



8-2002

Ruffed Grouse Nesting Ecology and Brood Habitat in Western North Carolina

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Recommended Citation

Fettinger, Jennifer L., "Ruffed Grouse Nesting Ecology and Brood Habitat in Western North Carolina." Master's Thesis, University of Tennessee, 2002.
https://trace.tennessee.edu/utk_gradthes/2058

To the Graduate Council:

I am submitting herewith a thesis written by Jennifer L. Fettinger entitled "Ruffed Grouse Nesting Ecology and Brood Habitat in Western North Carolina." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

David A. Buehler, Major Professor

We have read this thesis and recommend its acceptance:

Craig A. Harper, Arnold Saxton

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

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

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David A. Buehler
Major Professor

We have read this dissertation
And recommend its acceptance:
Craig A. Harper.

Arnold Saxton.

Accepted for the Council:

Anne Mayhew.
Vice Provost and
Dean of Graduate Studies

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

**RUFFED GROUSE NESTING ECOLOGY AND BROOD HABITAT
IN WESTERN NORTH CAROLINA**

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Jennifer L. Fettinger
August 2002

ACKNOWLEDGMENTS

I would like to thank Dr. David Buehler for providing guidance and support during my time as a student at the University of Tennessee. Dr. Buehler, Dr. Craig Harper, and Billy Minser shared their opinions, time, and expertise, while holding high expectations and encouraging me to do the best I could. For that I am grateful. Thanks to Dr. Arnold Saxton and Gordon Warburton for their technical input and guidance.

Several groups deserve recognition for their contributions to the project. In particular, the Department of Forestry, Wildlife, and Fisheries at the University of Tennessee, North Carolina Wildlife Resources Commission, U.S. Forest Service, Ceweeta Hydrologic Laboratory, the Ruffed Grouse Society, and the Appalachian Cooperative Grouse Research Project deserve a great deal of thanks. The faculty, staff, and students in the Department provided support and numerous opportunities to gain valuable experience. The Franklin and Andrews NCWRC crews provided much needed manpower and logistical support, and without them, this project could not have been completed. Ceweeta provided the use of their facilities on numerous occasions. The Ruffed Grouse Society provided opportunities to get the word out about the project and meet people who were genuinely interested in the grouse population in the southern Appalachians. Gary Norman and the ACGRP deserve recognition and thanks for pioneering an ambitious and worth-while long-term research effort that will, with the help of forest managers, ensure the future of ruffed grouse in the Appalachian region.

Several individuals deserve mention for their efforts in the project. An enthusiastic thank you is extended to George Taylor, my technician, for doing whatever it took to get the job done, without fail. I am genuinely grateful for your effort and positive

attitude when conditions weren't always favorable. In addition, Carrie Schumacher, my graduate student predecessor, laid the groundwork and jumped through many hoops before I began on the project and deserves thanks for her efforts and friendship. Thanks also to Ben Jones who, in taking over the project, will provide future data and insight into ruffed grouse ecology in the region. I am also grateful to my work-study students Rachel Patty and Todd Watson, and my summer assistant Martin Clark for providing assistance with invertebrate collection and processing.

Fellow graduate students Laura Lake, Jenny Fiedler, Jim Giocomo, Dan Kim, Aaron Keller, Vijak Chimchome, Chris Graves, Andy Edwards, Daniel Moss, and Allison Mains will always be remembered fondly for their humor and companionship. Finally, my family, boyfriend Matt, and friends back in Michigan never let me lose faith in myself and always let me know how proud they were of my accomplishments. Your support and confidence in me are the reasons I am the person I am today. Thanks a million times over.

ABSTRACT

Ruffed grouse (*Bonasa umbellus*) population densities are lower in the southern Appalachians compared to more northern parts of grouse range. Southern forests lack an aspen (*Populus* spp.) forest component, which provides year-round habitat in the North. The absence of aspen and low productivity have been cited as possible causes for low grouse densities in the southern Appalachians. In addition, habitat quality in the eastern United States may be decreasing as forests mature. These factors contribute to concerns that the region may be experiencing long-term ruffed grouse population declines. Productivity and breeding habitat must be characterized to foster better forest management strategies and ensure viable ruffed grouse populations in the southern Appalachians. The objective of this study was to quantify productivity and characterize habitat at nest and brood locations in the Nantahala National Forest, North Carolina.

Radio-collared hens were monitored in April - July 2000 and 2001 to determine nesting rate, clutch size, nesting chronology, and nest survival. Habitat characteristics were measured at nests ($n = 19$), and brood locations ($n = 115$) for 14 hens. Invertebrate samples ($n = 932$) were taken at each brood and random location during the first 6 weeks post-hatch to determine food availability for young ruffed grouse chicks. Nest and brood locations were paired with random locations to compare used versus available habitat.

Mean incubation initiation dates varied between years ($P = 0.0050$) and ranged from 10 April to 29 April. Hen incubation rate (84%), Mayfield nest survival (76%), mean clutch size (10.1 eggs/nest), and egg hatching success (95%) did not differ between years or age classes ($P > 0.05$). Hens selected nest locations with more dense vertical cover (83%) than random.

No chicks ($n = 48$) survived past 4 weeks post-hatch ($n = 5$ broods) in 2000. In contrast, all broods ($n = 9$) had at least one chick survive through the entire brooding season in 2001. Brood habitat selection differed between years ($P < 0.05$).

Early brood locations (hatch - 3 weeks) in 2001 ($n = 64$) had greater % ground cover (54%, $P < 0.0001$), were more frequently on eastern slope aspects than northern aspects (34% of locations on east aspects, $P = 0.0013$), were closer to streams (301 m, $P = 0.0071$), and had greater densities of invertebrates in preferred orders (78 invertebrates/ m^2 , $P < 0.0001$) than random locations. Brood locations in the late period (4 - 10 weeks, $n = 30$) had greater % ground cover (65%, $P = 0.0037$), lower basal area ($14.5\text{ m}^2/\text{ha}$, $P = 0.0444$), greater % vertical cover (72%, $P = 0.0257$), and greater densities of invertebrates in preferred orders (59 invertebrates/ m^2 , $P < 0.0040$) than random locations.

Broods selected 6 to 30-year-old stands (50% of locations) more frequently than random ($P < 0.0001$), but did not select habitat based on forest cover-type ($P > 0.05$).

Grouse management strategies for brood habitat should include practices that increase forb and fern ground cover during the summer months, because brood habitat may be limiting during that time. Prescribed fire and forest thinnings that allow sunlight to reach the forest floor may be useful tools in accomplishing this goal. Wildlife openings and logging roads should consist of forbs which allow chicks to move and forage efficiently while providing protective overhead cover. Forest regeneration cuts should be separated in time and space, so that a mosaic of forest age-classes is produced.

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I. INTRODUCTION

The ruffed grouse (*Bonasa umbellus*) is an important game bird throughout its range across North America from northern Georgia to Alaska. The southern limit of the species' range is located in the southern Appalachian Mountains where the subspecies *B. u. monticola* inhabits the eastern deciduous forest (Aldrich 1963, Johnsgard 1973).

Grouse in the North are strongly associated with aspen (*Populus* spp.), which is responsible for the high densities in that region (Bump et al. 1947; Sharp 1963; Gullion and Svoboda 1972; Gullion 1972, 1977a). Large populations and the popularity of ruffed grouse as a game species have led to extensive research in the northern part of the range.

Preferred habitat in the North varies with seasonal life history requirements so that juxtaposition of several forest successional stages is recommended (Berner and Gysel 1969, Gullion 1972, 1984, Stauffer and Peterson 1985, Thompson et al. 1987). In forests dominated by aspen, small clear-cuts creating a mosaic of multiple age classes provides the variety of habitats needed throughout the year (Gullion 1972, Kubisiak 1985, Dessecker and McAuley 2001). Areas devoid of an aspen component provide lower quality habitat and produce lower grouse densities (Bump et al. 1947; Gullion 1972, 1977b; Kubisiak et al. 1980, Thompson and Dessecker 1997). Areas without aspen or early successional habitat produce fewer grouse still (Dessecker and McAuley 2001). Management in these areas is more difficult to prescribe because no one vegetation type provides the variety of food and cover required through all seasons.

Grouse densities and productivity are lower in the southern Appalachians compared to more northern parts of grouse range. Southern forests lack an aspen component and consequently provide sub-optimal habitat (Bump et al. 1947, Sharp 1963,

Gullion 1972, Gullion and Svoboda 1972, Gullion 1977*a*, Rusch and Destefano 1989).

Maturation of eastern forests may be further lowering habitat quality and compounding the effects of low productivity.

Long-term population declines may be occurring in the southern Appalachians (Dessecker 1997, 2001). North Carolina grouse harvest declined from over 30,800 birds in 1972 to fewer than 11,800 in 1996, signaling a decrease in grouse population size, hunter effort, or both (Dessecker 2001). Flush rate data indicate long-term declines in Tennessee and Virginia ruffed grouse populations (Dessecker 2001). As a result, interest in proactive forest management for ruffed grouse in the southern Appalachians has increased.

Forest management for ruffed grouse in the southern Appalachians requires a complete understanding of grouse habitat requirements throughout the year (Bump et al. 1947, Stauffer and Peterson 1985, Fearer 1999). The presence of quality habitat during spring and summer is essential for maintenance of viable populations through reproduction and recruitment. In particular, brood range is a critical component of grouse habitat (Stewart 1956, Sharp 1963, Berner and Gysel 1969) because survival during the first weeks of life may limit populations (Haulton 1999). Close proximity of the nest to quality brood habitat may be important to chick survival in the first days of life (Bump et al. 1947).

Habitat characteristics at nest sites, nesting chronology, and invertebrate abundance and habitat at brood locations have been described for much of ruffed grouse range (Bump et al. 1947, Edminster 1947, Hungerford 1951, Sharp 1963, Godfrey 1975, Gullion 1977*a*, Maxson 1978*a*, Stauffer and Peterson 1985, Thompson et al. 1987, Boyd

1990, Haulton 1999, Dobony 2000). Habitat at nest sites is variable, and data for North Carolina are lacking entirely. Characterization of habitat at nest and brood sites in terms of topography, vegetative structure and composition, and invertebrate availability as prey for chicks may help guide management practices to ensure reproductive success. In addition, dates of egg laying, incubation, hatching, and their relation to weather conditions and green-up are needed for a full understanding of ruffed grouse reproductive ecology in North Carolina. Therefore, the objectives of this study were to:

1. Document nesting chronology of ruffed grouse in western North Carolina;
2. Document nest success, clutch size, and hatching success;
3. Describe ruffed grouse nest site habitat in terms of vegetative structure;
4. Describe ruffed grouse brood habitat in terms of vegetative structure and invertebrate abundance.

II. STUDY AREA

The study was conducted on 4,465-ha (11,485-ac) of the Wine Spring Creek Study Area (WSCA) in western Macon County, North Carolina ($35^{\circ}15'N$ latitude, $83^{\circ}35'W$ longitude, Figure 1, all figures are located in Appendix A). The area is located in the Wayah Ranger District of the Nantahala National Forest and has been designated an ecosystem management area by the U.S. Forest Service (USFS). The area lies in the southern Blue Ridge physiographic province.

Topography of the area is characteristic of the southern Appalachian Mountains. Elevation ranges from 915 m (3000 ft) to 1,644 m (5450 ft). Slopes range from 8% grade at the lowest elevations to 90% in some areas (USDA 1996). Three main tributaries run through the area and drain into Nantahala Lake, adding to the rugged terrain (Elliott and Hewitt 1997). Soils at higher elevations are well drained and range from sandy loam to rock outcrops, while soils in coves and lower elevations are more mesic (USDA 1996).

The WSCA is > 99% forested and contains a mixture of northern hardwood, oak (*Quercus* spp.) – hickory (*Carya* spp.), pine (*Pinus* spp.), mixed hardwood-pine, mesophytic hardwoods, and mixed mesophytic hardwood-pine forests (Table 1, all tables are located in Appendix B). Tree species include northern red oak (*Quercus rubra*), chestnut oak (*Q. prinus*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), sweet birch (*B. lenta*), yellow-poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), black cherry (*Prunus serotina*), pin cherry (*P. pensylvanica*), and hickory (*Carya* spp.). The mid-story contains rosebay rhododendron (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), and azalea (*Rhododendron* spp.). Forest openings are comprised mainly of wildlife food plots and

logging roads originally seeded with orchard grass (*Dactylis glomerata*) and white-dutch clover (*Trifolium repens*).

The area has a moist, temperate climate. Average annual snowfall in Macon County is 19 cm (7.5 in) and annual rainfall is 132 cm (52 in, USDA 1996). Minimum January and maximum July temperatures in extreme years can reach -18°C (0°F) and 34°C (93°F) respectively, although the average annual temperature is 13°C (55°F , USDA 1996).

The WSCA has a long history of disturbance, dating back to before 1850 when the Cherokee used semiannual burning to create openings for wildlife and livestock (Elliott and Hewitt 1997). Over time, the Nantahala National Forest has been managed for timber, wildlife, recreation, and a variety of other uses (USFS 1987). In 1986, the USFS set 6 goals for the Nantahala National Forest (USDA 1987). Those goals were created to provide a forest that has multiple uses such as timber production, recreation, and wildlife habitat (USDA 1987).

In 1995 - 1997, various silvicultural treatments were implemented to determine the effects on forest composition, condition, hydrology, and wildlife. The WSCA has not received any clear-cutting treatments since 1995. Regeneration methods were applied to 11 high-elevation northern red oak stands and included 2 control treatments, 3 shelterwood treatments, 3 two-age shelterwood treatments, and 3 group selection treatments. Shelterwood treated stands were left with $5.0 - 7.5 \text{ m}^2/\text{ha}$ ($20-30 \text{ ft}^2/\text{ac}$) basal area. Several small $0.4 - 0.8 \text{ ha}$ (1 - 2 ac) cuts made up group selection treatments. All forest stands in the WSCA have been classified into age classes according to the timing of the last regeneration cut (Table 2).

The University of Tennessee, the USFS, North Carolina Wildlife Resources Commission (NCWRC), the Ruffed Grouse Society, and the Appalachian Cooperative Grouse Research Project (ACGRP) have collaborated to work on the wildlife focus of Phase II of the Wine Spring Ecosystem Management Demonstration Project.

III. RUFFED GROUSE PRODUCTIVITY AND NESTING HABITAT USE IN WESTERN NORTH CAROLINA

INTRODUCTION

Ruffed grouse population densities are historically lower in the southern Appalachians than in the range of aspen (*Populus* spp., Bump et al. 1947), and may be experiencing long-term population declines (Dessecker 2001). Low productivity combined with forest maturation may influence grouse populations in the southern Appalachians (Bergerud 1988, Dessecker 1997, Dessecker and McAuley 2001). Identifying causes for lower productivity in this region is essential to determining whether changing forestry practices are negatively impacting grouse populations.

Grouse productivity in the South may depend on several factors, including nesting rate, egg production, hatching rate, nest success, and re-nesting rates. Nearly all hens attempt to incubate nests in the North (Bump et al. 1947, Maxson 1978a, Small et al. 1996) while only 82% attempted to incubate in the central and southern Appalachians (Haulton 1999). In addition, egg production may be lower in the South, where smaller clutch sizes have been reported (Haulton 1999). Mean clutch size was 9.5 eggs per nest ($n = 60$) in the central and southern Appalachians for 1997 – 1998 (Haulton 1999), whereas mean clutch size in the North ranges from 11.0 ($n = 77$, Small et al. 1996) to 12.7 eggs per nest ($n = 30$, Larson 1998). Egg hatching rate was 94% ($n = 482$) in the southern Appalachians (Haulton 1999), and 97% ($n \sim 5700$) in New York (Bump et al. 1947), suggesting few infertile or under-developed eggs are produced by ruffed grouse. Slightly lower hatching rate may result from low-quality eggs produced because of a diet low in protein (Beckerton and Middleton 1982). Servello and Kirkpatrick (1987)

suggested that low grouse densities in the South may result from the poor nutritional quality of evergreen leaves dominating the late winter diet.

Reported nest success rates in the South appear to be greater than rates reported from northern populations and is probably not a factor in lowering productivity. In the southern Appalachians, 82% ($n = 105$) of nests hatched at least one egg (Haulton 1999), compared to 58% ($n > 5400$) in New York (Bump et al. 1947), 60% ($n = 15$) in Minnesota (Maxson 1978b), and 48% ($n = 21$) in Wisconsin (Small et al. 1996). Re-nesting rates may be lower in the South and add to the effects of nest depredation on productivity. Only 6% of hens with unsuccessful nests ($n = 33$) attempted to re-nest in the southern Appalachians (Haulton 1999), compared to re-nesting rates as high as 67% in Michigan ($n = 9$, Larson 1998). Greater nest depredation may be the cause of more nest failures in the South, and may account for lower productivity (Bergerud 1988). Further, habitat at the nest site and proximity of the nest to a road or forest management-induced edge may impact depredation rates (Yahner and Mahan 1997).

Hens appear to select nest sites at the micro-habitat scale. Although most nests are placed in second growth forest stands, forest stand age and forest type are not as important as the cover they provide (Bump et al. 1947, Larson 1998). Nests are usually located at the base of a tree, stump, or log (Bump et al. 1947, Johnsgard and Maxson 1989) and vegetation immediately surrounding the nest is moderately dense (Bump et al. 1947). High stem densities provide protection from avian predators (Gullion 1972).

Hatching in the North occurs a week or two later than in the South. Peak hatching occurs the first or second week of June in the North (Bump et al 1947, Kubisiak 1978, Larson 1998) and the second or third week of May in the southern Appalachians (Haulton

1999), including eastern Tennessee (Boyd 1990). Reproduction is dependent on photoperiod, but may be proximally influenced by weather so that earlier hatching dates in the South reflect photoperiod and weather condition variations between regions (Larsen and Lahey 1958, Johnsgard et al. 1989).

Factors influencing grouse productivity have been described for much of ruffed grouse range (Bump et al. 1947, Edminster 1947, Hungerford 1951, Sharp 1963, Godfrey 1975, Gullion 1977, Maxson 1978a, Stauffer and Peterson 1985, Thompson et al. 1987, Larson 1998). However, few studies have focused on grouse productivity in the southern Appalachians (Norman and Kirkpatrick 1984, Boyd 1990, Haulton 1999, Dobony 2000), and data for North Carolina are lacking entirely. Documentation of grouse productivity and nesting habitat in North Carolina is needed for comparison with other studies from the southern Appalachians and the North, to gain a better understanding of regional variation in grouse population densities and to recommend forest management to sustain viable ruffed grouse populations. Consequently, the objective of this study was to determine productivity and characterize habitat at ruffed grouse nest sites in the mountains of western North Carolina.

METHODS

Trapping and monitoring females

Ruffed grouse were trapped using clover-leaf traps during the fall, 1999 and 2000, and spring 2001 (Liscinsky and Bailey 1955). Captured birds were sexed and aged as juvenile (hatch year) or adult (after hatch year) according to Davis (1969), Roussel and Ouellet (1975), and Kalla and Dimmick (1995). Birds were then equipped with mortality-sensitive radio collars (Advanced Telemetry Systems, Inc., Isanti, MN),

banded, released, and tracked throughout the year using 3-element yagi antennas and ATS and Telonics receivers (Advanced Telemetry Systems, Inc., Isanti, MN, Telonics Inc., Mesa, AZ). Collared females were located by triangulation (Cochran and Lord 1963) or homing of the radio signal at least 3 times per week during the first weeks of April 2000 – 2001. When 3 or more consecutive locations were limited to a 0.25-ha area for an individual hen, it was assumed incubation had begun (Maxson 1978a). Nests were located by homing in on the radio-collared hen and circling the signal, taking a compass bearing and flagging at ~20 m. The same area was visited the next day and if the hen was in the same location, an attempt was made to visually locate the nest. Anticipated hatch date was calculated by adding 24 days to the date the hen was first found in that area (Bump et al. 1947).

Productivity

Nesting hens were monitored daily using triangulation and variability of the radio signal to determine whether the hen was on or off the nest. If a hen was moving, the nest was visited briefly to determine its fate. Clutch size was determined at that time if the nest was intact. Hens were flushed once late during incubation if the clutch size was not previously determined. No nests failed as a result of such visits.

Nest survival was calculated using the Mayfield method (Mayfield 1961, 1975). Nests having at least one egg hatch were considered successful (Miller and Johnson 1978). The number of unsuccessful nests divided by the total exposure (# of days from first incubation observation to nest fate of all nests combined) determined the daily mortality rate (Mayfield 1975). The probability of a nest surviving from initiation to hatching was found by raising the daily survival rate (1-daily mortality rate) to the power

of the number of exposure days per nest (Mayfield 1975). Egg hatching success was determined from the proportion of the total number of eggs in successful nests that successfully hatched.

Egg shells and fragments left in the nest were examined post-hatch and after the hen and brood left the nest. The number of unhatched eggs was subtracted from the total number of eggs in the clutch to determine the initial brood size. Hatching success was calculated by the number of successfully hatched eggs divided by the total number of eggs in successful nests (Mayfield 1961).

Nesting chronology

A timeline documenting nest initiation and incubation was constructed using telemetry and nesting data. Incubation initiation date was calculated by subtracting 24 days from the hatch date (Bump et al. 1947). The initiation of egg laying was calculated by subtracting the number of incubation days (24) and the number of egg laying days (# eggs in clutch*1.5 days) from the hatch date (Bump et al. 1947, Maxson 1977). Hens with destroyed nests and those that lost broods were monitored along with non-nesting hens. Re-nesting was documented in the same manner as initial nests.

Monitoring weather conditions

Daily high and low temperatures and mean precipitation were recorded by the Coweeta Hydrologic Laboratory (Coweeta LTER, Otto, NC) using a permanent weather station on the study area.

Nest habitat sampling

Within 2 days after the hen and brood left the nest, the nest location was georeferenced using GPS units (Trimble Navigation Limited Inc., Sunnyvale, CA).

Vegetative and topographic data were collected within nested circular plots with the nest at plot center to quantify nest micro-habitat (Harper 1998). A paired, randomly selected site 100 m (328 ft) from the nest was also sampled to compare used versus available micro-habitat. Slope, aspect, and distance to an object were measured from plot center. ArcView GIS software was used to determine distance to a road, stream, and forest opening. A 2.5 m²/ha basal area prism was used from plot center to determine basal area. Species and counts of all trees determined to be “in” using the basal area prism were recorded. Trees recorded within the plot were classified as deciduous or evergreen. Snags (dead, standing trees) were recorded separately. Counts and species of woody mid-story (sapling) stems < 11.4 cm (< 4.5 in) dbh and > 1.4 m (> 4.6 ft) tall were taken within a 5.7 m (18.7 ft) radius plot. Stems were classified into < 2.54 cm (< 1 in) dbh, 2.54-5.08 cm (1-2 in) dbh, 5.08-7.62 cm (2-3 in) dbh, and > 7.62 cm (> 3 in) dbh diameter classes to determine small woody stem density within the plot (Noon 1981). Counts and species of woody under-story (seedling) stems < 1.4 m (< 4.6 ft) tall were recorded in 3.6 m (11.8 ft) plots and categorized as deciduous or evergreen. Vertical density was measured as percent area covered in each 0.2 m (8 in) section of a 2 m (6.6 ft) tall density board and was recorded 15 m (49 ft) from plot center on uphill and downhill slope positions. GIS coverages including roads, streams, openings, forest type, and stand age obtained through the U.S. Forest Service (USFS) and the Southern Appalachian Assessment (SAA) were combined with micro-habitat measurements.

In all, data for 24 variables were collected: SLOPE, ASPECT, DOBJ, DROAD, DSTR, DOPEN, BA, OSP, MIDA, MIDB, MIDC, MIDD, MIDT, MIDSP, USTEM, USP, VCVRA, VCVRB, VCVRC, VCVRD, VCVRE, VCVRM, FCVR, and AGECLS

(Table 3). All mid-story stem density and vertical cover measurements were highly correlated ($r > 0.7$), so only the total mid-story stem density and mean vertical cover density was used in further analysis.

Data Analysis

The nesting rate (percentage of hens with 3 locations per week that attempted to nest), mean clutch size, hatching success, and mean dates of egg laying, incubation, and hatch were compared between years and hen age classes using 2-sample t-tests. Nest survival was compared between years and age classes using Fisher's exact test. Monthly means of minimum, maximum, and average daily temperature, and precipitation were compared between years using 2-sample t-tests.

A micro-habitat model predicting nest site selection was created using logistic regression (PROC LOGISTIC, SAS 2000). A set of potentially biologically important habitat variables (ASPECT, BA, MIDT, USTEM, VCVRM, DOBJ, DROAD, DOPEN, FCVR, AGECLS) was selected for use in the model. Logistic regression (PROC LOGISTIC, SAS 2000) was run using stepwise selection (slstay = 0.1) to determine variable entry and retention in the model. Model performance was evaluated based on the Hosmer – Lemeshow goodness of fit statistic, a maximum – rescaled R^2 value, and percent correct classification rates (Hosmer and Lemeshow 1989).

RESULTS

Productivity

Nineteen radio-collared females were monitored for nesting during the 2000 ($n = 7$) and 2001 ($n = 12$) reproductive seasons. Seven additional hens were killed during April (2 in 2000, 5 in 2001), and were not included in productivity parameter

calculations. Two hens caught in spring 2001 were of unknown age and therefore not used in age-class comparisons.

Hen nesting rate pooled over years and age-classes was 84% (Table 4). Nesting rate did not differ between 2000 (71%) and 2001 (92%, $P = 0.2700$) or between adults (88%) and juveniles (83%, $P = 1.0$, Table 4).

Mayfield nest survival, pooled over years and age-classes, was 76% ($n = 19$, Table 4). Nest survival did not differ between 2000 (85%) and 2001 (79%, $P = 0.7900$) or between adults (90%) and juveniles (80%, $P = 0.5710$, Table 4). Apparent nest success for first nesting attempts was 86% pooled over years and age classes. Only 4 nests were unsuccessful, including one from an uncollared hen, two from juvenile hens and one second nesting attempt. No egg shells or fragments were found in or around unsuccessful nests to determine how the nests were destroyed.

Egg hatching success, pooled over years and age-classes, was 95% ($n = 145$, Table 5). Hatching success did not differ between 2000 (98%) and 2001 (94%, $P = 0.3132$) or between adult (98%) and juvenile (94%) nests ($P = 0.2621$, Table 5).

Mean clutch size for first nesting attempts, pooled over years and age-classes, was 10.1 eggs per nest ($n = 18$, Table 5). Mean clutch size did not differ between 2000 (9.5) and 2001 (10.3, $P = 0.2570$) or between adult (10.7) and juvenile (9.9) nests ($P = 0.2519$, Table 5).

Nesting chronology

Egg laying began earlier in 2000 (10 April) than 2001 (14 April, $P = 0.0152$); nest incubation started earlier in 2000 (25 April) than 2001 (29 April, $P = 0.0048$); and mean hatch dates were earlier in 2000 (19 May) than 2001 (24 May, $P = 0.0057$, Table 6).

Mean hatch dates ranged from 15 May to 27 May (Figure 2). Mean initiation dates of egg laying, incubation, and hatch differed between years ($P < 0.05$). Nesting chronology was similar between age classes (egg laying: $P = 0.1242$; incubation: $P = 0.7933$; hatch: $P = 0.4220$, Table 6). The only documented re-nesting attempt was by a juvenile in 2001 and the nest was depredated within the first week of incubation on 24 May.

Weather conditions

Monthly weather conditions differed between 2000/2001 for March and April (Table 7). March 2001 was cooler than in 2000 ($P = 0.0006$) and April 2000 was significantly colder ($P = 0.0438$) and wetter than in 2001 ($P = 0.0480$, Table 7).

Nest habitat characteristics

Nineteen nests were sampled for habitat parameters (Figure 3). Although all nests were located next to or under an object, the variable DOBJ could not be included in the analysis because it resulted in a quasi-complete separation of the data. Stepwise selection (slstay = 0.1) resulted in 1 variable remaining in the model ($R^2 = 0.42$, $\chi^2 = 6.91$, $P = 0.4386$): VCVRM ($\beta = 0.064$, SE = 0.021 $P = 0.0004$, Table 8, 9). Vertical cover was more dense at nest sites than random locations (Table 8). No other variables were significant at the $\alpha = 0.1$ level in logistic regression (Table 8, 9, 10, 11). Other variables measured were not different between nest and random locations ($P > 0.1$, Table 12).

DISCUSSION

Productivity

Differences in ruffed grouse densities from North to South can be explained by differential productivity, survival, or both. In this study, nesting rate was similar to the Ridge and Valley region in Virginia and West Virginia (82%, $n = 71$, Haulton 1999), but

lower than studies in the range of aspen. All radio-tagged females attempted to incubate a nest in Minnesota ($n = 15$, Maxson 1978a) and Wisconsin ($n = 26$, Small et al. 1996).

In New York, 75 – 100% of hens incubated a nest, and all nested during most years and on most study sites (Bump et al. 1947). Bergerud (1988) suggested that, in species with short expected life spans (0 – 4 years), all females should attempt to nest in a given year.

Ruffed grouse nesting rate appears to decrease from north to south. However, hens that lost their nests prior to or early in the incubation stage would not have been included in the nesting rate, thereby negatively biasing the results. It is nearly impossible to detect egg laying in grouse, since hens spend very little time at the nest during that time (Maxson 1978a). A radio-transmitter with a 2 – 4 hour inactivity switch may aid in detecting the onset of incubation, but may produce other unwanted effects. Future research should explore ways to accurately determine nesting rate, particularly early in the season.

Apparent nest success (86%, $n = 18$) was similar to that reported for the southern Appalachians (82%, $n = 105$, Haulton 1999), but greater than in the central Appalachians and the North. Dobony (2000) found 71% nest success ($n = 40$) in West Virginia, with 92% of unsuccessful nests depredated. Bump et al. (1947) had 58% nest success from over 5400 nests in New York. In Minnesota, 60% of first nests ($n = 15$) were successful, with all failures attributed to predators (Maxson 1978a). Small et al. (1996) reported 48% nest success ($n = 21$) in Wisconsin.

All nest failures on the WSCA were caused by nest depredation. The 4 unsuccessful nests (including one uncollared hen nest and a second-nest) were found with

no trace of egg shells, and were otherwise undisturbed. Depredation dates ranged from the third day of incubation to 3 days prior to the expected hatch date.

Re-nesting was observed for one juvenile hen in 2001 who lost her nest early in the incubation period. The hen that lost her nest late in the season and five hens that lost their entire broods in 2000 did not attempt to incubate a second nest. Haulton (1999) had a 6% re-nesting rate in the southern Appalachians, but proposed that that rate may have been negatively biased due to sampling methods. Dobony (2000) did not have any re-nesting attempts from 12 destroyed nests. In the northern states, re-nesting rates are as high as 56% in Wisconsin ($n = 9$, Small et al. 1996) and 67% in Michigan ($n = 9$, Larson 1998).

Nests on the WSCA that were incubated long enough to be detected had a high probability of surviving until hatch. However, nest success may have been positively biased by undetected nests that were destroyed prior to or early in the incubation stage. The re-nesting rate on the WSCA was high (50%) because only two first nests were destroyed. More data are needed to accurately measure the re-nesting on the WSCA.

The re-nesting rate in the southern Appalachians may be low (Haulton 1999), but may not be as critical to productivity since nest success appears relatively high. If nesting success is higher, it may offset the effects of lower re-nesting rates.

Nearly all eggs in successful nests hatched, suggesting few infertile or under-developed eggs were produced. This finding is similar to previous studies. Hatching success ranged from 87 – 99% in New York ($n \sim 5700$, Bump et al. 1947) and was 90% in southern Ontario (Cringan 1970).

Mean clutch size averaged 10.1 eggs per nest ($n = 18$) for the 2000/2001 seasons, slightly greater than the 9.5 eggs per nest found in the central and southern Appalachians ($n = 60$, Haulton 1999), but lower than clutch sizes further north. Bump et al. (1947) found a mean clutch size of 11.5 for nearly 1500 nests in New York; mean clutch size in Wisconsin was 11.0 ($n = 77$, Small et al. 1996); and clutches averaged 12.7 eggs per nest in northern Michigan ($n = 30$, Larson 1998). First nest clutch sizes in North Carolina ranged from 8 to 13, and did not significantly vary from previous findings. Rusch et al. (2000) reported first nest clutch sizes across North America ranging from 9 to 14 eggs per nest.

Clutch size appears to decrease from north to south. While fewer eggs are produced in the South, hatching rate remains relatively stable, indicating that the quality of eggs produced does not significantly vary by region. Lower quality winter habitat in the South may lead to poor hen condition entering the breeding season. The findings of this study are consistent with this theory, and suggest that the quantity of eggs may be sacrificed to ensure the quality of those eggs produced. Such a trade-off between quality and quantity of eggs produced, if a regional phenomenon, may be linked to poor nutritional quality in the winter diet. If this relationship exists, an increase in high quality forage during the winter months may potentially increase grouse productivity in the region. Therefore, this relationship between forage quality and productivity warrants further investigation.

The overall purpose for determining nest success, re-nesting rates, clutch size, and egg hatchability is to quantify potential ruffed grouse productivity. Based on the results of this study and Haulton (1999), it appears that the effects of low re-nesting rates may be

offset by high nest success. In addition, slightly fewer eggs are produced but have hatchability similar to the North. Future research should attempt to determine whether hen condition entering the breeding season is poorer than in the North, is a direct result of poor nutritional value of winter forage, and influences egg production. If this is found to be true, management practices that increase the availability of higher quality winter forage may lead to the production of more eggs and therefore higher ruffed grouse productivity.

Nesting chronology

Mean dates for egg laying, incubation, and hatch varied between 2000 and 2001 seasons. Egg laying is initiated within 7 days of mating at an approximate rate of 1 egg per 1.5 days (Bump et al. 1947). Once all eggs are laid, they are incubated for approximately 24 days (Bump et al. 1947). Therefore, nest incubation dates depend on the date of nest initiation (onset of egg laying) and clutch size.

The onset of egg laying is determined primarily by photoperiod, but may be proximally influenced by weather (Larsen and Lahey 1958). Warmer temperatures in 2000 may be responsible for the disparity found in between-year nesting date comparisons. Warmer weather in March may have prompted reproduction earlier in the 2000 season (first incidence of egg laying April 7 in 2000 and April 15 in 2001), and therefore influenced dates of incubation and hatch. Cooler and wetter weather occurred after 10 April 2000 ($P < 0.05$), after most hens began laying eggs, and therefore did not influence nesting chronology.

Peak hatching occurred 19 May 2000 and 24 May 2001, earlier than in the northern states, but similar to central and southern Appalachian data. Haulton (1999)

reported an overall mean hatch date of 25 May 1997/1998 for study sites in Kentucky, Maryland, Ohio, Virginia, and West Virginia. Hatching occurred between 6-22 May in eastern Tennessee (Boyd 1990), 1 – 2 weeks earlier than more northern states. Wisconsin nests hatched during the last week of May and into July (Kubisiak 1978). In northern Michigan, the median nest hatching date was 10 June (Larson 1998). Hatching in New York occurs around 1 June (Bump et al. 1947). Earlier hatching dates are probably caused by photoperiod and weather condition variations between regions (Johnsgard et al. 1989).

Nest habitat characteristics

All nests were next to or under an object, similar to other studies (Thompson et al. 1987, Johnsgard and Maxson 1989, Larson 1998), but the presence of an object may not be critical. Maxson (1978b) and Bump et al. (1947) reported some nests not associated with an object. No preference for object type was found in North Carolina. Rocks or rock outcrops, logs or slash, tree or shrub bases, and stumps were selected. When possible, it appeared that a hen would place the nest with the object providing some overhead cover in addition to cover from one or more directions. One nest was completely underneath a rock that jutted out from the mountainside. Such cover would provide protection from rain or snow in addition to preventing detection by avian predators.

Nest site selection , in general, did not differ at the micro-habitat scale from random sites, with only the % vertical cover differing between randomly selected locations and nest sites at the $\alpha = 0.1$ level ($R^2 = 0.42$, $\chi^2 = 6.91$, $P = 0.4386$). Vertical cover was denser at nest sites ($P = 0.0004$), presumably dense vertical cover provides

protection from avian predators (Gullion 1972). Other studies have found moderately dense vegetation immediately surrounding the nest (Thompson et al. 1987, Larson 1998). In northern Michigan, stem density at nest sites varied from 1,300 to 30,200 stems/ha in 11 different over-story vegetation types (Larson 1998). In Missouri, nests occurred on sites with an average of 3,955 woody tree stems/ha and 2,314 shrub stems/ha (Thompson et al. 1987).

Although vertical cover at nest sites was dense, it was not necessarily a reflection of stand age. Nests were placed in stands ranging from over 40 years old to the edge of a 5-year-old shelterwood cut. Larson (1998) similarly found that forest stand age was not as important as the cover it provided. Nests are usually found in second-growth forests (Bump et al. 1947), however nearly all of the WSCA is in regenerating stands, and therefore this could not be tested.

Forest-type selection did not differ from random, although most nests were found in oak-hickory or northern hardwood types. Selection was probably not detected since those two cover-types make up over 75% of the WSCA (Schumacher 2002) and random sites may not have been far enough from nests (100 m) to detect stand-level differences. However, a strong preference for hardwood stands was found in New York and Minnesota (Bump et al. 1947, Maxson 1978*b*), supporting the findings of this study.

Intensive nesting habitat management is likely unnecessary, because ecological conditions on the site and past forest management have created conditions favorable for high nest survival rates. Sapling stands and mature stands with an under-story of azalea, mountain laurel, or blueberry have produced areas of dense vertical cover that increases nest habitat quality and availability. Slash and stumps left after timber harvests have also

enhanced nesting habitat, although there is no evidence that the presence of such objects limits the availability of nest sites. Future forest management that continues to create areas of dense vertical cover will produce suitable nesting habitat.

IV. RUFFED GROUSE BROOD HABITAT USE IN WESTERN NORTH CAROLINA

INTRODUCTION

Brood habitat and diet during the first weeks of life may be a limiting factor to ruffed grouse populations because mortality is high during this time (Stewart 1956, Berner and Geysel 1969, Haulton 1999, Dobony 2000). For this reason, close proximity of the nest to quality brood habitat is important to chick survival in the first days of life (Bump et al. 1947). Lack of quality brood habitat increases the chances of chick mortality and may negatively impact recruitment into fall populations (Sharp 1963).

Brood habitat must provide cover from predators and inclement weather in addition to forage for chicks and brooding hens. Quality brood habitat has been described for northern ruffed grouse range as containing ample herbaceous ground cover and high stem densities (Bump et al. 1947, Berner and Geysel 1969, Porath and Vohs 1972, Godfrey 1975, Kubisiak 1978, Maxson 1978*a*, Harris 1981, Kimmel and Samuel 1984, Stauffer and Peterson 1985). Haulton (1999) found that herbaceous ground cover was taller and covered more ground at brood locations in Virginia, agreeing with the northern studies, although stem densities were not greater at brood locations.

Herbaceous ground cover supports forage for young grouse chicks in the form of invertebrates. The diet of young grouse chicks consists primarily (> 90%) of invertebrates during the first 3 weeks (Kimmel and Samuel 1984). Invertebrates provide a critical source of protein and calcium essential for chick development and survival (Nestler et al. 1945, Robel et al. 1995). Therefore, invertebrate abundance and biomass are two primary factors determining brood habitat quality (Stuen and Spidsø 1988, Hurst 1992, Peoples et al. 1996) and have been linked to variations in breeding success

(Southwood and Cross 1969). Sites used by hens with broods in Virginia and West Virginia had a greater abundance of arthropods than random locations in the first three weeks after the hatch date (Haulton 1999).

Abundant quality forage within good cover is essential for ruffed grouse chick survival in the first weeks of life (Bergerud 1988). A comparison of brood habitat characteristics and availability may provide insight into mechanisms underlying variations in grouse population densities between regions. Therefore, the objectives of this study were to characterize brood habitat in the mountains of western North Carolina in terms of cover and invertebrate availability.

METHODS

Trapping and monitoring females

Ruffed grouse were trapped using clover-leaf traps during the fall, 1999 and 2000, and spring 2001 (Liscinsky and Bailey 1955, Schumacher 2002). Captured birds were sexed and aged as juvenile (hatch year) or adult (after hatch year) according to Davis (1969), Roussel and Ouellet (1975), and Kalla and Dimmick (1995). Birds were then equipped with mortality-sensitive radio collars (Advanced Telemetry Systems, Inc., Isanti, MN), banded, released, and tracked throughout the year using 3-element yagi antennas and ATS and Telonics receivers (Advanced Telemetry Systems, Inc., Isanti, MN, Telonics Inc., Mesa, AZ). Collared females were located by triangulation (Cochran and Lord 1963) or homing of the radio signal at least 3 times per week during the first weeks of April 2000/2001. When 3 or more consecutive locations were limited to a 0.25-ha area for an individual hen, it was assumed incubation had begun (Maxson 1978a).

Nests were located by homing in on the radio-collared hen and circling the signal, taking a compass bearing, and flagging at ~20 m. The same area was visited the next day and if the hen was in the same location, an attempt was made to visually locate the nest. Anticipated hatch date was calculated by adding 24 days to the date the hen was first found in that area (Bump et al. 1947). Nesting hens were monitored daily using triangulation and variability of the radio signal to determine hatch date.

Monitoring weather conditions

Daily high and low temperatures and mean precipitation were recorded by the Coweeta Hydrologic Laboratory (Coweeta LTER, Otto, NC) using a permanent weather station on the study area.

Brood habitat sampling

Hens with broods were located 1 to 6 times per week at various times of day using either triangulation or homing in on the brood. When hens were located by homing to within 20 – 50 m using the strength of the radio signal, a compass bearing and estimated distance to the brood was recorded, and the area was flagged. To confirm that homing locations and estimated distances were accurate, radio-collared males were located in a similar way and then flushed to verify the distance estimate. Between 1 to 7 days after the hen and brood left the area, the location was re-visited and georeferenced using GPS units (Trimble Navigation Limited Inc., Sunnyvale, CA) and habitat data were gathered.

Hens were flushed periodically to determine whether chicks remained with the hen. In 2000, hens were flushed every 5 days because of concerns that chicks had died. In 2001, hens were only flushed at 21 and 35 days. Some hens ran along the ground to lead the investigator away from the chicks. The investigator would then sit quietly where

the hen began to run and listen for chick or hen calls. Generally chicks began to call within 5 to 30 minutes and the hen would return to the area. Chicks were assumed to remain with the hen if “broody” behavior was observed, even if no chicks were seen or heard. If the hen flushed from > 20 m or ran and did not return to the area within 50 minutes, it was assumed that no chicks remained with her. Subsequent flushes were conducted 3 days later to verify a loss of brood.

Micro-habitat data were collected within nested circular plots with the brood location at plot center (Harper 1998). A paired, randomly selected site was also sampled to compare used versus available micro-habitat. The random location was chosen from the hen’s home range using the numbers-from-a-hat method to determine direction and a distance between 50 – 400 m (164 – 1,312 ft) from the brood location and at a paired, randomly-selected site. Slope and aspect were measured from plot center. A 2.5 m²/ha basal area prism was used from plot center to determine basal area. Species and counts of all trees determined to be “in” using the basal area prism were recorded. Snags (dead, standing trees) were recorded separately. Species and counts of woody mid-story (sapling) stems < 11.4 cm (< 4.5 in) dbh and > 1.4 m (> 4.6 ft) tall were taken within a 5.7 m (18.7 ft) radius plot. Stems were classified into < 2.54 cm (< 1 in) dbh, 2.54-5.08 cm (1-2 in) dbh, 5.08-7.62 cm (2-3 in) dbh, and > 7.62 cm (> 3 in) dbh diameter classes to determine small woody stem density within the plot (Noon 1981). Counts and species of woody under-story (seedling) stems < 1.4 m (< 4.6 ft) tall were recorded in 3.6 m (11.8 ft) plots and categorized as deciduous or evergreen. Percent herbaceous cover was determined from three transects (0°, 120°, and 240°) within the 3.6 m (11.8 ft) radius plots. Percent of the ground covered by non-woody under-story vegetation < 1.4 m (<

4.6 ft) tall was classified as forb, fern, grass, briar, or blackberry (*Rubus* spp.). Vertical density was measured as percent area covered in each 0.2 m (8 in) section of a 2-m (6.6-ft) tall density board and was recorded 15 m (49 ft) from plot center on uphill and downhill slope positions.

Broader-scale (macro-habitat) parameters were determined using GIS coverages obtained through the U.S. Forest Service (USFS) and the Southern Appalachian Assessment (SAA). GIS coverages included roads, streams, openings, forest type, stand age, and management type. Brood locations collected by homing and triangulation (only locations with an error ellipse of < 2 ha were included) were compared with random locations created using a random points generator extension in ArcView. Random points were created within an effective study area created using a 1-km radius buffer around all brood locations.

In all, data on 32 variables were collected: SLOPE, ASPECT, DROAD, DSTR, DOPEN, DCUT, BA, OSP, PCTDEC, MIDA, MIDB, MIDC, MIDD, MIDT, MIDSP, USTEM, USP, AVFO, AVFRN, AVGR, AVBRAM, AVGCVR, VCVRA, VCVRB, VCVRC, VCVRD, VCVRE, VCVRM, FCVR, AGECLS, COND, and FMGT (Table 13, 14). All mid-story stem density and vertical cover density measurements were highly correlated ($r > 0.7$) so that only the total mid-story stem density and mean vertical cover density were used in further analysis.

Invertebrate sampling

Invertebrate samples were collected using a terrestrial vacuum sampler (Harper and Guynn 1998) and 0.10-m² frame box with lid for the first 6 weeks of brood locations (King 1969, Kimmel and Samuel 1978) or as long as the brood was believed to contain at

least one chick. This method allowed invertebrates flying, clinging to vegetation, and those in the top layer of leaf litter to be collected simultaneously, providing a representation of all invertebrates present. Care was taken not to sample beneath the top layer of leaf litter because grouse chicks tend to glean from vegetation, rarely flipping leaves or scratching for invertebrates (Bump et al. 1947, Kimmel and Samuel 1978). Five samples were collected from the perimeter of a 15-m radius circle around brood locations and paired, randomly-selected sites.

Samples were preserved in different ways in 2000 and 2001 because of differences in drying oven availability. In 2000, sample-bags with invertebrate samples were oven-dried for 48 hours at 60°C (Murkin et al. 1996) and stored for later processing. Sample bags from 2001 were frozen until sorting could take place, because drying ovens were no longer available. In fall 2001, samples were placed into white trays under bright lighting where invertebrates were separated and picked from debris using sieves and forceps. Arthropods were identified to class or order according to Borror et al. (1989). Invertebrates were then placed in a vial, dried (2001 samples), and weighed. All sorting and weighing was conducted by four observers during fall 2001.

Data Analysis

Weather data were collected for May, June, and July, 2000/2001. Daily and monthly means for minimum, maximum, average daily temperature, and precipitation were compared between years using 2-sample t-tests.

Separate logistic regression models were run to determine brood habitat selection on the macro- and micro-habitat scales (PROC LOGISTIC, SAS 2000). A set of potentially biologically important variables (SLOPE, ASPECT, BA, MIDT, AVGCVR,

VCVRM, AGECLS, DROAD, DOPEN, DSTR, DCUT) was selected for use in the micro-habitat model. Only brood locations obtained by homing were used in micro-habitat analysis. Locations were classified as hatch – 3 weeks post-hatch (early period) and 4 – 10 weeks post-hatch (late period). The macro-habitat model included locations obtained by telemetry and homing. The frequency of brood and random locations in each sub-group of the variables FCVR, AGECLS, COND, and FMGT were used in the macro-habitat model (Table 14). Logistic regression was used to check for differences between years and time-periods and differences between vegetative and topographic characteristics during each year and time-period.

Both macro- and micro-habitat models used logistic regression with stepwise selection ($\text{slstay} = 0.05$) to determine variable entry and retention. Model performance was evaluated based on the Hosmer – Lemeshow goodness of fit statistic, a maximum – rescaled R^2 value, and percent correct classification rates (Hosmer and Lemeshow 1989).

Mean euclidean distance to the nest site was calculated weekly for homing locations in 2000 and 2001. Weekly distances were compared between years using 2-sample t-tests.

Ruffed grouse chicks are known to prefer several invertebrate orders: Coleoptera (beetles and larva), Diptera (flies, mosquitoes), Hymenoptera (ants), Homoptera (leafhoppers, aphids), and Arachnida (spiders, Bump et al. 1947, Stewart 1956, King 1969, Kimmel and Samuel 1984). Therefore, invertebrate data were separated into 3 levels of classification to compare prey availability. Data were pooled to obtain total invertebrate density and biomass, classified by preferred invertebrate order, and classified as “preferred” (preferred orders pooled) and “other” (other orders pooled). The

UNIVARIATE procedure was used to evaluate normality of invertebrate data and equality of variance was checked (SAS 2000). Log transformations were performed on all invertebrate data to obtain normality. Homoptera data were too severely skewed to be transformed, and were only analyzed as part of pooled data. Invertebrate data at brood and random locations were compared between years and time-periods using a mixed model with observer as a random effect (PROC MIXED, SAS 2000).

Invertebrate samples were preserved by drying in 2000 and freezing in 2001. There was concern that a false year effect would be detected in the data because of differences in preservation method. A test was conducted to determine whether the method of preservation changed the detectability of invertebrates or certain invertebrate orders (e.g., were Lepidoptera larva missed once the sample had been dried). Ten frozen debris samples were sorted and all invertebrates were counted, classified, and placed back into the debris as sorting took place (i.e. not removed and placed back all at once). The samples were then dried and re-sorted. Results from each sample were compared using paired t-tests.

RESULTS

Weather conditions

May 2001 was cooler than in 2000 ($P = 0.0089$), but June and July temperatures did not differ (Table 15). Average precipitation did not differ between years (Table 15). Weather during the first 3 weeks post-hatch did not differ between years (Table 15).

Brood habitat

Hen flushes at 3 and 5 weeks post hatch revealed that no chicks survived past 4 weeks post-hatch in 2000 while all hens in 2001 had at least one chick past 70 days

(Tabke 16). Consequently, fewer brood locations were collected in 2000 than 2001 (Table 17). In 2000, 5 hens with broods produced 21 brood habitat locations representing the early period (Table 17). Hens 134 and 1971 were killed at 6 and 7 days post-hatch, respectively. Hen 813 was off site and yielded just 2 locations. Flushes at 15 and 29 days revealed that no chicks remained with her. Hen 734 acted broody at 14 days, but did not have chicks at 20 or 32 days. Hen 244 had chicks through 21 days, but subsequent flushes provided no evidence of chicks. In 2001, 9 hens with broods produced 95 brood locations representing the first 10 weeks post-hatch (Table 17).

Vegetative, topographic, and invertebrate data were collected at 115 pairs of brood and random locations. Brood habitat differed between years for the early period (Table 18, 19) and between time-periods in 2001 (Table 20, 21). Year 2000 data for the late period did not exist and therefore only data from the early period in 2001 was used in the between-year analysis. Likewise, 2000 data were not included in analyses for time-period differences. Brood locations in 2000 had less ground cover ($P < 0.0001$) and were closer to streams ($P = 0.0203$), forest openings ($P < 0.0001$), and cut edges ($P = 0.0478$) than in 2001 (Table 18, 19). In 2001, brood locations in the early period had greater basal area ($P = 0.0439$) and less dense vertical cover ($P = 0.0063$) than during the late period (Table 20, 21).

Separate logistic regression models were run on brood and random data for the 2000 season, 2001 early period, and 2001 late period to further explore brood micro-habitat selection. The 2000 brood micro-habitat model ($R^2 = 0.32$, $\chi^2 = 5.44$, $P = 0.7101$) retained 2 variables: AVGCVR ($\beta = -0.0378$, SE = 0.02), and DSTR ($\beta = -0.007$, SE =

0.003, Table 22, 23). Brood locations had less herbaceous ground cover ($P = 0.0319$) and were closer to streams ($P = 0.0300$) than random locations (Table 22, 23).

The 2001 early period brood micro-habitat model ($R^2 = 0.34$, $\chi^2 = 14.86$, $P = 0.0620$) retained 3 variables: AVGCVR ($\beta = 0.0421$, SE = 0.010), ASPECT ($\beta_{\text{East}} = 0.790$, SE = 0.378; $\beta_{\text{North}} = -0.432$, SE = 0.391; $\beta_{\text{South}} = 1.1795$, SE = 0.481), and DSTR ($\beta = -0.005$, SE = 0.002, Table 24, 25). Brood locations had more herbaceous cover ($P < 0.0001$), were more frequently on eastern slopes ($P = 0.0367$), less frequently on northern slopes ($P = 0.0002$), and closer to streams ($P = 0.0071$) than random locations (Table 24, 25).

The 2001 late period brood micro-habitat model ($R^2 = 0.48$, $\chi^2 = 6.34$, $P = 0.6091$) retained 3 variables: BA ($\beta = -0.085$, SE = 0.042), AVGCVR ($\beta = 0.037$, SE = 0.013), and VCVRM ($\beta = 0.026$, SE = 0.012, Table 26, 27). Brood locations had lower basal area ($P = 0.0444$), more herbaceous ground cover ($P = 0.0037$), and greater percent vertical cover ($P = 0.0275$) than random locations (Table 26, 27).

The macro-habitat model ($R^2 = 0.26$, $\chi^2 = 0.00$, $P = 1.0$) retained 2 variables: AGECLS 6 – 15 years ($\beta = -1.302$, SE = 0.178), and AGECLS 16 – 30 years ($\beta = -0.743$, SE = 0.204, Table 28). More brood locations were in young (6 – 30 year-old) stands than were randomly available (Table 28). Other variables measured did not differ between brood and random locations ($P > 0.05$, Table 29).

Weekly distance from nest locations did not differ between years ($P > 0.05$). Locations increased in distance with time for both years (Figures 4 - 17).

Invertebrate availability

One thousand one hundred fifty 0.10-m² samples were collected from 230 paired brood and random locations. A total of 932 samples were sorted and weighed, representing 4 samples per brood or random location. Invertebrates were collected from class Gastropoda (subclass Pulmonata) and 15 orders from 6 classes in Phylum Arthropoda: classes Arachnida (orders Acari, Araneae, Opiliones, and Pseudoscorpiones); Chilopoda; Diplopoda; Hexapoda (orders Coleoptera, Collembola, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Mecoptera, Orthoptera, and Psocoptera); and Malacostraca (order Isopoda).

The 10 samples tested for preservation effects showed no significant differences between dried and frozen treatments ($P = 0.1580$, Table 30). Therefore, it was assumed that year effects were not due to preservation method.

Invertebrate density was lower at brood and random locations in 2000 than in 2001 ($P < 0.0001$, Table 31). Invertebrate biomass was lower in 2000 at random locations ($P = 0.0088$), but brood locations did not differ in biomass between years (Table 32). In 2001, invertebrate density was significantly greater at the random locations in the late period ($P = 0.0005$), but brood locations did not show a significant time-period change in overall density (Table 33). However, both brood and random locations had greater invertebrate biomass in the late period ($P < 0.02$, Table 34). Brooding hens were, therefore, selecting areas with larger, although not more, invertebrates later in the brooding season.

Total invertebrate density was greater at brood locations than random during both years and the early period in 2001 (Table 31, 33). The late period did not differ in overall

invertebrate density, but density of preferred invertebrate orders was greater at brood locations than at random locations (Table 33). Preferred order density was greater at brood locations in 2000, 2001, and both the early and late periods (Table 31, 33). In 2000, Coleoptera and Hymenoptera densities were greater at brood locations, but in 2001 only Diptera density was greater (Table 31). Diptera density was greater at brood locations during the early period in 2001. Hymenoptera and Hemiptera densities were marginally greater at brood locations in the late period (Table 33). Other orders showed greater densities in 2000, 2001, and the early period in 2001 (Table 31, 33).

Total invertebrate biomass was greater at brood than random locations in 2000, but did not differ in 2001 or during the early or late periods (Table 32, 34). Biomass of all preferred orders pooled did not differ in 2000, but was greater at brood locations in 2001 overall, and during the early and late periods (Table 32, 34). Coleoptera and Hymenoptera biomass was greater at brood locations in 2000 while Diptera and Araneae biomass was greater at brood locations in 2001 overall and in the early and late periods respectively (Table 32, 34). Biomass of all other orders pooled was greater at brood locations in 2000, and during the late period in 2001 (Table 32, 34).

DISCUSSION

Brood habitat selection

Brood habitat is often associated with the dense vertical cover and high mid-story stem densities from aspen clear-cuts and alder thickets (Godfrey 1975, Gullion 1977a, Kubisiak 1978). Broods used aspen stands with 19,000 – 25,000 stems/ha in Minnesota (Gullion 1977b) and stands with up to 33,000 stems/ha in Wisconsin (Kubisiak 1978). However, broods south of the range of aspen use areas that are relatively more open

(Hein 1970, Harris 1981, Thompson et al. 1987, Haulton 1999). In this study, measured stem densities ranged from 4,500 to 9,100 stems/ha, although the mid-story stem densities of over 24,000 stems/ha are available on the WSCA (Table 35, Harper 1998). In Missouri, Thompson et al. (1987) found broods in areas with greater stem density than random, but densities averaged about 5,800 stems/ha; Haulton (1999) found broods in areas with lower stem densities than were randomly available, and suggested that the scale at which habitat measurements were taken may influence results.

Broods selected stands 6 to 30-years-old and with lower mid-story stem densities in 2001 than in 2000, suggesting that successful young broods were using areas that were relatively open within moderately dense stands, similar to the findings of Haulton (1999). However, mid-story stem density was not an important characteristic for habitat selection in either year. Broods did select areas with dense % vertical cover during late period in 2001. Available areas averaged 42% vertical cover, while broods selected areas with over 70% cover after 3 weeks post-hatch. The shift to areas with dense vertical cover may reflect the chicks' diet shift from invertebrates to vegetation. In addition, dense vertical cover may increase in importance as chicks age and become more mobile and visible to predators. Dense vegetation would provide protection from avian and mammalian predators (Gullion 1972).

Brooding hens in 2001 selected areas with greater herbaceous ground cover than random in both the early and late time-periods, agreeing with previous findings that herbaceous ground cover is an important characteristic of brood habitat (Bump et al. 1947, Sharp 1963, Berner and Geysel 1969, Porath and Vohs 1972, Godfrey 1975, Kubisiak 1978, Harris 1981, Stauffer and Peterson 1985, Thompson et al. 1987, Scott et

al. 1998, Haulton 1999). Moderately dense fern cover in open forest provided brood habitat in Wisconsin (Maxson 1978a); Scott et al. (1998) found broods in areas with greater % cover of live ground vegetation in central Pennsylvania; and Kimmel and Samuel (1984) found that herbaceous growth provided brood forage and cover in West Virginia. Herbaceous cover has also been shown to provide protection and food for wild turkey poult (*Meleagris gallopavo*) in forested areas and in clearings (Healy and Nenno 1983, Healy 1985, Harper et al. 2001).

Not all ground cover provides the same quality of habitat. The type, density, and structure of ground vegetation changes the quality of habitat for chicks. Healy (1985) found that wild turkey poult found adequate amounts of insect foods in forested and open areas where at least 50% of the ground cover consisted of forbs and ferns and where total ground coverage was between 60% and 100%. Successful broods in this study selected areas with high fern and forb cover, which provided overhead protection while allowing free movement along the ground and an ample supply of invertebrate food items (Healy 1985).

Vegetation in some wildlife openings (e.g. those planted in orchardgrass) provide extremely dense ground cover, but the thatch produced at ground level is too dense for young chicks to travel through and effectively forage (Nenno and Lindzey 1979, Healy 1985). In this study, only 4 of 115 brood locations were on the edge of wildlife openings. No broods were located further than 10 m from the inside edge of wildlife openings dominated by orchardgrass. This may imply either that areas with orchardgrass are avoided by grouse broods or, more likely, reflects a tendency for ruffed grouse to avoid large open areas.

Broods were statistically closer to streams than random locations during the early period, although mean distance to a stream was > 300 m. This result may be more reflective of grouse selecting for mid-slope topographic positions than actually showing an affinity for riparian habitat. Other studies, however, have revealed an affinity for moist areas. Stewart (1956) found broods in lowland areas along streams during the first weeks post-hatch in Virginia; Godfrey (1975) found the majority of brood locations in lowland sites with moist soils in Minnesota; and Thompson et al. (1987) found broods at lower slope positions, where soils are typically more mesic. Site quality and soil moisture influence vegetative cover and invertebrate biomass (Whittaker 1952), thus enhancing brood habitat. However, riparian zones in the mountains of North Carolina typically have rhododendron under-stories, which shades out the herbaceous cover broods are typically seeking.

Broods selected east-facing slopes in the early period 2001, presumably because there was greater herbaceous ground cover on those aspects. Soils tend to be more moist on north and east-facing slopes, producing greater amounts of organic matter in soils, and thus having greater productivity (Hicks 1998). East- and north-facing slopes also produce greater % herbaceous cover (Harper et al. 2001). North-facing slopes, however, were avoided by broods in the early period, possibly because green-up was retarded on those aspects. No attempt was made during this study to sample all slope aspects in order to compare the amount of herbaceous cover, however, and no final conclusions can be drawn.

Brood locations radiated away from the nest site with time, suggesting that brood habitat availability near nest sites may have been inadequate. Brood movements over

relatively long distances often were associated with linear corridors (i.e., logging roads or trails). Broods in Virginia were often found along secondary roads and trails (Stewart 1956). In Minnesota, Godfrey (1975) noted that when patches of good brood habitat were spaced far apart, brood home ranges expanded as broods traveled through less desirable habitat to occupy the preferred type. Maxson (1978a) also found that hens with broods used larger areas than hens without broods in Minnesota and attributed the increase to the increase in chick mobility and increasing food requirements. Continued brood movements over time may also help prevent predators from concentrating in the area.

The availability and distribution of quality brood habitat is an important factor influencing ruffed grouse populations (Bump et al. 1947). Habitat availability during the first 3 weeks post-hatch, which occurs during the last weeks of May in western North Carolina, is especially important since chick survival is lowest during that time (Rusch et al. 2000). In particular, close proximity of the nest to quality brood habitat may improve chick survival by reducing the need for the brood to travel through less desirable habitat to occupy a more suitable area. Linear wildlife openings (i.e. converted 2-track logging roads with thick cover along the edges) will provide an excellent source of invertebrates and a corridor from poor to higher quality habitat when seeded with clover and annual grasses.

Two years of data yielded two very different data sets representing brood micro-habitat. No chicks survived past 4 weeks in 2000, while all broods contained at least 1 chick through 10 weeks post-hatch in 2001. Similarly, researchers in the Appalachian Cooperative Grouse Research Project recorded poor chick survival in 2000 (Tom Allen,

personal communication). Brood habitat data in 2000 may have been biased toward habitat selection of one hen, since hen 244's locations made up about half of the data set. Further, locations were skewed toward the first week post-hatch in 2000. A between-year comparison of habitat use during the first 3 weeks post-hatch showed that unsuccessful broods (i.e., those in 2000) used areas with less herbaceous ground cover and fewer invertebrates than successful broods. Because of the distribution of data towards the first week post-hatch in 2000, this difference may reflect the fact that herbaceous vegetation had not yet fully emerged. This especially makes sense when considering that hatch occurred nearly a week earlier in 2000 than in 2001.

The difference in habitat selection coupled with poor survival in 2000 may suggest that chick survival is at least partially influenced by the amount of herbaceous ground cover. However, the limited sample size and possible biases in the data may be partially responsible for the differences observed between years, and such a conclusion would be premature at this time. Future research into the causes of chick mortality and habitat differences between successful and unsuccessful broods may provide valuable insight into what influences chick survival and therefore recruitment into fall populations.

Invertebrate availability

Invertebrates are a critical component in the diet of young upland game birds (Handley 1931, Nestler 1940, Barwick et al. 1973, Nenno and Lindzey 1979), providing protein and calcium essential for chick development and survival (Nestler et al. 1945). Brooding hens selected areas with greater invertebrate density through the third week post-hatch, when high levels of protein for rapid growth is critical (Nestler et al. 1945, Southwood and Cross 1969, Nenno and Lindzey 1979, Robel et al. 1995). In addition,

broods were found in areas with greater densities of preferred invertebrate orders through the sixth week post-hatch, when the diet consists mainly of animal matter (Bump et al. 1947, Stewart 1956, King 1969, Kimmel and Samuel 1978, 1984).

Invertebrate biomass increased from the early and late time-periods, while invertebrate density did not change. Kimmel and Samuel (1978) noted that the diet of ruffed grouse chicks includes larger invertebrates and a greater amount of plant material as the chicks age. The diet shift from invertebrates to plant material generally begins after the 3rd week post-hatch until the diet becomes dominated by plant material after the 6th week (King 1969, Kimmel and Samuel 1978). King (1969) found that invertebrates formed the majority of chick diets until 6 – 8 weeks; Kimmel and Samuel (1978) report that invertebrates dominate the diet until the 6th week in West Virginia; Haulton (1999) hypothesized that the shift in diet occurred after week 6 and was evidenced by possible use of areas with greater sapling stem densities, although the latter could not be confirmed from his data. In this study, broods were found in areas with lower basal area, more stems per acre, more dense vertical cover, and were closer to the edge of a cut during the late period than expected, suggesting a shift in habitat and presumably diet occurred. Not enough data were collected between the 4th and 10th week, however, to detect a weekly shift in diet.

Invertebrate availability for young chicks varies with weather conditions (Taylor 1963, Murkin et al. 1996) and ground cover structure and density (Healy 1985, Metzler and Speake 1985, Hollifield and Dimmick 1995, Harper et al. 2001). Cooler and wetter conditions tend to decrease invertebrate availability (Murkin et al. 1996), while increased herbaceous ground cover, particularly forbs, increases invertebrate abundance (Healy

1985, Hollifield and Dimmick 1995, Harper et al. 2001). Hollifield and Dimmick (1995) found that arthropod abundance was greater in mature hardwoods with abundant herbaceous ground cover than forests devoid of ground cover. Healy (1985) and Harper et al. (2001) found that areas with a mixed forb and fern ground cover provided high quality wild turkey (*Meleagris gallopavo*) brood habitat, providing chicks with relatively open ground for easy movement, high invertebrate availability for food, and dense overhead cover for protection from predators and inclement weather.

Weather conditions were cooler in 2001 immediately after hatch, but invertebrate density at brood locations was greater during that time. This supports the hypothesis that habitat differences, particularly ground cover, had more of an impact on prey availability between years than weather. Dense herbaceous ground cover with an open under-story to allow free movement provides grouse chicks with the cover and invertebrates that are crucial to chick survival during the first weeks. Forest management that encourages the growth of herbaceous ground cover will help provide brood habitat that is crucial for viable grouse populations.

Management implications

The availability and distribution of quality brood habitat appears to be an important factor influencing ruffed grouse populations. Habitat availability during the first 3 weeks post-hatch, which occurs during the last weeks of May in western North Carolina, is especially important since chick survival is lowest during that time (Rusch et al. 2000). In particular, close proximity of the nest to quality brood habitat may improve chick survival by reducing the need for the brood to travel through less desirable habitat to occupy a more suitable area.

Presently, ruffed grouse brood range on the WSCA is characterized by an abundance of herbaceous ground cover and relatively dense vertical cover in 6 to 30-year-old forested stands regenerated using an even-aged method of regeneration. The most important component of quality brood habitat is the abundance of herbaceous ground cover. Ideally, the ground should be covered by herbaceous material consisting of forb or weedy plant species. This composition will produce invertebrates for food, allow the chicks to move and forage efficiently, and provide protective overhead cover.

Forest management strategies should be concentrated in oak-hickory and northern hardwood stands because over 90% of all brood locations were in those two forest types. Forest regeneration cuts should be separated in time and space, so that a mosaic of forest age-classes is present at any given time across the landscape. In areas managed for sawtimber (60 – 80 year rotations), approximately 35% of forest stands should be in the 6 – 30-year-old age-class at any given time. Currently, approximately 12% of the WSCA is in this age-class.

Timber stand improvement for ruffed grouse broods may include prescribed fire and forest thinnings to allow sunlight to reach the forest floor and encourage herbaceous growth. Management practices for wild turkey broods may also benefit grouse and include roundwood and firewood thinnings and storm salvage cuts (Harper 1998). Recommendations from Luckett (1980) which include retention of soft mast producing species and at least 50% of mast-bearing hardwoods should be followed. Such measures may increase brood habitat quality in the late-period when the diet shifts to plant material.

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APPENDICES

APPENDIX A

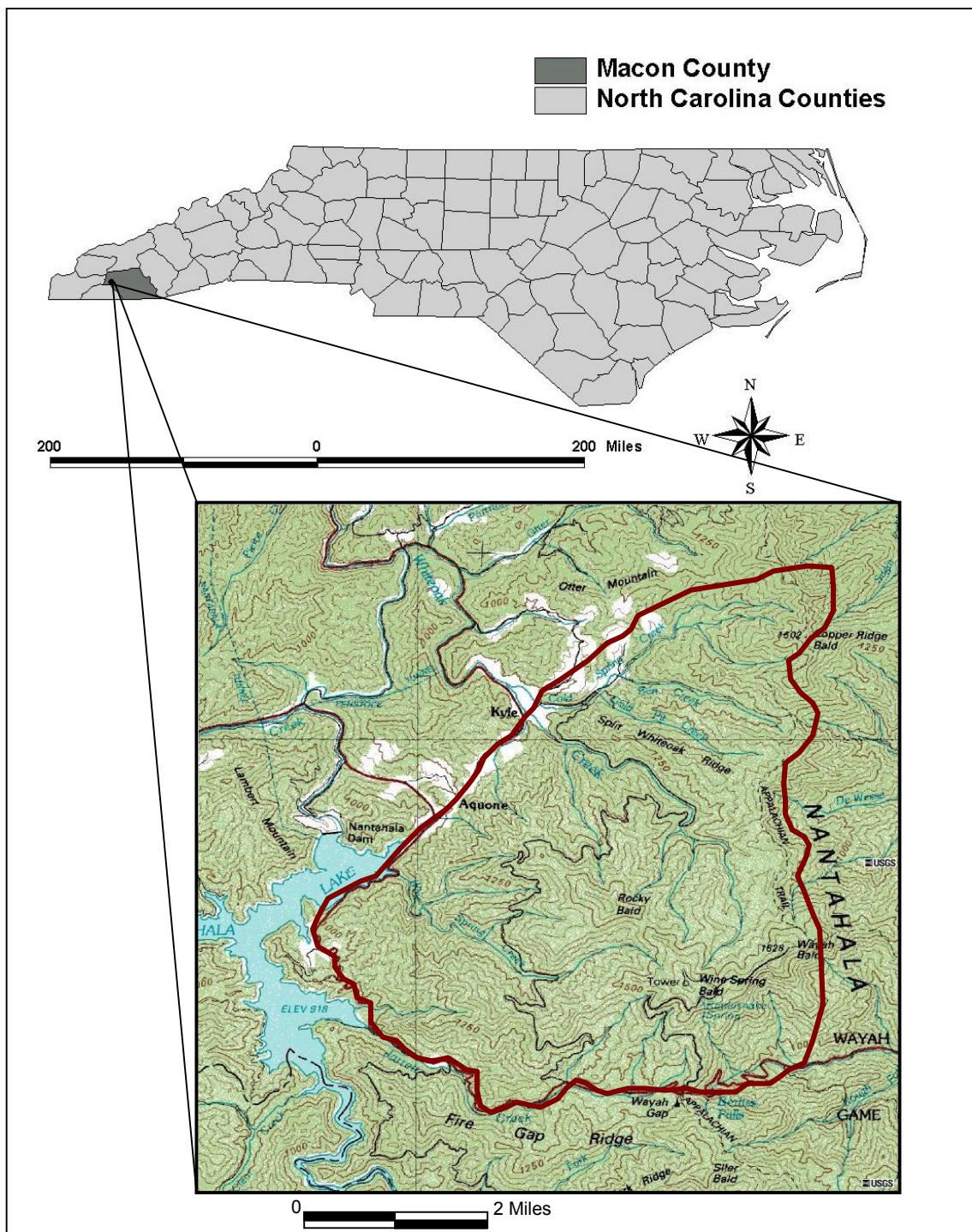


Figure 1. Location of the Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina.

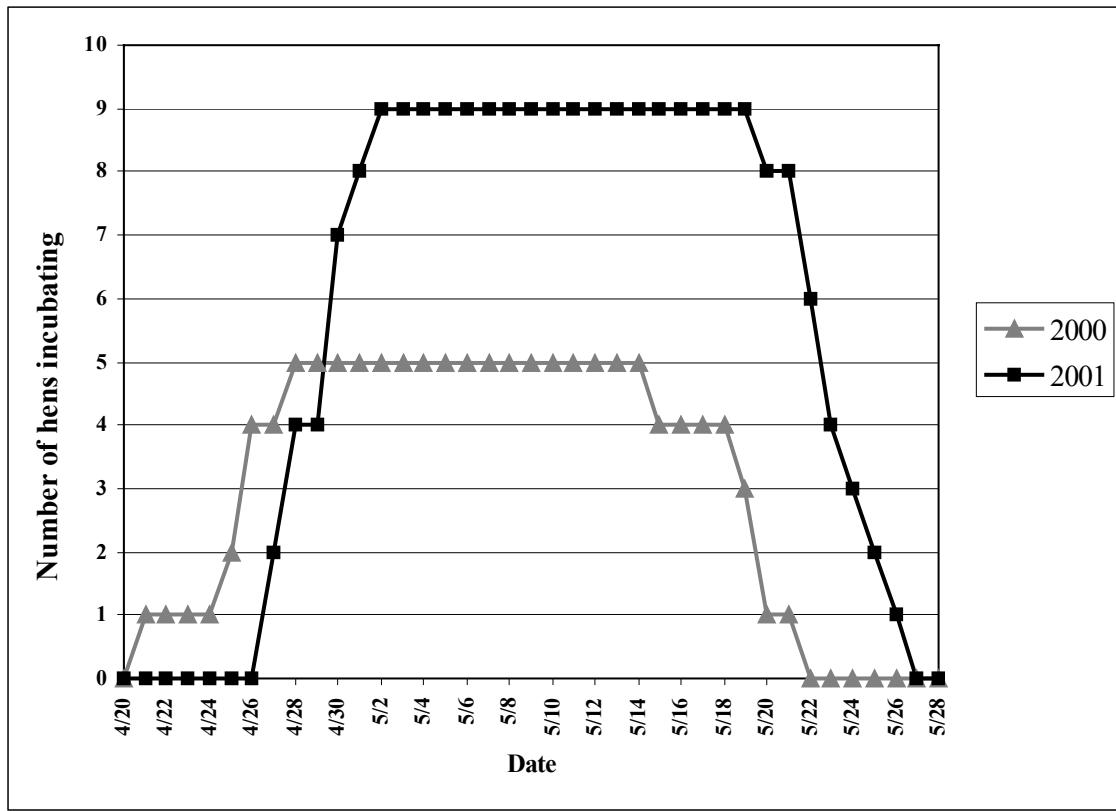


Figure 2. Chronology of ruffed grouse nest incubation on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 – 2001.

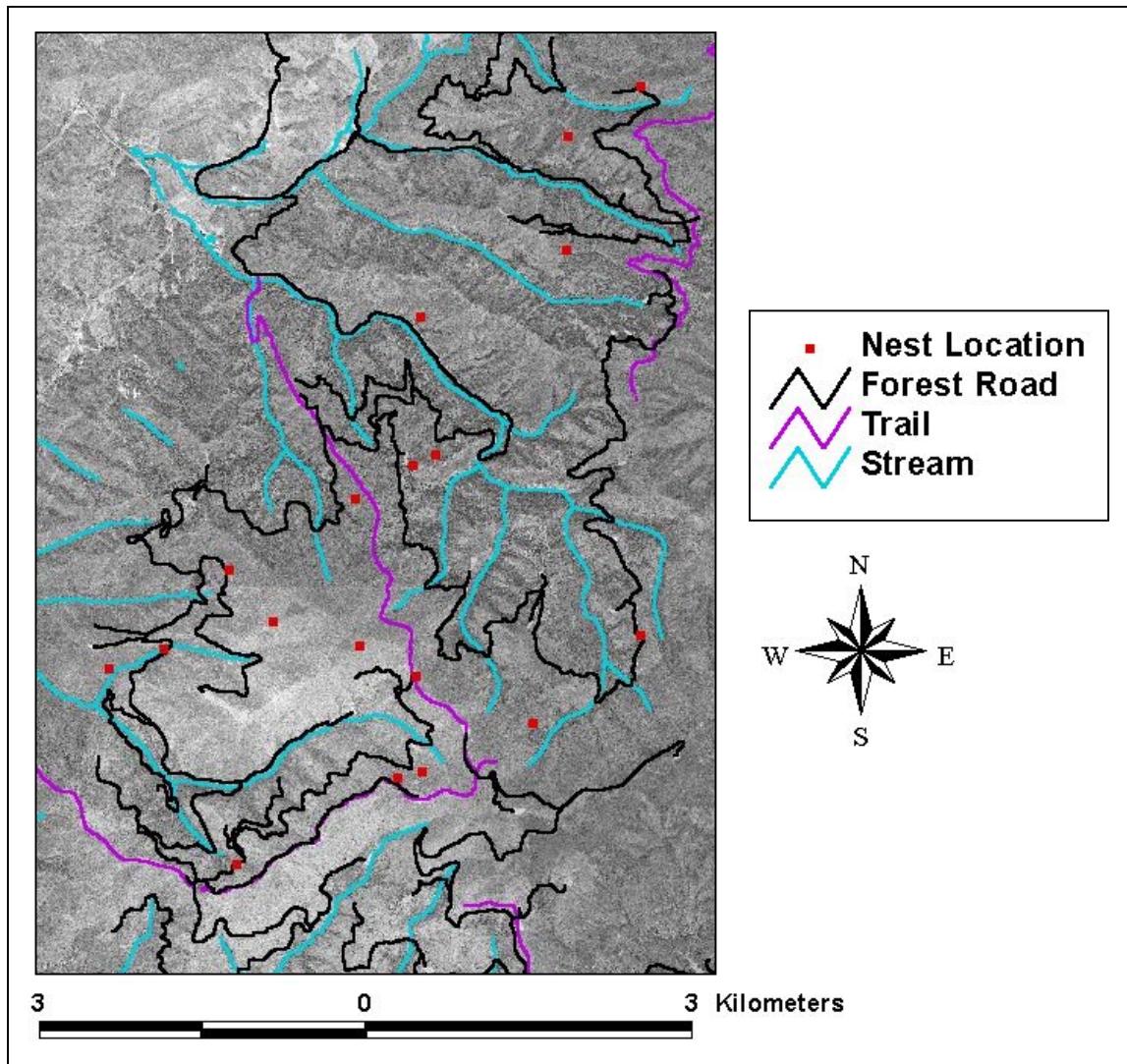


Figure 3. Ruffed grouse nest locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 – 2001.

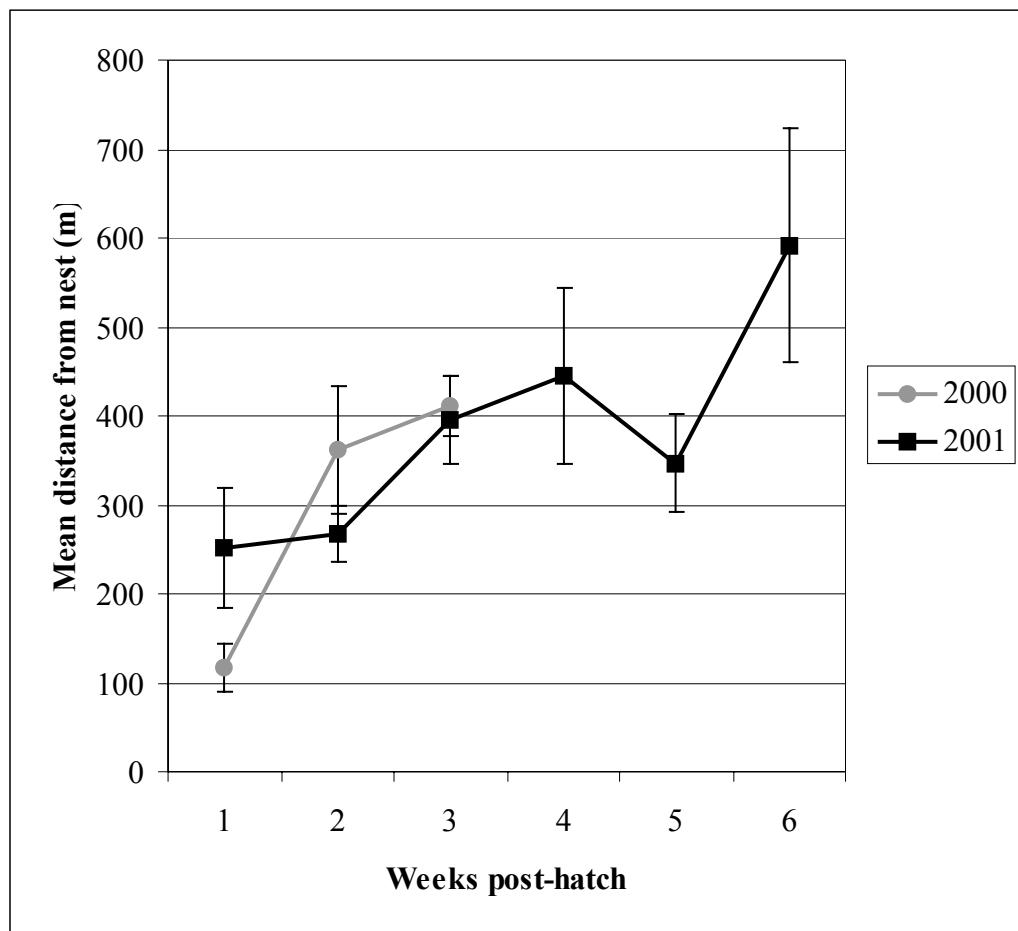


Figure 4. Ruffed grouse brood mean distance from nest by week on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

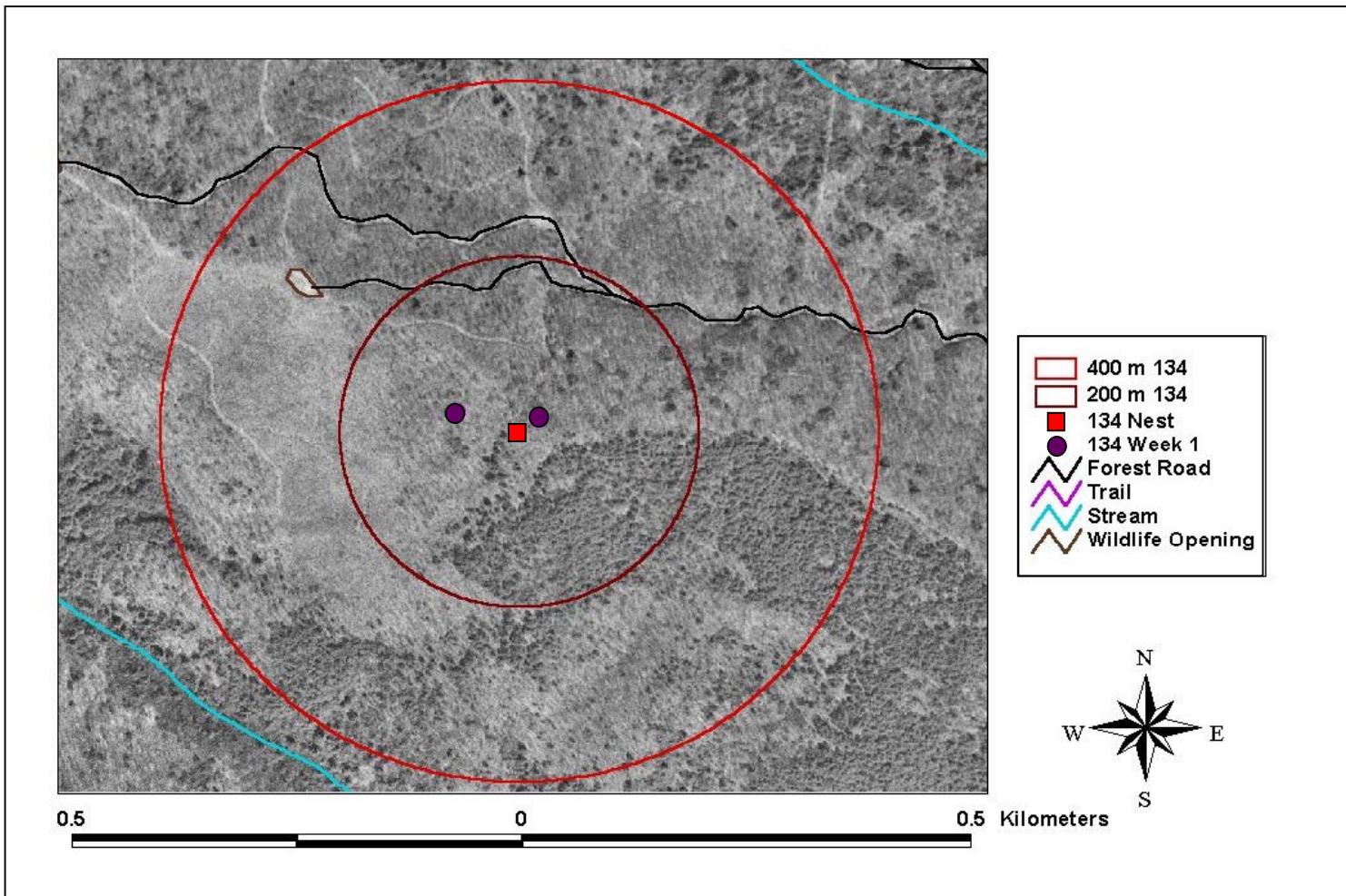


Figure 5. Ruffed grouse brood micro-habitat locations for brooding hen 134 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000.

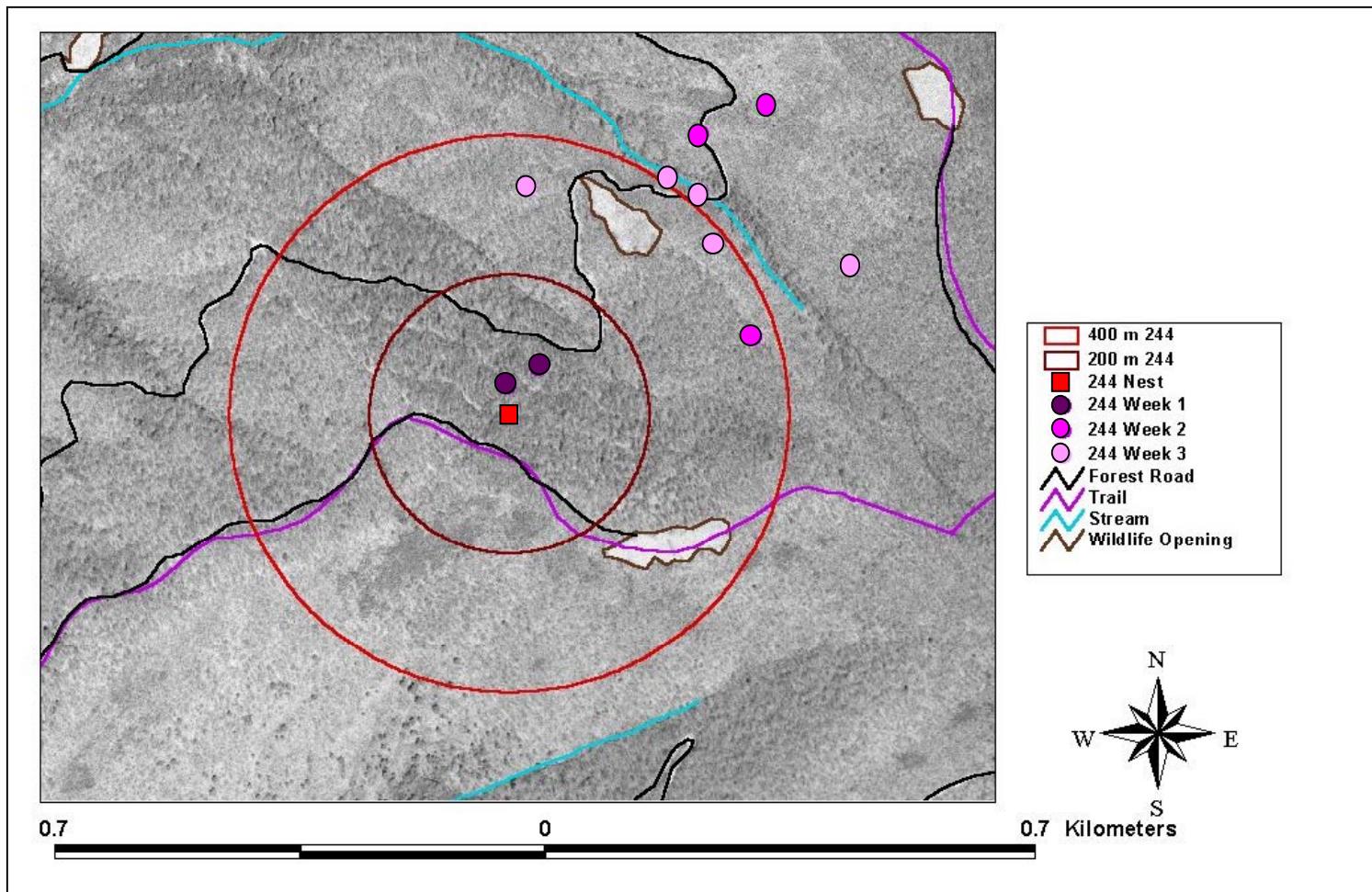


Figure 6. Ruffed grouse brood micro-habitat locations for brooding hen 244 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000.

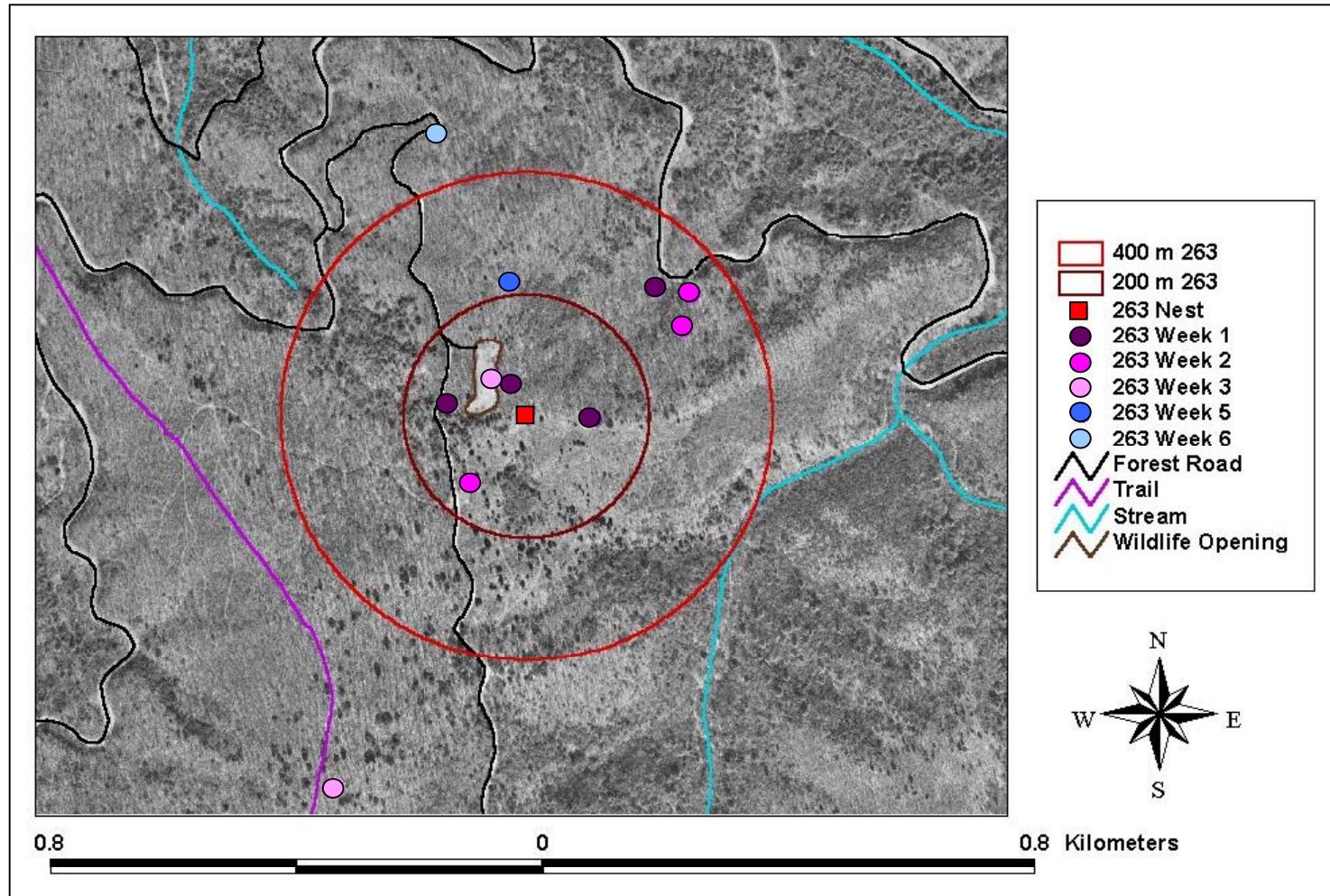


Figure 7. Ruffed grouse brood micro-habitat locations for brooding hen 263 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

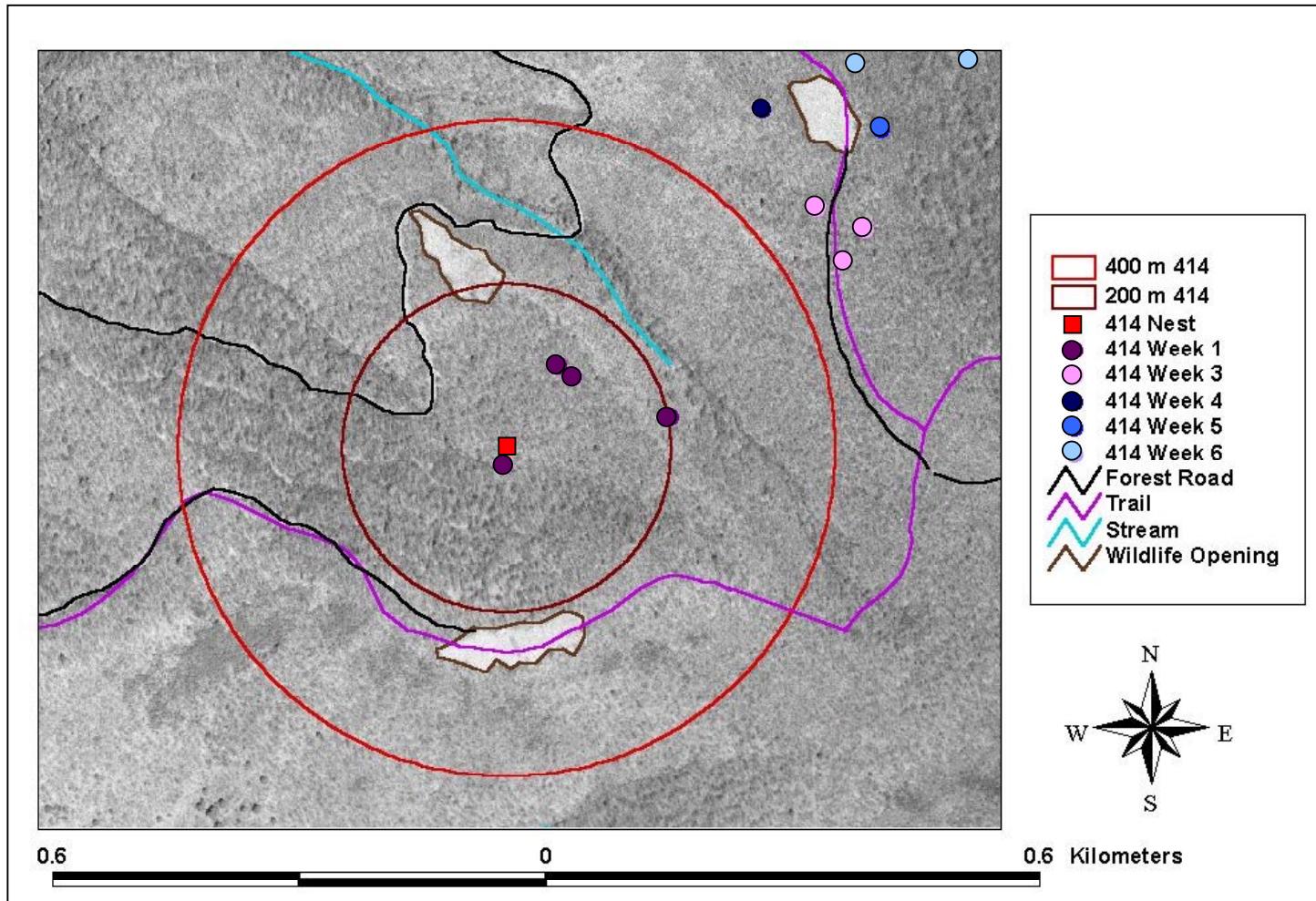


Figure 8. Ruffed grouse brood micro-habitat locations for brooding hen 414 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

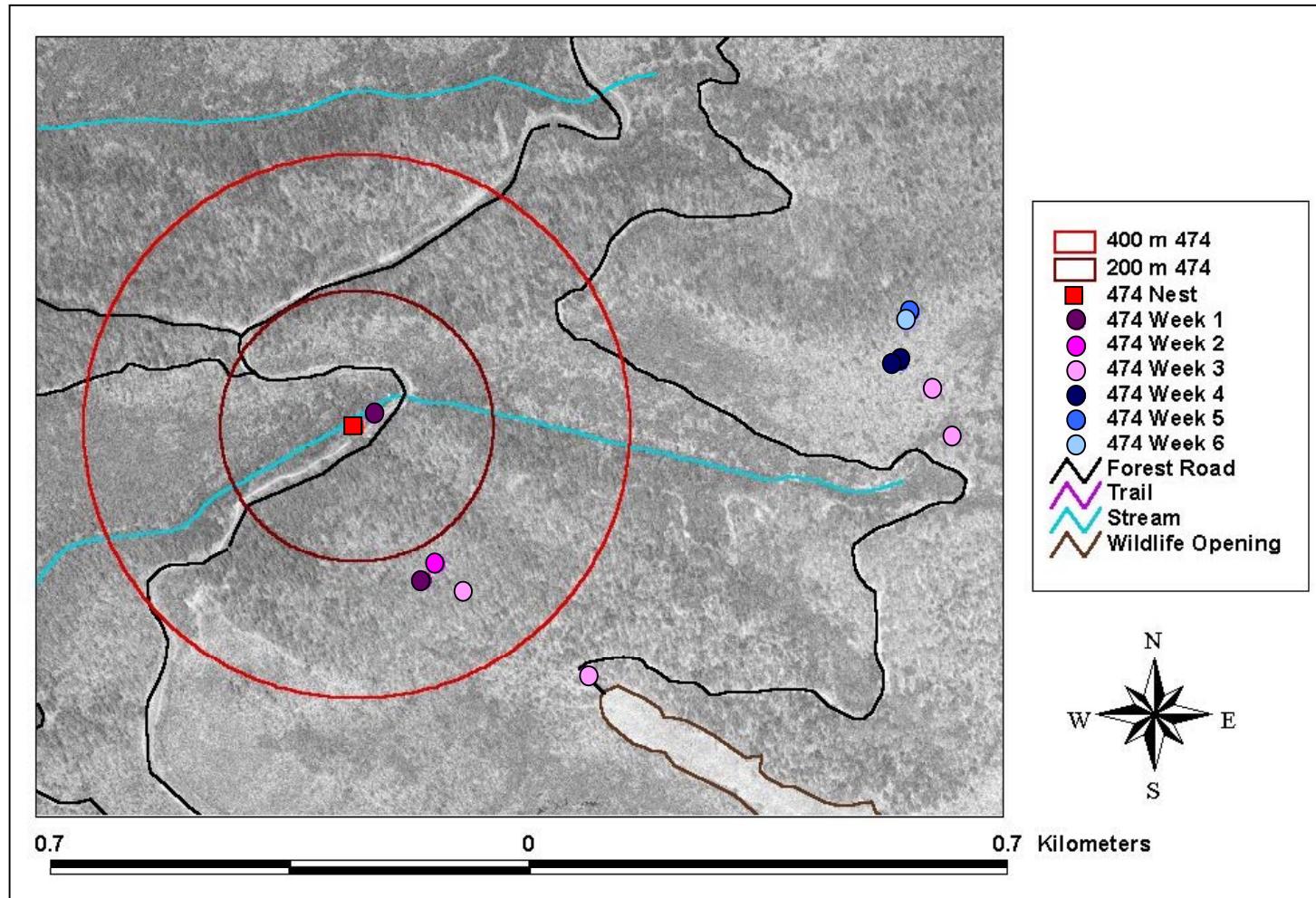


Figure 9. Ruffed grouse brood micro-habitat locations for brooding hen 474 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

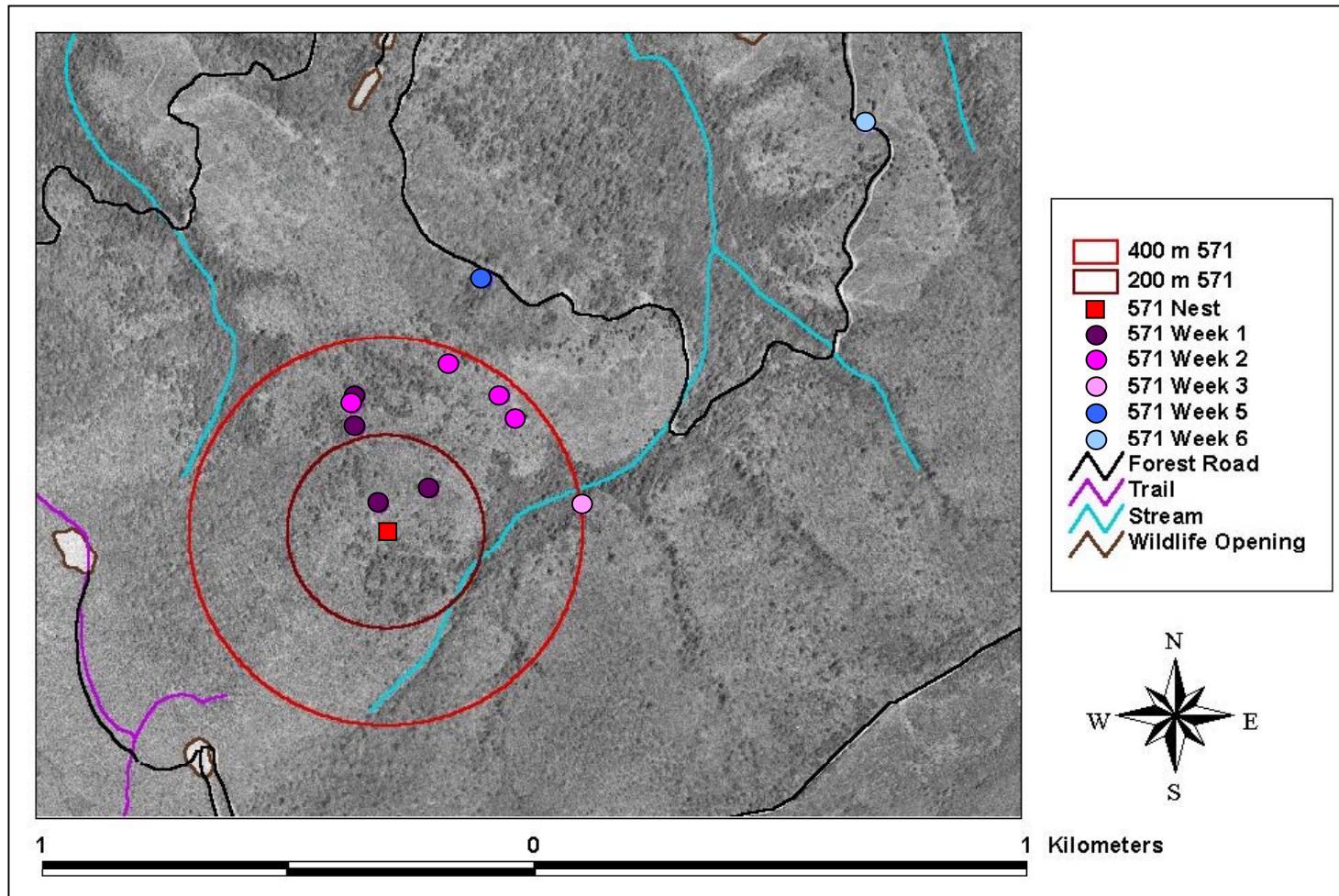


Figure 10. Ruffed grouse brood micro-habitat locations for brooding hen 571 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

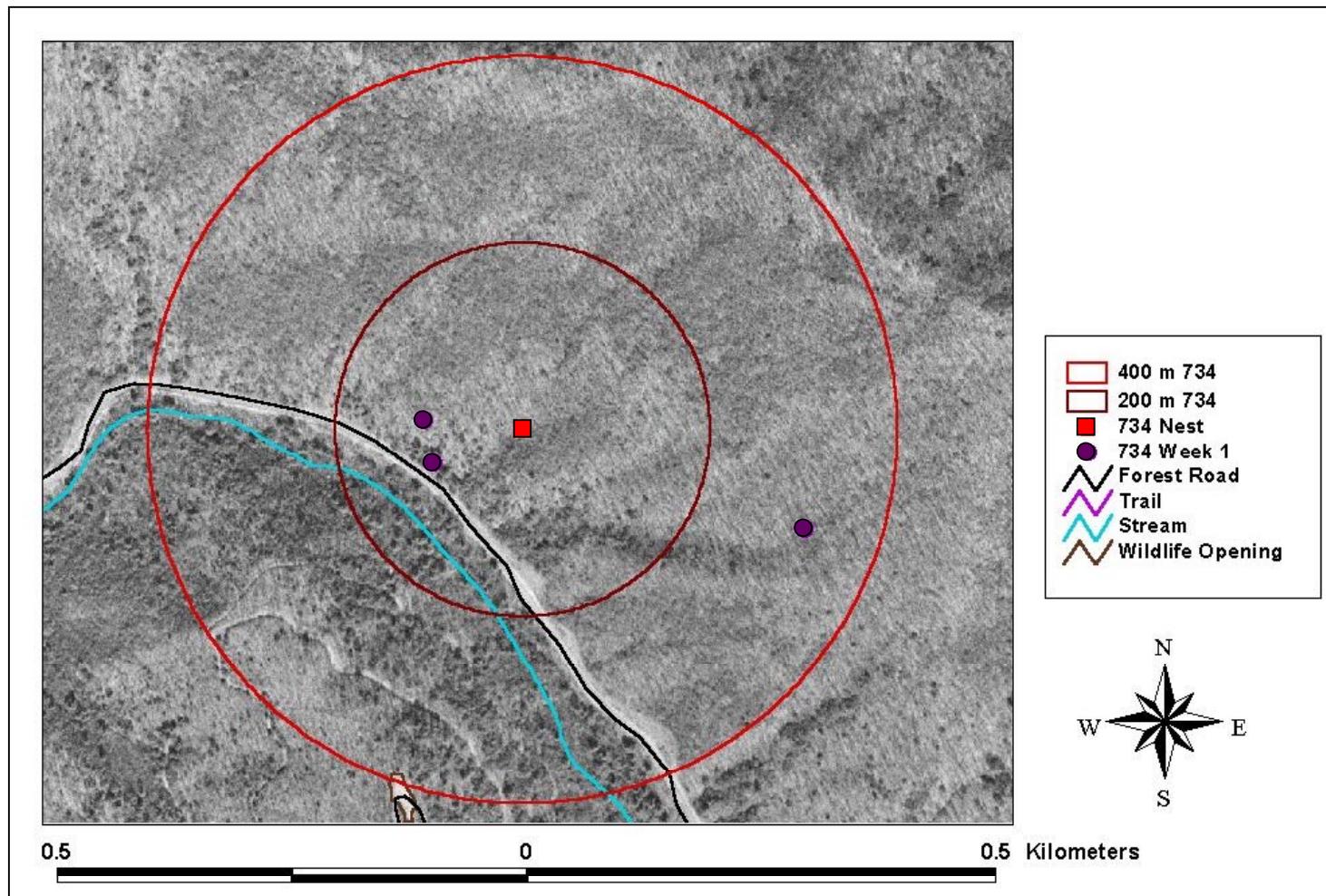


Figure 11. Ruffed grouse brood micro-habitat locations for brooding hen 734 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000.

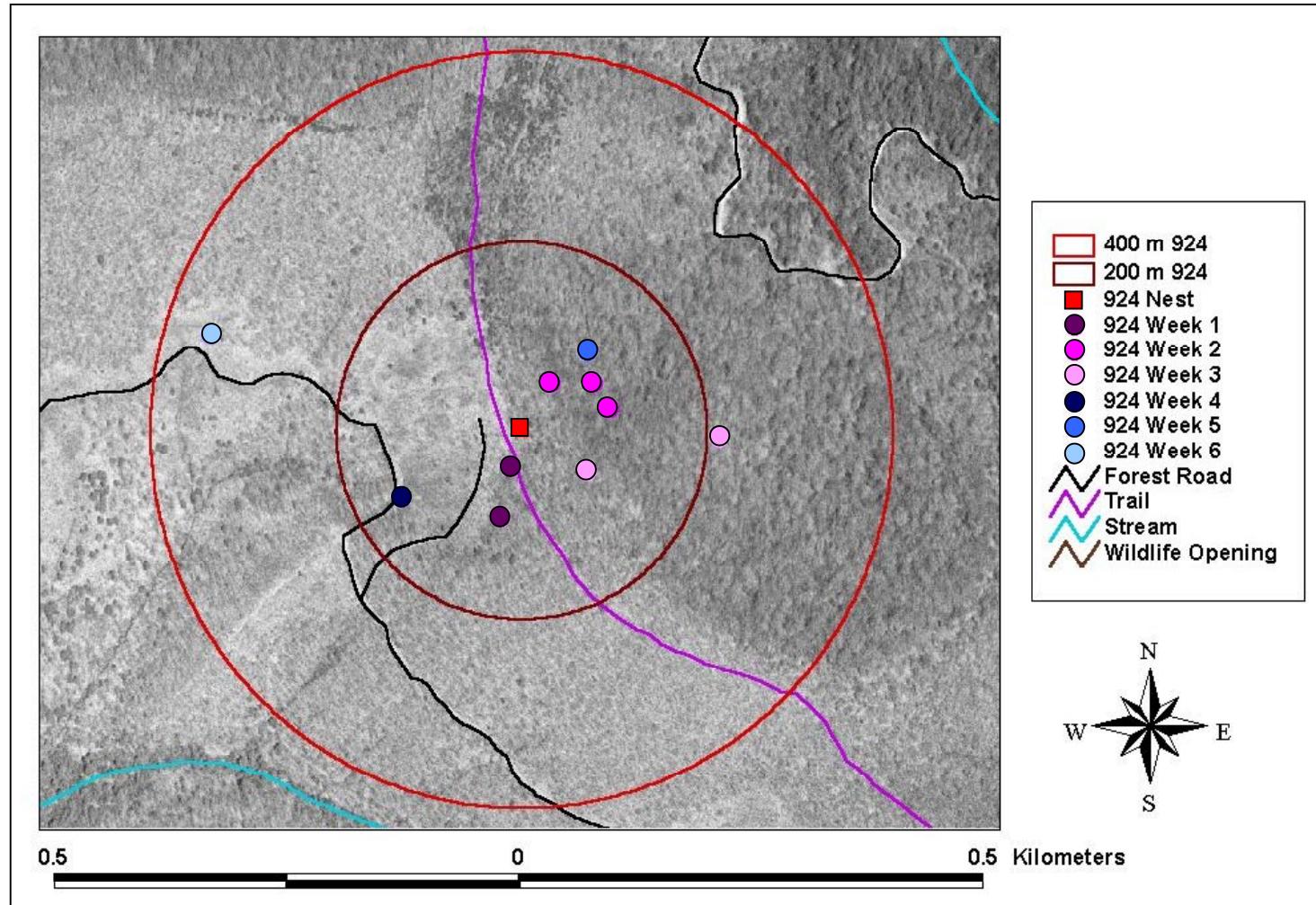


Figure 12. Ruffed grouse brood micro-habitat locations for brooding hen 924 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

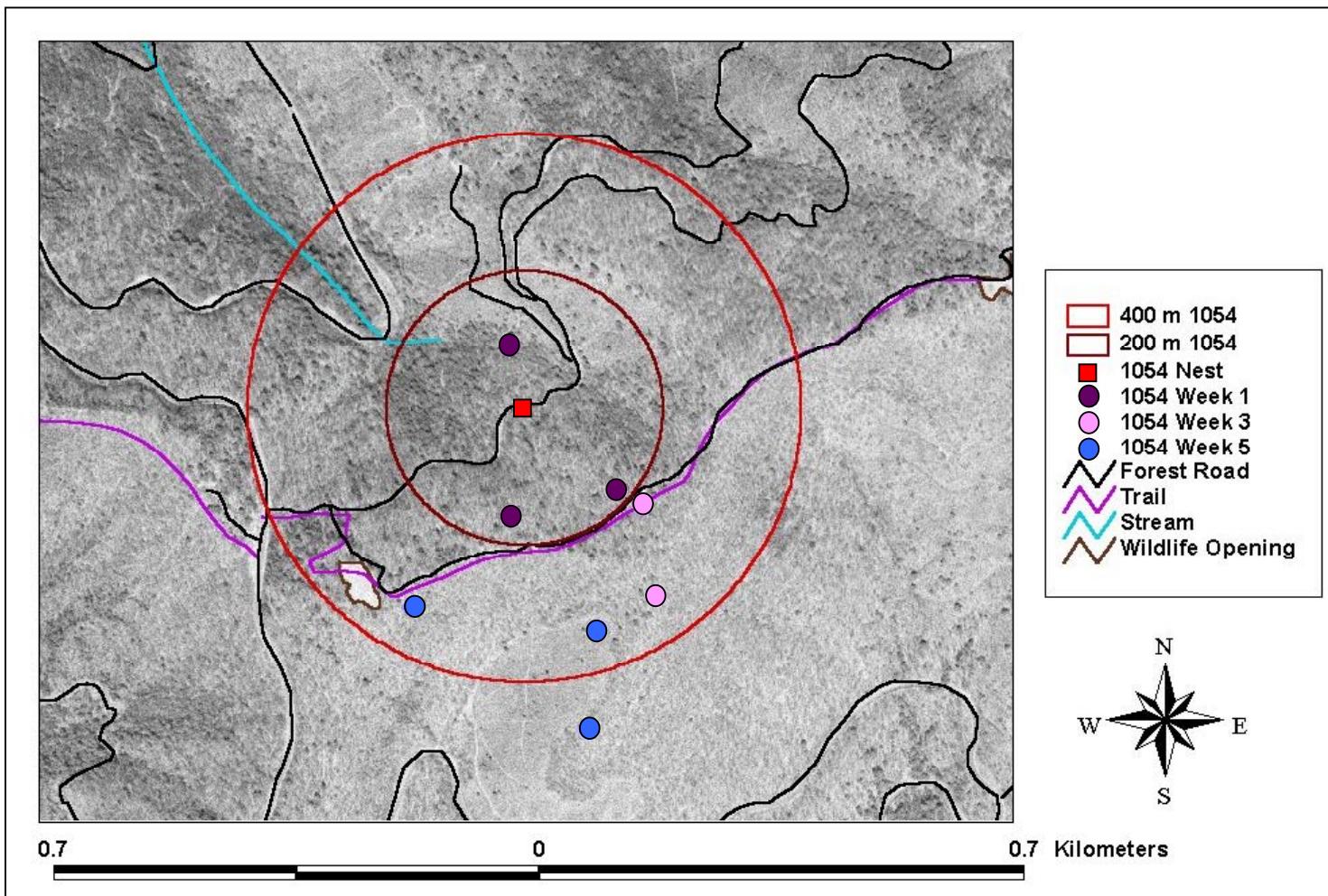


Figure 13. Ruffed grouse brood micro-habitat locations for brooding hen 1054 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

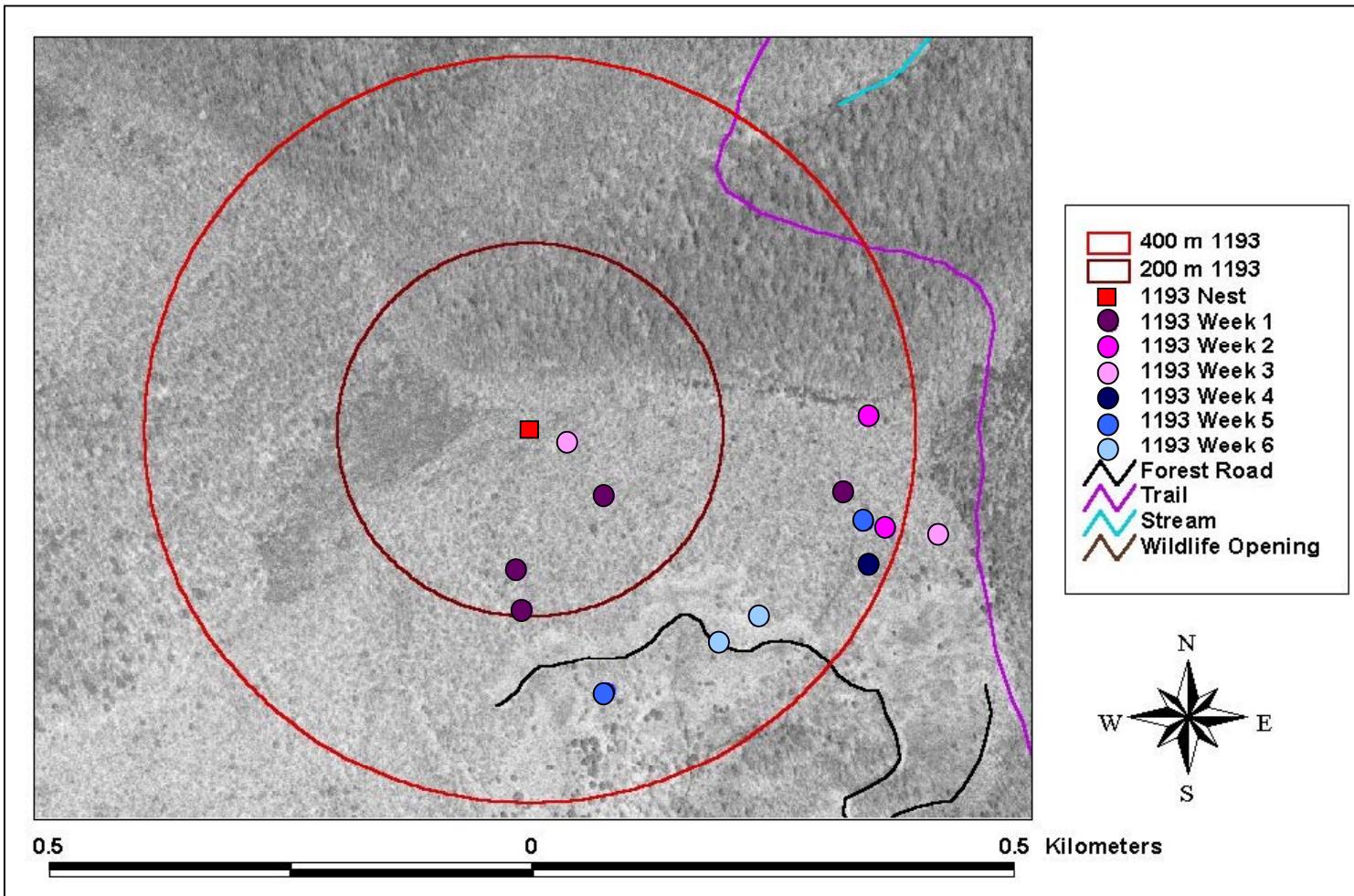


Figure 14. Ruffed grouse brood micro-habitat locations for brooding hen 1193 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

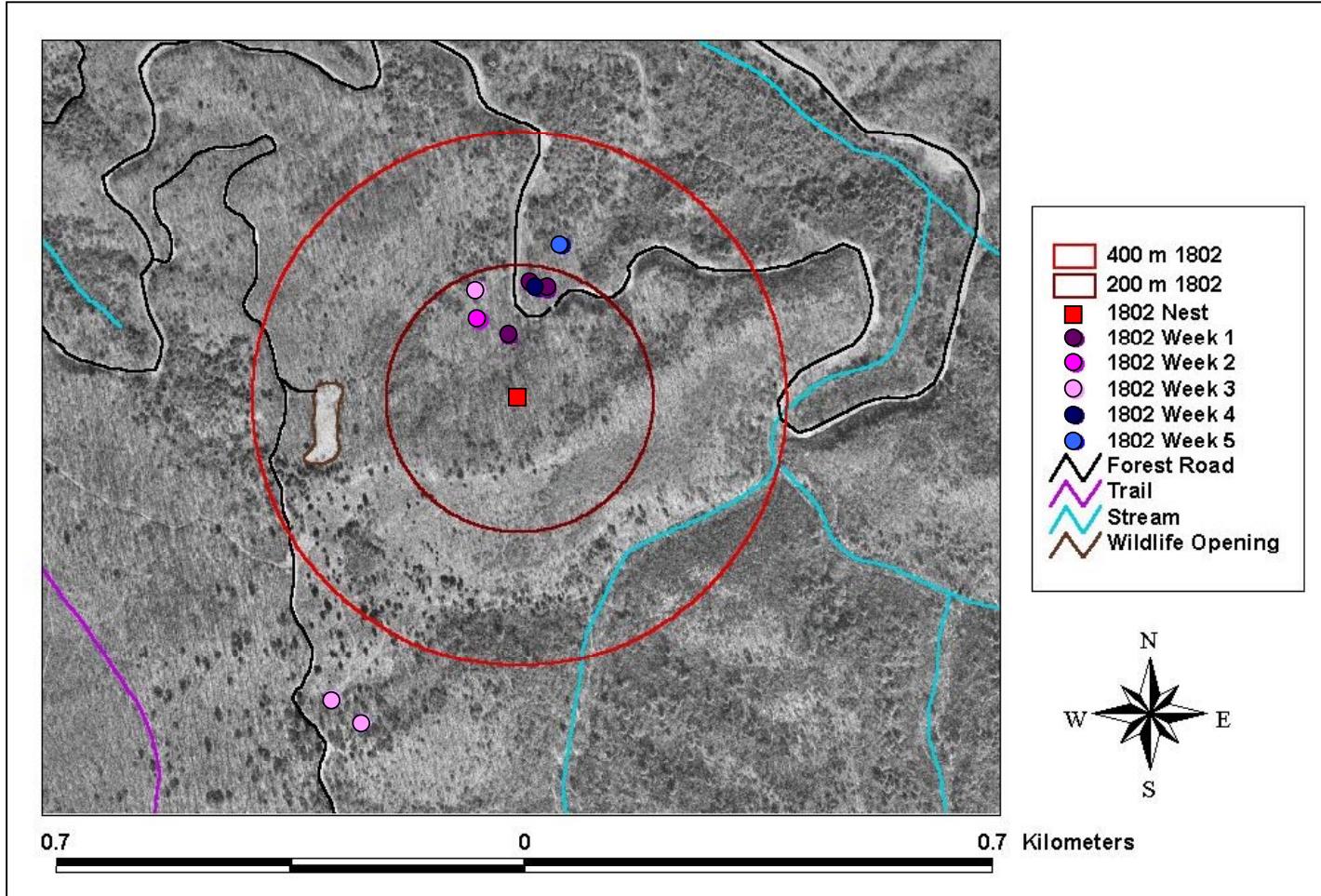


Figure 15. Ruffed grouse brood micro-habitat locations for brooding hen 1802 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

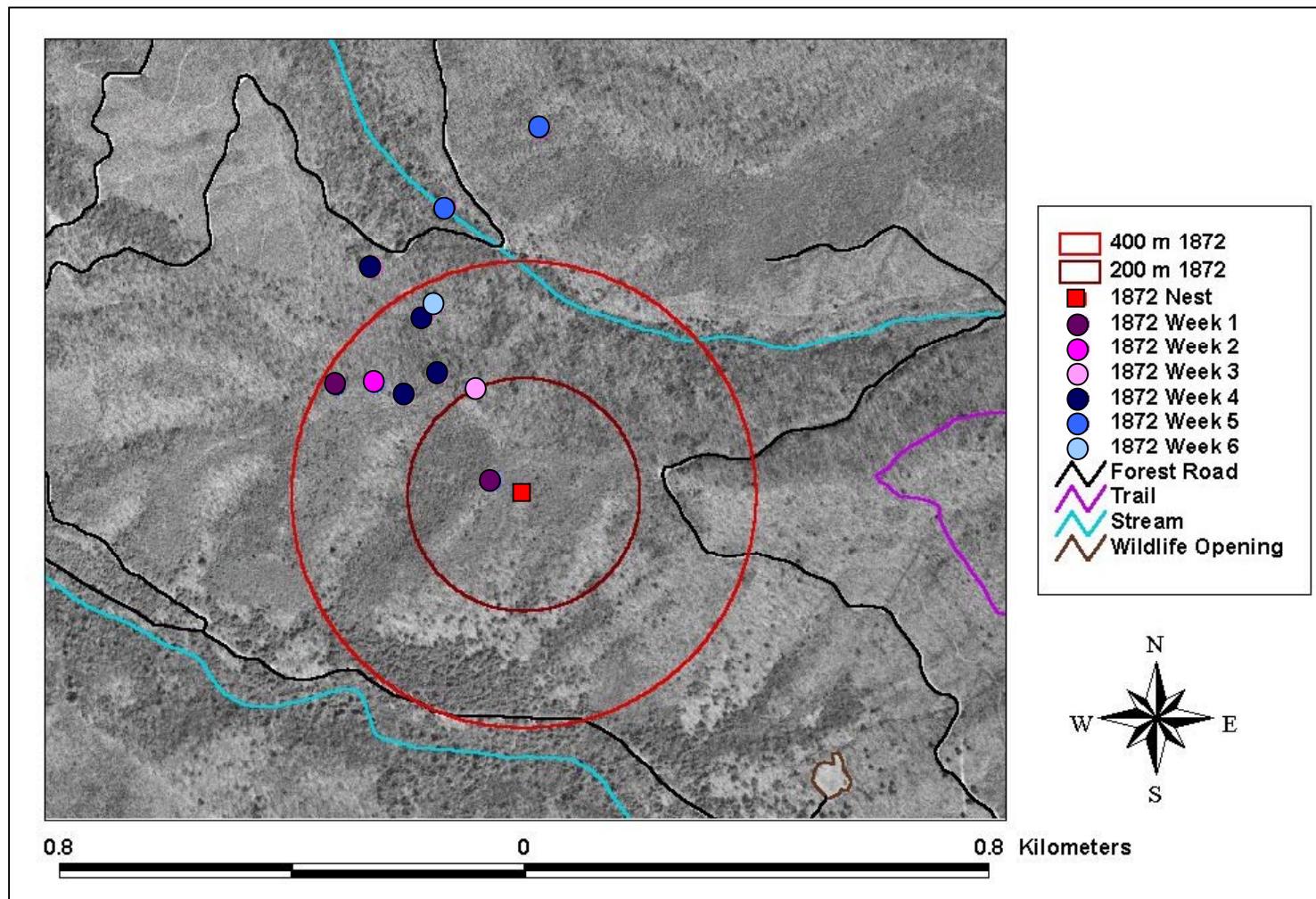


Figure 16. Ruffed grouse brood micro-habitat locations for brooding hen 1872 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

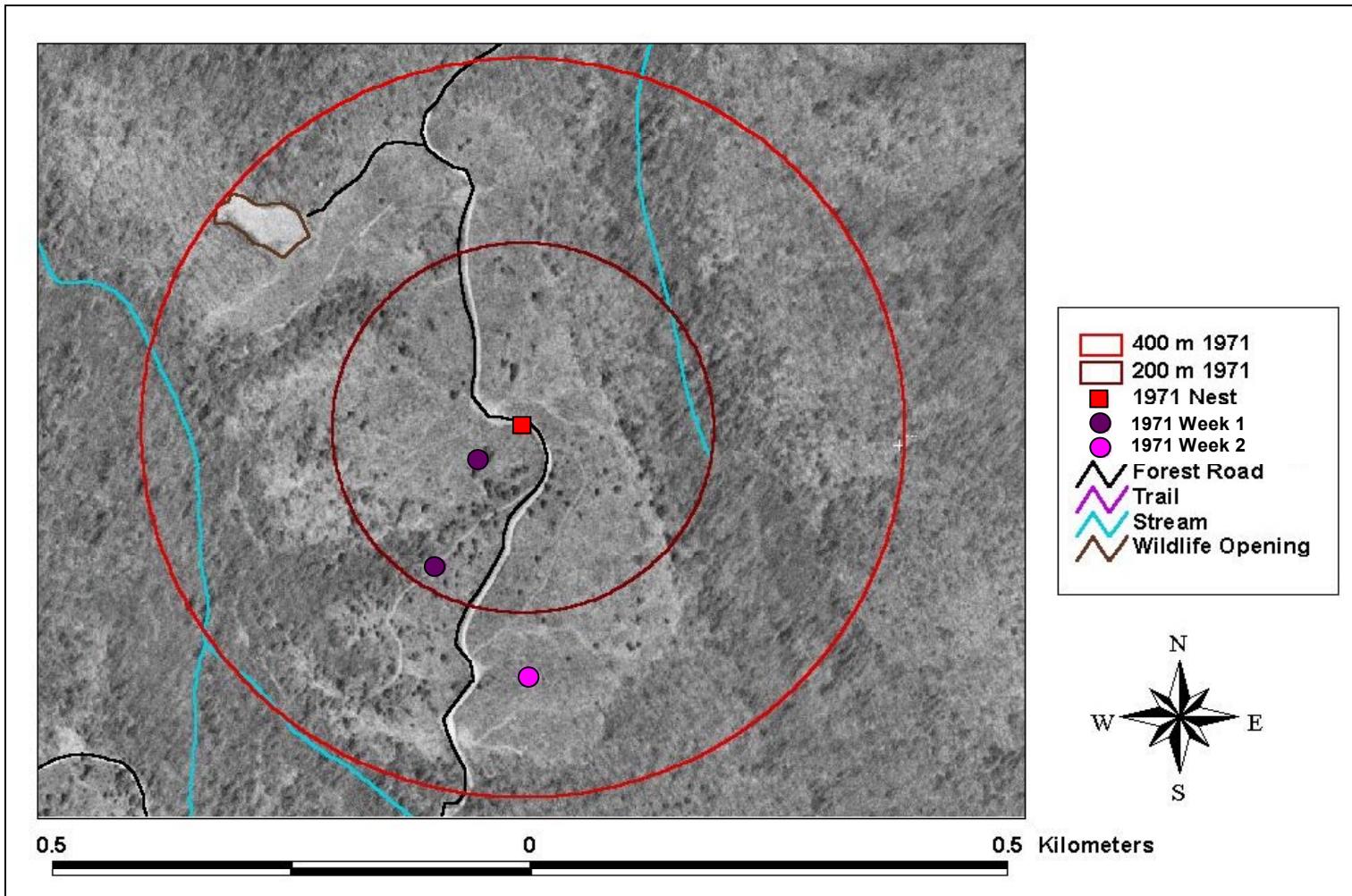


Figure 17. Ruffed grouse brood micro-habitat locations for brooding hen 1971 on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000.

APPENDIX B

Table 1. Forest type distribution on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Forest Cover-Type	Dominant /Codominant Species*	USFSCode	% of WSCA
Northern Hardwood	Sugar Maple/Beech/Birch	81	22.3
Oak - Hickory	Northern Red Oak	55	3.2
	Chestnut Oak	52	1.6
	Scarlet Oak	59	0.2
	White Oak/Northern Red Oak/Hickory	53	50.9
	Chestnut Oak/Scarlet Oak	60	2.9
Pine	White Pine	03	0.8
	Red Spruce/Frasier Fir	07	0.1
Pine - Hardwood	White Pine/Upland Hardwood	10	0.7
	Pitch Pine/Oak	15	0.2
	Upland Hardwood/White Pine	42	1.9
	Chestnut Oak/Scarlet Oak/Yellow Pine	45	1.7
Mesophytic Pine - Hardwood	Hemlock/ Hardwoods	08	1.3
	Cove Hardwoods/White Pine/Hemlock	41	6.5
Mesophytic Hardwood	Yellow-Poplar	50	0.6
	Yellow Poplar/White Oak/Northern Red Oak	56	5.0

*Source: USFS. 1996. National Forests Stands (CISC) for the Southern Appalachian Assessment (SAA) Study Area

Table 2. Forest age-class distribution on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Age-class	Hectares	Acres	% of WSCA
0 – 5 years	45	111	1.0
6 – 15 years	377	932	8.1
16 – 30 years	203	501	4.4
31 – 40 years	75	184	1.6
> 41 years	3,955	9,770	85.0

Table 3. Variables measured at ruffed grouse nest and random locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Variable Code	Variable Description
SLOPE	% Slope
ASPECT	Slope aspect: North, South, East, West
DOBJ	Distance from nest to object (m)
DROAD	Distance from nest to paved or 2-track road (m)
DSTR	Distance from nest to stream (m)
DOPEN	Distance from nest to a forest opening (m)
BA	Basal area (m^2/ha)
OSP	# Over-story species
MIDA	# Stems/ha >1.4 m tall and < 2.5 cm dbh
MIDB	# Stems/ha >1.4 m tall and 2.5 – 5 cm dbh
MIDC	# Stems/ha >1.4 m tall and 5 – 7.5 cm dbh
MIDD	# Stems/ha >1.4 m tall and \geq 7.5 cm dbh, but not in BA
MIDT	Total # Stems/ha >1.4 m tall and not in BA
MIDSP	# Mid-story species
USTEM	# Woody stems <1.4 m tall
USP	# Woody under-story species
VCVRA	Vertical cover density (% covered) 0 – 40 cm
VCVRB	Vertical cover density (% covered) 41 – 80 cm
VCVRC	Vertical cover density (% covered) 81 – 120 cm
VCVRD	Vertical cover density (% covered) 121 – 160 cm
VCVRE	Vertical cover density (% covered) 161 – 200 cm
VCVRM	Mean vertical cover density (% covered)
FCVR	Forest type classification
AGECLS	Age of stand (0 – 5 yr, 5 – 15 yr, 15 – 30 yr, 30 – 40 yr, >40 yr)

Table 4. Nesting rate and nest survival (%) by year and hen age of adult and yearling ruffed grouse on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Year/Age^a	n^b	Nesting Rate^c	n^d	Nest Survival^e	n^f
2000	7	71 A	5	85 A	6
2001	12	92 A	11	79 A	13
Adult	8	88 A	7	90 A	7
Juvenile	11	83 A	9	80 A	10
Pooled	19	84	16	76	17

Nesting rate and nest survival estimates with the same letter within each classification are not significantly different ($P > 0.05$)

^aAdult: After hatch year, Juvenile: Hatch year

^bTotal number of radio-tracked hens located >3 times/week

^cProportion of hens attempting to nest

^dNumber of hens with nesting attempts

^eNest survival using the Mayfield method for calculating nest success (Mayfield 1961)

^fTotal number of nests with known fate, including a second nest and two uncollared hens

Table 5. Hatching success (%) and mean clutch size of first nests by year and hen age for ruffed grouse on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Year/Age^a	n^b	Hatching Success^c	n^d	Mean Clutch	SE
2000	49	98 A	6	9.5 A	0.6
2001	96	94 A	12	10.3 A	0.4
Adult	66	98 A	7	10.7 A	0.5
Juvenile	79	94 A	9	9.9 A	0.5
Pooled	145	95	18	10.1	0.4

Hatching success estimates and mean clutch sizes with the same letter within each classification are not significantly different ($P > 0.05$)

^aAdult: After hatch year, Juvenile: Hatch year

^bNumber of eggs in successful nests (≥ 1 egg hatching)

^cProportion of eggs hatching from successful nests

^dNumber of nests with known clutch size

Table 6. Mean initiation dates for egg laying, nest incubation and hatching by year and hen age for ruffed grouse on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Year/Age^a	Mean Laying	Mean Incubation	Mean Hatch	n^b
2000	10-April A	25-April A	19-May A	5
2001	14-April B	29-April B	24-May B	9
Adult	12-April A	28-April A	22-May A	6
Juvenile	14-April A	28-April A	22-May A	8
Pooled	12-April	28-April	22-May	14

Initiation dates with the same letter within each classification are not significantly different ($P > 0.05$)

^aAdult: After hatch year, Juvenile: Hatch year

^bNumber of nests with known hatch dates

Table 7. Mean monthly precipitation (mm) and average daily temperature (C) during summer on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Month	2000		2001	
	Precipitation	Temperature	Precipitation	Temperature
March	18	7.5	17	2.8
April	28	8.6	8.1	11.2
May	3.0	15.8	5.2	15.0

Table 8. Means and frequencies of habitat variables measured at ruffed grouse nest and random locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Variable	Nest	SE	Random	SE	P-value^a
ASPECT ^b	--	--	--	--	0.7013
BA (m ² /ha)	20	1.2	20	2.1	0.4846
MIDT (stems/ha)	9,839	3,960	5,426	907	0.7392
USTEM (stems/ha)	23,930	6,765	21,455	5,514	0.5494
VCVRM (%)	84	4	55	5	0.0004*
DOBJ (m)	0	0	1.1	0.3	0.6124
DROAD (m)	251	117	266	113	0.6426
DOPEN (m)	643	154	577	130	0.4725
FCVR ^c	--	--	--	--	0.3307
AGECLS ^d	--	--	--	--	0.9087

^a P-values from stepwise logistic regression model ($R^2 = 0.42$, $\chi^2 = 6.91$, $P = 0.4386$)

^b ASPECT is a categorical variable and therefore is presented in a separate table

^c FCVR is a categorical variable and therefore is presented in a separate table

^d AGECLS is a categorical variable and therefore is presented in a separate table

*Retained by logistic regression model at $\alpha = 0.1$

Table 9. Ruffed grouse nest and random locations classified by aspect on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

ASPECT	Nest	% of Total	Random	% of Total
North	7	37	6	31
East	3	16	2	11
South	3	16	4	21
West	6	31	7	37

Table 10. Ruffed grouse nest and random location distribution by forest type on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

FCVR	Nest	% of Total	Random	% of Total
Northern Hardwood	5	26	6	32
Oak - Hickory	13	68	10	54
Pine - Hardwood	1	5	1	5
Mesophytic Hardwood	0	0	2	11

Table 11. Ruffed grouse nest and random location distribution by forest stand age class on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

AGECLS	Nest	% of Total	Random	% of Total
0 – 5 years	0	0	0	0
6 – 15 years	3	16	2	11
16 – 30 years	3	16	3	16
31 – 40 years	1	5	1	5
> 41 years	12	63	13	68

Table 12. Means for habitat variables measured at ruffed grouse nest locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001, but not included in logistic regression to test for nest site selection.

Variable	Nest Mean	SE
SLOPE (%)	41	3
DSTR (m)	262	26
OSP (#)	4	0
MIDA (stems/ha)	3,458	690
MIDB (stems/ha)	1,089	225
MIDC (stems/ha)	532	115
MIDD (stems/ha)	347	87
MIDSP (#)	8	1
USP (#)	7	1
VCVRA (%)	78	5
VCVRB (%)	56	6
VCVRC (%)	48	6
VCVRD (%)	46	7
VCVRE (%)	45	8

Table 13. Micro-habitat variables measured at ruffed grouse brood and random locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Variable Code	Variable Description
SLOPE	% Slope
ASPECT	Slope aspect: North, South, East, West
DROAD	Distance from brood to road (m)
DSTR	Distance from brood to stream (m)
DOPEN	Distance from brood to a forest opening (m)
DCUT	Distance from brood to the edge of nearest cut (m)
BA	Basal area (m^2/ha)
OSP	# Over-story species
PCTDEC	Percent deciduous over-story trees
MIDA	# Stems/ha >1.4 m tall and < 2.5 cm dbh
MIDB	# Stems/ha >1.4 m tall and 2.5 – 5 cm dbh
MIDC	# Stems/ha >1.4 m tall and 5 – 7.5 cm dbh
MIDD	# Stems/ha >1.4 m tall and ≥ 7.5 cm dbh, but not in BA
MIDT	Total # Stems/ha >1.4 m tall and not in BA
MIDSP	# Mid-story species
USTEM	# Woody stems <1.4 m tall
USP	# Woody under-story species
AVFO	% Ground covered by forbs
AVFRN	% Ground covered by ferns
AVGR	% Ground covered by grass
AVBRAM	% Ground covered by brambles
AVGCVR	% Ground covered by herbaceous plants
VCVRA	Vertical cover density (% covered) 0 – 40 cm
VCVRB	Vertical cover density (% covered) 41 – 80 cm
VCVRC	Vertical cover density (% covered) 81 – 120 cm
VCVRD	Vertical cover density (% covered) 121 – 160 cm
VCVRE	Vertical cover density (% covered) 161 – 200 cm
VCVRM	Mean vertical cover density (% covered)

Table 14. Macro- habitat variables measured at ruffed grouse brood and random locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Variable	Description	Sub-groups
FCVR	Forest type based on species of trees that comprise the canopy	<ul style="list-style-type: none"> • Northern Hardwood • Oak - Hickory • Pine • Pine - Hardwood • Mesophytic Pine - Hardwood • Mesophytic Hardwood
AGECLS	Age of stand	<ul style="list-style-type: none"> • 0 – 5 Years • 6 – 15 Years • 16 – 30 Years • 30 – 40 Years • > 40 Years
COND	Stage of growth (even-aged stands only)	<ul style="list-style-type: none"> • Seedling/Sapling • Poletimber • Sawtimber
FMGT	Forest management type	<ul style="list-style-type: none"> • Group selection • Individual tree selection

Table 15. Mean monthly precipitation (mm) and average daily temperature (C) for summer on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Month	2000		2001	
	Precipitation	Temperature	Precipitation	Temperature
May	1.6	18.7	2.1	16.9
June	3.8	21.1	5.0	20.7
July	2.4	22.9	3.4	22.9
15 May – 18 June	2.5	19.8	2.6	19.0

Table 16. Ruffed grouse brood flush counts on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 – 2001.

Hen	Hatch date	Initial brood size	3-week chick count	5-week chick count
134	5/20/00	7	Died 5/26/00	--
244	5/21/00	11	Hen Broody	0
734	5/19/00	11	0	0
813	5/15/00	9	0	0
1971	5/22/00	10	Died 5/29/00	--
263	5/22/01	9	7	5
414	5/24/01	11	7	10
474	5/26/01	9	4	4
517	5/23/01	13	8	5
924	5/27/01	10	2	3
1054	5/25/01	10	8+	10 (2 hens)
1193	5/23/01	10	2	6 (2 hens)
1802	5/20/01	9	6	4
1872	5/22/01	8	8	5

Table 17. Number of ruffed grouse brood habitat locations collected by week on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Bird	2000					2001								
	134	244	734	813	1971	263	414	474	571	924	1054	1193	1802	1872
Week 1	2	2	2	1	2	4	5	2	4	2	3	4	3	2
Week 2	0	3	1	1	1	3	0	1	4	3	0	2	1	2
Week 3	0	5	0	0	0	3	3	2	1	2	2	2	3	3
Week 4	0	0	0	0	0	0	1	2	0	1	0	1	2	1
Week 5	0	0	0	0	0	2	0	1	1	1	3	2	1	2
Week 6	0	0	0	0	0	1	1	1	1	1	0	2	0	1
Total	2	10	3	2	3	13	10	9	11	10	8	13	10	11

Table 18. Ruffed grouse brood micro-habitat variable means compared between years on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Variable	2000	SE	2001	SE	P-value^a
SLOPE (%)	39	3	33	2	0.2504
ASPECT ^b	--	--	--	--	0.7644
BA (m ² /ha)	18.9	2.2	20.7	1.4	0.4696
MIDT (stems/ha)	8,504	1,119	5,975	582	0.6782
AVGCVR (%)	27.3	4	53.7	3	< 0.0001*
VCVRM (%)	56	6	55	3	0.9882
DROAD (m)	71	15	130	14	0.4712
DSTR (m)	182	30	301	17	0.0203*
DOPEN (m)	239	30	444	30	<0.0001*
DCUT (m)	52	12	56	6	0.0478*

^a P-values from stepwise logistic regression model ($R^2 = 0.67$, $\chi^2 = 3.68$, $P = 0.8163$)

^b ASPECT is a categorical variable and therefore is presented in a separate table

*Retained by logistic regression model at $\alpha = 0.05$

Table 19. Ruffed grouse brood locations classified by aspect and year on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

ASPECT	2000	% of Total	2001	% of Total
North	10	45	14	22
East	0	0	22	34
South	2	9	12	19
West	10	45	16	25

Table 20. Ruffed grouse brood micro-habitat variable means compared between early (hatch – 3 weeks) and late (4 – 10 weeks) time-periods on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

Variable	Early 2001	SE	Late 2001	SE	P-value^a
SLOPE (%)	33	2	34	3	0.6392
ASPECT ^b	--	--	--	--	0.3756
BA (m ² /ha)	20.7	1.4	14.5	1.8	0.0439*
MIDT (stems/ha)	5,975	582	9,179	1,187	0.5672
AVGCVR (%)	54	3	65	6	0.2098
VCVRM (%)	55	3	71	5	0.0063*
DROAD (m)	130	14	116	16	0.7663
DSTR (m)	301	17	345	18	0.0679
DOPEN (m)	444	30	460	48	0.6446
DCUT (m)	56	6	34	8	0.1096

^a P-values from stepwise logistic regression model ($R^2 = 0.22$, $\chi^2 = 8.53$, $P = 0.3839$)

^b ASPECT is a categorical variable and therefore is presented in a separate table

*Retained by logistic regression model at $\alpha = 0.05$

Table 21. Ruffed grouse brood locations classified by aspect and time-period on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

ASPECT	Early 2001	% of Total	Late 2001	% of Total
North	14	22	5	17
East	22	34	7	23
South	12	19	14	47
West	16	25	4	13

Table 22. Variables used to model ruffed grouse brood micro-habitat selection on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000.

Variable	Brood	SE	Random	SE	P-value^a
SLOPE (%)	39	3	37	3	0.8707
ASPECT ^b	--	--	--	--	0.7944
BA (m ² /ha)	19	2	24	2	0.4486
MIDT (stems/ha)	8,503	1,119	5,561	919	0.7037
AVGCVR (%)	27	4	45	6	0.0319*
VCVRM (%)	56	6	59	6	0.2513
DROAD (m)	71	15	117	20	0.2535
DSTR (m)	182	30	270	19	0.0300*
DOPEN (m)	239	30	282	38	0.0837
DCUT (m)	52	12	57	9	0.5053

^a P-values from stepwise logistic regression model ($R^2 = 0.32$, $\chi^2 = 5.44$, $P = 0.7101$)

^b ASPECT is a categorical variable and therefore is presented in a separate table

*Retained by logistic regression model at $\alpha = 0.05$

Table 23. Ruffed grouse brood and random locations classified by aspect on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000.

ASPECT	Brood 2000	% of Total	Random 2000	% of Total
North	10	45	11	55
East	0	0	0	0
South	2	9	2	10
West	10	45	7	35

Table 24. Variables used to model ruffed grouse brood micro-habitat selection during the early period (hatch – 3 weeks) on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

Variable	Brood	SE	Random	SE	P-value^a
SLOPE (%)	33	2	33	2	0.7418
ASPECT ^b	--	--	--	--	0.0013*
BA (m ² /ha)	20.7	1.4	20.9	1.3	0.9032
MIDT (stems/ha)	5,975	582	4,598	514	0.1446
AVGCVR (%)	54	3	37	3	< 0.0001*
VCVRM (%)	55	3	44	3	0.0725
DROAD (m)	130	14	111	13	0.1419
DSTR (m)	301	17	321	17	0.0071*
DOPEN (m)	444	30	446	31	0.0913
DCUT (m)	56	6	58	7	0.1868

^a P-values from stepwise logistic regression model ($R^2 = 0.34$, $\chi^2 = 14.86$, $P = 0.0620$)

^b ASPECT is a categorical variable and therefore is presented in a separate table

*Retained by logistic regression model at $\alpha = 0.05$

Table 25. Ruffed grouse brood and random early period (hatch – 3 weeks) locations classified by aspect on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

ASPECT	Early Brood	% of Total	Early Random	% of Total
North	14	22	27	43
East	22	34	11	17
South	12	19	7	11
West	16	25	18	29

Table 25. Ruffed grouse brood and random early period (hatch – 3 weeks) locations classified by aspect on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

ASPECT	Early Brood	% of Total	Early Random	% of Total
North	14	22	27	43
East	22	34	11	17
South	12	19	7	11
West	16	25	18	29

Table 26. Variables used to model ruffed grouse brood micro-habitat selection during the late period (4 – 10 weeks) on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

Variable	Brood	SE	Random	SE	P-value^a
SLOPE (%)	34	3	33	3	0.2299
ASPECT ^b	--	--	--	--	0.2514
BA (m ² /ha)	14.5	1.8	21.4	1.5	0.0444*
MIDT (stems/ha)	9,179	1,187	5,674	1,012	0.4615
AVGCVR (%)	65	6	34	4	0.0037*
VCVRM (%)	72	5	44	6	0.0257*
DROAD (m)	116	16	115	21	0.9595
DSTR (m)	345	18	293	21	0.2052
DOPEN (m)	460	48	485	44	0.9569
DCUT (m)	34	8	42	6	0.8927

^a P-values from stepwise logistic regression model ($R^2 = 0.48$, $\chi^2 = 6.34$, $P = 0.6091$)

^b ASPECT is a categorical variable and therefore is presented in a separate table

*Retained by logistic regression model at $\alpha = 0.05$

Table 27. Ruffed grouse brood and random late period (4 – 10 weeks) locations classified by aspect on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

ASPECT	Late Brood	% of Total	Late Random	% of Total
North	5	17	10	32
East	7	23	7	23
South	14	47	3	10
West	4	13	11	35

Table 28. Ruffed grouse brood macro-habitat selection on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001. Values represent frequency of occurrence in each variable sub-group.

Variable	Sub-groups	Brood	Random	P - value
FCVR	<ul style="list-style-type: none"> • Northern Hardwood • Oak - Hickory • Pine • Pine - Hardwood • Mesophytic Pine - Hardwood • Mesophytic Hardwood 	<ul style="list-style-type: none"> 39 163 2 1 4 12 	<ul style="list-style-type: none"> 47 116 2 0 13 13 	<ul style="list-style-type: none"> 0.9942 0.3418 0.9106 0.2846 0.1878 0.9285
AGECLS	<ul style="list-style-type: none"> • 0 – 5 Years • 6 – 15 Years • 16 – 30 Years • 30 – 40 Years • > 40 Years 	<ul style="list-style-type: none"> 1 85 25 1 110 	<ul style="list-style-type: none"> 6 10 9 4 168 	<ul style="list-style-type: none"> 0.1807 < 0.0001* < 0.0001* 0.3883 0.1106
COND	<ul style="list-style-type: none"> • Seedling/Sapling • Poletimber • Sawtimber 	<ul style="list-style-type: none"> 79 41 85 	<ul style="list-style-type: none"> 16 51 120 	<ul style="list-style-type: none"> 0.5368 0.9038 0.3271
FMGT	<ul style="list-style-type: none"> • Group selection • Individual tree selection 	<ul style="list-style-type: none"> 11 0 	<ul style="list-style-type: none"> 1 0 	<ul style="list-style-type: none"> 0.2640 --

^aP-values from stepwise logistic regression model ($R^2 = 0.26$, $\chi^2 = 0.00$, $P = 1.0$)

*Retained by logistic regression model at $\alpha = 0.05$

Table 29. Means for habitat variables measured at ruffed grouse brood locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001, but not included in logistic regression to test for nest site selection.

Variable	2000	SE	Early 2001	SE	Late 2001	SE
OSP (#)	3	0	3	0	3	0
PCTDEC (%)	95	3	97	1	96	2
MIDA (stems/ha)	5,002	639	4,539	501	7,033	999
MIDB (stems/ha)	2,637	498	835	88	1,529	253
MIDC (stems/ha)	557	98	380	56	376	49
MIDD (stems/ha)	263	65	222	28	203	35
MIDSP (#)	8	1	7	0	8	1
USTEM (stems/ha)	11,787	2,210	16,699	2,701	32,416	9,090
USP (#)	5	1	5	0	7	1
AVFO (%)	11	2	31	5	37	8
AVFRN (%)	13	3	23	3	31	5
AVGR (%)	2	1	5	1	11	5
AVBRI (%)	0	0	1	0	1	1
AVBLK (%)	1	1	3	1	3	1
VCVRA (%)	65	6	81	3	86	4
VCVRB (%)	54	6	61	4	77	5
VCVRC (%)	52	7	49	4	69	5
VCVRD (%)	55	7	44	4	64	6
VCVRE (%)	55	7	39	4	63	6

Table 30. Invertebrate detection in dried and frozen debris samples at brood and random locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Class	Order	Dried	SE	Frozen	SE	P-value^a
Gastropoda	Pulmonata	3.2	1.1	1.5	0.3	0.1013
Chilopoda		2.0	0.8	1.9	0.5	0.8243
Diplopoda		2.4	0.6	2.1	0.4	0.5222
Malacostraca		6.0	3	6.5	3.5	0.5000
Arachnida	Acari	2.1	0.5	1.3	0.4	0.2110
	Araneae	3.3	0.6	3.7	0.7	0.5911
	Opiliones	1.0	0.0	1.0	0.0	--
	Pseudoscorpiones	0.0	0.0	0.0	0.0	--
Hexapoda	Coleoptera	2.1	0.7	1.7	0.5	0.1996
	Collembola	3.9	1.8	10.8	5.9	0.1893
	Diptera	3.1	0.6	4.0	0.6	0.1589
	Hemiptera	1.0	0.0	0.0	0.0	--
	Homoptera	1.3	0.5	2.0	0.6	0.2815
	Hymenoptera	1.7	0.2	0.8	0.3	0.0864
	Lepidoptera (Adult)	1.0	0.0	0.0	0.0	--
	Lepidoptera (Larva)	1.0	0.0	1.5	1.5	0.7952
	Mecoptera	0.5	0.5	1.0	0.0	0.5000
	Orthoptera	1.0	0.0	0.5	0.5	0.5000
	Psocoptera	0.0	0.0	0.0	0.0	--
TOTAL		27.8	5.2	37.9	6.7	0.1580

^aP-values from paired t-tests

Table 26. Variables used to model ruffed grouse brood micro-habitat selection during the late period (4 – 10 weeks) on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

Variable	Brood	SE	Random	SE	P-value^a
SLOPE (%)	34	3	33	3	0.2299
ASPECT ^b	--	--	--	--	0.2514
BA (m ² /ha)	14.5	1.8	21.4	1.5	0.0444*
MIDT (stems/ha)	9,179	1,187	5,674	1,012	0.4615
AVGCVR (%)	65	6	34	4	0.0037*
VCVRM (%)	72	5	44	6	0.0257*
DROAD (m)	116	16	115	21	0.9595
DSTR (m)	345	18	293	21	0.2052
DOPEN (m)	460	48	485	44	0.9569
DCUT (m)	34	8	42	6	0.8927

^a P-values from stepwise logistic regression model ($R^2 = 0.48$, $\chi^2 = 6.34$, $P = 0.6091$)

^b ASPECT is a categorical variable and therefore is presented in a separate table

*Retained by logistic regression model at $\alpha = 0.05$

Table 27. Ruffed grouse brood and random late period (4 – 10 weeks) locations classified by aspect on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

ASPECT	Late Brood	% of Total	Late Random	% of Total
North	5	17	10	32
East	7	23	7	23
South	14	47	3	10
West	4	13	11	35

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FCVR	<ul style="list-style-type: none"> • Northern Hardwood • Oak - Hickory • Pine • Pine - Hardwood • Mesophytic Pine - Hardwood • Mesophytic Hardwood 	<ul style="list-style-type: none"> 39 163 2 1 4 12 	<ul style="list-style-type: none"> 47 116 2 0 13 13 	<ul style="list-style-type: none"> 0.9942 0.3418 0.9106 0.2846 0.1878 0.9285
AGECLS	<ul style="list-style-type: none"> • 0 – 5 Years • 6 – 15 Years • 16 – 30 Years • 30 – 40 Years • > 40 Years 	<ul style="list-style-type: none"> 1 85 25 1 110 	<ul style="list-style-type: none"> 6 10 9 4 168 	<ul style="list-style-type: none"> 0.1807 < 0.0001* < 0.0001* 0.3883 0.1106
COND	<ul style="list-style-type: none"> • Seedling/Sapling • Poletimber • Sawtimber 	<ul style="list-style-type: none"> 79 41 85 	<ul style="list-style-type: none"> 16 51 120 	<ul style="list-style-type: none"> 0.5368 0.9038 0.3271
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^aP-values from stepwise logistic regression model ($R^2 = 0.26$, $\chi^2 = 0.00$, $P = 1.0$)

*Retained by logistic regression model at $\alpha = 0.05$

Table 29. Means for habitat variables measured at ruffed grouse brood locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001, but not included in logistic regression to test for nest site selection.

Variable	2000	SE	Early 2001	SE	Late 2001	SE
OSP (#)	3	0	3	0	3	0
PCTDEC (%)	95	3	97	1	96	2
MIDA (stems/ha)	5,002	639	4,539	501	7,033	999
MIDB (stems/ha)	2,637	498	835	88	1,529	253
MIDC (stems/ha)	557	98	380	56	376	49
MIDD (stems/ha)	263	65	222	28	203	35
MIDSP (#)	8	1	7	0	8	1
USTEM (stems/ha)	11,787	2,210	16,699	2,701	32,416	9,090
USP (#)	5	1	5	0	7	1
AVFO (%)	11	2	31	5	37	8
AVFRN (%)	13	3	23	3	31	5
AVGR (%)	2	1	5	1	11	5
AVBRI (%)	0	0	1	0	1	1
AVBLK (%)	1	1	3	1	3	1
VCVRA (%)	65	6	81	3	86	4
VCVRB (%)	54	6	61	4	77	5
VCVRC (%)	52	7	49	4	69	5
VCVRD (%)	55	7	44	4	64	6
VCVRE (%)	55	7	39	4	63	6

Table 30. Invertebrate detection in dried and frozen debris samples at brood and random locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

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Gastropoda	Pulmonata	3.2	1.1	1.5	0.3	0.1013
Chilopoda		2.0	0.8	1.9	0.5	0.8243
Diplopoda		2.4	0.6	2.1	0.4	0.5222
Malacostraca		6.0	3	6.5	3.5	0.5000
Arachnida	Acari	2.1	0.5	1.3	0.4	0.2110
	Araneae	3.3	0.6	3.7	0.7	0.5911
	Opiliones	1.0	0.0	1.0	0.0	--
	Pseudoscorpiones	0.0	0.0	0.0	0.0	--
Hexapoda	Coleoptera	2.1	0.7	1.7	0.5	0.1996
	Collembola	3.9	1.8	10.8	5.9	0.1893
	Diptera	3.1	0.6	4.0	0.6	0.1589
	Hemiptera	1.0	0.0	0.0	0.0	--
	Homoptera	1.3	0.5	2.0	0.6	0.2815
	Hymenoptera	1.7	0.2	0.8	0.3	0.0864
	Lepidoptera (Adult)	1.0	0.0	0.0	0.0	--
	Lepidoptera (Larva)	1.0	0.0	1.5	1.5	0.7952
	Mecoptera	0.5	0.5	1.0	0.0	0.5000
	Orthoptera	1.0	0.0	0.5	0.5	0.5000
	Psocoptera	0.0	0.0	0.0	0.0	--
TOTAL		27.8	5.2	37.9	6.7	0.1580

^aP-values from paired t-tests

Table 31. Invertebrate density (#/m²) at ruffed grouse brood and random locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Class	Order	2000					2001				
		Brood	SE	Random	SE	P-value	Brood	SE	Random	SE	P-value
Arachnida	Araneae	2.7	1.1	2.4	1.0	0.7426	8.2	2.1	6.8	1.7	0.2104
Hexapoda	Coleoptera	6.2	1.3	2.3	0.6	<0.0001	1.1	0.2	1.2	0.2	0.5383
	Diptera	0.7	0.6	1.4	0.8	0.1760	7.7	2.2	3.8	1.2	<0.0001
	Hemiptera	0.6	0.1	0.4	0.1	0.2753	0.2	0.1	0.1	0.1	0.1898
	Hymenoptera	7.2	1.3	3.6	0.7	0.0099	1.9	0.3	1.4	0.2	0.2148
	Preferred	23.8	7.6	17.1	5.4	0.0499	58.1	15.2	37.3	9.8	<0.0001
Other		17.0	11.9	5.1	4.0	<0.0001	39.7	25.4	27.8	17.9	0.0082
All Invertebrates		56.8	22.7	30.8	12.4	<0.0001	137.4	51.5	94.2	35.3	<0.0001

Table 32. Invertebrate biomass (mg/m^2) at ruffed grouse brood and random locations on the Wine Spring Creek Study Area, Macon County, North Carolina, 2000 - 2001.

Class	Order	2000					2001				
		Brood	SE	Random	SE	P-value	Brood	SE	Random	SE	P-value
Arachnida	Araneae	0.37	0.09	0.40	0.09	0.8278	0.86	0.11	0.68	0.09	0.0203
Hexapoda	Coleoptera	0.59	0.12	0.27	0.06	0.0106	0.12	0.02	0.16	0.03	0.2048
	Diptera	0.06	0.04	0.09	0.04	0.2930	0.38	0.07	0.17	0.04	<0.0001
	Hemiptera	0.06	0.02	0.07	0.02	0.5384	0.02	0.01	0.01	0.01	0.3681
	Hymenoptera	0.29	0.05	0.15	0.03	0.0181	0.13	0.02	0.09	0.02	0.0919
	Preferred	2.70	0.66	2.23	0.53	0.3953	4.32	0.66	3.06	0.46	0.0109
Other		9.89	7.18	1.80	1.35	<0.0001	6.48	4.15	4.95	3.17	0.2053
All Invertebrates		18.14	8.12	6.46	2.87	<0.0001	20.34	7.75	16.76	6.36	0.1734

Table 33. Invertebrate density (#/m²) compared between ruffed grouse brood and random locations during the early (hatch-3 weeks) and late (4 – 10 weeks) brooding periods on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

Class	Order	Early					Late				
		Brood	SE	Random	SE	P-value	Brood	SE	Random	SE	P-value
Arachnida	Araneae	9.5	2.5	7.9	2.1	0.1940	11.1	3.0	9.0	2.5	0.3022
Hexapoda	Coleoptera	1.4	0.5	1.6	0.5	0.6159	2.8	0.7	2.3	0.6	0.3152
	Diptera	11.7	3.6	5.9	2.0	<0.0001	4.5	1.6	4.7	1.7	0.8702
	Hemiptera	0.2	<0.0	0.1	<0.0	0.1600	0.4	<0.0	0.2	<0.0	0.0700
	Hymenoptera	3.2	1.2	2.5	0.1	0.1628	4.5	1.6	2.9	1.1	0.0504
	Preferred	78.0	25.7	49.9	16.5	<0.0001	58.5	19.5	39.8	13.3	0.0040
Other		21.0	8.1	14.8	5.8	0.0074	38.1	14.6	42.0	15.9	0.5836
All Invertebrates		112.5	31.0	77.9	21.6	<0.0001	116.4	32.3	104.6	29.0	0.2620

Table 34. Invertebrate biomass (mg/m^2) compared between ruffed grouse brood and random locations during the early (hatch-3 weeks) and late (4 – 10 weeks) brooding periods on the Wine Spring Creek Study Area, Macon County, North Carolina, 2001.

Class	Order	Early					Late				
		Brood	SE	Random	SE	P-value	Brood	SE	Random	SE	P-value
Arachnida	Araneae	0.94	0.18	0.73	0.14	0.1757	1.26	0.27	0.72	0.16	0.0257
Hexapoda	Coleoptera	0.13	0.03	0.18	0.04	0.2499	0.36	0.08	0.25	0.06	0.1860
	Diptera	0.51	0.12	0.25	0.07	<0.0001	0.18	0.06	0.22	0.07	0.3530
	Hemiptera	0.02	<0.00	0.01	<0.00	0.2201	0.03	<0.00	0.01	<0.00	0.1249
	Hymenoptera	0.17	0.04	0.12	0.03	0.0804	0.21	0.05	0.14	0.04	0.0761
	Preferred	5.87	1.46	4.12	1.03	0.0079	5.85	1.51	3.25	0.84	0.0015
Other		2.98	0.97	2.34	0.76	0.2489	6.35	2.15	11.08	3.67	0.0481
All Invertebrates		13.37	2.58	11.28	2.16	0.2045	19.88	4.11	23.03	4.68	0.4255

Table 35. Mid-story stem density (stems/ha) by forest type (as defined by Harper 1998) and age class on the Wine Spring Creek Study Area, Macon County, North Carolina.

Forest Type	Forest Age Class		
	0 – 12	13 – 39	>40
Xeric Mixed Pine-Hardwood	20,380	7,430	10,400
03 White Pine			
10 White Pine-Upland Hardwood			
15 Pitch Pine-Oak			
42 Upland Hardwood-White Pine			
45 Oak-Yellow Pine			
59 Scarlet Oak			
60 Chestnut Oak-Scarlet Oak			
Mesic Oak	24,240	10,010	3,887
52 Chestnut Oak			
53 White Oak-Northern Red Oak-Hickory			
55 Northern Red Oak			
Mixed Mesophytic Hardwood	20,240	4,330	3,400
08 Hemlock-Hardwood			
41 Cove Hardwood-White Pine-Hemlock			
50 Yellow Poplar			
56 Yellow Poplar-White Oak-Northern Red Oak			
Northern Hardwood	25,240	4,490	3,647
81 Sugar Maple-Beech-Yellow Birch			

VITA

Jennifer L. Fettinger was born in Lansing, Michigan on July 26, 1977. She graduated from Grand Ledge High School in 1995 and received her Bachelor of Science degree with honor in 1999 from Michigan State University. While at MSU she traveled to Kenya, Africa to study African wildlife ecology and management abroad and worked with the Michigan Department of Natural Resources. After graduation, she worked as a game bird intern at Tall Timbers Research Station in Tallahassee, Florida and as a moose research assistant with MSU in the upper peninsula of Michigan. She began her graduate research at the University of Tennessee in January 2000 and completed her research in May 2002. Jennifer began working with the Michigan Natural Features Inventory as an Associate Zoology Program Leader in May 2002.