edge per unit area cut (Franklin and Forman 1987), group selection will likely result in a greater increase of edge-related nest predation on birds in the forested portions of managed stands than would clearcutting (Thompson 1993).

Because the habitat created by group selection does not satisfy the habitat requirements of a substantial proportion of the early successional shrubland bird community, and the creation of groupcuts disrupts bird communities in the remaining mature forest in managed stands, sole reliance on group selection represents an ineffective compromise between the habitat requirements of early successional and mature forest birds. We suggest that a more effective strategy would be to consolidate mature and regenerating forest into larger blocks as suggested by Hagan et al. (1997), which would maximize the utility of the resulting habitat for both mature forest and early successional shrubland species.

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Appendix 1. Nests (n = 290) found in clearcuts and groupcuts on 6 plots on the White Mountain National Forest, New Hampshire, 1994–96.

Common name	Scientific name	Number of nests
Chestnut-sided warbler	(*Dendroica pensylvanica*)	217
American redstart	(*Setophaga ruticilla*)	20
Swainson's thrush	(*Catharus ustulatus*)	8
Veery	(*Catharus fuscesens*)	8
Rose-breasted grosbeak	(*Pheucticus ludovicianus*)	6
Alder flycatcher	(*Empidonax alnorum*)	6
Black-throated blue warbler	(*Dendroica caerulescens*)	5
Magnolia warbler	(*Dendroica magnolia*)	4
White-throated sparrow	(*Zonotrichia leucophrys*)	3
Common yellowthroat	(*Geothlypis trichas*)	3
Indigo bunting	(*Passerina cyanea*)	2
Red-eyed vireo	(*Vireo olivaceous*)	2
Gray catbird	(*Dumetella carolinensis*)	2
Hermit thrush	(*Catharus guttatus*)	2
American goldfinch	(*Carduelis tristis*)	1
Cedar waxwing	(*Bombycilla cedrorum*)	1

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Management and Conservation

Resource Selection by Indiana Bats During the Maternity Season

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ABSTRACT Little information exists on resource selection by foraging Indiana bats (*Myotis sodalis*) during the maternity season. Existing studies are based on modest sample sizes because of the rarity of this endangered species and the difficulty of radio-tracking bats. Our objectives were to determine resource selection by foraging Indiana bats during the maternity season and to compare resource use between pregnant and lactating individuals. We used an information theoretic approach with discrete choice modeling based on telemetry data to evaluate our hypotheses that land cover, percent canopy cover, distance to water, and prescribed fire affected the relative probability a point was used by a foraging Indiana bat. We fit models for individual bats and a population-level model based on all individuals with a random factor to account for differences in sample size among individuals. We radio-tracked 29 individuals and found variation in resource selection among individuals. However, among individuals with the same supported covariates, the magnitude and direction of the covariates were similar. Eighteen bats selected areas with greater canopy closure and 5 of 6 bats that had areas burned by low-intensity prescribed fire in their home range selected burned areas. Resource selection was related to land cover for 13 individuals; they selected forest and shrubland over agricultural land, which composed >50% of the landscape within 10 km. We found no support for our hypothesis that resource selection was related to individual reproductive condition or Julian date in our population-level model indicating habitat selection was not determined by reproductive status or date within the maternity season. Land use or forest management that greatly reduces canopy cover may have a negative impact on Indiana bat use. Maintaining forest cover in agricultural landscapes is likely critical to persistence of maternity colonies in these landscapes. Sites managed with low severity prescribed fire may be selected by some individuals because of reduced understory vegetation. © 2013 The Wildlife Society.

KEY WORDS discrete choice, foraging, Indiana bat, Missouri, *Myotis sodalis*, resource selection.

Human populations are increasingly modifying landscapes and causing extinctions or decreases in abundance of many wildlife species (Haila 2002, Fischer and Lindenmayer 2007). The Indiana bat (*Myotis sodalis*) has been on the United States Endangered Species List since 1967. Knowledge of how landscape and forest management affect forest wildlife, like the Indiana bat, will allow resource managers to make more informed management decisions that will aid in the recovery of species. Silvicultural practices such as selective harvesting, girdling, and other methods create forest patches with different tree densities and increase snags per hectare for bats and other wildlife (Thomas 1988, Patriquin and Barclay 2003). These management practices may provide roosting and foraging habitat for bats by reducing the structural clutter in the understory (e.g., small trees and shrubs) while keeping the canopy intact, especially during the maternity season (Crampton and Barclay 1998, Patriquin and Barclay 2003). Management techniques that mimic small-scale natural disturbances by wind or fire may be compatible with bat conservation, whereas removal of mature forests likely eliminates bat use since Indiana bats require large trees for roosting (Gardner et al. 1991, Callahan et al. 1997, Britzke et al. 2003, Kurta 2005).

Conservation efforts require better knowledge of foraging resource requirements for female Indiana bats during the maternity season. Most summer studies have focused on roost locations (Gardner et al. 1991, Callahan et al. 1997, Menzel et al. 2001, Britzke et al. 2003, Kurta 2005), whereas few have documented foraging habitats. Indiana bat activity is generally greatest in riparian corridors, upland forests, and bottomland forests (Menzel et al. 2005, Sparks et al. 2005, Carter 2006, Tuttle et al. 2006). Foraging height varies but is typically 2–30 m above the ground and under the forest canopy (Humphrey et al. 1977). Past studies of the summer ecology of Indiana bats did not consider selection at the individual level or by reproductive condition (i.e., pregnancy, lactation, and post-lactation), likely because of the small number of individuals studied (Menzel et al. 2005, Sparks

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et al. 2005). Distances traveled between foraging and diurnal roosting locations are highly variable between reproductive stages (i.e., pregnant or lactating) as well as variable among individuals in the same reproductive status in Indiana (Sparks et al. 2005). However, Sparks et al. (2005) did not investigate differences in resource selection among individuals or reproductive classes. Flight distance and home range size are smaller during lactation than pregnancy in little brown bats (*M. lucifugus*; Henry et al. 2002). Henry et al. (2002) monitored over 50 individuals and demonstrated the importance of studying individual behavior and an adequate sample size. Understanding how bats select resources to meet specific reproductive needs and variation among individuals will aide managers in determining what resources are important for sustaining Indiana bat populations.

Discrete choice models were designed to evaluate customer behavior in the social sciences based on the economic utility theory (Berry 1994) but are also used for wildlife resource selection studies to predict the relative probability of selecting a resource compared to available resources (Cooper and Millspaugh 1999). Our objectives were to determine resource selection by foraging Indiana bats during the maternity season and to compare resource use among pregnant and lactating individuals. We hypothesized Indiana bats would select vegetative conditions that optimize flight and prey capture based on wing morphology and echolocation design (Norberg 1994, Jacobs 1999, Fenton and Bogdanowicz 2002). Indiana bats have low wing loading and aspect ratio, adaptations for slow maneuverable flight around or within clutter. Therefore, we predicted they would prefer managed forest stands with high canopy coverages that were relatively close to water. We used an information theoretic approach with discrete choice modeling to evaluate our hypotheses that land cover, percent canopy cover, distance to water, and prescribed fire affected habitat use by foraging Indiana bats. We fit models for individuals to examine variability in resource selection and a population-level model to evaluate the relationship between resource selection and reproductive status and Julian date. Although we acknowledge that looking at resource selection across sites or landscapes is desirable, we studied individuals intensively at a site to be able to address questions concerning variation among individuals in resources selection—a question not generally addressed for bats.

STUDY AREA

We studied bats during May–July, 2008–2010, at Charles Heath Memorial Conservation Area (CHMCA) in Clark County, Missouri. The 662-ha CHMCA is managed by the Missouri Department of Conservation and is composed of 596 ha of mature upland and bottomland forests and 66 ha of grasslands or idle fields. The uplands are dominated by mature oak-hickory forest typically found in northern Missouri and the mature bottomland forest consists of typical mix species for northern Missouri, including silver maple (*Acer saccharinum*), sycamore (*Platanus occidentalis*), cottonwood (*Populus deltoides*), river birch (*Betula nigra*), and bottomland associated oak species (i.e., pin [*Querus palustris*], swamp [*Querus bicolor*], white [*Querus alba*], bur [*Querus macrocarpa*]). The only recent forest management activities on CHMCA were 2 prescribed fire units (18.2 ha and 14.56 ha) in upland forests managed first in either April 2005 or 2006 and burned annually each April until 2009. The composition of the landscape defined by a 10-km buffer around the center of CHMCA was 56% agricultural (corn, soybeans, and pasture), 27.8% forested (mostly CHMCA), 6.8% shrubland, 3.6% developed, and 4.5% wetland based on the National Land Cover Database 2001 (NLCD; Homer et al. 2004).

METHODS

Capture and Handling

We captured bats with mist nets and harp traps (Tuttle 1974, Kunz and Kurta 1988). We placed each bat in a muslin bag until it was processed. We cleaned bags and equipment and followed the white-nose syndrome decontamination protocol at the time of capture (U.S. Fish and Wildlife Service 2012). We attached radio transmitters weighing 0.43–0.53 g (Holohil Systems Ltd., Carp, ON, Canada) to female Indiana bats that were large enough to carry a transmitter (i.e., transmitter did not exceed 5% of the bat's weight). We trimmed the hair between the shoulder blades of bats with surgical scissors and forceps and glued (Osto-Bond, Montreal Ostomy Inc., Vaudreuil-Dorion, QC, Canada) transmitters to the skin. We placed bats with radio transmitters in a holding bag for 15 minutes to allow the glue to cure. We tried to place transmitters on up to 5 female Indiana bats at a time to maximize field efficiency. Animal procedures were approved under Missouri Department of Conservation permit 14529, Federal permit TE06809A, and University of Missouri Animal Care and Use Committee protocol #4451.

Telemetry

We radio tracked bats by obtaining simultaneous compass bearings from at least 2 locations and triangulated bat locations (Amelon et al. 2009); antennae were either roof-mounted on vehicles (RA-4A model, Teleonics, Mesa, AZ) or on a fixed location 30-foot tower (VHF model, Teleonics). We created a daily monitoring schedule to obtain bearings at intervals of 5–10 minutes, depending on the number of radio tagged animals, and synchronized times of each bearing by using atomic clocks. We tracked all bats from dusk (around 2100 hour) to night roost (0100–0230 hours) and again from about 0300 to dawn (around 0500 hour); monitoring times varied because of variability in individual's night roost time. We monitored all individuals with radio transmitters until the last bat went to night roost for at least 30 minutes. We triangulated locations from bearings and estimated error polygons using the program GTM3 (Sartwell 2000) and excluded locations with error polygons >200 m^2 (mean 42 ± 2.66 m^2) from the analysis.

We selected 3 random points as the choice set for comparison to each bat location. We calculated the maximum distance that an individual bat traveled each night as the greatest distance between all pair wise combinations of locations from a night. We then created a buffer around each location for each bat for that night using the maximum distance (mean: 2,089 m; range: 289–7,826 m) as the diameter. We selected 3 random points within each bat's buffer area using Hawths tools (ArcGIS; ESRI, Redlands, CA).

Model Covariates

We derived land cover classes and percent canopy cover from the National Land Cover Database from 2001 (NLCD; Homer et al. 2004). We verified the dependability of these coverages by comparing them to National Agriculture Imagery Program 2009 (NAIP) aerial photographs of the study area. Water features in the study area were underrepresented in the NLCD so we digitized all water features from NAIP 2009 photographs and United States Geological Survey quad maps using ArcGIS (ESRI, ver. 9.1). We grouped land use and land cover types from the NLCD into the following land cover categories: shrub-grassland, agriculture, bottomland forest, and upland hardwood forest and assigned each bat location and random point to one of these land cover categories. Since agriculture was the dominant land cover, we used agriculture as the reference category and excluded it from models to avoid linearly dependent covariates. Developed land and wetlands occurred within the 10-km buffer of our study area but no used or random points fell within either category so we did not include them in the analysis. We created an additional land cover category for upland hardwood forest managed with prescribe fire (mULHW) based on boundaries delineated in a polygon shape file provided by Missouri Department of Conservation. We calculated the distance from water (DisW) for each bat location and random point using the near tool in ArcGIS.

Data Analysis

We used an information theoretic approach to evaluate a priori hypotheses using Akaike's Information Criterion (AIC) to rank candidate models in terms of their ability to explain the empirical data for each individual bat and at the population level (Burnham and Anderson 2002). For resource selection by individuals, we compared bat locations to random points in the choice set using conditional logit discrete choice models (Proc MDC, SAS/ETS 9.2; SAS Institute, Cary, NC; SAS, 2010). Conditional logit discrete choice models consider the effects of the choice set attributes on each choice probability (Bonnot et al. 2009). The candidate models consisted of single covariate models with percent canopy cover, distance to water, and our land cover variables; all additive combinations of these covariates; and a null (intercept only model).

To examine resource selection at the population level, we pooled observations from all individuals and used mixed logit discrete choice models, which allow for random effects. We included a random effect for individuals to acknowledge heterogeneity among individuals and to account for varying sample sizes among individuals by treating individuals as subjects in the model. We evaluated support for reproductive condition (pregnant or lactating) and Julian date by comparing support for models with and without interactions between reproductive condition and Julian date with land cover, percent canopy cover, and distance to water and with percent canopy cover and distance to water; we also considered a null model with only an intercept parameter.

Traditional goodness-of-fit methods are not appropriate because discrete choice models use unique choice sets for each known location; therefore, we validated the top ranking model for each individual and the population using a modified *k*-fold approach (Boyce et al. 2002). We randomly removed 20% of the cases, fit the model with the remaining data, and tested the ability of the fit model to identify used points versus random points for the 20% of cases withheld, and repeated this 5 times. We report the mean percent concordance averaged over the 5 data subsets as the percentage of the time the used points had a greater predicted probability of use than the 3 random points in the choice set; values >25% indicate the model performed better than randomly selecting the used point (Bonnot et al. 2009).

We examined occurrence of covariates in the most supported models across individuals to assess variation among individuals. We evaluated the magnitude and 95% confidence intervals of model averaged coefficients for a confidence set of models ($w_i \geq 0.95$; Burnham and Anderson 2002); except where specifically noted, we only interpret covariates with 95% confidence intervals that did not overlap zero. We used the most supported population-level model to predict relative probability of use (±95% CI) over the observed range of supported covariates, while holding other covariates at their mean; we rescaled plots of continuous covariates so the maximum probability was 1 to facilitate comparison among covariates (McDonald et al. 2006).

RESULTS

We obtained 3,124 foraging locations for 29 female Indiana bats during summer 2008–2010. We monitored 14 pregnant, 12 lactating, 1 non-reproductive, and 2 post-lactating individuals but excluded non-reproductive and post-lactating individuals from population analysis (Table 1). We monitored individuals on average 5 nights (range: 2–9) and did not use individuals in analyses with <30 triangulated locations (range: 32–208). Bats moved on average 810 m (range: 25–1,025 m) in a 5- to 10-minute period so we concluded selection of use points by bats were sufficiently independent for discrete choice analysis.

We removed the land cover category, managed upland hardwood forest, from the models for 9 individuals (Bats 151238, 151400, 151440, 151481, 151538, 151759, 151799, 51839, 151859) because no used and <2% of random points were in the managed units and the coefficient could not be estimated (Supplementary Table S1, available online at www.onlinelibrary.wiley.com). The null model was not the most supported model for any bat. Percent concordance was 27–97% and exceeded that expected by chance (Table 1). We found variation in resources selected among individuals. Canopy cover, distance to water, and land cover classes appeared in the top model for 15, 14, and 13 bats; respectively (Table 1). For all but 2 individuals, model selection uncertainty existed so we model averaged parameter estimates and predictions (Supplementary Tables S1, S2; available online at www.onlinelibrary.wiley.com). The relative

Table 1. Reproductive condition and top supported discrete choice models for 29 individual Indiana bats study in northeast Missouri, 2008–2010. Akaike weight (w_i) is the weight of evidence for the top model relative to other candidate models, percent concordance is a measure of model fit, and *n* is the number of use and random points in the discrete choice model.

Bat ID	Reproductive condition	*n*	Model[a]	w_i	% Concordance
150181	Lactating	136	CAN	0.616	39
151078	Lactating	316	CAN + DisW	0.283	31
151538	Lactating	276	CAN	0.266	30
151759	Lactating	512	CAN	0.268	61
151177	Lactating	460	LAND^1 + DisW	0.500	47
151440	Lactating	664	LAND^2 + DisW	0.705	45
151839	Lactating	315	CAN + DisW	0.306	35
151481	Lactating	104	DisW	0.285	44
151578	Lactating	480	DisW	0.349	27
150000	Lactating	296	LAND^1	0.329	52
151718	Lactating	240	LAND^1	0.410	27
151900	Lactating	416	LAND^1 + DisW	0.559	43
151118	Pregnant	160	CAN	0.631	27
151859	Pregnant	100	CAN	0.258	42
151929	Pregnant	368	CAN	0.263	36
151238	Pregnant	368	LAND^2	0.361	56
151799	Pregnant	876	LAND^1 + DisW	0.734	55
151970	Pregnant	320	CAN + DisW	0.558	42
151018	Pregnant	376	LAND^1 + DisW	0.685	97
151539	Pregnant	616	LAND^1 + CAN + DisW	0.449	54
151878	Pregnant	272	DisW	0.654	43
151400	Pregnant	136	DisW	0.473	38
151098	Pregnant	260	LAND^1	0.294	54
151428	Pregnant	240	LAND^1 + CAN	0.546	53
151898	Pregnant	140	CAN	0.299	40
151913	Pregnant	384	CAN	0.247	40
151638	Non Reproductive	400	LAND^1 + CAN	0.238	41
151677	Post-lactating	420	CAN	0.506	36
151618	Post-lactating	300	LAND^1 + DisW	0.512	54

[a] CAN = percent canopy coverage; DisW = distance to water (m); LAND^1 = 4 dummy variables representing upland hardwood forest, upland hardwood forest managed with prescribed fire, bottomland hardwood forest, and shrubland-grassland; LAND^2 = excludes upland hardwood forest managed with prescribed fire, all other variables are included from previous LAND model; agricultural land use was the reference category.

probability a point was selected increased 1.2–5.3% for a 10% increase in canopy cover for the 4 individuals that the confidence interval did include 0 (Fig. 1). The relative probability a point was selected increased 2.2–7.1% for a 10-m increase in distance to water for the 8 individuals that the confidence interval did include 0 (Fig. 1). We found a positive relationships of shrubland, bottomland hardwood, upland hardwood, and managed upland hardwood forest with resource selection for 6, 9, 7, and 4 individuals, respectively, for which confidence intervals did not overlap 0 (Figs. 1 and 2; Supplementary Table S2). The increase in the relative probability a point was selected ranged across individuals, 84–227% if it was shrubland, 76–256% if it was bottomland hardwoods, 86–288% if it was upland hardwoods, and 46–629% if it was managed upland hardwoods versus agriculture (Figs. 1 and 2; Supplementary Table S2). Confidence intervals for model averaged coefficients did not include zero for 20–30% of individuals, and in all these cases the relationships with selection were positive.

For the population-level analysis, the percent canopy cover + distance to water + land cover model received overwhelming support ($w_i = 0.998$; % concordance = 0.38) with virtually no support for the model with the interactive terms for reproductive condition or Julian date (Table 2). The relative probability a point was selected increased 6% for a 10% increase in canopy cover and 3% for a 10-m increase in distance to water (Table 3). The relative probability a point was selected increased 545%, 940%, 527%, and 347% if it was bottomland forest, managed upland forest, shrubland, or upland forest, respectively, compared to agricultural land cover (Table 3). The predicted relative probability a point was selected increased across the range of distance to water and canopy cover, and was greatest for managed upland forest followed by bottomland forest, shrubland, and upland forest compared to agricultural land cover (Fig. 3).

DISCUSSION

We evaluated resource selection by individuals to identify variation in habitat use by Indiana bats that may have been unapparent or averaged out in the population-level model and to understand how individuals select resources (Cooper and Millspaugh 1999, Bolnick et al. 2002, Svanback and Bolnick 2007). We studied females during the maternity season because of the importance of reproduction and proximate high quality foraging sites to the conservation of the species. We found strong support for relationships between selection and canopy cover, distance to water, and land cover for only 20–30% of individuals and, overall, these relationships were supported at the population level. We think that some covariates were not supported at the individual level because of true variation among individuals, whereas for others large confidence intervals resulting from smaller

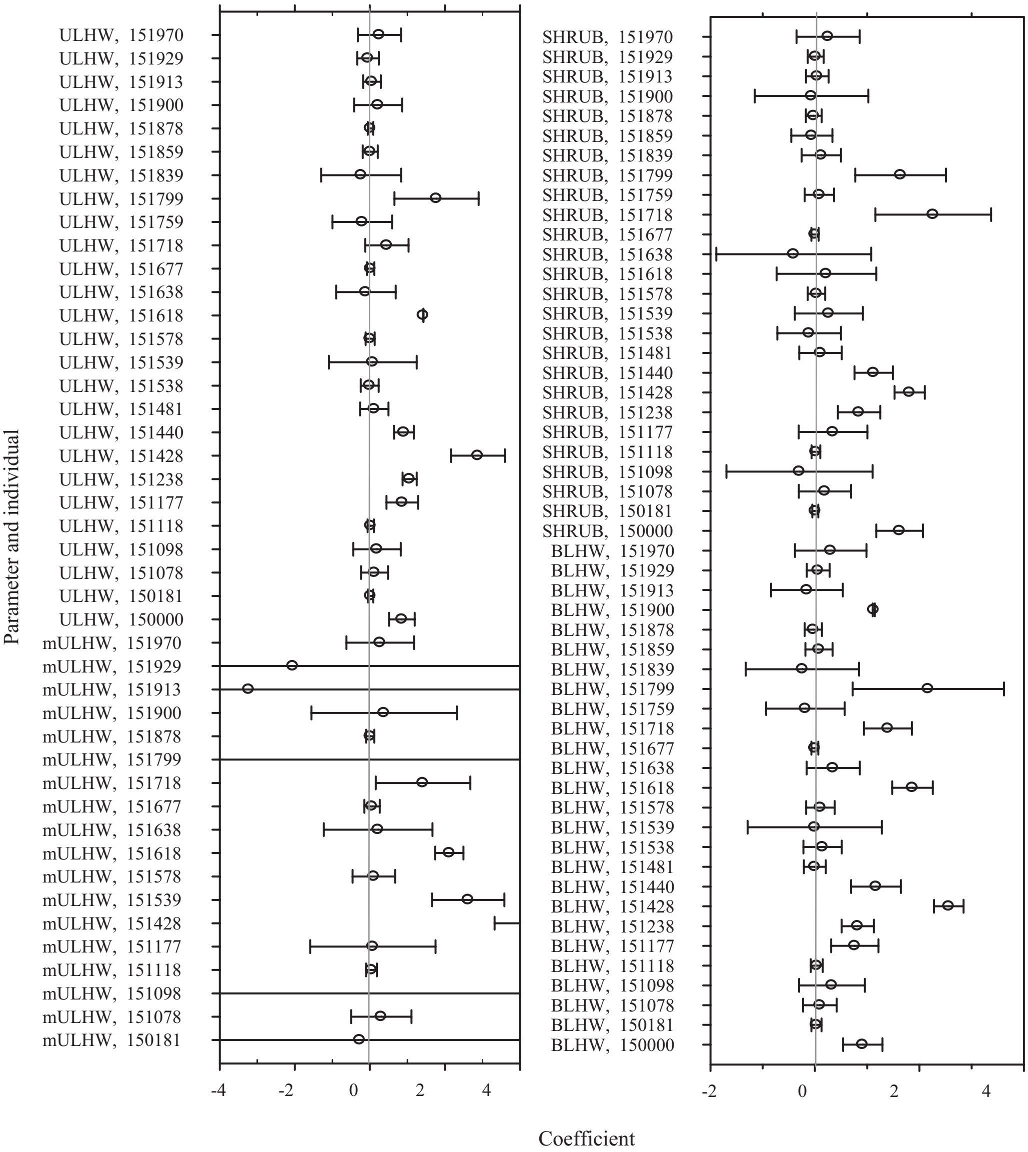

Figure 1. Model averaged coefficients (open circles) and 95% confidence intervals (bars) for discrete choice models for 29 individual Indiana bats in northeast Missouri, 2008–2010. Coefficients are for binary variables representing use of upland hardwood forest managed with prescribed fire (mULHW), upland forest (ULHW), open shrubland-grassland (SHRUB), or bottomland hardwoods (BLHW) versus agricultural land use.

sample sizes could have contributed to a lack of support. The magnitude of coefficients in the population model were in the lower range of coefficients in individual models, likely because any particular covariate was only supported for about half the individuals. However, population models do not necessarily represent what all individuals select, but rather an average across potentially substantial individual variability.

Intra-specific variation in resource selection, foraging behavior, and diet is known or suspected in a wide variety of species including insects (Howard 1993, Cronin et al. 1999), reptiles (Daltry et al. 1998), birds (Giraldeau and Lefebvre 1985, Annett and Pierotti 1999), ungulates (Clutton-Brock et al. 1982), bats (Fleming and Heithaus 1986), and mammalian carnivores (Kruuk and Moorhouse 1990, Ragg 1998). Foraging resources and diet breadth at the population level could be affected by differences in population size or strong intraspecific competition for limiting resources. The concept of variation in foraging behavior in Indiana bats is not especially surprising for a species living in a diverse environment with a large number of potential prey species and high temporal or spatial variability in prey populations. Individual foraging variation may have ramifications to population ecology. Reproductive success often depends upon the ability to compete for limiting resources. Although individual variation in diet remains largely unexplored from the standpoints of both theory and empirical detail, an individual may succeed or fail through their ability to obtain enough to eat.

A positive relationship of canopy cover with selection was the most frequently supported covariate for individuals and was supported in the population model. Increased use of areas with high canopy cover is consistent with others studies showing Indiana bats are found in areas with high canopy coverage (Humphrey et al. 1977, Menzel et al. 2005).

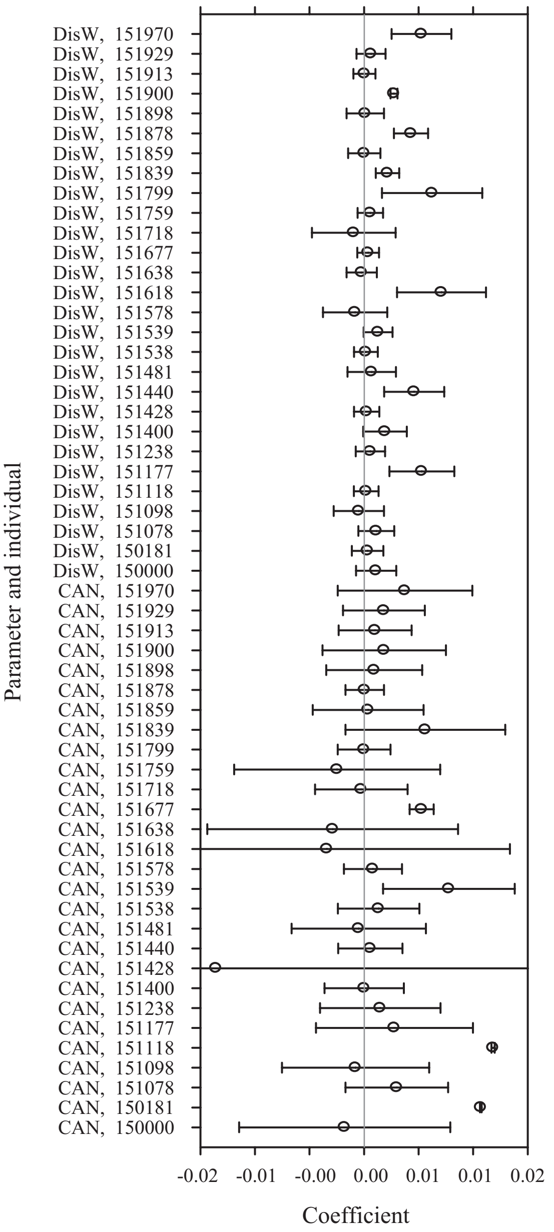

Figure 2. Model averaged coefficients (open circles) and 95% confidence intervals (bars) for discrete choice models for 29 individual Indiana bats in northeast Missouri, 2008–2010. Coefficients represent relationships of percent canopy cover (CAN) and distance to water (DisW) measured in meters with the probability of use.

Indiana bats' small body size, low wing loading, and high echolocation frequency allow them to navigate well in high clutter environments such as closed canopy forest (Owen et al. 2004). The distribution of canopy cover values for use and random points was skewed toward 0% and 100% with approximately 25% of points with 0% canopy cover and 25% with >90% canopy cover; nevertheless, we recorded values throughout the range. This distribution of canopy cover reflected the distribution of use and random points among land cover types; 68% and 59% of use and random points, respectively, were in forested land covers and the balance in shrub or agricultural land. Therefore, the positive relationship with canopy cover was largely driven by the contrast between forest and non-forest, although bats did make frequent use of non-forested or open areas 25% of the time. In addition to being adapted to foraging in closed canopy forest, Indiana bats may be associated with high canopy cover forest for roosting habitat. Out of 48 Indiana bat roost trees in Missouri, 32 were in closed-canopy forest, 12 in intermediate canopy cover, and 4 in open-canopy areas (Gardner et al. 1991).

We found a greater relative probability of use of areas managed with fire for 5 of 20 individuals that we were able to evaluate. We did not observe negative relationships with forest managed with prescribed fire for any individual, and a positive relationship was also supported in the population model. Other studies have also shown increased use by foraging Indiana bats of forests treated by prescribed fire that opened up the understory while keeping the mature forest canopy intact (Owen et al. 2004). Besides lower understory density, increased use of forests managed with prescribed fire could also be related to prey density. Lacki et al. (2009) found greater prey densities and northern long-eared bat (*Myotis septentrionalis*) activity in Kentucky forests managed with prescribed fire; however, insect prey densities were not greater in the stands with fire that we studied (Womack 2011). We think that Indiana bats likely selected sites treated with prescribed fire because of more open understories.

We found no support for temporal changes in resource use by females associated with reproductive condition or day of year in our population model. Brigham et al. (1992) also found no differences in habitat use between 4 reproductive classes (pregnant, lactating, post-lactating, and juveniles) of Yuma bats (*Myotis Yumanensis*) and attributed this finding to

Table 2. Support for population-level discrete choice models based on 29 female Indiana bats in a resource selection study in northeast Missouri, 2008–2010 ($n = 8{,}831$). Model support is indicated by Akaike's Information Criterion (AIC), the difference in AIC between the top model and indicated model (ΔAIC), Akaike weights (w_i), log likelihood value (log(L)), and number of estimated parameters in the model (K).

Model[a]	K	log(L)	AIC	ΔAIC	w_i
LAND + CAN + DisW	7	−2,861	5,736		0.998
LAND × jul + CAN × jul + DisW × jul	7	−2,867	5,748	12	0.002
CAN + DisW	3	−2,887	5,780	43	0.000
LAND × rc + CAN × rc + DisW × rc	7	−2,883	5,780	45	0.000
CAN × jul + DisW × jul	3	−2,894	5,794	58	0.000
CAN × rc + DisW × rc	3	−2,900	5,806	69	0.000
NULL	1	−3,061	6,124	389	0.000

[a] CAN = percent canopy coverage; DisW = distance to water (m); LAND represents 4 dummy variables for bottomland hardwood forest, shrubland-grassland, upland hardwood forest, upland hardwood forest managed with prescribed fire; jul = Julian date; rc = reproductive condition (pregnant or lactating); NULL = intercept only model.

Table 3. Model coefficients, standard errors, confidence intervals, and selection ratios for the most supported population-level discrete choice model based on 29 female Indiana bats in a resource selection study in northeast Missouri, 2008–2010.

Variable	Estimate	SE	95% CI	Selection ratio
Canopy cover (%)	0.006	0.0011	0.0039–0.0138	1.006
Distance to water (m)	0.003	0.0002	0.0028–0.0087	1.003
Bottomland forest[a]	0.545	0.120	0.31–1.152	1.725
Managed upland forest[a]	0.940	0.212	0.524–1.968	2.560
Shrubland[a]	0.527	0.099	0.333–1.180	1.694
Upland forest[a]	0.347	0.119	0.114–0.57	1.415

[a] Dummy variables coded as 1 if the point fell in the defined land cover type; agricultural land was the reference category.

the rarity of foraging areas (i.e., forests) in the system, which is similar to the landscapes we studied. In red bats (*Lasiurus borealis*), differences were noted between reproductive stages relative to selection for percent canopy cover and landscape percent water (Amelon 2007). Indiana bats have a different behavioral structure than red bats; Indiana bats roost in colonies under tree bark, whereas red bats are a solitary foliage roosting species. Henry et al. (2002) determined home range size differs between pregnant and lactating little brown bats, but they did not investigate resource selection by reproductive stage. Bat ecology studies in the future need to consider the individuals within populations to more fully understand what resources are selected by the species.

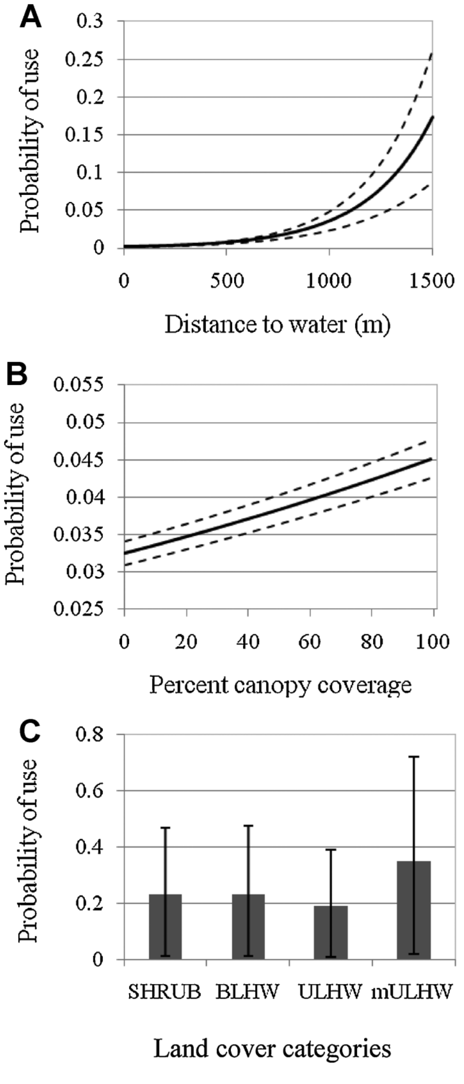

Figure 3. Predicted relative probability of site use for a population of female Indiana bats ($n = 29$) as a function of (A) distance to water in meters; (B) percent canopy cover; and (C) Land cover categories: shrub-grassland (SHRUB), bottomland forest (BLHW), upland forest (ULHW), and managed upland forest (mULHW).

Our resource selection results for land cover types are generally consistent with previous foraging studies for Indiana bats. Sparks et al. (2005) reported Indiana bats preferred closed-canopy forest over agricultural land and Murray and Kurta (2004) found most individuals foraged in forest in a landscape dominated by agriculture. Indiana bat maternity colonies generally occur in forest and in landscapes with 10–80% forest, 55–67% agriculture, 0–19% wetland, and 0–6% urban (Gardner et al. 1991, Kurta et al. 2002). Our landscape was 28% forest, which is at the lower end of percent forest composition for Indiana bats. In regions with very limited forest cover, Indiana bats may be constrained to landscapes with enough suitable forest cover. Differences in spatial foraging dynamics exhibited between forest-dominated versus agriculture-dominated landscapes have been described for this species as well as other *Myotis* species (Britzke et al. 2003, Sparks et al. 2005, Henderson and Broders 2008).

Our finding that relative probability of use increased with distance to water may not seem consistent with previous studies reporting high use of riparian corridors by foraging Indiana bats (Menzel et al. 2005, Carter 2006, Yates and Muzika 2006). However, water was abundant on our study area and all bat locations were within 1.5 km of water, well within the area of use for each individual. Therefore, no individuals were ever truly distant from water (i.e., >1,500 m).

Our use of discrete choice modeling differs from previous approaches used to determine resource selection by foraging Indiana bats, such as compositional analysis (Sparks et al. 2005). Compositional analysis is usually used to compare habitat use and availability within an individual's home range. Bats are capable of moving large distances compared to other mammals similar in size. Therefore, limiting the available area for potential use to home range is likely an underestimation of the potential foraging habitat available to individuals (Kurta 2001). To address this issue of availability, we used the maximum distance an individual flew each night to define an area from which we sampled points to be in our choice set. The use of discrete choice modeling also let us consider relationships with continuous covariates, unlike compositional analysis, which considers use of vegetation or land cover types.

MANAGEMENT IMPLICATIONS

Discrete choice models were a valuable tool for determining resource selection of individual foraging bats and provided insight into variability in resource selection by individuals not possible from population models. The probability a bat selected a point was greater for shrubland and forest habitats than agricultural habitat and increased with canopy cover. Therefore, practices that eliminate forest or greatly reduce canopy cover over large areas may have negative impacts on Indiana bats. Our study supports the premise that bats will use a broad array of vegetation types for foraging. Maintaining forest cover within landscapes dominated by agriculture is likely critical to persistence of Indiana bat maternity colonies in these landscapes. A positive relationship of selection with prescribed fire in upland forest was supported for 25% of the individuals that had managed stands available to them and no individuals had a negative relationship with fire; therefore, prescribed fire may improve habitat for Indiana bats and its use for this purpose warrants further research. Although our results suggest Indiana bats were selecting mature forests with relatively high canopy closure for foraging locations, we recommend further examination of the relationship between these forest structures, bat foraging, and bat fitness. We recommend that management activities proceed under an adaptive management framework to monitor bat population response to management such as partial tree harvest and prescribed fire.

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Review of the Forest Habitat Relationships of the Indiana Bat (*Myotis sodalis*)

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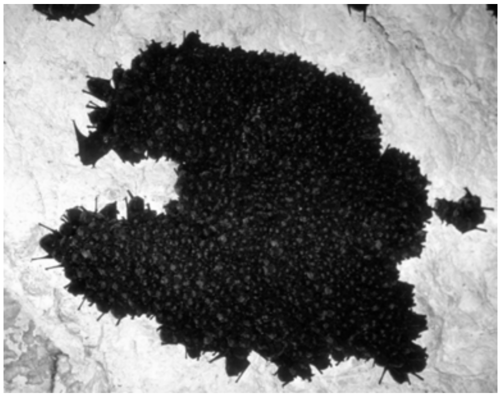

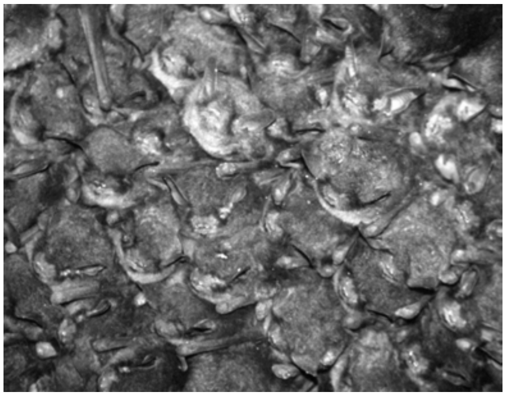

Abstract

Reviews the available literature on the ecology of the endangered Indiana bat (*Myotis sodalis*), including its selection of and use of hibernacula, roost trees, and foraging habitat. An extensive list of published references related to the Indiana bat is included.

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Contents

Introduction

The estimated population of the small, insectivorous Indiana bat (*Myotis sodalis*) totaled approximately 350,000 following a census conducted in 1995-97. This represents a decrease in population of nearly 400,000 since the 1960's (USDI Fish and Wildl. Serv. 1996). Officially listed as an endangered species in 1967, *M. sodalis* has seen its population continue to decline despite efforts to protect its winter habitat. As a result, scientists are studying how forest management techniques affect the summer habitat and foraging areas of the Indiana bat.

The Indiana bat closely resembles other *Myotis* species, all of which have brown pelage and a nondescript appearance. *M. sodalis* commonly are mistaken for the little brown myotis (*Myotis lucifugus*), but is differentiated from other myotid bats within its range by the presence of short toe hairs (not extending beyond knuckle), a small foot (9 mm), and a keeled calcar. The pelage is generally dull and pinkish-brown dorsally. Length measurements of the Indiana bat throughout its area of distribution produced the following ranges (in mm): total length, 70.8 to 90.6, tail, 27 to 43.8, hind foot, 7.2 to 8.6, forearm, 36 to 40.4. Measurements of weight ranged from 5 to 11 g (Whitaker and Hamilton 1998).

The distribution of this species is generally associated with limestone caves in the Eastern United States. The northern extent of the range extends southward from New England to the panhandle of Florida (excluding the Atlantic Coast). The western margins of the range include the Ozark Plateau of Missouri, Arkansas, and Oklahoma. *M. sodalis* roost in trees during the summer and hibernates in caves and mines during the winter. Most of the Indiana bat population occupies only nine winter hibernacula located in Indiana, Kentucky, and Missouri (USDI Fish and Wildl. Serv. 1996).

We conducted an extensive review of the literature on the natural history of the Indiana bat, particularly those aspects that might be influenced by forest management. We particularly sought information on hibernacula selection, tree roosts in spring, summer, and fall, and use of foraging habitat in summer and during fall swarm. Information on hibernacula, roosting, and foraging is summarized in Tables 1-3 in the Appendix.

Indiana Bat Hibernacula

Distribution of Caves

Since 1960, most (85+ percent) Indiana bats have used nine Priority I hibernacula caves/mines in Indiana (*n*=3), Kentucky (*n*=3), and Missouri (*n*=3) (Hall 1962; Humphrey 1978; Richter et al. 1978; USDI Fish and Wildl. Serv. 1996). Priority I hibernacula contain at least 30,000 bats (USDI Fish and Wildl. Serv. 1996). The remaining 15 percent of Indiana bats have been or currently are distributed among 50+ Priority II and III hibernacula in the aforementioned states and Alabama, Arkansas, Connecticut, Georgia, Illinois, Iowa, Massachusetts, Michigan, New Jersey, New York, Ohio, Oklahoma, Pennsylvania, Tennessee, Virginia, West Virginia, and Wisconsin (Humphrey 1978; Dunn and Hall 1989; USDI Fish and Wildl. Serv. 1996). Priority II and III caves contain 500 to 30,000 and fewer than 500 hibernating bats, respectively. The small number of Priority I hibernacula means that fewer, peripheral hibernacula have significant importance in the protection of Indiana bats (Gates et al. 1984; Hobson and Holland 1995). Most hibernacula are found west of the Appalachian Mountains (though some are found in the Ridge and Valley and the southern Blue Ridge provinces) and are centered on the lower Ohio River Valley area of southern Indiana, eastern and central Kentucky, and the eastern Ozark Plateau region in Missouri. Hall (1962) hypothesized that this distribution is related to both cave suitability/availability and proximity to major river courses that are used for annual migration. Most Indiana bats return to the same cave or localized cave cluster each fall (Griffin 1940; Hall 1962; LaVal and LaVal 1980).

Cave Characteristics

Because the number of Indiana bat hibernacula is limited relative to other species (Raesly and Gates 1986), the physical and microclimatic characteristics of the known hibernacula are well documented (Hall 1962; Myers 1964; Henshaw 1965; Henshaw and Folk 1966; Barbour and Davis 1969; LaVal et al. 1976; LaVal and LaVal 1980; Clawson 1984; Harvey and McDaniel 1986; Brack et al. 1984; Raesly and Gates 1986; Saugey et al. 1990; USDI Fish and Wildl. Serv. 1999; Tuttle and Kennedy 1999). Variables that influence the suitability of caves for hibernacula include size of cave entrance, size and configuration of cavern room and passageway, ceiling structure, airflow, temperature, fluctuation in seasonal temperatures, humidity, previous occupancy by Indiana bats, and occupancy by other species (Hall 1962; Raesly and Gates 1986).

Occupied hibernacula have noticeable airflow (Henshaw 1965). Tuttle and Kennedy (1999) hypothesized that Indiana bats prefer hibernacula with the lowest nonfreezing temperatures possible. Core range (Indiana, Kentucky, and Missouri), midwinter cave temperatures of 2° to 5°C have been reported for Indiana bat cluster sites (Hall 1962; Henshaw 1965; Henshaw and Folk 1966; Thomson 1982). However, Barbour and Davis (1969) and Humphrey (1978) found hibernacula temperatures ranging from −1.6° to 17°C across the entire wintering season and hibernating range. Using continually recording data loggers, Tuttle and Kennedy (1999) recorded an overwinter range of −8.3° to 13.1°C from 15 important hibernacula in Kentucky (4), Illinois

(1), Indiana (5), Missouri (3), Tennessee (1), and Virginia (1). A retrospective analysis of temperature and population trend for some of these caves revealed population increases in four of six caves where overwinter temperatures ranged from 3° to 7.2°C and population declines in all four caves/mines where overwinter temperatures exceeded 8.1°C or were less than 0°C (Tuttle and Kennedy 1999). Hibernacula temperatures in Arkansas and Oklahoma and in Maryland, Virginia, and West Virginia typically are warmer (7° to 10°C) than caves in other portions of the range (Harvey and McDaniel 1986; Raesly and Gates 1987; Saugey et al. 1990). Warmer temperatures may increase metabolic rates in Indiana bats and cause premature fat depletion during the hibernation period (Richter et al. 1993). Stable midwinter temperatures of 1° to 10°C may represent a thermal threshold for hibernacula occupancy by *M. sodalis* (Clawson 1984).

Relative humidity ranged from 70 to nearly 100 percent in most hibernacula surveyed (Hall 1962; LaVal et al. 1976; Humphrey 1978; Tuttle and Kennedy 1999). Large caves, such as those in the Mammoth Cave and nearby systems in Kentucky, generally are too dry for the Indiana bat (Hall 1962). Raesly and Gates (1986) quantitatively compared hibernacula microhabitat and microclimate variables for Indiana bats, eastern pipistrelles (*Pipistrellus subflavus*), little brown myotis, northern long-eared myotis (*M. septentrionalis*), and big brown bats (*Eptesicus fuscus*). Relative to cave conditions chosen by other bat species, Indiana bats occupied open cave ceiling areas where the ambient air temperature and cave wall temperature were lowest, relative humidity was highest, and airflow was greatest. Because Indiana bats cluster in large groups in most hibernacula, intraspecific spacing was lowest among all species surveyed. *M. sodalis* clusters can reach densities of 3,000 per m^2 (Barbour and Davis 1969). Raesly and Gates (1986) also compared microhabitat and microclimate variables between occupied (n = 8) and unoccupied (n = 42) caves and mines. They found that Indiana bat hibernacula tended to have larger openings (9.7 vs. 2.8 m^2) and cave passages (858.8 vs. 131.6 m), and higher ceilings (13.2 vs. 6.3 m) than unoccupied sites.

Hibernation Chronology and Ecology

Indiana bats arrive at hibernacula or hibernacula areas (< 5 km radius of hibernacula) from mid-August to October (Kiser and Elliot 1996) and November (Hall 1962; Humphrey 1978). Copulation occurs during this time (LaVal and LaVal 1980), though ovulation, fertilization, and implantation do not occur until females have left hibernacula in the spring (Thomson 1982). Intense foraging and subsequent fat deposition critical for the wintering period occur after arrival at hibernacula and prior to cessation of aboveground activity in October for females and November for males (Humphrey 1978; Kiser and Elliot 1996).

In late summer and fall, Indiana bats swarm or gather in large numbers near cave entrances. The reason for this swarming behavior is not completely understood, but is possibly related to mating behavior. Early researchers mistakenly believed that sex ratios were skewed toward males because their netting efforts occurred in the late swarm after most females had entered hibernacula for the winter season (Hall 1962). Intercave movements may occur from the latter portion of the swarm to the early portion of the hibernation period. Consequently, population estimation using banding and mark-recapture techniques is unreliable if focused solely on single caves within this period (Clawson and Sheriff 1982).

Arrival weights of bats at the hibernacula range from 6 to 10 g (Hall 1962; Kiser and Elliot 1996). During the early swarm, *M. sodalis* roost in the warmer portions of the hibernacula and forage nightly to build fat reserves (Hassel 1967; Kiser and Elliot 1996). Prior to hibernation, females reach a maximum mass of 8.9 g vs. 8.0 g for males (LaVal and LaVal 1980). Fecal analysis of netted Indiana bats revealed that prehibernation diets were dominated by Lepidoptera (28.5 to 34 percent), Coleoptera (15.9 to 40.2 percent), Homoptera (4.5 to 15.3 percent), and Diptera (14.8 to 28.2 percent).

Exposure to and accumulation of environmental contaminants could occur during the prehibernation period of intense foraging and rapid fat deposition (Reidinger 1972). Contaminants were directly implicated in some local extirpations and are suspected as a factor in the decline of insectivorous bat species in North America (Clark 1981). Body burdens of organochlorine insecticides (now banned for agricultural use in the United States) in insectivorous bats were higher in modified agricultural landscapes than in wild or seminatural landscapes (Reidinger 1976). Clark and Prouty (1976) found lower pesticide burdens in eastern pipistrelles, northern long-eared myotis, and big brown bats near known *M. sodalis* hibernacula sites in forested areas of West Virginia where industrial facilities and agricultural land were largely absent. McFarland (1998) reported that Indiana bats in northern Missouri were routinely exposed to agricultural pesticides. Little brown myotis and northern long-eared myotis collected in northern Missouri in 1996 contained residues of eight historically applied organochlorine insecticides and two synthetic pyrethroids. Further, depressed brain acetylcholinesterase levels in these bats showed evidence of exposure to organophosphate and/or carbamate insecticides (McFarland 1998). Little is known about Indiana bat-pesticide relationships (USDI Fish and Wildl. Serv. 1996).

During the prehibernation swarming period in the mountainous and heavily forested Cumberland Escarpment and Cliff section of eastern Kentucky, Kiser and Elliot (1996) used radiotelemetry to determine that

Indiana bats foraged more on upper slopes and xeric ridgelines with second-growth chestnut oak (*Quercus prinus*)-pine (*Pinus* spp.) and oak-hickory (*Carya* spp.) forests than in riparian areas or moist slope-cove forests. LaVal et al. (1977) and Brack (1983) reported that chemiluminescent light-tagged Indiana bats foraged over oak-hickory forested hillsides and ridgetops in Missouri and upland habitats in Indiana, respectively, during the early swarm, prehibernation period. Kiser and Elliot (1996) hypothesized that cooler autumn temperatures (and subsequent cold-air drainage in locations with hilly or mountainous relief) limit insect abundance and activity in riparian areas and sheltered cove forests, whereas upper slopes and ridgelines have more favorable "warm" exposures. The maximum size of Indiana bat foraging areas during October, including the cave site, was 318 ha in 1994 and 194 ha in 1995; travel distances from the cave site were ≤ 2.5 km (Kiser and Elliot 1996).

Indiana bats periodically use tree roosts during the fall swarm. In eastern Kentucky, these roosts were located predominately in medium-size hardwood snags (mean diameter breast height [d.b.h] of 27.0 cm) within small forest openings or canopy gaps (Kiser and Elliot 1996). On the Fernow Experimental Forest in West Virginia, Indiana bats chose similar-size tree roosts (mean d.b.h. of 33.1 cm) in the early swarm period. However, 80 percent of the roosts were in live trees rather than snags (Thomas Schuler, Northeastern Research Station, unpubl. data). Neither study quantitatively measured use versus availability of tree roosts.

The relationship between hibernacula of *M. sodalis* and landscape features is poorly understood (USDI Fish and Wildl. Serv. 1996). Raesly and Gates (1986) found that hibernacula occupied by Indiana bats in Maryland, Virginia, and West Virginia (*n* = 8) tended to have more surrounding forest cover and less area in cultivated fields within a radius of 1 km than unoccupied caves and mines (*n* = 42). However, the authors cautioned that more meaningful habitat analyses during the swarm period must include measures of insect abundance and availability.

Kiser and Elliot (1996) suggested that all snags within 2.5 km of hibernacula be retained and encouraged snag creation through girdling and reforestation of abandoned pastures and reclaimed surface mines with native hardwood tree species. Clawson (1984) reported that deforestation around hibernacula has decreased available foraging habitat throughout the Indiana bat's range during prehibernation.

Wintering

The inactive hibernation period for Indiana bats is approximately 190 days (October to April for females, November to May for males) depending on the hibernacula (Hall 1962). Indiana bats form large clusters in cooler hibernacula or cooler portions within hibernacula and smaller, more transient clusters in warmer hibernacula (Hall 1962; Thomson 1982). Indiana bats are true hibernators (Guthrie 1933; Thomson 1982); though, they arouse every 8 to 10 days (Hardin and Hassell 1970). *M. sodalis* that use low roosts in Great Scott Cave in Missouri moved throughout winter to areas within the cave with more optimal temperatures (Tuttle and Kennedy 1999).

Arousal following disturbance (e.g., by spelunkers, scientists, predators) can be detrimental, and may be one of the greatest threats to *M. sodalis* (Hall 1962; Myers 1964; LaVal et al. 1976; Humphrey 1978; LaVal and LaVal 1980; Brack et al. 1984; Clawson 1984). Mild sound and light stimuli can initiate arousal (Humphrey 1978), as can a drop in cave humidity below 85 percent (Tuttle and Kennedy 1999). Sudden arousal is accompanied by excessive agitation, movement and in-cave flight that can expend 20 to 30 days of stored energy reserves (Daan 1973). Sudden arousal events can accelerated fat depletion, result in premature emergence from hibernacula, and lower body condition and survival in spring (Clawson 1984; Tuttle and Kennedy 1999). Even in the absence of disturbance, weight loss in early winter is rapid. Bats lose 0.016 g/day, slowing to 0.008 g/day by mid- to late winter (Hall 1962).

Indiana bats are particularly vulnerable to vandalism during hibernation (Dunn and Hall 1989) as many instances of wanton destruction of bat colonies have been documented (Hall 1962; Myers 1964; LaVal et al. 1976; Humphrey 1978; LaVal and LaVal 1980; Brack et al. 1984; Clawson 1984). Potential or historic hibernacula that regularly are disturbed will not support wintering *M. sodalis*. In most instances, recolonization following cave protection has not occurred (Harvey and McDaniel 1986). Entry by humans into Indiana bat hibernacula should be prohibited from September through May (Humphrey 1978; LaVal and LaVal 1980; Clawson 1984; USDI Fish and Wildl. Serv. 1996).

Improperly designed cave gates that alter cave airflow regimes (particularly trapping warm air) reduce and in some instances make hibernacula unsuitable (Tuttle 1977; Humphrey 1978; Richter et al. 1993; Tuttle and Kennedy 1999). Tuttle and Kennedy (1999) suggested restoring airflow or improving temperature regimes in 15 Indiana bat hibernacula by removing entrance obstructions, building cold-air dams, or installing ventilation shafts. Cave-specific recommendations are dependent on cave characteristics and the extent of anthropogenic alteration.

Numerous instances of intra- and inter-hibernacula movements by Indiana bats have been documented (Myers 1964; Hardin and Hassell 1970; Fenton and Morris 1976). Although most movement were attributed to cave disturbance by humans (Myers 1964; LaVal and LaVal 1980), *M. sodalis* will move within caves during hibernation to roost sites where microclimatic conditions are better (Tuttle and Kennedy 1999). Generally, midwinter movements are limited to intra-hibernacula sallies in colonies that are minimally disturbed; colonies subjected to frequent or intense human disturbance will shift hibernacula (Myers 1964). Hall (1962) believed that Indiana bats wintering in Coach Cave, Kentucky, engaged in midwinter feeding during warm weather based on the presence of fresh fecal discharge of chitin.

Indiana bats in hibernacula also are vulnerable to natural disturbances. Local catastrophes can have tremendous conservation implications because of the limited number of hibernacula (Hall 1962). Midwinter flooding of caves can cause significant mortality by drowning trapped bats or inducing energy-expensive arousal (Cope and Ward 1965). Hibernating *M. sodalis* can freeze to death in caves that trap and hold cold air during periods of unseasonably frigid temperatures (Humphrey 1978; Richter et al. 1993). Ceiling collapses, which have killed Indiana bats and blocked passageways in mine sites (Hall 1962; Humphrey 1978), can occur in caves and mines (USDI Fish and Wildl. Serv. 1996).

Emergence

Indiana bats emerge from hibernacula from mid-April through May (Hobson and Holland 1995). Females typically leave caves before males (Humphrey 1978; LaVal and LaVal 1980); they are not visibly pregnant at emergence (LaVal and LaVal 1980). The chronology and patterns of female movements to maternity areas are unknown. Smaller caves in the hibernacula area may serve as "spring movement" roosts for Indiana bats following initial emergence (Myers 1964). Hobson and Holland (1995) tracked a single radio-marked male Indiana bat for 2 weeks following mid-May hibernacula emergence in western Virginia. The bat traveled 16 km from the hibernaculum to forage over a 625-ha patch of mature, second-growth, oak-hickory forest with a hemlock (*Tsuga canadensis*) riparian component. Diurnal roosting during this period occurred in a mature shagbark hickory (*C. ovata*) with other male Indiana bats. Additional identification of postemergence foraging and roosting habitat may be required for meaningful efforts designed to protect Indiana bats (Hobson and Holland 1995).

Research Questions and Needs

There are several important research questions related to Indiana bat hibernacula that remain to be addressed:

1. What landscape-scale characteristics and biological factors are ecologically important to Indiana bats with respect to hibernacula? Since all Priority I and II, and most Priority III, hibernacula sites probably are known, an attempt should be made to distinguish landscape and land-use features for hibernacula where *M. sodalis is* increasing, stable, or declining. The effects of forest management directly around hibernacula on the microclimate and suitability of the mines/caves should be identified. Researchers should use remote-sensing and GIS technologies with data from Indiana, Kentucky, and Missouri to examine the relationship of forest cover, type, and structure/age to population trends of hibernacula. Because only three radiotelemetry studies have addressed pre- and posthibernation habitat and roost selection, a geographically expanded program using radiotelemetry should be undertaken for a more complete understanding of Indiana bat foraging and roost selection. If bats rely on this period to accumulate overwinter energy stores, this aspect of the biology of *M. sodalis* may prove the most crucial to conservation efforts. Concomitant efforts are needed to more clearly identify Indiana bat food habits during prehibernation and postemergence across its entire range. The relation between insect abundance and availability and *M. sodalis* population densities and trends among hibernacula also should be explored.

2. What is the continued vulnerability of Indiana bats to pesticide exposure during the prehibernation swarm and postemergence? Considering the proximity of large agricultural landscapes to most Priority I hibernacula, is there a continued and measurable bioaccumulation of organochlorines? What other unknown environmental contaminant burdens do Indiana bats currently face, e.g., organophosphate insecticides and heavy metals? Could environmental contaminants that singularly occur at harmless tissue concentrations act in synergistic fashion to cause Indiana bat mortality or to lower overall fitness and survival? What role does insecticide use play in decreasing insect abundance and *M. sodalis* foraging efficiency during the prehibernation swarm or postemergence?

3. Should wintering colonies of Indiana bats be considered in the context of genetically or evolutionarily significant management units because of the extreme philopatry they show toward an individual hibernaculum, and because breeding occurs upon hibernacula arrival during the swarm? Accordingly, natural recolonization and use of historical but abandoned hibernacula following restoration and protection may not occur or at a rate too slow to overcome population declines. How can recolonization of historical hibernacula by Indiana bats be encouraged or enhanced via active management?

Spring, Summer, and Fall Roosting Habitat

General Roosting Ecology

Female Indiana bats form small maternity colonies (usually <100) under exfoliating bark during the summer months (Whitaker and Hamilton 1998). A single young is born in early summer (Mumford and Calvert 1960). Maternity colonies usually are composed only of females and young (Humphrey et al 1977) with the males roosting separately (Hall 1962). Young usually are volant by early to mid-July (Humphrey et al. 1977). Maternity roosts most commonly are located in bottomland or riparian areas (Gardner et al. 1991b; Callahan et al. 1997). However, maternity roosts occasionally have been found in other areas, e.g., pastures and upland hardwoods (Kurta et al. 1993a; Whitaker and Hamilton 1998). Male summer roosts can be found in a variety of locations. In Illinois, bachelor colonies of 1,000 to 1,500 were located in an abandoned mine. Other roosts of males have been found under exfoliating bark (Gardner et al. 1991b).

Indiana bat roosts used during spring, summer, and autumn can be placed into one of two categories: primary or alternate (Callahan et al. 1997). Primary roosts are trees that are used by more than 30 bats on more than one occasion. Alternate roosts are used by fewer individuals. Both roost types are essential to meet the maternity requirements of *M. sodalis*. Although a 30-bat threshold may not be applicable to all colonies (especially to those with fewer than 30 bats), the concept of primary and alternate roosts is used throughout this section.

Tree Species Used/Preferred

One of the earliest reported maternity roosts of the Indiana bat was a primary roost in a bitternut hickory (*C. cordiformis*) snag and an alternate roost in a live shagbark hickory (*C. ovata*; Humphrey et al. 1977). Roosts in living trees are most commonly found in shagbark hickory (Gardner et al. 1991b; Callahan et al. 1997). Indiana bats roost in snags of many tree species, including red (*Acer rubrum*), silver (*A. saccharinum*), and sugar (*A. saccharum*) maple, bitternut, shagbark, and pignut (*C. glabra*) hickory, cottonwood (*Populus deltoides*), white (*Fraxinus americana*), black (*F. nigra*), and green (*F. pennsylvanica*) ash, American sycamore (*Platanus occidentalis*), white (*Q. alba*), scarlet (*Q. coccinea*), shingle (*Q. imbricaria*), northern red (*Q. rubra*), and post (*Q. stellata*) oak, eastern hemlock (*Tsuga* canadensis), sassafras (*Sassafras albidum*), and American (*U. americana*) and slippery (*Ulmus rubra*) elm (Brack 1983; Gardner et al. 1991b; King 1992; Kurta et al. 1993a; Caryl and Kurta 1996; Kurta et al. 1996; Salyers et al. 1996; Callahan et al. 1997). In Kentucky, Indiana bats may roost in Virginia pine (*P. virginiana*) and shortleaf pine (*P. echinata*) and females also may use sourwood (*Oxydendum arboreum*) in autumn and early spring (Kiser and Elliott 1996; MacGregor et al. 1999).

Some biologists consider the previously mentioned tree species as "acceptable" (Gardner et al. 1991b; Rommé et al. 1995). However, new tree species frequently are added to this list (MacGregor et al. 1999), so it may be premature to consider the list as definitive. Except for Kurta et al. (1996), all reports of roost-tree preference are observational. Statistical designs were not used to test preference, though Kurta et al. demonstrated that Indiana bats prefer green ash to silver maple. Silver maple also was documented as a roost tree in other studies (Gardner et al. 1991b; Callahan et al. 1997).

The use of snags by Indiana bats may be influenced by bark characteristics. Because virtually all maternity roosts are found under exfoliating bark, the characteristics of a species as a snag may be more important than the tree species on which the bark is present (Rommé et al. 1995).

Indiana bats also use artificial roost structures. In central Indiana, Salyers et al. (1996) found two male *M. sodalis* roosting in a bat box. Using radiotelemetry, they tracked one bat to other bat boxes and a cedar shake garland. Butchkoski and Hassinger (2001) found a maternity colony roosting in the attic of a church in Pennsylvania. Wilhide et al. (1999) found a male Indiana bat roosting under the metal brackets of a utility pole top in the Ozark National Forest in Arkansas, and Mumford and Cope (1958) made two references to *M. sodalis* males roosting under bridges in Indiana.

Tree Condition

Although, some alternate roosts occur in living trees (primarily shagbark hickory), most Indiana bats roost in dead or dying trees. One of the two roost trees reported by Humphrey et al. (1977) was a live shagbark hickory. About 10 percent of the roost trees from Illinois reported by Gardner et al. (1991b) and 28 percent of the trees reported by Callahan et al. (1997) were classified as live. Live and dead trees may differ in protection from rain and solar radiation provided by their canopy as rates of heat loss (Humphrey et al. 1977; Garner et al. 1991b; Callahan et al. 1997).

Structural Characteristics of Roost Trees

Few maternity colonies have been located in tree cavities. Most primary maternity roosts are situated under exfoliating bark. The ability of a tree species to produce exfoliating bark probably influences Indiana bat use (Callahan et al. 1997; Rommé et al. 1995). Both Kurta et al. (1996) and Callahan et al. (1997) found that the quantitative amount of loose, peeling bark did not differ between roost trees used and random snag samples not used. These studies did not address the qualitative features of exfoliating bark.

Most maternity roosts are found in large trees. The average diameter for all roosts described by Gardner et al. (1991b) was 36.7 (range: 8 to 83 cm); the four roosts with the largest numbers of bats averaged 40 cm d.b.h. Primary roost trees described by Callahan et al. (1997) averaged 58.4 ± 4.5 cm d.b.h. Alternate roosts averaged 53.0 ± 4.1 cm d.b.h. Kurta et al. (1996) found that the average diameter of Indiana bat tree roosts (0 = 40.9 ± 1.2 cm; range: 30 to 52 cm) were significantly less variable than the average diameter of random trees (0 = 33.4 ± 1.4 cm; range: 11 to 70 cm).

The results of studies examining roost tree size effect on selectivity are conflicting (Kurta et al. 1996; Callahan et al. 1997). Gardner et al. (1991b) arbitrarily concluded from 48 roost trees that dead trees at least 22 cm d.b.h provided essential *M. sodalis* roosting habitat, but their designation of appropriate species was limited to tree species that they documented. Additionally, Indiana bats sometimes roost in snags smaller than 22 cm d.b.h and in species not found in Gardner et al.'s (1991b) list. The spring and autumn roosts of male Indiana bats do not differ greatly in size from those used during summer. Autumn and spring roosts reported from western Virginia and Kentucky ranged from 8.4 to 86.6 cm d.b.h, with a mean of 31 cm (Hobson and Holland 1995; Kiser and Elliott 1996; MacGregor et al. 1999).

Solar Exposure and Spatial Relation to Neighboring Trees

Most primary roosts are well exposed to extensive solar radiation. However, some alternate roosts are completely shaded while others are totally exposed. Indiana bats may pick maternity roosts with high solar exposure to increase the roost temperature, which might decrease the time of fetal development and juvenile growth (Callahan et al. 1997). However, because males are not associated with maternity colonies and the need for high roosting temperatures (Callahan et al. 1997), they may seek cooler roosts to conserve energy.

Gardner et al. (1991b) reported that most Indiana bat roosts in Illinois were beneath the forest canopy. However, canopy closure was estimated using multiple readings with a spherical densiometer taken near tree bases. These readings would most accurately reflect canopy closure of the forest where the roost was located rather than solar exposure of the roost. Callahan et al. (1997) considered roosts as open (exposed to solar radiation) or interior (less than 50 percent canopy cover) and found all primary roosts in open snags. Live interior roost trees averaged 70 percent canopy closure and were more open on the western aspect than random live trees. Interior snags used as roosts averaged 60 percent canopy closure and were more open on all aspects than random interior snags. MacGregor et al. (1999) reported that canopy closure ranged from 20 to 93 percent for male Indiana bat roosts (0 = 80 percent). However, MacGregor et al. (1999) noted that there is no effective method for measuring the canopy closure (solar exposure) at the actual roost. And tools such as the spherical densiometer, fisheye photography, and competition indexes used to assess canopy closure can yield different results (Cook et al. 1995; Comeau et al. 1998).

Different methodologies might explain discrepancies among studies of primary roosts and solar exposure. Reports of solar exposure for alternate roosts range from complete shade to total exposure. Alternate roosts are used when conditions in the primary roost are suboptimal (Callahan et al. 1997). Because conditions that make roost sites temporarily uninhabitable can vary (e.g., extreme high or low temperatures, precipitation), the structural characteristics of alternate roosts also vary.

In addition to canopy cover, roost height also affects the degree of solar exposure. The average height of closed-canopy roost trees used as primary maternity roosts in Illinois was 7.8 m (Gardner et al. 1991b). The average height of alternate roosts used by females was 6.4 m in areas under a forest canopy, 5.2 m in areas with a "patchy" forest canopy, and 2.7 m in trees in the open. Although not compared statistically, this trend shows that females tended to roost higher in the canopy in closed-canopy forests.

Roost heights may vary with canopy cover so that bats can to maintain a relatively constant level of solar exposure. Callahan et al. (1997) reported that 45 percent of maternity roosts in Missouri were in open areas and that more Indiana bats used open-area than closed-canopy roosts. The maternity colony in Michigan roosted in snags in the middle of a flooded pasture turned wetland (Kurta et al. 1996). All snags were unshaded and the mean roost height was 9.9 m (± 0.9; range: 1.4 to 18 m).

Male Indiana bats exhibit different habits with regard to roosting height and solar exposure. Gardner et al. (1991b) found that the average roost height used by males was 4.2 m (4.9 m in closed canopy and 3 m in "patchy" canopy). They also reported only one male roost from an open canopy at a height of 4 m. A male Indiana bat tracked in western Virginia by Hobson and Holland (1995) roosted at a height exceeding 8 m each night for 19 consecutive nights.

Canopy Cover of Stands

The canopy cover in stands used by Indiana bats is described inadequately, though stand characteristics can be inferred from Gardner et al. (1991b), Kurta et al. (1996), and Callahan et al. (1997). Methods used by Gardner et al. to measure canopy closure best describe closure at the stand level. Of 48 roosts that they found in forested habitats, 32 were in closed-canopy forests, 12 were in intermediate forests, and 4 were in open-canopy forests. All roosts reported by Kurta et al. (1996) were from a 5-ha flooded wetland where all trees were dead or dying. This wetland had an open canopy. The American sycamore roost reported by Kurta et al. (1993a) was unshaded indicating reduced canopy closure. In Missouri, Callahan et al. (1997) calculated the canopy closure of random trees located within the stand as an indication of stand canopy closure. Forest canopy closure averaged nearly 70 percent for all non-used trees.

Spatial Relationship of Roost to Water Sources and Foraging Areas

The proximity of Indiana bat roosts to water sources and foraging areas has not been well studied. Two roost trees reported by Humphrey et al. (1997) in Indiana were located less than 200 m from the creek that *M. sodalis* used for foraging. A roost tree described by Brack (1983) was on the bank of the Blue River in Indiana. Also in Indiana, Kurta et al. (1993a) reported a hollow sycamore roost that was 28 m from a dry intermittent stream and 2 km from the nearest perennial stream. Roost trees described by Kurta et al. (1996) were located within a 5-ha Michigan wetland inundated with as much as 1 m of water. The bats left this area each night to feed in the surrounding landscape that was composed of agricultural lands (pasture and corn), woodlots, and an extensive riparian strip of woods. All colonies reported by Callahan et al. (1997) were located near a stream or river.

Gardner et al. (1991b) reported distances from roosts to foraging areas in Illinois as great as 3,200 m (post-lactating female), with approximately equal distances for pregnant and lactating bats (1,000 m). Juveniles and adult males traveled about half the distance of females as their roosts were closer to streams than any other habitat feature measured. The mean distance between all Indiana bat roost trees tracked to the nearest intermittent stream was 124 m. In western Virginia, a single adult male Indiana bat repeatedly traveled 1 km from its roost site to foraging areas that included a stream and a road (Hobson and Holland 1995).

Spatial Relationship to Other Roost Trees

There is considerable variation in the distances that Indiana bats travel between roost trees within a colony. In Indiana, Humphrey et al. (1977) reported that two roost trees they observed were approximately 30 m apart. In Illinois, Gardner et al. (1991b) collected one of the largest data sets to date of *M. sodalis* roost trees, but did not associate roosts with particular colonies or report distances among roost trees that were used by each Indiana bat. In Michigan, Kurta et al. (1996) found that the average distance between roosts used by a single Indiana bat colony was 38.7 ± 7.1 m (range 1 to 147 m). In Missouri, Callahan et al. (1997) did not report the distance between roosts but provided the diameter of a circle that would encompass all roosts used by a single maternity colony. The smallest and largest "colony areas" had diameters of 1.6 and 3 km, respectively. In Kentucky, MacGregor et al. (1999) reported that distances between autumn roosts of males ranged from 48 m to 2,688 m encompassing areas from 0.4 to 568 ha.

Density of Potential Roost Trees

There is little information on densities of potential tree roosts for Indiana bat maternity colonies primarily because there is no universally accepted definition of a potential roost. Gardner et al. (1991b) listed the optimal number of roost trees as 64 per ha for upland habitat and 41 per ha for floodplains. Rather than describing a quantitative method for obtaining these data, their numbers were derived from a snag density survey (d.b.h. > 22 cm) of acceptable species within the study area. Bark characteristics and decay classes were not reported. As part of a mitigation project, Salyers et al. (1996) reported a potential roost density of 15 trees/ha, which was raised to 30.4 roost sites/ha after instillation of artificial roost structures.

In Missouri, Callahan et al. (1997) reported the largest distances between roosts of a single maternity colony. Although all roosts were not discovered, the highest density was 0.25 roost tree/ha. In a 5-ha Michigan wetland, Kurta et al. (1996) found that Indiana bats roosted in 23 different trees at a density of 4.6 ha. They reported that there were 66 available roost trees in the wetland (13.2 potential roost trees/ha), an unusually high snag density.

Due to features such as species, size, and bark characteristics, not all snags make acceptable Indiana bat roosts (Gardner et al. 1991b; Kurta et al. 1996; Callahan et al. 1997). These features vary from area to area with no predictable pattern (Kurta et al. 1996; Callahan et al. 1997). As a result, a variety of snag types must be maintained to maximize the chance that snags with suitable structural characteristics for Indiana bats will be present. Additional information is needed to define what constitutes suitable Indiana bat roost.

The number of roost trees needed by an Indiana bat colony is unknown and probably varies by colony size and roost availability. Roost use also can change in response to unpredictable climatic conditions. Roost attrition precludes managers from being able to set aside a minimum number of potential roosts. Also, the unpredictable nature of natural roost destruction hinders managers in predicting the longevity of current roost trees, and the time needed for a tree to become "suitable" for Indiana bats is unknown and probably varies by tree species and location.

Stand Composition

There are no quantitative descriptions of stand composition for forests surrounding Indiana bat roosts. However, all studies provide descriptions of the study areas. Based on most descriptions, the stands surrounding roosts do not differ substantially in composition from the list of species used as roosts (see Tree Species Used/Preferred). Kurta et al. (1996) commented that, although there were 99 green ash, 34 silver maple, and 9 American elm trees in their study area, only green ash trees were used as roosts. However, Indiana bat roosts have been found in both silver maple and American elm in other studies (Gardner et al. 1991b). Tree species reported in study areas that have not been used as roosts by Indiana bats include box elder (*A. negundo*), black walnut (*Juglans nigra*), and willow (*Salix* sp.). Further study is needed to elucidate how tree species composition at the landscape scale affects roost site selection by Indiana bats.

Stand Structure

The stand structure surrounding Indiana bat maternity colonies have not been described quantitatively, though there have been comparisons with roost trees to randomly located potential roosts within a stand. In Michigan, Kurta et al. (1996) found that roost trees within in the stand were larger (d.b.h.) and less variable in diameter than randomly located potential roost snags. However, Callahan et al. (1997) found that roost-tree characteristics such as d.b.h. or bark cover did not differ statistically from potential roosts within a stand in Missouri.

Roost trees occur in many habitat types with different stand structures. Gardner et al. (1991b) found roosts in grazed uplands (n = 26), nongrazed uplands (n = 9), nongrazed floodplains (n = 8), a clearcut (n = 1), a hoglot (n = 1), and a pasture (n = 1). Kurta et al. (1993a) also reported a roost tree from the middle of a heavily grazed pasture. Recent research has documented maternity colony use in a green-tree reservoir and along swamp edges in southern Illinois where tree mortality was substantial due to from flooding of the Mississippi River during 1993 and 1995 (T. C. Carter, unpubl. data).

MacGregor et al. (1999) reported that two-age shelterwood harvests on the Daniel Boone National Forest in Kentucky can produce different amounts of autumn roosting habitat for Indiana bats depending on the harvests' snag retention. Their guidelines called for retention of all snags, hollow trees, live trees with large dead limbs, and shagbark hickories. These guidelines produced stands with 15 times the roost trees retained with conventionally managed two-age shelterwoods (5 snags/ha). Roost sites were also found in burned areas managed for the red-cockaded woodpecker (*Picoides borealis*). Although this information is anecdotal, it suggests that Indiana bats may be more tolerant of limited disturbance of the roosting area. Practices such as even-age and uneven-age management can be used provided they include provisions for snag retention and favor oaks and shagbark hickories (Callahan et al. 1997). Still, there is little quantitative information on the effect of timber management practices on roost selection by Indiana bats.

Forest Type and Topography

Indiana bat roosts have been commonly found among mixed mesophytic hardwood and mixed hardwood-pine habitat types. Humphrey at al. (1977) and Brack (1983), located roosts in riparian habitats in Indiana. In Illinois, Gardner et al. (1991b) found 37 roost in uplands and 11 roosts in bottomlands. All roosts located by Kurta et al. (1996) were in a Michigan wetland habitat. In Missouri, Callahan et al. (1997) located roosts in riparian and upland habitats. In eastern Kentucky, MacGregor et al. (1999) reported that male Indiana bats roosted in pine-dominated forests during the autumn.

Size of Area Surrounding Roosts

The area used by Indiana bats surrounding their roosts varies among colonies. However, it is not always known where colony members forage and whether or not all colony roosts were discovered. Indiana bats tracked by Kurta et al. (1996) traveled outside their immediate roosting area to forage, but the exact location or extent was not known (Allen Kurta, Eastern Michigan University, pers. commun.). Humphrey et al. (1977) observed that bats traveled from their roosts to a nearby stream where they foraged along a 0.81-km section. Indiana bats have been observed foraging among and adjacent to roosts, and in areas disjunct from roosts.

Landscape Structure

Gardner et al. (1991b) made the only attempt to document composition of landscape habitat. Within the study area, 65 percent was cropland or old fields, 2 percent other agriculture, 33 percent forested (30 percent upland and 2.2 percent floodplain), and 0.1 percent impounded water habitat. At a larger scale, Illinois was 63 percent agricultural, 1.6 percent urban, 33 percent forested, 6.4 percent forested wetlands, and 1.3 percent impounded water. The impact of forest fragmentation on roost availability of Indiana bats at the landscape scale is unknown.

We are not aware of studies that have examined the effect of landscape-level disturbance regimes (e.g., fire, timber harvest) on availability of Indiana bat roosts. As suggested by the Indiana Bat Recovery Plan (USDI Fish and Wildl. Serv. 1996), the effect of availability of stands with "suitable" roosting habitat must be examined.

Rommé et al. (1995) used previously published data to develop a Habitat Suitability Index model for Indiana bats that asses habitat quality across the landscape. We are not aware of studies that have applied or validated the HSI model.

Research Questions and Needs

1. Further study of the Indiana bat's summer roosting habitat is needed as the mechanisms influencing roost selection remain unknown. We know that Indiana bat colonies use multiple trees to meet maternity requirements, but we do not know what resources each of these roosts provides or how resources change under different conditions. Also needed are studies of the factors that affect Indiana bat roosting behavior.

2. Research is needed on the effects of forest management on Indiana bat roosting ecology. It is not known how different management practices affect the quantity and quality of roosting structure and roosting habitat.

3. No studies have examined the reproductive output of an Indiana bat colony. This information is crucial to understand the species' capacity to recover from its current decline. Bats have relatively low reproductive outputs (Findley 1993). Without an understanding of Indiana bat reproduction, the period needed for this species to rebound from past disturbances cannot be assessed accurately. Claims of short-term declines or increases in populations (local or species wide) require an understanding of recruitment.

4. The relationships between stand structure and Indiana bat reproduction should be evaluated. Little or no work has investigated the impacts of timber harvests on maternity colonies. However, anecdotal evidence suggests that *M. sodalis* may benefit from limited disturbance around potential roosting areas. Limited disturbance can create potential roost trees and open the canopy around potential roost trees (Gardner et al. 1991b; Kurta et al. 1993a). It is important that such research evaluates how these practices affect both colony behavior and individual fitness. Disturbances from forest management that change behavior but do not adversely affect fitness may be benign.

Foraging Habitat

Species Composition/Vegetational Community Type

Indiana bats often forage in riparian areas (Humphrey et al. 1977; LaVal and LaVal 1980; Kessler et al. 1981; Brack 1983), woodlots (Mumford and Cope 1958), and upland forests (Easterla and Watkins 1969; LaVal et al. 1977; LaVal and LaVal 1980; Brack 1983). In summarizing past captures of Indiana bats, Mumford and Whitaker (1982) noted that some individuals had been collected (shot) when foraging around the crowns of oak and hickory trees. Brady (1983) observed in east-central Indiana that in riparian areas where four *M. sodalis* maternity colonies were located, 90 percent of the tree species were (in frequency of occurence) boxelder, silver maple, ash, sycamore, snags, sugarberry (*Celtis occidentalis*), American elm, willow, cottonwood, black walnut, honey locust (*Gleditsia triacanthos*), Ohio buckeye (*Aesculus glabra*), and slippery elm. Brack (1983) noted that at net sites where Indiana bats were captured, oaks or hickories (or both) dominated.

In Missouri, LaVal et al. (1977) observed 69 Indiana bats to which Cylalume Chemical Lightsticks (chemoluminescent tags) had been attached. The bats foraged under the forest canopy in dense wooded areas along ridges and hilltops. Their observations supported previous reports that Indiana bats primarily forage 2 to 30 m above the ground (Humphrey et al. 1977). Their results also indicated that Indiana bats forage in a greater diversity of habitat types, including uplands, than reported by Humphrey et al. (1977). LaVal et al. (1977) rarely observed Indiana bats foraging directly over water and suggested that low capture rates over streams experienced by Humphrey et al. supported these observations. However, the latter noted that low capture rates over water probably were related to the ability of Indiana bats to avoid nets rather than to the absence of bats along stream corridors. A study by Gardner et al. (1989) supported this hypothesis.

Brack (1983) observed chemoluminescent-tagged Indiana bats foraging in riparian areas, upland forests, and over a pond, a pasture, and an old field in Indiana. Most foraging occurred along habitat edges. Foraging occurred above, below, and around tree canopies in forested habitats, along the forest/stream edge in riparian areas, and along the edge of pastures and old fields.

Clark et al. (1987) captured Indiana bats in mist nets along narrow, disturbed riparian strips, wooded floodplains, and upland forests. Nearly 43 percent of Indiana bats (n = 12) were netted during nine nights of sampling at a highly disturbed, fragmented riparian strip. Cooling degree- days in May, heating degree-days in June, June maximum temperature, and June minimum temperature best predicted the presence of Indiana bats. These and other climatic factors may serve as environmental covariates when testing the significance of vegetation structure and vegetational community type on the presence of *M. sodalis*.

Bowles (1981) used mist-net surveys to document Indiana bat occurrence at four sites in Iowa. He captured reproductively active females at sites that varied greatly in structure and vegetational composition. These included highly disturbed, narrow (< 15 m) riparian habitats containing young trees (< 15 m tall and < 40 cm d.b.h.), mature riparian areas, and mature upland forests. Bowles suggested that Indiana bats are at least somewhat opportunistic in selecting summer foraging habitat.

Hobson and Holland (1995) used triangulation techniques, direct observation, and the receiver's attenuator to delineate foraging areas of radio-tagged bats. The 625-ha foraging area used by one male Indiana bat was an 80-year-old oak-hickory, mixed deciduous forest with a conifer component. The bat foraged in an elliptical pattern at canopy height. The authors did not indicate how many foraging locations were used to delineate the foraging area, how many points were obtained using triangulation or direct observation, or the degree of error associated with the radiotelemetry.

LaVal and LaVal (1980) captured Indiana bats along narrow riparian strips and in forest patches adjacent to streams in eastern Missouri. If riparian forests were the preferred foraging habitat for Indiana bats, then their summer foraging habitat was reduced greatly. However, if one uses the metric "one colony/km suitable riparian habitat and 12 colonies/county," the available habitat was not fully utilized.

Examination of fecal pellet also can provide insight into the foraging habitats of *M. sodalis*. Most myotids are opportunistic foragers and the differences observed between bat diets and available insects are a result of bats foraging in specific habitats and randomly feeding on insects rather than randomly foraging across habitats and selecting specific types of insects (Belwood and Fenton 1976; Fenton and Morris 1976; Whitaker 1995). If this is true for Indiana bats, foraging habitat can be assessed by examining the insects consumed.

Analyses of Indiana bat diets suggest that foraging habitats differ between their southern and northern distributions (Kurta and Whitaker 1998). Studies by Belwood (1979) and Brack (1983) in Missouri indicate that *M. sodalis* commonly forages in upland habitats in the southern portion of its range. Conversely, in Michigan, Kurta and Whitaker (1998) found that Indiana bats forage primarily in wetland habitats. Additional information is needed on the Indiana bat's diet and foraging habitat selection throughout its range.

Selection and Avoidance at Stand Scale

Humphrey et al. (1977) used Indiana bats tagged with fluorescent bands to determine relative levels of foraging activity among different vegetation communities. The bats foraged exclusively in riparian habitats despite the availability of upland forests, pastures, cornfields, upland hedge rows, and treeless creek banks. Although no statistical comparison of use versus available habitat was conducted to test for foraging habitat selection, the study indicated that *M. sodalis* forages primarily in wooded riparian areas and did not use other habitats. A criticism of fluorescent bands is that researchers must make visual contact with the marked bats. Another source of bias is the implicit assumption that foraging Indiana bats were equally visible among all habitat types examined. Humphrey et al. (1977) also assumed (albeit unstated) that if no marked Indiana bats were observed foraging in the individual forest stand, pasture, cornfield, upland hedge row, or treeless creek bank they surveyed, then these habitat types were not used elsewhere. It is unclear whether these assumptions were valid. Their results show that Indiana bats foraged in wooded riparian areas, but do not confirm that wooded riparian areas were preferred over the other habitat types they observed.

Following LaVal et al. (1977), Brack (1983) used chemoluminescent tags to compare the proportion of sightings in riparian habitat to that expected based on the availability of riparian habitats in the study area. Brack observed that foraging occurred mostly in upland woods, though his statistical analyses comparing habitat availability and use indicated that *M sodalis* did not preferentially forage in, or avoid, riparian habitats (Brack 1983, 1991). Brack (1983) also compared the proportion of foraging activity that occurred in forested habitats to that expected based on forested habitat abundance in the study area. Forested areas were selected over open areas (e.g., pastures, old fields) by foraging Indiana bats. These results provide one of the most quantitative examinations of foraging habitat selection by *M. sodalis*. However, the authors relied on the assumption that the probability of observing light tagged Indiana bats did not differ among riparian and nonriparian habitats, and among forested or nonforested habitats.

In Illinois, Gardner et al. (1989, 1991b) used radiotelemetry to analyze the foraging habits of the Indiana bat and to determine the size of the foraging ranges of 17 *M. sodalis* (2 pregnant, 6 lactating, 1 postlactating, 2 juvenile females, 3 juvenile males, 3 adult males). The study area in each foraging range was divided into 11 cover types: cropland, hayfield or pasture, old field, other agricultural land, upland forest with closed, intermediate, or open canopy, and floodplain forest with closed, intermediate, or open canopy, and pond. Foraging areas consisted primarily of cropland (49 percent), closed canopy floodplain forest (14.8 percent), and closed canopy upland forest (11.6 percent). Hayfield and pastures accounted for 7.1 percent, as did old fields.

Gardner et al. quantitatively tested for differences between proportions of habitat used and available using the program PREFER. Foraging Indiana bats selected closed-canopy (80 to 100 percent closure) floodplain forest. However, Gardner et al. used the minimum convex polygon method to define foraging ranges. Large areas unused by *M. sodalis* may have been included in the home range analysis (see White and Garrott 1990). For example, on average, 49 percent of minimum convex polygon foraging areas was composed of row crops. However, this does not necessarily mean that the bats spent 49 percent of their time foraging in row crops. Thus, the results presented by Gardner et al. (1991b) may not have reflected the amount of use for each habitat type. Determining the proportion of actual foraging locations in each habitat type would have been a more useful analysis of habitat use.

Another potential limitation of the analyses by Gardner et al. (1991b) is their definition of available habitat. Thomas and Taylor (1990) suggested that habitat use and availability be compared at multiple spatial scales. The size of the available foraging area (3,672 ha) defined by Gardner et al. (1991b) seems reasonable based on distances that Indiana bats traveled between roost and foraging areas. However, they reported use versus availability for only one spatial scale, and comparison among studies will be difficult unless the same spatial scale is used in future studies.

Gardner et al. (1991b) characterized habitats in 340-, 1,809-, and 5,278-ha concentric circles around sampling sites where Indiana bats had been captured. There was great variability in habitat use, e.g., deciduous forest (5 to 98 percent), evergreen forest (5 to 26.7 percent), total forest (5 to 98 percent), forested wetlands (0.07 to 59.6 percent), and cropland (zero to 95 percent). Although. these results support Bowles' (1981) observation that *M. sodalis* are somewhat opportunistic in selecting summer foraging habitats, they should be interpreted with caution. This type of analysis assumes that Indiana bats are captured near the center rather than at the edge of their home range, and gives equal importance to abundance of habitats 1 to 4 km from capture locations and habitats immediately surrounding the point of capture.

Foraging Height

Using ultrasonic detectors, Humphrey et al. (1977) found that Indiana bat foraging height was 2 to 30 m. Because of atmospheric sound attenuation, the ability to detect foraging bats with ultrasonic detectors decreases with increasing distance. Therefore, most myotid calls are difficult to detect with ultrasonic detectors at distances beyond 30 m. It is unclear how Humphrey et al. considered the relationship between distance and observability, both visually and with ultrasonic detectors. Thus, Indiana bat foraging activity at heights greater than 30 m may not have been observed due to limitations associated with methods used rather than a lack of foraging activity above this height.

On the basis of mist-netting captures, Brack (1983) found that Indiana bat capture rates were significantly greater at heights of 7.6 to 10.6 m than at 0.6 to 7.5 m. No bats were captured at heights less than 0.60 m. When interpreting data on capture per unit effort from mist nets, one must assume equal observability (in this case observability = capturability) among all treatments. If capture probability is unequal among treatments, differences in capture rates may result from differences in capture probability rather than from actual differences among treatments. Brack (1983) did not address potential differences in capture probability among vertical sampling strata, and it is unclear whether the assumption of equal capture probability was valid. Although Brack's results support Humphrey's observations, neither study provides conclusive evidence that Indiana bats selectively forage in specific strata within the forest canopy. Results of Brack's light-tagging experiment supported his mist-netting data with respect to preferred foraging heights used by *M sodalis* in the upper canopy.

Stand Structure/Canopy Cover

Brack (1983) noted that net sites where Indiana bats were captured had openings (gaps) in the forest canopy. Callahan (1993) located Indiana bat maternity roosts in northern Missouri in a stand that had been heavily logged within the past 20 years and in a hoglot where many overstory trees had been killed. He noted that these habitat modifications may have benefited *M. sodalis* by removing most of the canopy cover and leaving many standing dead trees. It is unclear how structural changes caused by logging or the girdling of overstory trees in the hoglot affected the use of these areas by foraging bats.

In Illinois, Indiana bats forage in areas that had been selectively harvested (Gardner et al. 1991b; J. MacGregor pers. observ.). These observations suggest that Indiana bats forage in areas where some timber harvesting has occurred, but they are not useful in determining preference or avoidence of harvested areas. Research is needed on the effect of timber harvest (e.g., shelterwood, deferment, and clearcuts) on the suitability of Indiana bat foraging habitat.

Relationship Between Habitat Selection and Stand Structure

Humphrey et al. (1977) suggested that Indiana bats forage only in riparian areas with some vertical structure, i.e., *M. sodalis* were not observed foraging along riparian areas denuded of woody vegetation. In addition, although there were other habitats with little or no vertical structure (e.g., pastures, cornfields) near the maternity roosts monitored, Humphrey et al. did not observe Indiana bats foraging in them.

Brack (1983) found that forest stand structural components that significantly influenced Indiana bat captures included (in order of importance): (1) whether the habitat was riparian or nonriparian, (2) amount of vegetation in the understory, (3) overstory species richness, and (4) understory species richness. The probability of capturing an Indiana bat in a mist net increased if habitat was riparian, understory density was low, overstory species richness was high, and understory species richness was low. However, these results depend on the assumption that the probability of bat capture did not differ among the 35 netting sites and that none of the factors listed affected capture probability. If Indiana bats are easier to net in riparian than in nonriparian areas, the observed differences in capture rates may be a reflection of differences in capture probability rather than actual differences in habitat use.

Assumptions associated with capture probability must be considered when indices are used. Brack (1983) recognized problems associated with using mist nets to determine bat spatial activity patterns. Many researchers have a feel for where a species can be captured, and when to try and capture it, but there is little quantitative evidence available for most species as to where, how high, and when they are active. There are problems associated with any capture method that is intended to show true abundance of an organism at a given place or time. The same is true for mist netting.

Forest Type and Topography

The relationship between stream corridors and Indiana bat foraging activity is unclear. Humphrey et al. (1977) suggested that Indiana bats forage preferentially in areas near streams (i.e., riparian corridors). However, most foraging activity observed by LaVal et al. (1977) occurred in upland forests. Sampling both riparian and nonriparian areas, Brack (1983) found that capture per unit effort of *M. sodalis* was higher in riparian areas, though the effect of stream proximity on Indiana bat foraging activity remains unknown.

Size of Home Range or Colony Foraging Area

Humphrey et al. (1977) found that foraging area used by one Indiana bat maternity colony in Indiana ranged from 1.5 to 4.5 ha. However, it is possible that maternity colony foraging areas were much larger than observed. As bats disperse from a central location such as roost trees, density decreases and observability declines. This also is true for radiotelemetry studies, and it becomes more severe as detection distance decreases. The extent to which decreased observability with distance from roost affected results of Humphrey et al. is unknown.

Humphrey et al. (1977) also suggested that foraging area is influenced by the time of summer and the level of development of young bats in the colony. Because they studied the foraging range of a single colony during two periods of a single summer, the significance of the observed change in size of foraging area is difficult to determine. All light-tagged Indiana bats observed by LaVal et al. (1977) were within 2 km of their release point, supporting the assertion by Humphrey et al. that Indiana bats use smaller foraging areas than other myotids (LaVal et al. 1977; Menzel et al. 2000).

Spatial Relations Between Roost and Foraging Areas

Foraging areas may be unimodal (one area with no patches of activity elsewhere) in and near summer roosts (usually ≤ 1,000 m; see Gardner et al. 1991b). LaVal and LaVal (1980) used a helicopter to observe two light-tagged male Indiana bats foraging (in July) 5 km from their roost in Great Scott Cave in Missouri. Using radiotelemetry, Hobson and Holland (1995) documented a male Indiana bat foraging within 1 km of the roost tree.

Foraging Site Philopatry

Indiana bats migrate yearly between hibernacula and summer maternity areas. Cope et al. (1973), Humphrey et al. (1977), and Gardner et al. (1991b, 1996) suggested that some individuals return to the same summer breeding areas each year. Data provided by Gardner et al. (1991b, 1996) are quantitative and therefore reliable. One individual tracked by radiotelemetry in 1986 and 1988 in the same summer breeding area exhibited a high degree of foraging area overlap. Gardner et al. (1991b) also found a high degree of overlap used by a Indiana bat colony in Illinois in 1987 and 1988.

Proportion of Landscape in Foraging Habitat

At the landscape scale, Miller et al. (1996) compared abundances of several habitat types, forest perimeter, tree species present, d.b.h., and percent canopy cover between sites in Missouri where Indiana bats had and had not been captured. They found no difference in percent coverage of forest, row crop, grassland, or water cover between capture and noncapture sites. However, sites where Indiana bats were present contained a significantly greater number of large-diameter trees than sites where *M. sodalis* were absent. Miller et al. used mist netting to verify the presence or absence of Indiana bat maternity colonies. It is relatively easy to verify Indiana bat presence via mist nets, but failure to capture an Indiana bat does not verify absence.

Callahan (1993) characterized roost types selected by *M. sodalis* maternity colonies. He also attempted to elucidate "habitat characteristics of areas used by maternal Indiana bat colonies." He defined the use areas in two ways: (1) the smallest circle that encompassed all maternal roost tees located in a colony (defined as the minimum roost range), and (2) a 3-km circle centered around the minimum roost range. Callahan classified the habitat types in these two areas surrounding four Indiana bat maternity colonies as forest, row crop, or field/pasture. The average minimum roost range and 3-km circle surrounding the four colonies was 39 percent forest, 12 percent row crop, and 49 percent field/pasture, and 24 percent forest, 8 percent row crop, and 65 percent field/pasture, respectively. No information about actual use of foraging habitats was provided.

Research Questions and Needs

1. Quantitative studies of Indiana bat foraging habitat selection are needed. Methods previously used to determine foraging areas used by *M. sodalis* include unaided visual observations, visual observations of light-tagged individuals and reflectively banded individuals, comparison of netting sites where Indiana bats have and have not been captured, examination of diet, and radiotelemetry. Indiana bat calls can be differentiated from the calls of other myotids. If technology continues to improve, future studies may rely more on the use of bat detectors. However, radiotelemetry currently is most reliable method for gathering data related to foraging habitat selection. Obviously, it will be important to sample throughout the night and to minimize error polygons.

2. Foraging point distribution (i.e., the vegetational community types and habitat structure where they fall) should be statistically compared to a random distribution of locations from the available foraging area (or the proportion of each vegetative community type in the study area). How available foraging areas are defined should be better described and should be spatially related to roosts. Error associated with radiotelemetry should be quantified and described. Differences between the distribution of foraging locations and randomly located points also should be examined in relation to abiotic factors (e.g., streams, roads, buildings). Efforts should be made to conduct these studies on colonies inhabiting areas near forests that have recently been subjected to disturbance, e.g., timber harvests and road construction.

3. Large portions of the Indiana bat's home range can occur over agricultural fields. Additional data on point foraging are needed to determine the extent to which *M. sodalis* forage over agricultural fields. If agricultural fields are used appreciably, the direct or indirect (by affecting preferred insects) effect of pesticides on Indiana bats should be quantified.

Conclusion

Indiana bat hibernacula and hibernacula characteristics have been well documented by numerous observational studies reported in the literature. However, reported research on foraging and roosting habitat use during the prehibernation swarm and posthibernation emergence is limited. We are aware of only three studies, one in eastern Kentucky and one each in north-central West Virginia and western Virginia, on the perhiphery of this species' range. Similarly, food habits during these critical periods are poorly documented. The implications of exposure to environmental contaminants such as agricultural pesticides during prehibernation and posthibernation emergence are not understood. Issues such as winter hibernacula protection to minimize or prevent Indiana bat disturbance and manage cave airflow are well understood and must be addressed on a cave-by-cave basis.

Outside the hibernation period, Indiana bats use both live trees and snags for roosts. Although roosts have been documented in a wide array of hardwood and pine species, trees and snags that have exfoliating bark, such as shagbark hickory, may be important. Indiana bat roost trees have been reported within forests above and below the canopy and among isolated trees or single trees in open areas such as wetlands, fields, and pastures with correspondingly wide ranges in solar exposure. Distances from known roosts to water, foraging areas, and alternative roost trees also are variable, ranging up to 3 km, depending on landscape and topography. Roost-tree density necessary to support Indiana bats is not understood and negative or positive biological thresholds linked to roost abundance are unknown. Similarly, there are no quantitative studies that adequately describe species composition of forest stands or stand structure surrounding occupied roosts. Forest cover around Indiana bat roosts ranges from less than 33 percent in the agricultural Midwest to virtually 100 percent in the Appalachians. In the Midwest, Indiana bats have been observed roosting in or near both bottomland/wetland forest habitats and upland forest habitats; in the eastern and southeastern peripheries of their distribution in the Appalachians, *M. sodalis* have been observed roosting in upland forests.

Indiana bats use many habitats for foraging, including riparian areas, upland forests, ponds, and fields. *M. sodalis* may forage in specific vertical strata in these habitats, though the preferred heights are unknown. The effects of timber harvesting on Indiana bat foraging patterns also is unknown. Research is needed to understand the effects forest management on the foraging habitats of *M. sodalis* during the spring and fall swarm and during summer. Size of foraging habitat seems to be dependent on the sex and age of the bat and location of the foraging area. Indiana bats have smaller foraging ranges than other myotids, and the foraging ranges of individual bats commonly overlap. There also is evidence that Indiana bats return to the same summer foraging areas each year.

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Appendix

Table 1.—Issues and techniques in studies of Indiana bat hibernacula

Study	Issue	Technique	Comment
Barbour and Davis (1969)	General biology	Review paper	
Brack (1983)	Swarm foraging	Light tags	Foraged over oak-hickory uplands
Brack et al. (1984)	Hibernacula characteristics	Observation	
Clark (1981)	Contaminants	Review paper	Includes many species of bats
Clark and Prouty (1976)	Contaminants	Bioassay	Examined other bats near Indiana bat hibernacula in mid-Atlantic
Clawson (1984)	General biology	Review paper	Identifies management issues
Clawson and Sheriff (1982)	Population estimation at hibernacula	Observation	
Cope and Ward (1965)	Natural mortality	Observation	Identifies cave flooding as mortality agent
Dunn and Hall (1989)	Population status	Observation	
Gates et al. (1984)	Cave habitat analysis	Observation	Only study that addresses landscape characteristics as environmental variables influencing cave use and Indiana bat populations
Griffin (1940)	General biology	Observation	
Kiser and Elliot (1996)	Swarm foraging	Radiotelemetry	Identified habitat use, roost tree use and food habits in prehibernation swarm
Hall (1962)	General biology	Observation	Comprehensive review of Indiana bat biology up to 1962
Hardin and Hassell (1970)	Hibernation activity	Observation	
Harvey and McDaniel (1986)	Population status	Observation	Population decline in Arkansas
Hassell (1967)	Hibernation activity	Observation	
Henshaw (1965)	Hibernation physiology	Observation	
Henshaw and Folk (1966)	Hibernation physiology	Observation	
Hobson and Holland (1995)	Posthibernation emergence	Radiotelemetry	Notes movement of single male in western Virginia
Humphrey (1978)	Hibernacula characteristics	Review paper	Comprehensive discussion of hibernacula conservation
LaVal et al. (1976)	Habitat analysis	Observation	
LaVal et al. (1977)	Foraging activity	Light tags	
LaVal and LaVal (1980)	Hibernacula characteristics	Observation	
McFarland (1998)	Contaminants	Bioassays and LD_{50} trials	Used surrogate myotids
Myers (1964)	Hibernacula characteristics	Observation	
Rasely and Gates (1986)	Hibernacula characteristics	Observation	
Reidinger (1976)	Contaminants	Bioassays	Does not include Indiana bats
Richter et al. (1993)	Cave airflow	Observation	Changed airflow from modified cave entrances is responsible for some declining Indiana bat populations
Richter et al. (1978)	Population status	Observation	Documents discovery of unknown hibernacula
Saugey et al. (1990)	Population status	Observation	
Thomson (1982)	General biology	Review paper	Mammalian species account
Tuttle (1977)	Cave gating	Review paper	
Tuttle and Kennedy (1999)	Hibernacula characteristics	Observation	Detailed microclimatic conditions in major Indiana bat hibernacula
U.S. Fish and Wildl. Serv. (1996)	General biology	Review paper	Recovery plan

Table 2.—Issues and techniques in studies of Indiana bat roosting habitat

Study	Issue	Technique	Comment
Brack (1983)	Maternity roost-tree selection	Observation	Single roost tree
Brady (1983)	Summer ecology	Review paper	Discusses cause of endangerment, summer habitat, and threats; makes recommendations
Callahan et al. (1997)	Maternity roost-tree selection	Telemetry	Data collected in early 1990s; four different colonies
Carly and Kurta (1996)	Maternity roost	Observation	Abstract only; preliminary work
Gardner et al. (1996)	Roost-tree selection (male and female)	Telemetry, observation	Same data set as in publications from 1990, 1991a
Harvey and McDaniel (1986)	Population decline	Review paper	
Hobson and Holland (1995)	Spring roost-tree selection	Telemetry, observation	Single roost tree
Humphrey et al. (1977)	Maternity roost-tree selection	Roost destruction, observation	First report of roost trees
King (1992)	Michigan	Telemetry, observation	Initial discovery of location for Kurta et al. 1993a, 1996
Kiser and Elliott (1996)	Autumn roost-tree selection	Telemetry, observation	Habitat and roost-tree use and food habits in prehibernation swarm
Kurta et al. (1993a)	Maternity roost-tree selection	Telemetry, observation	
Kurta et al. (1993b)	Maternity roost-tree selection	Telemetry, observation	Pilot study of Kurta et al. 1996
Kurta et al. (1996)	Maternity roost-tree selection	Telemetry	Northern edge of *M. sodalis* range; small flooded wetland
MacGregor et al. (1999)	Autumn roost-tree selection	Telemetry, observation	22 males tracked to 102 trees
Mumford and Cope (1958)	Indiana	Observation	One roost tree and one bridge
Salyer et al. (1996)	Artificial roosts	Observation	Two trees and first use of bat box
Tingle and Mitchell (1985)	Habitat delineation	HSI Model	No data based on Gardner et al. (1991)

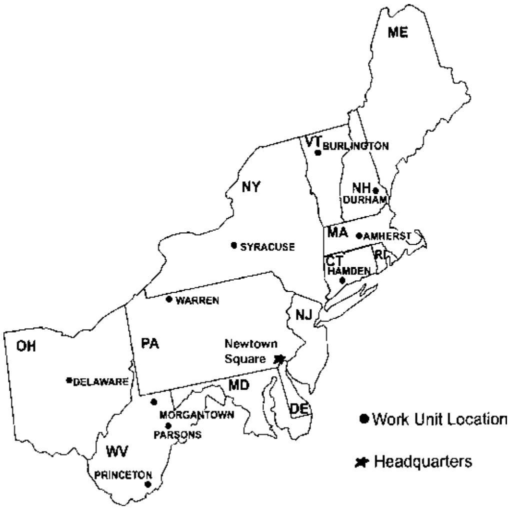
Table 3.—Issues and techniques in studies of Indiana bat foraging habitat

Study	Issue	Technique	Comment
Belwood (1979)	Feeding ecology	Fecal analysis	Morphology, prey selection
Belwood and Fenton (1976)	Diet	Observation	Includes *Myotis lucifugus*
Bowles (1981)	Summer status	Observation	
Brack (1983)	Swarm foraging	Light tags	Foraged over oak-hickory uplands
Brady (1981)	Recovery plan	Review paper	Abstract
Callahan (1993)	Summer habitat	Radio-telemetry	Includes roost trees
Clark et al. (1987)	Summer distribution	Mistnetting	
Cope et al. (1973)	Maternity colony	Mistnetting	Elm tree maternity roost
Esterla and Watkins (1969)	Maternity colony	Observation	
Fenton and Morris (1976)	Foraging	Observation	Opportunistic feeders
Gardner et al. (1991b)	Foraging behavior	Radiotelemetry	Includes roosting sites
Gardner et al. (1996)	Summer distribution	Banding	Cave surveys in Illinois
Gardner et al. (1989)	Capture technique	Mistnetting	Emphasis on *M. sodalis*
Hobson and Holland (1995)	Posthibernation emergence	Radiotelemetry	Notes movement of single male in western Virginia
Humphrey (1977)	Summer habitat	Banding	Foraging habitat
Kessler et al. (1981)	Summer survey	Mistnetting	Maternity colony indentified
Kurta and Whitaker (1998)	Diet	Fecal pellets	Opportunistic feeders
LaVal and LaVal (1980)	Hibernacula characteristics	Observation	
Mumford and Cope (1958)	Summer records	Observation	
Miller et al. (1996)	Habitat use	Mistnetting	Summer habitat patterns
Romme et al. (1995)	Habitat suitability model	Review paper	Foraging habitat
Whitaker (1995)	Food habits	Fecal pellets	Includes *Eptesicus fuscus*

Menzel, Michael A.; Menzel, Jennifer M.; Carter, Timothy C.; Ford, W. Mark; Edwards, John W. 2001. **Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*).** Gen. Tech. Rep. NE-284. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 21 p.

Reviews the available literature on the ecology of the endangered Indiana bat (*Myotis sodalis*), including its selection and use of hibernacula, roost trees, and foraging habitat. An extensive list of published references related to the Indiana bat is included.

Keywords: foraging habitat, hibernacula, tree roosts, silviculture



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Benjamin Colter Jones
University of Tennessee - Knoxville

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To the Graduate Council:

I am submitting herewith a dissertation written by Benjamin Colter Jones entitled "Ruffed Grouse Habitat Use, Reproductive Ecology, and Survival in Western North Carolina." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

Craig A. Harper, Major Professor

We have read this dissertation and recommend its acceptance:

David A. Buehler, Frank T. van Manen, Arnold M. Saxton

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

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Vice Chancellor and Dean of
Graduate Studies

(Original signatures are on file with official student records.)

RUFFED GROUSE HABITAT USE, REPRODUCTIVE ECOLOGY, AND SURVIVAL IN WESTERN NORTH CAROLINA

A Dissertation
Presented for the
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Benjamin Colter Jones
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ABSTRACT

Ruffed grouse populations are lower in the Appalachians compared to the Great Lakes states, the geographic core of grouse distribution. Theories to explain lower numbers in the Appalachians include inadequate foods, lower reproduction, lower survival, and loss of habitat. To provide insight into ruffed grouse ecology in the Appalachians, habitat use, reproduction, and survival were studied on Nantahala National Forest in western North Carolina. Radiotagged grouse (*n* = 276) were monitored through the year. Seasonal 75% kernel home ranges (*n* = 172) averaged 15–59 ha across sexes, ages, and seasons. Home range size was related to habitat with smaller ranges occurring where 6–20-year-old mixed oak (SUBXER2) and forest roads (ROAD) were interspersed with other habitats. Across seasons, sexes and ages, SUBXER2 and ROAD were among preferred habitats. Compared to males, females used greater diversity of habitats, including >40-year-old stands. Use of older stands may have been influenced by food availability (i.e., hard mast). Nests (*n* = 44) were located to determine fate. The majority of nests (86%) were on mid and upper slopes in mature stands >40-years old. Proportion of successful nests was 81%. Mayfield nest survival was 0.83 (± 0.084 SE) and did not differ between juveniles and adults. Nesting rate was 73% and did not differ between juveniles and adults. One female renested, though high nest success precluded opportunities for documenting extent of renesting. Mean first nest clutch was 10.1 eggs. Broods (*n* = 35) were monitored intensively following hatch. Brood sites had greater herbaceous ground cover, vertical cover, midstory stem density, and invertebrate density compared to random sites. Mean home range size was 24.3 ha (±4.0 SE) using 75% kernel methods and 40.0 ha (± 4.0 SE) using MCP. Preferred habitats were mixed oak

0–5, 6–20, and >80-years old, forest roads, and edges of maintained clearings. Mean annual survival of grouse >3 months old was 0.39 (± 0.052 SE). Of mortalities, 43% were from mammalian predators, 27% avian, 13% unknown predation, 11% hunter harvest and 7% other causes. Scavenging prior to transmitter recovery may have inflated mammalian predation rates. Relatively low hunter harvest did not appear to be additive to natural mortality. Spring population density, estimated from drumming counts, decreased from 11.4 grouse/100ha in 2000 to 5.88 grouse/100 ha in 2004. Fall population density indexed by catch per unit effort also decreased during the study from 0.96 grouse/100 trap-days in 1999 to 0.19 grouse/100 trap-days in 2003. The fall population index was inversely related to annual survival ($r^2 = 0.76$, $P = 0.054$). The inverse relationship may have been a function of habitat availability. Annual recruitment indexed by proportion of juveniles in fall captures was less than reports from the northern core of ruffed grouse range. Overall percentage of juveniles in fall captures was 59.6%, ranging from 46.2–66.7%. Recommendations to increase grouse density include creating a diversity of forest types and age classes interspersed across the landscape. Alternative regeneration techniques such as shelterwood, irregular shelterwood, and group selection can be used to intersperse food and cover, thus improving grouse habitat.

PREFACE

Data presented here were collected over 5 years (1999–2004) on Wine Spring Creek Ecosystem Management Area (WSC) in Macon County, North Carolina. In addition to addressing local topics of interest, data collected from April 1999 to September 2002 were contributed to a regional research effort, the Appalachian Cooperative Grouse Research Project (ACGRP). Of 12 ACGRP study sites in 8 states (Kentucky, Maryland, North Carolina, Ohio, Pennsylvania, Rhode Island, Virginia, and West Virginia), WSC was at the most southerly extent of ruffed grouse range.

University of Tennessee graduate students, Carrie Schumacher and Jennifer Fettinger, presented partial reports from data collected 1999–2001 in their Master's theses. I led field data collection from August 2001 through study completion and analyzed the complete data set for presentation herein. The primary focus of this research was to investigate ruffed grouse habitat use, particularly as it related to forest management practices. Radiotagging ruffed grouse also presented opportunities to investigate other aspects of population ecology, including reproduction and survival. While investigating these parameters, efforts were made to relate results to habitat quality and identify potential for improvements. Chapters of this dissertation were submitted individually to peer-reviewed journals, and each represents an aspect of ruffed grouse ecology.

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PART I.

USE OF SPRING DRUMMING COUNTS TO INDEX RUFFED GROUSE POPULATIONS IN THE SOUTHERN APPALACHIANS

ABSTRACT

Drumming surveys are used as an index to monitor ruffed grouse (*Bonasa umbellus*) populations across the species' range; however, most reports of drumming behavior are from the Great Lakes Region. Ruffed grouse drumming behavior was studied in the southern Appalachian Mountains of North Carolina. Drumming counts were conducted from late March through mid-April, 2002 – 2004. Concurrent with drumming counts, radio-tagged males (n = 30) were monitored to determine proportion of males drumming. Drumming activity increased from late March (20% of males drumming) to a peak in mid-April (56 – 69% of males drumming). Consistent drumming coincided with mean nest initiation date by females (12 April, n = 44). Drumming count results suggested a decreasing population trend similar to fall trapping success on the study area. Drumming counts appear to be an effective tool to monitor grouse population trends in the southern Appalachians. In North Carolina, drumming counts should be conducted during the peak drumming period of 9–16 April.

Key words: Appalachians, *Bonasa umbellus*, drumming, North Carolina, population index, ruffed grouse.

INTRODUCTION

In the southeastern United States, ruffed grouse are distributed across 190,000 km^2 of forest in the Appalachian Mountains of Alabama, Georgia, Kentucky, Maryland, North Carolina, South Carolina, Tennessee, Virginia and West Virginia (Cole and Dimmick 1991). Ruffed grouse are associated with a mosaic of early-, mid-, and late-successional habitats. During the past decade, forest maturation and reduced forest management have resulted in contiguous areas lacking early successional components, causing population declines (Dessecker 2001).

Because of their close association with early seral stages, ruffed grouse (hereafter, grouse) are a Management Indicator Species (MIS) on many National Forests. The National Forest Land and Resource Management Plan requires that MIS be monitored to index population responses to habitat management (U.S. Department of Agriculture Forest Service 1982). State wildlife agencies often work in cooperation with the Forest Service on such monitoring efforts. Further, as grouse have gained popularity among hunters following a regional decline in northern bobwhite (*Colinus virginianus*), state agencies are interested in monitoring grouse population trends to assist in setting hunting seasons and bag limits (Cole and Dimmick 1991).

Drumming behavior of male grouse provides a basis for estimating their numbers. From telephone surveys with state agency personnel in the southern portion of grouse range, it was determined spring drumming counts were used to varying extents in Georgia, Kentucky, North Carolina, Ohio, Virginia, and West Virginia and a proposal for their use has been drafted in Tennessee. Drumming count methodology has been well described (Petraborg et al. 1953, Dorney et al. 1958, Gullion 1966). In short, number of grouse heard drumming along survey routes is recorded and reported as density per unit area sampled. Frequently, results are extrapolated to a population estimate with assumptions made regarding sex ratio, sampling area, and proportion of males drumming over time. Although these assumptions have been studied in the Great Lakes states (Gullion 1981, Rodgers 1981), no studies have explored chronology of spring drumming and efficacy of drumming counts to index grouse populations in the Southeast.

Objectives were to: (1) estimate drumming intensity from late March through April, (2) determine period of peak drumming activity, and (3) examine efficacy of drumming counts as a population index in the southern Appalachians.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (WSC) within the Nantahala National Forest in Macon County, North Carolina. The area is within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1644 m. Terrain was typical of the southern Blue Ridge with broad ridges, steep valleys and long connecting slopes (McNab and Browning 1993). Mean annual temperature was 10.4º C, and mean annual precipitation was 192 cm. Mixed deciduous hardwood, primarily oak (*Quercus* spp.) with some northern hardwoods on north and east aspects above 1219m elevation dominated (>99%) the area. Rhododendron (*Rhododendron maximum*) was a primary midstory component along stream drainages while mountain laurel (*Kalmia* spp.) and huckleberry (*Gaylussacia* spp.) were present on drier upland sites. The U.S. Forest Service purchased the Wine Spring area in 1912. Since then, timber has been harvested on an 80–100-year rotation, making it representative of most Forest Service lands within the southern Appalachians. Approximately 9% of the area was in the 6–20-year age class.

Grouse Capture and Population Monitoring

Grouse were captured using intercept traps (Liscinsky and Bailey 1955) during August –November and March–April, 1999–2003, fitted with 12-g necklace-style radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota) and released at capture sites. Two hundred seventy six grouse were radiotagged.

Spring drumming counts were conducted 24 March to 30 April 2001–2004. Observers walked designated routes (i.e., gated forest roads) on two consecutive mornings beginning 30 minutes before sunrise and ending three hours after sunrise. The starting point on the second morning was the endpoint from the first morning. Routes were selected across the area such that approximately 20% of the study area was sampled. Drumming counts were cancelled when winds were >13 km/h because of reduced ability of observers to hear drumming. Observers listened for drumming while walking continuously at a steady pace. When a drumming male was heard, distance to drummer, time, and an azimuth to the bird were recorded. Approximate location for each drumming grouse was plotted on a geographic information system (GIS). Drumming male locations were buffered by 150 m because grouse may use alternate drumming sites (Lovallo et al. 2000). If two locations from consecutive days fell within the same 150 m buffer, they were considered the same bird.

Population estimates (grouse/100 ha) were calculated by doubling number of drumming males heard to account for females under the assumption of a 1:1 breeding season sex ratio (Bump et al. 1947, Gullion and Marshall 1968, Rusch and Keith 1971). For these density estimates, it was necessary to determine effective sampling area. This was achieved by estimating radius of audibility, the maximum distance at which drumming grouse could be heard (Petraborg et al. 1953). Audibility trials (n = 10) were conducted opportunistically during routine fieldwork. When a drumming grouse was located, one observer remained close to the drumming site and raised a flag when drumming occurred. A second observer moved away from the drumming site in 25 m increments until drumming could no longer be heard. When visibility was limited between observers, hand-held radios were used to retain contact. Radius of audibility may vary with changes in topography and hearing ability of observers; however, time did not permit replication necessary to identify these sources of variation. The estimate should be viewed as a general, conservative estimate of audibility. Consistent with Petraborg et al. (1953), 200 m was determined as the maximum audibility distance; therefore, 400 m buffers around each route (i.e., 200 m on each side) defined sampling area.

In 2001, one drumming count was conducted during the week of 9–16 April (period 3). During 2002–2004, counts were conducted during each of the weekly periods, 24–31 March (period 1), 1–8 April (period 2), and 9–16 April (period 3). In 2004, additional counts were conducted 17–24 April (period 4), and 25 April–2 May (period 5). Population estimates were calculated for each period to identify temporal changes in drumming. This allowed comparison of estimates among periods within the same year. Because grouse populations should not fluctuate greatly (especially increase) over 4 weeks in April, it was assumed variation within the same spring was a result of changes in drumming behavior.

Drumming intensity is the percentage of radiotagged males heard drumming during a specific morning (Gullion 1966). To determine drumming intensity, radiotagged males were located and approached them within 50 m using care not to disturb the bird. After an initial quiet-down period of one minute, occurrence or non-occurrence of drumming was recorded during a 5-minute interval. A distance of 50 m was used a because it was well within the audible range of drumming, but not so close as to disturb the bird.

Observations were concurrent with drumming count periods in 2002 and 2003, allowing examination of within year changes in drumming intensity.

Porath and Vohs (1972) suggested peak of drumming in northeastern Iowa corresponded with copulation. To explore this relationship, telemetry data were used to estimate mean nest (*n* = 44) initiation date (Chapter II). Copulation occurs 3–7 days prior to laying the first egg (Bump et al. 1947); therefore, mean copulation date was estimated by subtracting this range from mean nest initiation date. Estimated copulation range was then compared graphically to drumming chronology.

Across year population trends were compared from Period 3 drumming counts to several data sources, including grouse hunter surveys, ancillary observations, and trapping success the following fall. The North Carolina Wildlife Resources Commission collects grouse hunter surveys annually. To identify population trends from those data, number of grouse flushed per hunter hour on public lands was calculated within the southern mountain region of North Carolina during the 2001–2004 hunting seasons. The 16-county southern mountain region included the WSC study area. Ancillary observations were recorded by research technicians on WSC. During routine radiotracking, technicians recorded kilometers driven and grouse observed along roads. Grouse seen per 100 km during the period, 15 March–30 April were compared to drumming counts. Fall trapping success on WSC, measured by grouse captured/100 trap-days, also was compared to drumming count data. Pearson correlation coefficients were calculated between drumming count population estimates and other indices using SAS (SAS Institute, Cary, North Carolina, USA).

RESULTS

Within each year, more drumming males were heard during period 3 than in periods 1 and 2. In 2004, number of drumming males heard decreased through periods 4 and 5, suggesting peak drumming activity in period3 (Figure 1.1; tables and figures are located in the Appendix). Population estimates from period 3 were 243%, 38%, and 242% greater than those from period 1 in 2002, 2003, and 2004, respectively.

Similar to drumming counts, drumming intensity generally increased from period 1 through period 3. In 2002, proportion of radiotagged males drumming was 20% ($n = 15$) in period1, 67% ($n = 13$) in period 2, and 69% ($n = 9$) in period 3. In 2003, proportion of radiotagged males drumming was 20% ($n = 10$), 18% ($n = 11$), and 56% ($n = 9$) in periods 1, 2, and 3, respectively. When further delineated by age, the above sample sizes were too small to detect meaningful differences in drumming intensity between juveniles and adults.

Estimated copulation was 5–9 April, just prior to annual peaks in drumming. Greatest drumming activity coincided more closely with nest initiation ($\overline{x}$ = 12 April, 10–14 April 95% CI) than mean copulation date across years.

Fall trapping success and drumming counts suggested decreasing population trends from 2001–2003 (Table 1.1). Pearson's correlation coefficient between these methods was not significant ($P = 0.332$). Lack of significance was likely a function of small sample size ($n = 3$ years). Hunter flush rates were consistent across years, and did not indicate population change. Ancillary observations suggested overall decline from

2001–2004, with an apparent population increase in 2003. Drumming counts were not correlated with hunter flush rates ($R = 0.351$, $P = 0.649$) or ancillary observations ($R = 0.225$, $P = 0.775$).

DISCUSSION

Of the four methods examined, all but hunter flush rates indicated population decline. There may be several reasons hunter surveys did not indicate population change. First, surveys were conducted across 16 counties, and decreasing population trends may not have been as pronounced regionally as they were on WSC; however, conversations with hunters and U.S. Forest Service personnel suggested grouse numbers were decreasing across North Carolina's southern mountain region. Second, hunter surveys may be insensitive to population changes as hunters continually return to areas where they experience success, rather than "sampling" new or unproductive coverts. Perceived population changes from hunter surveys may reflect shifting hunter patterns as old coverts mature and new ones are discovered.

Ancillary observations suggested a decline in grouse numbers between 2001 and 2004 despite a population spike in 2003 that was not apparent in drumming counts or trapping success (Table1.1). Ancillary observations can be sensitive to changes in observer travel patterns. While radiotracking a female grouse in 2003, frequent trips were made through an area where grouse often were observed along a forest road. These daily travels may have positively biased 2003 ancillary data. Data collected by wildlife agency and U.S. Forest Service personnel during fieldwork may be similarly biased as their travel routes probably would not be consistent over time. Amman and Ryel (1963) reported grouse observations made by U.S. Postal Service employees were an effective population index because mail carriers traveled the same distances and routes; however, in western North Carolina, mail carriers seldom travel through higher elevations that constitute grouse range in the region.

Drumming counts have been used extensively to monitor population trends and responses to habitat management in the Appalachians and across ruffed grouse range (Kubisiak 1985, Wiggers et al. 1992, McCaffery et al. 1996, Dimmick et al. 1998, Storm et al. 2003). Drumming counts conducted in mid-April can provide an effective means to monitor population trends in North Carolina. Due to non-drumming males, drumming surveys tend to underestimate number of birds on an area (Gullion 1966). Fortunately for managers attempting to inventory grouse populations, error remains rather constant across years until maximum population densities are reached (Gullion 1981). The greatest proportion of males drumming on any morning on WSC was 69%. Without a method to estimate proportion of males drumming concurrent with counts (i.e., radiotelemetry), it is not possible for managers to extrapolate accurate spring population estimates; therefore, drumming counts are best used as an index to population trends over time.

There are two main drumming count techniques; the walking method described for this study and others (Rodgers 1981, Dimmick et al. 1998), and roadside counts developed by Petraborg et al. (1953). Roadside counts involve driving a route and stopping at predefined listening points for 4–5 minutes before proceeding to the next point. Roadside counts are an effective method to determine population trends and allow coverage of a large area with relatively few observers (Petraborg et al. 1953, Stoll 1980). Walked routes are better suited to sampling smaller, specific areas of interest, such as wildlife management areas or research study sites. The utility of either technique to determine population trends depends on consistency of methods and timing of counts. Peaks of drumming activity occur at approximately the same time each spring (Gullion 1966); therefore, identifying peak periods and planning counts accordingly lends to consistency across years.

Earliest onset of spring drumming was recorded 9 March 2002. Ruffed grouse drumming activity on WSC peaked during the week of 9–16 April. Beyond the mid-April peak, drumming had nearly ceased by the first week in May. Studies in Minnesota and Wisconsin identified plateaus in drumming within 7 days of 1 May (Dorney et al. 1958, Gullion 1966). In Ohio and Iowa, drumming peaked between 15 and 25 April (Donohoe 1965, Porath and Vohs 1972). Hale et al. (1982) reported drumming activity began in mid-March in northern Georgia, but did not indicate when peak drumming occurred. Those data support the contention of Bump et al. (1947) that onset and peak of drumming behavior occur earlier in southerly latitudes.

Because drumming counts were conducted once each week, within-period error could not be assessed; however, field observations provided insight into variability over time. During all years, drumming remained sporadic through the end of March and during that period, occurred only on clear days with no precipitation and little wind. By mid-April (period 3), drumming became more consistent and males drummed despite overcast skies, precipitation and other inclement weather, including snow. Managers may not have flexibility to schedule drumming counts according to weather; therefore, planning surveys during peak drumming appears most advantageous. Nonetheless, high winds hinder the ability of observers to hear drumming, and surveys should be suspended if winds exceed 13 km/h (Petraborg et al. 1953).

On WSC, peak drumming coincided with nest initiation by females. Drumming behavior serves a dual purpose, to advertise territories and attract females (McBurney 1989). As females became preoccupied with nesting, males may have spent greater time on drumming logs attempting to attract mates. Incubation chronology compiled by Devers (2005) for the Appalachian Cooperative Grouse Research Project was backdated to estimate regional nest initiation dates (Table 1.2). Regional nest initiation dates should provide insight to managers regarding peak drumming for their area of interest.

Prompted by population declines in the southern extent of ruffed grouse range, managers are developing strategic plans for grouse in the Appalachians. Monitoring population trends and response to habitat manipulation over time is an integral part of any strategy. With appropriate planning and consistency, spring drumming counts provide an effective population index. Roadside counts and walked routes are equally viable techniques and choice of method depends on scale of area to be sampled (i.e., regional vs. management area). To reduce within- and across-year variability, surveys should be planned to coincide with peak drumming periods.

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APPENDIX

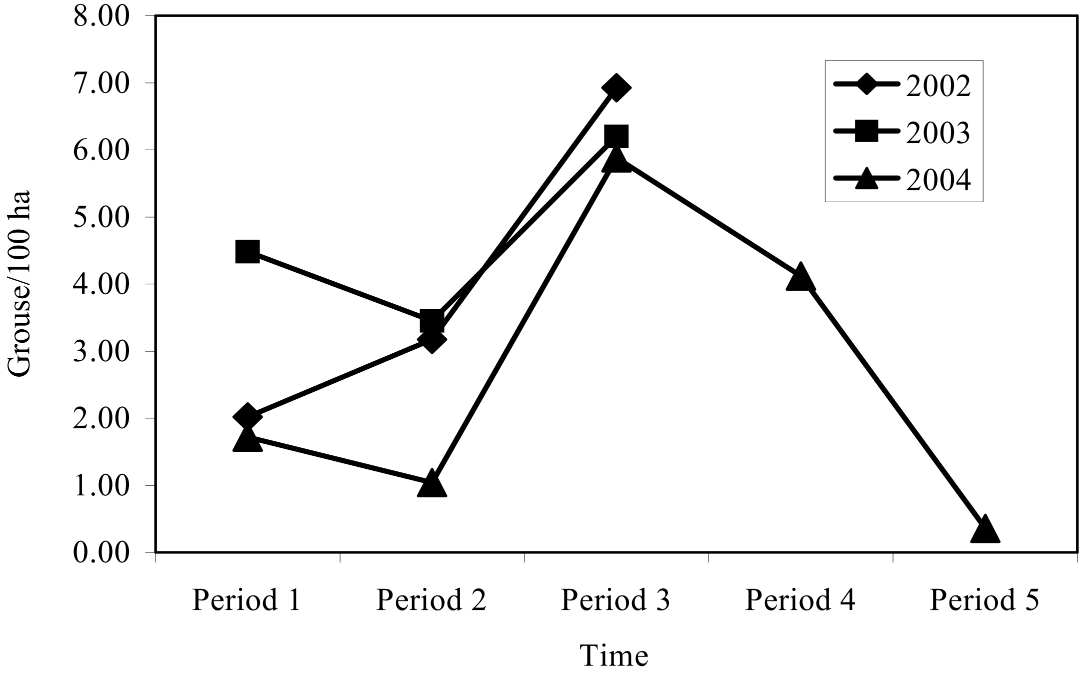

Figure 1.1. Ruffed grouse population estimates extrapolated from drumming counts conducted 24–31 March (period 1), 1–8 April (period 2), 9–16 April (period 3), 17–24 April (period 4), and 25 April–2 May (period 5), 2002–2004, on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina.

Table 1.1. Ruffed grouse population indices from drumming counts (grouse/100 ha), trapping success (grouse/100 trap-days), ancillary observations (grouse/100 km), and hunter surveys (flushes/hour), 2001–2004 on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina.

	Year			
Index	2001	2002	2003	2004
Drumming counts	11.40	6.93	6.20	5.88
Trapping success	0.68	0.48	0.19	NA
Ancillary observations	4.64	3.69	6.15	2.90
Hunter surveys	0.56	0.56	0.54	0.55

Table 1.2. Nest initiation dates and associated 95% confidence intervals for ruffed grouse on Appalachian Cooperative Grouse Research Project study sites, 1997–2002, adapted from Devers (2005).

State	County	Nest initiation	95% CI
Rhode Island	Washington	25 April	20–30 April
Pennsylvania	Clearfield	23 April	21–25 April
Ohio	Coshocton	10 April	4–15 April
Ohio	Athens	8 April	6–10 April
Maryland	Garrett	17 April	15–19 April
West Virginia	Randolph	16 April	13–19 April
West Virginia	Greenbrier	15 April	10–21 April
Kentucky	Lawrence	8 April	5–12 April
Virginia	Augusta	15 April	11–18 April
Virginia	Botetourt	14 April	11–16 April
Virginia	Smyth, Washington	17 April	15–19 April
North Carolina	Macon	12 April	10–14 April

PART II.

RUFFED GROUSE REPRODUCTIVE ECOLOGY AND NESTING HABITAT IN WESTERN NORTH CAROLINA

ABSTRACT

Poor reproduction may be responsible for lower ruffed grouse (*Bonasa umbellus*) populations in the southern Appalachians compared with northern parts of the species' range. Nutritional stress imposed by poor quality habitat and greater nest predation have been cited as negative influences on reproduction in the region. From 1999–2004, ruffed grouse reproductive ecology was studied in the Appalachian Mountains of North Carolina. Female grouse (*n* = 138) were radio tagged and monitored through the year. Nests (*n* = 44) were located to determine fate and habitat characteristics. Mayfield estimated nest survival was 0.83 (± 0.084 SE). Proportion of successful nests was 81%, among the greatest reported across ruffed grouse range; however, nesting rate (73%) was lower than many reports. Only 1 female (1/9) attempted a renest. Mean first nest clutch size of 10.1 eggs was within the range reported for the Appalachians, but less than those reported for the Great Lakes states. Females nested in various forest types, and microhabitat at nests did not differ from paired, random locations. Nesting habitat did not appear to be limiting; however, improvements in winter and early spring habitat quality could improve physical condition of females prior to nesting, potentially increasing nesting rate.

Key words: Appalachians, *Bonasa umbellus*, clutch, habitat, nest, reproduction, ruffed grouse, weather.

INTRODUCTION

In southern portions of their range, ruffed grouse (*Bonasa umbellus*) generally are generally less abundant than in northern latitudes (Bump et al. 1947). Several theories have been proposed to explain lower grouse numbers in the Appalachians, including additive mortality during extended hunting seasons (Stoll and Culbertson 1995), nutritionally inadequate foods (Servello and Kirkpatrick 1987), and loss of early successional habitat (Dessecker and McAuley 2001). Together, these factors may contribute to lower annual reproductive output in the Appalachians compared with the core of grouse range (Stewart 1956, Haulton 1999, Dobony 2000).

Understanding reproductive parameters is necessary to evaluate management scenarios for ground-nesting birds (Peterson et al. 1998). Nesting rate, clutch size, and nest success are important factors in grouse population ecology. Improving reproductive success could be a focus of management strategies (Bergerud 1988*a*). Habitat manipulation may affect reproduction by enhancing physical condition of females prior to nesting (Devers 2005), and decreasing nest predation (Tirpak and Giuliano 2004). In addition to habitat, extrinsic factors such as weather may play a role in reproduction (Larsen and Lahey 1958, Ritcey and Edwards 1963). Although climatic conditions may seem out of the proximate control of managers, Larsen and Lahey (1958:67) stated, "The correlation between grouse density and maximum temperature pattern does not imply that the correlation is with maximum temperature alone, but rather that it is with those environmental conditions that maximum temperature patterns induce or reflect." To provide a comprehensive management strategy for ruffed grouse in the Appalachians, managers require estimates of reproduction and insight into environmental conditions that can be altered to enhance reproductive success.

Until recently, most reproduction studies were conducted in the core of ruffed grouse range. As part of the Appalachian Cooperative Grouse Research Project (ACGRP), Devers (2005) examined population ecology on study sites across the central and southern Appalachian region; however only partial data (2 of 4 years) from this study site in western North Carolina were included. Tirpak (in press) reported nesting habitat characteristics for ACGRP sites, but omitted data from North Carolina because unique forest associations typical of the southern Blue Ridge amplified variability of the data set. Additional insight can be gained from this study, as the North Carolina site was the most southerly and is the first study to provide comprehensive estimates of reproduction at the southern extent of ruffed grouse range. Objectives were to (1) estimate reproductive parameters including nesting rate, nest success, clutch size, hatchability, hen success, and brood survival; (2) identify microhabitat characteristics of nest sites; and (3) examine associations among weather and reproductive parameters.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (WSC, 3,230 ha), within the Nantahala National Forest in western Macon County, North Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1,644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges that connect upper elevations to narrow valley floors (Whittaker 1956). Mean annual temperature was 10.4ºC, and mean annual precipitation was 160 cm. The area was predominantly forested with <1% coverage in small openings. The U.S. Forest Service purchased WSC in 1912 after it was logged. Since then, forest management practices included salvage harvest of blight-killed American chestnut (*Castanea dentata*), thinning, clearcutting, and diameter-limit cutting (McNab and Browning 1993). In 1997, 9 stands were harvested (3 shelterwood, 3 two-age, and 3 group selection) to study the effects of alternative regeneration techniques on vegetation response and wildlife habitat.

Habitats were classified by a combination of vegetative community type and stand age. Communities were stratified into 3 land classes (xeric, subxeric, and mesic) defined by elevation, landform, soil moisture, and soil thickness (McNab and Browning 1993; Table 2.1; tables are located in the Appendix). Additional land classes included gated forest roads (ROAD) and wildlife openings (WLO). Gated forest roads were defined by a buffer width of 5 m from road center on each side. The 10-m width included the road and adjacent berm maintained by mowing. Wildlife openings were small, open areas (0.50 ± 0.12 ha SE, $n = 24$) and also were maintained by mowing. Stand ages were determined by years since harvest or stand establishment in categories deemed important to ruffed grouse (0–5, 6–20, 21–39, 40–80, >80). Gated forest roads, wildlife openings and rhododendron (*Rhododendron maximum*)-dominated understory were not assigned age categories because they are in a state of arrested succession and their structural characteristics do not change appreciably over time (Phillips and Murdy 1985).

Habitat types were delineated in a geographic information system (GIS) developed for the study site. Oak and mixed oak-hickory stands in the >80-year age class (SUBXER5) made up the greatest proportion of the study site (31.5%) and wildlife openings (WLO) made up the least (0.2%; Table 2.2). Early successional habitats in the 6–20-year age class (XERIC2 and SUBXER2) occupied 9.3% of the area. The 0–5, 6–20, and 21–39-year age classes were not represented on mesic sites. There were 52.6 km of gated forest roads (1.1% of total area).

Capture and Telemetry

Grouse were captured using interception traps (Gullion 1965) during two annual periods, late August–early November, and early March–early April, 1999–2003. Gender and age (juvenile or adult) were assessed by feather characteristics and molt patterns (Kalla and Dimmick 1995). Grouse tagged as juveniles in fall graduated to be adults at the end of the following summer. Grouse were weighed, leg-banded, fitted with 12-g necklace-style radiotransmitters with a 3-hour mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA), and released at capture sites. Tagged birds ($n = 276$) were located $\geq$3 times per week from permanent telemetry stations. To adequately represent diurnal time periods, an equal number of locations were recorded during the periods, morning (0700–1100), mid-day (1101–1500), and evening (1501–1900). Stations were geo-referenced using a Trimble Global Positioning System (Trimble Navigation Limited Inc., Sunnyvale, CA). Transmitter signals were received using Telonics TR-2 receivers (Telonics Inc., Mesa, AZ), Clark model H7050 headphones (David Clark Company Inc., Worcester, MA), and hand-held 3-element yagi antennas.

Beginning in April, females were located daily to monitor nesting activity. When 2 consecutive locations occurred within a 0.25-ha area for an individual, she was assumed to be nesting. During the second week of continuous incubation, the nest was examined briefly to determine clutch size. Thereafter, nests were remotely monitored to minimize disturbance at the nest site. If a female was located away from the nest for >24 hours, the nest site was examined within 1 day to determine fate and clutch size. For successful nests, number of eggs hatched was determined by eggshell fragments. For unsuccessful nests, cause of nest failure was categorized as predation or abandonment. Unsuccessful females were monitored daily after failure to determine renesting effort.

Nest Microhabitat

Microhabitat data were collected in nested, circular plots centered on the nest site within 2 days of hatch or nest destruction. For comparison, a corresponding site was sampled 100 m in a random direction from each nest. Basal area was estimated from plot center with a 2.5 m^2/ha prism. Overstory composition of trees $\geq$11.4 cm diameter at breast height (DBH) was recorded within a 0.04-ha plot. Species and number of midstory saplings and shrubs <11.4 cm DBH and $\geq$1.4 m height was recorded for 4 DBH classes (<2.54 cm, 2.54–5.08 cm, 5.09–7.62 cm, and 7.63–11.4 cm) within a 0.01-ha plot. Woody seedlings <1.4 m in height were recorded within a 0.004-ha plot.

Nest Macrohabitat

Locations of nest and random sites were determined with a Trimble Global Positioning System (Trimble Navigation Limited Inc., Sunnyvale, California, USA) and incorporated in the GIS. Patch Analyst 3.0 (Elkie et al. 1999) was used to calculate edge density (m/ha) within 100-m radius buffers around nests and random sites used for microhabitat sampling. Distance to nearest opening also was measured from these points. Openings included forest roads, wildlife openings, and 0–5-year-old forest. Small canopy gaps created by natural disturbance of one or a few trees were not included, as these features were not available in the GIS stand coverage. At the study area scale, additional points were generated within a nesting habitat availability polygon to compare distances from random and nest sites to preferred brood-rearing habitats. The availability polygon was defined by merging fall and winter home ranges of females because female ruffed grouse are thought to sample potential nesting habitats during these seasons (Bergerud and Gratson 1988). Home ranges (95% fixed kernel) were calculated in ArcView GIS 3.2 (Environmental Systems Research Institute Inc., Redlands, California, USA) using the Animal Movement Extension to ArcView with least squares cross validation (Hooge and Eichenlaub 1997). Ninety-five percent kernel estimates were used because they incorporate home range periphery (Seaman et al. 1999) as available nesting habitat. Brood habitats were identified through intensive telemetry from hatch to 5 weeks post-hatch. Relative preference of SUBXER1, SUBXER2, SUBXER5, and ROAD within SUBXER5 stands for brood rearing was determined through compositional analysis (Aebischer et al. 1993, Chapter III). For distance measurements, points that fell within a preferred brood habitat were assigned a value of 0.

Nesting Chronology and Reproductive Parameters

Onset of continuous incubation was calculated by subtracting 24 days from the hatch date (Bump et al. 1947). Nest initiation dates were calculated by adding the number of incubation days (24) with the number of egg laying days (number of eggs in clutch * 1.5 days) and subtracting the sum from the hatch date (Bump et al. 1947). Nesting rate was the proportion of females alive in the 3 April radio-marked population known to reach incubation of an initial nest. April 3 was used because it was the earliest nest initiation date recorded on WSC. Nest success was the proportion of females that successfully hatched ≥ 1 egg in an initial nesting attempt. Renesting rate was the proportion of females, unsuccessful in an initial nesting attempt that reached incubation of a second nest. Renest success was the proportion of renesters that successfully hatched ≥ 1 egg. Hen success was the proportion of females alive in the 3 April radio-marked population that successfully hatched $\geq$1 egg in an initial or renesting attempt. Annual reproductive parameters were calculated across individuals within each year. Mean parameters and standard errors were calculated across years. Small sample sizes precluded calculation of annual reproductive parameters for juveniles and adults separately, therefore age-specific reproductive parameters were calculated with years pooled. Clutch size was the mean number of eggs in initial nests, determined by flushing the female once during the second week of incubation. Hatchability was the proportion of eggs in successful nests that hatched. Nest initiation date, nesting rate, clutch size, and nest success were compared across years between juveniles and adults.

Nest survival also was estimated using methods described by Mayfield (1975). Mayfield daily nest survival was calculated by dividing number of nests lost by total number of days nests were observed and subtracting from 1. Daily nest survival raised to a power of 24 (total incubation days) provided a survival estimate over the entire incubation period. An estimate of nest survival during laying and incubation was calculated by adding laying days to incubation days. During laying, female ruffed grouse lay approximately 1 egg every 1.5 days (Bump et al. 1947); therefore, laying days were estimated by multiplying mean clutch size by 1.5. Daily nest survival during laying and incubation was raised to a power of 39 (mean laying days + incubation days).

Weather

Coweeta Long Term Ecological Research Station (Coweeta LTER, Otto, North Carolina, USA) recorded weather data at a permanent weather station on the study site. Minimum and maximum temperature and precipitation (tipping bucket) were recorded daily. Weather data collected between 12 April (mean nest initiation date) and 21 May (mean hatch date) were used to explore correlations with annual nest success. Variables of interest included mean maximum temperature (MAXTEMP), mean minimum temperature (MINTEMP), number of days with temperatures <7^{o}C (COLDAYS), total rainfall (RAIN), and number of days with rainfall events (RAINDAYS).

Data Analysis

Mean reproductive parameters were calculated by averaging across individuals within each year, then averaging across years. An information-theoretic approach (Burnham and Anderson 1998) was used to evaluate differences in habitat characteristics between nest and random sites. A set of a-*priori* candidate models (Table 2.3) was created using combinations of microhabitat characteristics (basal area, midstory stem density, understory stem density) and landscape features (edge density, distance to opening). An estimate of ĉ was calculated from the global model to test for over dispersion of the data. Data were not over dispersed (ĉ = 0.515); therefore, bias-corrected Akaike's Information Criterion (AIC_c) and weight of evidence (w_i) were used to rank and select model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). Logistic regression was used to calculate 2log-likelihood values for each model with nest sites = 1 and random sites = 0 (Procedure GLM, SAS Institute, Cary, North Carolina, USA.). Log-likelihoods were then used to calculate Akaike's Information Criterion.

Difference in clutch size between juveniles and adults and distance to brood habitat were analyzed using the Generalized Linear Models (GLM) procedure in SAS. Nest survival was compared between juveniles and adults using chi-square methods described by Mayfield (1975). Relationships of weather data with nest success were examined using multiple regression (Procedure REG) in SAS.

RESULTS

Reproductive Parameters

One hundred thirty-eight female ruffed grouse were radio-tagged. Fate was recorded for 44 nests (35 successful, 9 unsuccessful). Mean annual nesting rate was 73% (6.8 SE), ranging from 50–92% across years (Table 2.4). Mean annual nest success was 81% (6.4 SE), based on proportion of nests that hatched $\geq$1 egg. Nests were observed for a total of 850 nest-days. Mayfield nest survival during incubation across years was 0.83 (± 0.084 SE). Nest survival during laying and incubation across years was 0.84 (± 0.076 SE).

Only 1 female of 9 (a juvenile) reached incubation of a second nest after an initial nesting attempt failed. Mean hen success was 61% (8.2 SE), ranging from 33% to 75%. Mean clutch size was 10.1 eggs (0.17 SE) with a mean hatchability of 97% (1.2 SE). Clutch size did not differ between juveniles ($\bar{x}$ = 9.4 ± 0.37 SE) and adults ($\bar{x}$ = 10.6 ± 0.53 SE, P = 0.0654, Table 2.5). Overall nesting rate was 74% (29/39) for juveniles and 88% for adults (15/17). Overall nest success was 87% (13/15) for adults and 76% (22/29) for juveniles. Nest survival did not differ between juvenile and adults ($\chi_2^2 = 1.42$, $P >$ 0.500).

Nesting Chronology

Females initiated first nests on a mean date of 12 April (0.84 days SE; Table 2.6). Mean dates were similar between juveniles ($\bar{x}$ = 14 April ± 1.35 SE) and adults ($\bar{x}$ = 13 April ± 2.36 SE). Nest initiation dates ranged over a 3-week period from 3 April–26 April. Start of continuous incubation occurred 21 April–10 May ($\bar{x}$ = 27 April ± 0.74

days SE). Mean hatch date was 21 May (0.74 days SE) with 80% of hatch occurring during the 10-day period of 17 May–27 May.

Nest Habitat

The majority of nests (86%) were on mid and upper slopes in mature sawtimber stands >40-years old (Table 2.7). Two nests (5%) were in 6–20-year-old stands, 2 (5%) were in rhododendron, 1 was in a 5-year-old two-aged stand, and 1 was in a 21–39-year-old pole stand. Small sample size of nests relative to habitat types resulted in expected habitat use values <1, preventing statistical analysis of use versus availability at the stand scale. Weight of evidence was low ($\omega_i \leq 0.217$) for all microhabitat nest site selection models, and Δ_i values indicated similar strength of evidence among members of the candidate set (Table 2.8). Habitat variable means were similar between nest and random sites; 95% confidence intervals overlapped for all variables (Table 2.9). Stem density at nest sites was 5,732 stems/ha (4,041–7,420, 95% CI) in the midstory, and 19,000 stems/ha (9,610–28,389, 95% CI) in the understory. Mean basal area was 18m^2/ha (15–20, 95% CI), and mean distance to edge was 195 m (115–275, 95% CI). Total edge density within 100-m buffers around nests was 394 m/ha (352–435, 95% CI), compared to 399 m/ha (344–454, 95% CI) for random sites. All nests were situated next to an object, 43% against stumps or fallen trees, 35% against standing trees, and 22% against rocks. Mean distance to preferred brood-rearing habitats did not differ between nests ($\overline{x}$ = 61 $\pm$ 19.0 m SE) and random points ($\overline{x}$ = 83 $\pm$ 11.3 m SE, $P = 0.327$).

Habitat models for nest fate were not created because sample size of unsuccessful nests was small (n = 9); however, mean habitat values were similar between successful and unsuccessful nests (Table 2.10). Annual nest success was not related to MINTEMP

($r^2 = 0.864$, $P = 0.136$, $n = 5$), COLDAYS ($r^2 = 0.627$, $P = 0.323$, $n = 5$), RAIN ($r^2 = 0.377$, $P = 0.623$, $n = 5$), RAINDAYS ($r^2 = 0.070$, $P = 0.930$, $n = 5$) or MAXTEMP ($r^2 = 0.865$, $P = 0.070$, $n = 5$).

DISCUSSION

Nesting Chronology

Increasing day length activates physiological changes that prepare ruffed grouse for reproduction, though annual variation in nesting phenology can be influenced by latitude and weather (Bump et al. 1947). Ruffed grouse in southern portions of their range nested earlier than those in northern areas. On WSC, incubation began on a mean date of 27 April across years. By comparison, incubation began approximately 17 May in northern Michigan (Larson et al. 2003), 14 May in Minnesota (Maxson 1978), and 7 May in New York (Bump et al. 1947). Across the Appalachians, Devers (2005) noted earlier nesting on more southerly sites, with incubation onset occurring 10 May in Rhode Island, 8 May in Pennsylvania, 29 April in southern West Virginia, and 27 April in central Virginia.

Nesting phenology in southerly latitudes may be driven by early occurrence of warming spring temperatures compared with northern areas. In New York, Bump et al. (1947) attributed annual fluctuations in nesting to weather. They noted advanced nesting dates when average minimum temperature during the pre-nesting period was above normal. Data from WSC support this contention, as the earliest mean incubation date (in 2001), coincided with greatest mean minimum temperature during pre-nesting (15

March–14 April). Although photoperiod determines the general timing of reproduction, annual and latitudinal fluctuations may in part be determined by climate.

Clutch Size and Hatchability

Mean clutch size of 10.1 eggs was within the range of 9.2–11.3 reported by Devers (2005) for the Appalachians. Clutches in the northern United States and southern Canada were generally larger, with reports of 11.4 in Ontario (Cringan 1970), 11.6 in Alberta (Rusch and Keith 1971), 11.5 in New York (Bump et al. 1947), 11.0 in Wisconsin (Small et al. 1996), and 12.7 in Michigan (Larson et al. 2003). Hatchability of 97% on WSC was similar to the 95% average from northern studies, but greater than the mean of 86% for ACGRP (Devers 2005).

Variation in clutch size has been related to latitude in many bird species (Kulesza 1990, Gaese et al. 2000). Within the Appalachians, Devers (2005) attributed differences in clutch size to latitude, with smaller clutches occurring on more southerly study areas. Variation in clutch size with latitude may be related to food availability (Cody 1966, Perrins and Jones 1974, James 1983, Findlay and Cook 1987). Food availability plays the greatest role in clutch size on marginal or poor habitats (Nager et al. 1997). For ruffed grouse, females in poor physiological condition tend to lay smaller clutches (Beckerton and Middleton 1982). In the Appalachians, habitats with nutritionally inadequate foods can cause physiological stress prior to nesting (Servello and Kirkpatrick 1987) that may result in decreased egg production. This presents an opportunity for management to improve reproductive output. Habitat manipulations that improve nutrition, especially in winter and early spring may alleviate stress and positively influence clutch size and other reproductive parameters.

Nesting Rate

Estimates of nesting rate and nest success from telemetry studies tend to be biased because most nests are not located prior to onset of continuous incubation. Nesting rate may be negatively biased, as nests destroyed during laying are not discovered. For the same reason, nest success estimates may be artificially high. Larson et al. (2003) suggested the extent of bias in nest success reports can differ among areas, and comparisons among study sites may be inappropriate. Mayfield (1975) outlined several potential problems in reports of apparent nest survival, including a mixture of nests discovered early and late, nests with unknown outcomes, and observer bias in ability to locate nests. By using intensive radio telemetry during this study, nests were located within 3 days of incubation onset, and once located, fate was determined for all nests. Use of radio telemetry minimizes observer bias among observers, and methodology on WSC was consistent with other ruffed grouse studies in Minnesota (Maxson 1978), Wisconsin (Small et al. 1996), and the Appalachian region (Devers 2005). For consistency with other research, reports herein included apparent nesting rate and apparent nest success as well as Mayfield nest survival.

Nesting rates averaged 73%, which was lower than estimates of 100% from the Great Lakes States (Maxson 1978, Small et al. 1996). In New York, Bump et al. (1947) used systematic nest searching methods to estimate rates of 75–100%, with all females attempting to nest in all but 3 of 13 years. Of 11 study sites in the central and southern Appalachians, nesting rates were 69–100% (Devers 2005). Only one area, located in northern Virginia (VA1), had rates lower than those reported here (Devers 2005). Seven ACGRP study sites (KY1, MD1, OH1, OH2, PA, RI1, and VA3) had nesting rates of

100%, while 3 (WV1, VA2, WV2) reported 98%, 96%, and 85%, respectively (see Devers 2005 for study site locations and acronyms).

Habitat quality and resultant food availability may influence physiological condition and nesting by ruffed grouse in the Appalachians (Servello and Kirkpatrick 1987, Long et al. 2004). Devers (2005) proposed nesting rate was lower on ACGRP sites dominated by oak-hickory forest, where grouse are dependent on annually variable hard mast production, compared with mixed mesophytic forests where alternate food sources, such as herbaceous plants, were plentiful. The WSC study area was classified as mixed mesophytic by ACGRP; however, nesting rates were lower than similarly classed sites in Maryland, Pennsylvania, West Virginia, and Virginia (Devers 2005). Larson (1998) believed that despite an apparent nesting rate of 65% in Michigan, all hens attempted to nest, with some losses occurring prior to incubation. The nesting rate on WSC may have reflected habitat quality, nest predation during the laying period, or a combination of these factors.

Nest Success

Although nesting rates on WSC were lower, nest success (81%) was greater than the range of 47–78% reported from 10 ACGRP study areas (Devers 2005). Only 1 ACGRP site had nest success >81% (92%, Augusta County, Virginia). Estimates also were greater than those from the core of grouse range. Using telemetry techniques, Maxson (1978), Larson et al. (2003), and Small et al. (1996) reported apparent nest success of 75%, 70% and 46% in Minnesota, Wisconsin, and Michigan, respectively. Nest success on WSC likely was biased high because nests were not located prior to incubation; however, methods were similar to other studies and relative comparisons seem appropriate.

Nest survival rates calculated using the Mayfield method were available from 1 other study (Larson et al. 2003). Their survival of first nests (0.44) was considerable lower than a survival rate of 0.83 on WSC. No other studies have estimated nest survival through the laying and incubation periods.

Correlations between weather variables and nest success were not identified. Devers (2005) found a positive relationship between ACGRP nest success and mean minimum temperature in April and May, and proposed colder temperatures necessitate females to make more frequent feeding trips away from the nest. In New York, Bump et al. (1947) concluded weather had a negligible effect on nest success, despite frequent bouts of cold spring weather coupled with snow during their 13-year study period. Results from WSC support the latter contention, as no relationship of nest success with mean minimum temperature and maximum temperature was observed.

Age may influence nest success, as nesting experience gained by juveniles could benefit future attempts (Bergerud 1988*b*). Supporting this contention, Small et al. (1996) found greater adult nest success compared with juveniles in Wisconsin. Conversely, success did not differ with age in northern Michigan (Larson et al. 2003), or across the central and southern Appalachians (Devers 2005). Similar to the latter studies, nest survival on WSC did not differ between juveniles and adults. Availability of nesting habitat (i.e., mature forest) may have resulted in greater opportunity for successful nesting for both juveniles and adults.

Renesting Rate

Renesting was recorded for one female (a juvenile). High success of initial nests precluded the opportunity to document subsequent attempts. Bump et al. (1947) argued renesting contributes little to annual reproductive output. Renesting rates determined by radio telemetry were 46% in Michigan (Larson 1988) and 56% in Wisconsin (Small et al. 1996). In the Appalachians, Devers (2005) reported 23% renesting rate with a range of 0–50%.

Physiological condition largely determines the reproductive capacity of female ruffed grouse (Beckerton and Middleton 1982). In the absence of quality winter forage, Appalachian grouse experience nutritional deficiencies that can result in lower reproductive potential (Servello and Kirkpatrick 1987, Long et al. 2004). Nutritionally stressed grouse in the Appalachians may put more emphasis on initial nesting attempts because low physiological reserves make production of a second clutch difficult. Bergerud and Gratson (1988) suggested that, if disturbed, female grouse should abandon a nest and initiate another attempt, "…if certainty of a current loss outweighs the unpredictability of the loss of a future effort." On WSC, all females were flushed during the first 2 weeks of incubation to determine clutch size; however, no females abandoned nests after these disturbances. This may indicate grouse in the southern Appalachians put more effort in an initial nesting attempt, as opposed to abandoning a first attempt and renesting.

The probability of second nesting efforts also may decrease with increased time invested in an initial nest (Bump et al. 1947, Bergerud and Gratson 1988). In Minnesota, when nests were destroyed during incubation, females did not initiate a second attempt (Maxson 1978). Because nests were not located prior to incubation, potential existed to mistake renests (i.e., those following destruction during laying) for first attempts; however, second clutches are generally smaller (Bump et al. 1947, Maxson 1978, Larson et al. 2003, Devers 2005). Based on numbers reported in the literature, clutch sizes on WSC were not indicative of renests.

Hen Success

Mean annual hen success (63%) was within the range of 47–92% reported across ACGRP study areas (Devers 2005). Of 10 study sites, the WSC estimate was greater than PA1 and VA2, similar to MD1 and WV2, and less than KY1, OH1, OH2, RI, VA1, VA3, and WV1. Hen success has not been reported on other ruffed grouse research studies.

Hen success was defined as the proportion of females alive at the beginning of the reproductive period that successfully hatched ≥1 egg in an initial or renesting attempt. This definition differed from that provided by Vangilder and Kurzejeski (1995) for wild turkeys, as they considered only females that attempted to nest or survived through the reproductive season. As calculated here, hen success represents cumulative contributions of nesting rate, nest success, renesting rate, and renest success to annual reproductive output. On WSC, high nest success offset relatively low nesting and renesting rates.

Nest Habitat

Nesting habitat, particularly placement of nests in relatively open, mature forest, was similar to reports from across grouse range (Bump et al. 1947, Gullion 1977, Maxson 1978, Thompson et al. 1987). These studies and others (Larson et al. 2003, Tirpak et al. in press) suggested females conceal nests against trees or other objects in stands that permit detection of advancing predators. Inability to detect microhabitat differences may have been a function of proximity, as nests and random points (100 m distant) were usually within the same forest type.

Female grouse may select nesting sites based on predation risk (Bergerud and Gratson 1988). Habitat characteristics on WSC were similar between successful and unsuccessful nests; however, given high success rates, few unsuccessful nests were sampled. In Michigan, Larson et al. (2003) could not relate variability in microhabitat structure to nest fate. Conversely, Tirpak et al. (in press) described a positive relationship among nest success, basal area, and coarse woody debris. To decrease predator efficiency, they suggested females nest against trees or debris in stands with numerous potential nest sites. Results from WSC support this contention, as females nested in areas of contiguous habitat against objects, including trees, stumps, and fallen logs, and experienced high success rates.

MANAGEMENT IMPLICATIONS

Recent studies of ruffed grouse in the Appalachians suggest annual productivity is a limiting factor, and habitat management has been recommended to improve nest success and physiological condition of females prior to nesting (Whitaker 2003, Devers 2005, Tirpak et al. in press). Nest success on WSC was among the highest reported for the species, and nesting habitat did not appear to be limiting. Nesting rates, however, were lower than those reported for other areas and may be a function of habitat quality and nutrition.

Habitat manipulations that increase interspersion of quality food sources with suitable protective cover could improve pre-breeding condition of females resulting in greater nesting rates and larger clutches. Topography of the Appalachians creates diverse vegetation communities defined by changes in soil type, thickness, and moisture

(Whitaker 1956). With heterogeneity in soil characteristics, various communities and associated ecotones often occur in close proximity, presenting unique opportunities to intersperse forest types. The greatest diversity often occurs on midslope transition zones between xeric uplands and mesic lower slopes (Berner and Gysel 1969, McNab and Browning 1993). By placing timber harvests on midslope positions, managers can take advantage of diverse food sources while creating early successional cover in close proximity. Timber harvest on midslopes also can create corridors between upper and lower elevation habitats and connect disjunct patches. Such interspersion of cover types also would provide brood habitat in close proximity to stands used for nesting and could ultimately provide the greatest benefit to annual productivity.

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APPENDIX

Table 2.1. Forest stand associations, understory characteristics, and corresponding USDA Forest Service (USFS) and Society of American Foresters (SAF) codes for land classifications used to define ruffed grouse habitats on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina 1999–2004. Adapted from McNab and Browning (1993).

Land class	Moisture gradient	Forest associations	Understory	USFS	SAF
Xeric	Xeric	Pitch pine-oak	>75% ericaceous	59	NA
	.	Scarlet oak	>75% ericaceous	15	45
	.	Chestnut oak-scarlet oak	50-75% ericaceous	60	NA
	Subxeric	Chestnut oak	50-75% ericaceous	52	44
Subxeric	Subxeric	Chestnut oak	25-50% ericaceous	52	44
	.	White oak-red oak-hickory	25-50% ericaceous	55	52
	.	Northern red oak	Herbaceous	53	55
	Submesic	Yellow poplar-white oak-red oak	Herbaceous	56	59
Mesic	Submesic	Yellow poplar	Herbaceous	50	57
	.	Sugar maple-beech-yellow birch	Herbaceous	81	25
	.	Basswood-yellow buckeye	Herbaceous	41	26
	Mesic	Hemlock	75-100% rhododendron	8	23

Table 2.2. Land class, stand age (years), resultant ruffed grouse habitat types, number of stands (*n*), mean stand size (ha) and study area coverage (%) of Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Land class	Age	Habitat type	*n*	Mean ± SE	Coverage
Mesic	40-80	MESIC4	23	21 ± 5.3	9.7
Mesic	>80	MESIC5	12	37 ± 8.7	9.1
Mesic	NA	RHODO	18	53 ± 20.3	19.6
Subxeric	0-5	SUBXER1	30	2 ± 0.4	0.8
Subxeric	6-20	SUBXER2	40	10 ± 0.6	8.1
Subxeric	21-39	SUBXER3	7	11 ± 1.7	1.6
Subxeric	40-80	SUBXER4	8	16 ± 3.9	2.7
Subxeric	>80	SUBXER5	43	36 ± 4.3	31.5
Xeric	6-20	XERIC2	4	15 ± 4.4	1.2
Xeric	40-80	XERIC4	6	20 ± 3.4	2.4
Xeric	>80	XERIC5	15	39 ± 11.2	11.9
Roads	NA	ROAD	NA	NA	1.1
Openings	NA	WLO	24	0.5 ± 0.1	0.2

Table 2.3. A-*priori* candidate models used to evaluate nest site selection by ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Model structure	Model definition
USTEM[a]	Nest site selection a function of understory stem density
MDSTEM	Nest site selection a function of midstory stem density
MDSTEM+USTEM	Nest site selection a function of midstory and understory stem density
BASAL	Nest site selection a function of basal area
MDSTEM+BASAL	Nest site selection a function of midstory stem density and basal area
MDSTEM+USTEM+BASAL	Nest site selection a function of midstory and understory stem density, and basal area
ED	Nest site selection a function of edge density within 100 m radius buffer
ED+BASAL	Nest site selection a function of edge density and basal area
DIST	Nest site selection a function of distance to opening
ED+BASAL+MDSTEM	Nest site selection a function of edge density, basal area, and midstory stem density
ED+BASAL+MDSTEM+USTEM+DIST	Nest site selection a function of edge density, basal area, midstory stem density, and distance to opening

[a] USTEM = density of woody seedlings <1.4 m in height within 0.004-ha plots
MDSTEM = density of woody seedlings >1.4 m in height and <11.4 cm dbh within 0.004-ha plots
BASAL = basal area (m^2/ha)
DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year old forest
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites

Table 2.4. Annual and mean reproductive parameters for female ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

	Year						
Parameter	2000	2001	2002	2003	2004	Mean	SE
Nesting rate (%)	71 (5/7)	92 (11/12)	79 (15/19)	83 (10/12)	50 (3/6)	73	6.8
Nest success (%)	100 (5/5)	82 (9/11)	67 (10/15)	90 (9/10)	67 (2/3)	81	6.4
Renest rate (%)	0	50 (1/2)	0	0	0	10	9.8
Renest success (%)	NA	0 (0/1)	NA	NA	NA	NA	NA
Hen success (%)	71 (5/7)	75 (9/12)	53 (10/19)	75 (9/12)	33 (2/6)	61	8.2
Clutch size (eggs)	9.8	10.5	10.4	9.4	8.5	9.72	0.4
Hatchability (%)	98	93	95	97	100	97	1.2

Table 2.5. Reproductive parameters by age class (juvenile or adult) with years pooled for female ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Parameter	Age Juvenile	 Adult
Nesting rate (%)	74 (29/39)	88 (15/17)
Nest success (%)	76 (22/29)	87 (13/15)
Hen success (%)	56 (22/39)	76 (13/17)
Clutch size (eggs)	9.4 ± 0.37	10.6 ± 0.53
Initiation Date	14 April ± 1.35	13 April ± 2.36

Table 2.6. Nest initiation, incubation, and hatch dates and ranges for ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Year	Initiation	Range	Incubation	Range	Hatch	Range
2000	10 Apr	7 Apr–14 Apr	25 Apr	21 Apr–28 Apr	19 May	15 May–22 May
2001	13 Apr	9 Apr–18 Apr	29 Apr	26 Apr–3 May	23 May	20 May–27 May
2002	8 Apr	3 Apr–13 Apr	24 Apr	22 Apr–3 May	18 May	16 May–27 May
2003	15 Apr	11 Apr–16 Apr	28 Apr	26 Apr–3 May	22 May	20 May–27 May
2004	21 Apr	16 Apr–26 Apr	4 May	28 Apr–10 May	28 May	22 May–3 June
All Years	12 Apr	3 Apr–26 Apr	27 Apr	21 Apr–10 May	21 May	15 May–3 June

Table 2.7. Nesting habitat use and availability for ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Habitat	Number nests	Use (%)	Availability (%)
XERIC2	0	0	1
XERIC4	2	5	2
XERIC5	4	9	12
SUBXER1	1	2	1
SUBXER2	2	5	8
SUBXER3	1	2	2
SUBXER4	3	7	3
SUBXER5	16	37	32
MESIC4	8	19	10
MESIC5	4	9	9
RHODO	2	5	20
ROAD	0	0	1
WLO	0	0	<1

[a] XERIC2 = xeric uplands in 6–20-year age class
XERIC4 = xeric uplands in 40–80-year age class
XERIC5 = xeric uplands in >80-year age class
SUBXER1 = subxeric to submesic forest in 0–5-year age class
SUBXER2 = subxeric to submesic forest in 6–20-year age class
SUBXER3 = subxeric to submesic forest in 21–39-year age class
SUBXER4 = subxeric to submesic forest in 40–80-year age class
SUBXER5 = subxeric to submesic forest in >80-year age class
MESIC4 = mesic forest in 40–80-year age class
MESIC5 = mesic forest in >80-year age class
RHODO = forest with >75% midstory coverage in rhododendron
ROAD = gated forest roads
WLO = wildlife openings

Table 2.8. Comparison of Akaike's Information Criterion (AIC_c), differences in AIC_c, and model weights (w_i) for ruffed grouse nest site selection models on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Model	AICc	ΔAICc	*w*i
MDSTM	96.845	0.000	0.217
BASAL	97.198	0.353	0.182
DIST	98.348	1.503	0.102
USTEM	98.401	1.556	0.100
ED	98.425	1.580	0.099
MDSTM + USTEM	98.703	1.858	0.086
ED + MDSTEM	99.032	2.187	0.073
ED + BASAL	99.231	2.386	0.066
BASAL + MDSTM + USTEM	100.372	3.527	0.037
ED + BASAL + MIDSTEM	100.519	3.674	0.035
BASAL + MDSTEM + USTEM + DIST + ED	105.068	8.223	0.004

[a] USTEM = density of woody seedlings <1.4 m in height within 0.004-ha plots

MDSTEM = density ofwoody seedlings >1.4 m in height and <11.4 cm dbh in 0.004-ha plots

BASAL = basal area (m^2/ha)

DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year old forest

ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites

Table 2.9. Means and 95% confidence intervals for habitat variables at nest and paired random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

Variable	Sampling site			
	Nest		Random	
	Mean	95% CI	Mean	95% CI
USTEM	19,000	9,610-28,389	20,455	11,187-29,274
MDSTM	5,732	4,041-7,420	4,414	3,113-5,716
BASAL	18	15-20	19	17-22
DIST	195	115-275	213	128-299
ED	394	352-435	399	344-454

[a]USTEM = density of woody seedlings <1.4 m in height/ha
MDSTEM = density ofwoody seedlings >1.4 m in height and <11.4 cm dbh/ha
BASAL = basal area (m^2/ha)
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites
DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year old forest

Table 2.10. Means and 95% confidence limits for habitat variables at successful and unsuccessful nest sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

	Nest Fate			
Variable	Successful		Unsuccessful	
	Mean	95% CI	Mean	95% CI
USTEM	18,024	7,768-28,281	27,550	10,464-44,636
MDSTM	7,371	2,444-12,298	5,480	3,339-7,621
BASAL	17	15-20	21	15-26
DIST	216	122-311	189	32-346
ED	407	358-457	378	290-465

[a]USTEM = density of woody seedlings <1.4 m in height/ha
MDSTEM = density ofwoody seedlings >1.4 m in height and <11.4 cm dbh/ha
BASAL = basal area (m^2/ha)
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites
DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year old forest

PART III.

RUFFED GROUSE BROOD HOME RANGE AND HABITAT USE IN WESTERN NORTH CAROLINA

ABSTRACT

Ruffed grouse brood habitat is an important consideration in management of the species.We measured brood habitat characteristics at forest stand and microhabitat scales in the Appalachian Mountains of western North Carolina. From 2000–2004, radiotagged females with broods (N = 36) were monitored from hatch to 5 weeks post-hatch, resulting in 372 microhabitat plots (186 brood, 186 random). Brood sites had greater percent herbaceous ground cover, greater percent vertical cover 0–2 m, greater density of midstory stems <11.4 cm DBH, and greater invertebrate density compared with random. Seventeen broods survived the 5-week post-hatch period and were available for home range analysis. Mean 75% kernel home range was 24.3 ha. Top-ranked habitats for relative preference were mixed oak in the 0–5, 6–20, and >80-year age classes, forest roads, and edges of maintained wildlife openings. Broods often were associated with managed stands, and forest management may be used to further enhance brood habitat in the southern Appalachians.

Key words: Appalachians, *Bonasa umbellus*, broods, habitat use, home range, ruffed grouse.

INTRODUCTION

Provision of brood habitat is an important aspect of ruffed grouse (*Bonasa umbellus*) management. Female grouse promote chick survival by seeking areas that allow optimal foraging near the safety of protective cover (Bergerud and Gratson 1988). Realizing the inherent relationship between cover and chick survival, Bump et al. (1947) suggested brood habitat quality ultimately determines an area’s reproductive potential.

Prompted by population declines, biologists in the central and southern Appalachians (CSA) are developing management strategies to address ruffed grouse habitat needs. Provision of quality brooding areas may be a cornerstone of such plans, as fulfilling specific brood requirements also improves conditions for adults throughout the year. The reverse, however, may not be true, as broods are less able to adjust to unfavorable conditions (Berner and Gysel 1969).

Characteristics of brood habitat during the first few weeks after hatch are well documented from the core of ruffed grouse range. Requirements include ample invertebrates, a diversity of moderately dense, herbaceous groundcover and a high density of midstory shrubs and woody stems (Berner and Gysel 1969, Porath and Vohs 1972, Godfrey 1975, Gullion 1977, Kubisiak 1978, Maxson 1978). The diversity of forest stands exhibiting these conditions included lowland speckled alder (*Alnus rugosa*, Godfrey 1975), mature alder-aspen (*Populus tremuloides, P. grandidentata*, Kubisiak 1978), and various combinations of forest openings and edge habitats (Berner and Gysel 1969, Porath and Vohs 1972, Maxson 1978).

Several studies have examined brood habitat in the CSA (Stewart 1956, Scott et al. 1998, Haulton et al. 2003); however, conflicting reports exist regarding forest types preferred by grouse broods in the region. Similar to other areas within grouse range, results emphasized importance of diverse herbaceous cover with varying descriptions of forest stand types and ages that provided optimal conditions. In Virginia and West Virginia, broods frequented mature, closed canopy hardwoods (Haulton et al. 2003). Also in Virginia, Stewart (1956) located broods in moist forest ravines and near canopy gaps in otherwise mature forest. On an intensively managed mixed oak (*Quercus* spp.) forest in Pennsylvania, brood hens selected 10-year-old clearcuts (Scott et al. 1998). The range of forest types reportedly used by grouse broods, from closed canopy mature stands to young clearcuts, may complicate decision-making for managers choosing among silvicultural options for improving ruffed grouse brood habitat in the CSA.

Most forest management plans are implemented at stand and compartment scales. Within forest stands, vegetation characteristics (i.e., microhabitat) are altered by natural disturbances and management activities including timber harvest and prescribed burning. Within compartments, or multiple stands, habitat is influenced albeit at a coarser resolution. Habitat selection can occur at one or both of these scales (Johnson 1980); therefore, a comprehensive understanding of forest management effects on wildlife can be gained through habitat investigations at multiple spatial scales. Such a study could provide valuable information pertinent to forest management for ruffed grouse in the CSA.

Ruffed grouse brood habitat was studied in the southern Appalachian Mountains of North Carolina. Objectives were to (1) compare habitat use versus availability at the forest stand scale; (2) examine vegetation structure of brood habitat; (3) investigate invertebrate availability in brood habitats; and (4) identify forest management options for creating, maintaining, and improving brood habitat in the CSA.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (WSC; 3,230 ha), within Nantahala National Forest in western Macon County, North

Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges connecting upper elevations to narrow valley floors (Whittaker 1956). Mean annual temperature was 10.4ºC, and mean annual precipitation was 160 cm. The area was predominantly forested with <1% coverage in small openings. The U.S. Forest Service purchased WSC in 1912 after it was logged. Since then, forest management practices included salvage harvest of blight-killed American chestnut (*Castanea dentata*), thinning, clearcutting, and diameter-limit cutting (McNab and Browning 1993).

Habitats were classified by a combination of vegetative community type and stand age. Communities were stratified into 3 land classes (i.e., xeric, subxeric, and mesic) defined by elevation, landform, soil moisture, and soil thickness (McNab and Browning 1993; Table 3.1; tables are located in the Appendix). Within communities, variation in plant species occurrence existed along a moisture continuum, similar to that described by Whittaker (1956). Xeric communities were on high elevation, steep, south and west aspects characterized by shallow, dry soils. Tree species included scarlet oak (*Quercus coccinea*), black oak (*Q. velutina*), pitch pine (*Pinus rigida*) and chestnut oak (*Q. prinus*) in the overstory with ericaceous plants including huckleberry (*Gaylussacia baccata*), lowbush blueberry (*Vaccinium vacillans*), and mountain laurel (*Kalmia latifolia*) in the understory. Subxeric communities were at middle elevations and upper elevations on less exposed aspects. Soil characteristics were between xeric and mesic, or subxeric and submesic (Whittaker 1956). Overstory was dominated by chestnut oak, white oak (*Q. alba*), hickory (*Carya* spp.), northern red oak (*Q. rubra*), red maple (*Acer* *rubrum*), and yellow poplar (*Liriodendron tulipifera*). Ericaceous understory occupied 25–50% groundcover on drier microsites, whereas herbaceous plants occupied more mesic sites. Mesic communities occurred on north and east aspects, on lower slopes, and in sheltered coves. Stands were comprised of yellow poplar, eastern hemlock (*Tsuga canadensis*), northern hardwoods including sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and birch (*Betula* spp.), and mixed mesophytic obligates including American basswood (*Tilia americana*) and yellow buckeye (*Aesculus octandra*). Understory was herbaceous except where rhododendron (*Rhododendron maximum*) inhibited groundcover. Sites with 75–100% cover in rhododendron were placed in a separate habitat classification (RHODO).

Additional land classes included gated forest roads (ROAD) and wildlife openings (WLO). Gated forest roads were defined by a buffer width of 5m from road center on each side. The 10-m width included the road and adjacent berm. Wildlife openings were small, permanent clearings (0.50 ± 0.12 ha SE). Management of roads and openings included an initial planting of orchardgrass (*Dactylis glomerata*), tall fescue (*Festuca arundinacea*) and white-dutch clover (*Trifolium repens*) maintained by annual or biennial mowing.

Stand ages were determined by years since harvest or stand establishment in categories deemed important to ruffed grouse (0–5, 6–20, 21–39, 40–80, >80). Grouse reportedly begin use of regenerating mixed hardwood and oak stands approximately six years after harvest (Kubisiak 1987, Thompson and Dessecker 1997). At approximately 20 years of age, habitat quality decreases as the upper canopy closes and woody stem density and herbaceous ground cover decrease (Kubisiak 1987, Storm et al. 2003). Mixed hardwood stands remain in this “pole stage” for up to 40 years. By age 40, most oak species have reached reproductive maturity and are capable of producing significant acorn crops (Guyette et al. 2004). By 80–120 years, oak stands are considered full rotation age (U.S. Forest Service 1994). Beyond 120 years, natural mortality of upland oaks increases (Guyette et al. 2004), resulting in canopy gaps. Wildlife openings, roads and rhododendron-dominated understory were not assigned age categories because they are in a state of arrested succession and their structural characteristics do not change appreciably over time (Phillips and Murdy 1985).

Stands in the 6–20-year age class were predominantly clearcuts (1.3–24.6 ha, *n* = 44) harvested in the late 1980s and early 1990s. Alternative regeneration harvests (i.e., shelterwood, irregular shelterwood, group selection) were cut 1996–1997, and represented the 0–5-year category (SUBXER1) for most of the study. Target residual basal area was 9.0 m^2/ha for shelterwood harvests. Prescriptions called for a final removal cut of residuals approximately 10 years after the initial harvest. Ruffed grouse data were collected prior to removal of residuals in these stands. Mean size of shelterwood stands was (5.56 ± 0.42 ha SE, *n*=3). For irregular shelterwood, target residual basal area was 5.0 m^2/ha. Residuals in irregular shelterwood were to be retained through the next rotation, resulting in 2-aged stands. Mean size of 2-aged stands created by irregular shelterwood was (4.68 ± 0.18 ha SE, *n* =3). Group selection was implemented in 3 stands with 4–9 groups/stand. Mean group size was 0.36 ha (± 0.05 SE). All shelterwood, irregular shelterwood, and group selection harvests were implemented on subxeric sites and represented the SUBXER1 habitat type.

Subxeric oak and mixed oak-hickory in the >80 year age class (SUBXER5) made up the greatest proportion of the study site (31.5%) and wildlife openings (WLO) made up the least (<1.0%; Table 3.2). Early successional habitats in the 6–20-year age class (XERIC2 and SUBXER2) occupied 9.3% of the area. The 6–20-year, and 21–39-year age classes were not represented on mesic sites. There were 52.6 km of gated forest roads (1.1% of total area).

Capture and Telemetry

Grouse were captured using intercept traps (Gullion 1965) during two annual periods, late August–early November and early March–early April, 1999–2003. Gender and age (juvenile or adult) were assessed by feather characteristics and molt patterns (Kalla and Dimmick 1995). Grouse were weighed, leg-banded, fitted with a 12-g necklace-style radiotransmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA) and released after processing.

Females with broods were monitored intensively from hatch to 5 weeks post-hatch, a critical period when chick mortality is greatest and survival may depend on habitat characteristics (Bump et al 1947, Larson et al. 2001). Brood females were located 1-2 times daily by triangulation and 2-3 times weekly by homing. Homing provided visual locations necessary to confirm brood survival and sites for vegetation and invertebrate sampling. Intensive monitoring continued as long as a female had $\geq$1 surviving chick or until 5 weeks post-hatch. When possible, flush counts were avoided, as frequent disturbance may influence brood movements and survival. Instead, broods were approached cautiously to determine presence or absence through observation of brooding behavior or direct observation of chicks. In this way, field personnel were successful in determining brood presence or absence without flushing chicks.

Microhabitat Sampling

Microhabitat data were collected in nested circular plots centered on brood locations. For comparison, corresponding random locations were sampled at a random distance (200–400 m) and azimuth (0–359°) from a location recorded the previous day. This allowed availability to differ among observations as broods moved within the study area (Arthur et al. 1996). The 200–400 m distance was chosen because it represented mean daily movement distance of grouse chicks (Godfrey 1975, Fettinger 2002).

Basal area was estimated from plot center with a 2.5 m^2/ha prism. Overstory composition of trees $\geq$11.4 cm diameter at breast height (DBH) was recorded within a 0.04-ha plot. Species and number of midstory saplings and shrubs <11.4 cm DBH and $\geq$1.4 m height was recorded for 4 DBH classes (<2.54 cm, 2.54–5.08 cm, 5.09–7.62 cm, and 7.63–11.4 cm) within a 0.01-ha plot. Woody seedlings <1.4 m in height were recorded within a 0.004-ha plot. Mean percent herbaceous groundcover was estimated from 3, 3.6-m transects (0°, 120°, 240°). Groundcover was expressed as a total and within the categories fern, forb, grass, and briar. Briar included blackberry, raspberry (*Rubus* spp.), and greenbriar (*Smilax* spp.). Vertical vegetation density was estimated using a 2.0 m vegetation profile board divided into 0.2-m sections (Nudds 1977). Mean percent vertical coverage of vegetation was estimated 10 m from plot center at 4 sample points, one for each cardinal direction. During 2002–2004, mean percent overstory canopy also was estimated from these points using a densiometer. Standard deviation of the 4 canopy measurements was calculated to measure canopy continuity.

Invertebrates were sampled within a 15 m radius of plot center using a 0.10-m^2 bottomless box and a terrestrial vacuum sampler (Harper and Guynn 1998). During 2000–2001, 5 subsamples were collected at each plot. After 2001, power analysis revealed 4 subsamples were adequate to estimate mean invertebrate density within plots (Fettinger 2002). Invertebrate samples were frozen pending sorting in the laboratory. Arthropods were sorted from leaf litter and detritus and identified to order according to Borror et al. (1989). After sorting, arthropods were placed in glass vials, oven-dried for 48 hours at 60°C (Murkin et al. 1996), and weighed by order. Orders frequently consumed by ruffed grouse chicks, including Araneae, Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, and Orthoptera, were grouped in a unique category (Bump et al. 1947, Stewart 1956, Kimmel and Samuel 1984).

Weather

Coweeta Hydrologic Lab (Coweeta LTER, Otto, North Carolina) recorded weather data at a permanent weather station on the study site. Minimum and maximum temperature and precipitation (tipping bucket) were recorded daily. Weather data collected between 25 May (mean hatch date) and 30 June each year were used to explore correlations with brood survival. Variables of interest included, mean maximum temperature (MAXTEMP), number of days with temperatures $< 7^oC$ (COLDAYS), total rainfall (RAIN), and number of days with rainfall events (RAINDAYS). Linear relationships of weather data with 5-week brood survival were examined using the REG procedure in SAS.

Habitat Modeling

An information-theoretic approach (Burnham and Anderson 1998) was used to evaluate differences in habitat characteristics between brood and random sites. A set of a-*priori* candidate models was created using combinations of microhabitat characteristics previously determined important to ruffed grouse broods (Stewart 1956, Berner and Gysel 1969 Porath and Vohs 1972, Godfrey 1975, Kubisiak 1978, Maxson 1978, Kimmel and Samuel 1984, Thompson et al. 1987, Scott et al. 1998, Fettinger 2002, Haulton et al 2003). Variables included in models were percent total groundcover, percent vertical cover $\leq$2 m, midstory stems $\leq$11.4 cm DBH, and density of invertebrates in orders preferred by ruffed grouse chicks. Bias-corrected Akaike's Information Criterion (AIC_c) and weight of evidence (w_i) were used to rank and select the model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). Logistic regression was used to calculate 2log-likelihood values for each model with brood sites = 1 and random sites = 0 (Procedure GLM, SAS Institute, Cary, North Carolina, USA.). Log-likelihoods were then used to calculate Akaike's Information Criterion. Multicollinearity of explanatory variables was assessed for each model with variance inflation factor (VIF) output by the REG Procedure in SAS. Goodness of fit of the most parsimonious models was assessed with Hosmer and Lemeshow goodness of fit test (Hosmer and Lemeshow 1989).

Habitat characteristics were compared between broods that survived to 5-weeks post hatch and those that did not. Linear distance from nest sites to preferred brood habitats was measured for both categories. Nests located within a preferred brooding habitat were assigned a value of 0. Inherently small sample size of vegetation plots for non-surviving broods (n = 32) prevented model development. Therefore, habitat variable means and 95% confidence intervals were calculated for comparisons.

Second Order Habitat Selection

Habitat use was compared with availability at the study area scale (i.e., second-order selection; Johnson 1980). Use was represented by the proportion of habitats within brood home ranges. The Animal Movement Extension to ArcView GIS 3.2 (Environmental Systems Research Institute Inc., Redlands, CA; Hooge and Eichenlaub 1997) was used to calculate fixed kernel home ranges (Worton 1989). Estimates were based on 75 percent kernel contours to define central portions of a home range and exclude "occasional sallies" (Burt 1943, Seaman et al. 1999). To determine adequate sampling (minimum locations), home range area was plotted against number of locations to determine sampling level at which area variation decreased and became asymptotic. Only broods with $\geq$1 chick surviving at 5 weeks post-hatch and home ranges that became asymptotic were used for analysis.

Home ranges were overlaid on a Geographic Information System (GIS) created for the area using color infrared aerial photographs, 1:24,000 U.S. Geologic Survey 7.5-min quadrangles, U.S. Forest Service Continuous Inventory of Stand Condition (CISCS), and ground truthing. Home ranges were clipped from the coverage to determine proportional use of each habitat type. The Animal Movement Extension also was used to calculate home range size by 95% kernel and minimum convex polygon (MCP) methods for comparison with other studies.

Second-order habitat availability was defined by 1,200 m circular buffers around successful nest sites. Grouse chicks are capable of moving up to 1200 m during the 5 weeks following hatch (Godfrey 1975, Fettinger 2002); therefore, this distance represented habitats available to broods based on their movement potential. Use was compared with availability using compositional analysis (Aebischer et al. 1993). Relative ranks of habitat use were assigned by calculating pair-wise differences in use versus availability for corresponding habitat log-ratios. To control Type I error, data were examined for 0% observations in any available habitat (Bingham and Brennan 2004). Shapiro-Wilk's test was used to test for normality in log-ratio differences, and randomization tests were used to determine differences in use versus availability for non-normal data. Significance tests ($\alpha = 0.05$) were used to examine differences in relative preference among ranked habitats (Aebischer et al. 1993).

RESULTS

From 2000–2004, 36 brood females were monitored resulting in 372 microhabitat plots (186 brood, 186 random). Seventeen brood females had $\geq$1 chick alive at 5 weeks post-hatch. Whole brood survival varied across years with 0% (0/5), 100% (9/9), 70% (7/10), 22% (2/9), and 33% (1/3) surviving to 5 weeks post-hatch in 2000, 2001, 2002, 2003, and 2004, respetively. Annual brood survival was not correlated with MAXTEMP ($r^2 = 0.015$, $P = 0.984$), COLDAYS ($r^2 = -0.613$, $P = 0.387$), RAIN ($r^2 = 0.034$, $P = 0.966$), or RAINDAYS ($r^2 = 0.047$, $P = 0.953$).

Mean home range size was 24.3 ha ($\pm$ 4.0 SE) using 75% kernel methods and 40.0 ha ($\pm$ 4.0 SE) using MCP. At second order selection, log-ratio differences were non-normal (Wilk's $\lambda = 0.90$). Randomization tests recommended for non-normal log-ratios (n=10,000; Aebischer et al. 1993) indicated use differed from availability ($P < 0.001$).

Top-ranked habitats for relative preference were SUBXER1, SUBXER2, SUBXER5, ROAD, and WLO (Table 3.3). Lack of significant differences in use indicated ranks among these habitats were interchangeable.

The most parsimonious microhabitat model included an intercept term, percent total herbaceous groundcover, percent vertical cover, density of midstory stems <11.4 cm DBH, and preferred invertebrate density ($\mathrm{AIC}_c = 482.36$, $\omega_i = 0.965$; Table 3.4). Cross-validation revealed the model correctly classified 66.3 % of brood locations, and lack of fit was rejected by Hosmer and Lemeshow goodness of fit test ($\chi^2 = 6.02$, $P = 0.645$; Hosmer and Lemeshow 1989). Explanatory variables in the best model were not linearly related (VIF <1.38).

Compared with random plots, brood sites had greater percent herbaceous groundcover (brood = 55.7 ± 2.0 SE, random = 44.8 ± 2.0 SE), greater percent vertical cover (brood = 52.3 ±2.0 SE, random = 41.5 ± 2.0 SE), greater midstory stems/ha <11.4 cm DBH (brood = 6,250 ± 441 SE, random = 4,963 ± 355 SE), and greater number of invertebrates/m^2 (brood = 58.9 ± 5.0 SE, random = 44.3 ± 2.4 SE; Tables 3.5, 3.6). Herbaceous groundcover on both brood and random plots was evenly distributed between forb and fern with lesser amounts of grass and briar (Table 3.5). Vertical vegetation coverage 0–2 m in height also was evenly distributed across 0.4 m sections. The greatest difference in preferred invertebrate density was within the order Hymenoptera (i.e., bees, wasps, ants; Table 3.6). Mean Hymenopteran density was 13.5/m^2 (± 4.3 SE) on brood plots and 7.7/m^2 (± 1.5 SE) on random plots. Invertebrate biomass did not differ between brood and random plots (Table 3.7).

Microhabitat variables did not differ among plots measured for broods that survived to 5 weeks post-hatch and those that did not (Table 3.8). Mean linear distance from nest sites to brood habitats was 41 m (8–73 m, 95% CI) for surviving broods; and 90 m (16–165, 95%CI) for non-surviving broods; however, variability resulted in overlap between confidence intervals.

DISCUSSION

Whole brood survival varied widely from 0–100% across years; however, this statistic should not be viewed as a reliable indicator of chick survival. For example, if brood survival in a given year was 2/10 (20%) with 3 chicks/brood, the number of chicks surviving would actually be greater than during a year with 5/10 broods surviving (50%) with 1 chick/brood. Flush count data do not provide an alternative, as brood mixing and a wide range of observer bias may occur (Godfrey 1975*b*). Given difficulties in estimating chick survival without radiotagged individuals (Larson et al. 2001), whole brood longevity was the best estimator available on WSC.

Brood survival was not related to weather variables examined on WSC. It seems reasonable to theorize cold weather and rainfall would influence ruffed grouse chick survival during the first weeks after hatch when chicks are unable to thermo regulate and the brooding female provides protection from the elements. Spring weather has been shown to influence recruitment in other gallinaceous game birds including wild turkeys (*Meleagris gallopavo*, Roberts and Porter 1998) and northern bobwhite (*Colinus virgianus*, Lusk et al. 2001); however, such relationships have not been identified for ruffed grouse (Bump et al. 1947, Larson and Lahey 1958, Gullion 1970). As a northern species, ruffed grouse may have adapted to efficiently brood chicks during periods of inclement spring weather frequently encountered in northern latitudes. In the CSA, there may be even less of an impact as weather extremes are less severe compared with northern parts of their range.

Brood MCP home ranges were smaller than those reported from other studies in mixed oak forests. On 2 study sites in Virginia and West Virginia, brood home ranges averaged 90 ha (Haulton 1999). In Pennsylvania, Scott et al. (1998) reported overall home range of 84 ha, with smaller ranges occurring on intensively managed sections of the study area. Although home range size may be a function of habitat quality (Schoener 1968, Smith and Shugart 1987, Renken and Wiggers 1989), larger use areas reported from other studies may have resulted from these researchers monitoring broods through late summer when ranges often shift to take advantage of diverse food sources. Home ranges in this study were estimated during the early brood period, ending in early July. Nonetheless, considerably smaller estimates from the core of ruffed grouse range of 12.9 ha (Godfrey 1975) and 16.0 ha (Maxson 1978) may indicate more desirable habitat conditions in mixed hardwood-aspen forests of the Great Lakes Region.

With respect to forest types, broods used mixed oak stands in the 0–5, 6–20, and >80-year age classes. Site conditions were submesic to subxeric with northern red oak and red maple dominant in the overstory and flame azalea, American chestnut sprouts, red maple, serviceberry, and northern red oak, in the midstory (Tables 3.9, 3.10). The 0–5-year class was represented by use of 3–4-year-old group selection cuts and edges of 2 recently harvested irregular shelterwood (i.e., 2-aged) stands. Broods also utilized edges of 6–20-year-old mixed oak clearcuts, but seldom ventured into their interior.

There may be an apparent contradiction between use of younger age classes and >80-year-old mixed oaks. During the mid-1980s an extensive drought in the southeastern United States resulted in increased overstory tree mortality and canopy gap formation in late-rotation oak forests (Clinton et al. 1993). These canopy openings promoted localized patches of early successional structure similar to that found in younger stands. Broods often were associated with such canopy openings as evidenced by greater variability in canopy closure at brood locations (Table 3.5).

In addition to the aforementioned forest types, broods used other openings, including edges of permanent clearings (i.e., wildlife openings) and forest roads. All wildlife openings and roads used by broods were located within late-rotation mixed oak stands. Management included an initial planting of orchardgrass (*Dactylis glomerata*), tall fescue (*Festuca arundinacea*) and white-dutch clover (*Trifolium repens*) maintained by annual or biennial mowing. Dense understory conditions created by perennial cool-season grasses prevented chick movement through these areas; however, broods were observed foraging along their periphery. Herbaceous and woody stem cover provided by various forbs, brambles, shrubs, and regenerating hardwoods created desirable conditions for foraging and concealment along margins of clearings. Microclimates created by moderate forb cover in conjunction with overstory shrubs create ideal conditions for both grouse chicks and their invertebrate prey (Kimmel and Samuel 1984). Maxson (1978) also noted broods foraging along field edges and within hardwood strips between open fields and hardwood forest. In Virginia, Stewart (1956) observed broods using linear openings created by forest roads. These studies and ours suggest permanent clearings and forest roads can be managed to create and improve brood habitat in oak forests.

With the exception of Haulton et al. (2003), most habitat studies in mixed oaks have noted an association of ruffed grouse broods with forest openings. In Missouri, Freiling (1985) found broods near canopy gaps in mature sawtimber stands. Porath and Vohs (1972) and Stewart (1956) gave similar reports from Iowa and Virginia, respectively. In New York, Bump et al. (1947:140) cited brood use of "spot-lumbered hardwoods." These areas seem to be similar to group selection stands on WSC. A common theme across studies is the young age and diversity of vegetation in brood habitats.

Microhabitats selected by broods had greater vertical vegetation cover, herbaceous groundcover, and midstory stem density compared to availability. Random plots were frequently within the same stand type as use locations, suggesting broods selected within stand microsites based on vegetation structure. Other brood habitat studies in mixed-oak forests emphasized the importance of 0.0–2.0 m vertical cover (Scott et al. 1998, Haulton et al. 2003) and percent groundcover in the 50–60% range (Porath and Vohs 1972, Thompson et al. 1987, Scott et al. 1998, Haulton et al. 2003); however, there is disagreement regarding importance of midstory stem density. Supporting desirability of high stem density, Scott et al. (1998) found broods used 10-year-old clearcuts with 21,100 stems/ha. In Missouri, Thompson et al. (1987) reported moderate stem density of 5,558 stems/ha at brood locations. Conversely, in Virginia and West Virginia, Haulton et al. (2003) suggested broods preferred more open conditions (i.e., 3,581–3,822 stems/ha) though more dense stands were available. Discrepancies in stem density reports may be a function of herbaceous cover conditions. Broods may select sites based on herbaceous structure with midstory stems providing additional cover when available. On WSC, desirable herbaceous cover and moderate stem density (6,250 stems/ha) occurred along edges of timber harvests and in canopy gaps.

Differences in habitat structure were not observed between surviving and non-surviving broods. Conditions that created canopy gaps were widespread (Clinton et al. 1993), resulting in patches of desirable cover across ≥80-year-old subxeric mixed oak stands. Interspersion of 3, 5–12 ha clearcuts and 1, 5 ha two-aged harvest created additional habitat on a 513 ha ridge used by 14 broods. This together with moderate overall brood survival (53%) may suggest brood habitat for the first 5 weeks following hatch was not limiting on WSC; however, to maintain habitat quality, continued disturbance may be necessary as clearcut stands were nearing pole-stage and gaps created 17–20-years prior were nearing closed canopy conditions.

Invertebrates are a primary food source for grouse chicks <5 weeks old (Bump et al. 1947, Stewart 1956, Kimmel and Samuel 1984). Density of preferred orders, primarily ants (Hymenoptera) and leafhoppers (Homoptera), was greater on brood plots compared to random (Table 3.6). Using human-imprinted ruffed grouse chicks, Kimmel and Samuel (1984) observed ants and leafhoppers were the most frequently consumed invertebrates. They also noted herbaceous cover that presents feeding opportunities and protective cover provide optimal habitat conditions.

Rather than selecting habitats based on food availability, birds may use proximate cues related to prey abundance (Schoener 1968, Smith and Shugart 1987). Based on microhabitat characteristics at use locations, broods appeared to select sites based on vegetation structure. This structure also provided invertebrates (especially those of the order Hymenoptera) as a food source. For wild turkey poults, which consume similar invertebrates to ruffed grouse chicks, authors have recommended forest management practices that may increase invertebrate density by promoting herbaceous communities (Hurst 1978, Rogers 1985, Pack et al. 1980). On WSC, Harper et al. (2001) also recommended habitat evaluations focus on vegetation structure to improve invertebrate density.

MANAGEMENT IMPLICATIONS

A comprehensive understanding of forest management effects on wildlife can be gained through habitat investigations at multiple spatial scales. Information is provided on forest stand types and microhabitat characteristics within stands used by ruffed grouse broods. Similar to other studies, vertical cover, herbaceous groundcover, and midstory stem density were important components of brood habitat on WSC. These requirements were met where openings in the forest canopy encouraged herbaceous plant growth and woody stem regeneration. Interspersion of forest age classes creates areas of desirable cover in close proximity (Sharp 1963, Berner and Gysel 1969, Gullion 1977, Kubisiak 1978). Where mature, undisturbed forests have closed canopies, timber management activities including group selection harvests, thinning, shelterwood, and irregular shelterwood harvests and prescribed burning can promote improved cover conditions. In mature (>40 years), mixed oak stands with closed canopies, timber management activities will allow sunlight to reach the forest floor, resulting in diverse understory communities favored by grouse broods. On forest roads and permanent clearings, eliminating perennial cool season grasses and maintaining forb communities through minimal maintenance should be a priority (Healy and Nenno 1983, Harper et al. 2001).

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APPENDIX

Table 3.1. Forest stand associations, understory characteristics, and corresponding USDA Forest Service (USFS) and Society of American Foresters (SAF) codes for land classifications used to define ruffed grouse habitats on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina 1999–2004. Adapted from McNab and Browning (1993).

Land class	Moisture	Forest associations	Understory	USFS	SAF
Xeric	Xeric	Scarlet oak	>75% ericaceous	59	NA
	.	Pitch pine-oak	>75% ericaceous	15	45
	.	Chestnut oak-scarlet oak	50-75% ericaceous	60	NA
	Subxeric	Chestnut oak	50-75% ericaceous	52	44
Subxeric	Subxeric	Chestnut oak	25-50% ericaceous	52	44
	.	White oak-red oak-hickory	25-50% ericaceous	55	52
	.	Northern red oak	herbaceous	53	55
	Submesic	Yellow poplar-white oak-red oak	herbaceous	56	59
Mesic	Submesic	Yellow poplar	Herbaceous	50	57
	.	Sugar maple-beech-yellow birch	Herbaceous	81	25
	.	Basswood-yellow buckeye	Herbaceous	41	26
	Mesic	Hemlock	75-100% rhododendron	8	23

Table 3.2. Land class, stand age (years), resultant ruffed grouse habitat delineations, number of stands, mean stand size (ha) and study area coverage (%) of Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Land class	Age	Habitat	*n*	Mean ± SE	Coverage
Mesic	40-80	MESIC4	23	21 ± 5.3	9.7
Mesic	>80	MESIC5	12	37 ± 8.7	9.1
Mesic	NA	RHODO	18	53 ± 20.3	19.6
Subxeric	0-5	SUBXER1[a]	30	2 ± 0.4	0.8
Subxeric	6-20	SUBXER2	40	10 ± 0.6	8.1
Subxeric	21-39	SUBXER3	7	11 ± 1.7	1.6
Subxeric	40-80	SUBXER4	8	16 ± 3.9	2.7
Subxeric	>80	SUBXER5	43	36 ± 4.3	31.5
Xeric	6-20	XERIC2	4	15 ± 4.4	1.2
Xeric	40-80	XERIC4	6	20 ± 3.4	2.4
Xeric	>80	XERIC5	15	39 ± 11.2	11.9
Roads	NA	ROAD	NA	NA	1.1
Openings	NA	WLO	24	0.5 ± 0.1	0.2

[a] Represented alternative regeneration treatments (i.e., shelterwood, irregular shelterwood, and group selection).

Table 3.3. Ranks of habitats used versus availability at the study area scale for female ruffed grouse with broods on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it with corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Wlo	Subxer2	Subxer5	Subxer1	Road	Rhodo	Mescov4	Mescov5	Subxer3	Xeric2	Xeric4	Subxer4	Xeric5	Rank
Wlo	▨	+	+	+	+	+++	+++	+++	+++	+++	+++	+++	+++	1
Subxer2		▨	+	+	+	+++	+++	+++	+++	+++	+++	+++	+++	2
Subxer5			▨	+	+	+++	+++	+++	+++	+++	+++	+++	+++	3
Subxer1				▨	+	+++	+++	+++	+++	+++	+++	+++	+++	4
Road					▨	+++	+++	+++	+++	+++	+++	+++	+++	5
Rhodo						▨	+	+	+	+++	+	+++	+	6
Mescov4							▨	+	+	+	+	+++	+	7
Mescov5								▨	+	+	+	+	+	8
Subxer3									▨	+	+	+	+	9
Xeric2										▨	+	+	+	10
Xeric4											▨	+	+	11
Subxer4												▨	+	12
Xeric5													▨	13

Table 3.4. A-*priori* candidate models, number of parameters estimated (K), bias-corrected Akaike's Information Criterion (AIC_c), and model weights (w_i) used to evaluate ruffed grouse brood microhabitat on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model[a]	K	AICc	ΔAIC	w_i
Gcvr + lat + midstem + arthropods	4	482.358	0.000	0.965
Gcvr + lat	2	489.757	7.399	0.024
Gcvr + lat + midstem	3	491.246	8.888	0.011
Gcvr	1	502.026	19.668	0.000
Arthropods	1	502.212	19.854	0.000
Lat	1	502.935	20.577	0.000
Lat + midstem	2	504.821	22.463	0.000
Midstem	1	512.816	30.458	0.000

[a] Gcvr = percent herbaceous groundcover
Lat = percent vertical vegetation cover 0.0 – 2.0 m in height
Midstem = density of woody stems <11.4 cm dbh
Arthropods = density of invertebrates in orders preferred by ruffed grouse chicks

Table 3.5. Microhabitat variables measured at sites used by ruffed grouse females with broods ($n = 35$) and corresponding random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

	Brood				Random			
Variable	Mean	*n*	SE	95% CI	Mean	*n*	SE	95% CI
Basal area (m^2/ha)	17.0	186	0.7	15.5–8.5	17.9	186	0.8	16.4–19.4
Canopy cover (%)	76.3	90	2.0	72.4–80.3	82.0	90	1.8	78.5–85.5
Std. dev. (%)[a]	12.1	90	1.1	9.9–14.3	6.9	90	0.7	5.6–8.2
Stem density (/ha)	6250	186	441	5380–7120	4963	186	355	4263–5662
Shrub (/ha)	2947	186	379	2198–3695	2172	186	309	1562–2781
Hardwood (/ha)	3303	186	217	2875–3732	2791	186	186	2424–3159
Lateral cover (%)								
0.00-2.00 m	52.3	186	2.0	48.4–56.3	41.5	186	2.0	37.6–45.3
0.00-0.40 m	77.1	186	1.8	73.6–80.6	65.3	186	2.0	61.4–69.2
0.41-0.80 m	57.0	186	2.3	52.5–61.5	45.7	186	2.2	41.4–49.9
0.81-1.20 m	47.6	186	2.3	43.0–52.1	36.6	186	2.3	32.0–41.1
1.21-1.60 m	41.7	186	2.4	36.9–46.4	32.6	186	2.3	28.0–37.2
1.61-2.00 m	38.4	186	2.5	33.4–43.3	27.1	186	2.3	22.7–31.6
Ground cover (%)								
Forb	23.5	186	1.6	20.3–26.7	21.1	186	1.6	17.8–24.3
Fern	23.3	186	1.9	19.6–27.0	17.6	186	1.5	14.7–20.5
Grass	5.6	186	0.8	4.0–7.2	4.3	186	0.8	2.6–5.9
Briar[b]	3.3	186	0.7	2.0–4.6	1.9	186	0.4	1.1–2.7
Total	55.7	186	2.0	51.8–59.7	44.8	186	2.0	40.8–48.7

[a] Standard deviation of 4 canopy measurements taken at each site

[b] included coverage in greenbriar (*Smilax* spp.), blackberry, and raspberry (*Rubus* spp.)

Table 3.6. Density of invertebrates (number/m^2) preferred by ruffed grouse chicks at sites used by females with broods (*n* = 35) and corresponding random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

		Brood (*n* = 186)			Random (*n* = 186)		
Class	Order	Mean	SE	95% CI	Mean	SE	95% CI
Arachnida							
	Araneae	13.1	0.8	11.4–14.8	12.4	0.7	11.1–13.7
Hexapoda							
	Coleoptera	4.8	0.4	3.9–5.7	3.5	0.3	2.9–4.2
	Diptera	15.5	1.4	12.7–18.3	12.4	1.2	10.2–14.7
	Hemiptera	1.3	0.2	1.0–1.7	1.5	0.4	0.7–2.3
	Homoptera	8.0	1.2	5.7–10.3	5.0	0.5	4.0–6.1
	Hymenoptera	13.5	4.3	5.1–21.9	7.7	1.5	4.9–10.6
	Lepidoptera (Adult)	0.5	0.1	0.3–0.7	0.5	0.1	0.3–0.7
	Lepidoptera (Larval)	1.6	0.2	1.1–2.1	0.8	0.1	0.6–1.1
	Orthoptera	0.5	0.1	0.3–0.7	0.3	0.1	0.1–0.4

Table 3.7. Biomass of invertebrates (grams/m^2) preferred by ruffed grouse chicks measured at sites used by ruffed grouse females with broods (*n* = 35) and corresponding random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

		Brood (*n* = 186)			Random (*n* = 186)		
Class	Order	Mean	SE	95% CI	Mean	SE	95% CI
Arachnida							
	Araneae	0.033	0.003	0.026–0.039	0.025	0.002	0.021–0.029
Hexapoda							
	Coleoptera	0.014	0.002	0.10–0.018	0.016	0.003	0.010–0.021
	Diptera	0.008	0.001	0.006–0.009	0.006	0.001	0.005–0.007
	Hemiptera	0.002	0.001	0.001–0.003	0.003	0.001	0.001–0.004
	Homoptera	0.007	0.001	0.005–0.009	0.005	0.001	0.003–0.007
	Hymenoptera	0.010	0.003	0.003–0.017	0.005	0.001	0.003–0.007
	Lepidoptera (Adult)	0.002	0.001	0.000–0.004	0.003	0.001	0.000–0.005
	Lepidoptera (Larval)	0.014	0.004	0.007–0.021	0.009	0.003	0.003–0.014
	Orthoptera	0.011	0.003	0.004–0.017	0.012	0.004	0.004–0.021

Table 3.8. Means, associated standard error, and 95% confidence intervals for microhabitat variables, and density (number/m^2), and biomass (grams/m^2) of invertebrates preferred by ruffed grouse chicks measured at sites used by successful ($\geq$1 chick alive at 5 weeks post-hatch) and unsuccessful broods on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

	Successful (*n* = 63)			Unsuccessful (*n* = 34)		
Variable[a]	Mean	SE	95% CI	Mean	SE	95% CI
Basal Area (m^2/ha)	18.5	1.4	15.7–21.2	17.5	1.7	14.1–20.9
Stem Density (/ha)	4857	560	3,737–5,977	5,688	867	3,924–7,452
Lateral cover 0-2 m (%)	41.6	3.2	35.2–48.1	50.8	4.4	41.9–59.8
Ground cover (%)	52.8	3.0	46.7–58.9	45.6	5.1	35.4–55.9
Arthropod density	4.6	0.4	3.9–5.3	6.0	0.6	4.8–7.3
Arthropod biomass	0.0087	0.0009	0.0069–0.0105	0.0083	0.0018	0.0047–0.0119

[a] Stem desnity = density of woody stems <11.4 cm dbh/ha
Ground cover = percent herbaceous groundcover
Lateral cover = percent vertical vegetation cover 0–2 m in height
Arthropods = density of invertebrates in orders preferred by ruffed grouse chicks

Table 3.9. Frequency of occurrence (%) and percent of total stems ≥ 11.4 cm dbh measured on sites used by ruffed grouse females with broods on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Species	Percent occurrence in plots	Percent total stems
Quercus rubra	78.6	23.7
Acer rubrum	65.5	15.7
Amalanchier arborea	42.9	12.4
Fraxinus americana	35.7	7.7
Prunus serotina	35.7	6.1
Quercus alba	29.2	5.5
Betula alleghaniensis	22.6	4.1
Carya spp.	22.0	3.5
Robinia pseudoacacia	17.3	3.1
Betula lenta	12.5	2.7
Fagus grandifolia	11.3	2.5
Acer saccharum	10.1	1.5
Liriodendron tulipifera	6.5	1.9
Quercus montana	6.5	1.4
Tilia heterophylla	6.5	1.1
Magnolia acuminata	5.4	0.5
Halesia tetraptera	5.4	0.8
Aesculus flava	4.8	0.7
Quercus velutina	3.6	0.5
Prunus pennsylvanicum	2.4	0.2
Oxydendrum arboreum	1.8	0.3
Nyssa sylvatica	1.2	0.2
Sassafras albidum	1.2	0.0
Tsuga canadensis	1.2	2.5
Magnolia fraseri	0.6	1.5
Pinus strobus	0.6	0.0

Table 3.10. Frequency of occurrence (%) and percent of total stems ≤ 11.4 cm dbh measured on sites used by ruffed grouse females with broods on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Species	Percent occurrence in plots	Percent total stems
Castanea dentata	74.1	14.3
Acer rubrum	65.7	5.6
Amalanchier arborea	56.6	4.2
Quercus rubrum	55.9	4.3
Rhododendron calendulaceum	42.7	34.3
Acer pennsylvanicum	39.2	1.8
Rubus spp.	32.9	6.9
Ilex ambigua	30.8	1.9
Fraxinus americana	30.8	1.3
Robinia pseudoacacia	26.6	1.6
Carya spp.	26.6	1.5
Fagus grandifolia	25.9	4.8
Prunus serotina	24.5	1.3
Vaccinium spp.	23.1	2.8
Hamamelis virginiana	18.2	2.4
Magnolia acuminata	17.5	1.2
Sassafras albidum	16.8	1.4
Quercus alba	15.4	1.0
Betula alleghaniensis	14.0	1.1
Acer saccharum	13.3	1.1
Tsuga canadensis	9.8	0.4
Pyrularia pubera	9.1	0.5
Liriodendron tulipifera	7.0	0.4
Rhododendron maximum	6.3	1.0
Betula lenta	6.3	0.5
Kalmia latifolia	5.6	0.7
Gaylussacia ursina	5.6	0.2
Quercus montana	4.9	0.2

PART IV.

RUFFED GROUSE HABITAT USE AND INFLUENCE OF SEASON, SEX, AGE, AND LANDSCAPE CHARACTERISTICS ON HOME RANGE SIZE

ABSTRACT

Ruffed grouse (*Bonasa umbellus*) in the Great Lakes states (the geographic core of their distribution) have shown positive population responses to forest management. Because of differences in seasonal habitat requirements, forest management recommendations include interspersion of stand types to meet biological needs throughout the year. Managers in the southern Appalachians require an understanding of seasonal habitat use to manage for the species at the southern extent of its distribution. Ruffed grouse home ranges and habitat use were studied in the Appalachian Mountains of western North Carolina. The study area was divided into 3 distinct watersheds to examine effects of landscape characteristics on home range size. Habitat preference was determined through compositional analysis. Grouse (n = 276) were radiotagged and monitored $\geq$3 times/week. Seasonal 75% kernel home ranges (n =172) were estimated for 85 individuals. Mean home ranges were 15–59 ha depending on sex, age, and season. The best home range model included one explanatory variable, watershed (AIC_c = 1,729.0, ω_i > 0.999). There was no support for models with sex, age, and season. The watershed with smallest home ranges had more patches of 6–20 year-old mixed oak with less distance among patches and greater interspersion compared to watersheds with larger home ranges. Forest roads and 6–20 year-old mixed oak were habitats preferred by all sex and age classes during all seasons. Early successional stands used by grouse had been harvested via clearcut, and alernative regeneration techniques (i.e., shelterwood and irregular shelterwood). Early successional forest is an important component of grouse habitat, though habitat quality may ultimately be determined by interspersion of young stands with other habitat types. Alternative regeneration techniques can be useful in interspersing habitat components.

Key words: Appalachians, *Bonasa umbellus*, habitat, home range, landscape characteristics, ruffed grouse.

INTRODUCTION

Home range is the area traversed by an animal during its normal activities over a specified period of time (Burt 1943, Kernohan et al. 2001). Home range size depends on individual traits, life history functions, environmental factors, and their interactions. For birds, home range size may be related to sex, age, food supply, breeding status, population density, and habitat distribution (Schoener 1968). McNab (1963) discussed home range size as a function of body size and food resource availability (i.e., bioenergetic demand). To optimize foraging and reduce risks associated with increased movement, animals should attempt to establish the smallest possible home range in habitats that meet all their needs (Badyaev et al. 1996); therefore, home range size may be a useful indicator of habitat quality, with smaller occupancy areas occurring on higher quality sites. Several studies of birds have shown inverse relationships between home range size and resource availability (Smith and Shugart 1987, Renken and Wiggers 1989, Whitaker 2003). Recent efforts have examined relationships of home range size with landscape features (Leary et al. 1998, Elchuck and Wiebe 2003).

Understanding landscape-scale habitat characteristics contributes information about ecological processes that impact wildlife (McGarigal and Marks 1995). Spatial characteristics including patch size, edge density, dispersion, interspersion, and juxtaposition have been shown to affect avian territory size, survival, and recruitment (e.g., Schmitz and Clark 1999, Hinsley 2000, Thogmartin and Schaeffer 2000, Elchuck and Wiebe 2003). Recently, Fearer and Stauffer (2003), and Whitaker (2003) identified landscape characteristics related to variations in home range size of ruffed grouse.

Ruffed grouse are forest-dwelling game birds distributed across boreal forests of Canada and the northern United States. In the eastern U.S., their range extends southward through the central and southern Appalachians. In the northern U.S. and southern Canada, where population densities are greatest, ruffed grouse are closely associated with aspen (*Populus tremuloides, P. grandidentata.*). Mature male aspen buds are an important winter food and regenerating stands of aspen provide year-round cover (Rusch and Keith 1971, Doer et al. 1974, Svoboda and Gullion 1972). South of the range of aspen, Appalachian grouse rely on a diversity of alternate food and cover resources (Servello and Kirkpatrick 1987).

Although forest types vary, a common characteristic of ruffed grouse habitat is dense woody cover with 17,000–34,000 stems/ha in hardwood saplings and brush considered optimal (Gullion 1984*a*). Suitable conditions often are found in young (5–20-year-old) forests created by timber harvest or natural disturbance; however, various age classes and forest types are used as biological activities and food availability changes through the year (Gullion 1972, Kubisiak et al. 1980, Whitaker 2003). Bump et al. (1947) advocated interspersion of habitats long before landscape analyses were commonplace. Since then, creating a mosaic of diverse habitat patches via forest management has been recommended throughout the literature (e.g., Berner and Gysel 1969, Gullion 1984*b*, Kubisiak 1998); however, most inferences are drawn from areas where aspen is a forest component.

Ruffed grouse studies in mixed oak forests have confirmed importance of early successional habitat (Stoll et al. 1995, Storm et al. 2003, Whitaker 2003). In the central and southern Appalachians (CSA), interspersion of forest types and age classes is especially important as grouse use diverse food sources (i.e., hard and soft mast, and herbaceous plants) in the absence of aspen (Whitaker 2003). Although clearcutting is generally recommended as a grouse habitat management practice, public land managers in the central and southern Appalachians are interested in use of esthetic alternatives to clearcutting. In addition to improved esthetics, techniques such as shelterwood, two-age, and group selection may be used to regenerate desirable species and influence hard mast production. Although these techniques have implications for creating grouse habitat, no studies have investigated their use by grouse in the CSA.

Managers require information regarding optimal size, shape, and placement of forest management units for ruffed grouse. Whitaker (2003) and Fearer and Stauffer (2003) studied relationships of home range size to habitat features in the Appalachian region. Both studies examined spatial features within home ranges, and found amount of edge and interspersion were indicators of habitat quality. Although these studies provided valuable insight into landscape composition effects on grouse home range size, many landscape measures of interest to managers, including patch size, patch shape, dispersion, interspersion, and juxtaposition were not included in home range models.

Ruffed grouse home range and habitat use were studied in the mountains of western North Carolina. Objectives were to (1) examine the relationship between sex and age on home range size; (2) determine temporal (seasonal) variability in home ranges; (3) estimate relative habitat preference; (4) identify landscape features of available habitats and their relationship to home range size; and (5) examine grouse use of stands harvested via alternative regeneration techniques.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (3,230 ha), within Nantahala National Forest in western Macon County, North Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges that connect upper elevations to narrow valley floors (Whittaker 1956). Wine Spring Creek, White Oak Creek, Cold Spring Creek, and surrounding ridges naturally divided the study site into 3 distinct watersheds. Mean annual temperature was 10.4º C, and mean annual precipitation was 160 cm. The area was predominantly forested with <1% coverage in small herbaceousopenings. The U.S.D.A. Forest Service purchased WSC in 1912 after it had been logged. Since then, forest management practices included salvage harvest of blight-killed American chestnut (*Castanea dentata*), thinning, clearcutting, and diameter-limit cutting (McNab and Browning 1993).

Habitats were classified by a combination of vegetative community type and stand age. Communities were stratified into 3 land classes (i.e., xeric, subxeric, and mesic) defined by elevation, landform, soil moisture, and soil thickness (McNab and

Browning 1993; Table 4.1; tables and figures are located in the Appendix). Within communities, variation in plant species occurred along a moisture continuum, similar to that described by Whittaker (1956). Xeric communities were on high elevation, steep, south and west aspects characterized by thin, dry soils. Tree species included, scarlet oak (*Quercus coccinea*), black oak (*Q. velutina*), pitch pine (*Pinus rigida*) and chestnut oak (*Q. prinus*) in the overstory with ericaceous plants including huckleberry (*Gaylussacia baccata*), lowbush blueberry (*Vaccinium vacillans*), and mountain laurel (*Kalmia latifolia*) in the understory. Subxeric communities were at middle elevations and upper elevations on less exposed aspects. Soil characteristics were between xeric and mesic, or subxeric and submesic (Whitaker 1956). Overstory was dominated by chestnut oak, white oak (*Q. alba*), hickory (*Carya* spp.), northern red oak (*Q. rubra*), red maple (*Acer rubrum*), and yellow poplar (*Liriodendron tulipifera*). Ericaceous understory occupied 25–50% groundcover on drier microsites whereas herbaceous plants occupied more mesic sites within this category. Mesic communities occurred on north and east aspects, on lower slopes, and in sheltered coves. Stands were comprised of yellow poplar, eastern hemlock (*Tsuga canadensis*), northern hardwoods, including sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), and mixed mesophytic obligates, including American basswood (*Tilia americana*) and yellow buckeye (*Aesculus octandra*). Understory was herbaceous except where rhododendron (*Rhododendron maximum*) inhibited groundcover. Sites with 75–100% cover in rhododendron were placed in a separate habitat classification (RHODO).

Additional land classes included gated forest roads (ROAD) and wildlife openings (WLO). Gated forest roads were defined by a buffer width of 5m from road center on each side. The 10-m width included the road and adjacent berm. Wildlife openings were small, permanent clearings (0.50 ± 0.12 ha SE). Management of roads and openings included an initial planting of orchardgrass (*Dactylis glomerata*), tall fescue (*Festuca arundinacea*) and white-dutch clover (*Trifolium repens*) maintained by annual or biennial mowing.

Stand ages were determined by years since harvest or stand establishment in categories deemed important to ruffed grouse (0–5, 6–20, 21–39, 40–80, >80). Grouse reportedly begin use of regenerating mixed hardwood and oak stands approximately six years after harvest (Kubisiak 1987, Thompson and Dessecker 1997). At 15–20 years of age, habitat quality decreases as the upper canopy closes and woody stem density and herbaceous ground cover decrease (Kubisiak 1987, Storm et al. 2003). Mixed hardwoods remain in a "pole stage" until 40 years of age, when most oak species have reached reproductive maturity and are capable of producing significant acorn crops (Guyette et al. 2004). By 80–120 years, oaks stands are considered full rotation age (U.S. Forest Service 1994). Beyond 120 years, natural mortality of upland oaks increases (Guyette et al. 2004), resulting in canopy gaps. Gated forest roads, wildlife openings and rhododendron-dominated understory were not assigned to age categories because they are in a state of arrested succession and their structural characteristics do not change appreciably over time (Phillips and Murdy 1985).

Stands in the 6–20-year age class were predominantly clearcuts (1.3–24.6 ha, *n* = 44) harvested in the late 1980s and early 1990s. Alternative regeneration harvests (i.e., shelterwood, irregular shelterwood, group selection) were cut 1996–1997, and represented the 0–5-year category (SUBXER1) for most of the study. Target residual basal area was 9.0 m^2/ha for shelterwood harvests. Prescriptions called for a final removal cut of residuals approximately 10 years after the initial harvest. Ruffed grouse data were collected prior to removal of residuals in these stands. Mean size of shelterwood stands was (5.56 ± 0.42 ha SE, *n* = 3). For irregular shelterwood (aka shelterwood with reserves), target residual basal area was 5.0 m^2/ha. Residuals in irregular shelterwood were to be retained through the next rotation, resulting in 2-aged stands. Mean size of 2-aged stands created by irregular shelterwood was (4.68 ± 0.18 ha SE, *n* = 3). Group selection was implemented in 3 stands with 4–9 groups/stand. Mean group size was 0.36 ha (± 0.05 SE). All shelterwood, irregular shelterwood, and group selection harvests were implemented on subxeric sites and represented the SUBXER1 habitat type.

Oak and mixed oak-hickory stands in the >80 year age class (SUBXER5) made up the greatest proportion of the study site (31.5%) and wildlife openings (WLO) made up the least (0.2%; Table 4.2). Early successional habitats in the 6–20-year age class (XERIC2 and SUBXER2) occupied 9.3% of the area. The 0–5, 6–20-year, and 21–39-year age classes were not represented on mesic sites. There were 52.6 km of gated forest roads (1.1% of total area).

Capture and Telemetry

Grouse were captured using intercept traps (Liscinsky and Bailey 1955, Gullion 1965) during two annual periods, late August–early November, and early March–early April, 1999–2003. Gender and age (juvenile or adult) were assessed by feather characteristics and molt patterns (Kalla and Dimmick 1995). Grouse tagged as juveniles in fall graduated to the adult age class at the end of the following summer. Grouse were weighed, leg-banded, fitted with 12-g necklace-style radiotransmitters with a 3-hour mortality switch (Advanced Telemetry Systems, Isanti, Minnesota), and released at capture sites. Tagged birds (*n* = 276) were located ≥3 times per week from permanent telemetry stations. To adequately represent diurnal time periods, an equal number of locations were recorded during the periods, morning (0700–1100), mid-day (1101–1500), and evening (1501–1900). Stations were geo-referenced using a Trimble Global Positioning System (Trimble Navigation Limited Inc., Sunnyvale, California, USA). Transmitter signals were received using Telonics TR-2 receivers (Telonics Inc., Mesa, Arizona, USA), Clark model H7050 headphones (David Clark Company Inc., Worcester, Massachusetts, USA), and hand-held 3-element yagi antennas. For each grouse location, time, azimuths (*n* = 3–5) to nearest degree, grouse activity (moving or still), and a relative measure of signal strength (1 = weakest, 5 = strongest) were recorded. A maximum of 20 minutes was allotted between first and last azimuths to minimize error from animal movement. While in the field, locations were plotted on paper maps to check precision of azimuths. Telemetry data were entered in Microsoft Excel and converted to x and y UTM coordinates using program LOCATE II (Nams 2000). Error was assessed by mean error ellipse of grouse locations and from test beacons (*n*=10) placed at central points (Jennrich and Turner 1969) in randomly selected grouse home ranges. Grouse locations with error ellipses >7 ha were culled from the data set. All field personnel triangulated beacons 4 times during March and June to account for potential foliage effects.

Home Range and Daily Movement

The Animal Movement Extension (Hooge and Eichenlaub 1997) to ArcView GIS 3.2 (Environmental Systems Research Institute Inc., Redlands, California, USA) with least squares cross validation was used to calculate seasonal fixed kernel home ranges (Worton 1989). Estimates were based on 75% kernel contours to define central portions of a home range (Seaman et al. 1999) and exclude the "occasional sallies" described by Burt (1943). To determine adequate sampling (minimum locations), home range area was plotted against number of locations to determine sampling level at which area variation decreased and became asymptotic. Only grouse with sufficient locations for home ranges to become asymptotic were used for analysis.

Four 91-day seasons were defined by plant phenology and grouse biology. Fall (15 September–14 December) was a period of food abundance and dispersal among juveniles. Winter (15 December–15 March) was defined by minimal food resources and physiological stress. Spring (16 March–14 June) coincided with vegetation green-up and breeding activity. Summer (15 June–14 September) was a period of low stress with maximum cover and food availability. Effect of breeding status on home range was evaluated by comparing spring (breeding) to fall and winter pooled (non-breeding). Summer was not included in seasonal analysis because only females with broods were monitored intensively in summer (Chapter III). In spring, home ranges of females known to nest included all locations prior to the onset of continuous incubation. To be included in a season, a grouse must have survived ≥75% of that season (68 days).

Daily movements were monitored by diurnal telemetry (focal runs). During a focal run, grouse were located once every 1.5–2.0 hours. Precision is necessary to ensure movements are reflective of grouse mobility, rather than a measure of telemetry error; therefore, focal locations with error ellipses >1 ha were excluded from analysis. To minimize error, grouse were monitored from proximate stations to prevent disturbing the bird and influencing its movement pattern. If a grouse was disturbed, the focal run was stopped and data were excluded from analysis. Data were collected for 10–20 grouse seasonally, fall 2000–spring 2004. Total daily movement for an individual was the sum of sequential travel distances (m/day), and movement rate was total daily movement divided by total locations (m/1.5 hrs).

Data Analysis

A geographic information system (GIS) was developed using color infrared aerial photographs, 1:24,000 U.S. Geologic Survey 7.5-min quadrangles, U.S. Forest Service Continuous Inventory of Stand Condition (CISCS), and ground truthing. Wine Spring (WSP; 842 ha), White Oak (WOC; 1,399 ha) and Cold Spring (CSP; 987 ha) watersheds were extracted from the GIS to examine landscape features of available habitat and their effects on home range size. Use of landform to define availability prevented spurious results that can be caused by geometric definition of landscapes (i.e., circular or square buffers). Grouse tended to remain within their watershed of capture. Birds that occupied >1 watershed (n = 3) were not included in analysis.

Program FRAGSTATS (McGarigal and Marks 1995) was used to calculate landscape metrics. FRAGSTATS output values at landscape, patch, and class (habitat) scales (Table 4.3). At the class scale, spatial characteristics of 6–20-year-old mixed oak (SUBXER2) and gated forest roads (ROAD) were examined because of their importance as grouse habitat in the Appalachians (Whitaker 2003). Metrics were chosen based on ability to describe features relevant to grouse habitat management and their relationships with each other (McGarigal and Marks 1995, Hargis et al. 1998). Of particular interest were metrics that described patch size, shape, dispersion, interspersion, and edge. Edges were weighted by contrast from 0 (low) to 1 (high) by increments of 0.25. For example, high contrast edges occurred along forest roads, wildlife openings, and boundaries between 0–20- and >40-year-old stands. Medium contrast edges occurred where 21– 39-year-old stands met 6–20-year-old and >40-year-old stands. Low contrast edges occurred between 40–80-and >80-year-old stands (Table 4.4). Vector data were converted to 10-m grids in ArcView 3.2. Analysis window size was defined by mean total daily movement distance of grouse.

An information-theoretic approach (Burnham and Anderson 1998) was used to evaluate sources of variation in home range size. A set of a-*priori* candidate models (Table 4.5) was created using combinations of sex, age, season, and watershed. A bias-corrected version of Akaike's Information Criterion (AIC_c), and weight of evidence (w_i), were used to rank and select the model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). The generalized linear models procedure (Proc GLM; SAS Institute Inc., Cary, North Carolina, USA) was used to calculate –2log-likelihood values for each model. Log-likelihoods were then used to calculate AIC_c. Generalized linear models also were used to test for effects of sex, age, and season on diurnal movements.

Habitat use was compared with availability at the study area scale (second-order selection; Johnson 1980). Use was defined by the proportion of habitats within home ranges. Availability was defined by topographic features surrounding the study area. Road systems facilitated access to most tagged grouse. If a bird traveled beyond the steep ridges surrounding the study area, use could not be measured; therefore, those areas were not included in availability. Use was compared with availability using compositional analysis (Aebischer et al. 1993). Relative ranks of habitat use were assigned by calculating pair-wise differences in use versus availability for corresponding habitat log-ratios. Shapiro-Wilk test was used to test for normality in log-ratio differences. An advantage of compositional analysis is that it allows testing for between group differences in habitat use. Differences were tested between age groups (juvenile and adult), within sexes and seasons. Significance tests ($\alpha = 0.05$) also were used to examine differences in relative preference among ranked habitats (Aebischer et al. 1993). To control Type I error, data were examined for 0% observations in any available habitat (Bingham and Brennan 2004). Wildlife openings had 0% observations and were <1% of available habitats; therefore, in the habitat coverage, openings were incorporated into the surrounding habitat type and excluded from analysis.

RESULTS

Home Range and Movements

Telemetry bearing error on beacons was $\pm$ 6.53°. Mean grouse location error ellipse (*n*=6,656) was 1.9 ha ($\pm$ 0.06 SE). Diurnal data were available for 24 grouse (6 adult female, 3 juvenile female, 7 adult male, 8 juvenile male) in fall, and 10 grouse (5 adult male, 5 juvenile male) in spring. Total mean daily movement (874 $\pm$ 72.1 m SE) did not differ between spring and fall or among sex and age classes ($F_5 = 0.9$, $P = 0.492$); therefore, 874 m was used as the analysis window for landscape analysis.

Seasonal home ranges (*n*=172) were estimated for 85 individuals (4.6). Mean locations/home range was 27 ($\pm$ 3.1 SE). The most parsimonious home range model included one explanatory variable, watershed ($AIC_c = 1729.0$, $\omega_i > 0.999$). There was no evidence of support for home range models with sex, age, season, breeding status, and their interactions as explanatory variables (Table 4.7). Pooled seasonal home ranges were smallest on CSP (14.6 ± 2.8 ha SE) and greatest on WSP (36.2 ± 3.6 ha SE; Table 4.8). To examine effects of sex, age, season, and their interactions on home range size, an *a-posteriori* model of these variables was run in the absence of watershed. No variables in the model were significant ($P > 0.293$).

Landscape Features

There were differences in several landscape and patch metrics among watersheds (Tables 4.9, 4.10). Mean nearest neighbor distance (MNN) for 6–20 year old mixed oak stands (SUBXER2) was 31 m on CSP, 100 m on WOC, and 103 m on WSP, indicating less distance between neighboring SUBXER2 patches on CSP. Mean proximity index (MPI) of SUBXER2 was 142% and 198% greater on CSP compared with WOC and WSP, respectively, indicating more SUBXER2 patches within the analysis window on CSP. Interspersion juxtaposition index (IJI) of SUBXER2 was closer to the maximum of 100% on CSP (76%), compared with WOC (55%), and WSC (60%). Proportion (PROP), mean patch size (MPS), and mean shape index (MSI) of SUBXER2 were similar among watersheds. Gated access roads (ROAD) were not considered for MNN and MPI because roads were included as single linear patches in the GIS, and FRAGSTATS requires ≥2 patches of a corresponding type for these calculations. For ROAD, IJI was 85%, 76%, and 78% on CSP, WOC, and WSC, respectively, indicating similar interspersion of forest roads with other habitat types across watersheds. Proportion of ROAD also was similar on the 3 areas.

Fall Habitat Use

Differences in log-ratios were normally distributed for all sex and age classes within seasons (Shapiro-Wilk > 0.950, $P < 0.001$). Habitat use did not differ between juvenile and adult females ($P = 0.449$); therefore, female age classes were pooled for fall ($n = 29$). Habitat use by females differed from availability ($P < 0.001$). Top-ranked habitats were SUBXER1, SUBXER2, ROAD, RHODO, and MESIC4, with no difference among habitats (Table 4.11). Least ranked habitats were MESIC5 and XERIC4. Fall habitat use differed between adult and juvenile males ($P < 0.001$). There were fewer juvenile males than habitat types in the sample; therefore compositional analysis could not be used to assess habitat use by juvenile males. For adult males ($n = 30$), use differed from availability ($P < 0.001$). Greatest ranked habitats for adult males in fall were SUBXER2 and ROAD, with no difference between these types (Table 4.12). Least ranked habitats were SUBXER3, SUBXER4, XERIC4, XERIC5, and MESIC5.

Winter Habitat Use

Similar to fall, female habitat use in winter did not differ between juveniles and adults ($P = 0.460$); therefore female age classes were pooled. Female ($n = 28$) habitat use differed from availability ($P < 0.001$). Habitats preferred by females in winter were SUBXER1, SUBXER2, SUBXER5, ROAD, RHODO, and XERIC5 (Table 4.13). These habitats did not differ among each other. Least ranked habitats were XERIC4 and MESIC5, with no difference between them. For males in winter, habitat use did not differ between juveniles and adults ($P = 0.725$); therefore, age classes were pooled. Habitat use for males ($n = 28$) differed from availability ($P < 0.001$). Greatest ranked habitats were

SUBXER2 and ROAD with no difference between these types (Table 4.14). Least ranked habitats were XERIC4, XERIC5, and MESIC5.

Spring Habitat Use

Habitat use in spring did not differ between age classes for females ($P = 0.313$) or males ($P = 0.160$) in spring. Habitat use by females ($n = 32$) differed from availability ($P < 0.001$). Habitats preferred by females in spring were SUBXER1, SUBXER2, ROAD, and MESIC4, with no differences among habitats (Table 4.15). Least ranked habitats were XERIC4, SUBXER4, and MESIC5. Habitat use by males ($n = 34$) differed from availability ($P < 0.001$). The most preferred habitat for males in spring was ROAD (Table 4.16). Least ranked habitats were XERIC4, SUBXER4, and MESIC5, with no differences among habitats.

DISCUSSION

Habitat Use

Forest roads were among preferred habitats for all sex and age classes, during all seasons. Several studies cite the importance of roads as grouse habitat in the central and southern Appalachians (Stewart 1956, Endrulat 2003, Whitaker 2003). Roads can provide an herbaceous food source especially important during winter and early spring and in years of low mast production (Whitaker 2003). In Minnesota, where aspen nourishes grouse in winter, Gullion (1984*b*) suggested roads were a marginal habitat used when optimal areas were not available. In the Appalachians, herbaceous plants serve as quality forage for ruffed grouse (Stoll et al. 1980, Servello and Kirkpatrick 1987), and can provide a crucial winter food source in the absence of aspen. Cinquefoil (*Potentilla* spp.)

and wild strawberry (*Fragaria virginiana*) were plant protein sources especially important to females in the central and southern Appalachians prior to nesting (Long and Edwards 2004). These and other forbs often germinate from the seedbank following forest road closure. Preference of ROAD by males during the breeding season was influenced by their juxtapositon to other habitat types. Males on the study area established drumming territories on upper slopes and ridge tops with dense mid-story structure (Schumacher et al. 2001). Drumming sites often were in close proximity to ROAD, where males could attract females while remaining near safety of dense cover (Figure 4.1; Bergerud and Gratson 1988). In northern Georgia, Hale et al. (1982) also reported that drumming logs were in dense cover, close to forest openings (79% within 50 m of an opening).

Subxeric mixed oak in the 6–20-year age class was among habitats preferred by females in fall, winter, and spring, and by males in fall and winter. Association of ruffed grouse with early seral stages is well documented (Dessecker and McAuley 2001); however, interspersion of diverse forest types and age classes ultimately determines habitat quality (Bump et al. 1947, Berner and Gysel 1969, Gullion 1972, Kubisiak 1985). Interspersion of young stands for cover (i.e., high stem density) with mature stands for food (i.e., hard mast) is important, as grouse must optimize the balance between energy gain and predation risk (Cowie 1977). Nutritional constraints posed by reproduction may cause females to spend more time in foraging habitats, while males opt for cover (Whitaker 2003). Data from WSC support this contention. In fall and winter, adult males used fewer habitats compared to females, and selection for escape cover was evident in relative preference for 6–20-year-old subxeric mixed oak.

In fall, winter, and spring, females had ≥ 5 habitats ranked highest in preference, with no difference among them. Habitats that may have been preferred because of cover were RHODO, SUBXER1, and SUBXER2 in all seasons. Potential foraging habitats represented a topographic cross section and included MESIC4, ROAD, and SUBXER5 in fall, and ROAD, SUBXER5, and XERIC5 in winter. Inclusion of more xeric habitat in winter likely indicates a shift in diet to evergreen leaves such as laurel and trailing-arbutus (*Epigaea repens*) available on dry upper slopes (Servello and Kirkpatrick 1987).

Foraging habitats used by females were juxtaposed to escape cover (Figure 4.2.). Subxeric mixed oak stands in the 6–20-year age class provided cover and additional foraging opportunities between mature stands on upper and lower slopes. An example of juxtaposition as a proximate cue to females selecting foraging habitat was a high preference rank for MESIC4 and low preference for MESIC5 in fall. Food availability in terms of mast should be similar between these habitats; however, MESIC5 existed in several large patches, poorly interspersed with escape cover, whereas MESIC4 patches were irregularly shaped and juxtaposed to cover. Further, use of MESIC4 by females in spring was influenced by 6 females that used a stand selectively thinned to approximately 75% residual canopy cover in 1993, which likely resulted in increased midstory and herbaceous groundcover, and improved conditions for grouse in this stand.

With the exception of males in fall, habitat use did not differ between juveniles and adults. Juvenile males had greater proportions of ROAD, SUBXER1, SUBXER2, and MESIC5 in fall home ranges, compared with availability; however, sample size was insufficient ($n = 8$) to test differences statistically. After brood break-up in early fall, juvenile males disperse and seek potential breeding territories for the following spring (Hale and Dorney 1963, Small and Rusch 1989). The largest home ranges observed on this study were of juvenile males in fall (59.1 ± 27.4 ha SE). Relatively large home ranges and diverse habitat use may have resulted from occupation of unfamiliar areas and sampling of habitats for suitable spring territories. Such wandering was apparently complete by winter, when home range size decreased (21.5 ± 6.9 ha SE), and juvenile males selected habitats similar to those used by adults.

Use of shelterwood and 2-aged stands was indicated by inclusion of SUBXER1 among habitats preferred by females in fall, winter, and spring. Stands harvested via alternative regeneration techniques were restricted to the southern third of the study site (i.e., WSP watershed). Nonetheless, 22 of 89 grouse on WSP (7 juvenile females, 1 adult female, 7 juvenile males, 7 adult males) included shelterwood and 2-aged stands in their home ranges, although these stands were 0–5-years-old for most of the study and had not yet reached the 6–20-year age class. Grouse began using shelterwood and 2-aged stands 3 years after harvest and continued through the end of the study, 6 years post-harvest. Onset of use was consistent with findings of Stoll et al. (1999) in mixed oak-hickory clearcuts in Ohio, but earlier than reports of 7 years from Pennsylvania (Storm et al 2003) and Wisconsin (McCaffery et al. 1997). Gullion (1984) observed that grouse first utilized regenerating clearcuts when hardwood stems were naturally thinned to ≤37,000 stems/ha. Stem densities at 3 years post-harvest in this study were approximately 38,269 stems/ha and 49,117 stems/ha, in shelterwood and 2-aged stands, respectively (Elliott and Knoepp 2005). Group selection cuts were not used extensively in fall, winter or early spring; however, they were important brood habitats in late spring and summer (see Chapter III).

Shelterwood and 2-aged stands can provide sufficient regenerating stem densities for cover and mature mast-producing trees for food within the same stand. Studies in the central and southern Appalachians showed similar stem densities among shelterwood, 2-aged, and traditional clearcuts at 5–10 years after harvest (Beck 1986, Smith et al. 1989, Miller and Schuler 1995). Regarding food availability, acorns are a high quality food for Appalachian ruffed grouse (Servello and Kirkpatrick 1987). Two-aged stands moderate the time lag in acorn production that normally follows clearcutting (Beck 1986, Smith et al. 1989) and can increase number of acorns produced by individual trees (Stringer 2002). Shelterwood has a similar positive effect, though for a shorter time, prior to removal of residual overstory. Canopy disturbance and improved light conditions promote other grouse food sources in addition to acorns. In southwestern Virginia, herbaceous species richness increased following group selection, shelterwood, irregular shelterwood, and clearcutting (Wender et al. 1999). Miller and Schuler (1995) noted prevalence of wild grape (*Vitus* spp.), flowering dogwood (*Cornus florida*), pin cherry (*Prunus pennsylvanica*), and American hophornbeam (*Carpinus caroliniana*) in a 2-aged stand 10 years after harvest in West Virginia. Norman and Kirkpatrick (1984), and Servello and Kirkpatrick (1987) cited leaves of herbaceous plants and soft fruits as important foods for Appalachian grouse, and suggested silvicultural practices that encourage these foods may increase carrying capacity. Thus, compared to clearcutting, shelterwood and irregular shelterwood have the unique ability to create diverse food resources and cover in the same stand, and their application could positively impact grouse populations. Potential benefits of irregular shelterwood over shelterwood include greater stem density (Elliott and Knoepp 2005) and retention of mature mast-producing trees throughout the rotation.

Home Range and Landscape Characteristics

Ruffed grouse home range size has been reported across the species' range. Earlier studies used minimum convex polygon methods (MCP; Mohr 1947) to estimate utilization distributions (Table 4.17; White and Dimmick 1978, Kurzejeski and Root 1989, Thompson and Fritzell 1989, McDonald et al. 1998), and differences in methodology make comparisons across studies difficult (Lawson and Rodgers 1997). Use of 75% kernel methods allowed comparisons between this study and Appalachian Cooperative Research Project (ACGRP) results pooled across 9 study areas in Kentucky, Maryland, Pennsylvania, Rhode Island, Virginia, and West Virginia (Whitaker 2003). Female home ranges in fall, winter, and spring (Table 4.6) were similar to pooled estimates from other ACGRP sites (Table 4.17). Males had larger mean home ranges compared to ACGRP during all seasons. For fall-winter, mean home range size for males pooled across ACGRP sites was 17 ha, compared with 47 ha and 23 ha in fall and winter, respectively in this study. Mean spring-summer home range size for males on ACGRP sites was 10 ha compared with 22 ha reported here for spring only. Some differences in home range size may have resulted from comparisons of fall-winter, and spring-summer seasons used by ACGRP, with individual fall, winter, and spring estimates reported here. Greater number of locations collected during pooled seasons may have resulted in condensed 75% kernel contours and smaller home range areas on ACGRP sites.

Mean home range sizes were 2 times greater on WOC and WSP watersheds compared to CSP. Season, sex, and age were not predictors of home range size; therefore, structure and composition of available habitat were examined to explain differences among the 3 areas. Use of timber harvest to sustain a proportion of early seral stages is one of the most important aspects of grouse management (Gullion 1984*b*). Fifty percent coverage in the 5–15-year age class has been recommended in aspen communities (Gullion 1972). For mixed oak, prescriptions range from 12% (Stoll et al. 1999) to 20% (Storm et al. 2003). In this study, CSP had slightly less proportional coverage in SUBXER2 (7%) than WOC (9%) and WSP (9%); however, these differences were small and likely negligible in their effect on home range size. In the Appalachians, Endrulat (2003) found no relationship of home range size to habitat quality based on proportion of early successional habitats alone.

Size, dispersion, juxtaposition, and interspersion of habitats also must be considered. Mean size of SUBXER2 stands on CSP was 4.16 ha (0.8 SE). Gullion (1972) cited 4.2 ha as the optimal management unit for ruffed grouse habitat. Patches of SUBXER2 on WOC (7.81 ± 1.0 ha SE) and WSC (5.71 ± 1.0 ha SE) were larger than CSP, and slightly greater than the 0.5–5.0 ha range recommended for the Appalachians by Fearer and Stauffer (2003); however, they were within the 2–8 ha range suggested by Stoll et al. (1999) on mixed-oak sites in Ohio.

Mean nearest neighbor, MPI, and IJI revealed SUBXER2 patches were in closer proximity to each other and had greater interspersion and juxtaposition with other habitats on CSP. The combination of size, dispersion, juxtaposition, and interspersion of SUBXER2 likely influenced home range size. Dispersion of early successional forest stands on CSP allowed grouse to minimize movements between patches of cover while interspersion with uncut stands provided additional food sources in close proximity. In Ohio's mixed mesophytic forests, Stoll et al. (1980) found that in addition to suitable cover, early successional stands ranked highest in production of preferred grouse foods.

Mature, uncut stands also provide important foods in the form of hard mast and herbaceous plants (Stoll et al. 1980, Servello and Kirkpatrick 1987). Interspersion of these forest types on CSP may have created relatively greater habitat quality, resulting in smaller home ranges.

Forest roads can be an important habitat for grouse in the Appalachians, providing an herbaceous food source especially important during winter and early spring and in years of low mast production (Whitaker 2003). Forest roads initially planted with a mix of clover and annual grasses, then mowed annually, also produce arthropods important to grouse chicks (Harper et al. 2001). In this study, ROAD was a preferred habitat for all sex and age classes during all seasons. Gated forest roads intersected most SUBXER2 patches on CSP, but not on the other watersheds. The intersection of SUBXER2 with ROAD decreased patch size and increased interspersion and juxtaposition. Similar to the relationship of SUBXER2 with mature forest, ROAD juxtaposed to SUBXER2 presented food and cover in immediate proximity.

Amount of edge in a landscape and its impact on grouse has been debated. Males tend to use drumming sites near edges (Kubisiak et al. 1980), where they can attract females while remaining near the safety of dense cover (Bergerud and Gratson 1988). Attesting to potential edge benefits to grouse, Fearer and Stauffer (2003) found high contrast edge had an inverse relationship with home range size. Conversely, Gullion (1984) suggested apparent edge use by grouse was a function of preference for interspersed habitats and extensive use indicated poor habitat quality. McCaffery et al. (1996) found that grouse abandoned edges in uncut forest when early successional habitats were made available. In this study, edge density was similar across watersheds despite greater intersperion of patch types on CSP. The presence of high contrast edge, such as along roads and clearcuts, did not appear to influence home range size; however, edge relationships with other aspects of population ecology, including nest success and survival, deserve further investigation (Donovan et al. 1997).

Amount of edge on a landscape is influenced by patch shape. Some studies propose regularly shaped cuts to provide habitat for ruffed grouse (Gullion 1984*b*, Fearer and Stauffer 2003, Storm et al. 2003). On some sites, topography, aspect, moisture, tract size, forest type, and stand age distribution are the most important considerations in prescribing management unit shape (Kubisiak 1985, Whitaker 2003). In this study, mean shape index (MSI) was used to quantify patch form. For MSI calculations in FRAGSTATS, regularly shaped features (circles or squares) are assigned a value of 1, and MSI increases without limit as shape becomes more irregular (McGarigal and Marks 1995). Mean shape index of SUBXER2 stands was <1.9 across watersheds, indicating regularly shaped patches. Based on similarity among watersheds, patch shape did not appear to affect home range size. In the central and southern Appalachians, where steep ridges are intersected by ephemeral and permanent drainages and paralleled by mesic lower slopes, landform and forest characteristics should influence patch shape. The ability to intersperse early successional stands according to site-specific features is the most important determinant of patch shape.

MANAGEMENT IMPLICATIONS

Provision of early successional forest habitat is a cornerstone of ruffed grouse management. To maximize benefits of silvicultural practices, land managers in the

Appalachians require information on size, shape, dispersion, interspersion, and juxtaposition of management units. Home range size can serve as an indicator of habitat quality and may be related to survival (Thompson and Fritzell 1989, Clark 2000). Insight was provided through description of landscape-scale features of available habitats associated with reduced home range size. The area with smallest home ranges had the following landscape characteristics when compared to 2 other areas with larger home ranges: (1) less distance between stands of mixed oak forest in the 6–20 year age class; (2) more patches of early successional forest within the mean daily movement distance of grouse; and (3) greater interspersion and juxtaposition of early successional habitats with gated forest roads and other forest types.

Topography of the southern Blue Ridge creates diverse vegetation communities defined by changes in soil type, thickness, and moisture (Whittaker 1959). Often, various communities and associated ecotones occur in close proximity. The diverse features of southern Appalachian forests offer a unique opportunity to provide a mosaic of habitat types preferred by ruffed grouse.

Management prescriptions should be based on interspersion and juxtaposition of early successional habitats to other preferred types. On this study site, in addition to 6–20-year-old mixed oak, important habitats included gated forest roads, 40–80-year old mixed oak, 80–130-year-old mixed oak, and 40–80-year-old mesic-mixed hardwood. Regarding patch size, early successional habitat created by several smaller cuts can increase interspersion compared to a single, larger cut, provided the smaller units are placed in close proximity to each other and to other important habitats. Based on home range differences across watersheds, ideal patch size was 4 ha (mean SUBXER2 patch size on CSP), though the range of 0.5–8.0 ha should be acceptable.

Results from this study support the contention that habitat management for ruffed grouse should include a diversity of forest types, age classes, and openings that provide food and cover in close proximity. In the Appalachians, leaves of herbaceous plants, soft mast, and hard mast are important food items. Herbaceous plants can be provided on forest roads and in mature stands, especially on mesic and subxeric sites. Soft fruits such as greenbriar (*Smilax* spp.), blackberry, raspberry (*Rubus* spp.), and hawthorn (*Crataegus* spp.) are found along roads, in forest openings, and in stands 0–5-years-old, whereas more shade tolerant fruit producers, including flowering dogwood, blueberry, and huckleberry occur under closed or partial canopies. Substantial hard mast production from oaks and beech requires trees ≥30 years old. These trees can be in mature tracts or as residuals in shelterwood and 2-aged stands. The main focus is to recognize ruffed grouse food sources (or potential food sources), and use silviculture to augment and intersperse these areas with early successional habitats.

The traditional approach to creating early successional cover for grouse relies on clearcutting. Currently, public land managers find litigation a difficult barrier limiting forest management options. Given their ability to produce food and cover and their utility as an esthetic alternative to clearcutting, alternative regeneration techniques (i.e., shelterwood, irregular shelterwood, and group selection) can be important tools in forest management for Appalachian ruffed grouse. Whether through traditional even-aged or alternative regeneration methods, creation of early successional habitat should occur on mid-slope subxeric sites to join mesic lower slopes with xeric uplands. Conditions also could be improved through timber harvest on upland and mesic sites. Placement of harvest units according to landform will allow site-specific flexibility and interspersion of habitat types across vegetation communities and moisture gradients.

Habitat could be improved further through a minimal maintenance approach to forest roads (Healy and Nenno 1983). By seeding a mixture of an annual grain such as winter wheat (*Triticum aestivum*) with clover (*Trifolium* spp.), roads can be stabilized to prevent erosion while providing food sources for grouse and other wildlife. Over time, forbs germinating from the seed bank should maintain vegetation on the site and further enhance habitat quality (Harper et al. 2001, Long et al. 2004). Opening the forest canopy along roads (i.e., daylighting) could be used to stimulate herbaceous plant growth and create adjacent midstory stem cover.

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APPENDIX

Table 4.1. Forest stand associations, understory characteristics, and corresponding USDA Forest Service (USFS) and Society of American Foresters (SAF) codes for land classifications used to define ruffed grouse habitats on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina 1999–2004. Adapted from McNab and Browning (1993).

Land class	Moisture	Forest associations	Understory	USFS	SAF
Xeric	Xeric	Scarlet oak	>75% ericaceous	59	NA
	.	Pitch pine-oak	>75% ericaceous	15	45
	.	Chestnut oak-scarlet oak	50-75% ericaceous	60	NA
	Subxeric	Chestnut oak	50-75% ericaceous	52	44
Subxeric	Subxeric	Chestnut oak	25-50% ericaceous	52	44
	.	White oak-red oak-hickory	25-50% ericaceous	55	52
	.	Northern red oak	Herbaceous	53	55
	Submesic	Yellow poplar-white oak-red oak	Herbaceous	56	59
Mesic	Submesic	Yellow poplar	Herbaceous	50	57
	.	Sugar maple-beech-yellow birch	Herbaceous	81	25
	.	Basswood-yellow buckeye	Herbaceous	41	26
	Mesic	Hemlock	>75% rhododendron	8	23

Table 4.2. Land class, stand age (years), resultant ruffed grouse habitat delineations, number of stands, mean stand size (ha) and study area coverage (%) of Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Land class	Age	Habitat	*n*	Mean ± SE	Coverage
Mesic	40-80	MESIC4	23	21 ± 5.3	9.7
Mesic	>80	MESIC5	12	37 ± 8.7	9.1
Mesic	NA	RHODO	18	53 ± 20.3	19.6
Subxeric	0-5	SUBXER1	30	2 ± 0.4	0.8
Subxeric	6-20	SUBXER2	40	10 ± 0.6	8.1
Subxeric	21-39	SUBXER3	7	11 ± 1.7	1.6
Subxeric	40-80	SUBXER4	8	16 ± 3.9	2.7
Subxeric	>80	SUBXER5	43	36 ± 4.3	31.5
Xeric	6-20	XERIC2	4	15 ± 4.4	1.2
Xeric	40-80	XERIC4	6	20 ± 3.4	2.4
Xeric	>80	XERIC5	15	39 ± 11.2	11.9
Roads	NA	ROAD	NA	NA	1.1
Openings	NA	WLO	24	0.5 ± 0.1	0.2

Table 4.3. Metrics used to quantify landscape-scale habitat variables for ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Metric	Scale	Description
Total area	Landscape	Landscape area (ha)
Shannon's diversity index	Landscape	Measure of diversity by richness
Shannon's evenness index	Landscape	Measure of diversity by evenness
Largest patch index	Landscape	Proportion of the landscape occupied by the largest patch (%)
Mean patch size	Landscape, patch	Mean size (ha) of habitat patches
Mean shape index	Landscape, patch	Shape complexity of habitat patches
Total core area index	Landscape, patch	Proportion of core area within patches
Contrast weighted edge density	Landscape, patch	Total edge, weighted by contrast values, per unit area
Interspersion-juxtaposition index	Landscape, patch	Distribution of patch adjacencies
Proportions	Class	Proportion of landscape covered by each patch type
Mean nearest neighbor	Patch	Degree of isolation of habitat patches
Mean proximity index	Patch	Degree of isolation and fragmentation of habitat patches

* See McGarigal and Marks (1995) for formulas and detailed descriptions of habitat metrics.

Table 4.4. Edge weights used in evaluating ruffed grouse habitat at the landscape scale on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Habitat 1	Habitat 2	Edge Weight
MesCov4	MesCov5	0.00
Subxer4	Subxer5	0.00
Subxer2	Xeric2	0.00
Xeric4	Xeric5	0.00
Subxer4	MesCov4	0.25
Subxer5	MesCov4	0.25
Subxer4	MesCov5	0.25
Subxer5	MesCov5	0.25
Subxer3	MesCov4	0.50
Subxer3	MesCov5	0.50
Subxer3	Subxer4	0.50
Subxer3	Subxer5	0.50
Rhodo	Xeric4	0.50
Subxer3	Xeric4	0.50
Subxer4	Xeric4	0.50
Rhodo	Xeric5	0.50
Subxer4	Xeric5	0.50
Subxer5	Xeric5	0.50
MesCov4	Xeric4	0.75
MesCov5	Xeric4	0.75
Subxer5	Xeric4	0.75
MesCov4	Xeric5	0.75
MesCov5	Xeric5	0.75

Table 4.4. continued.

Habitat 1	Habitat 2	Edge Weight
Subxer1	Rhodo	1.00
Subxer2	Rhodo	1.00
Subxer3	Rhodo	1.00
Subxer4	Rhodo	1.00
Subxer5	Rhodo	1.00
MesCov4	Road	1.00
MesCov5	Road	1.00
Rhodo	Road	1.00
Subxer1	Road	1.00
Subxer2	Road	1.00
Subxer3	Road	1.00
Subxer4	Road	1.00
Subxer5	Road	1.00
Subxer1	Subxer2	1.00
Subxer1	Subxer3	1.00
Subxer2	Subxer3	1.00
Subxer1	Subxer4	1.00
Subxer2	Subxer4	1.00
Subxer1	Subxer5	1.00
Subxer2	Subxer5	1.00
MesCov4	WLO	1.00
MesCov5	WLO	1.00
Rhodo	WLO	1.00
Road	WLO	1.00
Subxer1	WLO	1.00
Subxer2	WLO	1.00
Subxer3	WLO	1.00
Subxer4	WLO	1.00
Subxer5	WLO	1.00
Xeric2	WLO	1.00
Xeric4	WLO	1.00

Table 4.4. continued.

Habitat 1	Habitat 2	Edge Weight
Xeric5	WLO	1.00
MesCov4	Xeric2	1.00
MesCov5	Xeric2	1.00
Rhodo	Xeric2	1.00
Road	Xeric2	1.00
Subxer1	Xeric2	1.00
Subxer3	Xeric2	1.00
Subxer4	Xeric2	1.00
Subxer5	Xeric2	1.00
Road	Xeric4	1.00
Subxer1	Xeric4	1.00
Subxer2	Xeric4	1.00
Xeric2	Xeric4	1.00
Road	Xeric5	1.00
Subxer1	Xeric5	1.00
Subxer2	Xeric5	1.00
Xeric2	Xeric5	1.00

Table 4.5. A-*priori* candidate models used to evaluate variation in home range size of ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model structure	Model definition
HR(age)	HR differs by age
HR(sex)	HR differs by sex
HR(season)	HR differs among seasons
HR(watershed)	HR differs among watersheds
HR(sex*age)	HR differs by sex and age
HR(sex*age*season)	HR differs by sex and age among seasons
HR(sex*season)	HR differs by sex among seasons
HR(age*season)	HR differs by age among seasons
HR(age*watershed)	HR differs by age among watersheds
HR(sex*watershed)	HR differs by sex among watersheds
HR(season*watershed)	HR differs by season among watersheds
HR(sex*age*watershed)	HR differs by sex and age among watersheds
HR(spring≠[fall=winter])	HR in breeding season differs from non-breeding seasons
HR(sex*age*spring≠[fall=winter])	HR differs by sex and age and by breeding or non-breeding seasons
HR(watershed*sex*age*season)	Global model used to assess overdispersion

Table 4.6. Mean home range size (ha), sample size, standard error (SE), and 95% confidence intervals for ruffed grouse by sex, age and season on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Season	Sexage[a]	*n*	Mean	SE	LCL	UCL
Fall	AF	17	28.3	7.4	12.7	43.9
	JF	9	41.2	9.5	19.3	63.0
	AM	27	35.2	10.4	13.7	56.7
	JM	8	59.1	27.4	5.6	123.8
Winter	AF	11	22.1	5.1	10.7	33.4
	JF	12	28.1	6.1	14.7	41.6
	AM	21	24.5	4.3	15.5	33.5
	JM	6	21.5	6.9	3.8	39.2
Spring	AF	13	31.6	4.3	22.2	41.1
	JF	16	30.9	4.9	20.4	41.4
	AM	18	15.0	3.7	7.3	22.7
	JM	14	28.2	6.6	13.9	42.4

[a] Sex and age classes
AF = adult female
JF = juvenile female
AM = adult male
JM = juvenile male

Table 4.7. Comparison of number of parameters estimated (K), Akaike's Information Criterion (AIC_c), differences in AIC_c, and model weights (w_i) for ruffed grouse home range size models based on sex, age, season and location (watershed) on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model	K	AICc	ΔAICc	*w*i
HR(watershed)	4	1729.03	0.00	0.999999
HR(age)	3	1764.01	34.98	0.000001
HR(sex)	3	1765.07	36.04	0.000000
HR(spring≠[fall=winter])	3	1768.51	39.48	0.000000
HR(season)	4	1769.99	40.96	0.000000
HR(sex*age*spring≠[fall=winter])	6	1770.84	41.81	0.000000
HR(sex*watershed)	9	1771.25	42.22	0.000000
HR(age*watershed)	9	1772.11	43.08	0.000000
HR(sex*age)	5	1772.49	43.46	0.000000
HR(sex*season)	9	1772.62	43.59	0.000000
HR(age*season)	9	1776.85	47.83	0.000000
HR(season*watershed)	13	1779.33	50.30	0.000000
HR(sex*age*watershed)	13	1789.97	60.94	0.000000
HR(sex*age*season)	17	1790.26	61.23	0.000000

Table 4.8. Mean home range size (ha), sample size, standard error (SE), and 95% confidence intervals for ruffed grouse on 3 watersheds on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Watershed	*n*	Mean	SE	LCL	UCL
Cold Spring	40	14.6	2.8	9.0	20.2
White Oak	43	29.3	5.9	17.4	41.3
Wine Spring	89	36.2	3.6	29.0	43.4

Table 4.9. FRAGSTATS landscape indices calculated for habitats available to ruffed grouse on 3 locations (watersheds) on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Metric	Units	Watershed		
		Cold Spring	White Oak	Wine Spring
Total landscape area	ha	841.85	1,399.10	987.31
Shannon's diversity index	none	2.05	1.82	1.75
Shannon's evenness index	none	0.86	0.76	0.73
Mean patch size	ha	10.79	16.86	10.18
Largest patch index	%	7.88	15.45	16.18
Mean shape index	none	2.26	2.15	2.32
Total core area index	%	91.51	93.07	91.56
Contrast weighted edge density	m/ha	96.33	79.34	105.01
Interspersion juxtaposition index	%	83.86	72.82	76.47

Table 4.10. FRAGSTATS patch and class indices calculated for habitats available to ruffed grouse on 3 locations (watersheds) on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

			Watershed		
Habitat type[a]	Metric	Units	Cold Spring	White Oak	Wine Spring
SUBXER2	Proportion of habitat type	%	7.30	8.70	8.60
SUBXER2	Mean patch size	ha	4.16	7.81	5.71
SUBXER2	Largest patch index	%	1.42	1.00	1.21
SUBXER2	Mean shape index	none	1.73	1.67	1.83
SUBXER2	Total core area index	%	88.99	92.01	90.21
SUBXER2	Contrast weighted edge density	m/ha	25.59	21.09	27.89
SUBXER2	Mean nearest neighbor	m	30.52	99.84	102.83
SUBXER2	Mean proximity index	none	2,375.60	1,670.20	1,200.40
SUBXER2	Interspersion juxtaposition index	%	75.97	54.99	60.16
ROAD	Proportion of habitat type	%	1.40	0.70	1.50
ROAD	Mean patch size	ha	NA	NA	NA
ROAD	Largest patch index	%	NA	NA	NA
ROAD	Mean shape index	none	NA	NA	NA
ROAD	Total core area index	%	NA	NA	NA
ROAD	Contrast weighted edge density	m/ha	39.18	24.29	40.61
ROAD	Mean nearest neighbor	m	NA	NA	NA
ROAD	Mean proximity index	none	NA	NA	NA
ROAD	Interspersion juxtaposition index	%	85.20	76.02	77.56

[a] SUBXER2 = mixed oak stands in the 6–20-year age class
ROAD = gated forest roads

Table 4.11. Ranks of habitats used versus availability at the study area scale for female ruffed grouse in fall on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it with corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Subxer2	Road	Rhodo	Subxer1	Mesic4	Subxer5	Xeric2	Xeric5	Subxer3	Subxer4	Mesic5	Xeric4	Rank
Subxer2		+	+	+	+	+++	+++	+++	+++	+++	+++	+++	1
Road			+	+	+	+++	+++	+++	+++	+++	+++	+++	2
Rhodo				+	+	+	+++	+	+++	+++	+++	+++	3
Subxer1					+	+	+	+	+	+++	+++	+++	4
Mesic4						+	+	+	+	+++	+++	+++	5
Subxer5							+	+	+	+++	+++	+++	6
Xeric2								+	+	+++	+	+++	7
Xeric5									+	+	+	+	8
Subxer3										+	+	+++	9
Subxer4											+	+	10
Mesic5												+	11
Xeric4													12

Table 4.12. Ranks of habitats used versus availability at the study area scale for adult male ruffed grouse in fall on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it with corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Subxer2	Road	Subxer1	Rhodo	Mesic4	Subxer5	Xeric2	Subxer3	Xeric5	Xeric4	Subxer4	Mesic5	Rank
Subxer2		+	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	1
Road			+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	2
Subxer1				+	+	+	+++	+++	+++	+++	+++	+++	3
Rhodo					+	+	+	+++	+	+++	+++	+++	4
Mesic4						+	+	+++	+++	+++	+++	+++	5
Subxer5							+	+++	+	+++	+++	+++	6
Xeric2								+	+	+++	+++	+++	7
Subxer3									+	+	+	+	8
Xeric5										+	+	+	9
Xeric4											+	+	10
Subxer4												+	11
Mesic5													12

Table 4.13. Ranks of habitats used versus availability at the study area scale for female ruffed grouse in winter on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it to corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at $\alpha = 0.05$.

Habitat	Road	Rhodo	Subxer2	Subxer1	Subxer5	Xeric5	Mesic4	Subxer3	Xeric2	Subxer4	Xeric4	Mesic5	Rank
Road		+	+	+	+	+	+++	+++	+++	+++	+++	+++	1
Rhodo			+	+	+	+	+++	+++	+++	+++	+++	+++	2
Subxer2				+	+	+	+	+++	+++	+++	+++	+++	3
Subxer1					+	+	+	+++	+++	+++	+++	+++	4
Subxer5						+	+	+	+++	+++	+++	+++	5
Xeric5							+	+	+	+	+++	+	6
Mesic4								+	+	+	+	+++	7
Subxer3									+	+	+++	+++	8
Xeric2										+	+	+++	9
Subxer4											+	+	10
Xeric4												+	11
Mesic5													12

Table 4.14. Ranks of habitats used versus availability at the study area scale for male ruffed grouse in winter on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it WITH corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Subxer2	Road	Rhodo	Subxer1	Mesic4	Subxer5	Xeric2	Subxer3	Subxer4	Xeric5	Xeric4	Mesic5	Rank
Subxer2		+	+	+++	+++	+++	+++	+++	+++	+++	+++	+++	1
Road			+	+++	+++	+++	+++	+++	+++	+++	+++	+++	2
Rhodo				+	+	+	+	+++	+++	+++	+++	+++	3
Subxer1					+	+	+	+	+++	+++	+++	+++	4
Mesic4						+	+	+	+++	+++	+++	+++	5
Subxer5							+	+	+++	+	+++	+++	6
Xeric2								+	+++	+++	+++	+++	7
Subxer3									+++	+	+++	+++	8
Subxer4										+	+	+	9
Xeric5											+	+	10
Xeric4												+	11
Mesic5													12

Table 4.15. Ranks of habitats used versus availability at the study area scale for female ruffed grouse in spring on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it with corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Road	Rhodo	Subxer1	Subxer2	Mesic4	Subxer5	Subxer3	Xeric2	Xeric5	Mesic5	Subxer4	Xeric4	Rank
Road		+	+	+	+	+++	+++	+++	+++	+++	+++	+++	1
Rhodo			+	+	+	+	+++	+++	+++	+++	+++	+++	2
Subxer1				+	+	+	+++	+++	+++	+++	+++	+++	3
Subxer2					+	+	+++	+++	+	+++	+++	+++	4
Mesic4						+	+++	+++	+++	+++	+++	+++	5
Subxer5							+	+++	+	+	+++	+++	6
Subxer3								+	+	+	+	+++	7
Xeric2									+	+	+	+++	8
Xeric5										+	+	+	9
Mesic5											+	+	10
Subxer4												+	11
Xeric4													12

Table 4.16. Ranks of habitats used versus availability at the study area scale for male ruffed grouse in spring on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Statistical significance among habitat types is examined by following a habitat type across a row and comparing it to corresponding types in columns. A triple plus sign (+++) indicates significant relative preference at α = 0.05.

Habitat	Road	Subxer1	Subxer2	Subxer5	Rhodo	Mesic4	Subxer3	Xeric2	Mesic5	Xeric4	Subxer4	Xeric5	Rank
Road	▨	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	1
Subxer1		▨	+	+	+++	+++	+++	+++	+++	+++	+++	+++	2
Subxer2			▨	+	+	+	+	+	+++	+++	+++	+++	3
Subxer5				▨	+	+	+	+++	+++	+++	+++	+++	4
Rhodo					▨	+	+	+	+++	+++	+++	+++	5
Mesic4						▨	+	+	+	+++	+++	+++	6
Subxer3							▨	+	+	+++	+++	+++	7
Xeric2								▨	+	+++	+++	+++	8
Mesic5									▨	+	+	+	9
Xeric4										▨	+	+	10
Subxer4											▨	+	11
Xeric5												▨	12

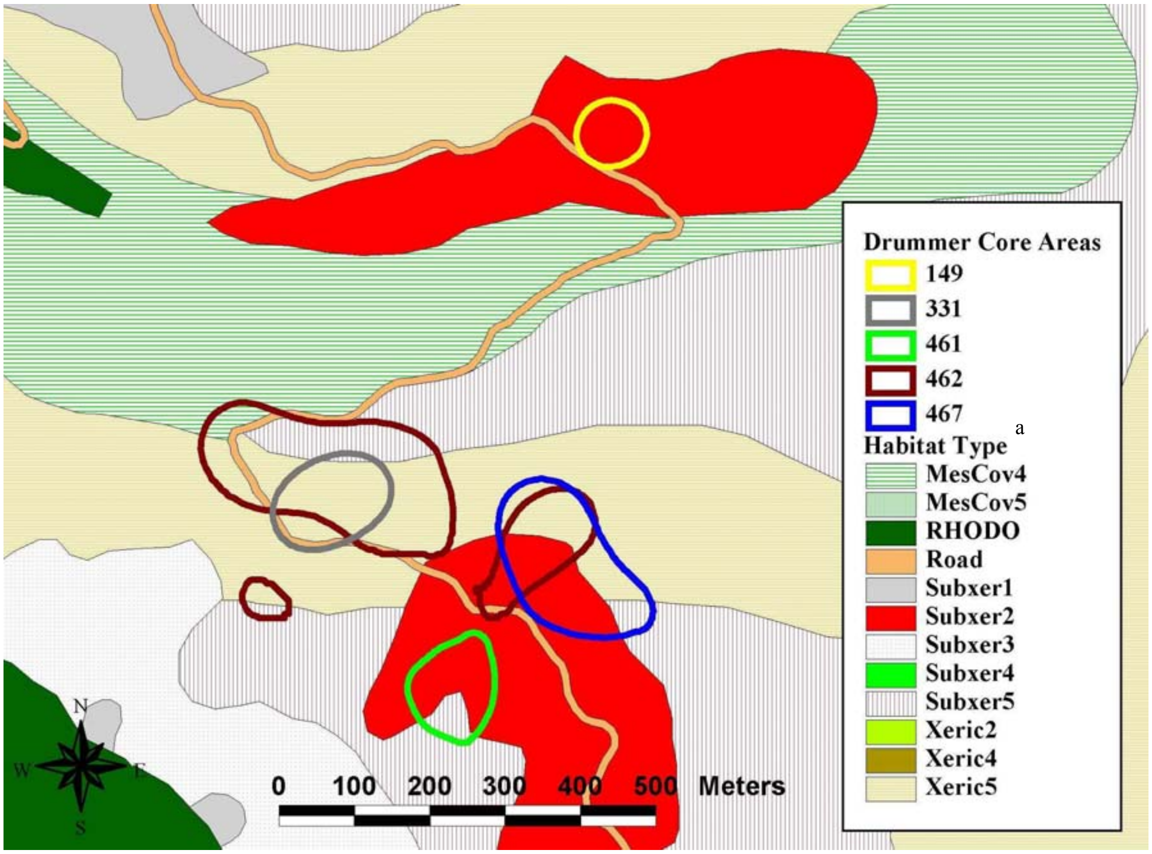

Figure 4.1. Example of core areas (50% kernel) of male ruffed grouse positioned near gated forest roads on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004. Apparent overlap resulted from projecting core areas across years.

[a] MESIC4 = mesic forest in 40–80-year age class
MESIC5 = mesic forest in >80-year age class
RHODO = forest with >75% midstory coverage in rhododendron
ROAD = gated forest roads
SUBXER1 = subxeric forest in 0–5-year age class
SUBXER2 = subxeric forest in 6–20-year age class
SUBXER3 = subxeric forest in 21–39-year age class
SUBXER4 = subxeric forest in 40–80-year age class
SUBXER5 = subxeric forest in >80-year age class
XERIC2 = xeric uplands in 6–20-year age class
XERIC4 = xeric uplands in 40–80-year age class
XERIC5 = xeric uplands in >80-year age class
WLO = wildlife openings

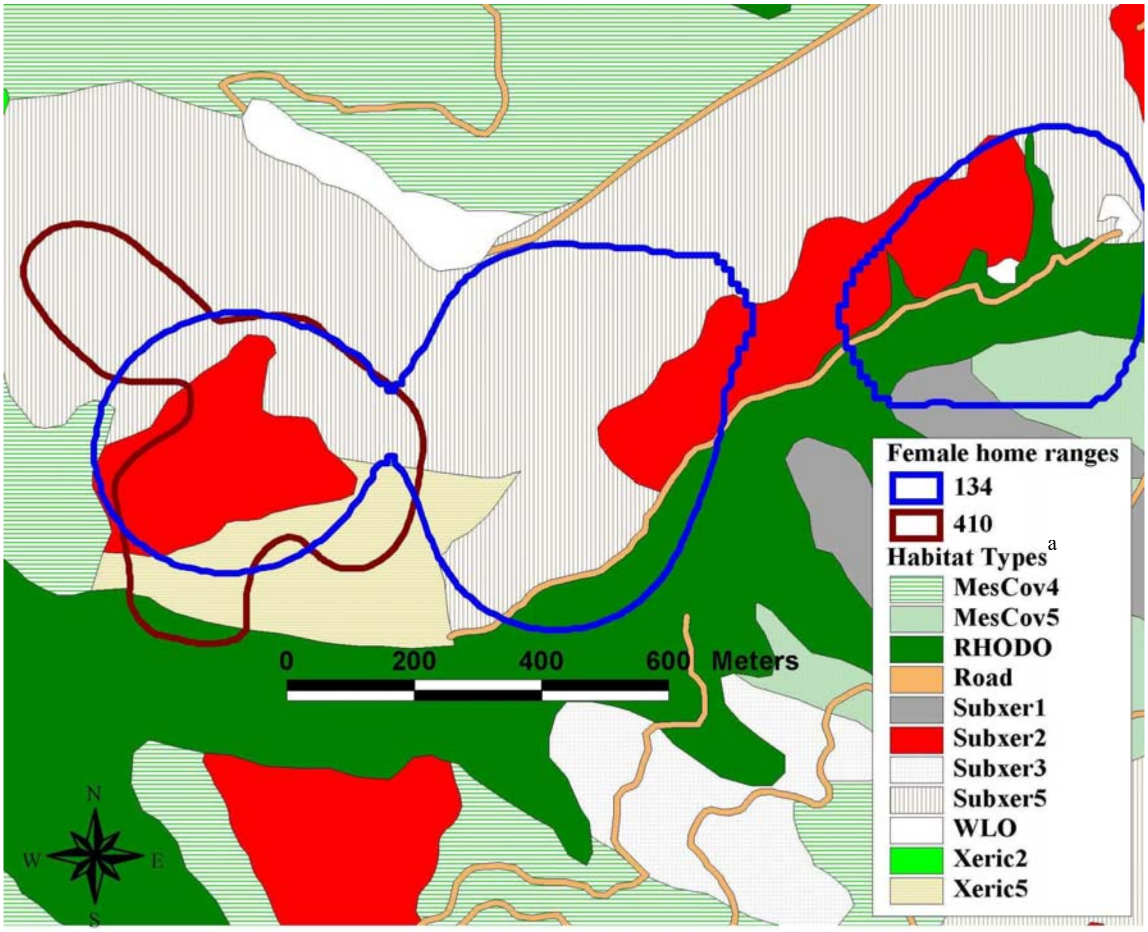

Figure 4.2. Example of female ruffed grouse use (75% kernel home range) of mature forest juxtaposed to early successional stands in winter on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

[a] MESIC4 = mesic forest in 40–80-year age class
MESIC5 = mesic forest in >80-year age class
RHODO = forest with >75% midstory coverage in rhododendron
ROAD = gated forest roads
SUBXER1 = subxeric forest in 0–5-year age class
SUBXER2 = subxeric forest in 6–20-year age class
SUBXER3 = subxeric forest in 21–39-year age class
SUBXER4 = subxeric forest in 40–80-year age class
SUBXER5 = subxeric forest in >80-year age class
XERIC2 = xeric uplands in 6–20-year age class
XERIC4 = xeric uplands in 40–80-year age class
XERIC5 = xeric uplands in >80-year age class
WLO = wildlife openings

Table 4.17. Comparison of mean ruffed grouse home range size (ha) reported by season, sex, and estimation method from ruffed grouse studies outside the range of aspen.

Study area[a]	Season	Sex	Method	Mean
ACGRP	fall-winter	male	75% kernel	17
ACGRP	spring-summer	male	75% kernel	10
ACGRP	fall-winter	female	75% kernel	25
ACGRP	spring-summer	female	75% kernel	25
PA	spring	male	MCP	5
MO	spring	male	MCP	43
MO	spring	male	MCP	230
MO	spring	female	MCP	202
MO	fall-winter	male	MCP	507
MO	fall-winter	female	MCP	505
TN	fall	male and female	MCP	133

[a] ACGRP=Appalachina Cooperative Grouse Research Project, mean of Kentucky, Maryland, Pennsylvania, Rhode Island, Virginia, and West Virginia, Whitaker (2003).
PA=Pennsylvania, McDonald et al. (1998)
MO1=Missouri, Thompson and Fritzell (1989)
MO2=Missouri, Kurzejeski and Root (1989)
TN=Tennessee, White and Dimmick (1978)

CHAPTER V.

RUFFED GROUSE SURVIVAL AND POPULATION STRUCTURE IN WESTERN NORTH CAROLINA

ABSTRACT

Sound management of ruffed grouse (Bonasa umbellus) populations requires an understanding of survival and cause-specific mortality; however, these parameters have not been investigated at the southern extent of the species' range. Ruffed grouse were studied in the mountains of western North Carolina. Grouse ($n = 276$) were radiotagged and monitored ≥ 3 times/week. Mean annual survival was 0.39 ($\pm$ 0.052 SE) and did not differ between sex and age classes. Seasonal survival was greatest in summer (0.87, 95% CI = 0.81–0.91), followed by fall (0.77, 95% CI = 0.73–0.80), winter (0.76, 95% CI = 0.72–0.80), and spring (0.74, 95% CI = 0.68–0.79). The most parsimonious survival model included a year*season interaction as the only explanatory variable ($AIC_c = 1964.7$, $\omega_i = 0.9999$). Of 155 mortalities, the greatest proportion was attributed to mammalian predators (42.6%), followed by avian (26.5%), unknown predation (12.9%), hunter harvest (11.0%), and other (7.0%). Scavenging prior to transmitter recovery may have positively biased mammalian predation rates. Mean hunter harvest rates based on band returns was 0.06 ($\pm$ 0.005 SE). Population densities were 5.9–11.4 grouse/100 ha and were not negatively associated with hunter harvest. The most viable option for increasing grouse abundance is through creation and maintenance of habitat.

Key words: Appalachians, *Bonasa umbellus*, hunting, mortality, population, ruffed grouse, survival.

INTRODUCTION

Survival and cause-specific mortality are important population parameters relevant to setting hunting seasons and bag limits for upland gamebirds.

For ruffed grouse, difficulties in setting harvest are further complicated by 10-year population cycles across northern parts of the species' range (Dorny and Kabat 1960). Most ruffed grouse survival studies have been conducted to determine acceptable harvest rates from hunter-submitted wings, tails, and band returns (Fischer and Keith 1974, Kubisiak 1984, Rusch et al. 1984, DeStefano and Rusch 1986). Although these methods provide valuable information, they reveal little about seasonal and cause-specific mortality. Alternatively, radiotelemetry studies can provide comprehensive information by monitoring individuals across time periods and ascertaining mortality from all sources, not just hunting (Heisey and Fuller 1985).

Most ruffed grouse survival studies have been conducted in northern states. Differences in population ecology, including lower population abundance (Johnsgard 1973), lower reproductive output (Devers 2005), different fall age structure (Davis and Stoll 1973), extended hunting seasons (Stoll et al 1995), and apparent lack of a 10-year population cycle preclude application of northern harvest recommendations to southern portions of ruffed grouse range.

In recent years, survival was estimated via radiotelemetry in the central and southern Appalachians as part of the Appalachian Cooperative Grouse Research Project (ACGRP; Devers 2005). Compared with telemetry studies in northern states, survival estimates for Appalachian ruffed grouse were greater. Across ACGRP sites, mean annual survival was 42% (Devers 2005). Also in the Appalachians, survival was 62% in Kentucky (Triquet 1989) and 39% in Ohio (Swanson et al. 2003). By comparison, survival was 25% in Wisconsin (Small et al. 1991), 11% in Minnesota (Gutierrez 2003), and 25–37% in Michigan (Clark 2000).

Partial data from this study (2 of 5 years) were included in ACGRP results (Devers 2005). More detailed results from the complete data set are presented here. Further, the North Carolina study site was the most southerly of ACGRP studies, and no other studies have examined ruffed grouse survival and cause-specific mortality at the southern tip of the species' range.

Objectives were to (1) identify temporal patterns in ruffed grouse survival; (2) investigate sex and age-specific survival; (3) identify mortality causes; and (4) compare population structure at the southern extent of ruffed grouse range to other areas.

METHODS

Study Area

Research was conducted on Wine Spring Creek Ecosystem Management Area (WSC, 3230 ha), within Nantahala National Forest in western Macon County, North Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 m to 1,644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges that connect upper elevations to narrow valley floors (Whittaker 1956). Mean annual temperature was 10.4° C, and mean annual precipitation was 160 cm. The area was predominantly forested. Forest types included, mixed oak >40 years-old (34.2%), rhododendron (*Rhododendron maximum*) dominated midstory (19.6%), mixed mesophytic and northern hardwood >40 years-old (18.8%), xeric upper elevation oak >40 years-old (14.3%), regenerating mixed oak 6–20 years-old (9.3%), pole-stage mixed oak 21–39 years-old

(1.6%), regenerating mixed oak 0–5 years-old (0.8%), and maintained herbaceousclearings (0.2%). There were 52.6 km of gated forest roads (1.1%).

Capture and Telemetry

Grouse were captured using intercept traps (Gullion 1965) during late August – early November, and 1 March–8 April, 1999–2003. Gender and age (juvenile or adult) were assessed by feather characteristics and molt patterns (Kalla and Dimmick 1995). Grouse tagged as juveniles in fall graduated to the adult age class at the end of the following summer. Grouse were weighed, leg-banded, fitted with 12-g necklace-style radiotransmitters with a 3-hour mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA), and released at capture sites after processing. Notification of a $25 reward and contact information were printed on transmitters for hunter return. The proportion of bands returned by hunters (i.e., crude return rates) was calculated for comparison to other studies.

Grouse were checked for survival 3–5 times/week during routine telemetry. When a mortality signal was emitted, the transmitter was located and cause of death ascertained from evidence at the site. Transmitters were located within a few hours (i.e., the length of time it took to traverse terrain and home on the signal) after detection of a mortality signal. At mortality sites, predator sign (i.e., tracks, scat, whitewash), presence of cache, evidence of feeding on remains, and various site characteristics were recorded. For example, chewed bones cached under a log indicated mammalian predation. Picked bones and whitewash indicated avian. If conflicting sign was present, the mortality was classified as unknown predation. Additional causes of mortality included hunter harvest, and “other” (disease, crippling loss, vehicle/tree collision). Date of death was recorded as the midpoint between the last known alive date and detection of mortality (Pollack et al. 1989).

Population Estimates

Grouse caught per unit effort (grouse/100 trap-days) was calculated as an index to population density from fall capture data. These data should provide an index to population density as trapping methods and effort were similar across years.

Population density estimates also were obtained from spring drumming counts. For drumming counts, observers walked designated routes (i.e., gated forest roads) on 2 consecutive mornings beginning 30 minutes before sunrise and ending three hours after sunrise. The starting point on the second morning was the endpoint from the first morning. Routes were selected such that approximately 20% of the area was sampled. Effective sampling area was defined by 400 m buffers around each route (i.e., 200m on each side, see Chapter I). Drumming counts were cancelled when winds were >13 km/h because of reduced ability to hear drumming. Observers listened for drumming while walking selected routes. When a drumming male was heard, distance to drummer, time, and an azimuth to the bird were recorded. An approximate location for each drumming grouse was plotted on a geographic information system (GIS) created for the study area. Locations of drumming males were buffered by 150 m because grouse may use alternate drumming sites (Lovallo et al. 2000). If two locations from consecutive days fell within the same 150 m buffer, they were considered the same bird. Population estimates (grouse/100 ha) were calculated by doubling number of drumming males to account for females under the assumption of a 1:1 breeding season sex ratio (Bump et al. 1947, Gullion and Marshall 1968, Rusch and Keith 1971).

Fall sex and age ratios were calculated from fall capture data as a recruitment index. Although capture data may be biased due to greater vulnerability of juveniles to trapping (Destefano and Rusch 1982), capture data should provide an index for comparison to other studies.

Data Analysis

Survival was analyzed using the known fates procedure in Program MARK (White and Burnham 1999). Known fates uses a staggered entry (Pollack et al. 1989) modification of the product limit estimator (Kaplan and Meier 1958). A 30-day time step was used. A bird was "at risk" during an encounter occasion if it was captured during the first 15 days of the interval. If it was captured from day 16-30 in an interval, it was entered in the next encounter occasion. If contact was lost when a bird left the study area or a transmitter failed, it was right-censored (Pollack et al. 1989). Right censoring indicated contact was lost without specifying fate. Juvenile grouse that survived through the year were right-censored 14 August following capture and re-entered as an adult on 15 August. Cause-specific mortality is defined as losses to a given mortality source in the absence of all other sources, or competing risks (Heisey and Fuller 1985:670); therefore, cause-specific estimates were calculated in MARK by retaining the mortality source of interest while right-censoring all other mortalities. Grouse were entered in survival analysis after a 7-day period to exclude mortalities potentially caused by capture stress.

Annual survival was calculated from 15 September–14 September. Each year was further delineated into 4, 91-day seasons defined by plant phenology and grouse biology. Fall (15 September–14 December) was a period of food abundance and dispersal among juveniles. Winter (15 December–15 March) was defined by minimal food resources and physiological stress. Spring (16 March–14 June) coincided with vegetation green-up and breeding activity. Summer (15 June–14 September) was a period of low stress with maximum cover and food availability.

Ridges surrounding Wine Spring Creek, White Oak Creek, and Cold Spring Creek watersheds naturally divided the study area into 3 distinct sections. Grouse tended to remain within their watershed of capture; therefore, in survival analysis, each watershed was treated as a separate area and used as an explanatory variable to examine effects of available habitat on survival. Radiotagged grouse that occupied >1 watershed ($n = 3$) were not included in analysis.

An information-theoretic approach (Burnham and Anderson 1998) was used to evaluate sources of variation in survival. A set of a-*priori* candidate models was created using combinations of sex, age, year, season, and watershed. Models were assessed in program MARK using a bias-corrected version of Akaike's Information Criterion (AIC_c), and weight of evidence (w_i) to rank and select the model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). Bootstrapping was used to analyze goodness of fit and overdispersion (Cooch and White 2001). Relationships between fall population density and annual survival were investigated using multiple regression (Proc REG) in SAS (SAS Institute Inc., Cary, North Carolina, USA).

RESULTS

Two hundred seventy-six grouse were radiotagged over 5 years (Table 5.1; tables are located in the Appendix). The overall percentage of juveniles in fall captures was 59.6%, ranging from 46.2–66.7% Twenty-two grouse died during the initial 7-day period after capture. Of these, 11/22 were juveniles captured in fall 2000; therefore, survival estimates may have been biased low due to capture-induced stress during that year. Contact was lost during the initial 7-day period for an additional 7 grouse. Recapture of censored birds suggested faulty transmitters were most likely to fail within a few days following capture; therefore, these censors may have been due to transmitter failure rather than unrecovered mortalities.

Two hundred-thirty two grouse were available for survival analysis. Of these, 155 mortalities were observed. Across years, the greatest proportion was attributed to mammalian predators (42.6%), followed by avian (26.5%), unknown predation (12.9%), hunter harvest (11.0%), and other (7.0%). Mean annual hunter harvest (i.e., proportion of annual mortalities due to hunting) based on band returns was 6% (± 0.5 SE). The "other" category included 9 unknown causes, 1 vehicle collision, and 1 death from *Aspergillosis* (Schumacher 2002). Mean annual cause-specific rates (i.e., risk of death to individual mortality sources) followed the same pattern as raw proportions, with mammalian predation being most common (0.31 ± 0.074 SE) followed by avian (0.22 ± 0.044 SE), unknown predation (0.13 ± 0.044 SE), hunter harvest (0.10 ± 0.028 SE), and other (0.07 ± 0.033 SE). The seasonal risk of mammalian predation was lowest in summer (0.07), and relatively constant across fall (0.11), winter (0.10), and spring (0.11). Risk of avian predation was greatest in spring (0.09) compared with fall (0.06), winter (0.06), and summer (0.05).

Mean annual survival was 0.39 (± 0.052 SE), ranging from 0.26–0.56. Seasonal survival was greatest in summer (0.87, 95% CI = 0.81–0.91), followed by fall (0.77, 95% CI = 0.73–0.80), winter (0.76, 95% CI = 0.72–0.80) and spring (0.74, 95% CI = 0.68–

0.79). Overlapping confidence intervals suggest similar survival rates among fall, winter, and spring. By sex and age classes, mean annual survival was 0.39 (95% CI = 0.28–0.51) for adult males, 0.42 (95% CI = 0.31–0.52) for juvenile males, 0.32 (95% CI = 0.13–0.50) for adult females, and 0.40 (95% CI = 0.36–0.43) for juvenile females.

The most parsimonious model contained a YEAR*SEASON interaction (AIC_c = 1964.7, $\omega_i = 0.9999$), indicating seasonal survival differed among years (Table 5.2, 5.3). Bootstrapping revealed data were not overdispersed ($\hat{c} = 1.11$). There was no support for models with combinations of sex, age, or watershed as explanatory variables ($\omega_i < 0.0001$).

Annual survival showed an inverse relationship with the population index calculated from fall trapping data ($r^2 = 0.76$, $P = 0.054$, Figure 5.1). Spring population density, estimated from drumming counts, ranged from 5.88 grouse/100 ha in 2004 (the year of greatest survival) to 11.4 grouse/100ha in 2000 (the year of lowest survival).

DISCUSSION

Survival and Cause-Specific Mortality

Compared with other radiotelemetry studies, annual survival (39%) was greater than reports from northern areas, and within the range of estimates for the Appalachians. Devers (2005) estimated 42% survival with a range of 17%–57% across the central and southern Appalachians. Of 11 ACGRP study areas, mean annual survival on WSC was similar to KY1 (40%), greater than MD1 (35%), OH2 (17%), PA1 (29%), RI1 (30%), and VA3 (33%), and less than OH1 (55%), VA1 (56%), VA2 (49%), WV1 (47%), and WV2 (57%, see Devers 2005 for study locations and acronymns). By comparison, annual survival rates were 11% in Minnesota (Gutierrez et al. 2003), and 25–37% in Michigan (Clark 2000). In Wisconsin, annual survival was 25% for adults and 7% for juveniles (Small et al. 1991).

The trend for greater survival in the Appalachians may be partially explained by differences in predator communities. In the core of ruffed grouse range, species such as the northern goshawk (*Accipiter gentiles*) have adapted to prey specifically on grouse. The presence of these efficient predators can lead to greater mortality (Bergerud and Gratson 1988). Survival may be enhanced in the Appalachians because specialists are largely replaced by generalist predators that prey on grouse opportunistically (Bumann and Stauffer 2004).

Even though goshawks are not a frequent threat in the Appalachians, avian predators, including red-tailed hawks (*Buteo jamaicensis*), red-shouldered hawks (*Buteo lineatus*) broad-winged hawks (*Buteo platypterus*), Cooper's hawks (*Accipiter cooperii*), and great horned owls (*Bubo virginianus*) are important mortality sources (Bumann and Stauffer 2004). Avian predation is frequently cited as a leading cause of ruffed grouse mortality. As determined from evidence at mortality sites, mammalian rather than avian predation accounted for the greatest proportion of losses on WSC. Bumann and Stauffer (2002) found mammals scavenged >65% of placed carcasses and warned of potential for overestimating mammalian predation of ruffed grouse. The narrow margin between mammalian and avian predation on WSC may have resulted from such bias.

Survival estimates did not differ between juveniles and adults, as the most parsimonious survival model did not include an age effect. Similar results were reported in Minnesota (Gutierrez et al. 2003) and across ACGRP study sites (Devers 2005). An age effect was apparent in Wisconsin (Small et al. 1991) and other non-telemetry studies in New York (Bump et al. 1947) and Alberta (Rusch and Keith 1971). These authors proposed greater juvenile mortality was a function of dispersal. A combination of factors, including exposure to predators during extended movements, increased energetic demand, and traversing unfamiliar space may lead to increased risk for dispersing juveniles (Small and Holzwart 1993, Yoder et al. 2004). There may be several reasons age-specific differences in survival were not observed. First, there actually may not have been a difference in survival between juveniles and adults. Second, trapping efforts were conducted in fall, concurrent with dispersal. Juveniles may have completed or nearly completed dispersal at their time of capture. Juveniles radiotagged during a dispersal movement may have been passing through the study area, and were subsequently right-censored when contact was lost. As a result, only those grouse that completed dispersal movements were monitored, hence obscuring survival differences for dispersing juveniles.

Seasonally, survival was greatest in summer (87%) and similar among fall, winter, and spring (74–77%). Slightly lower survival in spring may have been a function of reproductive activities (i.e., nesting and drumming) coinciding with raptor migrations. Further, mortality risk to avian predators was greatest during spring. Relatively high survival in summer might be expected considering it is a period of maximum vegetation cover and food availability. Similarly, Swanson et al. (2003) reported survival of Ohio ruffed grouse was greatest in summer, and lowest in spring and fall. Other studies also showed greatest survival in summer (Small et al. 1991, Devers 2005), though these reports indicated seasonal rates were lowest in winter. Winter survival on WSC (76%)

was similar to other ACGRP sites (72%, Devers 2005) and greater than in Wisconsin (55–57%, Small et al. 1991). Greater survival of Appalachian grouse in winter compared with northern areas may have been influenced by less severe winters in southern portions of ruffed grouse range.

Hunter Harvest

Concern has been raised regarding potential additive mortality effects of hunting seasons that extend through the winter (DeStefano and Rusch 1982, Bergerud 1985, Stoll and Culbertson 1995). On WSC, mean harvest rate based on band recoveries (6%) was considerably lower than harvest rates of 17–49% in Wisconsin (Kubisiak 1984, Rusch et al. 1984) and 13–20% in New York (Bump et al. 1947). Harvest recommendations in northern latitudes were 20–23%, with sustained harvests $\geq$23% viewed as potentially additive and detrimental to populations (Kubisiak 1984, Rusch et al. 1984).

Appalachian harvest rates were somewhat lower compared to northern areas with a range of 4–13% on ACGRP sites (Devers 2005) and 4–20% in Ohio (Stoll and Culbertson 1995). Devers (2005) conducted a compensatory mortality experiment by comparing survival between areas open and closed to hunting. He found no increase in survival in the absence of hunting and suggested conservative harvest rates <20% would be compensatory in the Appalachians. Using flush counts to index population density, Monschein (1974) determined grouse density was not affected by varying levels of hunting pressure in northwestern North Carolina.

Harvest rates on WSC were among the lowest reported. Although hunting seasons extended through the end of February, 65% of harvests occurred during the first 9 weeks of the season (October–December). Given relatively high annual survival and low harvest, there appeared to be no evidence that hunting was detrimental to the WSC grouse population. Further, spring population density was at its highest level (11.4 grouse/100 ha) following the year of greatest hunter harvest (7%), indicating hunting mortality may have been compensatory.

Population Structure

Spring population density estimated from drumming counts was 5.88–11.4 grouse/100 ha, with a decreasing trend observed throughout the study. As density decreased, an increase in survival was observed (Figure 5.1). The inverse relationship between survival and population density may have been caused in part by habitat availability. As density increased, some grouse may have used marginal habitats, thus decreasing survival by increasing efficiency of generalist predators. Predators switching from other prey as grouse became more abundant may have compounded this effect (Bergerud 1988). Survival of juveniles and adults may exert the greatest influence on population density in the central and southern Appalachians, compared with other population parameters (Tirpak 2005). Increasing survival observed over time on WSC could have increased density; however, this effect may not have been realized in the absence of sufficient suitable habitat.

Recruitment, the addition of individuals to a population through reproduction and immigration (Krebs 1994), is an important aspect of population ecology. As a recruitment index, ruffed grouse studies have used hunter-submitted wings and tails to estimate proportion of juveniles in fall populations (Davis and Stoll 1973, Destefano and Rusch 1982, Norman et al. 1997). On WSC, hunter band returns were limited to radiotagged grouse; therefore, proportion of juveniles in fall captures provided the only recruitment index. Although this index may have been biased because juveniles are more susceptible to capture than adults (Destefano and Rusch 1986), it serves as a basis for comparison with other studies. Despite potential positive bias, proportion of juveniles in fall on WSC (47–67%) was less than means of 76% in Alberta ((Rusch and Keith 1971) and 78% in Wisconsin (Dorney 1963). Means from harvest data in Ohio (42–56%, Davis and Stoll 1973) and Virginia (22–59%, Norman et al. 1997) also were lower than reports from Wisconsin and Alberta. In the Appalachians, lower recruitment may be influenced by habitats with nutritionally inadequate foods that cause physiological stress and decreased reproductive output (Servello and Kirkpatrick 1987). Although nest success was relatively high on WSC (see Chapter II), the recruitment index suggested other aspects (i.e., chick survival and immigration) might have been limiting. Because chicks were not radiotagged on WSC, reliable estimates of chick survival (Larson et al. 2001) were not available.

In addition to reproduction, immigration and emigration influence recruitment. During dispersal in early fall, juvenile grouse move 1– 6 km from their natal ranges (Bump et al. 1947, Chambers and Sharp 1958, Godfrey and Marshall 1969, Small and Rusch 1989). During this time, 50% of juveniles may emigrate from an area (Chambers and Sharp 1958), with a greater proportion dispersing when habitat was limiting (Bump et al. 1947). Recruitment and resultant population density on WSC may have been affected by losses to emigration that were not balanced by equal immigration. The landscape within a 5-km radius surrounding WSC contained 5% coverage in 6–20-year-old mixed oak forest (a preferred habitat type, see Chapter IV). At such low levels, interspersion of age classes is probably limited andmay fall below a minimum threshold for ruffed grouse. Relatively poor habitat in the surrounding area may have resulted in WSC acting as a source population that contributed birds, surrounded by a sink that did not replace these losses.

MANAGEMENT IMPLICATIONS

In the core of ruffed grouse range, densities may exceed 50 grouse/100 ha on areas under intensive aspen management (Kubisiak 1985, Gullion 1990). Increasing the proportion of landscapes in the 0–25-year age class has been shown to increase grouse density on these areas. In Wisconsin, grouse density increased from 14 to 32 grouse/100 ha as proportion of early successional forest increased from 13% to 55% (Kubisiak 1985). Forest management and interspersion of aspen age classes also increased grouse density on the Stone Lake Area in Wisconsin (McCaffrey et al. 1996).

Although population responses following management are well documented in aspen forests, similar grouse densities in Pennsylvania mixed oak forest were achieved by interspersing age classes and maintaining 20% coverage in the 0–20-year age class (Storm et al. 2003). In mixed mesophytic and mixed oak forests in Ohio, grouse abundance increased 50–100% following creation of early successional habitat on 12% of the study area (Stoll et al. 1999).

Approximately 9% of WSC was in the 6–20-year age class. As discussed, habitat availability may have influenced the inverse relationship between survival and population density. With habitat improvement (i.e., creation of early successional forest interspersed with other habitat types), grouse density may increase as it has done on other mixed oak-dominated areas. In the absence of forest management, the proportion of forest in the 6–

20-year age class on WSC will be reduced to 2% by 2010, potentially causing further population decline. Potential for unbalanced emigration and immigration stresses the need to manage whole landscapes as opposed to creating habitat islands surrounded by an otherwise unsuitable matrix.

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APPENDIX

Table 5.1. Capture period, capture effort (trap-days), number of grouse tagged, capture rate (grouse/100 trap-days), and sex and age of grouse captured during ruffed grouse research on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Period	Trap-days	Captured	Rate	Ad fem[a]	Juv fem	Ad male	Juv male
Fall							
1999	6,770	65	0.96	14 (22)[b]	24 (37)	21 (32)	6 (9)
2000	9,040	63	0.70	5 (8)	29 (46)	16 (25)	13 (21)
2001	10,350	70	0.68	8 (11)	22 (31)	17 (24)	23 (33)
2002	9,576	46	0.48	7 (15)	17 (37)	10 (22)	12 (26)
2003	8,560	16	0.19	2 (13)	4 (25)	5(31)	5 (31)
Spring							
2000	94	4	4.26	0	0	4 (100)	0
2001	938	6	0.64	2 (33)	0	4 (67)	0
2002	96	1	1.04	1 (100)	0	0	0
2003	114	5	4.39	1 (20)	1(20)	2 (40)	1 (20)
Total	39,538	276	0.70	40 (14)	97 (35)	79 (29)	60 (22)

[a] Ad fem = adult female
Juv fem = juvenile female
Ad male = adult male
Juv male = juvenile male

[b] Values in parentheses are percentage of total capture during the period.

Table 5.2. Comparison of Akaike's Information Criterion (AIC_c), differences in AIC_c, and model weights (w_i) for ruffed grouse survival models based on year, season, area, sex, and age on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model[a]	K	AICc	ΔAICc	*w*i
{Year*season}	20	1964.7	0.0	0.9999
{Year}	5	2001.7	37.0	<0.0001
{Season}	4	2003.2	38.6	0.0000
{Area*season}	12	2004.8	40.1	0.0000
{Season*sex}	8	2008.6	43.9	0.0000
{Season*age}	8	2008.8	44.2	0.0000
{Area}	3	2009.5	44.8	0.0000
{Age}	2	2011.5	46.9	0.0000
{Sex}	2	2012.0	47.4	0.0000
{Sex*age}	4	2013.6	48.9	0.0000
{Season*sex*age}	16	2018.8	54.1	0.0000
{Area*year*season}	60	2018.8	54.1	0.0000
{Global}	236	2221.5	256.9	0.0000

[a] Year = annual period from September 15–September 14.
Season = fall (15 September–14 December)
winter (15 December–15 March)
spring (16 March–14 June)
summer (15 June–14 September)
Sex = male, female
Age = juvenile, adult
Area = watershed

Table 5.3. Survival rates of ruffed grouse by year and season on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Annual survival for all years was calculated as an across year average. Seasonal survival for all years was calculated with years pooled.

			Season							
	Annual		Fall		Winter		Spring		Summer	
Year	Survival	95% CI	Survival	95% CI	Survival	95% CI	Survival	95% CI	Survival	95% CI
1999–2000	0.32	0.23–0.40	0.69	0.59–0.77	0.83	0.72–0.90	0.64	0.50–0.75	0.91	0.79–0.97
2000–2001	0.26	0.18–0.34	0.69	0.59–0.77	0.67	0.56–0.77	0.73	0.59–0.83	0.81	0.67–0.90
2001–2002	0.37	0.29–0.45	0.78	0.70–0.85	0.78	0.68–0.85	0.80	0.69–0.87	0.76	0.62–0.85
2002–2003	0.43	0.33–0.54	0.79	0.69–0.86	0.73	0.61–0.82	0.82	0.67–0.91	1.00	1.00–1.00
2003–2004	0.56	0.41–0.69	1.00	1.00–1.00	0.81	0.68–0.90	0.64	0.45–0.79	1.00	1.00–1.00
All years	0.39	0.29–0.49	0.77	0.73–0.80	0.76	0.72–0.80	0.74	0.68–0.79	0.87	0.81–0.91

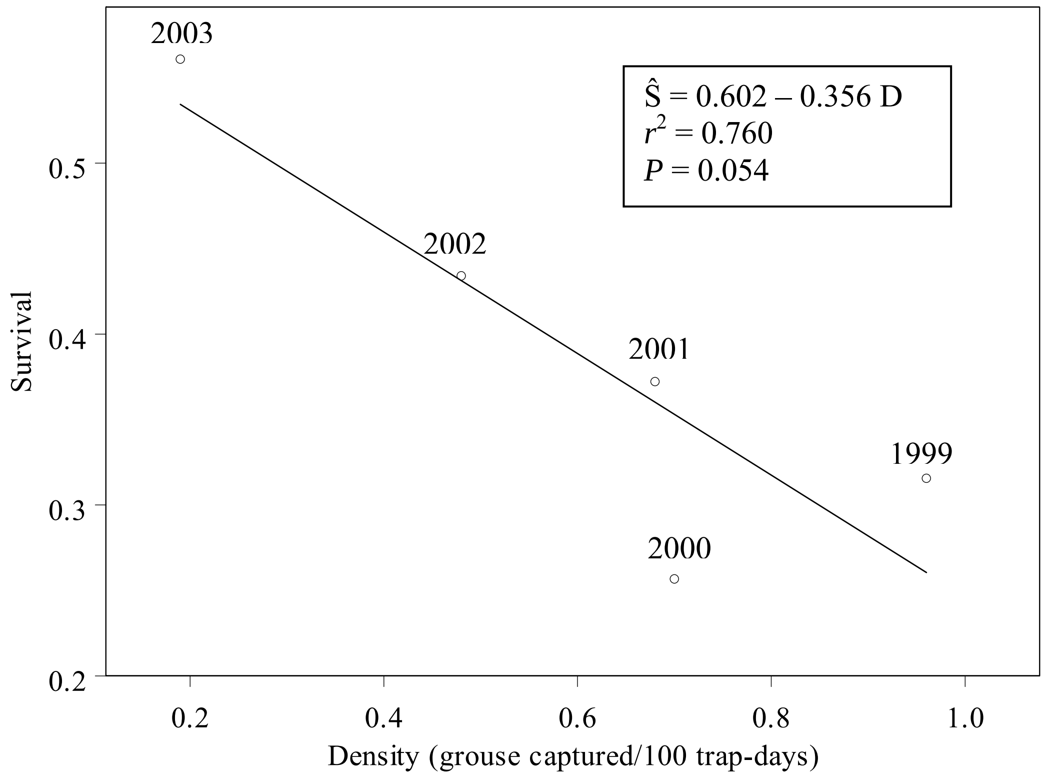

Figure 5.1. Relationship of ruffed grouse annual survival with a population density index calculated from fall trapping success on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

CHAPTER VI.

MANAGEMENT IMPLICATIONS OF RUFFED GROUSE RESEARCH ON WINE SPRING CREEK ECOSYSTEM MANAGEMENT AREA

INTRODUCTION

Ruffed grouse in the central and southern Appalachian Mountains have unique population structure and habitat needs that differ from the core of the species' range. In the mid-1990s, a regional research effort, the Appalachian Cooperative Grouse Research Projects (ACGRP), was undertaken to gain an understanding of ruffed grouse ecology in the region. The ACGRP was a partnership among state and federal agencies, universities, and private conservation groups on 12 study sites in 8 states.

Research conducted on Wine Spring Creek Ecosystem Management Area (WSC) in North Carolina was designed to contribute to this regional effort and address local topics of interest. The WSC study site was unique among ACGRP sites in that its location was at the southern extent of grouse range. Previously, no studies had undertaken such a comprehensive effort to identify grouse habitats and population structure at the southern end of the Blue Ridge Mountains.

During the 5-year study (1999–2004), 276 grouse were radiotagged, resulting in information on habitat use, reproduction, and survival. Management implications from WSC are relevant to mixed hardwood forests in western North Carolina (including over 200,000 ha of national forest) and similar forest types in northern Georgia and eastern Tennessee.

RECRUITMENT AND POPULATION STRUCTURE

Annual population density indexed using spring drumming counts and fall trapping success decreased from 1999–2004. Yet, during that period, annual survival increased (Chapter V). These observations may be an indication of low recruitment.

Indeed, proportion of juveniles in fall captures suggested recruitment on WSC was lower than in northern portions of grouse range (Chapter V). However, nesting rates and nest success were relatively high (Chapter II) and whole brood survival during the 5 weeks following hatch was moderate (Chapter III). It is possible that chick losses during summer may have resulted in low recruitment but a more reliable estimate of chick survival was not available as chicks could not be radiotagged and monitored through fall.

Low recruitment also may have been influenced by an imbalance between emigration and immigration. During dispersal in early fall, juvenile grouse move 1– 6 km from their natal ranges and during this time, >50% of juveniles may emigrate from an area. There was proportionally more forest in the 6–20-year age class (an important habitat component) on WSC compared with the surrounding landscape. WSC may have been a source population that contributed birds, surrounded by a sink that did not replace those losses. If so, managing habitat at a landscape scale, as opposed to creating habitat islands within a matrix of unsuitable habitat, may offset losses to emigration with additions from immigration.

The inverse relationship between population density and survival may have been caused in part by habitat availability on WSC. As density increased, some grouse may have used marginal habitats, thus decreasing survival. Increases in survival over time could exert a positive influence on the population; however, such an effect may not be realized as the proportion of early successional forest on WSC declines from 9% to 2% by 2010.

HABITAT PREFERENCE

Grouse on WSC used a variety of habitats as food and cover availability and life-history functions changed through the year (Chapters III, IV). In the absence of aspen (*Populus tremuloides, P. grandidentata*), grouse depended on a diversity of food sources, including hard mast, buds, soft mast, and herbaceous plants. In general, cover was provided by young forest stands in the 6–20-years age class. Mature stands presented an important food source in the form of acorns and beechnuts, and gated forest roads with forbs and legumes provided herbaceous forage. Grouse homeranges were smallest (an indicator of habitat quality) where these habitats were well interspersed. The greatest determinant of habitat quality was interspersion and juxtaposition of food with cover.

METHODS TO IMPROVE HABITAT

Alternative regeneration techniques including shelterwood, irregular shelterwood, and group selection can be used to create and improve grouse habitat (Chapter IV). Shelterwood and irregular shelterwood can maximize interspersion by providing food (i.e., hard mast) and cover (i.e., regenerating stems) in the same stand. Techniques that retain mature, mast-producing trees (i.e., 2-age systems) may have the greatest long-term benefits.

In managing landscapes for grouse, group selection can be used to increase interspersion by connecting otherwise disjunct habitat patches. Perhaps the greatest utility for group selection is in creating small canopy gaps used by broods during the first few weeks after hatch (Chapter III). Brood habitat also could be improved by converting perennial cool-season grass cover in wildlife openings to more desirable structure afforded by forbs and legumes. Broods used edges of wildlife openings, and thinning these areas could further enhance vegetation structure.

Timber stand improvement techniques increase sunlight to the forest floor, promoting herbaceous plant growth and hardwood regeneration. Habitat use by female ruffed grouse suggested thinnings on mesic sites resulted in desirable conditions on WSC (Chapter IV). Thinnings also could be used to connect group selection cuts, soften edges along harvest boundaries, and increase herbaceous cover on forest roads.

Gated forest roads were important habitats for grouse during all seasons. By seeding a mixture of an annual grain such as winter wheat (*Triticum aestivum*) with clover (*Trifolium* spp.), roads can be stabilized to prevent erosion while providing food sources for grouse and other wildlife. Over time, forbs germinating from the seed bank should maintain vegetation on the site and further enhance habitat quality (Chapter IV). Opening the forest canopy along roads (i.e., daylighting) could be used to stimulate herbaceous plant growth and create adjacent midstory stem cover.

SUMMARY

The grouse population on WSC declined through the study period. Habitat improvement on the study site and surrounding area is the most feasible approach to increasing ruffed grouse abundance. Prescriptions that maximize diversity of forest types and age classes should satisfy ruffed grouse habitat requirements that change seasonally with life-history functions. Because ruffed grouse are associated with ephemeral habitats, a long-term approach is necessary to retain habitat quality and quantity over time.

VITA

Benjamin Colter Jones was born in New Castle, Pennsylvania on March 9, 1975. He was raised in rural Pennsylvania where he attended high school at Mansfield Junior-Senior High. He graduated from Pennsylvania State University in 1998 with a B.S. in Wildlife and Fisheries Science (Forest Science minor). He completed M.S. research in Wildlife and Fisheries Science at Mississippi State University in 2001. His research interests include impacts of silvicultural prescriptions on wildlife and the use of forest management for improving wildlife habitat. Ben is currently the Wildlife Planning Biologist with the Pennsylvania Game Commission.

United States Department of the Interior

FISH AND WILDLIFE SERVICE
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April 11, 2019

Mr. Dan Olsen
Forest Supervisor
Daniel Boone National Forest
1700 Bypass Rd
Winchester, KY 40391

Subject: FWS 2018-B-0293: Scoping Notice and Request for Comments on the Daniel Boone National Forest Plan Amendment Environmental Assessment

Dear Mr. Olsen:

The U.S. Fish and Wildlife Service's Kentucky Field Office (KFO) has reviewed the above-referenced scoping notice requesting comments on amending the existing Forest Plan for the Daniel Boone National Forest (DBNF). According to the scoping notice and March 2019 Draft Environmental Assessment (2019 Draft EA), revisions to the plan are necessary to incorporate new science applicable to the management of bat habitat, account for the increased number of federally listed species and designated critical habitat that occur on the DBNF since 2004, and to accommodate a landscape level approach to forest management. The Forest Plan would be amended to ensure that appropriate management of the DBNF occurs by (1) removing or rewording of the plan standards, (2) using the best available science to update the management direction, (3) updating the Significant Caves Prescription Area to match USFWS Priority Hibernacula, and (4) updating certain definitions. We provided comments to the DBNF on the initial scoping notice on March 20, 2018. Many of our concerns remain and are offered again for ease of reference. In addition, we provide comments for your consideration on the 2019 Draft EA specific to the proposed action.

Section 7(a)(1)

Section 7(a)(1) of the Endangered Species Act establishes the shared responsibility of all Federal agencies to utilize their authorities in furtherance of the purposes of the ESA by carrying out programs for the conservation of endangered and threatened species (50 CFR 402.01). Section 7(a)(1) actions do not take the place of section 7(a)(2) consultations; however, these actions do have the potential to promote the recovery and conservation of listed species while complementing, streamlining, and facilitating section 7(a)(2) consultations. While we understand the amendment to the forest plan is meant to provide flexibility for a landscape-level approach to forest management, these actions can result in unintended direct and indirect adverse effects on federally listed species. Given the potential widespread nature and magnitude of potential adverse effects that may occur during implementation of the amended Forest Plan, as currently proposed, development of a Section 7(a)(1) conservation plan for the DBNF may be warranted to promote the conservation and recovery of federally listed species affected by implementation of the amended Forest Plan. The KFO is willing to assist the DBNF in the development of a plan if the DBNF chooses to take this step.

General Comments

As stated in our March 20, 2018 letter, the KFO supports several of the changes proposed in the amendment, such as updating the definitions of significant caves, snags, and roost trees to be more consistent with terminology used across the range of these species. We also support taking a landscape-level approach to ensure that there is suitable habitat for federally listed bats, other federally listed species, and at-risk species throughout the DBNF. In our initial scoping comments, the KFO was concerned that the intended purpose of some of the replacement Forest Plan standards was unclear and recommended that the DBNF provide the rationale and supporting science for each replacement standard prior to finalizing the proposed action. We appreciate the inclusion of this information in the 2019 Draft EA. However, we still have concerns that the removal of several of the standards that are included in the current Forest Plan will result in increased adverse effects on listed bats.

Federally Listed Bat-Specific Comments

The KFO acknowledges the DBNF's need for flexibility when carrying out management activities and recognizes that several of the existing plan standards that are intended to protect the Indiana bat are unnecessarily restrictive. However, other standards were designed to protect Indiana bat swarming habitat and non-volant pups. The removal of these standards is likely to have significant negative effects on bat species.

Swarming Habitat: Upon arrival at a hibernaculum, Indiana bats "swarm," a behavior in which "large numbers of bats fly in and out of cave entrances from dusk to dawn, while relatively few roost in the caves during the day" (Cope and Humphrey 1977). Swarming continues for several weeks and, during this time, mating occurs, generally in the latter part of the period (USFWS 2007). Prior to hibernating, Indiana bats must also store sufficient fat to support metabolic processes during hibernation and until they emerge from hibernation in the spring. During fall swarming, fat supplies for Indiana bats are replenished as they forage in the vicinity of the hibernaculum (USFWS 2007).

The DBNF has proposed to remove standards DB-WLF-9, DB-WLF-10, DB-WLF-12, and 1.J-VEG-2, which were designed to protect Indiana bat swarming habitat and individual Indiana bats during the swarming period, and replace them with standard DB-WLF-7. DB-WLF-7 prohibits tree removal within a ¼-mile of a known hibernacula or maternity cave for gray bats and Virginia big-eared bats, unless the tree removal is meant to protect or enhance the microclimate of the hibernacula, rare species, or rare communities. However, Indiana and northern long-eared bats swarm in an area much broader than ¼ mile around cave entrances. Known swarming habitat encompasses a 10-mile buffer around P1/P2 hibernacula and a 5-mile buffer around P3/P4 hibernacula for Indiana bats (USFWS 2011).

Northern long-eared bat swarming habitat encompasses a 5-mile buffer around hibernacula (USFWS 2016). Therefore, the replacement standard offers significantly less protection to swarming habitat and individuals of both listed bat species during the swarming period than the current standards. While we understand the DBNF may need to carry out forest management activities in these areas over time, we recommend that tree removal in known swarming habitat, especially during the fall swarming period (August 16 to November 14), be limited to the greatest extent practicable. We also recommend that permanent tree removal be avoided in these areas when possible. In addition, tree removal that occurs in swarming habitat should be evaluated to ensure that a high percentage of suitable habitat is maintained around the hibernacula at all times.

Maternity Habitat: Several of the current Forest Plan standards provide a significant amount of direct protection to Indiana bats and northern long-eared bats during the spring staging and summer roosting period (April 1 to August 15), while also ensuring the integrity of summer roosting habitat. While the proposed replacement standards **(**DB-WLF-4, 5, 6, and 7) offer some level of protection, they primarily focus on "known maternity habitat" and "known maternity roost trees". For example, current standard DB-WLF-8 avoids direct impacts to Indiana bats during the summer occupancy period in known maternity habitat by prohibiting tree removal within 2.5 miles of an Indiana bat maternity colony from May 1 to August 15. The proposed replacement standard (DB-WLF-5) only applies to new construction projects and only avoids direct impacts in known maternity habitat during June and July. Therefore, tree removal associated with other activities in known maternity habitat, such as timber harvest, would be expected to result in direct effects on both adult Indiana bats and non-volant pups during the time that bats are present on the landscape, and these effects increase the likelihood of mortality, especially for non-volant pups.

DB-WLF-6, which is proposed as a replacement for DB-WLF-8, only protects within 150 feet of a known maternity roost tree. While the protection of a known roost tree is important, the 150-foot buffer was intended to ensure the removal of other trees in the vicinity did not unintentionally damage the known roost tree. It does not offer protection the numerous other roost trees outside of the 150-foot buffer that are likely to be used by the colony during the summer occupancy period. These additional roosts are important for maternity colony success, as Indiana bats frequently switch roosts (Callahan et al. 1997).

Little is known about the summer usage of the DBNF by Indiana bat. Limited survey efforts from over a decade ago have provided the location of some maternity colonies and roost trees. However, the DBNF has stated that some portion of the large number of bats that spend the winter in the large and medium-sized hibernacula on the DBNF are thought to remain in these areas throughout the summer (USFS 2003). Based on 2018 and preliminary 2019 winter bat count data, approximately 5,600 Indiana bats are estimated to hibernate on the DBNF during the winter (USFWS, internal data). In addition, the DBNF also indicated that Indiana bats from nearby hibernacula on Pine Mountain, Carter Caves, and in Campbell and Fentress Counties in Tennessee are thought to occur on the DBNF (USFS 2003). Based on this information, it appears likely that there are other Indiana bat and northern long-eared bat maternity colonies present that have not been documented. This habitat and the individual bats occupying these areas could be adversely affected by future forest management actions if there are no protective standards proposed for potential summer habitat for either species. Therefore, we recommend developing conservation measures in the BA that would avoid and minimize adverse effects. Several such measures were discussed during the November 2017 science meeting, including identifying and avoiding potential primary roost trees during tree removal activities and limiting the amount of tree removal that can occur during the occupied timeframe, especially during June and July when non-volant pups are present.

We also have concerns with the DBNF's conclusion that the proposed action will result in "no loss of viability or change in population of federally listed bat species due to the proposed action", particularly for the Indiana bat and northern long-eared bat" (Table A6 of the EA). While it is difficult to evaluate the full extent of adverse effects on these two species without a detailed analysis, we anticipate the proposed action could result in significant harm to these species, including the mortality of non-volant pups and pregnant females, which can have both individual- and local population-level effects. The loss of reproducing females and non-volant pups has the potential to causes declines in local numbers and could affect the viability of the Indiana bat at the recovery unit level. To address these issues, we encourage the DBNF to work with us to develop appropriate avoidance and minimization measures.

Conclusion

In general, we support the DBNF's proposal to amend the Forest Plan to be more consistent with the terminology recognized across the range of federally listed bat species and to focus on a landscape level approach to forest management. Once a final proposed action is identified, we anticipate that the DBNF will provide a biological assessment that clarifies how listed species and critical habitat will be affected and that the DBNF will make its effects determinations for the Forest Plan amendment for our consideration. If the DBNF determines that the proposed action may affect, and is likely to adversely affect federally listed species or critical habitat, formal consultation will be necessary.

We believe many of the anticipated adverse effects on federally listed species could be avoided or minimized if appropriate conservation measures are included as part of the proposed action in the BA. Please note that conservation measures intended to avoid and minimize anticipated incidental take in the BA are part of the section 7(a)(2) consultation process and do not necessarily need to be included as standards in the amendment to the Forest Plan to be considered in our analysis.

Thank you for the opportunity to comment on 2019 Draft EA. We look forward to continued coordination with your staff as the proposed action progresses. If you have any questions, please contact Carrie Allison at 502-695-0468, extension 103.

Sincerely,

Virgil Lee Andrews, Jr.
Field Supervisor

Literature Cited

Callahan, E.V., R.D. Drobney, and R.L. Clawson. 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. J. Mammalogy. 78:818-825.

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