Ruffed Grouse Reproductive Ecology and Nest Site Selection in Western North Carolina

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Abstract: Relatively low fecundity may be responsible for lower Ruffed Grouse (*Bonasa umbellus*) populations in the southern Appalachians compared to those in more northern areas of the species' range. Nutritional stress imposed by poor-quality habitat and greater nest predation have been cited as negative influences on reproduction in the region. We monitored 56 female grouse during the reproductive season in the Appalachian Mountains of North Carolina, 1999–2004, to measure reproductive success and evaluate cover used for nesting. Nests (*n* = 44) were located to determine fate and habitat characteristics. Nesting rate (78%) was lower than most reports, and mean first nest clutch size of 9.7 eggs was less than that reported in the Great Lakes states but was within the range reported in the central and southern Appalachians. Mayfield estimated nest survival was 0.83 (±0.084 SE) and the proportion of successful nests was 81%, which is among the greatest reported. Only 11% of females (1 of 9) renested following an initial nest failure, and overall hen success was only 61%. Females nested in various forest types with 86% occurring in stands >40 years old. Vegetation and topographic characteristics at nests did not differ from paired, random sites. Cover for nesting was not limiting. Increased nutrition during winter and early spring made available through increased forest management (regeneration harvests and improvement cuts) should lead to improved female physical condition and an increased nesting rate and overall hen success.

Ruffed Grouse (*Bonasa umbellus*) are less abundant in the southern portion of their range than in northern latitudes (Stauffer 2011). Several theories have been proposed to explain lower grouse numbers in the Appalachians, including additive mortality during extended hunting seasons (Stoll and Culbertson 1995), limited nutrition (Servello and Kirkpatrick 1987, Whitaker et al. 2007), and forest maturation (Dessecker and McAuley 2001). Together, these factors may contribute to lower annual reproductive output in the Appalachians compared to more northern populations (Stewart 1956, Haulton 1999, Dobony 2000).

Understanding reproductive parameters, including nesting rate, clutch size, and nest success, is necessary to evaluate management scenarios for ground-nesting birds (Peterson et al. 1998) because improving reproductive success may be a focus for management (Bergerud 1988). For example, habitat manipulation can affect reproduction by enhancing physical condition of females prior to nesting (Devers et al. 2007) and decreasing nest predation (Tirpak and Giuliano 2004).

Until recently, most ruffed grouse reproduction studies were conducted in the core of their range. As part of the Appalachian Cooperative Grouse Research Project (ACGRP), Devers et al. (2007) examined ruffed grouse population ecology on study sites across the central and southern Appalachians. However, only partial data (two of four years) from our study site in western North Carolina were included. Tirpak et al. (2006) reported characteristics at nests among ACGRP sites, but omitted data from North Carolina because unique forest associations typical of the southern Blue Ridge amplified variability of the data set. Additional insight can be gained from our study site because we provide estimates of reproduction near the southern-most extent of ruffed grouse range. Our objectives were to estimate nesting rate, clutch size, hatchability, nest success, and hen success to provide a measure of fecundity for ruffed grouse in the southern Appalachians. We also wanted to identify characteristics surrounding nest sites to determine potential limiting factors related to nesting that could be addressed through habitat management.

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Study Area

Our research site was the Wine Spring Creek Ecosystem Management Area (WSC, 3,230 ha) within the Nantahala National Forest in western Macon County, North Carolina. WSC lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915-1,644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges that connect upper elevations to narrow valley floors (Whittaker 1956). Mean annual temperature was 10.4 C, and mean annual precipitation was 160 cm. The area was predominantly forested with <1% in openings. The U.S. Forest Service purchased WSC in 1912 after it was logged extensively during the timber boom of the early 1900s. Forest management practices have since included salvage harvest of blight-killed American chestnut (*Castanea dentata*), thinning, clearcutting, and diameter-limit cutting (McNab and Browning 1993). In 1997, nine stands were harvested (three shelterwood, three two-age, and three group selection) to study the effects of these regeneration techniques on vegetation and wildlife response.

A Geographic Information System was developed for the study area. Vegetation communities were stratified into three categories (xeric, subxeric, and mesic) defined by elevation, landform, soil moisture, and soil thickness (McNab and Browning 1993). These moisture regimes were highly relevant to habitat classification with diverse forest types occurring across the study area (e.g., pitch pine-oak on dry ridge tops to basswood-buckeye in moist coves; Table 1). Additional areas included gated forest roads (ROAD) and small 0.25–0.5 ha wildlife openings (WLO). Stand ages were determined by years since harvest or stand establishment in cat-

egories deemed important to ruffed grouse (0–5, 6–20, 21–39, 40–80, >80). ROAD, WLO, and rhododendron (*Rhododendron maximum*)-dominated understory were not assigned age categories because they were in a state of arrested succession and their structural characteristics did not change appreciably over time (Phillips and Murdy 1985).

As a contributing study site to the Appalachian Cooperative Grouse Research Project, our study site was classified as "mixed mesophytic" by Devers et al (2007). However, mixed oak was the most common forest type and oak and mixed oak-hickory forest in the >80-year age class made up the greatest proportion of the study site (31.5%). Wildlife openings made up the least (0.2%) and young forest in the 6-to 20-year age class occupied 9.3% of the area.

Methods
Capture and Telemetry

Grouse were captured using interception traps (Gullion 1965) during late August–early November and early March–early April, 1999–2003. Sex and age (juvenile or adult) were assessed by feather characteristics (Kalla and Dimmick 1995). Grouse tagged as juveniles in fall graduated to adults at the end of the following summer. Grouse were weighed, leg-banded, fitted with 12-g necklace-style radiotransmitters with a 3-hour mortality switch (Advanced Telemetry Systems, Isanti, Minnesota), and released at capture sites. Tagged birds were located ≥3 times weekly throughout the year via triangulation from permanent geo-referenced (Trimble Navigation Limited Inc., Sunnyvale, California) telemetry stations. We used Telonics TR-2 receivers (Telonics Inc., Mesa, Arizona) and hand-held 3-element yagi antennas.

Females were located daily beginning 1 April to monitor nesting activity. A hen was assumed incubating when two consecutive locations occurred within a 0.25-ha area as estimated by the observer. We flushed females during the second week of incubation to visually locate the nest and determine clutch size. Thereafter, we monitored nests remotely to minimize disturbance. When a female was located away from the nest for >24 hours, we determined fate and clutch size within 1 day. For successful nests, we determined number of eggs hatched by eggshell fragments. We categorized unsuccessful nest fate as predation or abandonment (Jones 2005). Unsuccessful females were monitored daily after failure to determine if re-nesting occurred.

Nesting Chronology and Reproductive Parameters

We determined onset of continuous incubation by subtracting 24 days from the hatch date of each nest (Bump et al. 1947). We determined nest initiation dates by adding the number of incubation days (24) to the number of egg laying days (number of eggs

Table 1. Forest stand associations, understory characteristics, and corresponding USDA Forest Service (USFS) and Society of American Foresters (SAF) codes for land classifications on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Adapted from McNab and Browning (1993).

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

in clutch * 1.5 days) and subtracting the sum from the hatch date (Bump et al. 1947). Nesting rate was the proportion of females alive on 3 April ($n = 52$) known to reach incubation of an initial nest. We used 3 April because it was the earliest nest initiation date recorded on WSC. Nest success was the proportion of females that hatched ≥1 egg in an initial nesting attempt. Renesting rate was the proportion of females, unsuccessful in an initial nesting attempt that reached incubation of a second nest. Renest success was the proportion of renesting females that hatched ≥1 egg. Hen success was the proportion of females alive on 3 April that hatched ≥1 egg in an initial or renesting attempt. Clutch size was the mean number of eggs in initial nests, determined by flushing females during the second week of incubation. Hatchability was the proportion of eggs that hatched in successful nests.

Mayfield (1975) outlined several potential problems in reports of apparent nest survival (i.e., nesting rate and nest success), including a mixture of nests discovered early and late, nests with unknown outcomes, and observer bias in ability to locate nests. By using intensive radio telemetry, we located nests within three days of incubation onset, and once located, fate was determined for all nests. Use of radio telemetry minimizes observer bias among observers, and methodology on WSC was consistent with other ruffed grouse studies in Minnesota (Maxson 1978), Wisconsin (Small et al. 1996), and the Appalachian region (Whitaker 2003, Devers 2005, Tirpak et al. 2006, Devers et al. 2007). Therefore, for consistency with other research, reports herein include apparent nesting rate and apparent nest success as well as Mayfield nest survival during laying and incubation. We calculated Mayfield daily nest survival by dividing the number of failed nests by the total number of days nests were monitored and subtracting from 1 (Mayfield 1975). We calculated a survival estimate for the incubation period by raising daily nest survival by a power of 24.

We calculated annual reproductive parameters across individuals within each year. Mean parameters and standard errors were calculated across years. We calculated age-specific reproductive parameters with years pooled because small sample sizes precluded calculation of annual reproductive parameters for juveniles and adults separately. Difference in clutch size between juveniles and adults and distance to brooding sites were analyzed using the Generalized Linear Models (GLM) procedure in SAS. Nest survival was compared between juveniles and adults using chi-square methods described by Mayfield (1975).

Nest Site Selection

We collected vegetation data at nest sites within two days of determining nest fate. We sampled a paired random site 100 m in a random direction from each nest. We used 100 m because it represented the localized area within which the female could have nested. We estimated basal area from plot center with a 2.5 m²/ha prism and recorded trees ≥11.4 cm diameter at breast height (DBH) within a 0.04-ha plot. We recorded species and number of midstory saplings and shrubs <11.4 cm DBH and ≥1.4 m height within 4 DBH classes (<2.54 cm, 2.54–5.08 cm, 5.09–7.62 cm, and 7.63–11.4 cm) within a 0.01-ha plot. Woody understory seedlings <1.4 m in height were recorded within a 0.004-ha plot. Distance to nearest object such as a tree, rock, or other "backstop" also was recorded.

We recorded locations of nest and random sites with a Trimble Global Positioning System (Trimble Navigation Limited Inc., Sunnyvale, California) and incorporated them in the GIS. We used Patch Analyst 3.0 (Elkie et al. 1999) to calculate edge density (m/ha) within 100-m radius buffers around nests and random sites. We measured distance to nearest opening from these points. Openings included forest roads, wildlife openings, and 0- to 5-year-old forest. Small canopy gaps created by natural disturbance of one or a few trees were not included, as these features were not available in the GIS stand coverage.

At the study area scale, we generated additional points within a nesting area availability polygon to compare distances from random and nest sites to preferred brood-rearing cover (Jones et al. 2008). The availability polygon was defined by merging fall and winter home ranges of females because female ruffed grouse are thought to sample potential nest sites during these seasons (Bergerud and Gratson 1988). We calculated home ranges (95% fixed kernel) in ArcView GIS 3.2 (Environmental Systems Research Institute Inc., Redlands, California) using the Animal Movement Extension to ArcView with least squares cross validation (Hooge and Eichenlaub 1997). We used 95% kernel estimates because they incorporate home range periphery (Seaman et al. 1999) as available for nesting. We identified areas used for brooding through intensive telemetry from hatch to 5 weeks post-hatch (Jones et al. 2008). Relative preference of SUBXER1, SUBXER2, SUBXER5, and ROAD within SUBXER5 stands for brood rearing was determined through compositional analysis (Aebischer et al. 1993, Jones et al. 2008). For distance measurements, points that fell within preferred brooding cover were assigned a value of 0.

Statistical Analyses

We used an information-theoretic approach (Burnham and Anderson 1998) to evaluate nest and random site differences. We created a set of *a priori* candidate models (Table 2) using combinations of vegetation (basal area, midstory stem density, understory stem density) and landscape features (edge density, distance to opening). We calculated an estimate of ĉ from the global model to test for

Table 2. *A-priori* candidate models used to evaluate nest site selection by ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

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

a. USTEM = density of woody seedlings <1.4 m in height within 0.004-ha plots
MDSTEM = density of woody seedlings >1.4 m in height and <11.4 cm dbh within 0.004-ha plots
BASAL = basal area (m²/ha)
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites
DIST = distance to nearest opening including forest roads, wildlife openings, and 0–5-year-old forest

Table 3. Annual and mean reproductive parameters for female ruffed grouse on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Parameter	2000	2001	2002	2003	2004	Mean	SE
Nesting rate (%)	71 (5/7)	92 (11/12)	79 (15/19)	83 (10/12)	50 (3/6)	78	6.8
Nest success (%)	100 (5/5)	82 (9/11)	67 (10/15)	90 (9/10)	67 (2/3)	81	6.4
Renest rate (%)	0	50 (1/2)	0	0	0	10	9.8
Renest success (%)	NA	0 (0/1)	NA	NA	NA	NA	NA
Hen success (%)	71 (5/7)	75 (9/12)	53 (10/19)	75 (9/12)	33 (2/6)	61	8.2
Clutch size (eggs)	9.8	10.5	10.4	9.4	8.5	9.7	0.4
Hatchability (%)	98	93	95	97	100	97	1.2

over dispersion of the data. The data were actually under-dispersed ($\hat{c}=0.515$). We used bias-corrected Akaike's Information Criterion (AIC_c) and weight of evidence (w_i) to rank and select model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). We used logistic regression to calculate 2log-likelihood values for each model with nest sites=1 and random sites=0 (Procedure GLM, SAS Institute, Cary, North Carolina). Log-likelihoods were used to calculate Akaike's Information Criterion.

Results
Nesting Chronology and Reproductive Parameters

We radio-tagged 138 female ruffed grouse (97 juvenile, 41 adult). As a result of mortality and censoring, our sample size was reduced, allowing us to monitor 52 individuals during the spring reproductive season; 4 were monitored for multiple reproductive seasons. Females initiated first nests on a mean date of 12 April (0.84 days SE). Mean dates were similar between juveniles ($\bar{x}=14$ April± 1.35 SE) and adults ($\bar{x}=13$ April± 2.36 SE). Initial nest initiation dates ranged from 3 April–26 April. Start of continuous incubation ranged from 21 April–10 May ($\bar{x}=27$ April± 0.74 days SE). Mean hatch date was 21 May (0.74 days SE) with 80% of hatch occurring 17 May–27 May.

We recorded fate for 44 nests (35 successful, 9 unsuccessful). Mean annual nesting rate was 78% (6.8 SE; Table 3) and ranged from 50%–92%. Overall nesting rate was 74% ($^{29}/_{39}$) for juveniles and 88% for adults ($^{15}/_{17}$). Mean clutch size was 9.7 eggs (0.17 SE) and did not differ between juveniles ($\bar{x}=9.4\pm 0.37$ SE) and adults ($\bar{x}=10.6\pm 0.53$ SE, $P=0.0654$). Mean hatchability was 97% (1.2 SE).

Mean annual nest success was 81% (67%–100%; 6.4 SE). Overall nest success was 87% ($^{13}/_{15}$) for adults and 76% ($^{22}/_{29}$) for juveniles. Nest success did not differ between juveniles and adults ($\chi^2=1.42$, $P>0.500$). Mayfield nest survival during incubation across years was 0.83 (± 0.084 SE).

Only 11% of females (1 of 9) reached incubation of a second nest after initial nesting failure. Mean hen success was 61% (8.2 SE) and ranged from 33% to 75%.

Nest Site Selection

Most nests ($^{37}/_{43}$; 86%) were on mid- and upper slopes in mature mixed oak stands >40 years old, with a smaller percentage occurring in 6- to 20-year-old stands, rhododendron thickets, 5-year-old two-aged stands, and 21- to 39-year-old pole stands (Table 4). Small sample size of nests relative to forest types and age classes resulted in expected habitat use values <1, preventing statistical analysis of use versus availability at the stand scale. Weight of evidence was low ($\omega_i \leq 0.217$) for all nest site selection models, and Δ_i values indicated similar strength of evidence among members of the candidate set (Table 5). Nest site variable means were similar between nest and random sites with 95% confidence intervals overlapping for all variables (Table 6). Mean stem density at nest sites was 5,732 stems/ha (4,041–7,420, 95% CI) in the midstory and 19,000 stems/ha (9,610–28,389, 95% CI) in the understory. Mean basal area was 18m²/ha (15–20, 95% CI), and mean distance to nearest edge was 195 m (115–275, 95% CI). Total edge density was 394 m/ha (352–435, 95% CI), compared to 399 m/ha (344–454, 95% CI) for random sites. All nests were situated next to an object, 43% against stumps or fallen trees, 35% against standing trees, and 22% against rocks. Mean distance to preferred brood-rearing cover

Table 4. Ruffed grouse nest site selection and availability by moisture gradient and forest age class on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Moisture gradient and forest age class	Number nests	Use (%)	Availability (%)
XERIC2[a]	0	0	1
XERIC4	2	5	2
XERIC5	4	9	12
SUBXER1	1	2	1
SUBXER2	2	5	8
SUBXER3	1	2	2
SUBXER4	3	7	3
SUBXER5	16	37	32
MESIC4	8	19	10
MESIC5	4	9	9
RHODO	2	5	20
ROAD	0	0	1
WLO	0	0	<1

a. XERIC2 = dry oak, oak-pine uplands in 6–20-year age class
XERIC4 = dry oak, oak-pine uplands in 40–80-year age class
XERIC5 = dry oak, oak-pine uplands in >80-year age class
SUBXER1 = mixed oak hardwoods, oak-hickory forest in 0–5-year age class
SUBXER2 = mixed oak hardwoods, oak-hickory forest in 6–20-year age class
SUBXER3 = mixed oak hardwoods, oak-hickory forest in 21–39-year age class
SUBXER4 = mixed oak hardwoods, oak-hickory forest in 40–80-year age class
SUBXER5 = mixed oak hardwoods, oak-hickory forest in >80-year age class
MESIC4 = cove hardwood and northern hardwood forest in 40–80-year age class
MESIC5 = cove hardwood and northern hardwood forest in >80-year age class
RHODO = forest with >75% midstory coverage in rhododendron
ROAD = gated forest roads
WLO = wildlife openings

Table 5. Comparison of Akaike's Information Criterion (AIC$_c$), differences in AIC$_c$, and model weights (w_i) for ruffed grouse nest site selection models on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Model	AIC$_c$	ΔAIC$_c$	w_i
MDSTM[a]	96.845	0.000	0.217
BASAL	97.198	0.353	0.182
DIST	98.348	1.503	0.102
USTEM	98.401	1.556	0.100
ED	98.425	1.580	0.099
MDSTM + USTEM	98.703	1.858	0.086
ED + MDSTEM	99.032	2.187	0.073
ED + BASAL	99.231	2.386	0.066
BASAL + MDSTM + USTEM	100.372	3.527	0.037
ED + BASAL + MIDSTEM	100.519	3.674	0.035
BASAL + MDSTEM + USTEM + DIST + ED	105.068	8.223	0.004

a. MDSTEM = density of woody seedlings >1.4 m in height and <11.4 cm dbh in 0.004-ha plots
BASAL = basal area (m²/ha)
DIST = distance (m) to nearest opening including forest roads, wildlife openings, and 0–5-year old forest
USTEM = density of woody seedlings <1.4 m in height within 0.004-ha plots
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites

Table 6. Means and 95% confidence intervals for habitat variables at nest and paired random sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

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

a. USTEM = density of woody seedlings <1.4 m in height/ha
MDSTEM = density of woody seedlings >1.4 m in height and <11.4 cm dbh/ha
BASAL = basal area (m²/ha)
DIST = distance (m) to nearest opening, including forest roads, wildlife openings, and 0–5-year-old forest
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites

Table 7. Means and 95% confidence limits for habitat variables at successful and unsuccessful nest sites on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

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

a. USTEM = density of woody seedlings <1.4 m in height/ha
MDSTEM = density of woody seedlings >1.4 m in height and <11.4 cm dbh/ha
BASAL = basal area (m²/ha)
DIST = distance (m) to nearest opening, including forest roads, wildlife openings, and 0–5-year-old forest
ED = total edge density (m/ha) within 100-m radius buffers around nest and random sites

was similar ($P = 0.327$) between nest ($\bar{x} = 61 \pm 19.0$ m SE) and random points ($\bar{x} = 83 \pm 11.3$ m SE). Habitat models for nest fate were not created because sample size of unsuccessful nests was small ($n = 9$). However, mean habitat values were similar between successful and unsuccessful nests based on 95% confidence interval overlap (Table 7).

Discussion

Recent studies of ruffed grouse in the Appalachians suggest annual productivity is a limiting factor (Whitaker 2003, Devers 2005, Tirpak et al. 2006). We documented two components of fecundity (nesting rate and clutch size) that were low compared to areas with larger grouse populations supporting the hypothesis that nutrition is a limiting factor for grouse in the southern Appalachians. However, nest success and hatchability were consistent with those in areas of high-quality grouse habitat.

Reproductive Parameters and Nesting Chronology

The average nesting rate at WSC (78%) was lower than estimates of 100% from the Great Lakes States (Maxson 1978, Small et al. 1996). In New York, Bump et al. (1947) used systematic nest searching methods to estimate rates of 75%–100%, with all females attempting to nest in all but 3 of 13 years. Of 11 study sites in the Appalachians, nesting rates were 69%–100% (Devers et al. 2007). Only one area, located in northern Virginia (VA1), had rates lower than those reported here (Devers 2005). Seven ACGRP study sites (KY1, MD1, OH1, OH2, PA, RI1, and VA3) had nesting rates of 100%, whereas 3 (WV1, VA2, WV2) reported 98%, 96%, and 85%, respectively. Estimates of nesting rate and nest success from telemetry studies tend to be biased because most nests are not located prior to onset of continuous incubation. Nesting rate may be negatively biased as nests destroyed during laying are not discovered. For the same reason, nest success estimates may be artificially high. Larson et al. (2003) suggested the extent of bias in nest success reports can differ among areas, and comparisons among study sites may be inappropriate.

Habitat quality, especially food availability, may influence physiological condition and nesting by ruffed grouse in the Appalachians (Servello and Kirkpatrick 1987, Long et al. 2004). Devers et al. (2007) proposed nesting rates were lower on ACGRP sites dominated by oak-hickory forest, where grouse are dependent on annually variable hard mast production, compared with mixed mesophytic forests where alternate food sources, such as herbaceous plants and buds of more desirable species, were plentiful. The WSC study area was classified as mixed mesophytic by ACGRP; however, nesting rates were lower than similarly classed sites in Maryland, Pennsylvania, West Virginia, and Virginia (Devers 2005). Although our study site did have some mixed mesophytic forest (i.e., basswood-poplar coves), it was dominated by mixed oak and oak-hickory. Our lower nesting rates compared to other mixed mesophytic sites may have been a function of this greater dominance of oak on WSC.

Mean clutch size of 9.7 eggs was within the range of 9.2–11.3 reported by Devers (2005) for the Appalachians. However, clutches in the northern United States and southern Canada are generally larger, with reports of 11.4 in Ontario (Cringan 1970), 11.6 in Alberta (Rusch and Keith 1971), 11.5 in New York (Bump et al. 1947), 11.0 in Wisconsin (Small et al. 1996), and 12.7 in Michigan (Larson et al. 2003).

Variation in clutch size has been related to latitude in many bird species (Kulesza 1990, Gaese et al. 2000). Devers et al. (2007) attributed differences in clutch size within the Appalachians to latitude, with smaller clutches occurring on more southerly study areas. Variation in clutch size with latitude may be related to food availability (Cody 1966, Perrins and Jones 1974, James 1983, Findlay and Cook 1987) with the greatest role occurring on areas of poor site quality (Nager et al. 1997). Food availability plays the greatest role in clutch size on poor habitat (Nager et al. 1997). Ruffed grouse females in poor physiological condition tend to lay smaller clutches (Beckerton and Middleton 1982). In the Appalachians, nutritionally inadequate foods can cause physiological stress prior to nesting (Servello and Kirkpatrick 1987) that may result in decreased egg production.

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

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

Age may influence nest success, as nesting experience gained by juveniles could benefit future attempts (Bergerud 1988). Small et al. (1996) reported greater adult nest success compared with juveniles in Wisconsin. However, nest survival at WSC did not differ between juveniles and adults, similar to studies in northern Michigan (Larson et al. 2003) and across the central and southern Appalachians (Devers et al. 2007).

We recorded only one female (a juvenile) to renest at WSC. High success of initial nests precluded the opportunity to document subsequent attempts. Bump et al. (1947) argued renesting contributed little to annual reproductive output. Renesting rates determined by radio telemetry were 46% in Michigan (Larson et al. 2003) and 56% in Wisconsin (Small et al. 1996). In the Appalachians, Devers (2005) reported 23% renesting rate with a range of 0–50%. We flushed all females during the first 2 weeks of incubation to determine clutch size, and no females abandoned their nest after the disturbance.

Mean annual hen success (63%) was within the range of 47%–92% reported across ACGRP study areas (Devers 2005). Hen success has not been reported on other ruffed grouse research studies. We defined hen success as the proportion of females alive at the

beginning of the reproductive period that successfully hatched ≥1 egg in an initial or renesting attempt. This definition differed from that provided by Vangilder and Kurzejeski (1995) for wild turkeys, as they considered only females that attempted to nest or survived through the reproductive season. We calculated hen success as the cumulative contributions of nesting rate, nest success, renesting rate, and renest success to annual reproductive output. At WSC, high nest success offset relatively low nesting and renesting rates. Hen success at WSC highlights low nesting rate and relatively high nest success. Perhaps more than any other, this parameter can guide management strategies to increase ruffed grouse populations, with the greatest priority directed to management that could improve nesting rate.

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

Nesting phenology in southerly latitudes may be driven by early occurrence of warming spring temperatures compared with northern areas. In New York, Bump et al. (1947) attributed annual fluctuations in nesting to weather. They noted advanced nesting dates when average minimum temperature during the pre-nesting period was above normal. Data from WSC support this contention, as the earliest mean incubation date (in 2001), coincided with greatest mean minimum temperature during pre-nesting (15 March–14 April; Jones 2005). Although photoperiod determines the general timing of reproduction, annual and latitudinal fluctuations are likely influenced by climate.

Nest Site Selection

Placement of nests in open, mature forest was similar to reports from across the ruffed grouse range (Bump et al. 1947, Gullion 1977, Maxson 1978, Thompson et al. 1987). These studies and others (Larson et al. 2003, Tirpak et al. 2006) suggest females conceal nests against trees or other objects in stands that permit detection of advancing predators. Our inability to detect fine-scale differences in vegetation or topographic features at nests and random points suggests cover for nesting was not a limiting factor within the stands selected.

Female grouse may select nest sites based on predation risk

(Bergerud and Gratson 1988). Habitat characteristics on WSC were similar between successful and unsuccessful nests. However, given high success rates, few unsuccessful nests were sampled. In Michigan, Larson et al. (2003) could not relate variability in nest site structure to nest fate. Conversely, Tirpak et al. (2006) described a positive relationship among nest success, basal area, and coarse woody debris. To decrease predator efficiency, they suggested females nested against trees or debris in stands with numerous potential nest sites. Results from WSC support this contention, as females nested against objects, including trees, stumps, and fallen logs, and experienced high success rates. The >40-year old forest stands used by nesting grouse on WSC were not limiting on the study area or the surrounding landscape. In fact, this forest age class is becoming more ubiquitous as the rate of forest management on public lands declines.

Management Implications

Our data suggest fecundity could be a limiting factor for ruffed grouse populations in the southern Appalachians. Increased forest management, specifically regeneration harvests, improvement cuts, and planting forest roads, increases availability of nutritious foods for ruffed grouse, such as herbaceous plants, soft mast, and buds, and thereby can lead to improved physiological condition of females prior to nesting (Long et al. 2011) and ultimately hen success. Variation in topography, soils, and moisture in the southern Appalachians promotes diverse vegetation communities, with the greatest diversity often occurring on midslope transition zones between xeric uplands and mesic lower slopes (Whittaker 1956, Berner and Gysel 1969, McNab and Browning 1993). We encourage land managers in the southern Appalachians to intersperse forest age classes and use silvicultural methods, such as two-aged shelterwood, that provide diverse food resources within suitable protective cover (Jones and Harper 2007, Harper et al. 2011).

Acknowledgments

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