



## Ruffed grouse-habitat preference in the central and southern Appalachians

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### ABSTRACT

Ruffed grouse (*Bonasa umbellus*; hereafter grouse) populations in the central and southern Appalachians (CSA) are declining due to widespread maturation of forest cover. Effective management of this species requires a sex- and age-specific understanding of habitat preferences at multiple temporal and spatial scales. We used multivariate logistic regression models to compare habitat within 1440 grouse home ranges and 1400 equally sized buffered random points across 7 CSA study areas. On most sites, grouse home ranges were positively associated with roads and young forest (<20 years old). Sex and age status affected habitat preference. In general, males used younger forest than females, likely because of differences in habitat use during reproductive periods. Juveniles had fewer vegetation types preferred by adult grouse and more of the avoided vegetation types within their home ranges, indicative of competitive exclusion. Adult females had the greatest specificity and selectivity of habitat conditions within their home ranges. Habitat selection varied among seasons and years on most sites. Winter habitat use reflected behavior that maximized energy conservation, with open vegetation types avoided in the winter on the northernmost study areas, and topography important on all areas. Summer habitat selection reflected vegetation types associated with reproductive activities. Scale influenced habitat preference as well. Although roads and forest age predominantly influenced grouse home range location within the landscape, mesic forest types were most important in determining core area use within the home range. This was likely a result of increased food availability and favorable microclimate. Habitat management efforts should attempt to maintain ~3–4% of the landscape in young forest cover (<20 years old), evenly distributed across management areas. Roads into these areas should be seeded as appropriate to enhance brood habitat and provide travel corridors connecting suitable forest stands.

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### 1. Introduction

Ruffed grouse are associated with aspen (*Populus* spp.) stands across most of their North American range (Svoboda and Gullion, 1972). However, in the CSA, grouse are found at the periphery of their range, where aspen is sparse (Cole and Dimmick, 1991). Although grouse populations in the CSA have historically occurred at lower densities than populations in aspen-dominated landscapes (Bump et al., 1947), data suggest further depressions in CSA grouse

numbers are a result of a decline in young forest cover (Dessecker and McCauley, 2001).

Ruffed grouse may be particularly sensitive to spatial and temporal changes at the landscape scale because the habitat they occupy has a limited “time window” and is continually lost through forest maturation (Pulliam, 1996). Although grouse in the CSA inhabit structurally similar young forest cover of birds in aspen-dominated landscapes, they are also found over a broader range of forest stand compositions and ages (Barber et al., 1989; Whitaker et al., 2007), topography (Fearer, 1999), and road density (Whitaker et al., 2007).

Clearly, forest composition and age influence reproduction and survival (Pulliam, 1988), and any shift in habitat use has impli-

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cations on grouse population dynamics (Pulliam and Danielson, 1991). Therefore, understanding habitat preference is critical to accurately predicting the future distribution and abundance of grouse in these landscapes. However, differential habitat use among male, female, adult, and juvenile birds complicates this effort (Stauffer and Peterson, 1985; Whitaker et al., 2006). Typically, assessment of habitat suitability ignores this heterogeneity and assumes similar limiting factors for all ages and sexes (Cade and Sousa, 1985; Hammil and Moran, 1986; Larson et al., 2003), which can lead to models with poor predictive power (Van Horne, 1986) and management actions that enhance habitat for one group while degrading it for another (Tirpak, 2005).

Grouse-habitat preference also varies temporally (e.g., diurnally [Tirpak et al., 2005], seasonally [e.g., Jones, 2005], and annually [e.g., Gullion, 1977]). Failure to incorporate the variability associated with these temporal scales may result in biased estimates of habitat use, preference, and suitability (Schooley, 1994; Thomas and Taylor, 1990; Zimmerman et al., 2009). Appropriate spatial scale is another critical element in habitat studies (Villard et al., 1998). However, multiple scales are rarely examined (Johnson, 1980), and models based on data from only one scale at one time period may lead to spurious conclusions (Pribil and Picman, 1997). Hence, to properly manage grouse and predict potential effects on population trajectories, it is important to understand how habitat physiognomy and composition affect age- and sex-specific grouse-habitat preference at different temporal and spatial scales (Turner et al., 1995). Therefore, our objectives were to quantify and compare habitat preference of ruffed grouse: (1) varying in sex and age, (2) intra- and interannually, and (3) at multiple spatial scales, in the central and southern Appalachians.

## 2. Materials and methods

### 2.1. Study areas

Seven study areas associated with the Appalachian Cooperative Grouse Research Project (ACGRP) were selected for this research based on logistical considerations. These study areas were located as follows: 1 each in MD (MD), NC (NC), and PA (PA) and 2 each in VA (VA2 and VA3) and WV (WV1 and WV2). These study areas encompassed the various land ownerships, physiographic regions, forest cover types, elevations, and land uses of the CSA (Tirpak, 2005). Detailed descriptions of each study area are provided in Fecske et al. (2002) for the MD site, Jones (2005) for the NC site, Tirpak et al. (2005) for the PA site, Haulton (1999) for the VA sites, and Dobony (2000) for the WV sites.

### 2.2. Data collection and analyses

Ruffed grouse were captured on each site using modified lily pad and mirror traps (Gullion, 1965) during the spring (March–April) and fall (August–October), 1995–2001. Trapping effort on individual sites varied among years, commencing on the WV1 site during 1995, on the WV2, VA2, VA 3, and MD study areas during 1996, in PA during 1998, and in NC in 1999. Trapping continued through 2000 on all sites except MD, which concluded trapping in 1999.

Upon capture, birds were aged and sexed according to standard feather criteria (Hale et al., 1954), equipped with a necklace-style radiotransmitter (10 g, 1–3% of body mass; Advanced Telemetry Systems, Isanti, MN) and uniquely numbered aluminum leg band (National Band and Tag, Newport, KY), and then immediately released at the capture site. All capture, handling, and marking techniques were approved by the Animal Care and Use Committees of collaborating institutions.

We established a network of telemetry receiving stations on each site. The Universal Transverse Mercator (UTM) coordinates

of each of these stations were obtained using a global positioning system and were differentially corrected to limit positional error to <5 m. Using portable receivers and Yagi antennas at these stations, observers relocated birds via triangulation 2–3×/week throughout the year. For each bearing, we recorded date, time, station, azimuth, signal strength, and mode (e.g., dead or alive).

For location attempts with  $\geq 3$  bearings collected within 30 min (White and Garrott, 1990), we calculated each bird position using Lenth's maximum likelihood estimator (Lenth, 1981). Based on error assessments of the observers, we used a mean bearing error of 7° to calculate the 95% confidence ellipses for location estimates. Locations with error ellipses >10 ha or >800 m from a telemetry station were considered unreliable and not used. This approach conservatively estimated positional error for each location at 160 m (Whitaker, 2003). Finally, bird locations in the first week following capture were censored to prevent any bias related to changes in behavior associated with capture or handling.

We used the Animal Movement Extension to ArcView 3.3 (Hooge and Ichenlaub, 1997) to construct 50% and 95% fixed-kernel home range estimates for grouse with  $\geq 30$  reliable telemetry locations (Seaman et al., 1999). Least squares cross validation was used to estimate the smoothing factor for all kernels (Seaman and Powell, 1996). Both annual (1 September–31 August) and seasonal (winter [1 September–28 February] and summer [1 March–31 August]) home ranges were constructed for each grouse. Dates were selected to reflect significant life history events for ruffed grouse: breeding in early March (Thompson et al., 1987) and brood breakup in early September (Godfrey and Marshall, 1969).

To characterize available habitat for use in assessing selection, we generated 200 random points per site and buffered each with a circle equivalent to the average circular home range area of grouse on that site. To determine exact habitat compositions of both grouse and random home ranges, we used the Xtools extension to ArcView 3.3 (Delaune, 2003) to intersect the kernel home ranges and buffered random points with maps depicting 15 habitat types from 5 main variables: topographic moisture index, overstory type, understory type, age, and roads (Table 1; Tirpak, 2005). Maps were derived from a combination of classified Landsat TM imagery, digital elevation models, and preexisting datasets (Tirpak, 2005). The area of each habitat variable within each home range (i.e., habitat used) and random buffer was determined and converted to a percentage.

We used multivariate logistic regression to develop habitat preference models. To reduce the number of potential variables in the candidate models, we first eliminated those with  $P > 0.200$  in univariate analyses (Hosmer and Lemeshow, 2000), and then eliminated one variable from any highly correlated pairs ( $r \geq 0.70$ ). The variable retained was the one with the greatest  $F$ -ratio derived from an ANOVA comparing grouse and random home ranges (McGarigal et al., 2000). This correlation analysis also relaxed unit-sum constraints (i.e., a vegetation type is selected because another is avoided) by requiring each variable to be independent (Aebischer et al., 1993). Finally, “best” models ( $P \leq 0.05$ ) were fit from the remaining variables using backward stepwise procedures with  $P$ -to-enter and  $P$ -to-leave = 0.150.

To determine how sex and age differences affected habitat selection patterns, we developed models for each of the following: all birds, females, males, adults, juveniles, adult males, adult females, juvenile males, and juvenile females. Birds were considered juveniles until 1 September of the year following their hatch (i.e., ~1.5 years post-hatch). Because ruffed grouse have large interannual shifts in the location and size of home ranges (Whitaker et al., 2007), habitat selection patterns of individual birds likely vary widely among years. Therefore, we treated each home range as the experimental unit and used multiple home ranges from the same bird when possible. To investigate potential intra- and interannual

**Table 1**  
Ruffed grouse-habitat features (%) within study areas, central and southern Appalachians, 1995–2001.

Habitat class Habitat type	Study areas						
	MD	NC	PA	VA2	VA3	WV1	WV2
Topographic moisture index							
Mesic	10.2	1.9	23.4	5.3	11.9	7.4	0.0
Mesoxeric	26.3	14.3	32.0	34.2	36.2	18.2	53.7
Xeric	63.5	83.8	44.6	60.5	51.9	74.4	46.3
Overstory type							
Agriculture <sup>a</sup>	8.8	1.4	0.2	1.4	5.2	0.7	1.6
Bare ground <sup>b</sup>	4.5	2.8	1.0	2.0	5.2	2.5	1.8
Evergreen overstory	8.9	20.3	10.9	15.2	17.0	12.2	18.8
Hardwood overstory	38.6	36.1	51.9	24.0	32.0	53.2	29.3
Oak overstory	37.6	39.4	35.4	57.2	40.2	31.3	47.2
Water	1.6	<0.1	0.6	0.2	0.501	<0.1	1.2
Forest stand age							
1–10 years old forest	0.2	1.8	0.0	4.4	0.2	2.3	4.6
10–20 years old forest	0.0	5.9	9.6	11.6	1.1	1.0	6.4
>20 years old forest	84.9	88.1	88.6	80.5	87.9	93.4	84.4
Understory type							
Non-evergreen understory	67.9	32.6	66.9	46.6	44.8	41.7	46.4
Evergreen understory	8.4	42.9	20.4	34.6	27.4	42.8	30.1
Road							
Road <sup>c</sup>	3.7	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

<sup>a</sup> This category contained agricultural areas, including pastures and hayfields, gas wells, planted wildlife clearings, and larger log landings (these could not be differentiated using our classification system [Tirpak, 2005]).

<sup>b</sup> This category included new clearcuts lacking plant regrowth, rock outcrops, strip mines, and gravel pits (these could not be differentiated using our classification system [Tirpak, 2005]).

<sup>c</sup> Road included all paved (~10%) and unpaved (~90%) roads, and unmaintained trails wide enough for a vehicle, all with a large edge buffer of herbaceous vegetation. Road area included the road itself and a 15 m buffer on either side (Tirpak, 2005).

differences in habitat selection patterns, models were developed based on annual home ranges for each year of the study and seasonal home ranges from all years. These models were developed at Johnson's level II scale (i.e., home range within the landscape). To assess the effect of changing scale, models were also developed at Johnson's level III scale (i.e., habitat within the home range). While level II analyses compared habitat composition of the 95% kernel grouse home ranges to that of the buffered random points, Level III analysis compared differences in the habitat composition between 50% and 95% kernel home ranges with differences in the habitat composition between random point buffers representing 50% and 95% area averages (Johnson, 1980). All random point buffer sizes were adjusted to reflect the different average home range size of birds in each set. Each study area was modeled separately due to large differences in sample sizes among sites (Erickson et al., 2001). Models were not constructed for any set represented by <5 individuals, a liberal criterion that ensures a maximum number of comparisons could be made among sites (Hosmer and Lemeshow, 2000).

Following model building, we determined the importance of each habitat variable by arranging the variables in each model (excepting the intercept) by the magnitude of their coefficients. Variables not included in a model were considered neutral and assigned a coefficient of 0. Because all variables in the model represent the percentage of that habitat class, use of the coefficients for each variable is analogous to ordering each by its odds ratio. To compare variable coefficients between models, we employed the Wald statistic (Hosmer and Lemeshow, 2000). Sets with no differences between coefficients among variables were considered equivalent. We considered tests significant at  $P \leq 0.05$  to prevent unwarranted segregation of classes. All tests were conducted using SYSTAT software (SYSTAT, 1999).

### 3. Results

Between 1995 and 2001, 637 different grouse were trapped on the 7 study areas. From these birds, we were able to estimate 637 annual, 333 summer, and 406 winter home ranges, representing

511, 276, and 321 individuals, respectively, with 211 adult, 96 juv, and 1 unknown-age males and 197 adult, 122 juv, and 8 unknown-age females.

#### 3.1. All birds

Grouse home ranges contained greater road and young forest and less agricultural area than random sites, and were the most important covariates on the majority of study areas. Other variables either occurred only in site-specific models or exhibited no clear pattern among sites (Table 2). Models differed among all sites (minimum  $W = 0.390$ ,  $P = 0.004$ ), except PA and VA3 (minimum  $W = 0.014$ ,  $P = 0.059$ ).

#### 3.2. Age and sex

Adult home ranges contained greater road area than random areas on all but the WV sites, where avoidance of agricultural fields and older forest occurred (Table 3). Home ranges of juveniles exhibited similar patterns (Table 3). However, these habitat features were not as abundant in juvenile home ranges as in adult home ranges (road area was lower on the MD and VA sites and older forest more abundant on both WV sites). Adult and juvenile models were equivalent only on the NC and PA sites (Supplementary Appendix A).

Roads were the most important parameter in habitat models of male home ranges on the NC and VA sites. Alternatively, in PA and on both WV sites, males were mostly associated with young forest cover (Table 4). Female home ranges were similarly dominated by roads on the NC, PA, and VA sites. However, avoidance of open agricultural and barren areas was a critical feature of female habitat use on MD and WV sites. Females on all sites secondarily responded to young forest, particularly in the 10–20 years age class (Table 4). Male and female selection differed on all sites. Males were associated with more roads than females on the MD and NC sites, greater evergreen understory area on the MD and VA3 sites, and younger forest, particularly in the 1–10 years age class, on the VA2 and WV study sites (Tables 4 and 5).

**Table 2**  
Maximum likelihood estimates of logistic models predicting the probability of ruffed grouse use from habitat composition, all birds, central and southern Appalachians, 1995–2001.

Variable	MD		NC		PA		VA2		VA3		WV1		WV2	
	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P
Intercept	-0.51 ± 1.17	0.665	-2.90 ± 0.47	<0.001	-4.76 ± 0.65	<0.001	-7.18 ± 2.23	0.001	-2.32 ± 0.88	0.009	2.87 ± 1.15	0.013	7.07 ± 0.72	<0.001
Mesic	0.03 ± 0.01	0.021									0.11 ± 0.04	0.002		
Xeric							0.03 ± 0.01	0.044	-0.04 ± 0.01	0.002				
Agriculture	-0.10 ± 0.03	<0.001	-1.39 ± 0.90	0.121							-0.87 ± 0.41	0.032		
Bare ground														
Evergreen overstory														
Hardwood overstory	-0.08 ± 0.03	0.007												
Oak overstory	-0.09 ± 0.03	0.001												
Water														
1–10 years old forest					0.07 ± 0.01	<0.001								
10–20 years old forest									0.08 ± 0.04	0.029	0.14 ± 0.04	0.001		
>20 years old forest											-0.04 ± 0.01	0.005	-0.09 ± 0.01	<0.001
Non-evergreen understorey	0.07 ± 0.03	0.003												
Evergreen understorey	0.08 ± 0.04	0.023	0.155 ± 0.05	0.001	0.22 ± 0.07	0.003	0.20 ± 0.05	<0.001	0.24 ± 0.05	<0.001	-0.04 ± 0.01	0.001		
Road														

Models of adult male home range habitat contained many variables important in both the aggregated adult and male categories. Roads were the first model component on all but the WV sites, where selection of young forest and avoidance of old forest were the most important parameters (Table 5). Juvenile male home ranges exhibited similar patterns on the VA3 and WV1 sites. However, roads were more important than young forest on the WV2 site, and neither of these habitat features was important to juvenile males on the MD or VA2 sites (Table 5). Too few juvenile male home ranges were available on the NC or PA sites to develop models.

Models of adult female home range habitat associations also contained roads as an important covariate on most non-WV sites and 10–20 years old forest on the WV sites. Additionally, models of adult female home ranges on all but the WV2 site included either overstory composition or topographic moisture index. MD, VA2, VA3, and WV1 sites contained >1 habitat class from each (Table 6). These additional habitat covariates resulted in poor fit between adult female and either adult or juvenile male models (minimum  $W=4.760$  and  $4.225$ ,  $P=0.029$  and  $0.040$ , respectively), except on the NC site (minimum  $W=2.453$  and  $2.796$ ,  $P=0.117$  and  $0.095$ , respectively). Habitat models of juvenile female home ranges were slightly more cosmopolitan. Although they contained more roads and 10–20 years age forest common to adult females, only topographic moisture index was an important secondary model variable (Table 6). Still, differences among these variables were large enough to warrant separate models for adult and juvenile females on all sites except NC (Supplementary Appendix B).

### 3.3. Year and season

Models varied among years on most sites. At the extreme, on the MD site, the most important variable differed for each year of the study and 6 variables were unique to a single model (Supplementary Appendix C). We observed a similar discordance among years on the PA and WV2 sites. Other sites exhibited greater consistency among years. Roads were the most important variable for 3 of 5 years on the VA2 site and 4 of 5 years on the VA3 site (Supplementary Appendix C). On the WV1 study area, 10–20 years old forest occurred in 5 out of 6 models and mesic habitats in 4 (Supplementary Appendix C). Still, only on the NC site were models similar between any two years, 1999 and 2000, the only available for that site ( $W=0.020$ ,  $P=0.887$ ).

Models differed between most study areas each year. However, in 1999, 10–20 years old forest was the most important selection factor on 5 of 7 study areas (VA2, MD, PA, VA3, and WV1). The latter 4 also all contained an overstory variable. Roads were the most important variable on the other two sites, of which, WV2 contained an overstory variable.

Sufficient winter home range estimates were available to develop habitat models on all but the NC site (Table 7). Road area was greater in winter home ranges than in random areas on all sites and the most important covariate on the WV2 and both VA sites. On the MD, PA, and WV1 sites, avoidance of agricultural and barren lands dominated habitat models.

Road and 10–20 years old forest area dominated models of summer habitat (Table 7). Roads were the most important variable on the NC, PA, and two VA sites, while 10–20 years old forest was the most important variable on the two WV sites. Roads were secondarily important on the WV1 site, and 10–20 years old forest was secondarily important on the PA and VA3 sites. Avoidance of agricultural and oak-dominated areas were the two most important covariates on the MD site. Winter and summer models differed by at least 1 variable on all sites; however, no consistent differences were observed between seasons among sites (Supplementary Appendix D).

**Table 3**  
Maximum likelihood estimates of logistic models predicting the probability of ruffed grouse use from habitat composition, adult and juvenile birds, central and southern Appalachians, 1995–2001.

Age Variable	MD		NC		PA		VA2		VA3		WV1		WV2	
	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P
<b>Adult</b>														
Intercept	-2.38 ± 1.45	0.100	-3.18 ± 0.49	<0.001	-1.93 ± 2.83	0.496	-8.450 ± 1.89	<0.001	-3.64 ± 1.14	0.001	2.68 ± 1.21	0.027	6.20 ± 0.80	<0.001
Mesic											0.10 ± 0.04	0.013		
Mesoxeric	0.04 ± 0.02	0.032												
Xeric										-0.03 ± 0.01	0.034			
Agriculture	-0.15 ± 0.06	0.015												
Bare ground											-0.68 ± 0.38	0.075	-0.13 ± 0.08	0.130
Evergreen overstory					-0.16 ± 0.10	0.099					0.03 ± 0.01	0.005		
Hardwood overstory	-0.08 ± 0.04	0.061			0.07 ± 0.04	0.066								
Oak overstory	-0.09 ± 0.04	0.017							0.03 ± 0.01	0.016				
Water														
1–10 years old forest							0.05 ± 0.02	0.011						
10–20 years old forest					0.05 ± 0.01	<0.001			0.08 ± 0.04	0.048	0.14 ± 0.04	0.001		
>20 years old forest											-0.04 ± 0.01	0.006	-0.09 ± 0.01	<0.001
Non-evergreen understory	0.08 ± 0.04	0.022			-0.09 ± 0.05	0.075	0.05 ± 0.02	0.003						
Evergreen understory							0.06 ± 0.03	0.040			-0.03 ± 0.01	0.003	-0.03 ± 0.02	0.127
Road	0.14 ± 0.04	0.002	0.12 ± 0.05	0.020	0.22 ± 0.10	0.027	0.18 ± 0.05	<0.001	0.26 ± 0.06	<0.001				
<b>Juvenile</b>														
Intercept	0.20 ± 0.85	0.818	-5.50 ± 1.03	<0.001	-5.16 ± 0.93	<0.001	-3.47 ± 0.51	<0.001	-1.80 ± 0.98	0.067	-2.67 ± 0.34	<0.001	-3.46 ± 0.43	<0.001
Mesic											0.12 ± 0.04	0.005		
Mesoxeric														
Xeric	-0.03 ± 0.01	0.030								-0.04 ± 0.02	0.012			
Agriculture	-0.06 ± 0.02	0.015												
Bare ground														
Evergreen overstory	0.03 ± 0.02	0.053									0.03 ± 0.01	0.046		
Hardwood overstory														
Oak overstory														
Water														
1–10 years old forest											0.09 ± 0.03	0.004		
10–20 years old forest					0.07 ± 0.01	<0.001	0.06 ± 0.02	0.001			0.15 ± 0.06	0.009		
>20 years old forest														
Non-evergreen understory														
Evergreen understory	-0.08 ± 0.04	0.025												
Road			0.25 ± 0.09	0.004	0.19 ± 0.10	0.053			0.24 ± 0.06	<0.001			0.32 ± 0.05	<0.001

**Table 4**  
Maximum likelihood estimates of logistic models predicting the probability of ruffed grouse use from habitat composition, male and female birds, central and southern Appalachians, 1995–2001.

Sex Variable	MD		NC		PA		VA2		VA3		WV1		WV2	
	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P
<b>Male</b>														
Intercept	−4.00 ± 1.98	0.043	−4.02 ± 0.65	<0.001	−6.50 ± 1.35	<0.001	−7.03 ± 1.19	<0.001	−2.28 ± 1.21	0.060	−4.95 ± 2.15	0.021	6.24 ± 0.83	<0.001
Mesic									−0.08 ± 0.05	0.141	0.11 ± 0.04	0.005		
Mesoxeric	0.04 ± 0.02	0.033												
Xeric									−0.04 ± 0.02	0.025				
Agriculture	−0.07 ± 0.04	0.067												
Bare ground													−0.56 ± 0.26	0.033
Evergreen overstory											0.03 ± 0.01	0.015		
Hardwood overstory	−0.11 ± 0.07	0.106									−0.02 ± 0.01	0.031		
Oak overstory	−0.12 ± 0.07	0.072					0.04 ± 0.01	0.001						
Water														
1–10 years old forest							0.06 ± 0.02	0.005			0.14 ± 0.03	<0.001		
10–20 years old forest					0.08 ± 0.02	<0.001			0.07 ± 0.04	0.088	0.18 ± 0.05	<0.001		
>20 years old forest											0.03 ± 0.02	0.123	−0.09 ± 0.01	<0.001
Non-evergreen understory	0.14 ± 0.06	0.031												
Evergreen understory									0.05 ± 0.02	0.010			−0.03 ± 0.02	0.093
Road	0.10 ± 0.05	0.022	0.16 ± 0.06	0.008			0.18 ± 0.05	0.001	0.27 ± 0.06	<0.001				
<b>Female</b>														
Intercept	−3.15 ± 0.63	<0.001	−2.54 ± 0.30	<0.001	−4.74 ± 0.65	<0.001	−4.20 ± 0.84	<0.001	−2.94 ± 1.24	0.018	9.49 ± 2.07	<0.001	0.27 ± 1.13	0.809
Mesic											0.15 ± 0.05	0.001		
Mesoxeric	0.05 ± 0.02	0.006					−0.05 ± 0.02	0.017						
Xeric									−0.05 ± 0.02	0.005				
Agriculture	−0.07 ± 0.03	0.023									−0.76 ± 0.51	0.135		
Bare ground											−0.11 ± 0.04	0.007	−0.72 ± 0.43	0.094
Evergreen overstory	0.04 ± 0.01	0.003									0.02 ± 0.01	0.040		
Hardwood overstory							0.04 ± 0.01	0.005			−0.02 ± 0.01	0.029		
Oak overstory									0.03 ± 0.02	0.042				
Water														
1–10 years old forest														
10–20 years old forest					0.06 ± 0.01	<0.001	0.05 ± 0.01	0.005	0.12 ± 0.05	0.022			0.10 ± 0.02	<0.001
>20 years old forest											−0.11 ± 0.02	0.000		
Non-evergreen understory													−0.03 ± 0.01	0.014
Evergreen understory	−0.05 ± 0.03	0.051											−0.04 ± 0.02	0.063
Road			0.15 ± 0.06	0.009	0.21 ± 0.08	0.005	0.19 ± 0.06	0.002	0.23 ± 0.07	0.001				

**Table 5**  
Maximum likelihood estimates of logistic models predicting the probability of ruffed grouse use from habitat composition, adult and juvenile male birds, central and southern Appalachians, 1995–2001.

Age Variable	MD		NC		PA		VA2		VA3		WV1		WV2	
	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P
Adult														
Intercept	-13.98 ± 2.83	<0.001	-3.77 ± 0.65	<0.001	-7.70 ± 1.74	<0.001	-6.05 ± 1.00	<0.001	-5.46 ± 0.87	<0.001	-2.04 ± 0.23	<0.001	2.64 ± 1.47	0.073
Mesic														
Mesoxeric	0.07 ± 0.02	0.003												
Xeric														
Agriculture														
Bare ground														
Evergreen overstory														
Hardwood overstory														
Oak overstory														
Water														
1–10 years old forest							0.06 ± 0.02	0.002			0.10 ± 0.02	<0.001		
10–20 years old forest					0.07 ± 0.02	<0.001			0.07 ± 0.04	0.095	0.16 ± 0.04	<0.001		
>20 years old forest													-0.08 ± 0.01	<0.001
Non-evergreen understory	0.10 ± 0.03	<0.001					0.02 ± 0.01	0.024					0.03 ± 0.01	0.016
Evergreen understory									0.05 ± 0.02	0.031				
Road	0.21 ± 0.06	<0.001	0.12 ± 0.07	0.077	0.26 ± 0.15	0.075	0.1690.06	0.004	0.30 ± 0.06	<0.001				
Juvenile														
Intercept	-2.78 ± 0.70	<0.001					-8.73 ± 2.60	0.001	-2.68 ± 1.10	0.014	-6.05 ± 1.00	<0.001	-5.46 ± 0.87	<0.001
Mesic														
Mesoxeric	0.04 ± 0.02	0.069												
Xeric									-0.03 ± 0.02	0.087				
Agriculture	-0.06 ± 0.03	0.064												
Bare ground														
Evergreen overstory														
Hardwood overstory														
Oak overstory														
Water							0.07 ± 0.03	0.024						
1–10 years old forest											0.06 ± 0.02	0.002		
10–20 years old forest													0.07 ± 0.04	0.095
>20 years old forest														
Non-evergreen understory											0.02 ± 0.01	0.024		
Evergreen understory	-0.12 ± 0.08	0.105											0.05 ± 0.02	0.031
Road									0.18 ± 0.05	0.001	0.16 ± 0.06	0.004	0.30 ± 0.06	<0.001

**Table 6**  
Maximum likelihood estimates of logistic models predicting the probability of ruffed grouse use from habitat composition, adult and juvenile female birds, central and southern Appalachians, 1995–2001.

Age	MD		NC		PA		VA2		VA3		WV1		WV2	
	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P
Adult														
Intercept	−4.56 ± 0.89	<0.001	−3.30 ± 0.73	<0.001	3.57 ± 3.26	0.274	−5.81 ± 1.06	<0.001	−4.09 ± 1.51	0.007	7.54 ± 3.52	0.032	−2.99 ± 0.35	<0.001
Mesic							−0.38 ± 0.25	0.126						
Mesoxeric	0.06 ± 0.02	0.010												
Xeric									−0.03 ± 0.02	0.050	−0.10 ± 0.04	0.007		
Agriculture	−0.08 ± 0.05	0.145												
Bare ground														
Evergreen overstory	0.04 ± 0.02	0.021	−0.06 ± 0.04	0.117	−0.25 ± 0.12	0.043					0.02 ± 0.01	0.130		
Hardwood overstory					0.06 ± 0.04	0.098	0.03 ± 0.02	0.059			−0.01 ± 0.01	0.064		
Oak overstory									0.04 ± 0.02	0.037				
Water														
1–10 years old forest							0.04 ± 0.02	0.022	0.09 ± 0.05	0.090	0.10 ± 0.03	0.001		
10–20 years old forest											0.13 ± 0.05	0.009	0.09 ± 0.01	<0.001
>20 years old forest					−0.05 ± 0.01	<0.001								
Non-evergreen understory					−0.09 ± 0.05	0.076								
Evergreen understory														
Road			0.12 ± 0.07	0.094	0.21 ± 0.12	0.075	0.23 ± 0.08	0.002	0.22 ± 0.08	0.007				
Juvenile														
Intercept	−2.21 ± 1.07	0.038	−5.19 ± 1.02	<0.001	−5.68 ± 0.93	<0.001	−8.60 ± 2.46	<0.001	−8.23 ± 1.86	<0.001	−3.24 ± 0.41	<0.001	−3.93 ± 0.55	<0.001
Mesic	0.07 ± 0.04	0.063									0.14 ± 0.06	0.017		
Mesoxeric									0.07 ± 0.03	0.011				
Xeric							0.05 ± 0.03	0.094						
Agriculture	−0.08 ± 0.04	0.053												
Bare ground														
Evergreen overstory	0.03 ± 0.02	0.133												
Hardwood overstory							0.05 ± 0.02	0.016						
Oak overstory	−0.03 ± 0.02	0.110												
Water														
1–10 years old forest											0.11 ± 0.04	0.004		
10–20 years old forest					0.07 ± 0.01	<0.001	0.06 ± 0.03	0.022	0.21 ± 0.09	0.023	0.18 ± 0.06	0.005		
>20 years old forest														
Non-evergreen understory														
Evergreen understory														
Road			0.21 ± 0.09	0.024	0.21 ± 0.10	0.038			0.24 ± 0.10	0.014			0.29 ± 0.06	<0.001



**Table 7**  
Maximum likelihood estimates of logistic models predicting the probability of ruffed grouse use from habitat composition by season, all birds, central and southern Appalachians, 1995–2001.

Season	MD		NC		PA		VA2		VA3		WV1		WV2	
	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P
Winter														
Intercept	-2.15 ± 0.48	<0.001			-6.55 ± 1.56	-6.551	-3.71 ± 0.76	<0.001	-3.94 ± 1.14	0.001	0.82 ± 1.41	0.560	-2.84 ± 0.32	<0.001
Mesic					-0.16 ± 0.05	-0.157					0.09 ± 0.04	0.038		
Mesoxeric					0.04 ± 0.03	0.044	-0.05 ± 0.02	0.013						
Xeric	0.05 ± 0.02	0.001							-0.03 ± 0.01	0.016				
Agriculture	-0.13 ± 0.04	0.004									-0.93 ± 0.63	0.140		
Bare ground	-0.09 ± 0.06	0.146			-0.69 ± 0.26	-0.686								
Evergreen overstory					-0.12 ± 0.06	-0.117								
Hardwood overstory					0.05 ± 0.02	0.050								
Oak overstory									0.02 ± 0.01	0.108				
Water														
1–10 years old forest														
10–20 years old forest					0.08 ± 0.01	0.081	0.03 ± 0.02	0.025			0.13 ± 0.04	0.003		
>20 years old forest											-0.03 ± 0.02	0.031		
Non-evergreen understory														
Evergreen understory	-0.12 ± 0.04	0.002							0.05 ± 0.03	0.033				
Road	0.10 ± 0.05	0.037			0.13 ± 0.06	0.131	0.22 ± 0.06	<0.001	0.25 ± 0.06	<0.001	0.16 ± 0.04	<0.001	0.34 ± 0.04	<0.001
Summer														
Intercept	-1.34 ± 0.79	0.090	-3.492 ± 0.50	<0.001	-5.32 ± 0.79	<0.001	-9.02 ± 3.28	0.006	-2.40 ± 0.89	0.007	-7.03 ± 2.01	<0.001	-2.83 ± 0.32	<0.001
Mesic											0.07 ± 0.03	0.031		
Mesoxeric	0.04 ± 0.02	0.016												
Xeric														
Agriculture	-0.23 ± 0.10	0.019												
Bare ground														
Evergreen overstory														
Hardwood overstory									0.02 ± 0.01	0.132				
Oak overstory	-0.05 ± 0.02	<0.001									0.02 ± 0.01	0.031		
Water														
1–10 years old forest											0.12 ± 0.03	<0.001		
10–20 years old forest					0.06 ± 0.01	<0.001					0.19 ± 0.04	<0.001	0.10 ± 0.01	<0.001
>20 years old forest							-0.02 ± 0.02	0.119	0.07 ± 0.04	0.060	0.04 ± 0.02	0.033		
Non-evergreen understory							0.06 ± 0.03	0.033						
Evergreen understory							0.09 ± 0.04	0.031						
Road			0.145 ± 0.50	0.002	0.23 ± 0.08	0.006	0.19 ± 0.05	0.001	0.19 ± 0.05	<0.001	0.18 ± 0.03	<0.001		



Habitat differences between used and random sites varied for each age and sex on every site except NC. The overall low number of grouse home ranges on this site ( $n=28$ ) may have reduced the ability of the model to include some covariates that had small coefficients relative to their standard errors (Hosmer and Lemeshow, 2000); most habitat models contained only road as an important covariate. Of the 3 additional variables that occurred in habitat models, all had 95% confidence intervals on their odds ratios that included 1, indicative of no effect. Schumacher (2002) did find non-random use of different stand ages on this site, with grouse preferring 11–39 years old pole stands to sapling and mature forest. However, she assessed selection by evaluating the distribution of locations among vegetation types, an analysis that emphasizes time spent in rather than spatial extent of a vegetation type within the home range (Aebischer et al., 1993). Our preliminary univariate analysis indicated both juvenile and summer home ranges contained more 10–20 years old forest than random areas ( $9.21 \pm 3.51\%$  vs.  $3.35 \pm 0.43\%$ ,  $P=0.027$  and  $6.12 \pm 1.78\%$  vs.  $3.53 \pm 0.54\%$ ,  $P=0.169$ ; Tirpak, 2005). However, young forest was not retained as a covariate in either final model on this site. Roads may be of primary importance on this site because clearcut size was typically small ( $8.05 \pm 0.92$  ha) and less than the average grouse home range. Therefore, roads may connect regenerating cuts on these areas and provide suitable cover and food resources.

On all other sites, habitat models varied between adults and juveniles. These differences were not attributable to the parameters occurring in models, but rather the magnitude of their coefficients (i.e., not the vegetation types within the home range, but rather their abundance). Regardless of vegetation type, home ranges of juveniles contained fewer of the preferred and more of the habitat types avoided by adults. Assuming habitat selection cues are associated with habitat quality (but see Gates and Gysel, 1978; Van Horne, 1983), juvenile birds appear to have occupied poorer habitat than adults on most sites. Adults may be relegating juveniles to suboptimal habitat via territorial behavior, as observed in drumming males (Gullion, 1981; Rusch and Keith, 1971) and suspected for brooding females (Godfrey, 1975). However, this pattern may also reflect dispersal of grouse through unsuitable areas and continued sampling of unfamiliar areas during home range establishment (Small and Rusch, 1989; Small et al., 1993). Average home range size was larger for juveniles than adults in both sexes on most study areas. Juvenile home ranges may need to be larger to find required resources that may be more dispersed within areas occupied by these younger, subordinate birds.

Although home ranges for male and female grouse were associated with greater young forest cover, males predominantly used forests 1–10 years old, while females were found more often in 11–20 years old stands. In winter, grouse of different sex may form loose aggregations (Doerr et al., 1974) and have similar habitat requirements (Whitaker, 2003). Therefore, differences in habitat selection between sexes likely represent differences in habitat requirements during the breeding season. Males typically establish centers of activity immediately around drumming logs during fall or early spring (Gullion, 1967). These activity centers typically contain the highest stem densities of any area used by grouse during the year (Stauffer and Peterson, 1985; Thompson et al., 1987). On our sites, stem density was highest in 1–10 years old forests. Strong site fidelity to drumming logs even through summer results in small home ranges and dominance of young forest in annual models (Craven, 1989). Alternatively, areas used by nesting and brooding females are typically characterized by moderate stem densities, abundant groundcover, and closed canopies (Haulton et al., 2003; Jones et al., 2008; Thompson et al., 1987; Tirpak et al., 2006), more characteristic of 10–20 than 1–10 years old forests on our study areas.

Adult males were strongly associated with roads on all but the WV sites. On the MD and VA3 sites, young forest cover was extremely limited (<1.5% of the landscape), and the structure found along roads likely provided the only suitable cover with stem densities high enough to be selected by drumming males. On neither site did the habitat model contain young forest, likely because of the small number of birds that could even potentially occupy it because of its limited availability. Conversely, young forest cover was not limiting on the other sites. In particular, both WV sites were industrial forests with many large, interspersed regeneration cuts. In these areas, the structure found along roads was not unique and their role as travel corridors, areas with high stem densities, and/or herbaceous vegetation may be less important. Whitaker et al. (2006) observed a negative correlation between the selection for young and regenerating stands and access routes within home ranges of males on these study areas. The VA2 site was also an industrial forest with numerous clearcuts and the PA site contained a large swath containing high stem densities created by a tornado. However, road area on these sites was nearly twice that on either WV site. At such a high density, use of roads may increase, particularly where grouse populations are high in relation to the availability of young forest. Nonetheless, <20 years old forest was the second most important factor of adults on the PA and both VA sites.

Habitat of juvenile males appeared inferior to that of adult males (Tirpak, 2005). On the MD and VA2 sites, roads were the most important covariate for adult males, but were not important for juvenile males on either site. Similarly, on the WV sites, where young forest was the most important habitat feature for adult males, juvenile males were restricted to areas with high amounts of road. Gullion (1984) hypothesized that roads provided poorer habitat for ruffed grouse than young stands. While grouse may use some roads or roadside habitats, this suggests that other habitats (e.g., young forest) may be superior and preferred when available.

Models of adult female habitat contained variables for stand age and road, but also overstory type and topographic moisture index. The larger number of variables for adult females relative to other ages and sexes likely reflects higher selectivity and greater specificity for certain habitat features. In particular, brood habitat is considered to have the narrowest limits of any area used by grouse (Berner and Gysel, 1969). Specifically, grouse broods prefer areas containing abundant food associated with abundant ground vegetation and the security provided by dense cover (Jones et al., 2008; Tirpak et al., 2005). In the CSA, seeded logging roads adjacent to regenerating stands can provide these habitat characteristics (Harper et al., 2001; Hollifield and Dimmick, 1995), which may explain the importance of road area and stand age in many models. Additionally, mesic forest often supports lush herbaceous understories and can serve as important brood habitat (Haulton et al., 2003; Jones et al., 2008). Only the WV2 site did not contain topographic moisture index as a model variable, and it lacked mesic habitat. The importance of overstory composition on some sites likely reflects favorable habitat conditions associated with particular species. However, the lack of agreement among sites prevents any region-wide generalizations. Juvenile females, which had habitat covariates similar to adult females on most sites, often lacked overstory composition as an important feature.

The large variation in models among years both within and across sites may be related to low and uneven sample sizes of age and sex classes each year. On most sites, annual habitat selection patterns often reflected the dominant age and sex class of the bird's radiotracked during that year. Even the large sample sizes we had in this study may have been insufficient to adequately describe habitat selection, when separated into individual years by sex and age class. Randomization and resampling procedures can poten-

tially reduce this potential bias (Manly, 1997); however, we did not conduct them because of the limited number of available comparisons. Hosmer and Lemeshow (2000) recommended a minimum of 10 events (i.e., home ranges) to develop the most basic logistic model. Although they questioned whether this was too stringent a guideline, our results indicate it likely is not. Alternatively, the differences among years may not be a statistical artifact. Schooley (1994) cautioned against pooling data across years because of temporal changes in habitat selection. There is evidence grouse may alter habitat preferences among years based on varying weather patterns (Berner and Gysel, 1969), mast abundance (Devers et al., 2007), population density (Gullion, 1967; Zimmerman et al., 2009), and habitat management. Therefore, models developed from pooled datasets should be considered long-term trends that are not representative of any single year.

Seasonal models pooled data across years and were likely more representative as a result of larger and more even distribution of samples among age and sex classes. Winter selection patterns differed between the 3 northernmost and 3 southernmost study areas. Avoidance of agricultural and barren areas in the former may relate to a lack of food or cover or the increased heat loss associated with higher wind speeds in relatively open areas, which increases metabolic rates and energy costs of grouse occupying these areas (Thompson and Fritzell, 1988). Topographic position was also important on these sites, with avoidance of low-lying mesic areas on the PA site and selection of xeric areas on the MD site. Snow cover was more prevalent and common on ridgetops, which may allow snow roosting (Berner and Gysel, 1969). Alternatively, on the WV1 site and sites further south, xeric sites were avoided and mesic or mesoxeric sites selected. These sheltered areas may be used diurnally because of their lack of snow cover, greater food availability, and lower wind speeds (Whitaker and Stauffer, 2003). The importance of roads to grouse on 3 of the southernmost areas may relate to overall habitat quality. Birds on these sites may have relied on acorn mast as an important winter food resource (Devers et al., 2007). Oaks dominated the overstory on both the VA2 and WV2 sites, and birds on the mixed-mesophytic VA3 site selected oak stands in the winter as well. Oak mast has high spatial variability and is associated with mature oak trees (Healy et al., 1999), requiring grouse to move from young forest stands that provide protective cover to mature stands that contain greater acorn abundance (Fearer and Stauffer, 2003); with roads facilitating movement (Whitaker et al., 2006).

Summer habitat models were similar on the southernmost areas, with road area being the most important factor on both the VA and NC sites. Roads provided suitable habitat for broods in this region and the dominance of females in the summer samples, especially after 1999, may partially explain this result. An opposite trend existed on the MD site, with males dominating the summer sample, and this was the only site that did not have road as one of the two most important covariates.

Lastly, the scale of analysis affected habitat selection. Grouse selected mesic stands on all sites where available. Fearer (1999) also observed mesic stands as an important habitat component within home ranges of grouse on the VA sites. He attributed this to the greater stem density found in mesic stands. However, there were no differences in stem density in oak or hardwood stands among mesic, mesoxeric, or xeric sites on study areas. Overstory composition, however, did differ between these topographic moisture classes. Similarly, Whitaker et al. (2006) found mesic stands more strongly selected within the home range than within the landscape. However, he observed this pattern only on oak-hickory sites and not on the mixed-mesophytic areas. Our results indicate these sites may be important to grouse on all sites. Important in most other contexts (e.g., seasonal habitat selection), scale was less important to selection of roads, with grouse selecting roads at only

WV1 and VA2 sites, and avoiding them at the MD site. Avoidance at the MD site probably reflects the greater abundance of paved roads that provided unsuitable areas for grouse (Trombulak and Frissell, 2000). Although almost all roads had substantial herbaceous border edge areas and/or areas of high stem density that may provide suitable habitat, not separating paved (i.e., less suitable) from unpaved (i.e., more suitable) roads may have led to us underestimating the value of the unpaved road areas that dominated our study areas in all contexts.

Because of its overall importance to grouse, particularly adults, young forest cover should be considered the cornerstone of ruffed grouse management. Focusing management efforts on improving habitat conditions preferred by adults, will also improve habitat conditions for juvenile birds, and increase the overall carrying capacity of an area for grouse. As juveniles appeared relegated to suboptimal habitat, increased availability of higher quality habitat may result in more consistent selection patterns between ages and potentially higher and more stable population sizes. Selection for roads by grouse in most contexts illustrated their importance as a management consideration. Unpaved roads and roadsides were commonly used by grouse and we recommend managing roads by planting annual grains (i.e., wheat) and perennial clovers after timber harvests to encourage native forbs that provide soil stabilization, escape cover, and abundant arthropod and vegetative forage for grouse (Schumacher, 2002; Tirpak et al., 2005). However, in models of male habitat, the importance of roads likely reflected their use as travel corridors and suitable cover along the road edge in landscapes where young forest cover was limited. Road use was reduced where >2% of the landscape was in young forest cover, and we recommend this as a minimum for ruffed grouse. This value is below the 15% recommended by Dettmers (2003), but is in agreement with historical estimates of the amount of young forest available in the interior uplands of the northeastern United States (Litvaitis, 2003; Lorimer and White, 2003). Stand regeneration should be initiated evenly through time to ensure an adequate amount of young forest habitat for both sexes and replenish that lost to forest maturation. Further, cuts should be dispersed throughout the landscape to make their microclimates more hospitable to grouse during winter, when they are heavily used by both sexes. Finally, where possible, management activities should be concentrated in mesic stands to encourage the use of these areas by grouse.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.07.051.

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