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MULTISCALE HABITAT SELECTION BY RUFFED GROUSE AT LOW POPULATION DENSITIES

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Abstract. Theory suggests habitats should be chosen according to their relative evolutionary benefits and costs. It has been hypothesized that aspen (Populus spp.) forests provide optimal habitat for Ruffed Grouse (Bonasa umbellus). We used the low phase of a grouse population’s cycle to assess the prediction that grouse should occupy aspen and avoid other forest types at low population density because of the presumptive fitness benefits of aspen. On the basis of our observations, we predict how the Ruffed Grouse population will increase in different forest types during the next cycle. In conifer (Pinus spp., Abies balsamea, Picea spp.)-dominated and mixed aspen–conifer landscapes, grouse densities were highest where forest types were evenly distributed. Within these landscapes, male Ruffed Grouse selected young aspen stands that were large and round or square. Although Ruffed Grouse selected young aspen stands strongly, contrary to prediction, they also used other forest types even when young aspen stands remained unoccupied. The relative densities of Ruffed Grouse in aspen and conifer forests indicated that the aspen forest’s carrying capacities for grouse was higher than the conifer forest’s at least during the low and declining phases of the grouse’s cycle. On the basis of our observations, we predict that Ruffed Grouse populations in aspen-dominated landscapes will have higher population densities and fluctuate more than will populations in conifer-dominated landscapes. We suggest that studies of avian habitat selection would benefit from knowledge about the relative densities among habitats at differing population sizes because this information could provide insight into the role of habitat in regulating populations and clarify inferences from studies about habitat quality for birds.

Key words: Bonasa umbellus, habitat use, population density, population regulation, Ruffed Grouse, multiscale analysis.

Selección de Hábitat a Varias Escalas por Bonasa umbellus a Densidades Poblacionales Bajas

Resumen. La teoría sugiere que los hábitats deben ser escogidos de acuerdo a sus costos y beneficios evolutivos relativos. Se ha propuesto la hipótesis de que los bosques de Populus spp. proveen un ambiente óptimo para Bonasa umbellus. Usamos la fase de densidad poblacional pequeña del ciclo de una población de B. umbellus para evaluar la predicción de que estas aves deberían ocupar los bosques de Populus y evitar otros tipos de bosque al encontrarse en densidades bajas debido a los beneficios presumibles del ambiente de Populus para su adecuación. Con base en nuestras observaciones, predecimos cómo incrementaría la población de B. umbellus en diferentes tipos de bosque durante el siguiente ciclo. En paisajes dominados por coníferas (Pinus spp., Abies balsamea, Picea spp.) y en paisajes mixtos de Populus y coníferas, las densidades de B. umbellus fueron máximas donde los tipos de bosque estaban distribuidos uniformemente. Dentro de esos paisajes, los machos escogieron los rodales de Populus jóvenes que eran grandes y con forma redondeada o cuadrada. Aunque las aves escogieron mayormente los rodales de Populus jóvenes, de forma contraria a la predicción, también usaron otros tipos de bosque aún cuando algunos rodales de árboles jóvenes permanecían desocupados. Las densidades relativas de B. umbellus en bosques de Populus y de coníferas indicaron que las capacidades de carga de los bosques de Populus eran mayores que las de los de coníferas, al menos durante las fases de densidad poblacional baja y de declive del ciclo de B. umbellus. Con base en nuestras observaciones, predecimos que las poblaciones de B. umbellus en paisajes dominados por Populus serán más densas y fluctuarán más que las poblaciones de paisajes dominados por coníferas. Sugerimos que los estudios sobre la selección de hábitat por parte de las aves se beneficiarían del conocimiento de las densidades relativas entre diferentes hábitats a distintos tamaños poblacionales, pues esta información podría aclarar el papel del hábitat como regulador de las poblaciones y clarificar las inferencias hechas a partir de estudios sobre la calidad del hábitat de las aves.

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INTRODUCTION

Patterns of avian habitat selection are complex, which often impedes understanding of the influence of habitat selection on population regulation. Habitat and population size are important factors influencing population regulation in wildlife (Morris 2006). Furthermore, population dynamics depend on how the population grows when at low densities and declines when at high densities (Sibly et al. 2005). The Ruffed Grouse (Bonasa umbellus) is a model species for assessing the influence of habitat selection on population regulation because it undergoes population cycles with large changes in density over much of its range (Rusch et al. 2000). These population cycles have sparked the interest of ecologists because they provide an opportunity to examine variation in habitat use relative to variation in population density (Barber 1989, Rosenzweig 1991). Grouse in general, and the Ruffed Grouse in particular, are also of considerable interest to wildlife managers because they are economically important game birds (Johnsgard 1983).

The Ruffed Grouse is thought to depend on aspen (Populus spp.; Gullion and Alm 1983, Rusch et al. 2000) over much of its range. However, aspen either does not occur or is a relatively minor component of its habitat in the western, eastern, and southern extremities of its range, so it cannot be strictly dependent on aspen (Barber 1989). This rangewide difference in habitat use has been termed “the evergreen controversy” (Barber 1989: 328). This situation is not unlike many avian conservation issues, where species have developed evolutionary strategies to cope with spatially and temporally varying resources (Rhodes and Odum 1996). When applied to conservation or habitat management the variation in these strategies can require profoundly different types of management. In the case of the Ruffed Grouse, population densities are much higher in areas where aspen is found than where aspen is absent (Rusch et al. 2000). Consequently, management for the Ruffed Grouse focuses on aspen where this species occurs (Gullion and Alm 1983). Under some conditions, however, grouse may attain high densities in landscapes dominated by conifer plantations (Gullion 1990). These seemingly contradictory observations suggest that patterns of habitat selection by Ruffed Grouse are not well understood despite intensive historical observation, which illustrates the problem of generalizing habitat selection by any bird species on the basis of multiple studies, particularly for wide-ranging species like the Ruffed Grouse.

Two factors hypothesized to influence observed patterns of habitat selection in the Ruffed Grouse include population density and spatial scale. Over most of their range Ruffed Grouse undergo population cycles of approximately 10 years, and between high and low phases of cycles population densities can vary by a factor \( >3 \) (Rusch et al. 2000, Bump et al. 1947). Although aspen appears to be a key habitat, the use of other forest types by Ruffed Grouse when aspen is present may be due to density effects on habitat-settlement patterns (Rosenzweig 1991). Therefore, we studied the grouse’s habitat selection during the decline and low phase of a cycle (M. A. Larson, Minnesota Department of Natural Resources’ Ruffed Grouse monitoring coordinator, pers. comm.; Zimmerman et al. 2008) to assess patterns of habitat selection at low densities, when theory predicts that individuals should occupy only the best habitats (Fretwell and Lucas 1970). Because observed patterns of habitat use can be artifacts of habitat selection at other spatial scales (Wiens 1989a), we examined grouse habitat use at two spatial scales, a larger (landscape or transect) scale and a smaller (stand) scale. Our landscape scale encompassed the matrix of stands including and surrounding stands used by male grouse during the spring breeding season, which might also yield insight into potentially important forest types outside of the breeding season. We first account for imperfect detection of grouse during field surveys, a common problem in field studies of wildlife (Anderson 2001), and then use model selection to identify the strongest pattern in habitat selection among potential hypotheses. We then develop predictions about how the grouse’s relative population densities should change through the cycle.

METHODS

STUDY AREA

We studied Ruffed Grouse at the Cloquet Forestry Center (1386 ha; hereafter “Cloquet”) from 2002 to 2005, and in the Deep Portage Conservation Area (hereafter “Cass”) and the Chippewa National Forest (hereafter “Chippewa”) in 2005. Cloquet has been the site of long-term grouse studies, whereas the other areas were randomly located sites in central Minnesota. Cloquet is 36 km southwest of Duluth, Minnesota (46° 31’ N, 92° 30’ E); Cass is ~160 km west of Cloquet in Cass County (46° 56’ N, 94° 31’ E), and Chippewa is ~25 km west of Grand Rapids, Minnesota (47° 14’ N, 93° 32’ E). Chippewa is approximately 140 km west-northwest of Cloquet. Average annual precipitation (76 cm) falls mostly (~63%) as rain during the relatively warm summer months (Tester 1997). These areas are in the transition zone between the boreal and broadleaf deciduous forest biomes (Bailey 1995). Approximately 65% of Cloquet is upland habitat, with wetlands covering the remainder of the study area. We used the silvicultural definition of forest stand types (hereafter “forest types”) as a contiguous population of trees that (1) has at least 66% of the basal area dominated by a single species and age class [e.g., a “young red pine” (Pinus resinosa) stand is an area with at least 66% of the trees’ basal area consisting of red pine ≥20 cm in diameter] and (2) has a sufficiently uniform structure to be considered a uniquely identifiable unit (Smith et al. 1997:11). Stand size averaged 3.36 ha (SD = 3.95) and ranged from 0.12 to 121.51 ha. Many upland forest stands were experimentally...
FIELD TECHNIQUES
We identified sites of Ruffed Grouse breeding displays by locating males performing their conspicuous acoustical display (called drumming); this “drumming site” represents the center of a bird’s territory during the late winter and early spring (Archibald 1975, Boag 1976). At this time both males and females use similar habitats, environmental conditions are among the most stressful of the year, and annual mortality rates in our area are highest (Gullion and Alm 1983, Lauten 1995). Therefore, drumming sites commonly have been used to assess this species’ habitat use (Rusch et al. 2000).

Using a robust design comprising 15 repeated surveys within a breeding season (Zimmerman and Gutiérrez 2007), which lasted from the first week of April to the second week of June, we carefully searched for drumming males along bounded transects ranging in length from 3 to 5 km. Our probability of detecting a grouse that was present at least once during the breeding season was >99% (Zimmerman and Gutiérrez 2007). We sampled nine, three, and three transects at Cloquet, Cass, and Chippewa, respectively. We quantified habitat at the landscape (larger) scale and stand (smaller) scales. The landscape scale encompassed all habitats (forests, wetlands, nonforested uplands) within the bounded transects at Cloquet, Cass, and Chippewa. The bounds of each transect were 175 m from its center line, the approximate distance from which we could hear grouse under all conditions at Cloquet (Zimmerman and Gutiérrez 2007). Thus the spatial scale for this level of analysis ranged from 1.05 to 1.75 km². In a few instances at Cloquet, the 175-m boundary overlapped with boundaries of other transects. When this occurred, we assigned the overlapping area to one transect only to avoid double counting the same area. Consequently, not all transects at Cloquet were the same size, and we calculated grouse density at this scale by counts corrected for transect area. We classified habitats into one of 11 categories, including wetlands, nonforested uplands, and nine forest types. The forest types were young aspen (stands 10–25 years of age), mature aspen (>25 years of age), young spruce–fir (trunks <20 cm diameter at breast height [DBH]), mature spruce–fir (≥20 cm DBH), young pine (<20 cm DBH), mature pine (≥20 cm DBH), young northern hardwood (birch or maple 10–25 years of age), mature northern hardwood (birch or maple >25 years of age), and mixed hardwood–conifer (i.e., a stand where neither hardwoods nor conifers constituted ≥66% of the basal area). These divisions were based on habitat associations of grouse and their predators (Gullion and Alm 1983, Gullion 1990, Boal et al. 2005). Our sample of replicated landscapes was 15 (nine transects surveyed from 2002 to 2005 at Cloquet and six transects surveyed during 2005 at Cass and Chippewa). For statistical analyses at this spatial scale we pooled our nine forest types into four main types: aspen, northern hardwood, conifer, and mixed hardwood–conifer.

We used Geographical Information System (GIS)-based maps that we developed for Cloquet, Cass, and Chippewa and the PATCH extension of ArcView 3.2 (ESRI Inc., Redlands, CA) to estimate landscape metrics within our 1.75-km² transects. These landscape metrics included mean patch size, number of patches, total area of a habitat type, and mean patch shape (perimeter:area ratio) for each habitat type. Because male grouse may display in stands close to habitat types used by females for nesting and roosting (Rusch et al. 2000, Clark 2000), we calculated Shannon’s diversity index and Shannon’s evenness index (i.e., the distribution of total land area among habitat types) of the six habitats (aspen, conifer, northern hardwood, mixed forest, wetland, nonforested uplands) within each transect (McGarigal and Marks 1995).

Although we used transects to organize field sampling, the individual forest stands at Cloquet served as the sampling units for the stand scale because we sampled the entire Cloquet forest. Although grouse may use wetlands for cover during the winter, males did not use wetlands or nonforested uplands for breeding-display sites, and for this scale of analysis we limited our analysis to upland forests. We recorded the location of each detected grouse with a Global Positioning System (GPS 12XL, Garmin, Inc., Olathe, KS) and summarized the total number of grouse in each stand, regardless of the transect from which we initially detected the grouse. We did not include the forest stands at Cass and Chippewa for this scale of analysis because many stands extended beyond the bounds of our transects (i.e., beyond the limits of our transect distance we could not reliably detect displaying grouse). We used a GIS-based map of Cloquet and the PATCH extension of Arc View 3.2 to estimate the size (in ha), shape (area in ha divided by perimeter in km), and edge (in km) of each forest stand at Cloquet.

STATISTICAL ANALYSES
Landscape scale. We used model selection and mixed-effects models to assess the relationship between landscape metrics and Ruffed Grouse density within transects. We developed nine a priori hypotheses, which included relationships between Ruffed Grouse density and the following landscape metrics:
fragmentation of aspen and conifer stands, forest patch sizes, forest-stand shapes, landscape habitat diversity, and the evenness of habitats (Table 1). We expressed these hypotheses as statistical models, used hierarchical models (Thogmartin et al. 2004) in a Bayesian framework and Markov chain Monte Carlo simulations (MCMC) to estimate parameters within models, and ranked models by using deviance-information criteria (DIC) to determine the most parsimonious model (i.e., model with the lowest DIC value; Gelfand and Ghosh 2000). We considered models within 5 DIC units of the best model to be competitive with the best model (Spiegelhalter et al. 2003). Because DIC provides a measure of model performance relative to the models in the a priori set, we assessed the absolute performance of the top-ranked model by estimating an $R^2$ value for the best model.

We hypothesized that the total areas of aspen and conifer were critical factors influencing Ruffed Grouse populations (Barber 1989, Rusch et al. 2000, Gullion and Alm 1983). Therefore, we developed a set of a priori hypotheses that represented predictions about how the size, fragmentation, and shape of forested habitats may have influenced Ruffed Grouse density (Table 1). The metrics, mean patch size, and total area were correlated for both aspen and conifer (Pearson correlation coefficients $>0.85$, $P<0.01$). Because we considered models of fragmentation, which was a function of the number of patches and mean patch size, we used mean patch size of aspen and conifer to represent the total area of these forest types in the landscape and discarded total area of these forest types from the analysis. In addition, we included models that represented the correlation between diversity, evenness, and mean patch size of other habitat types with grouse density because previous research indicated associations between grouse and these habitats at various periods of the bird’s life history (Clark 2000, Rusch et al. 2000). Zimmerman (2006) presented a detailed discussion and supporting literature for a priori models.

We used multiple linear regression and the program WinBUGS (Spiegelhalter et al. 2003) to estimate the parameters in our statistical models and the DIC values for each model. We considered density of grouse within transects as our response variable and year as a random effect. We also considered Ruffed Grouse density to have a normal distribution with an unknown mean and variance. We assumed normal distributions for the random effect of year and used an inverse gamma distribution to estimate the unknown variance associated with the year effect (Link et al. 2002). We assumed that all habitat parameters were normally distributed, and we used noninformative priors ($\tau = 0, \sigma^2 = 1000 000$) to estimate their variances. Therefore, the general structure of these models was:

$$D_i = \mu + \tau + \sum_{k=1}^p \beta_k x_{ik}$$

where $D_i$ represented density calculated as the number of grouse divided by the area of each transect, $\mu$ represented an intercept, $\tau$ represented the random effect of year, and the $\beta_k$ represented parameters relating habitat covariates ($x_{ik}$) to density. We conducted 20 000 MCMC iterations to estimate parameters for each of the models. If the model showed adequate convergence (see below) for fixed parameter estimates during the first 10 000 iterations (i.e., the “burn-in” period), we used the last 10 000 estimates for assessing convergence, deriving median parameter estimates, and calculating DIC. We estimated two chains and two sets of initial values for the MCMC estimators in each model. We used starting values of zero for all habitat parameters in the first chain and estimated nonzero
starting values by using maximum-likelihood estimates for the second chain (PROC GENMOD in program SAS; SAS Institute, Cary, NC). We assessed convergence of the two chains in WinBUGS by using history plots, density plots, and the Gelman–Rubin statistic. We considered Gelman–Rubin statistic values <1.2 to indicate convergence of the two chains (Congdon 2003). We assessed the strength of particular variables within models with 95% credible intervals, which are analogous to frequentist confidence intervals. Variables with intervals that excluded zero were considered to be credibly correlated with grouse density.

Forest-stand scale. We used the same model-selection approach to assess forest-stand attributes used by drumming grouse as we used to assess density at the landscape scale. For this scale, we used the number of drumming grouse within each forest stand as the response variable and the different forest types as predictor variables. We developed 8 a priori models based on predictions about how stand type, age, and other attributes could influence counts of grouse within each stand (Table 2). We considered two sets of habitat classifications (a fine-scale classification with nine categories and a coarse-scale classification with five categories) and three forest-stand attributes (size, shape, and amount of edge) (Table 2). Zimmerman (2006) presented a detailed description of supporting literature for the a priori hypotheses.

We used a mixed-effects Poisson regression to estimate parameters for models at the forest-stand scale. We assumed that the number of drumming grouse within forest stands was Poisson distributed with an unknown mean. Data assumed to be generated from a Poisson model often contain a variance greater than the mean (Congdon 2003), so we estimated a noise parameter to assess the extent of overdispersion in our data (Thogmartin et al. 2004). We considered forest stand and year to be random effects. Therefore, the general form for the models estimated for this scale was:

$$\log(\lambda_i) = \log(A) + (\mu + \delta + \tau + \sum_{k=1}^{\rho} \beta_k X_{ik}) + \epsilon_i$$

where $A$ represented an area adjustment for each sample unit (i.e., each forest stand), $\mu$ represented an intercept, $\delta$ represented the random effect of forest stand, $\tau$ represented the random effect of year, $\beta_k$ represented parameters for stand-level covariates, and $\epsilon_i$ represented the overdispersion parameter for the Poisson model. If we did not detect large amounts of overdispersion, we removed the noise parameter from the model. We used a normal and noninformative prior for random year effects, with $\tau = 0$ and an unknown variance estimated from a noninformative ($r = 0.001, \mu = 0.001$) gamma prior. We assumed that prior parameters for the habitat covariates were normally distributed random variables with $\tau = 0$ and $\sigma^2 = 1\ 000\ 000$. We used DIC and followed the same estimation, model-assessment, and correlation-assessment protocol described for the landscape-scale analysis.

Predictions for habitat occupancy during cyclic increase. We used isodars (Morris 1988) to make predictions about habitat quality and patterns of habitat occupancy as our grouse population increases during the next 10-year cycle. Isodars are graphical lines that track the density of a species in different habitats at varying population sizes and relate the spatial distribution of individuals to habitat quality on the basis of predicted relationships between habitat selection and population regulation (Rosenzweig 1991, Morris 1988). We limit our isodar analysis to aspen and conifer forests because, among forest types, grouse occupying aspen stands are predicted to have the highest fitness (Gullion and Alm 1983, Rusch et al. 2000) and because of uncertainty about the ecological value.

### Table 2. A priori models and predicted relationships between forest-stand metrics and tree species composition on Ruffed Grouse density in Minnesota, 2002–2005. All forest-type variables are categorical.

<table>
<thead>
<tr>
<th>Model number</th>
<th>Model</th>
<th>Variables* and predictions^b</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Forest type</td>
<td>$\pm A_y$ $\pm A_m$ $\pm C_y$ $\pm C_{m}$ $\pm N_y$ $\pm N_{m}$ $\pm P_y$ $\pm P_{m}$ $\pm SF_y$ $\pm SF_{m}$</td>
</tr>
<tr>
<td>2</td>
<td>Forest type (pooled)</td>
<td>$\pm C_y$ $\pm C_{m}$ $\pm N_y$ $\pm N_{m}$ $\pm P_y$ $\pm P_{m}$ $\pm SF_y$ $\pm SF_{m}$</td>
</tr>
<tr>
<td>3</td>
<td>Patch shape</td>
<td>+SH</td>
</tr>
<tr>
<td>4</td>
<td>Patch edge</td>
<td>+PE</td>
</tr>
<tr>
<td>5</td>
<td>Patch shape + forest type</td>
<td>$\pm SH$ $\pm A_y$ $\pm A_m$ $\pm C_y$ $\pm C_{m}$ $\pm N_y$ $\pm N_{m}$ $\pm P_y$ $\pm P_{m}$ $\pm SF_y$ $\pm SF_{m}$</td>
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<tr>
<td>6</td>
<td>Patch shape + forest type (pooled)</td>
<td>$\pm SH$ $\pm A_y$ $\pm A_m$ $\pm C_y$ $\pm C_{m}$ $\pm N_y$ $\pm N_{m}$ $\pm P_y$ $\pm P_{m}$ $\pm SF_y$ $\pm SF_{m}$</td>
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<tr>
<td>7</td>
<td>Patch edge + forest type</td>
<td>$\pm PE$ $\pm A_y$ $\pm A_m$ $\pm C_y$ $\pm C_{m}$ $\pm N_y$ $\pm N_{m}$ $\pm P_y$ $\pm P_{m}$ $\pm SF_y$ $\pm SF_{m}$</td>
</tr>
<tr>
<td>8</td>
<td>Patch edge + forest type (pooled)</td>
<td>$\pm PE$ $\pm C_y$ $\pm C_{m}$ $\pm N_y$ $\pm N_{m}$ $\pm P_y$ $\pm P_{m}$ $\pm SF_y$ $\pm SF_{m}$</td>
</tr>
</tbody>
</table>

* $A$ = aspen, $C$ = conifer (pine or spruce–fir), $HC$ = mixed hardwood/conifer, $N$ = northern hardwoods (birch, maple, or oak), $NA$ = northern hardwood or aspen, $P$ = pine, $SF$ = spruce–fir, $PS$ = patch size, $SH$ = patch shape index, $PE$ = length of edge between patch and other patches. Subscript represents age: $m$ = mature, $y$ = young.
^b $+$ = predicted positive correlation, $-$ = predicted negative correlation, $\pm$ = correlation could be positive or negative.
of conifers to Ruffed Grouse (Barber 1989, Gullion 1990). We estimated isodars from regression, where the data consisted of grouse density in conifers as the predictor variable (x axis) regressed against grouse density in aspens as the response variable (y axis) within a study area at one point in time (Morris 1988). Positive intercepts would indicate that aspen supports higher densities than conifer regardless of overall population density. Morris (1988) noted that as the overall population increases, population growth rates would be expected to decline. Isodar slope values >1 would suggest that the growth rate declines more rapidly in conifers than in aspens, whereas a slope = 1 indicates that the growth rates within aspen and conifer decline at the same rate.

We estimated the isodar for Ruffed Grouse in aspen and conifer forests by estimating the density of grouse in each of those forest types at Cloquet in 2002, 2003, 2004, and 2005 (n = 4 isodar points) and the density of grouse in those forest types at Cass and Chippewa (n = 6 isodar points). We used linear regression to estimate the isodar [i.e., the intercept and slope for a line that best fits the densities of grouse in conifer forest (x axis) plotted against the density of grouse in aspen forests]. We used 95% Wald confidence intervals to assess whether the intercept of this isodar was >0 and the slope was >1 or equal to 1.

RESULTS

LANDSCAPE SCALE

The density of drumming male grouse within the nine Cloquet transects varied among the four years of surveys (range 0.00–0.26 per ha). The number of drumming males at Cloquet declined from 64 in 2002 to 46 in 2005. Thus, given the high probability of detecting a drumming grouse at least once during our 15 surveys of each transect each spring, we observed a 28% decline in grouse during our study. When only the 2005 data are considered, mean densities of drumming grouse were 0.04 ha⁻¹ (SD = 0.03) at Cloquet, 0.03 ha⁻¹ (SD = 0.01) at Cass, and 0.03 ha⁻¹ (SD = 0.02) at Chippewa.

Grouse had higher densities in landscapes that had a more even distribution of habitats. This model was 5.02 DIC units better then the second-ranked model, which indicated strong support that this was the best model (Table 3). The best model indicated that landscapes with an even distribution of habitats (i.e., conifer, aspen, hardwood, wetland) had a greater density of drumming grouse than landscapes where one type of habitat dominated (βShannon’s evenness = 2.01, 95% CI = 0.72 to 3.29). However, the r² value (0.28) indicated substantial uncertainty about the relationship between habitat evenness and grouse density at the landscape scale.

Habitat evenness could vary by landscape because the relationship of evenness in conifer-dominated landscapes could be different from the relationship of evenness in aspen-dominated landscapes. Therefore, we assessed some of the landscape characteristics within transects to gain a more clear biological interpretation of the best model. Although mean patch size of aspen was not correlated with mean patch size of conifer (r = −0.41, P = 0.13), the proportions of aspen and conifer within transects were correlated with habitat evenness. Specifically, transects with a higher density of grouse and more evenly distributed habitats also had a lower proportion of conifer (rconifer-evenness = −0.69, P < 0.001) and a higher proportion of aspen (rconifer-evenness = 0.70, P < 0.001) than transects with lower evenness values. Parameter estimates for mean patch size of conifer and mean patch size of aspen from the second-ranked model indicated a strong negative relationship between grouse density and conifer patch size (βMPS conifer = −0.01, 95% CI = −0.03 to −0.13), but no correlation between Ruffed Grouse density and aspen patch size (βMPS aspen = 0.01, 95% CI = −0.03 to 0.04).


<table>
<thead>
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<th>Model</th>
<th>$\hat{\beta}$</th>
<th>pd</th>
<th>DIC</th>
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<td>Shannon's evenness index: all cover types</td>
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<td>5.10</td>
<td>9.84</td>
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<td>5.86</td>
<td>14.86</td>
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<td>7.72</td>
<td>16.82</td>
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<tr>
<td>Fragmentation: aspen and conifer</td>
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<td>7.78</td>
<td>17.44</td>
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<td>Intercept-only model</td>
<td>13.83</td>
<td>3.66</td>
<td>17.49</td>
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<tr>
<td>Mean patch size: aspen</td>
<td>10.82</td>
<td>7.76</td>
<td>18.58</td>
</tr>
<tr>
<td>Mean patch shape: aspen and conifer</td>
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<td>5.68</td>
<td>18.91</td>
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<td>14.22</td>
<td>4.81</td>
<td>19.03</td>
</tr>
<tr>
<td>Fragmentation: aspen</td>
<td>13.69</td>
<td>5.98</td>
<td>19.67</td>
</tr>
</tbody>
</table>

*Posterior mean of the deviance.

Effective number of parameters; the number of parameters in hierarchical models with mixed effects can be a continuous number (Spiegelhalter et al. 2003).

Deviance information criterion.

FOREST–STAND SCALE

At Cloquet, from 2002 to 2005, we sampled 231 individual forest stands, which represented all of the forest stands not harvested during the study period. In the analysis at this scale the mean forest-stand size was 3.36 ha, with most stands between 0.12 and 36.78 ha. The only stand outside of this range was a reserve of old-growth pine covering 121.51 ha. The number of drumming Ruffed Grouse within individual stands ranged from zero to four. Seventy-five percent of forest stands at Cloquet were not occupied by a drumming grouse during any of the four years of surveys.

Our preliminary estimates of overdispersion were extremely small (<0.005), so we excluded an overdispersion parameter from habitat models. Forest-stand shape and a fine-scale classification of forest type (i.e., nine forest types) was the most parsimonious hypothesis for the gourse’s selection of
forest stands (Table 4). Estimates and confidence intervals for the parameters in the best model indicated that our stand-shape index was negatively correlated with density of drumming males ($\hat{B}_{\text{stand shape}} = 0.002, 95\% \text{ CI } = 0.005$ to $0.000$) and that counts were influenced by forest type. A model representing patch shape was within 5 DIC units of the second-ranked model, indicating further support for the effect of patch shape. Specifically, round or square stands (i.e., lower perimeter:area ratio) had higher counts of drumming grouse than did long narrow stands. Plots of the predicted values for each forest type using the mean-shape index (perimeter:area ratio) observed at Cloquet indicated that drumming grouse selected young aspen stands more often than other forest types (Fig. 1).

Although grouse appeared to select young aspen stands for drumming, we also observed grouse drumming in a variety of other forest types and age classes during this study (Fig. 1). The best model accounted for approximately 76% of the variation in the density of drumming grouse among forest stands. We had considered incorporating an intercept-only model prior to analysis but rejected doing so because of the copious information about grouse-habitat relationships, leading us to expect a strong relationship among at least some models we chose on the basis of the literature. However, a reviewer suggested including an intercept-only model, which we estimated post hoc. This model was 11.04 DIC units greater than the best model and was thus not competitive.

### Predictions for Habitat Occupancy

The isodar for aspen and conifer habitats indicated that grouse density changed in the same direction in both forest types as the overall population changed (Fig. 2). The regression model showed that the intercept was positive ($\hat{B}_{\text{intercept}} = 0.06, 95\% \text{ CI } = 0.03$ to $0.09$), and the slope of the best-fit line was >1 ($\hat{B}_{\text{slope}} = 3.05, 95\% \text{ CI } = 1.64$ to $4.45$), indicating that on the basis of occupancy patterns aspen stands were of higher quality than the other forest types. These results suggest that aspen forests are both qualitatively and quantitatively (sensu Morris 1988) better for Ruffed Grouse than conifer forest. Consequently, we expect that the grouse’s density will remain higher in and increase at a higher rate in aspen than in conifer forest as the population increases to cyclic high points.

![Figure 1](image1.png)

**Figure 1.** Predicted counts of drumming Ruffed Grouse males within nine forest-stand types estimated from the most parsimonious model, Cloquet Forestry Center, Minnesota, 2002–2005. Error bars represent 95% credible intervals for each predicted count.

![Figure 2](image2.png)

**Figure 2.** Observed density of drumming Ruffed Grouse in conifer and aspen forests at three areas (Cloquet from 2002 to 2005, Cass in 2005, and Chippewa in 2005) in Minnesota. The line represents the estimated regression of grouse density in aspen and conifer forests derived from the observed data (black dots).

### Table 4


<table>
<thead>
<tr>
<th>Model</th>
<th>$\hat{D}$</th>
<th>$p\hat{D}$</th>
<th>DIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Patch shape + forest type</td>
<td>571.19</td>
<td>70.91</td>
<td>642.10</td>
</tr>
<tr>
<td>Patch shape</td>
<td>568.18</td>
<td>76.10</td>
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<td>Patch edge + forest type</td>
<td>577.35</td>
<td>72.11</td>
<td>649.46</td>
</tr>
<tr>
<td>Patch edge</td>
<td>571.37</td>
<td>78.10</td>
<td>649.47</td>
</tr>
<tr>
<td>Forest type</td>
<td>579.14</td>
<td>71.35</td>
<td>650.50</td>
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<td>Patch edge + forest type (pooled)</td>
<td>577.98</td>
<td>73.64</td>
<td>651.62</td>
</tr>
<tr>
<td>Forest type (pooled)</td>
<td>580.685</td>
<td>72.53</td>
<td>653.21</td>
</tr>
<tr>
<td>Patch shape + forest type (pooled)$^d$</td>
<td>——</td>
<td>——</td>
<td>——</td>
</tr>
</tbody>
</table>

$^a$Posterior mean of the deviance.

$^b$Effective number of parameters; the number of parameters in hierarchical models with mixed effects can be a continuous number (Spiegelhalter et al. 2003).

$^c$Deviance information criterion.

$^d$Model did not converge.
DISCUSSION

For several decades, ecologists have hypothesized that birds use specific cues for selecting habitats (Hildén 1965, Wiens 1989b). Spatial scale and population density are two important factors that influence whether birds actually select habitats on the basis of those cues (Wiens 1989b, Newton 1998). From statewide counts and our data, Ruffed Grouse were in the decline and low phases of their population cycle throughout Minnesota during our multiscale study from 2002 to 2005 (M. Larson, Ruffed Grouse monitoring coordinator, Minnesota Department of Natural Resources, pers. comm., Zimmerman et al. 2008). Thus, theory predicts individuals should have selected habitats conferring the highest absolute fitness as a result of reduced intraspecific competition (Fretwell and Lucas 1970). On the basis of previous research in our study area (Gullion and Svoboda 1972, Gullion and Alm 1983), we predicted grouse should have selected aspen during this period of low population density. However, our observations suggested that habitat selection varied by spatial scale: grouse density was higher in landscapes with a diversity of habitats at a large scale and highest in aspen at the smaller stand scale. Furthermore, although our prediction was generally supported at the stand scale, some grouse selected seemingly suboptimal habitats.

RELATIONSHIPS BETWEEN GROUSE DENSITY AND LANDSCAPE CONDITIONS

In our study area Ruffed Grouse density was highest in landscapes having an even distribution of all habitat types. This result was difficult to interpret without understanding the composition of habitats within our transects (i.e., landscapes) because landscapes that had a high proportion of conifers had lower evenness values, whereas landscapes with a greater proportion of aspen had higher evenness values. Thus, grouse could have been (1) selecting sites in landscapes composed of an even distribution of forest types, (2) selecting landscapes composed primarily of aspen, or (3) avoiding landscapes composed primarily of conifers. Our results supported alternative 1 because the model hypothesizing a negative correlation between grouse density and mean patch size of conifers, which was correlated with total area of conifers, had less support than the evenness model, indicating that grouse were selecting landscapes with an even distribution, or higher diversity, of habitat types. The hypothesis related to mean patch size of aspens and number of patches had the least support (no support for alternative 2 above). Therefore, although drumming grouse occupied aspen at the scale of individual stands, our landscape-scale analysis suggested that densities of Ruffed Grouse were higher where there was an even distribution of the four habitats (i.e., wetlands, hardwoods, aspen, conifer) that we defined in our study (alternative 1). The correlation between grouse density and habitat evenness we found may have been related to different habitat needs for different life-history stages (e.g., drumming, nesting, brood rearing, and dispersal) and/or variable weather conditions that required birds to find shelter in different habitat types. Displaying birds may be more likely to attract mates when they occupy sites adjacent to nesting habitat. For example, Gullion and Svoboda (1972) and Gullion (1988) reported that females used forest stands structurally different from stands used by drumming males. In addition, Ruffed Grouse sometimes used conifer forests during the fall (Clark 2000) and winter when young aspen and snow roosts were not available as cover (Thompson and Fritzell 1988). Therefore, grouse may have selected aspen or hardwood stands adjacent to conifers for thermal cover (i.e., conifers provide shelter from cold more than aspens when snow roosting is not possible). Despite the apparent correlation of the evenness variable at the landscape scale, this model explained only a small proportion of variation in grouse density among landscapes.

RELATIONSHIPS BETWEEN GROUSE AND HABITAT AT THE FOREST-STAND SCALE

We detected the highest number of drumming grouse in young (10–25 years of age) and large aspen stands having a high area:perimeter ratio. Our results, with regard to patch shape as quantified from the area:perimeter ratio, were consistent with other studies in which grouse densities have been shown to be highest in round or square habitat patches (Gullion and Svoboda 1972, Fearer and Stauffer 2003). However, stand shape and stand size were correlated in our study area, so regularly round/square patches tended to be larger than elongated ones. Several studies have explored the influence of forest-stand size on Ruffed Grouse occupancy (e.g., Sharp 1963, Gullion and Alm 1983, McCaffery et al. 1996, Fearer and Stauffer 2003). In these studies, in which stand sizes ranged from 0.1 to almost 100 ha, the optimal stand size appeared to be 2–8 ha. However, McCaffery et al. (1996) reported that grouse densities did not vary greatly when stand size varied between 8 and 98 ha. Ruffed Grouse use of aspen stands between 10 and 25 years of age for drumming displays has been well documented (Gullion and Svoboda 1972, Gullion and Alm 1983, Rusch et al. 2000). Gullion and Alm (1983) suggested that this age class of aspen provides the best year-round cover for males and nonbreeding females. However, these observations were contrary to our observations of grouse using a variety of forest types at relatively lowest densities, when they should have occupied only the best habitats (i.e., aspen). During our study, grouse occupied some mature pine and spruce–fir stands, whereas some aspen stands remained unoccupied during all years. We also did not expect this pattern of habitat occupancy because other researchers have argued that Ruffed Grouse should incur their lowest level of fitness if they occupy mature pine stands, which put them at the greatest risk of predation from the Northern Goshawk (Accipiter gentilis) (Gullion and Alm 1983, Boal et al. 2005).
The hypothesis that animals will exhibit greater habitat selectivity at low population densities has received wide support (see Rosenzweig 1991 for a review). Studies of a wide range of birds, including raptors (Smallwood 1988), songbirds (Arcese 1987), and waterfowl (Ebbing 1992), have demonstrated that individuals occupy the best habitats at the lowest population densities. Further support for density-dependent habitat selection has been inferred from changes in density through time and changes in habitat-occupancy patterns as population density increased over a long period. For example, studies of songbirds indicate that density remains more stable in the best habitats because individuals occupy those habitats first and tend to use lower-quality habitats when population density is high (e.g., Probst and Hayes 1987, Bollinger and Gavin 1989). Although our study of a cyclic bird population adds additional support to the hypothesis that individuals occupy the best habitats at low densities, we do not know why some individuals occupied suboptimal habitat (i.e., conifer). Possible explanations included failure of individuals to locate young aspen stands because of imperfect knowledge (Gray and Kennedy 1994), presence of ground predators precluded grouse from occupying particular young aspen stands, shrub density within conifer stands provided adequate cover from predators (Zimmerman and Gutiérrez 2008), or some young aspen stands lacked a nearby winter food source (buds and catkins of mature aspen) (Gullion and Alm 1983). In addition, site fidelity has been shown to disrupt patterns of optimal habitat occupancy if individuals settle on sites where they successfully reproduced during a previous season even though higher-quality sites were available (Lanyon and Thompson 1986).

Our observation of differential habitat selection at different scales is consistent with that of several other avian taxa (e.g., Wiens et al. 1987, Newton 1998, Barbaro et al. 2008), likely as a result of scale-dependent costs associated with habitat selection (Morris 1987). For example, Chalfoun and Martin (2007) observed that Brewer’s Sparrows (Spizella breweri) apparently selected landscapes that would increase food availability and nest sites within those landscapes that reduced the risk of predation. Paralleling our study of Ruffed Grouse, Barbaro et al. (2008) reported that the Eurasian Hoopoe (Upupa epops) selected for a diversity of habitats at the landscape scale with stronger selection for specific attributes at smaller scales.

PREDICTIONS FOR HABITAT OCCUPANCY

The pattern of habitat use that we have observed has important implications for population regulation of the Ruffed Grouse and perhaps other cyclic species. Gullion and Marshall (1968) suggested that male grouse occupying conifer forests should have lower survival and might receive fewer visits from females, reducing their reproductive success in comparison to birds occupying aspen forests. Consequently, males selecting conifer stands should be less fit than those occupying aspen stands. Thus, patterns of male density in these two forest types at different population densities provide predictions about how changes in the proportions of these habitats across the landscape should influence grouse populations.

On the basis of the isodar analysis, we predict that the entire Ruffed Grouse population should have lower population densities and growth rates in conifer than in aspen. Although ecological traps and source–sink dynamics could lead to patterns similar to those we observed (Shochat et al. 2005), patterns of habitat selection and population dynamics across the range of the Ruffed Grouse support this prediction. For example, on a regional scale, grouse densities and rates of population growth are lower in boreal and other coniferous forests than in aspen-dominated regions (Rusch et al. 2000). Our prediction is also supported by rangewide differences in the Ruffed Grouse’s population dynamics. Regulated (e.g., stable populations or cyclic populations with bounded fluctuations [Murdoch 1994]) Ruffed Grouse populations that occur in the aspen-dominated portion of the species’ range show distinct population fluctuations, whereas regulated western, southern, and eastern populations that occupy regions not dominated by aspen have lower densities and are not cyclic (Keith and Rusch 1989, Rusch et al. 2000). Populations with higher intrinsic growth rates are more likely to fluctuate than those with lower intrinsic growth rates (Case 2000). Thus, individuals occupying aspen-dominated landscapes may incur greater fitness, as measured by intrinsic growth rates, than those occupying conifer-dominated landscapes. These patterns are not comparable to those of unregulated grouse populations (e.g., populations on the edge of a species’ range), whose dynamics may be highly unstable and strongly influenced by metapopulation dynamics (Murdoch 1994).

Rangewide differences in habitat selection by Ruffed Grouse have led to controversy among biologists and wildlife managers regarding the value of conifers to the grouse (Gullion and Alm 1983, Barber 1989, Gullion 1990). Our results suggest that Ruffed Grouse occupy conifer habitats even at low population densities, when they are predicted to occupy aspen, but it is not clear what effect this has on their population dynamics. Long-term monitoring of Ruffed Grouse populations through a 10-year cycle and estimates of individual fitness (e.g., survival and reproductive success) are needed to assess our prediction that although individuals occupy conifer stands when aspen is available, those individuals will likely be less fit and populations occupying conifer zones will have lower rates of population growth.

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LITERATURE CITED


JOHNSGARD, P. A. 1983. The grouse of the world. University of Nebraska Press, Lincoln, NE.


