Selection of Landscapes by Male Ruffed Grouse During Peak Abundance

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Dedication

My family, friends, and mentors along the way; those that have gone the extra mile to support my endeavors and have never ceased to believe in my ability to accomplish the goals that I have set.

Abstract

Most research on ruffed grouse (*Bonasa umbellus*) habitat selection has focused either on habitat structure within their activity centers or characteristics of forest stands containing activity centers. I studied the relationship between landscape configuration and density of male grouse during the high portion of their cycle. I located 290 and 230 male grouse during 2009 and 2010 respectively, on 30 landscapes encompassing 5,349 hectares. I used information theoretic model selection to examine two sets of *a priori* models. The top model in the first set was the null model (intercepts only), but a model representing Shannon's Evenness Index was competing. This competing model contained the second greatest cumulative weight ($AIC_c w_i = 0.203$). Shannon's Evenness Index was positively correlated with male grouse density (R= 0.43). The effect of Shannon's Evenness Index within landscapes was difficult to interpret because it was confounded by cover type dominance in landscapes. The proportion of the aspen cover type was positively correlated (R= 0.55), and the proportion of the conifer cover type was negatively correlated (R= -0.79) with Shannon's Evenness Index. The top ranked model in my second set of models was based on road density and had the greatest cumulative weight ($AIC_c w_i = 0.52$). Road density was negatively related to grouse density (R= -0.34), which could mean either that hunting pressure affects density or habitats were different in landscapes with higher road densities. The year only model indicated that male grouse density declined from 2009 to 2010 ($\beta_{Year} = -0.014$, 95% CI = -0.024 to -0.005).

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SELECTION OF LANDSCAPES BY MALE RUFFED GROUSE DURING PEAK ABUNDANCE.

INTRODUCTION

The ruffed grouse (*Bonasa umbellus*) is widely distributed in North America (Rusch et al. 2000). It is closely associated with early successional habitats, particularly aspen forest (*Populus* sp.; Rusch et al. 2000). Ruffed grouse are important game birds, and the most popular game bird in Minnesota (Rusch et al. 2000; M. Dexter, 2009 Minnesota Department of Natural Resources, unpublished report). Hence, their population trends and dynamics are of interest to wildlife managers and hunters (Rusch et al. 2000).

Although ruffed grouse occur in habitats other than aspen (Devers et al. 2007), they reach their highest density when there is a mosaic of different-aged aspen stands close to each other (Gullion and Alm 1983, Rusch et al. 2000). This suggests that aspen-dominated landscapes may confer higher fitness relative to other habitats because each age class of aspen provides different resources to grouse (Gullion and Marshall 1968, Svoboda and Gullion 1972, Gullion and Alm 1983, Giroux et al. 2007, Zimmerman et. al 2009). Therefore, a close juxtaposition of different age classes of aspen occurring in relatively small patches is believed to be optimal habitat for grouse.

In contrast, conifers have been suggested to have either negative or beneficial effects on grouse depending on the circumstances (Bump et al. 1947, Gullion and Marshall 1968, Gullion and Alm 1983). From one perspective, conifers provide no food resources and may provide hunting perches for their avian predators (Eng and Gullion 1962, Dessecker and McAuley 2001). However, conifers provide thermal cover and cover from predators during winter when snow roosts are not available (Thompson and Fritzell 1988, Whitaker and Stauffer 2003, Blanchette et al. 2007).

Most habitat-based research on ruffed grouse has focused on characteristics at smaller scales (i.e., territory or stand scale, e.g., Gullion 1967, Gullion and Alm 1983, Dessecker and McAuley 2001, Hansen et al. 2011). However, Zimmerman et al. (2009) examined the influence of landscape-scale characteristics on grouse density. They found that landscapes having an even distribution of habitats had the highest density of grouse, but their finding was confounded because landscapes that had higher Shannon’s Evenness Index values also had higher abundance of aspen and lower abundance of conifers (Zimmerman et al. 2009). Hence, it was not clear if grouse are selecting landscapes with higher Shannon’s Evenness Index values, selecting aspen, or avoiding conifers (Zimmerman et al. 2009).

The resolution of this issue is critical for two reasons:(1) proposals have been made to restore northern forests in Minnesota and elsewhere to perceived pre-settlement conditions by increasing conifer forests on the landscape, and (2) some forest industries prefer a higher proportion of conifers for economic reasons (Minnesota Department of Natural Resources 2009 [MNDNR]). Coincidentally, the MNDNR set a goal to increase the hunting harvest of ruffed grouse (Minnesota Department of Natural Resources 2010). If grouse habitat is optimal in an aspen-dominated landscape then this harvest goal may not be compatible with “forest restoration.” Therefore, my specific objectives were to evaluate the generality of Zimmerman et al.’s (2009) results because their study occurred in a unique environment to Minnesota and to assess which landscape characteristics were correlated with male ruffed grouse densities in landscapes dominated by either aspen or conifers.

STUDY AREA

I studied male ruffed grouse during 2009-2010 on the Red Lake Wildlife Management Area and Beltrami Island State Forest in Roseau, Beltrami, and Lake of the Woods Counties in North Central Minnesota. My study area encompassed approximately 251,038 ha and was located in the Laurentian Mixed Forest Province (Minnesota Department of Natural Resources 2003). This floristic province extended from north central Minnesota north to southern Canada and east to New England. This province was characterized by conifer forests, mixed hardwood and conifer forests, conifer bogs, and swamps. Annual precipitation in the study area was 55.8 cm for 2009 and 84.9 cm for 2010, with 34% (2009) and 67% (2010) of precipitation falling during the growing season (May-September, Mehmel 2010 Unpublished Data). Average daily low temperature for 2009 was -26.8º C during January, and the average daily high was 22º C during July. Average daily low for 2010 was -18.9º C during January and the average daily high was 26 º C in July. Topography was relatively flat, with elevations ranging from 369 m to 410 m (average ~384 m) above sea level. Approximately 33.9% of the study area was upland habitats (forested and un-forested uplands) and the remainder was lowlands (forested and un-forested wetlands).

I divided my study area into two sampling sites with the northern site (116,454 ha) of the study area dominated by conifer forests and the southern site (134,584 ha) dominated by aspen forests (Figure 1). Much of the lowland area in the northern site was lowland forest comprised of black spruce (*Picea mariana*), tamarack (*Larix laricina*), speckled alder (*Alnus incana spp. rugosa*), and eastern white-cedar (*Thuja occidentalis*). Upland areas in the northern site were primarily mixed or pure forests dominated by red pine (*Pinus resinosa*), aspen (primarily *Populus tremuloides*, and secondarily by *P. gradidentata*), balsam poplar (*Populus balsamifera*), jack pine (*Pinus banksiana*), and balsam fir (*Abies balsamea*), birch (*Betula papyrifera*, *B. alleghaniensis*), white pine (*Pinus strobus*), and some hardwoods such as green ash (*Fraxinus pennsylvanica*), black ash (*F. nigra*), and oak (*Quercus* spp.). In contrast, lowland forested habitats in the southern study site were dominated by ash species and tamarack. Upland sites in the southern study site were dominated by aspen, balsam poplar, white spruce, and balsam fir with some interspersed white pine and red pine stands. The understory of both study sites was dominated by hazel (*Corylus* spp.), mountain maple (*Acer spicatum*), red-osier dogwood (*Cornus sericea*), pin cherry (*Prunus pensylvanica*), choke cherry (*P. virginiana*), speckled alder, round-leaved juneberry (*Amelanchier sanguinea*), willow (*Salix* spp.), highbush cranberry (*Viburnum trilobum*), downy arrowwood (*Viburnum rafinesquianum*), and Labrador tea (*Ledum groenlandicum*) (Zager 2011).

METHODS

Landscape Selection

I estimated density of male grouse within landscapes and the characteristics of those landscapes. I defined landscapes in the following ways. I first selected 60 random points (30 within each study site) and then located the nearest road or trail as the starting point of each transect. I randomly selected the orientation of transect along roads or trails. I was restricted to roads and trails because much of the study area was covered with sphagnum bogs or swamps, which can be impassable during the spring and summer. Each transect was 3-5 km in length depending on local conditions. If a transect encountered a fork in the road or trail, I randomly selected the direction for the continuation of the transect until it reached the minimum length (3 km). If the direction I chose did not extend at least 3 km, I extended the transect in the direction opposite of the original starting point until it reached the minimum length. Zimmerman and Gutiérrez (2007) found that only 6% of their detections of drumming grouse were ≥200 m from similar transects. Therefore, I bounded each transect by a survey distance of 200 m on either side of the transect line (400 m total width, this area is considered the landscape). If selected transects were ≥50% unsuitable habitat (i.e., non-forested), I selected a new transect. I divided my 60 transects into three groups that represented three categories of cover type dominance— conifer dominated (hereafter "conifer"), aspen-birch dominated (hereafter "aspen"), and mixed (encompassing the intergrades between aspen or conifer transects). I randomly selected 10 transects from each of the three groups, regardless of study site.

Grouse Surveys

I surveyed for displaying (drumming) males using methods described by Zimmerman and Gutiérrez (2007). I conducted 1 drumming survey per transect per week over an 8-week period during April-May in 2009 and 2010. These periods represented the major portion of the grouse breeding season in northern Minnesota (Gullion 1984, Zimmerman 2006). I began surveys, on foot, 0.5 hours before sunrise and continued until the survey (transect) was completed (approximately 2.5-6 hours). I reversed the direction of each subsequent survey on each transect because drumming activity peaks near sunrise and then declines (Rusch et al. 2000, Zimmerman and Gutiérrez 2007). When I detected a displaying grouse during a survey, I determined its location by first triangulating the direction of the sound and then stealthily approaching the displaying bird. I attempted to observe each grouse on its drumming structure. If I flushed the bird before visually locating it, I searched the approximate area and identified the likely drumming structure by accumulation of fecal droppings on or next to a structure (Gullion and Marshall 1968). I used a handheld global positioning system (GPS) to determine the location of each drumming structure and then marked it with flagging and a numbered metal tag nailed to the structure. Grouse can use multiple structures within their activity center (Gullion 1967, Rusch et al. 2000). To avoid double counting birds and to identify primary drumming structures (the drumming structure used most often by a male grouse in its territory, structures used less frequently are referred to as secondary drumming structures), I confirmed subsequent detections that I suspected were originating from the same location by triangulating the sound of the drumming bird, cross checking the location with the GPS, and then observing the drumming male. By repeatedly observing males on their drumming structures I was able to distinguish between primary and secondary drumming structures (see also below).

Habitat Data

Although the search area for displaying male grouse during surveys was the 400-m-wide transect (landscape), I restricted measurement of landscape characteristics and grouse density to a 350-m-wide landscape (Figure 2). Assuming my probability of detecting a grouse during one survey was similar to Zimmerman and Gutierrez (2007) detection probability (0.31, 2006), the probability that I detected a drumming grouse within my 350 m transects at least once during 8 surveys was approximately 0.95. I also excluded all lands not owned by the state of Minnesota (i.e., private and Red Lake Ojibwe Nation-owned lands) from the landscapes to ensure access. The remaining area was considered the landscape. My cover type maps were based on MNDNR Forest Stand Inventory (FIM) (Minnesota Department of Natural Resources Forest Stand Inventory Version 2 2010) land cover layers.

I classified each patch within a landscape three separate times using unique classifications including two non-forest classes (Appendix 1)— (1) one of six cover types based on tree species composition (Zimmerman et al. (2009) Criteria column, Appendix 1), (2) one of nine cover types based on cover type associations of grouse, their predators, or their physiognomy without dividing forest by age class (Gullion and Alm 1983, Gullion 1990, Boal et al. 2005), and (3) one of 21 cover type associations of grouse, their predators, or their physiognomy as well as forest age class. To classify a forest stand to one of those cover types it had to be ≥66% by basal area of a particular species or age class (Loeffelholz and Zimmerman 2005, Unpublished Report). Stands with <66% dominance of a particular species or age class were assigned to a “mixed” cover type class (e.g., Mixed Hardwood Conifer for Zimmerman et al. (2009) Criteria and Mixed Hardwood Spruce-Fir or Mixed Hardwood Pine for 2009-2010 Criteria). In addition to classifying forest cover types, I designated other cover types as forested wetlands, non-forested wetlands, and non-forested uplands.

I used a Geographic Information System (GIS) and the PATCH Analyst 4.2.10 extension (Rempel et. al 2008) to estimate landscape metrics for each year because timber harvests, storms, and vegetation growth changed forest characteristics in some landscapes between years. For each of the 180 combinations of transect, year, and land cover classification I estimated mean patch size, number of patches, total area of a cover type, proportion of area a habitat type covers, and mean patch shape (perimeter:area ratio) within each landscape. In addition, I calculated Shannon's Diversity Index and Shannon's Evenness Index of cover types within each landscape using FRAGSTATS Spatial Pattern Analysis program (McGarigal and Marks 1995) in the PATCH extension. Shannon's Diversity Index measures the number of different cover types present within a landscape whereas Shannon's Evenness Index measures the relative abundance of a cover type or proportion of a cover type within a landscape. The equation for Shannon's Diversity index was:

$$H' = \sum_{i=1}^{S} p_i \ln p_i$$

Where, S is the number of cover types present within a landscape and p_i is the relative abundance of the i-th cover type. The equation for Shannon's Evenness Index was:

$$E = \frac{H'}{H_{max}}$$

Where, H' is the Shannon's Diversity index for a landscape and H_{max} is the greatest possible diversity that a landscape can have given the number of cover types present within that landscape. In addition, I calculated road density within the landscape by dividing the total length of a road (km) within an individual landscape by that landscape's total area (ha).

Designating Primary Drumming Structures

I located all drumming structures used by displaying male grouse within my landscapes. I differentiated primary from secondary structures to avoid overestimating grouse. Grouse activity centers are relatively small ~2.3 ha (Archibald 1975, Rusch et al. 2000). Moreover, grouse typically defecate while on their drumming structures and fecal droppings accumulate thereon with primary logs having larger accumulations of droppings than secondary logs (Gullion 1967). I used a variety of criteria (e.g., direct observation of grouse, distance between drumming structures, relative fecal accumulation, unnatural breaks in habitat such as roads) sequentially to distinguish grouse using primary or secondary drumming structures (Appendix 2, 3). I varied my criteria slightly between years because weather conditions and number of grouse were different between years (higher rainfall in 2010 led to more rapid deterioration of fecal droppings, and slightly higher density in 2009 required applying average distance between structures as a criterion to distinguish some primary from secondary structures). It was also apparent during the 2009 season that I could recognize seasonal changes in general diet composition from droppings. Buds were present in droppings during early surveys, followed by catkins, and vegetation during the late surveys, which I used to help distinguish activity centers (i.e., catkins were used during the height of drumming activity). Some of these criteria could have led to a slight underestimate of the number of male grouse present. For example, Rusch et al. (2000) stated that adjacent grouse will occasionally have activity centers in close proximity (as close as 52 m in Alberta), but if I was unable to simultaneous hear the two birds drumming on close structures, I randomly chose one structure to represent an activity center. I used these individual grouse activity centers to estimate grouse density within each landscape (i.e., number of grouse activity centers/total hectares within 175 m of a transect line).

Data Analysis

Model Development. I used a two-stage modeling approach. I designed Stage 1 models to examine the generality of results presented by Zimmerman et al. (2009) while also expanding on their analysis. I designed Stage 2 models to examine the effect of road density and attempt to unravel the confounding of Shannon’s Evenness Index with cover type dominance reported by Zimmerman et al. (2009). Both Stage 1 and Stage 2 model sets were created *a priori*. For my Stage 1 models I used all models developed by Zimmerman et al. (2009) as well as novel models to evaluate the relationship between landscape metrics and grouse density. Their models included the predicted influence of fragmentation of aspen and conifer stands, forest and non-forest patch sizes, forest stand shapes, and diversity of cover types (including Shannon’s Evenness Index) on ruffed grouse density (Table 1, models 1-9). My novel models for Stage 1 included dividing the conifer cover type into pine and spruce-fir cover types as well as several models that contained combinations of variables from their top ranked models (e.g. including Shannon's Evenness Index and mean patch size of aspen and conifer cover types in the same model). I designed several Stage 1 models to evaluate whether Shannon's Evenness Index was correlated with grouse avoiding conifers or selecting aspens (Table 1, models 10-18). In addition, I included age classes when classifying cover types to better assess the hypothesis that a mixture of different age classes of aspen is correlated with the highest density of male grouse at the landscape scale (Gullion and Alm 1983).

I considered 12 additional models in my Stage 2 model set (Table 2). Grouse cycle in abundance on my study area (Bump et al. 1947, Rusch et al. 2000). To account for cyclic variation I developed a year-effect-only model (model 19, Table 2) and included year as a variable in all models (Stage 1 and Stage 2), with the exception of the Stage 1 intercepts-only-model (model 9, Table 1). Zimmerman et al.'s (2009) study area was dominated by the conifer cover type, and the data used to classify cover types at two of their study areas did not permit fine scale classification of cover types (e.g., age classes allow inclusion of young (0-10 years) cover types that were classified as un-forested uplands using Zimmerman et al.'s (2009) criteria, Appendix 1). Zimmerman et al. (2009) suggested that the confounding effect of Shannon's Evenness Index and cover type might be partitioned by conducting future landscape scale grouse habitat selection research in an aspen-dominated landscape. My southern study site was aspen-dominated, and cover types within both study sites could be classified by species composition as well as age, the two characteristics needed to help resolve this confounding (Zimmerman et al. 2009). In model 20 I considered transect type as a factor (i.e., Aspen, Conifer, Mixed). In addition, I originally classified each study site as either conifer or aspen dominated (model 21, Table 2). If the presence of the conifer and aspen cover types had negative or positive effects on grouse populations, respectively (Gullion and Marshall 1968, Gullion and Alm1983), I predicted that grouse densities would be lower in the conifer study site and higher in aspen study site. I considered road density as a potentially informative variable because I was restricted to using roads or trails when selecting survey transects (models 22, 23, 28-31, Table 2). In addition, roads can have negative impacts on wildlife (Spellerberg 1998). Heavy hunting pressure occurs along roads within my study area. It has been observed that hunting mortality of grouse increases with proximity to roads (Fischer and Keith 1974). Thus, I predicted that the abundance of roads would be negatively correlated with grouse density. In addition to road-based models, I also predicted that the proportion of the aspen cover type within the landscape would be positively related to grouse density (models 24, 25, 30-31, Table 2). I also included a model with mean patch size of aspen stands >25 years old because male aspen trees in that age class produce the staminate flower buds used as a primary winter food by grouse (Svoboda and Gullion 1972, Jakubas and Gullion 1991; model 26, Table 2). I predicted that grouse density would be positively related to mean patch size of aspen in all age classes because grouse use aspen of different age classes. Thus, I developed a finer scale classification that recognized young aspen patches (Eng and Gullion 1962, Gullion and Alm 1983, Rusch 2000; model 27, Table 2).

Model Selection and Estimation of Parameters. My response variable was grouse density (the number of observed unique male grouse within a landscape divided by the total area (ha) of that landscape). For predictor variable values that were not designated (e.g., a mean patch size cannot be calculated for a cover type not present) I substituted the mean value for that continuous variable for all non-designated values (i.e., instead of using a 0 value). Using the mean value to designate a variable value does not influence the parameter estimates whereas a 0 value would influence the estimates.

I used mixed effects models in a linear regression framework to estimate the parameters in my statistical models. I used the 'nlme' package (Pinheiro et. al 2011) in program R (R Development Core Team 2010) to fit my models. I treated individual transects as a random effect (i.e., intercepts-only) and all other variables as fixed effects. The general structure of these models was:

$$D_{ij} = b_i + \sum_k x_{ijk}\beta_k + \varepsilon_{ij}$$

Where D_{ij} represented response variable grouse density for transect *i* of year *j* and b_i represented the random intercept for each transect *i*. The fixed effects were represented by the sum across all fixed effects, *k*, of the data (predictor variables, x_{ijk}), multiplied by the fixed-effect coefficients, β_k). The error for the observation from transect *i* in year *j* was represented by ε_{ij} and assumed to be multivariate normally distributed.

After fitting models to my data I used diagnostic plots to assess the assumptions of normality and constant variance of residuals. Three landscapes that had high grouse density contributed to apparent heteroscedasticity of the residuals. In order to mitigate this violation of model assumptions I applied transformations to the response variable (grouse density) and the predictor variables (e.g., Shannon's Evenness Index) in an attempt to normalize the residuals, and thus reduce the non-constant variance of the residuals. No transformation improved the normality and non-constant variance of the residuals; the residual pattern was likely caused by the three observations of high grouse density, which I determined to be accurate estimates. Therefore, I fitted my Stage 1 and Stage 2 models to my dataset using ordinary least squares regression. I then conducted a weighted least squares regression (Neter et al. 1996, pages 400-409) to reduce the influence of these observations.

I used information-theoretic model selection to assess the relative fit of models to my data (Burnham and Anderson 2002). I ranked my Stage 1 and Stage 2 model sets using small sample Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). I calculated AIC_c values using the 'qpcR' package (Ritz and Spiess 2008) in program R (R Development Core Team 2010).

RESULTS

Field Effort. I surveyed 30 transects (i.e., landscapes) 8 times each year (480 surveys) within my study area during 6 April- 29 May 2009 and during 5 April-28 May 2010. Individual landscapes varied from 121 ha to 156 ha and collectively encompassed 5,349 ha. I located 432 and 449 grouse drumming structures during 2009 and 2010, respectively. Of these structures, I estimated 290 (2009) and 230 (2010) were primary drumming structures and thus represented individual grouse activity centers (Archibald 1975, Boag 1976, Rusch 2000). The filtering criteria resulted in the uncertain determination of 24 structures in 2009 (12 randomly selected as primary, 12 selected as secondary, criteria 8, Appendix 2) and 0 structures in 2010. Densities of grouse varied from 0.013—0.151 grouse per hectare among transects in 2009 and from 0.012—0.143 grouse per hectare among transects in 2010. There was a decline in the estimated numbers of drumming grouse between 2009 and 2010 (β_{Year}= -0.014, 95% CI = -0.024 to -0.005).

Stage 1 Modeling. Regression coefficients estimated using weighted least squares methods did not differ substantially from the regression coefficients estimated using ordinary least squares. In addition, non-constant variance caused by three extreme values of grouse density was not improved using weighted least squares methods. Therefore, I based my inference on results from ordinary least squares.

Of the Stage 1 models, the intercepts only (null) model was the highest ranked model (model 9, Table 3). The ranking of the intercepts-only model suggests that no single covariate (fixed effect) improved the fit sufficiently to offset the 2-unit penalty that AIC_c imposes for each additional covariate added to a model (Table 3). In addition, the intercepts-only model is based on a random effect with transect-specific intercepts (i.e., a different intercept for each transect). It can be expected that a random-effects model that has a separate intercept for each individual transect would fit the data better than an intercepts-only model without the random effect for transect. The only competing model suggested that landscapes having a more even distribution of cover types had higher grouse densities (model 8, β_{Evenness}= 0.090, 95% CI = 0.017—0.163, Figure 3). There was a low coefficient of determination ($R^2 = 0.18$) for the effect of Shannon's Evenness

Index, which suggested that much of the variation in grouse density was not explained by this model. In addition, mean patch size aspen was correlated with mean patch size of conifer (Pearson Correlation Coefficient = -0.36, P= <0.001). More importantly, the proportions of aspen and conifer within landscapes were correlated with Shannon's Evenness Index. Landscapes having higher densities of grouse and more evenly distributed cover types also had a lower proportion of the conifer cover type (Pearson Correlation Coefficient= -0.79, P= <0.001, Figure 4) and a greater proportion of the aspen cover type (Pearson Correlation Coefficient= 0.55, P= <0.001, Figure 4). A model based on Shannon's Evenness Index within the landscape and age classes of aspen (model 16) was <2 Delta_i AIC_c points from the model based on Shannon's Evenness Index alone (model 8). However, both models had the same number of parameters, so the inclusion of aspen age class in the cover type classification did not improve the correlation between Shannon's Evenness Index and grouse density (model 16, $\beta_{\text{Evenness aspen age}}$= 0.058, 95% CI= 0.006—0.110).

Stage 2 Modeling. Of the Stage 2 models, a model based on road density was the top model for predicting grouse density within landscapes and ranked higher than all other Stage 1 and Stage 2 models (model 22, Tables 3 and 5). Although the confidence limits of the parameter estimate overlapped zero, the model indicated that the greater the length of road/landscape the lower the grouse density ($\beta_{\text{Road density}}$= -0.860, 95% CI = -1.76—0.04, Table 4). The wide confidence limits surrounding the predicted values from this model (Figure 5) indicated uncertainty about the effect of roads and a low coefficient of determination (R^2 = 0.12) indicated that much of the variation in grouse density was left unexplained. Shannon's Evenness Index within the landscape (model 8, Tables 4 and 5) was more highly correlated with grouse density than the proportion of aspen within a landscape (model 24, $\beta_{\text{Proportion aspen}}$= 0.066, 95% CI = 0.126—0.006, Tables 4 and 5). This observation supports the hypothesis that Shannon's Evenness Index within the landscape is a better indicator of grouse density than the proportion of the aspen cover type within a landscape. The third ranked stage 2 model based on the year effect alone suggested that grouse density declined from 2009 to 2010 (model 19, β_{Year}= -0.014, 95% CI = -0.024 to -0.005).

Model Selection Uncertainty. After ranking the combined Stage 1 and Stage 2 models that contained 95% of the AIC weights in their separate analyses, there were two competing models including the intercepts-only model and one that considered year and road density (Table 6). Several other models had less empirical support (>2 Delta AIC_c, Table 5).

DISCUSSION

I conducted my study during the high phase of the grouse cycle in contrast to Zimmerman et al. (2009) who conducted their study during the low phase of the grouse cycle. Consequently, the high density of grouse during my study may have obscured the importance of my landscape metrics for predicting grouse density and contributed to model selection uncertainty because grouse were found in almost all cover types and in all landscapes. If grouse follow an ideal-despotic distribution, dominant territorial males may have displaced subdominant males into less preferred habitats (Fretwell and Lucas

1970). Male ruffed grouse are territorial (Rusch 2000) and there is evidence that subdominant males are subjected to competitive exclusion (Tirpak et al. 2010). Thus, the ranking of the intercepts-only model as the top Stage 1 model would be consistent with theoretical predictions. In addition to model selection uncertainty, another reason for the high rank of the intercepts-only model may have been the result of AIC structure. The 2-unit penalty that AIC_c imposed for each covariate in a model may have given the intercepts-only model (2 covariates; intercept and error) an advantage over alternative models containing >2 covariates (and thus a larger penalty and AIC_c value).

In my study area, landscapes having higher Shannon's Evenness Index values also had higher grouse densities, an effect also observed by Zimmerman et al. (2009) during the low phase of the population cycle. Although my top ranked Stage 1 model suggested that no single covariate explained a substantial amount of variation in grouse density during my study, Shannon's Evenness Index within the landscape was still an important predictor of grouse density. Nevertheless, in my study, like Zimmerman et al. (2009) observed, landscapes with a high proportion of the conifer cover type also had lower Shannon's Evenness Index values and landscapes with a higher proportion of the aspen cover type had higher Shannon's Evenness Index values. Although I selected an aspen-dominated study site and used spatial data that allowed finer classifications of forest cover types by age and species, two criteria that Zimmerman et al. (2009) suggested might help partition this confounding effect, uncertainty remains as to whether grouse were selecting landscapes with a higher Shannon's Evenness Index value or greater area of the aspen cover type. However, models based on Shannon's Evenness Index within the landscape outranked a model based on the proportion of aspen within a landscape. Although not competing with the top models, the relative ranking of these models provides support for the hypothesis that Shannon’s Evenness Index is a better predictor than the presence of aspen within the landscape when grouse are selecting habitats at the landscape scale in northern Minnesota forests containing a mixture of aspen and conifer cover types.

The consistency between my study and Zimmerman et al. (2009), despite my specific design to resolve this confounding effect, suggested that either there may be an inherent ecological relationship between cover type and evenness or that landscapes managed for conifers lack spatial heterogeneity. For example, conifer species such as red pine in my study area were typically replanted as monocultures after harvest and often with site preparation that includes herbicide application to reduce competition with other species such as aspen. In contrast, aspen is often left to regenerate naturally after harvest, which resulted in spatial heterogeneity. Slight alterations in the way that conifer regeneration is managed may result in higher grouse densities in landscapes dominated by the conifer cover type. In addition, my results supported the prediction that Shannon’s Evenness Index was a more important predictor of grouse density at the landscape scale than cover type dominance. Models hypothesizing a positive correlation between grouse density and mean patch size aspen and proportion of aspen within the landscape as well as models hypothesizing a negative correlation between grouse density and mean patch size conifer had less support than the Shannon’s Evenness Index model, which supported the inference that Shannon’s Evenness Index was a better predictor of grouse density. The question of whether Shannon’s Evenness Index or cover type is more correlated with grouse density would best be answered by a manipulative experiment in which grouse populations are monitored during all phases of their population cycle in landscapes dominated by the conifer cover type with high Shannon’s Evenness Index values as well as in landscapes dominated by the aspen cover type with low Shannon’s Evenness Index values.

Zimmerman et al. (2009) suggested that the correlation between Shannon’s Evenness Index and grouse densities within the landscape may have been related to different habitat needs for different life history stages (e.g. male drumming vs. female nesting habitats). Female ruffed grouse nest in stands that are structurally different than habitats used by drumming males (Gullion and Svaboda 1972, Gullion1988). Males may select habitats in which they are more likely to attract mates with their drumming display. Zimmerman et al. (2009) also hypothesized that grouse select landscapes with an even distribution of cover types as a response to variable weather conditions (i.e., grouse may use different habitats during different weather). For example, grouse use conifer forests during the fall and winter when snow roosting is not available (Clark 2000, Thompson and Fritzell 1988) therefore male grouse may select stands that are suitable for drumming that are close to thick conifers (e.g. cedar, fir and spruce stands).

In my study area grouse density was highest in landscapes having a lower road density. My observation was different than recent observations made in the Appalachian region where grouse selected areas having higher road densities (Tirpak et al. 2010). However, Tirpak et al. (2010) suggested that grouse may have selected habitats associated with roads because the structure of vegetation (i.e., recently disturbed habitats resembling early successional stages) found along roads likely provided the only suitable habitat for grouse within their study area. The presence of young forest did not seem to be a limiting resource within my study area. It also has been observed that hunting mortality of adult territorial males increases with decreased distance to roads (Fischer and Keith 1974). Although many studies have concluded that mortality from sport hunting does not adversely affect populations of grouse, DeStefano and Rusch (1986) noted that such studies were conducted within large areas of contiguous habitat. Thus, they hypothesized that immigration of grouse during spring and fall dispersal may have mitigated local effects of hunting. After observing hunting mortality of ruffed grouse in central Wisconsin, Small et al. (1991) suggested that high hunting mortality could decrease ruffed grouse numbers when immigration was reduced because of fragmented habitat or where widespread heavy hunting pressure was associated with public ownership of land. My study area contained predominantly public-owned land and was characterized by upland habitat islands (e.g. sandy hills) surrounded by lowland areas, much of which is unsuitable habitat (e.g., sphagnum bog). Thus, grouse killed by hunters along roads in isolated areas might not be readily replaced by immigrant birds in my study area.

It was also possible that there were other differences important to grouse between landscapes having high or low road densities. The majority of roads occurred along drier ridgelines that could support road construction more easily than surrounding lowlands. Road density was positively correlated with the proportion of the conifer cover type and negatively correlated with the proportion of the aspen cover type within a landscape (Pearson’s Correlation Coefficient $_{\text{Conifer}}$ = 0.23, 95% CI= -0.03—0.46, Pearson’s Correlation Coefficient $_{\text{Aspen}}$ = -0.23, 95% CI= -0.45—0.03). Road density and Shannon’s Evenness Index within the landscape were negatively correlated (Pearson’s Correlation Coefficient $_{\text{Evenness}}$= 0.23, 95% CI= -0.03—0.46) suggesting that landscapes with higher road densities had lower Shannon’s Evenness Index values. Thus, it appears that drier upland areas can better support road construction and are potentially focal areas for conifer plantations for silvicultural and logistical reasons (year round access). One possibility is that because the conifers are often managed as a monoculture, increased area of the conifer cover type around roads results in lower diversity of vegetation types (and thus lower Shannon’s Evenness Index values).

It was also possible that it simply took less time for observers to survey transects that had a higher road density (i.e., roads are easier to traverse than trails). However, survey duration was partly a function of the number of displaying males on the survey route. Survey routes with many displaying males took longer to survey. The mean survey time (minutes) per unit area of landscape (ha) was more highly correlated with the average number of grouse in a landscape (Pearson’s Correlation Coefficient$_{\text{survey time-grouse density}}$= 0.7, 95% CI= 0.456—0.847, average count between 2009 and 2010) than it was with road density in a landscape (Pearson’s Correlation Coefficient$_{\text{survey time-road density}}$=-0.32, 95% CI= -0.608—0.048). This suggested that grouse density was a better predictor of survey duration than road density and suggested that the presence of roads was not affecting the number of grouse detected during surveys. Despite the apparent correlation of the

Shannon’s Evenness Index and road density variables at the landscape scale, the models that I considered explained only a small proportion of variation in grouse density within landscapes. This may have been due to the generally high abundance of grouse, thus masking effects of selection of optimal habitats or landscapes (Fretwell and Lucas 1970).

MANAGEMENT IMPLICATIONS

It is well established that grouse densities respond to habitat modification, particularly when aspen mosaics are favored (Gullion and Alm 1983, Rusch et al. 2000). However, my results suggest that management for conifers in my study area lacks spatial heterogeneity. Conifers, specifically red pine and jack pine, are managed primarily as plantation monocultures or occur in naturally regenerated large stands. Hence, when managing for conifers, if grouse are desired, managers should emphasize either mixed-species composition during replanting or conifer plantations interspersed with aspen or mixed aspen/hardwood-conifer patches to create a mosaic of more evenly distributed cover types.

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Table 1. Stage 1 models and predicted relationships between landscape characteristics and male ruffed grouse density in northern Minnesota during 2009-2010.

Model #	Model	K	Habitat Variables[a] and Predictions[b]
1	Mean Patch Size: Aspen and Conifer[d]	5	-Year$_{2010}$[c]±MPS$_{A}$-MPS$_{C}$
2	Mean Patch Size: All Cover Types[d]	8	-Year$_{2010}$[c]±MPS$_{A}$-MPS$_{C}$-MPS$_{N}$ –MPS$_{M}$ ±MPS$_{W}$
3	Fragmentation: Aspen[d]	5	-Year$_{2010}$[c]±NP$_{A}$ ±MPS$_{A}$
4	Fragmentation: Aspen and Conifer[d]	7	-Year$_{2010}$[c]±NP$_{A}$±MPS$_{A}$-NP$_{C}$-MPS$_{C}$
5	Mean Patch Shape: Aspen and Conifer[d]	5	-Year$_{2010}$[c]±MPAR$_{A}$+MPAR$_{C}$
6	Mean Patch Size and Shape: Aspen and Conifer[d]	7	-Year$_{2010}$[c]±MPS$_{A}$-MPS$_{C}$±MPAR$_{A}$+MPAR$_{C}$
7	Shannon's Diversity Index[d]	4	-Year$_{2010}$[c]±SDI$_{ACNMW}$
8	Shannon's Evenness Index: All Cover Types[d]	4	-Year$_{2010}$[c]±SEI$_{ACNMW}$
9	Intercept only	2	None

10	Mean Patch Size: Aspen and Conifer (Zimmerman 2006)[d] and Age Class[d]	9	$-\mathrm{Year}_{2010}^{c} \pm \mathrm{MPS}_{A,\ 0\text{-}7} \pm \mathrm{MPS}_{A,\ 8\text{-}25} \pm \mathrm{MPS}_{A,\ 26+} - \mathrm{MPS}_{C,\ 0\text{-}20} - \mathrm{MPS}_{C,\ 21\text{-}50} - \mathrm{MPS}_{C,\ 51+}$
11	Mean Patch Size: Aspen, Spruce-Fir, Pine[e]	6	$-\mathrm{Year}_{2010}^{c} \pm \mathrm{MPS}_{A} - \mathrm{MPS}_{P} \pm \mathrm{MPS}_{SF}$
12	Mean Patch Size and Shape: Aspen, Spruce-Fir, Pine[e]	9	$-\mathrm{Year}_{2010}^{c} \pm \mathrm{MPS}_{A} - \mathrm{MPS}_{SF} - \mathrm{MPS}_{P} \pm \mathrm{MPAR}_{A} + \mathrm{MPAR}_{SF} - \mathrm{MPAR}_{P}$
13	Fragmentation: Aspen, Spruce-Fir, and Pine[e]	9	$-\mathrm{Year}_{2010}^{c} \pm \mathrm{NP}_{A} \pm \mathrm{MPS}_{A} \pm \mathrm{NP}_{SF} \pm \mathrm{MPS}_{SF} - \mathrm{NP}_{P} - \mathrm{MPS}_{P}$
14	Shannon's Evenness Index: All Cover Types[e] (Zimmerman 2006) and Age Class[e]	4	$-\mathrm{Year}_{2010}^{c} \pm \mathrm{SEI}_{A,\ 0\text{-}7,\ A,\ 8\text{-}25,\ A,\ 26+,\ C,\ N,\ M,\ W}$
15	Shannon's Evenness Index: Aspen and Conifer[d]	4	$-\mathrm{Year}_{2010}^{c} \pm \mathrm{SEI}_{A,\ C}$
16	Shannon's Evenness Index: All Cover Types (Subdivided)[e]	4	$-\mathrm{Year}_{2010}^{c} \pm \mathrm{SEI}_{A,\ SF,\ P,\ N,\ MSF,\ MP,\ FW,\ NFW,\ NFU}$
17	Shannon's Evenness Index: All Cover Types [d] and Mean Patch Size: Aspen and Conifer[d]	6	$-\mathrm{Year}_{2010}^{c} \pm \mathrm{SEI}_{ACNW} \pm \mathrm{MPS}_{A} - \mathrm{MPS}_{C}$

18	Shannon's Evenness Index: All Cover Types [c] and Mean Patch Size and Shape: Aspen and Conifer	8	$-Year_{2010} \pm SEI_{ACNW} \pm MPS_A - MPS_C \pm MPAR_A + MPAR_C$

[a] NP = Number of patches, MPS= Mean Patch Size, MPAR= Mean perimeter to Area ratio, SDI= Shannon's diversity index, SEI= Shannon's Evenness Index, TT= Transect Type

Subscripts represent habitat types: A= Aspen, C= Conifer, N= Northern Hardwood, W= Wetland, M= Mixed Hardwood-Conifer, MP= Mixed Hardwood-Pine, MSF= Mixed Hardwood-Spruce-Fir, SF= Spruce Fir, P= Pine, FW= Forested Wetland, NFW= Non-Forested Wetland, NFU= Non-forested Uplands

[b] + = predicted positive correlation, −= predicted negative correlation, ± = correlation could be positive or negative.

[c] 2010= Year effect, 1 if 2009, 0 if 2010 survey year.

[d] Zimmerman et al. (2009) original model or variable classification.

[e] Zimmerman et al. (2009) combination of original models or finer scale variable classification.

Table 2. Stage 2 models and predicted relationships between landscape characteristics and male ruffed grouse density in northern Minnesota during 2009-2010.

Model #	Model	K	Habitat Variables[a] and Predictions[b]
19	Year Only	3	$-\mathrm{Year}_{2010}^{c}$
20	Transect Type	4	$-\mathrm{Year}_{2010}^{c}\pm\mathrm{TT}_{\mathrm{ACM}}$
21	Study Site	4	$-\mathrm{Year}_{2010}^{c}-\mathrm{SS}_{\mathrm{AC}}$
22	Road density	4	$-\mathrm{Year}_{2010}^{c}$ –RD
23	Road density and SEI.ACNMW[d]	5	$-\mathrm{Year}_{2010}^{c}-\mathrm{RD}\pm\mathrm{SEI}_{\mathrm{ACNMW}}$
24	Proportion of Aspen[d]	4	$-\mathrm{Year}_{2010}^{c}\pm\mathrm{Prop}_{\mathrm{A}}$
25	Proportion of Aspen and Shannon’s Evenness Index[d]	5	$-\mathrm{Year}_{2010}^{c}+\mathrm{Prop}_{\mathrm{A}}\pm\mathrm{SEI}_{\mathrm{ACNMW}}$
26	Mean Patch Size Aspen (Mature)[e]	4	$-\mathrm{Year}_{2010}^{c}\pm\mathrm{MPS}_{\mathrm{a},\ 26+}$
27	Mean Patch Size Aspen[e]	4	$-\mathrm{Year}_{2010}^{c}\pm\mathrm{MPS}_{\mathrm{a}}$

28	Road density and Mean Patch Size Aspen[d]	5	$-\text{Year}_{2010}{}^{c}\pm\text{MPS}_{A}\text{-RD}$
29	Road density, Mean Patch Size Aspen[d] and Shannon's Evenness Index[d]	6	$-\text{Year}_{2010}{}^{c}\pm\text{MPS}_{A}\text{-RD}\pm\text{SEI}_{ACNMW}$
30	Road density, Proportion of Aspen[d] and Shannon's Evenness Index[d]	6	$-\text{Year}_{2010}{}^{c}\pm\text{Prop}_{A}\text{-RD}\pm\text{SEI}_{ACNMW}$
31	Road density and Proportion of Aspen[d]	5	$-\text{Year}_{2010}{}^{c}\text{-RD}\pm\text{Prop}_{A}$

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[a] SS= Study Site, RD= Road density, Prop$_A$= Proportion of Aspen, MPS= Mean Patch Size

Subscripts represent habitat types: A= Aspen, a=Aspen Subdivided, C= Conifer, N= Northern Hardwood, W= Wetland, M= Mixed Hardwood-Conifer, MP= Mixed Hardwood-Pine, MSF= Mixed Hardwood-Spruce-Fir, SF= Spruce Fir, P= Pine, FW= Forested Wetland, NFW= Non-Forested Wetland, NFU= Non-forested Uplands

[b] + = predicted positive correlation, −= predicted negative correlation, ± = correlation could be positive or negative.

[c] 2010= Year effect, 0 if 2009, 1 if 2010 survey year.

[d] Zimmerman et al. (2009) variable classification.

[e] Finer scale classification (i.e., including younger age classes of aspen than Zimmerman et al. 2009).

Table 3. Stage 1 model selection results (only those models with w_i >0.001) for assessing the relationships between landscape characteristics and male ruffed grouse density in northern Minnesota during 2009-2010.

Model		Delta$_i$ AIC$_c$[a]	K[b]	AIC$_c$[c]	w_i[d]
9	Intercept Only Model	0	2	-250.680	0.490
8	Shannon’s Evenness Index: All Cover Types[e]	0.941	4	-249.740	0.306
14	Shannon’s Evenness Index: All Cover Types[e] and Aspen Age Class[f]	2.628	4	-248.052	0.132
16	Shannon’s Evenness Index: All Cover Types (Subdivided)[f]	5.018	4	-245.662	0.040
7	Shannon’s Diversity Index[e]	7.1434	4	-243.537	0.014
15	Shannon’s Evenness Index: Aspen and Conifer[e]	7.4721	4	-243.208	0.012
2	Mean Patch Size: All Cover Types[e]	8.5739	8	-242.107	0.001

[a] Difference in Akaike’s Information Criterion adjusted for small samples between model *i* and the model with the lowest AIC$_c$ value.

[b] Number of parameters in the model.

[c] Small sample Akaike's Information Criterion

[d] Akaike's weights.

[e] Zimmerman et al. (2009) original model or variable classification.

[f] Finer scale classification (i.e., including younger age classes of aspen than Zimmerman et al. 2009).

Table 4. Stage 2 model selection results (only those models with $w_i \geq 0.001$) for assessing the influence of landscape scale metrics on male ruffed grouse density in northern Minnesota during 2009-2010.

Model		Delta$_i$ AIC$_c^{a}$	K^{b}	AIC$_c^{c}$	w_i^{d}
22	Road density	0	4	-252.212	0.501
23	Road density and Shannon’s Evenness Index^{e}	2.325	5	-249.887	0.157
19	Year Only	2.571	3	-249.641	0.138
31	Road density and Proportion of Aspen^{e}	3.0486	5	-249.163	0.109
24	Proportion of Aspen^{e}	4.139	4	-248.073	0.063
25	Proportion of Aspen^{e} and Shannon’s Evenness Index^{e}	7.919	5	-244.293	0.010
30	Road density, Proportion of Aspen^{e} and Shannon’s Evenness Index^{e}	7.971	6	-244.241	0.009
21	Study Site	9.231	4	-242.981	0.005
28	Mean Patch Size Aspen^{f}	10.015	5	-242.197	0.003

26	Mean Patch Size Aspen[e]	10.022	4	-242.190	0.003
27	Mean Patch Size Aspen[f]	12.156	4	-240.056	

[a] Difference in Akaike's Information Criterion adjusted for small samples between model *i* and the model with the lowest AIC_c value.

[b] Number of parameters in the model.

[c] Small sample Akaike's Information Criterion

[d] Akaike's weights.

[e] Zimmerman et al. (2009) original model or variable classification.

[f] Finer scale classification (i.e., including younger age classes of aspen than Zimmerman et al. 2009).

Table 5. Model selection results for all models (both Stage 1 and Stage 2 models with w_i >0.001) for assessing the relationships between landscape characteristics and male ruffed grouse density in northern Minnesota during 2009-2010.

Model		Delta$_i$ AIC$_c$[a]	K[b]	AIC$_c$[c]	w_i[d]
22*	Road density	0	4	-252.212	0.501
9	Intercept Only Model[e]	1.531	2	-250.680	0.233
23*	Road density and Shannon’s Evenness Index[e]	2.325	5	-249.887	0.157
8	Shannon’s Evenness Index: All Cover Types[e]	2.472	4	-249.740	0.145
19	Year only Model	2.571	3	-249.641	0.138
31*	Road density and Proportion of Aspen[e]	3.048	5	-249.163	0.110
24*	Proportion of Aspen[e]	4.139	4	-248.073	0.063
14	Shannon’s Evenness Index: All Cover Types and Age Class[f]	4.160	4	-248.052	0.063
16	Shannon’s Evenness Index: All Cover Types[f]	6.549	4	-245.662	0.019
25*	Proportion of Aspen[d] and Shannon’s Evenness Index[e]	7.919	5	-244.293	0.010

30*	Road density, Proportion of Aspen[e] and Shannon's Evenness Index[e]	7.971	6	-244.241	0.009
7	Shannon's Diversity Index[e]	8.675	4	-243.537	0.007
15	Shannon's Evenness Index: Aspen and Conifer[e]	9.003	4	-243.208	0.006
21*	Study Site	9.231	21	-242.981	0.005
28*	Road density and Mean Patch Size Aspen[f]	10.015	5	-242.197	0.003
26*	Mean Patch Size Aspen (Mature)[f]	10.022	4	-242.190	0.003
2	Mean Patch Size: All Cover Types[e]	10.105	8	-242.107	0.001

[a] Difference in Akaike's Information Criterion adjusted for small samples between model *i* and the model with the lowest AIC_c value.

[b] Number of parameters in the model.

[c] Small sample Akaike's Information Criterion

[d] Akaike's weights.

[e] Zimmerman et al. (2009) original model or variable classification.

[f] Finer scale classification (i.e., including younger age classes of aspen than Zimmerman et al. 2009).

* represents Stage 2 models.

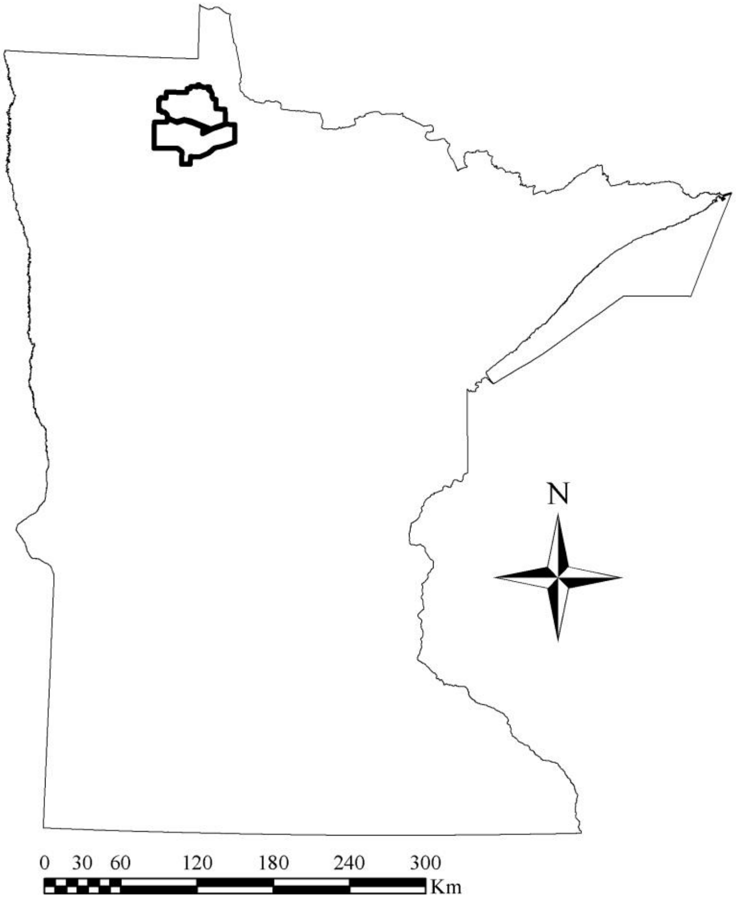


Figure 1. Location of ruffed grouse study area in Minnesota. Northernmost polygon represented the conifer study site and the southernmost polygon represented the aspen study site.

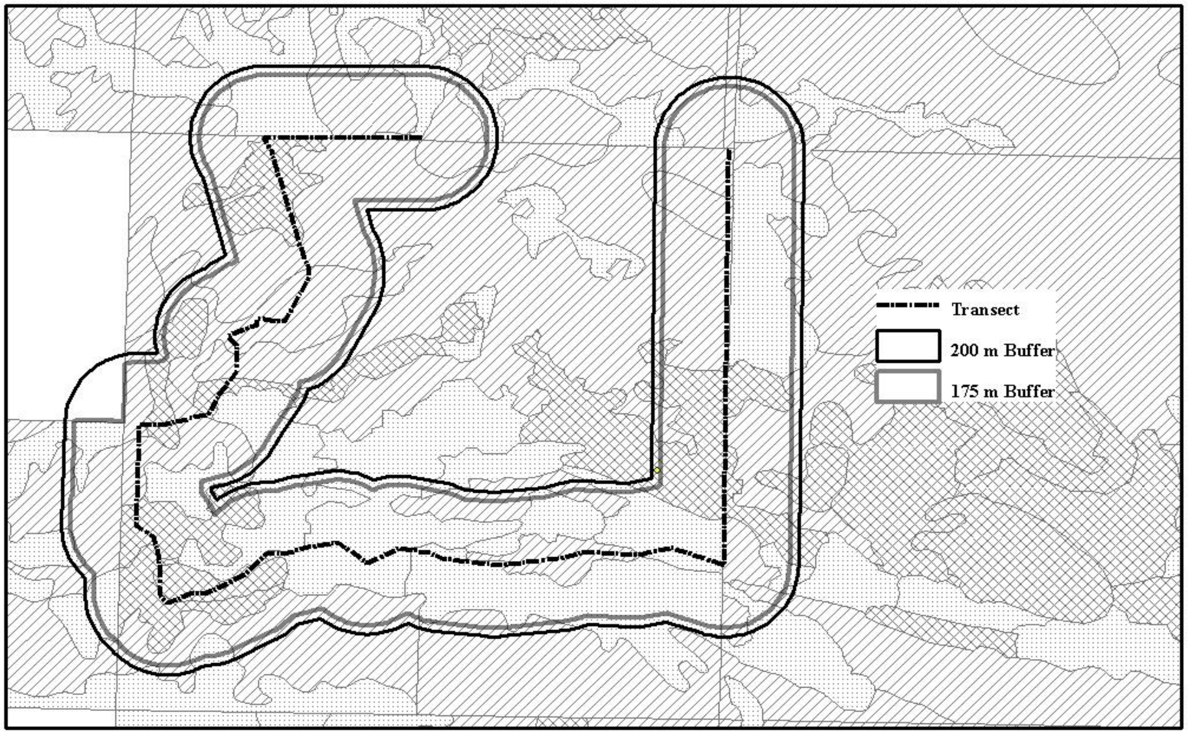


Figure 2. Example of a Transect (Landscape) within the study area with the 200 m search area and the 175 m sampling area defined by black and grey lines, respective

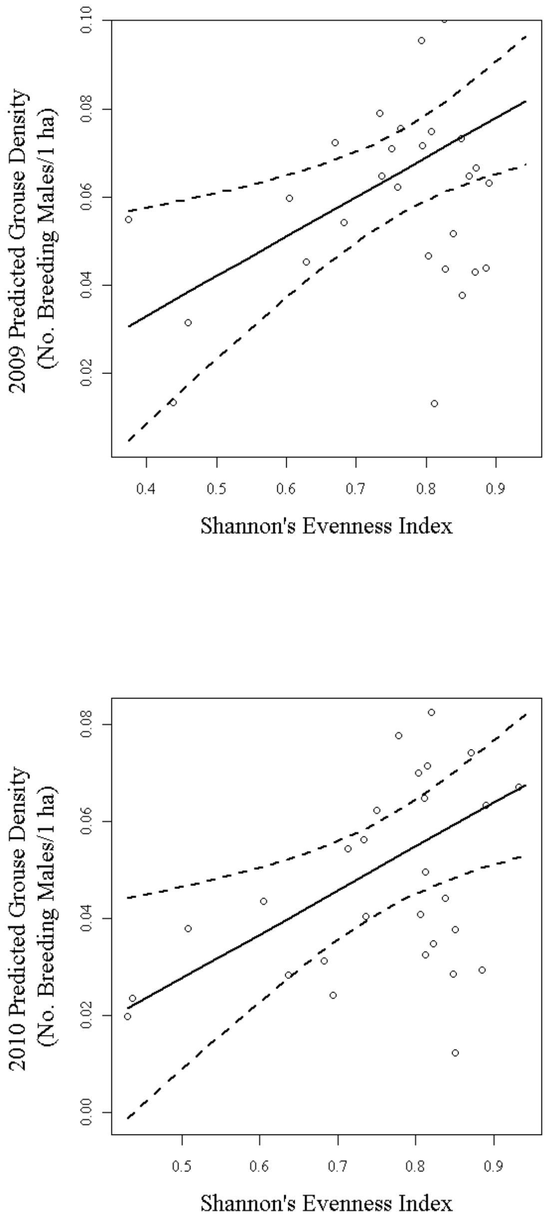
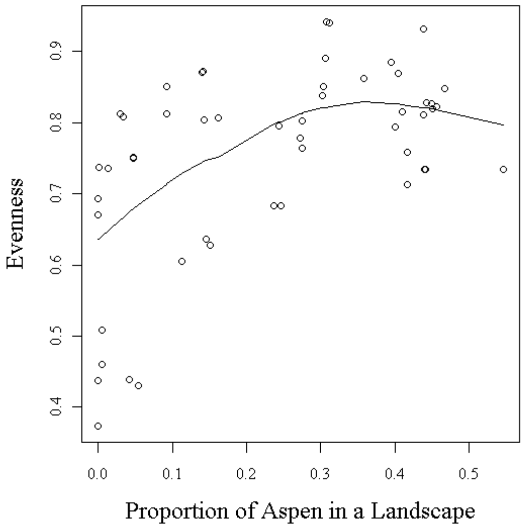


Figure 3. Predicted relationship between Shannon’s Evenness Index and male ruffed grouse density in northern Minnesota during 2009 and 2010. Dashed lines represent 95% confidence interval.



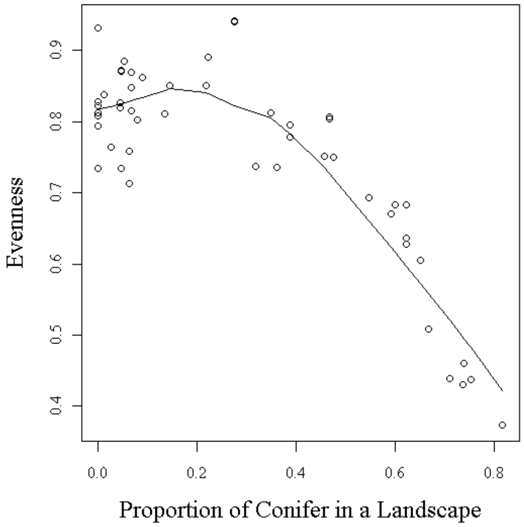


Figure 4. Observed relationship between Shannon's Evenness Index and the proportion of the aspen and conifer cover types within the landscape. Landscapes with higher Shannon's Evenness Index values tended to have a higher proportion of the aspen

cover type and landscapes with lower Shannon's Evenness Index values tended to have a higher proportion of the conifer cover type.

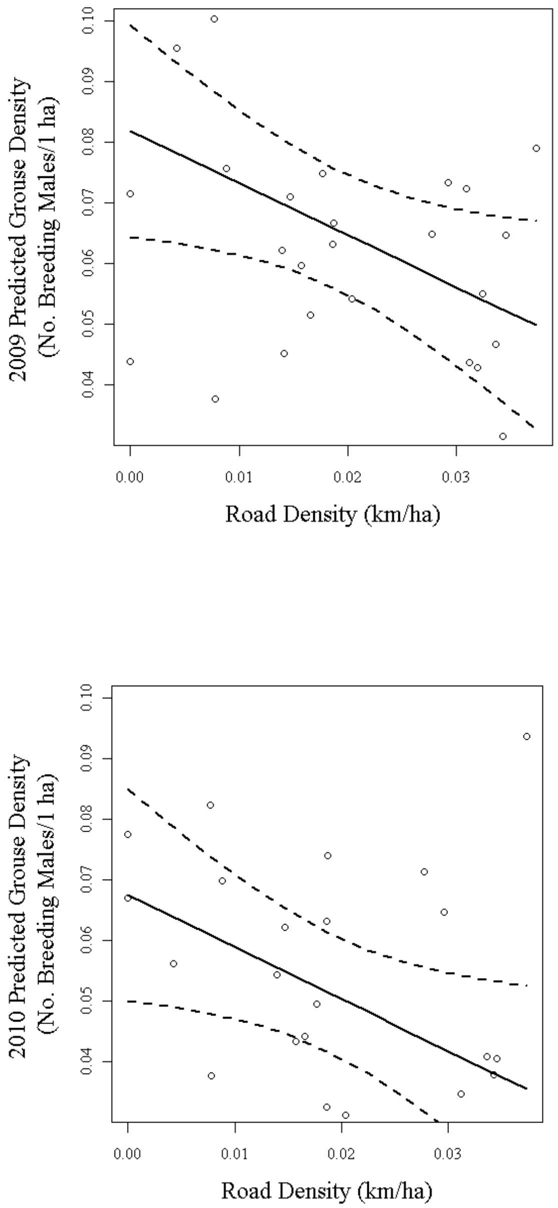


Figure 5. Predicted relationship between road density and male ruffed grouse density in northern Minnesota during 2009 and 2010. The dashed lines represent the 95% confidence interval.

Appendix 1. Classification of land cover types, using Minnesota Department of Natural Resources Forest Stand Inventory (2010, FIM) data.

MN_CTYPE	CTYPE_NAME	2009-2010 Criteria: Age Class	2009-2010 Criteria	Zimmerman et al. (2009) Criteria
12	Aspen	0-7 Aspen	Aspen	Aspen
78	Offsite Aspen	8-25 Aspen		
		26+ Aspen		
62	Balsam Fir	0-20 Spruce-Fir	Spruce-Fir	Conifer
74	Black Spruce, Upland	21-50 Spruce-Fir		
61	White Spruce	51+ Spruce-Fir		
53	Jack Pine	0-20 Pine	Pine	
52	Norway/Red Pine	21-50 Pine		
51	White Pine	51+ Pine		
01	Ash	0-7 Northern Hardwood	Northern Hardwood	Northern Hardwood
14	Balm of Gilead/Balsam Poplar	8-25 Northern Hardwood		
13	Birch	26+ Northern Hardwood		
30	Oak			
79	Offsite Oak			
NA	Various Hardwoods (incl. Aspen) and Pine[a]	0-7 Mixed Hardwood Pine 8-25 Mixed Hardwood Pine 26+ Mixed Hardwood Pine	Mixed Hardwood Pine	Mixed Hardwood Conifer
NA	Various Hardwoods (incl. Aspen) and Spruce-Fir[a]	0-7 Mixed Hardwood Spruce-Fir 8-25 Mixed Hardwood Spruce-Fir 26+ Mixed Hardwood Spruce-	Mixed Hardwood Spruce-Fir	

		Fir		
92	Industrial and Urban Development	Non-forested Uplands	Non-forested Uplands	Non-forested Uplands
82	Cutover Area			
84	Roads			
93	Recreation Development			
86	Upland Brush			
84	Upland Grass			
71	Black Spruce, Lowland	Forested Wetlands	Forested Wetlands	Wetlands
09	Lowland Hardwoods			
73	Northern White Cedar			
77	Stagnant Cedar			
75	Stagnant Spruce			
76	Stagnant Tamarak			
72	Tamarak			
85	Lowland Brush	Non-Forested Wetlands	Non-Forested Wetlands	
83	Lowland Grass			
98	Marsh			
88	Moss			
99	Muskeg			
97	Non-Permanent Water			
96	Permanent Water			

[a] The mixed cover types are a combination of the forested cover types in which no single cover type comprises more than 66% of the total area. I used the age of the younger maturing hardwood for the age criteria of the mixed cover types. Assuming grouse are selecting landscapes based on the dominant structure. As hardwoods mature at an earlier age in this forest type, the hardwoods would

most likely be the predominant structure within the landscape.

Appendix 2. Sequential criteria used in 2009 to distinguish primary drumming structures from secondary drumming structures on the Red Lake Wildlife Management Area, Roosevelt, MN.

Criterion	Criterion Description
1	Drumming structures where no other structures found within 85 represented an individual male ruffed grouse.
2	Drumming structures <85 m apart, but separated by a recreational trail or road were considered primary.
3	Drumming structures having 0-20 droppings that are <85 m of a drumming structure having= >21 droppings were secondary.
4	When two drumming structures were found <85 m apart and both had <21 droppings, the structure with higher dropping count was considered primary.
5	Food type present in droppings used to determine primary structures that have +21 dropping count and < 85 m apart. Structure with most dropping types present is primary.
6	Drumming structures with the same dropping count and the same dropping types present (hereafter, like-structures) < 85 m apart: If one structure was determined as secondary in the field was considered secondary. Some structures were designated as secondary in the field. This designation was given when field observers bumped the grouse from a structure and observed it display on another drumming structure.
7	If two like-structures < 85 m apart, 52 m distance was used. If the two like-structures >52 m apart then both were determined as primary.
8	If two structures were similar in all criteria but were < 52 m I then randomly selected one as primary and one as secondary.

Appendix 3. Sequential criteria used in 2010 to distinguish primary drumming structures from secondary drumming structures on the Red Lake Wildlife Management Area, Roosevelt, MN.

Criterion	Criterion Description
1	Drumming structures where no other structures found within 85 represented an individual male ruffed grouse.
2	Drumming structures <85 m apart, but separated by a recreational trail or road were considered primary unless field observer notes indicate otherwise (n=0).
3	Drumming structures having 0-20 droppings that are <85 m of a drumming structure having >21 droppings were secondary. Unless designated as a primary log by field observer notes.
4	When two drumming structures were found <85 m apart and both had <21 droppings, the structure with higher dropping count was considered primary. Unless conflicting observations were recorded in field observer notes.
5	Drumming structures with +21 dropping count and < 85 m apart were separated using field observer notes. If one structure is designated as a primary and the other as secondary then the structure designated as primary was assumed to be the primary log.
6	Drumming structures had >21 dropping count and were <85m apart were, the number of individual field observations made per drumming structure during the drumming survey season was used to determine the primary structure.
7	Drumming structures with the same dropping count and the same dropping types present (hereafter, like-structures) <85 m apart and field observer notes do not determine a primary drumming structure then I used 52 m distance. If two like-structures >52 m apart then both drumming structures are primary.

8	If the two like-structures are <52 m I then randomly selected one as primary and one as secondary.