Research Article

Factors Affecting Habitat Use by Appalachian Ruffed Grouse

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Abstract

*A goal of many resource selection studies is to identify those habitats selected by a species. However, favorability of a particular habitat feature is likely contingent on such factors as landscape composition, predation risk, and an individual's resource needs. Thus, habitat selection may vary depending on context, and identifying causes of variability in habitat use could increase our understanding of functional aspects of a species' habitat ecology. Clear-cuts afford ruffed grouse (*Bonasa umbellus*) important escape cover, whereas access routes (roads and trails) and mesic bottomlands are viewed as important foraging areas for this species. We present a study of factors influencing strength of selection (i.e., use–availability) for these 3 habitat features by individual ruffed grouse. We analyzed radiotelemetry data from $>$1,000 ruffed grouse monitored on 10 study sites in the central and southern Appalachians. Five sites were typified by mixed-mesophytic forests, and 5 were predominantly oak-hickory forests. Selection for clear-cuts was positively related to selection for access routes, but it was inversely related to selection for mesic bottomlands. Selection for mesic bottomlands and selection for access routes were positively related in oak-hickory forests, but they were unrelated in mixed-mesophytic forests. Clear-cuts were more strongly selected in mixed-mesophytic forests, and within each forest type, use of clear-cuts was strongest by adult males. Mesic bottomlands were only selected in oak-hickory forests, and within these forests they were most strongly selected by adult females. Following poor, hard-mast crops, use of access routes by female grouse increased. Use of clear-cuts and bottomlands increased for some or all sex and age classes of grouse following closure of hunting, suggesting that hunting discouraged use of these covers. Animals typically face a trade-off between survival and condition to maximize fitness, and our observations suggest that (relative to one another) male grouse favor refuging habitats whereas females favor foraging areas. At a landscape scale, grouse in areas having oak-hickory forests selected foraging habitats more strongly, whereas those inhabiting mixed-mesophytic forests made greater use of escape cover. Our findings indicate that habitat management prescriptions for Appalachian grouse can be tailored by forest type.* (JOURNAL OF WILDLIFE MANAGEMENT 70(2):460–471; 2006)

Key words

ACGRP, Appalachian Mountains, Bonasa umbellus, *habitat use, landscape composition, resource selection, ruffed grouse, strength of selection.*

A primary goal of many resource selection studies is to describe the pattern of habitat use by a species. However, the value of a vegetation type or habitat feature is likely contingent on a number of factors, so habitat use may vary depending on context (Block and Brennan 1993). Modifying factors might include, for example, predation risk, social status, weather, site productivity, food availability, and an individual's current resource needs. Availability of a habitat feature may also influence the degree to which it is used. For example, a resource may be strongly selected when rare but be used at, or below, background levels when abundant (Johnson 1980, Tonkovich and Stauffer 1993). Another important consideration is that, in situations where multiple resources can be limiting, the true process of habitat selection will be clouded if not considered in a multivariate context (Huston 2002). Consequently, once a species' basic habitat affinities have been described, a logical next step toward understanding its habitat ecology is to investigate factors and interactions that influence the habitat-selection process. These, in turn, affect the degree to which important habitat features are used.

Ruffed grouse are resident birds of temperate and boreal forests in North America. Because grouse are an important game species, they have been the focus of numerous studies, and fundamental patterns of habitat use are understood (Rusch et al. 2000). Although grouse make use of forests representing a variety of successional stages and stand types, it is clear that stands having high stem densities, particularly early successional stands created by natural disturbance or even-aged timber harvesting (i.e., clear-cutting), form the cornerstone of the species' habitat needs (Bump et al. 1947, Rusch et al. 2000, Dessecker and McAuley 2001).

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High stem-density stands provide important predator escape cover, and they have been shown to positively affect survival rates and grouse population density (Wiggers et al. 1992, Clark 2000, Dessecker and McAuley 2001), and even grouse occupying mature forests typically seek out microsites having locally high stem densities (Schumacher 2002, Whitaker and Stauffer 2003). A second widely reported aspect of ruffed grouse habitat ecology is that they make extensive use of wooded roads and other high-contrast forest edges (Bump et al. 1947, Stewart 1956, Schumacher 2002, Endrulat 2003). Various reasons for use of roadsides have been put forward, including abundant invertebrate, fruit, and herbaceous foods; access to grit for digestion; presence of bare ground for dust bathing; and use as travel corridors (Bump et al. 1947, Stewart 1956, Hollifield and Dimmick 1995, Schumacher 2002). However, it has also been suggested that use of forest roads and edges increases as availability of early successional habitat decreases, so edges are of secondary value by comparison (Bump et al. 1947, Gullion 1984*a*). Finally, although not always observed, several authors have reported that bottomlands are an important habitat for grouse in southeastern forests. Relatively abundant herbaceous vegetation may make these areas important foraging sites during winter (Fearer 1999), whereas this groundcover and the high number of insects it supports are important foods for grouse broods during spring and summer (Stewart 1956, Thompson et al. 1987, Fettinger 2002, Haulton et al. 2003). Size of home range for Appalachian ruffed grouse was inversely related to use of clear-cuts, woodland access routes, and bottomlands, suggesting that all 3 of these habitat features are of high quality (Whitaker 2003).

Here, we set out to investigate the habitat ecology of Appalachian ruffed grouse. However, rather than presenting a straightforward assessment of patterns of use, we explicitly investigated factors that influenced habitat selection, leading to variability in habitat use. We did this by evaluating the influence of a variety of factors on strength of selection (i.e., use–availability) by individual grouse for clear-cuts, woodland access routes (i.e., roads and trails), and mesic bottomlands. Factors we considered as potentially affecting use of these habitat features included grouse sex and age, aspects of space use, availability of a key food, forest type, season, availability and use of other habitats, and hunting. We took this approach to elucidate functional aspects of the species' habitat ecology in the region, for example, by identifying when and why important habitat features are selected. We then used the resulting information to make inferences about selective pressures acting at different times and on different groups within the regional grouse population.

Study Areas

Appalachian Cooperative Grouse Research Project (ACGRP) researchers radio-tracked >1,000 ruffed grouse at 10 study sites in the central and southern Appalachian Mountains (Fig. 1). Radio-tracking was conducted at most sites from September 1996 through April 2001 (55 months). Study sites ranged in size from 2,000–10,000 ha and were located on National Forest lands ($n = 2$), state forest and game management areas ($n = 5$), and industrial forestlands owned by MeadWestvaco Corporation ($n = 3$). Woodlands on each study site were typified by either oak-hickory (OH) or mixed-mesophytic (MM) forests (Fig. 1; Braun 1950).

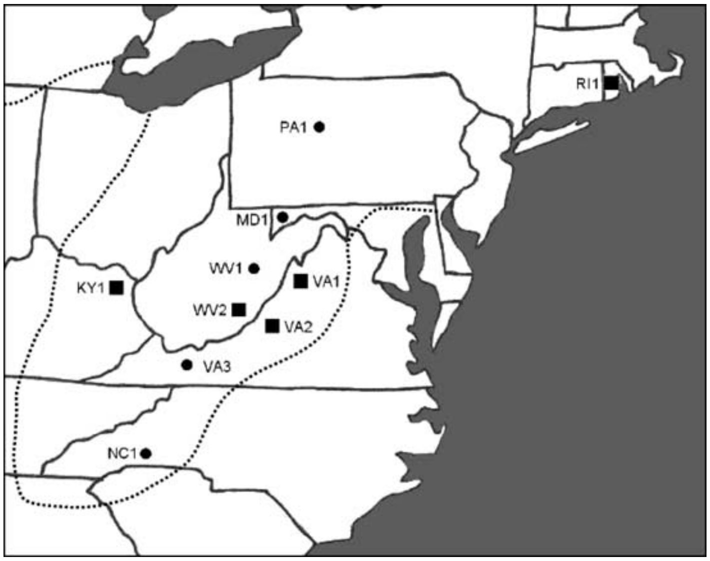

Figure 1. Locations of study sites in the eastern United States (1996–2001), with the southern limit of the geographic range of ruffed grouse indicated by the dotted line. Square markers identify study sites having predominantly oak-hickory forests, whereas those typified by mixed-mesophytic forests are identified with circles. Study sites were located in Kentucky (KY1), Maryland (MD1), North Carolina (NC1), Pennsylvania (PA1), Rhode Island (RI1), Virginia (VA1, VA2, and VA3), and West Virginia (WV1 and WV2).

Oak-hickory forests dominated cover on the KY1, RI1, VA1, VA2, and WV2 study sites. The most common tree on these sites was chestnut oak (*Quercus prinus*), and other important tree species included white, red, scarlet, and black oak (*Q. alba, Q. rubra, Q. coccinea*, and *Q. velutina*, respectively); shagbark, pignut, bitternut, and mockernut hickory (*Carya ovata, C. glabra, C. cordiformis,* and *C. tomentosa*, respectively); white, Virginia, pitch, and Table Mountain pine (*Pinus strobus, P. virginiana, P. rigida,* and *P. pungens*, respectively); eastern hemlock (*Tsuga canadensis*); red and sugar maple (*Acer rubrum* and *A. saccharum*, respectively); and beech (*Fagus grandifolia*; J. Tirpack and D. Whitaker, ACGRP, unpublished data). Hard mast produced by oaks and beech is a high-quality grouse food (Servello and Kirkparick 1987), and on average, these species constituted 42% of canopy trees on oak-hickory sites (Whitaker 2003; J. Tirpak, Fordham University, unpublished data). Where available, buds and flowers of cherries (*Prunus* spp.), birches (*Betula* spp.), and aspens (*Populus* spp.) afford ruffed grouse a stable supply of high-quality winter food (Servello and Kirkpatrick 1987), but these northern hardwoods averaged only 2% of canopy trees on oak-hickory sites (Whitaker 2003).

Woodlands on the MD1, NC1, PA1, VA3, and WV1 sites were dominated by the mixed-mesophytic forest association. The most abundant canopy tree species on each of these sites was red maple, although other important tree species included sugar maple, basswood (*Tilia americana*), sweet and yellow birch (*Betula lenta* and *B. alleghaniensis*, respectively), black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), white pine, American beech, northern red oak, eastern hemlock, and yellow poplar (*Liriodendron tulipifera*). Oaks and beech comprised 23% of canopy trees on mixed-mesophytic sites, and birches, cherries, and aspen constituted 22% of canopy trees (Whitaker 2003; J. Tirpak, Fordham University, unpublished data). Compared with oak-hickory forests, upland soils in mesophytic forests were more mesic (i.e., moist), and growing conditions were typical of more northerly climates (Devers 2005).

A key goal of the ACGRP was to experimentally test effects of hunting on grouse ecology. During Phase I (fall 1996–spring 1999), all study sites were open to fall–winter grouse hunting. During Phase II (fall 1999–fall 2002), hunting was closed on 3 sites (KY1, VA3, WV2) but remained open on all other sites (Devers 2005).

Methods

Data Collection and Processing

We used lily-pad traps to capture grouse during fall (Sep–Dec; Gullion 1965), with additional trapping being conducted during spring as necessary. We attempted to monitor 40–50 grouse on each study area, each year, and trapping effort was increased as necessary in an effort to maintain a study population exceeding 20 individuals at all times. We assessed sex and age (juvenile = <15 months posthatch, adult = ≥15 months posthatch) of captured grouse based on feather criteria (Kalla and Dimmick 1995). We then weighed grouse, fitted them with a necklace-style radio-transmitter (10 g, 1.25–2.5% of body mass; Advanced Telemetry Systems, Isanti, Minnesota), and released them at the site of capture. After release, grouse were given a 1-week conditioning period to acclimate to the collar and recover from capture stress, and they then entered into the study population. Grouse captured as juveniles were graduated to the adult age class on September 1 of their second year (≈15 months posthatch).

Detailed methods for collection, testing, and processing of radio-tracking data are provided in Whitaker (2003). Briefly, we attempted to locate each radioed bird at least twice weekly. Locations were collected between dawn and dusk and, thus, reflect diurnal habitat use. To triangulate grouse, observers used handheld receiving equipment to measure azimuths from ≥3 receiving stations over a period of <20 min (White and Garrott 1990). Location estimates were calculated using Lenth's maximum-likelihood estimator (Lenth 1981). We conducted a beacon study to quantify telemetry error (White and Garrott 1990), and we estimated mean location error to be <75 m (see Whitaker 2003). We censored observations when the mean distance from receiving stations to the location exceeded 800 m.

When location estimates may be imprecise (i.e., are potentially misclassified), it is preferable to define habitat use on an area basis (Erickson et al. 2001). Consequently, we used home ranges to measure habitat use by individuals. Fall–winter (1 Sep–31 Mar; 212 days) and spring–summer (1 Apr–31 Aug; 153 days) home ranges were delineated; these time periods approximate the nonbreeding and breeding seasons, respectively (Devers 2005). We used the fixed kernel method with least squares cross validation (LSCV; Worton 1989), which generally yields the least-biased estimates of home-range boundaries compared with other contemporary methods (Seaman and Powell 1996). We used a minimum of 30 locations (Seaman et al. 1999) and estimated boundaries for the 50, 75, and 95% probability kernels for each home range. Because we were interested in identifying areas that animals had selected for extended occupancy, we excluded dispersal movements from sets of locations used to estimate home ranges (see Whitaker 2003).

At the study area scale, we used the distribution of radioed grouse to define an available landscape each season by placing an 800-m buffer around any telemetry station falling within 800 m of a grouse location collected that season. This ensured that any habitat considered available was in the vicinity of an extant grouse home range and that portions of study areas where locations would be considered unreliable and censored (i.e., areas >800 m from telemetry stations) were not considered available.

Digital habitat maps were developed for each study site using remote-sensing data and ground surveys (see Whitaker 2003). Maps included layers for 0- to 20-year-old clear-cuts and access routes (including paved, unpaved, vegetated roads, and trails). When a new clear-cut or road was created, or when the age of a clear-cut reached 20 years, a revised map was created. Digital elevation models (DEMs) were used to develop a topographic moisture-index (TMI) layer (30 × 30-m resolution; U.S. Geological Survey, EROS Data Center, Sioux Falls, South Dakota). Topographic moisture-index values for each pixel were calculated based on slope, aspect, and landform, and we used these values to classify each pixel as xeric or mesic relative to the average for the landscape. Maps of mesic habitats (hereafter, mesic bottomlands) closely reflected the distribution of concave landforms in the landscape (e.g., hollows, valley bottoms, and riparian zones).

We recorded a number of variables for each home range (Table 1). These included grouse sex and age, natural log-transformed area of the 75% kernel home range (LN75), and the ratio in size between the 50 and 95% kernel home ranges (core). An index of hard-mast production was estimated for each site, each year, by ranking production by red/black, white, and chestnut oaks and beech on a 0–3 scale (0 = no mast, 1 = light, 2 = moderate, 3 = heavy) and then summing the 4 values (Whitaker 2003). From digital habitat maps, we calculated the percentage of cover by clear-cuts and mesic bottomlands, as well as the density of access

Table 1. Variables used in analyses of ruffed grouse habitat selection in the Appalachian region, 1996–2001.

Variable	Description
Acs	Landscape-level selectivity for access routes (m/ha)
Age	Age; hatch-year (juvenile) or after-hatch-year (adult)
CC	Landscape-level selectivity for clear-cuts (%)
Core	Core-area ratio (50% kernel home range ÷ 95% kernel home range)
For	Dominant forest type on each study site: oak-hickory or mixed-mesophytic
Ln75	Natural log-transformed area of the 75% kernel home range (ha)
LsAcs	Density of access routes in the landscape (m/ha)
LsCC	Availability of clear-cuts in the landscape (%)
LsTMI	Availability of mesic bottomlands in the landscape (%)
Mast	Index of hard mast production by chestnut, red/black, and white oaks and beech
Sex	Male or female
SA	Sex and age combined into 4 classes (AM, AF, JM, JF)
Sea	Season (spring–summer or fall–winter)
Site(For)	Study site, nested within forest type (*n* = 10; see Fig. 1)
TMI	Landscape-level selectivity for mesic bottomlands (%)

routes (m/ha) within the 50, 75, and 95% kernel home range of each grouse. Landscape-scale habitat information was extracted from the available landscape for each site, each season, using the same methods as for individual home ranges.

Data Analyses

We carried out all analyses at both the landscape and within-home-range scales of selection (i.e., second- and third-order selection, respectively; sensu Johnson 1980). We measured landscape-level strength of selection for clear-cuts, mesic bottomlands, and access routes by each grouse by subtracting the value for the available landscape from the value for its 75% kernel home range. For each grouse, we estimated within-home-range strength of selection for each habitat feature by subtracting the value from its overall (95% kernel) home range from that of its core (50% kernel) home range. Both landscape and within-home-range measures of strength of selection will be positive if a habitat feature is being selected and negative if it is being used less than expected by chance. Habitat features we studied were not mutually exclusive, in that a location could be classified as both mesic bottomland and clear-cut and have access routes passing through it. Consequently, selection for 1 habitat feature did not negate selection for the others, and unit sum constraints (Aebischer et al. 1993) were not a concern.

As a first step, we carried out tests to confirm that the habitat features we selected for study were on average used more than would be expected by chance at both the landscape and within-home-range scales. For this, we used one-tailed *t*-tests to determine whether the mean strength of selection for clear-cuts, access routes, and mesic bottomlands between used and available areas was greater than zero (Sokal and Rohlf 1995). This is analogous to a paired *t*-test comparing the extent of coverage in used and available areas (Sokal and Rohlf 1995). We then employed 3 analytic approaches to identify factors relating to variability in strength of selection for clear-cuts, access routes, and mesic bottomlands by ruffed grouse. First, we used information–theoretic model selection to evaluate a priori multivariate models describing hypothesized relations between various factors and habitat selection. Second, when an individual grouse was monitored for >1 season or year, we compared pairs of home ranges from individuals to test for effects of season, age, and fall hard-mast crops on habitat selection. Finally, we used an experimental, hypothesis-testing approach to evaluate the influence of hunting activity on habitat selection by ruffed grouse.

Habitat selection is a multivariate process (Jones 2001), and we hypothesized that many different factors could simultaneously influence strength of selection for clear-cuts, mesic bottomlands, and access routes. To investigate this dimensionality, we developed a priori sets of linear models specifying a variety of relations hypothesized to influence strength of selection for each of these 3 habitat features (see Whitaker 2003: appendix B for complete lists of a priori models). Candidate models ranged from simple univariate representations to complex multivariate models including hypothesized 2- and 3-way interactions. Categorical explanatory variables included the sex and age of grouse, season, study area, and forest type (Table 1). When both study site and forest type were included in a model, we specified that sites were nested within forest types. Continuous explanatory variables included our hard-mast index, core-area ratio, and availability of clear-cuts, mesic bottomlands, and access routes in the landscape (Table 1). To account for any area effects, we also included the (natural log-transformed) size of the 75% kernel home range. As there may be tradeoffs in the use of different habitat features, we included landscape-scale strength of selection for clear-cuts, mesic bottomlands, and access routes in model sets where that particular feature was not the response variable. Food availability is an important factor affecting habitat quality, and hard mast is a high quality food that varies in availability between seasons and years. Consequently, we specified a number of interactions between our mast index and other candidate variables. Because of differences in availability of this and other key foods (e.g., birch and cherry trees), we hypothesized that the habitat ecology of grouse would differ between forest types, so we specified a number of interactions with forest type. Also, we expected that selective pressures would differ between demographic groups, so we included several hypothesized interactions with sex and age. We computed Pearson's product-moment correlation coefficient for all pairs of continuous variables, and we censored 1 member of any pair having a correlation >0.6 (Sokal and Rohlf 1995).

For each habitat feature, we tested the same set of candidate models using both the landscape and within-home-range scale strength of selection as the response variable, with individual home ranges as the sampling unit. We followed some individuals during >1 year; to avoid pseudoreplication (Hurlbert 1984), we included only 1 home range per individual per season in our model evaluation data sets. When choosing between pairs of home ranges, we selected those estimated from the larger number of locations. Clear-cuts <20 years old were not present on the KY1, MD1, and NC1 study sites, so we dropped observations from these sites from the data set used to evaluate strength of selection for this habitat feature. Mast indices were not available for the NC1 study site, so we excluded this site from all model evaluation data sets.

We fit our a priori models as general linear models using JMP statistical software (Version 4.0.3; SAS Institute, Cary, North Carolina) and evaluated and ranked candidate models using information–theoretic model selection techniques (Burnham and Anderson 2002). To gain an appreciation of the explanatory power of our models, we included a null model (i.e., intercept only) in each set of candidate models. To assess model fit we inspected residual plots and carried out a goodness-of-fit test for the global model in each set. We evaluated and ranked models within each set based on Akaike's Information Criterion adjusted for sample size (AIC_c), AIC_c differences (Δ_i), R^2_{adj}, and Akaike weights (ω_i; Burnham and Anderson 2002). Increases in $AIC_c > 2$ indicate a substantial reduction in model fit, so for simplicity, we report only the null model plus those models having $\Delta_i \leq 2.0$.

Individual grouse followed for >1 season presented an opportunity to test factors that might modify habitat selection by individuals. We compared pairs of home ranges to assess the influence of 3 factors on strength of habitat selection. To assess age effects, we compared pairs of fall–winter home ranges used by individuals that were first monitored as juveniles and then as adults during the subsequent year. To test for seasonal differences, we compared spring–summer home ranges to fall–winter home ranges used by individual adult grouse. Finally, when individual adults were tracked for >1 fall–winter, we compared home ranges used during the year having the heavier hard-mast crop to that used during the lighter mast year. We tested males and females separately, and for tests of season and mast crop, the order in which we collected pairs of home ranges varied. For each of these comparisons, we tested for changes in strength of selection towards access routes, clear-cuts, and mesic bottomlands. Note that although a negative difference indicates that strength of selection is reduced, it does not necessarily imply that the habitat is being avoided. When testing selectivity for access routes, we pooled observations from all 10 study sites. For clear-cuts, we pooled observations from the 7 study sites having clear-cuts. Prior analyses of factors affecting home-range size indicated that the importance of mesic bottomlands may differ by forest type (Whitaker 2003), so we subdivided these tests by forest type. We used 2-tailed paired *t*-tests to test the null hypothesis that the mean difference in strength of selection between the 2 conditions would be zero (Sokal and Rohlf 1995).

Because treatments were applied following an experimental design, we employed a hypothesis-testing approach to assess the effect of hunting closure on selection of clear-cuts, access routes, and mesic bottomlands. Previous analyses indicated that grouse used smaller home ranges when hunting was closed (Clark 2000, Whitaker 2003), leading us to hypothesize that hunters push grouse out of important habitats. Consequently, we used a repeated-measures design to test the hypothesis that closure of hunting would result in stronger selection for important habitat features during fall–winter, the period when hunting would have occurred (Bennington and Thayne 1994; PROC MIXED, SAS Institute, Cary, North Carolina). We applied hunting treatments to study sites as a whole, so to avoid pseudoreplication, we took the mean selection index for each sex and age class of grouse, on each site, each year, as the response variable. Subjects of repeated measures were sites, which were nested within treatments. Treatment (experimental or control) and phase (pretreatment vs. hunting closed on experimental sites) were included as fixed effects. A significant phase × treatment interaction would indicate an effect of hunting on strength of selection for a habitat feature. We included natural log-transformed home range size (LN75), hard-mast index, and sex, age, or sex-age in models as control variables if they were found to influence selection for the habitat feature being tested (i.e., $P < 0.10$). Three-way interactions between sex, age, or sex-age and phase × treatment were tested to determine whether all sex and age classes responded similarly. Finally, a 3-way interaction between LN75 and phase × treatment was included to control for the effect of hunting on home-range size (Whitaker 2003).

For all analyses, we report mean ± SE parameter estimates. For multivariate models, we report least squares means; unless otherwise indicated, parameter estimates (i.e., slopes [β], or means for categories) resulting from model selection are from the model having the highest Akaike weight. For hypothesis tests, the level of significance was set at $\alpha = 0.05$.

Results

Averaged across all home ranges, clear-cuts and access routes were used 1.11–2.55× more than expected by chance (i.e., mean strength of selection was greater than zero) during both spring–summer and fall–winter and at both landscape and within-home-range scales (Table 2). At the landscape scale, mesic bottomlands comprised a greater proportion of home ranges than expected by chance during both spring–summer (1.11×) and fall–winter (1.06×; Table 2). Within home ranges, use of mesic bottomlands was 1.05× more than expected by chance during fall–winter, but on average was used in proportion to availability during spring–summer (Table 2).

Goodness-of-fit tests and residual plots indicated that the global model in each set of a priori models fit the data adequately. Model testing indicated that numerous factors influenced strength of selection for clear-cuts, access routes, and mesic bottomlands (Table 3). Study site (nested within forest type) was included in all best models.

Clear-cuts

Landscape-scale models.—At the landscape scale, several factors influenced strength of selection for clear-cuts by grouse (Table 3). Controlling for all other variables in the best model, the mean difference between use and availability of clear-cuts was ≈1.4 times greater in mixed-mesophytic forests (20.6 ± 1.4%) than in oak-hickory forests (15.0 ± 1.5%; note that evaluation of effect sizes for parameter estimates may be facilitated through comparison to mean rates of use and availability [Table 2]). All best models included the 4-level variable sex-age; selection was stronger by adult males (20.1 ± 1.6%) than by adult females (16.0 ± 1.6%) and juvenile males (16.2 ± 2.1%), and it was intermediate for juvenile females (18.9 ± 2.0%). Selection for clear-cuts was inversely related to home range size ($\beta = -5.9 \pm 1.0$ %/ln[ha]). Although a positive association with selection for access routes was observed ($\beta = 0.16 \pm 0.03$ %/m·ha^{-1}), there was an inverse relation between strength of selection for clear-cuts and mesic bottomlands ($\beta = -0.21 \pm 0.06$ %/%). However, the model also included a 3-way interaction between selection for mesic bottomlands, sex-age, and forest type. This resulted because the inverse relationship between selection for clear-cuts and mesic bottomlands was stronger in oak-hickory forests than in mixed-mesophytic forests, particularly for females (OH females, $\beta = -0.50 \pm 0.10$ %/%; MM females, $\beta = -0.29 \pm 0.13$ %/%). No relation between selection for clear-cuts and mesic bottomlands was observed for males in mixed-mesophytic forests.

Within-home-range models.—Best models of within-home-range scale strength of selection for clear-cuts were similar to those for landscape-scale selection, but they had reduced explanatory power (Table 3). As at the landscape scale, selection for clear-cuts was inversely related to both home range size ($\beta = -3.1 \pm 0.8$ %/ln[ha]) and strength of selection for mesic bottomlands ($\beta = -0.17 \pm 0.05$ %/%), and it was positively related to selection for access routes ($\beta = 0.09 \pm 0.03$ %/m·ha^{-1}). Also, all best models still included the 4-level variable sex-age, although mean strength of selection was greatest for juvenile males (7.5 ± 1.8%), weakest for adult females (3.9 ± 1.3%), and intermediate for juvenile females (6.7 ± 1.7%) and adult males (5.4 ± 1.4%). Unlike landscape-scale models, within-home-range strength of selection for clear-cuts was similar in mixed-mesophytic (6.0 ± 1.1%) and oak-hickory forests (5.7 ± 1.3%). Availability of clear-cuts in the landscape was included in 1 model in the best model set, although the effect was ambiguous ($\beta = -0.2 \pm 0.3$ %/%).

Table 2. Within-home-range (HR) and landscape-scale selection (i.e., use vs. availability) of access routes, clear-cuts, and mesic bottomlands by ruffed grouse in the Appalachians, 1996–2001. We used a 1-tailed *t*-test to verify that the mean difference between use and availability (i.e., strength of selection) was greater than zero, which would indicate that the habitat feature was being selected. Within-home-range analyses compared the 50% fixed kernel home range for each bird to the 95% fixed kernel; landscape analyses contrasted the 75% fixed kernel home range with habitat available in the landscape.

Season, scale		**Used**		**Available**			
Habitat feature	**n**	**Mean**	**SE**	**Mean**	**SE**	**t**	**P**
Spring–summer, within HR							
Access (m/ha)	356	36.09	1.91	32.42	0.95	2.51	0.006
Clear-cuts (%)	285	32.20	2.04	24.75	1.32	6.06	<0.001
Mesic bottomlands (%)	354	31.17	1.48	30.45	1.10	0.80	0.212
Spring–summer, landscape							
Access (m/ha)	356	36.00	1.42	21.34	0.26	10.64	<0.001
Clear-cuts (%)	285	29.93	1.74	11.73	0.50	12.06	<0.001
Mesic bottomlands (%)	354	31.34	1.27	28.36	0.92	3.55	<0.001
Fall–winter, within HR							
Access (m/ha)	535	34.78	1.58	31.03	0.74	3.01	0.001
Clear-cuts (%)	455	30.27	1.54	24.98	1.08	6.43	<0.001
Mesic bottomlands (%)	534	32.10	1.13	30.62	0.82	2.16	0.016
Fall–winter, landscape							
Access (m/ha)	535	33.83	1.12	20.61	0.21	12.33	<0.001
Clear-cuts (%)	455	28.66	1.36	11.82	0.39	14.37	<0.001
Mesic bottomlands (%)	534	31.54	0.97	29.71	0.69	2.73	0.003

Table 3. Best models to explain variation in within-home-range and landscape-level strength of selection (i.e., use–availability) for clear-cuts, access routes, and mesic bottomlands during fall–winter and spring–summer by ruffed grouse in the Appalachian Mountains, 1996–2001. For each habitat feature the same sets of a priori models (including the null model) were fit to both the within-home-range and landscape-level data sets. Only best models having AIC_c differences (Δ_i) ≤ 2.0 are presented.

Model[a]	**SSE**	**K**	**AIC_c**	**Δ_i**	**R^2**	**R^2_{adj}**	**ω_i**
Clear-cuts; landscape-level selectivity (n = 729)							
$Y = \beta_0$ + For + Site(For) + SA + Acs + TMI + Ln75 + (SA × For) + (SA × TMI) + (For × TMI) + (SA × For × TMI) + ε	317,449	24	4,479.4	0.0	0.315	0.294	0.93
$Y = \beta_0 + \varepsilon$ (null model)	463,759	2	4,710.0	230.6	0.000	0.000	0.00
Clear-cuts; within-home-range selectivity (n = 729)							
$Y = \beta_0$ + For + Site(For) + SA + Acs + TMI + Ln75 + ε	238,164	14	4,248.8	0.0	0.094	0.079	0.54
$Y = \beta_0$ + For + Site(For) + SA + Acs + TMI + Ln75 + (SA × For) + (SA × TMI) + (For × TMI) + (SA × For × TMI) + ε	231,924	24	4,250.6	1.8	0.118	0.090	0.22
$Y = \beta_0$ + For + Site(For) + SA + Acs + TMI + Ln75 + LsCC + ε	238,065	15	4,250.6	1.8	0.094	0.078	0.22
$Y = \beta_0 + \varepsilon$ (null model)	262,875	2	4,296.2	47.4	0.000	0.000	0.00
Access routes; landscape-level selectivity (n = 865)							
$Y = \beta_0$ + For + Site(For) + Sex + Sea + CC + TMI + Mast + Ln75 + (Mast × Sea) + (TMI × For) + ε	442,429	18	5,432.1	0.0	0.203	0.187	0.68
$Y = \beta_0 + \varepsilon$ (null model)	554,798	2	5,595.1	163.0	0.000	0.000	0.00
Access routes; within-home-range selectivity (n = 865)							
$Y = \beta_0$ + For + Site(For) + Sex + Sea + CC + TMI + Mast + Ln75 + (Mast × Sea) + (TMI × For) + ε	661,580	18	5,780.1	0.0	0.051	0.033	0.38
$Y = \beta_0$ + For + Site(For) + Sex + Sea + CC + TMI + Mast + (Mast × Sea) + (TMI × For) + ε	663,647	17	5,780.7	0.6	0.048	0.031	0.28
$Y = \beta_0 + \varepsilon$ (null model)	696,972	2	5,792.4	12.3	0.000	0.000	0.00
Mesic bottomlands; landscape-level selectivity (n = 865)							
$Y = \beta_0$ + For + Site(For) + Sea + CC + LsTMI + (For × Sea) + ε[b]	184,761	14	4,668.4	0.0	0.088	0.075	0.27
$Y = \beta_0$ + For + Site(For) + SA + Sea + CC + Acs + LsTMI + Ln75 + (SA × Acs) + (For × Sea) + ε	181,463	22	4,669.6	1.1	0.104	0.082	0.15
$Y = \beta_0$ + For + Site(For) + SA + Sea + CC + Acs + LsTMI + (SA × Acs) + (For × Sea) + ε	181,985	21	4,669.9	1.5	0.102	0.081	0.13
$Y = \beta_0 + \varepsilon$ (null model)	202,552	2	4,723.5	55.0	0.000	0.000	0.00
Mesic bottomlands; within-home-range selectivity (n = 865)							
$Y = \beta_0$ + For + Site(For) + SA + CC + Acs + Mast + LsTMI + (SA × For) + ε	213,746	20	4,807.0	0.0	0.092	0.072	0.42
$Y = \beta_0 + \varepsilon$ (null model)	235,355	2	4,853.3	46.3	0.000	0.000	0.00

[a] See Table 1 for definitions of explanatory variables, and Whitaker (2003; appendix B) for a list of all models tested.

Paired home ranges.—Comparison of pairs of home ranges from individual grouse did not identify any change in selection for clear-cuts between fall–winter and spring–summer, between juvenile and adult age classes, or between high- and low-mast years.

Access Routes

Landscape-scale models.—At the landscape scale, strength of selection for access routes was positively associated with strength of selection for clear-cuts ($\beta = 0.21 \pm 0.04$ m·ha^{-1}/%) and inversely related to home range size ($\beta = -3.2 \pm 1.0$ m·ha^{-1}/ln[ha]) (Table 3). There was an interaction between hard mast crops and season resulting from a positive influence of mast on selection of access routes during spring–summer ($\beta = 0.84 \pm 0.61$ m·ha^{-1}/unit mast) compared with an inverse trend during fall–winter ($\beta = -0.60 \pm 0.39$ m·ha^{-1}/unit mast). There was also an interaction between selection for mesic bottomlands and forest type. This resulted from the negative trend between selection for access routes and bottomlands on sites having mixed-mesophytic forests ($\beta = -0.08 \pm 0.08$ m·ha^{-1}/%), compared with a positive association on sites having oak-hickory forests ($\beta = 0.22 \pm 0.07$ m·ha^{-1}/%).

Within-home-range models.—The same model best explained variation in strength of selection for access routes at the within-home-range scale as at the landscape scale, although the explanatory power of the model was much lower (Table 3). As at the landscape scale, mast crop was inversely related to selection for access routes during fall–winter ($\beta = -1.11 \pm 0.50$ m·ha^{-1}/unit mast), and it was positively related during spring–summer ($\beta = 0.72 \pm 0.71$ m·ha^{-1}/unit mast). Within-home-range selection for access routes was positively related to landscape-level selection for clear-cuts ($\beta = 0.14 \pm 0.05$ m·ha^{-1}/%). Although parameter estimates were ambiguous, terms also were included for home-range size ($\beta = -1.95 \pm 1.20$ m·ha^{-1}/ln[ha]) and an interaction between the effects of forest type and selection for mesic bottomlands (MM forests, $\beta = -0.12 \pm 0.10$ m·ha^{-1}/%; OH forests, $\beta = 0.11 \pm 0.09$ m·ha^{-1}/%).

Paired home ranges.—Individual, adult, female grouse selected access routes more strongly during spring–summer than during fall–winter, with the difference being stronger at the within-home-range scale of selection (mean difference = 10.9 ± 3.6 m/ha, $n = 88$, $t = 3.07$, $P < 0.01$) than at the landscape scale (mean difference = 5.9 ± 2.3 m/ha , $n = 88$, $t = 2.58$, $P = 0.01$). Females also made greater use of access routes during fall–winters when hard-mast crops were poor, and again, the difference appeared to be strongest at the within-home-range scale (mean difference = 10.8 ± 3.5 m/ha, $n = 38$, $t = 3.07$, $P < 0.01$) compared with the landscape scale (mean difference = 7.3 ± 2.5 m/ha, $n = 38$, $t = 2.89$, $P = 0.01$).

Mesic Bottomlands

Landscape-scale models.—At the landscape scale, the best model (Table 3) indicated that strength of selection for mesic bottomlands was reduced as selection for clear-cuts increased ($\beta = -0.09 \pm 0.02$ %/%), but it increased as bottomland availability in the landscape increased ($\beta = 1.0 \pm 0.5$ %/%). There was an interaction between forest type and season; on sites having mixed-mesophytic forests strength of selection was similar between fall–winter and spring–summer (2.4 ± 1.0% and 2.1 ± 1.1%, respectively), whereas on sites having oak-hickory forests, bottomlands were not clearly selected during fall–winter (1.3 ± 1.0%), but they were selected during spring–summer (4.3 ± 1.2%). Other models in the best-model set included an interaction between sex-age and selection for access routes; this resulted from a positive relation with selection of bottomlands for juvenile males ($\beta = 0.11 \pm 0.05$ %/m·ha^{-1}), with no response by other classes. Considering findings for access routes (above), we conducted post hoc testing for an interaction between forest type and selection of access routes affecting selection for bottomlands. This revealed a positive relationship between selection for access routes and bottomlands on sites having oak-hickory forests ($\beta = 0.11 \pm 0.03$ %/m·ha^{-1}) compared with a lack of association on sites having mixed-mesophytic forests ($\beta = -0.03 \pm 0.03$ %/m·ha^{-1}).

Within-home-range models.—At the within-home-range scale, mesic bottomlands were selected on sites having oak-hickory forests but not those having mixed-mesophytic forests (2.8 ± 0.9% and −0.4 ± 0.6%, respectively). Though our best model also included a negative association with selection for clear-cuts, the parameter estimate was ambiguous ($\beta = -0.05 \pm 0.03$ %/%). Our a priori models suggested a positive association with selection for access routes ($\beta = 0.06 \pm 0.02$ %/m·ha^{-1}). However, post hoc tests revealed an interaction with forest type, where the relationship between selection of bottomlands and access routes was positive on oak-hickory sites ($\beta = 0.13 \pm 0.04$ %/m·ha^{-1}) and nonexistent on mixed-mesophytic sites ($\beta = 0.00 \pm 0.03$ %/m·ha^{-1}). The best model for mesic bottomlands included a term for availability of this habitat type in the landscape ($\beta = 1.1 \pm 0.6$ %/%) and also for fall hard-mast index ($\beta = 0.32 \pm 0.24$ %/unit mast), although effects for both of these terms were ambiguous. Finally, there was an interaction between sex-age and forest type. On sites having oak-hickory forests, adult females selected bottomlands (6.0 ± 1.6%), whereas other sex and age classes did not (1.5 ± 1.1%). On sites having mixed-mesophytic forests, use by adults (−1.7 ± 0.7%) was less than use by juveniles (1.8 ± 1.0%).

Paired home ranges.—Individual adult male grouse selected mesic bottomlands more strongly during fall–winter than during spring–summer on both oak-hickory sites (mean difference = 12.1 ± 5.4%, $n = 28$, $t = 2.22$, $P = 0.04$; within-home-range scale) and mixed-mesophytic sites (mean difference = 3.9 ± 1.7%, $n = 29$, $t = 2.28$, $P = 0.03$; landscape scale). In contrast, individual adult female grouse in oak-hickory forests increased use of mesic bottomlands during spring–summer (mean difference = 4.5 ± 1.9%, $n = 38$, $t = 2.44$, $P = 0.02$; landscape scale); we detected no seasonal difference for females inhabiting mixed-mesophytic forests. During fall–winter, female grouse inhabiting oak-hickory forests selected mesic bottomlands more strongly as adults than they had as juveniles (mean difference = 13.3 ± 4.2%, $n = 10$, $t = 3.16$, $P = 0.01$; landscape scale). Age did not affect selection of mesic bottomlands by females in mixed-mesophytic forests or males in either forest type.

Hunting Experiment

We found no change in landscape-scale strength of selection for clear-cuts in response to closure of hunting. In our within-home-range test, there was an interaction between phase and treatment, indicating a change in strength of selection for clear-cuts because

Table 4. Effect of hunting closure on selection of clear-cuts, access routes, and mesic bottomlands by ruffed grouse in the Appalachian Mountains, 1996–2001.[a] Parameter estimates are reported in Table 5.

Source	Numerator df	Denominator df	F *(Type III)*	P
Clear-cuts, within home range (n = 77)				
Phase	1	64.6	6.43	0.014
Treatment	1	22.4	0.11	0.741
Age	1	62.5	2.70	0.106
LN75[b]	1	21.8	7.59	0.012
Phase × treatment	1	64.6	7.42	0.008
LN75 × treatment	1	21.8	0.10	0.757
LN75 × phase	1	64.9	6.27	0.015
LN75 × phase × treatment	1	64.9	6.90	0.011
Age × treatment	1	62.5	0.97	0.327
Age×Phase	1	65	0.99	0.323
Age × phase × treatment	1	65	7.14	0.010
Access route, within home range (n = 106)				
Phase	1	84.6	2.00	0.161
Treatment	1	5.34	0.20	0.675
Sex-age	3	86.6	2.05	0.113
Phase × treatment	1	84.6	<0.01	0.964
Sex-age × treatment	3	86.6	1.77	0.158
Sex-age × phase	3	86.6	1.65	0.183
Sex-age × phase × treatment	3	86.6	2.31	0.081
Mesic bottomlands, landscape scale (n = 134)				
Phase	1	125	1.16	0.283
Treatment	1	7.4	1.99	0.199
Sex-age	3	121.0	2.27	0.084
LN75	1	126.0	11.91	0.001
Phase × treatment	1	125.0	4.95	0.028

[a] The response variable was the difference in strength of selection, averaged across grouse for each site each year. Data were analyzed using a repeated measure mixed-linear model fit using restricted maximum-likelihood (REML) estimation.

[b] LN75 is the mean natural log-transformed area of a 75% kernel home range.

of hunting closure (Table 4). However, there was also a 3-way interaction between phase, treatment, and age; strength of selection for clear-cuts by juveniles was 2.6× greater on treatments sites following closure of hunting than on controls, with no clear response by adults (Table 5).

We found no change in landscape-scale selection for access routes by grouse following closure of hunting. In our test of within-home-range selection, there also was no general effect of hunting closure on use of access routes. However there was some indication of a 3-way interaction between sex-age, phase, and treatment (Table 4). Exploratory tests by individual sex and age class suggested that on treatment sites use of access routes by adult

Table 5. Effect of hunting on strength of selection (i.e., use–availability) for access routes, clear-cuts, and mesic bottomlands by Appalachian ruffed grouse. During Phase I (fall 1996–spring 1999), hunting was open on all sites, whereas during Phase II (fall 1999–fall 2002), hunting was closed on treatment sites (*n* = 3) but remained open on control sites. ANOVA results are presented in Table 4.

Habitat and scale	Phase I (1996–1999)			Phase II (1999–2001)		
Class and treatment	***n***	**Mean**	**SE**	***n***	**Mean**	**SE**
Clear-cuts, within home ranges (%)						
Juveniles, control sites	7	12.73	3.90	12	5.67	2.97
Juveniles, treatment sites	9	0.31	3.79	6	14.73	4.32
Adults, control sites	9	1.61	3.42	15	3.18	2.65
Adults, treatment sites	11	8.06	3.00	8	3.59	3.80
Access routes, within home ranges (m/ha)						
Juvenile females, control sites	7	−1.41	7.35	6	19.27	7.99
Juvenile females, treatment sites	8	−4.17	6.84	4	12.90	9.81
Adult females, control sites	8	2.28	6.87	8	4.13	6.92
Adult females, treatment sites	8	0.01	6.84	5	−3.27	8.75
Juvenile males, control sites	6	−7.54	7.92	7	0.16	7.41
Juvenile males, treatment sites	5	3.93	8.75	4	−13.59	9.81
Adult males, control sites	7	4.04	7.33	9	−3.26	6.50
Adult males, treatment sites	9	4.24	6.44	5	29.49	8.75
Mesic bottomlands, landscape scale (%)						
All sex and age classes, control sites	44	2.68	2.10	40	0.83	2.01
All sex and age classes, treatment sites	31	3.43	2.68	19	8.79	2.95

males increased 7.0× following closure of hunting, though variability was high for all classes (Table 5).

Landscape-scale strength of selection for mesic bottomlands increased 2.6× for all sex and age classes of grouse following closure of hunting on treatment sites (Tables 4, 5). No change was detected for within-home-range selection of mesic bottomlands.

Discussion

We recognize that the ability of our a priori models to explain variation in our data set was modest. However, we expected a low signal-to-noise ratio for a number of reasons, and we believe our findings are still informative. Home ranges, boundaries that are likely only generally perceived by animals and are then imprecisely estimated from sets of telemetry locations, are a crude tool for studies of resource selection (Powell 2000). Also, of necessity, when making comparisons between many sites across a large region, we used unambiguous generalized features to estimate availability of important habitats; we took clear-cuts as a proxy for early successional forest, access routes as an index of forest-edge density, and used landform to identify sites having mesic soils. Undoubtedly, there were other sources of these habitats that were not captured in our classification (e.g., patches of early successional forest within mature stands resulting from natural disturbance). Consequently, we expect that low explanatory power (i.e., R^2_{adj}) resulted from our need for a robust analytical approach that could be generalized across a large region, and we feel that our findings still point to important aspects of the regional habitat ecology of ruffed grouse.

Although few studies have explicitly investigated variability in habitat use by a species, it is intuitive to expect that the importance of a habitat feature is dependant on ecological context (Block and Brennan 1993). Clear-cuts, access routes, and mesic bottomlands have been identified as important habitat features for Appalachian ruffed grouse, so one might predict that, on average, use of these habitats by this species would be greater than expected by chance. Indeed, this was what we observed in 11 of 12 tests of within-home-range and landscape-scale use of these habitat features during both the breeding and nonbreeding seasons (Table 2). However, we did not detect disproportionate use of bottomlands during spring–summer, and this exception highlights the importance of considering ecological context in habitat studies. Closer investigation revealed that, during this season, bottomlands were simultaneously weakly avoided by males, used in proportion to availability by females inhabiting mixed-mesophytic forests, and strongly selected by females inhabiting oak-hickory forests. When averaged across all individuals, this variability in use between sexes and forest types canceled out, masking the importance of this habitat. Even for the remaining habitat features, which were, on average, used more than expected by chance, strength of selection was not constant, and identification of factors influencing use yielded many insights into the regional habitat ecology of ruffed grouse.

It is not immediately obvious whether the magnitude of all of the effects we report here constitute biologically important differences. However we feel it is important to bear in mind that all 3 of the habitat features we studied were repeatedly found to be selected by ruffed grouse, and all confer important benefits to grouse in terms of survival or foraging opportunities. Consequently, we did not expect to see dramatic changes in use of these features, for example strong selection in some instances and avoidance in others. Rather, our belief is that even seemingly small differences in use of important habitats suggest important underlying differences in selective pressures. For example, use of clear-cuts is known to improve grouse survival and population size (Wiggers et al. 1992, Clark 2000, Dessecker and McAuley 2001), so 1.4× greater strength of selection for clear-cuts in mixed-mesophytic forests compared with oak-hickory forests suggests an important difference in the species' ecology between these forest types.

There was considerable interdependence in strength of selection among clear-cuts, access routes, and mesic bottomlands, and observed patterns suggest that these 3 habitat features were not equally favorable and/or that they were being selected to meet different needs. Previously, it has been suggested that access roads and other hard forest edges are more strongly selected when availability of (presumably higher-quality) early successional forest stands is low (Bump et al. 1947, Gullion 1984*a*), and this pattern was observed on our study sites (Whitaker 2003). In this context, the positive association we observed between strength of selection for clear-cuts and access routes was logical because both habitat features should be most strongly selected when clear-cuts are rare.

We observed an inverse relationship between strength of selection for clear-cuts and mesic bottomlands. Thick, early successional habitats, such as clear-cuts, are viewed primarily as escape cover for grouse, whereas mesic sites having well-developed groundcover are seen as a source of plant and invertebrate foods (Dessecker and McAuley 2001). Consequently, the inverse relationship may result because grouse are balancing 2 competing strategies; maximizing survival when energetic demands are low and accruing high-quality food when energetic needs are high. For example, males, who make no contribution to reproduction after mating, showed the strongest selection towards clear-cuts. In contrast, females need substantial nutrient reserves for egg production and then productive foraging sites for broods, and they are often under strong nutritional constraint in the Appalachian region (Devers 2005; B. Long, West Virginia University, Morgantown, W. Va., USA, unpublished data). Females selected bottomlands more strongly than did males, and they also exhibited a stronger trade-off between use of bottomlands and clear-cuts.

There was a positive association between selection for access routes and selection for mesic bottomlands in oak-hickory forests. In contrast, in mixed-mesophytic forests mesic bottomlands were not strongly selected, and there was no clear relationship between selection of this habitat and use of access routes. As with bottomlands, woodland access routes are often viewed as important foraging sites (e.g., Hollifield and Dimmick 1995). Accordingly, grouse selected access routes more strongly during fall–winters when hard-mast crops were poor and, in the case of females, during the breeding season. Stronger selection for mesic bottomlands and greater sensitivity to mast crops (Whitaker 2003) may be symptomatic of ruffed grouse inhabiting oak-hickory forests being under greater nutritional constraint than those in mixed-mesophytic forests (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1997, Devers 2005). The positive association between selection for access routes and bottomlands in oak-hickory forests may also result from this constraint.

Influence of Sex and Age

Divergence in habitat use by male and female grouse was greatest during the breeding season. During this time, males spend a considerable proportion of their time at displaying sites, and these drumming logs typically are located along ridges (Thompson et al. 1987, Schumacher 2002). Thus, the reduced use of bottomlands that we observed for males during spring–summer was likely an indirect result of this focus on ridge-top display sites during the breeding season. Males also select display sites in stands having high stem densities (Stoll et al. 1979, Stauffer and Peterson 1985, Thompson et al. 1987, Boyd 1990), and this may contribute to strong selection of clear-cuts by males. Further, juvenile males often have not yet settled on a perennial drumming site (Gullion 1981), and they may be excluded from high-quality sites by territorial adult males (Marshall 1965, Small 1985, Whitaker 2003), which would account for the stronger selection of clear-cuts by adult males.

During the breeding season, females most often nest in mature stands having open understories and make extensive use of bottomlands as brood foraging habitat (Stewart 1956, Stauffer and Peterson 1985, Thompson et al. 1987, Fettinger 2002, Haulton et al. 2003). At this time, it seems that the need for dense ground cover typical of mesic sites takes precedence over the species' general affinity for early successional stands. During winter, selection for mesic bottomlands by juvenile females was weak, presumably because they have not yet settled on future breeding sites (Small and Rusch 1989).

Influence of Forest Type

The ecology of ruffed grouse appears to differ in many important ways between mixed-mesophytic forests and oak-hickory forests. At the root of this dichotomy, ruffed grouse appear to endure greater nutritional stress in oak-hickory forests, and this constraint has direct demographic consequences (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1987, Whitaker 2003, Devers 2005). For example, adult grouse inhabiting oak-hickory forests increased home range size 2.5× following poor hard-mast crops, whereas those inhabiting mixed-mesophytic forests were unresponsive to mast crops (Whitaker 2003). Presumably, this nutritional constraint results in part from the rarity or absence of northern hardwood tree species (e.g., birch, aspen, and cherries) in oak-hickory forests; during winter and early spring, buds and flowers of these trees afford a dependable and accessible supply of high-quality grouse foods in northern forests (Braun 1950, Servello and Kirkpatrick 1987). Further, stands on (xeric) upland soils in oak-hickory forests may have limited value as foraging habitat because of the low abundance of ground cover vegetation they support (Braun 1950). Selection for mesic bottomlands was much stronger in oak-hickory forests, particularly for females, and it was associated with selection for access routes. There also was a pronounced difference in seasonal use of mesic bottomlands by females in oak-hickory forests. Stewart (1956) suggested that grouse rearing broods selected mesic bottomlands in oak-hickory forests because they more closely resembled mixed-mesophytic forests than did upland forests. Our analyses support this contention. Stronger selection for clear-cuts and a weaker trade-off between selection for bottomlands and clear-cuts on sites having mixed-mesophytic forests may have occurred because of the ubiquity of mesic soils, and the presence of northern hardwoods relaxed a constraint imposed by food scarcity in oak-hickory forests.

Influence of Hard-Mast Crops

In addition to affecting home-range size (Whitaker 2003), fall hard-mast crops influenced habitat use by ruffed grouse. Selection of access routes, particularly by female grouse, was stronger during fall–winter when mast crops were poor. This suggests that access routes provide alternate foraging areas for grouse. In oak-hickory forests, seeding and management of forest roads (e.g., Hollifield and Dimmick 1995) may provide food resources to help buffer negative consequences of poor mast crops. The positive association between hard-mast crops and selection of mesic bottomlands likely resulted from the association and productivity of trees producing high-quality hard mast with rich soils in bottomlands (e.g., white oak and beech; Servello and Kirkpatrick 1987). The lack of association between hard-mast crops and selection for clear-cuts may be related to the function of early successional stands as escape cover, as well as the absence of mature mast-producing trees in cut-overs. Also, clear-cuts were used more by males, who have lower energetic needs and are much more territorial than females, and so, they may be less responsive to transient environmental conditions.

Influence of Hunting on Habitat Use

A broadly supported prediction based on Darwinian fitness is that to balance increased risk of mortality, animals will reduce their movements when predation risk is increased (Lima 1998). However, ruffed grouse use smaller home ranges when hunting pressure is removed (Clark 2000, Whitaker 2003). This observation led us to hypothesize that hunters, who typically have a general knowledge of grouse habitat use and presumably allocate their hunting effort accordingly, pressure grouse out of important habitat types. We found evidence to support this; following closure of hunting, juvenile grouse made greater use of clear-cuts, all sex and age classes increased use of mesic bottomlands, and there was some evidence that adult males made greater use of access routes. No sex or age class reduced use of any of these habitat features following closure of hunting. Similar changes in habitat use in response to human disturbance have been reported for a range of taxa (reviewed in Frid and Dill 2002). In particular, studies have reported that hunters concentrate their activities around access routes (Lyon and Burcham 1998, Brøseth and Pedersen 2000), and that human activity (including hunting) typically leads to avoidance of disturbed areas by game (Kilgo et al. 1998, Frid and Dill 2002). Hunting-induced avoidance of important habitats may lead to indirect negative effects on populations of game animals. Avoidance of important refuging and foraging areas in response to hunting pressure may result in increased risk of predation and reduced body condition; ultimately, this could lead to reduced survival and reproductive success (Frid and Dill 2002). However, we did not detect any consequences of closure of hunting on the population ecology of ruffed grouse on our study sites (Devers 2005).

Management Implications

We recommend that consideration of forest type be incorporated into selection of locations for ruffed grouse management areas and into choice of habitat management prescriptions. In mixed-mesophytic forests, established approaches, primarily creation of early successional stands (e.g., Gullion 1984*b*, Thompson and Dessecker 1997), are appropriate. However in oak-hickory forests, food, particularly hard mast, is a limiting factor (Devers 2005), so management prescriptions should be aimed at alleviating this constraint. A low density of mature mast-producing trees should be retained in clear-cuts to stabilize masting and increase food availability within these patches of escape cover (Whitaker 2003). Brood habitat management should focus on mesic sites, particularly bottomlands, and be aimed at increasing ground cover vegetation and insect production. Whether females rearing broods would make preferential use of the combination of early successional stands on mesic sites is an open question not directly addressed here. However, it is likely that such sites would afford high-quality brood-rearing habitats, so this is an important topic for future investigation. Wooded roads should also be a focus of management and should be seeded and fertilized as a means to diversify foraging opportunities and to buffer mast failures. Also, we recommend gating roads and placing some management units far from access points, thereby, reducing hunting pressure in distant locations and minimizing disturbance resulting from other forms of road use (e.g., Brøseth and Pedersen 2000).

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