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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.

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

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee

Benjamin Colter Jones
December 2005

ACKNOWLEDGMENTS

Five years of intensive research is an expensive endeavor and would not have been possible without funding from Coweeta Hydrologic Lab, the University of Tennessee Department of Forestry, Wildlife and Fisheries, the North Carolina Wildlife Resources Commission, Bent Creek Experimental Forest, the Ruffed Grouse Society, and Orvis. Individuals responsible for funding included Jim Vose, George Hopper, Gordon Warburton, David Loftis, and Dan Dessecker.

Success of the "Grouse Project" was a result of hard work from many people to whom I am deeply indebted. Carrie Schumacher and Jennifer Fettinger got the project off the ground and provided invaluable data over the first 2 years. Many thanks for your hard work and persistence in the field. George Taylor worked tirelessly and without complaint collecting data during all 5 years of the study. In addition to being an unparalleled technician, George is an exceptional grouse hunting companion, and most importantly, a friend.

Monitoring grouse in the mountains is a labor-intensive process that would not have been possible without help from North Carolina Wildlife Resources Commission, especially Gordon Warburton, Joffrey Brooks, Jerry Anderson, Mike Parks, and David Allen. These folks helped with drumming counts, setting traps, tagging grouse, and keeping trucks running during the rigors of daily telemetry. Gentlemen, those trucks were broken when you gave them to me, I promise.

During my academic career, I have been blessed to work under mentors who serve as role models in science, conservation, and life. Walter Tzilkowski and James

Zaczek at Penn State, Jeanne Jones at Mississippi State, and now Craig Harper at the University of Tennessee. Dr. Harper molded and supported my desire to conduct research relevant to habitat management. We also spent invaluable time discussing the most important aspect in life, family. I am proud to have worked with you and I look forward to many more good hunts and long talks in the future.

Thanks also to my committee members and faculty in the UT Department of Wildlife and Fisheries, especially David Buehler, Frank van Manen, Billy Minser, and Arnold Saxton for insights and contributions throughout this endeavor. Thanks to companions in academic and wild game pursuits, Andy Edwards, Ryan Basinger, Kent Adams, and John Gruchy.

Thanks most of all to my family for supporting me in everything. To my parents, Ben and Mary Jo Jones, who have done so much more than I could ever put into words. You have nurtured, supported, and endured. To my grandparents, Robert C. and Helen French who taught me the values of hard work, love of the land, and life's simplest, most wonderful pleasures. Not a day passes when I don't think of you.

Wildlifers tend to be an obsessive lot in our careers and associated hobbies. My wife Michelle Lynne has inspired me to be the best possible husband and father above all else. Thanks are not enough.

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 ($\pm$ 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 ($\pm$4.0 SE) using 75% kernel methods and 40.0 ha ($\pm$ 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 ($\bar{x}$ = 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

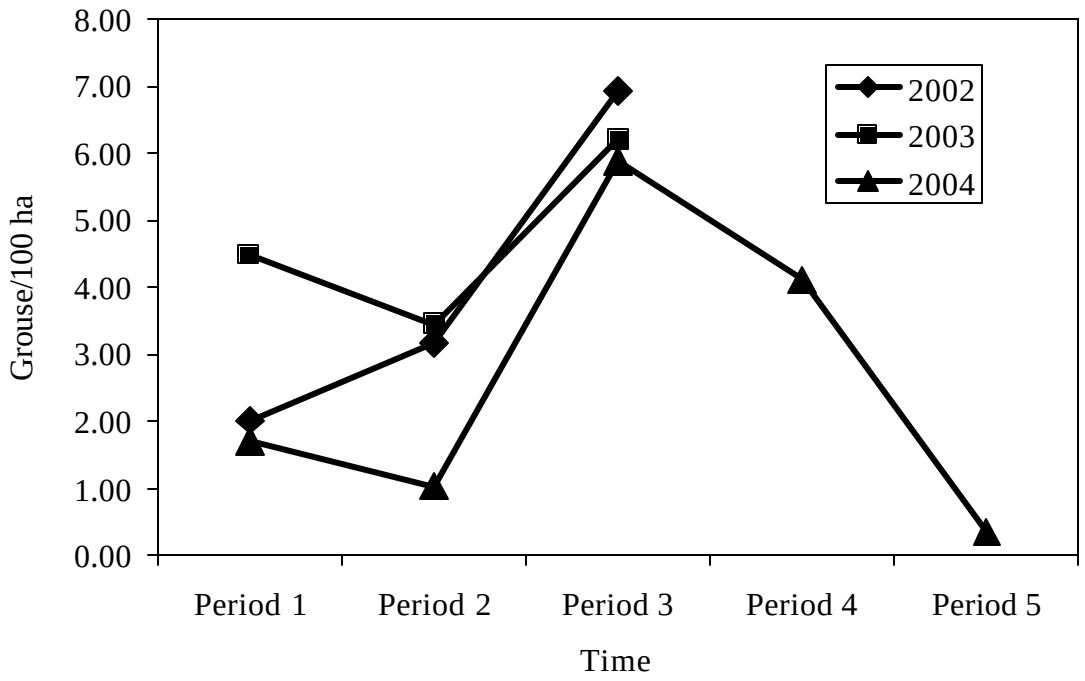

Figure 1.1. Ruffed grouse population estimates extrapolated from drumming counts conducted 24–31 March (period 1), 1–8 April (period 2), 9–16 April (period 3), 17–24 April (period 4), and 25 April–2 May (period 5), 2002–2004, on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina.

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 ($\pm$ 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*) 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 $\pm$ 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 $\geq$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 $\geq$1 egg. Hen success

was the proportion of females alive in the 3 April radio-marked population that successfully hatched ≥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°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 c was calculated from the global model to test for over dispersion of the data. Data were not over dispersed (c = 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$1 egg. Nests were observed for a total of 850 nest-days. Mayfield nest survival during incubation across years was 0.83 ($\pm$ 0.084 SE). Nest survival during laying and incubation across years was 0.84 ($\pm$ 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 $\pm$ 0.37 SE) and adults ($\bar{x}$ = 10.6 $\pm$ 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 ($?_2^2$ = 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 $\pm$ 1.35 SE) and adults ($\bar{x}$ = 13 April $\pm$ 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 $\pm$ 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 ($?_i \leq 0.217$) for all microhabitat nest site selection models, and $?_i$ 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 ($\bar{x}$ = 61 $\pm$ 19.0 m SE) and random points ($\bar{x}$ = 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 $\geq$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.

Parameter	Year					Mean	SE
	2000	2001	2002	2003	2004		
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.

	Age	
Parameter	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	?AICc	*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.

Variable	Nest Fate			
	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 $\pm$ 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 $\pm$ 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 $\pm$ 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 ($\pm$ 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°C (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 (a = 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 ? = 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 (AIC_c = 482.36, ? $_i$ = 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 (?^{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 $\pm$ 2.0 SE, random = 44.8 $\pm$ 2.0 SE), greater percent vertical cover (brood = 52.3 $\pm$ 2.0 SE, random = 41.5 $\pm$ 2.0 SE), greater midstory stems/ha <11.4 cm DBH (brood = 6,250 $\pm$ 441 SE, random = 4,963 $\pm$ 355 SE), and greater number of invertebrates/m^2 (brood = 58.9 $\pm$ 5.0 SE, random = 44.3 $\pm$ 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 ($\pm$ 4.3 SE) on brood plots and 7.7/m^2 ($\pm$ 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 a = 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	?AIC	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 (≥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, ? $_i$ > 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 $\pm$ 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 $\pm$ 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 ($\pm$ 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 $\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, 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 $\geq$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 (a = 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^{o}. 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, ? $_i$ > 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 $\pm$ 2.8 ha SE) and greatest on WSP (36.2 $\pm$ 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 $\geq$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 $\geq$ 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 $\pm$ 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 $\pm$ 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 $\leq$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 $\pm$ 1.0 ha SE) and WSC (5.71 $\pm$ 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 $\geq$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 relied 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	?AICc	*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 a = 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 a = 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 a = 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 a = 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 a = 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 a = 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

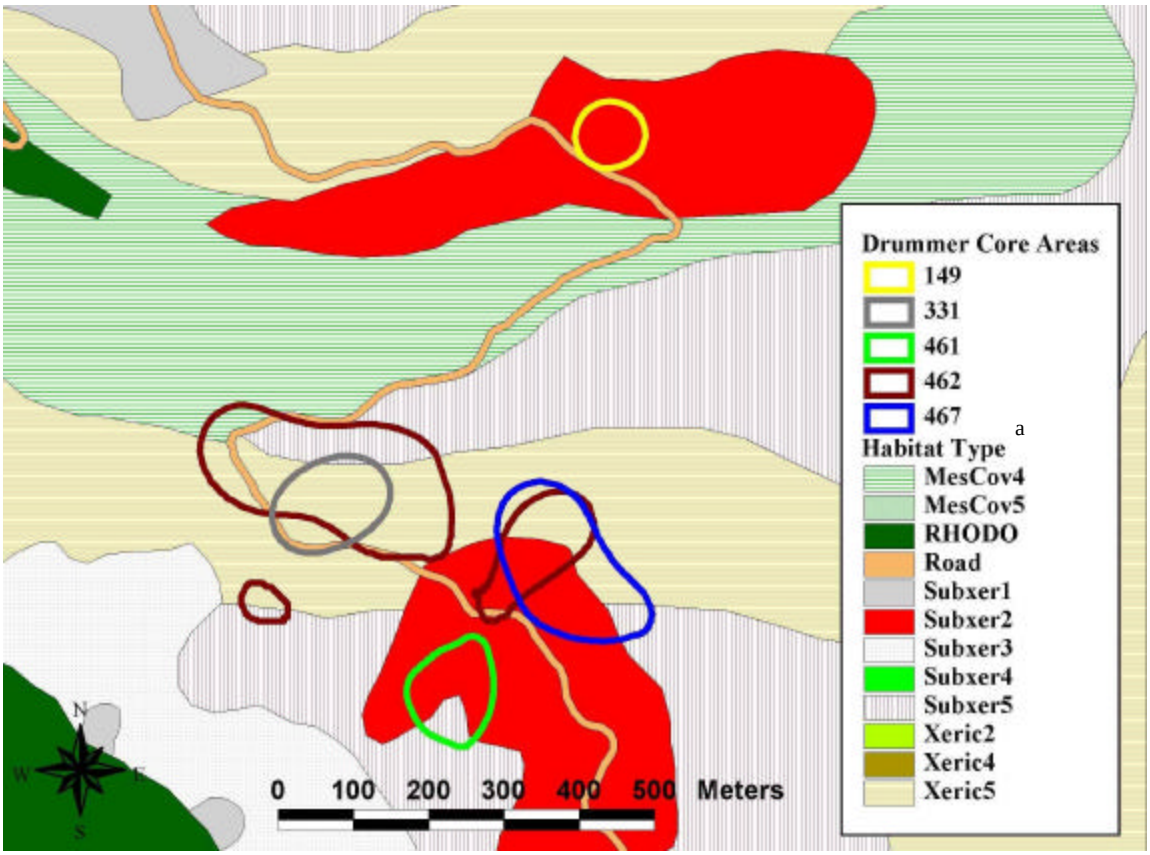

Figure 4.1. Example of core areas (50% kernel) of male ruffed grouse positioned near gated forest roads on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004. Apparent overlap resulted from projecting core areas across years.

[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

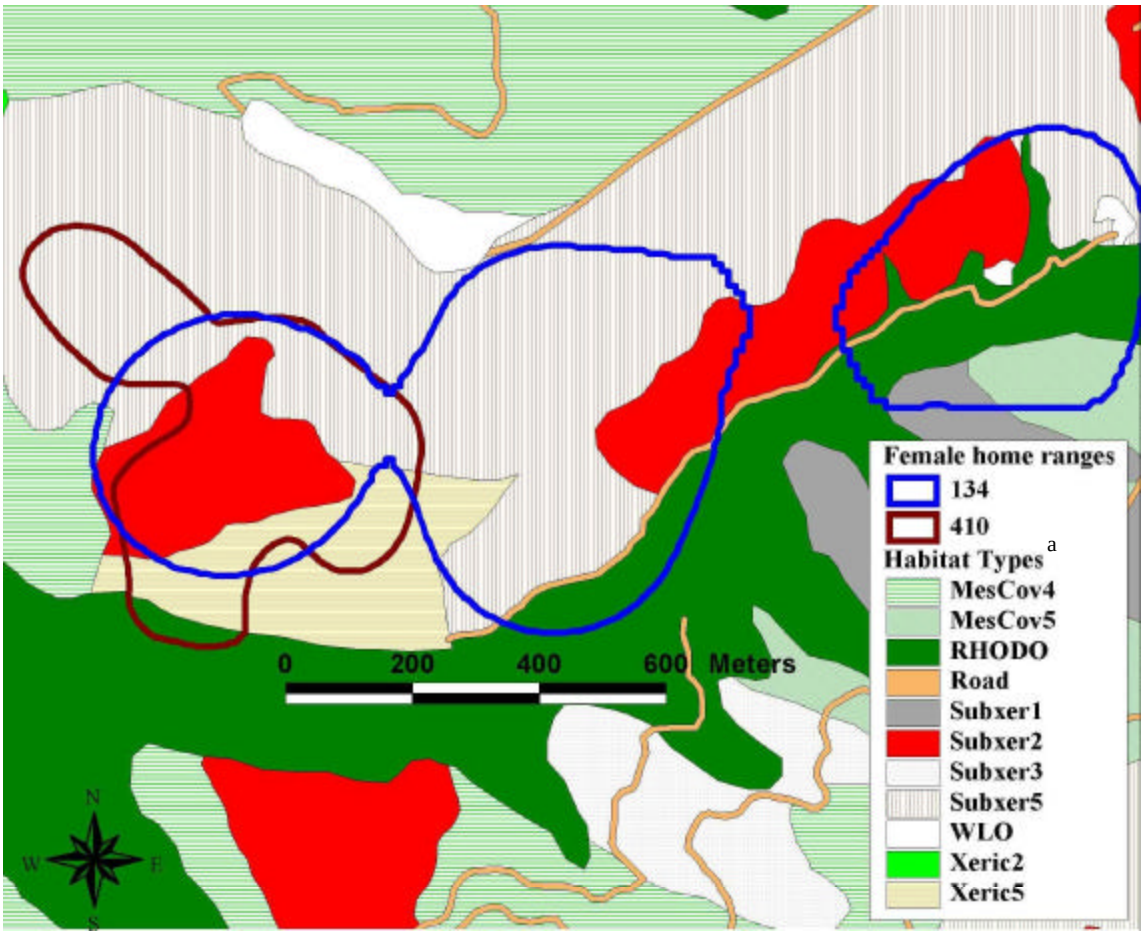

Figure 4.2. Example of female ruffed grouse use (75% kernel home range) of mature forest juxtaposed to early successional stands in winter on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999-2004.

[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 (± 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, ? $_i$ = 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 (± 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 10.4º 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% ($\pm$ 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 $\pm$ 0.074 SE) followed by avian (0.22 $\pm$ 0.044 SE), unknown predation (0.13 $\pm$ 0.044 SE), hunter harvest (0.10 $\pm$ 0.028 SE), and other (0.07 $\pm$ 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 ($\pm$ 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, ? $_i$ = 0.9999), indicating seasonal survival differed among years (Table 5.2, 5.3). Bootstrapping revealed data were not overdispersed (c = 1.11). There was no support for models with combinations of sex, age, or watershed as explanatory variables (? $_i$ < 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 ≥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	?AICc	*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

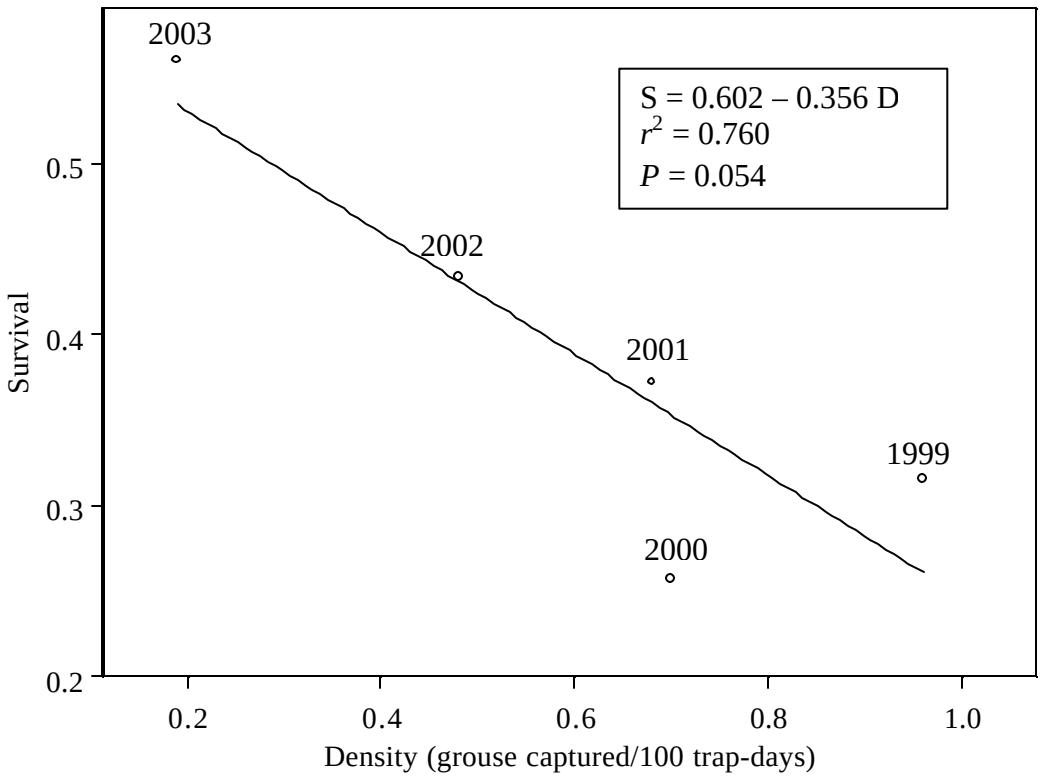

Figure 5.1. Relationship of ruffed grouse annual survival with a population density index calculated from fall trapping success on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

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 Public Lands Wildlife Planning Biologist with the Pennsylvania Game Commission.