Ruffed Grouse Survival and Population Structure in Western North Carolina

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Abstract: Sound management of ruffed grouse (*Bonasa umbellus*) populations requires an understanding of survival and cause-specific mortality; however, these parameters have not been investigated at the southern extent of the species' range. Ruffed grouse were studied in the mountains of western North Carolina. Grouse (*n* = 276) were radiotagged and monitored >3 times/week. Mean annual survival was greater than reports from the northern core of the species' range. Seasonal survival was greatest in summer, followed by fall, winter, and spring. Of 155 mortalities, the greatest proportion was attributed to mammalian, followed by avian, and unknown predation, hunter harvest, and other. Scavenging prior to transmitter recovery may have positively biased mammalian predation rates. Despite long hunting seasons that extended into winter, hunter harvest rates were among the lowest reported in the literature. Population densities, estimated annually in spring, were 5.9–11.4 grouse/100 ha and showed no association with hunter harvest. Survival rates showed an inverse relation with population density. Lower survival when population density was greatest may be related to habitat availability.

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

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

Prior to 1996, most ruffed grouse telemetry studies had been conducted in the geographic core of ruffed grouse range (i.e., northern states such as Wisconsin and Minnesota). Differences in abundance (Johnsgard 1973), survival and reproductive output (Devers et al. 2007), fall age structure (Davis and Stoll 1973), ex-

tended hunting seasons (Stoll et al. 1999), and apparent lack of a 10-year population cycle preclude applying northern study results to southern portions of ruffed grouse range.

In 1996, the Appalachian Cooperative Grouse Research Project (ACGRP) was initiated to examine the species' population dynamics in the central and southern Appalachian Mountains. The ACGRP provided considerable insight into ruffed grouse survival from Pennsylvania to southwestern Virginia (Devers et al. 2007). However, ACGRP results did not include information from the southern extent of ruffed grouse range, which includes the southern Blue Ridge Mountains of eastern Tennessee, western North Carolina, and northern Georgia. Ruffed grouse hunting is popular in this region, particularly on public land where state wildlife agencies work cooperatively with the U.S. Forest Service to monitor and manage ruffed grouse. Detailed cause-specific mortality and survival information is paramount to these management efforts.

This study represents survival information from the southern extent of ruffed grouse range. Objectives were to (1) identify tem-

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

Study Site

We conducted research on Wine Spring Creek Ecosystem Management Area (WSC, 3,230 ha), within Nantahala National Forest in western Macon County, North Carolina. The area lies within the Blue Ridge Physiographic Province and is part of the southern Nantahala Mountain Range. Elevation ranges from 915 to 1,644 m. Terrain is characterized by long, steep ridges with perpendicular secondary ridges that connect upper elevations to narrow valley floors (Whittaker 1956). The area is predominantly forested. The U.S. Forest Service purchased WSC in 1912 after extensive logging representative of the period. Since then, forest management included salvage harvest of blight-killed American chestnut (*Castanea dentata*), thinning, clearcutting, and diameter-limit cutting (McNab and Browning 1993). Beginning in 1995, shelterwood, two-aged shelterwood, and group-selection harvests were implemented as part of a study to examine effects of these practices on various ecosystem aspects (Elliott and Knoepp 2005).

During the study, vegetative types included, mixed oak (*Quercus* spp.) >40 years old (34.2%), mixed hardwoods with rhododendron (*Rhododendron maximum*) dominated midstory (19.6%), mixed mesophytic and northern hardwoods >40 years old (18.8%), xeric upper elevation oak >40 years old (14.3%), regenerating mixed oak 6–20 years old (9.3%), pole-stage mixed oak 21–39 years old (1.6%), regenerating mixed oak 0–5 years old (0.8%), and maintained herbaceous clearings (0.2%). The area included 52.6 km of gated forest roads (1.1%).

Methods
Capture and Telemetry

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

We monitored grouse for survival 3–5 times/week during routine telemetry. When a mortality signal was emitted, we located the transmitter and ascertained cause of death from evidence at the site. Transmitters were located within a few hours after detection of a mortality signal. At mortality sites, we recorded predator sign (e.g., tracks, scat, whitewash), presence of cache, evidence of feeding on remains, and various site characteristics. For example, chewed bones cached under a log indicated mammalian predation. Picked bones and whitewash indicated avian. If conflicting sign was present, we classified the mortality as unknown predation. Additional causes of mortality included hunter harvest and "other" (disease, wounding loss, vehicle/tree collision). We recorded date of death as the midpoint between the last known alive date and detection of mortality (Pollock et al. 1989).

Population Index

We indexed population density from spring drumming counts (Jones et al. 2005). During drumming counts, we walked designated routes (i.e., gated forest roads) on two consecutive mornings beginning 30 minutes before sunrise and ending three hours after sunrise. The starting point on the second morning was the endpoint from the first morning. We selected routes so that approximately 20% of the area was sampled. We defined effective sampling area with 200-m buffers on both sides of each route (Jones et al. 2005). We listened for drumming while walking selected routes. When a drumming male was heard, we recorded estimated distance to drummer, time, and an azimuth to the bird. We calculated population estimates (grouse per 100 ha) by doubling number of drumming males to account for females under the assumption of a 1:1 breeding season sex ratio (Bump et al. 1947, Gullion and Marshall 1968, Rusch and Keith 1971).

We calculated grouse caught per unit effort in fall (grouse per100 trap-days) as a population density index. These data provided an effective index because trapping methods and effort were similar across years. We also calculated sex and age ratios from fall capture data. Although greater vulnerability of juveniles to capture may present bias (DeStefano and Rusch 1982), capture data provided an index for comparison to other studies that used similar techniques.

Statistical Analysis

We analyzed survival using the Known Fates Procedure in Program MARK (White and Burnham 1999). Known Fates uses a staggered entry (Pollock et al. 1989) modification of the product-limit estimator (Kaplan and Meier 1958). We used a 30-day time step. A bird was "at risk" during an encounter occasion (included during a particular period) if it was captured during the first 15 days of the interval. If it was captured from day 16–30 in an inter-

val, it was entered in the next encounter occasion. If contact was lost when a bird left the study area or a transmitter failed, it was right-censored (Pollock et al. 1989). Right-censoring indicated contact was lost without specifying fate. Juvenile grouse that survived through the year were right-censored 14 August following capture and re-entered as an adult on 15 August. Cause-specific mortality is defined as losses to a given mortality source in the absence of all other sources, or competing risks (Heisey and Fuller 1985); therefore, we calculated cause-specific estimates in MARK by retaining the mortality source of interest while right-censoring all other mortalities. We entered grouse in survival analysis after a seven-day period to exclude mortalities potentially caused by captures stress.

We calculated annual survival from 15 September–14 September. We further delineated each year into four 91-day seasons defined by plant phenology and grouse biology; fall (15 September–14 December) was a period of food abundance and dispersal among juveniles; winter (15 December–15 March) was defined by minimal food resources and physiological stress; spring (16 March–14 June) coincided with vegetation green-up and breeding activity; and summer (15 June–14 September) was a period of relatively low stress with maximum cover and food availability. We constructed Parameter Index Matrices (PIMs) to allow season and year estimates in the same analysis (White and Burnham 1999).

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

We used an information-theoretic approach (Burnham and Anderson 1998) to evaluate sources of variation in survival. We established a set of *a priori* candidate models using combinations of sex, age, year, season, and watershed. These covariates were used to investigate effects of sex and age, as well as temporal (within and among years) and spatial patterns on survival. We assessed models in program MARK using a bias-corrected version of Akaike's Information Criterion (AIC_c), and weight of evidence (w_i) to rank and select the model(s) that most parsimoniously fit the data (Burnham and Anderson 1998). We used bootstrapping to analyze goodness of fit and overdispersion (Cooch and White 2001). We investigated relations between fall population density and annual survival using the multiple regression procedure in SAS, Version 8.2 (SAS 2006). Values presented in the Results section are means + SE.

Results

We radio tagged 276 grouse over five years (Table 1). The overall percentage of juveniles in fall captures was 59.6%, ranging from 46.2%–66.7%. Thirty-two grouse died during the initial seven-day period after capture. Contact was lost during the initial seven-day period for an additional 12 grouse. Recapture of censored birds suggested faulty transmitters were most likely to fail within a few days following capture; therefore, these early censors may have been due to transmitter failure rather than unrecovered mortalities.

Two hundred-thirty two grouse were available for survival analysis. Of these, 155 mortalities were recorded. Across years, the greatest proportion of mortality was attributed to mammalian predators (42.6%), followed by avian (26.5%), unknown predation (12.9%), hunter harvest (11.0%), and other (7.0%). The "other" category included nine unknown causes, one vehicle collision, and one death from *Aspergillosis* (Schumacher 2002). Mean annual hunter harvest (i.e., proportion of annual mortalities due to hunting) based on band returns was 6.0%. Mean annual cause-specific rates (i.e., risk of death to individual mortality sources) followed the same pattern as raw proportions, with mammalian predation being most common (0.31+0.074) followed by avian (0.22+0.044), unknown predation (0.13+0.044), hunter harvest (0.10+0.028), and other (0.07+0.033). The seasonal risk of mammalian predation was lowest in summer (0.07), and relatively constant across fall (0.11), winter (0.10), and spring (0.11). Risk of avian predation was greatest in spring (0.09) compared with fall (0.06), winter (0.06), and summer (0.05).

Mean annual survival was 0.39+0.052, ranging from 0.26–0.56

Table 1. Capture period, capture effort (trapdays), number of grouse tagged, capture rate (grouse/100 trapdays), sex, and age of grouse captured on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Period	Trapdays	Captured	Rate	Ad fem[a]	Juv fem[b]	Ad male[c]	Juv male[d]
Fall							
1999	6,770	65	0.96	14 (22)[e]	24 (37)	21 (32)	6 (9)
2000	9,040	63	0.7	5 (8)	29 (46)	16 (25)	13 (21)
2001	10,350	70	0.68	8 (11)	22 (31)	17 (24)	23 (33)
2002	9,576	46	0.48	7 (15)	17 (37)	10 (22)	12 (26)
2003	8,560	16	0.19	2 (13)	4 (25)	5 (31)	5 (31)
Spring							
2000	94	4	4.26	0	0	4 (100)	0
2001	938	6	0.64	2 (33)	0	4 (67)	0
2002	96	1	1.04	1 (100)	0	0	0
2003	114	5	4.39	1 (20)	1(20)	2 (40)	1 (20)
Total	39,538	276	0.7	40 (14)	97 (35)	79 (29)	60 (22)

a. Ad fem = adult female
b. Juv fem = juvenile female
c. Ad male = adult male
d. Juv male = juvenile male
e. Values in parentheses are percentages of total capture during the period.

Table 2. Comparison of Akaike's Information Criterion (AIC$_c$), differences in AIC$_c$, and model weights (w_i) for ruffed grouse survival models based on year, season, area, sex, and age on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

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

a. Year = annual period from September 15–September 14; season = fall (15 September–14 December), winter (15 December–15 March), spring (16 March–14 June), summer (15 June–14 September); sex = male, female; age = juvenile, adult; area = watershed

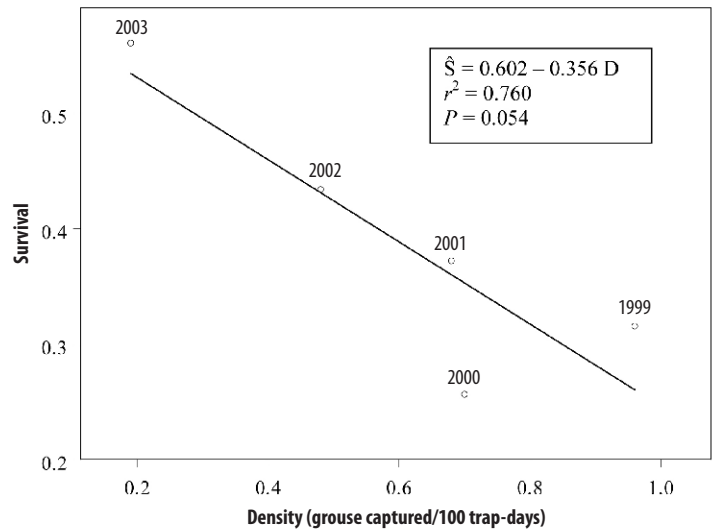b. K = number of model parameters

Figure 1. Relation of ruffed grouse annual survival with a population density index calculated from fall trapping success on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004.

Table 3. Survival rates of ruffed grouse by year and season on Wine Spring Creek Ecosystem Management Area, Macon County, North Carolina, 1999–2004. Annual survival for all years was calculated as an across year average. Seasonal survival for all years was calculated with years pooled.

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

(95% CI = 0.29–0.49). Seasonal survival was greatest in summer (0.87, 95% CI = 0.81–0.91), followed by fall (0.77, 95% CI = 0.73–0.80), winter (0.76, 95% CI = 0.72–0.80) and spring (0.74, 95% CI = 0.68–0.79). Overlapping confidence intervals suggested similar survival rates among fall, winter, and spring. Mean annual survival was 0.39 (95% CI = 0.28–0.51) for adult males, 0.42 (95% CI = 0.31–0.52) for juvenile males, 0.32 (95% CI = 0.13–0.50) for adult females, and 0.40 (95% CI = 0.36–0.43) for juvenile females.

The most parsimonious model contained a *year*season* interaction (AIC$_c$ = 1964.7, ω_i = 0.9999), suggesting seasonal survival differed among years (Tables 2, 3). Bootstrapping revealed data were not overdispersed (ĉ = 1.11). There was no support for models with combinations of *sex*, *age*, or *watershed* as explanatory variables (ω_i < 0.0001).

Annual survival showed an inverse relation with the popula-

tion index calculated from fall trapping data (r^2 = 0.76, P = 0.054, Figure 1). Spring population density index, estimated from drumming counts, ranged from 5.88 grouse/100 ha in 2003 (the year of greatest survival) to 11.4 grouse/100 ha in 2000 (the year of lowest survival).

Discussion

Survival and Cause-Specific Mortality

The *year*season* model may have been influenced by two seasons with no mortalities: summer and fall 2003. Because standard errors on mean annual and seasonal survival were small, we believe it appropriate to use these survival rates for discussion. To be conservative, we used confidence intervals around WSC means for comparison to other studies.

Compared with other telemetry studies, grouse annual survival

(95% CI = 29%–49%) was greater than reports from northern areas and similar to 42% reported by Devers et al. (2007) in the Appalachians. Of 11 other ACGRP sites, WSC survival was similar to studies in Virginia, West Virginia, Kentucky, Maryland, Rhode Island, and Pennsylvania. By comparison, survival rates in northern ruffed grouse range were 11% in Minnesota (Gutierrez et al. 2003), 25%–37% in Michigan (Clark 2000), and 25% for adults and 7% for juveniles in Wisconsin (Small et al. 1991).

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

Even though goshawks are not a frequent threat in the Appalachians, red-tailed hawks (*Buteo jamaicensis*), red-shouldered hawks (*Buteo lineatus*) broad-winged hawks (*Buteo platypterus*), Cooper's hawks (*Accipiter cooperii*), and great horned owls (*Bubo virginianus*) are important grouse mortality causes (Bumann and Stauffer 2004). However, evidence at our mortality sites showed mammalian predation accounted for the greatest losses. Bumann and Stauffer (2002) found mammals scavenged >65% of placed grouse carcasses and warned of overestimating mammalian predation based on mortality site evidence. The narrow margin between mammalian and avian predation on WSC may have resulted from such bias.

Survival estimates did not differ between juveniles and adults, indicated by lack of age effect in survival models. Similar results were reported in Minnesota (Gutierrez et al. 2003) and across the Appalachians (Devers et al. 2007). An age effect was apparent in Wisconsin (Small et al. 1991) and non-telemetry studies in New York (Bump et al. 1947) and Alberta (Rusch and Keith 1971). These authors proposed greater juvenile mortality was a function of dispersal. Combined factors, including exposure to predators during extended movements, increased energetic demand, and traversing unfamiliar space may increase risk for dispersing juveniles (Small and Holzwart 1993, Yoder et al. 2004).

There may be several reasons age-specific survival differences were not observed on WSC. First, there may not be real survival differences by age. Second, trapping efforts were concurrent with dispersal; therefore, juveniles may have completed or nearly completed dispersal at their time of capture. Juveniles tagged during a dispersal movement may have been passing through the study area, and were subsequently right-censored when contact was lost. As a result, only those grouse that completed dispersal were monitored, obscuring survival differences for dispersing juveniles.

Seasonal survival was greatest in summer (87%) and similar among fall (77%), winter (76%), and spring (74%). Slightly lower survival in spring may have been a function of reproductive activities (i.e., nesting and drumming) coinciding with raptor migrations. Further, mortality risk to avian predators was greatest during spring. Relatively high survival in summer might be expected considering it is a period of maximum cover and food availability. Swanson et al. (2003) reported survival of ruffed grouse in Ohio was greatest in summer and lowest in spring and fall. Other studies also showed greatest survival in summer (Small et al. 1991, Devers et al. 2007), indicating seasonal rates were lowest in winter. Winter survival on WSC (76%) was similar to ACGRP sites (72%; Devers 2005) and greater than Wisconsin (55%–57%; Small et al. 1991). Greater survival of Appalachian grouse in winter compared with northern areas may be influenced by less severe winters in southern ruffed grouse range.

Hunter Harvest

Concern exists regarding additive mortality from hunting seasons that extend through winter (DeStefano and Rusch 1982, Bergerud 1985, Stoll and Culbertson 1995). On WSC, mean harvest rate (6%) was considerably lower than 17%–49% in Wisconsin (Kubisiak 1984, Rusch et al. 1984) and 13%–20% in New York (Bump et al. 1947). Estimates of 4%–13% from the ACGRP also were lower than northern areas (Devers et al. 2007). During a compensatory mortality experiment comparing hunted and un-hunted areas, Devers et al. (2007) found no survival increase in the absence of hunting and suggested harvest rates <20% should be compensatory.

Harvest rates on WSC were among the lowest reported across grouse range. Although hunting seasons extended through late February, 65% of hunter returned bands were submitted during the first nine weeks of the season (October–December). Given relatively high annual survival and low harvest, there was no evidence that hunting was detrimental to the WSC grouse population. Further, the spring population index was greatest following the year of greatest hunter harvest, suggesting compensatory mortality.

Population Structure

Drumming surveys should be viewed as a population index rather than an absolute census of grouse. The index showed a decreasing trend throughout the study. As the density index decreased, an increase in survival was observed (Figure 1). This inverse relation between survival and population index may have been caused in part by habitat availability. At higher densities, some grouse may use marginal habitats, thus increasing generalist predator efficiency. As grouse numbers decrease, their suscep-

tibility to predation may decrease as availability of optimal cover increases. Predators then may concentrate on species other than grouse (Bergerud 1988). Grouse survival exerts an influence on population density in the Appalachians (Devers et al. 2007). Increased survival observed on WSC could have increased density; however, this effect may not have been realized in the absence of suitable habitat.

Recruitment is an important aspect of population ecology. As an index, ruffed grouse studies use hunter-submitted wings and tails to estimate proportion of juveniles in fall populations (Davis and Stoll 1973, DeStefano and Rusch 1982, Norman et al. 1997). On WSC, hunter band returns were limited to radiotagged grouse; therefore, proportion of juveniles in fall captures provided the only recruitment index. Although this index may be positively biased because juveniles are more susceptible to capture than adults (Destefano and Rusch 1986), it serves as a basis for comparison with other studies. The proportion of juveniles in fall (47%–67%) was less than means of 76% in Alberta (Rusch and Keith 1971) and 78% in Wisconsin (Dorney 1963) and similar to Ohio (42%–56%; Davis and Stoll 1973) and Virginia (22%–59%; Norman et al. 1997). Lower recruitment may be influenced by habitats with inadequate foods that cause physiological stress and decreased reproduction (Servello and Kirkpatrick 1987). Although nest success was relatively high on WSC (Jones 2005), the recruitment index suggested other aspects such as chick survival, immigration, or emigration might have been limiting. Because chicks were not radio tagged on WSC, reliable chick survival estimates were not available.

Immigration and emigration also influence population density. During dispersal, juvenile grouse move 1–6 km from natal ranges (Bump et al. 1947, Chambers and Sharp 1958, Godfrey and Marshall 1969, Small and Rusch 1989). During this time, 50% of juveniles may emigrate (Chambers and Sharp 1958), with a greater proportion dispersing when habitat is limiting (Bump et al. 1947). Population density on WSC may have been affected by losses to emigration that were not balanced by immigration. The landscape within a 5-km radius surrounding WSC contained 5% coverage in 6- to 20-year-old mixed oak forest, a highly selected vegetation type (Jones 2005). At such low levels, interspersion of forest age classes is limited and may fall below a minimum threshold for ruffed grouse. Relatively poor habitat in the surrounding area may have resulted in WSC acting as a source population that contributed birds, surrounded by a sink that did not replace these losses.

During this study, approximately 9% of WSC forest was in the 6- to 20-year age class. With habitat improvement (i.e., creation of young forest interspersed with other habitat types), grouse density may increase as it has done on other mixed oak-dominated areas.

In the absence of habitat management, the proportion of WSC forest in the 6- to 20-year age class will be reduced to 2% by 2010, possibly causing further population decline. Potential for unbalanced emigration and immigration stresses the need to manage entire landscapes as opposed to creating habitat islands surrounded by an otherwise unsuitable matrix.

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