OCCUPANCY MODELING OF RUFFED GROUSE IN THE BLACK HILLS NATIONAL FOREST

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

OCCUPANCY MODELING OF RUFFED GROUSE IN THE BLACK HILLS NATIONAL FOREST

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a candidate for the degree of master of sciences,

and hereby certify that, in their opinion, it is worthy of acceptance.

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OCCUPANCY MODELING OF RUFFED GROUSE IN THE BLACK HILLS NATIONAL FOREST

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ABSTRACT

Ruffed grouse (*Bonasa umbellus*) are important game birds and the management indicator species for quaking aspen (*Populus tremuloides*) in the Black Hills National Forest (BHNF). As a result, a robust monitoring protocol which reflects the status, trends, and habitat associations of ruffed grouse in the BHNF is necessary. To evaluate these processes, we used ruffed grouse drumming counts combined with occupancy modeling. Ruffed grouse occupancy in the BHNF was 0.13 (SE = 0.029) in 2007 and 0.11 (SE = 0.022) in 2008, and was positively influenced by the amount of aspen. Detection probability was 0.29 (SE = 0.052) in 2007 and 0.27 (SE = 0.063) in 2008, and was primarily influenced by date and wind speed. Using these estimates, we evaluated multiple occupancy sampling designs to determine which design required the least amount of effort to achieve occupancy estimates with a desired level of precision. The most appropriate sampling design was the standard multi-season design with 3 repeat surveys at each site, each season (i.e., year). Using this design, we estimated the necessary number of sites and repeat surveys at each site to achieve occupancy estimates which met precision requirements. Site requirements were high due to low ruffed grouse occupancy and detection rates in the BHNF; thus, managers must decide on the amount of effort they are able allocate towards monitoring and how to distribute that effort. We also addressed ruffed grouse micro-site selection of drumming sites (activity centers) to determine what structure and adjacent vegetative characteristics were correlated with selection of activity centers. Selection was driven by vegetative cover above 1 meter in height, suggesting ruffed grouse selected activity centers that provided protection from predators. By evaluating both broad-scale occupancy and small-scale activity center selection, forest management decisions to encourage ruffed grouse at both the population and individual level in the BHNF will be more robust.

CHAPTER I

OCCUPANCY MODELING OF RUFFED GROUSE IN THE BLACK HILLS NATIONAL FOREST

ABSTRACT

Ruffed grouse (*Bonasa umbellus*) are an important game bird and the management indicator species (MIS) for quaking aspen (*Populus tremuloides*) in the Black Hills National Forest (BHNF) because of their strong association with aspen communities. As a result, a robust monitoring protocol is required to evaluate trends in ruffed grouse populations in the BHNF. We used roadside drumming surveys in spring 2007 and 2008 to estimate ruffed grouse occupancy, detection, colonization, and local extinction probabilities in the BHNF while simultaneously assessing the influence of sampling and site covariates on these processes. We detected only 2 ruffed grouse during autumn surveys so these data were not considered further. Ruffed grouse occupancy estimates in spring ($\Psi_{2007} = 0.13$, $\Psi_{2008} = 0.11$) were influenced by the extent of aspen, white spruce (*Picea glauca*), and ponderosa pine (*Pinus ponderosa*) vegetation and by the amount of dense sapling (i.e., > 70% sapling canopy cover) forest. Model-averaged estimates suggested that increasing the extent of aspen had the largest positive effect on occupancy, while spruce had less of a positive effect, and pine and dense sapling cover had essentially no effect. Average colonization rates were low ($\gamma = 0.005$) and positively influenced by aspen patch size while average extinction probabilities ($\varepsilon = 0.20$) were negatively influenced by aspen patch size. Detection probabilities in spring ($p_{2007} = 0.29$, $p_{2008} = 0.27$) were influenced by survey date in a quadratic form and negatively influenced by wind. Collectively, our results suggested that ruffed grouse occupancy in the BHNF was low and the highest occupancy was associated with increasing amounts and size of aspen patches. Additionally, model validation procedures suggested our model had high predictive ability for spatial trends in occupancy throughout the BHNF. Monitoring ruffed grouse occupancy should be conducted during the peak of drumming (mid-May) and during favorable weather (e.g., little wind or precipitation) conditions to maximize the probability of detecting ruffed grouse.

INTRODUCTION

Ruffed grouse are popular game birds and habitat specialists (Barber et al. 1989, Madison 1969) that are valuable to resource management agencies for achieving hunter satisfaction as well as monitoring the health of specific habitats. Ruffed grouse inhabit early succession forest (e.g., aspen [*Populus* spp.]) for cover from predators and acquisition of food (Gullion 1977, Kubisiak 1985, Johnsgard et al. 1989, Maxson 1989, Sharpe et. al. 1997). Because ruffed grouse depend on multiple forest age-classes and dense woody cover, they are considered an important indicator species for the condition and abundance of aspen communities (Barber et al. 1989). Fire suppression, cattle grazing, and pine (*Pinus* spp.) encouragement for timber harvest have caused drastic changes in the vegetative species composition in the Black Hills National Forest (BHNF) (Ball et. al. 1992, Bartos and Shepperd 2003). Primarily, aspen communities have declined and been replaced by either white spruce (*Picea glauca*) or ponderosa pine (*Pinus ponderosa*). Thus, management strategies (e.g., burning, cutting, and fencing) have been used in the last 20 years in an attempt to slow aspen declines (U.S. Forest Service 1997, Bartos and Shepperd 2003). To evaluate whether aspen management and associated strategies have been effective in encouraging ruffed grouse in the BHNF, monitoring is a necessity. Monitoring will provide managers with important ruffed grouse status, trend, and habitat association information that will be crucial towards management of ruffed grouse in the BHNF.

Recent monitoring activities of ruffed grouse in the BHNF have not effectively evaluated ruffed grouse population trends due to the inconsistency of surveys, inherent bias from conducting surveys only in vegetative types where ruffed grouse were expected to occur, and the failure to consider imperfect detection (SAIC 2005). Occupancy modeling is one alternative for monitoring ruffed grouse in the BHNF that overcomes many of the current deficiencies. Occupancy models have recently become popular because they do not assume all individuals are detected, only require the investigator to determine the presence or absence of the species from repeated surveys, and can be robust predictors of the proportion of the study area occupied when appropriate predictor variables are considered (MacKenzie et al. 2002, Crossland et al. 2005, MacKenzie et al. 2006). Additionally, using a multi-season design, the metapopulation dynamics of the species can be examined by evaluating local extinction and colonization trends of habitat sites in the study area (Hanski 1994, MacKenzie et al. 2003, MacKenzie et al. 2006). Trends in extinction and colonization offer a robust evaluation of the population trends of a species (Hanski 1994, MacKenzie et al. 2003, MacKenzie et al. 2006) and can therefore be useful for future monitoring purposes as well as prescribing effective management strategies.

We used ruffed grouse roadside drumming counts to estimate occupancy and detection probability, assess the influence of covariates (e.g., vegetation area, date of survey, weather conditions) on ruffed grouse occupancy and detection probability, and evaluate the metapopulation dynamics (e.g., colonization and local extinction) of ruffed grouse in the BHNF during 2007 and 2008. In addition to understanding the status and habitat associations of ruffed grouse in the BHNF, our research was intended to improve future ruffed grouse monitoring in the BHNF.

STUDY AREA

The BHNF was located in the western portion of South Dakota and included the Bear Lodge Mountains of northeastern Wyoming. Elevation ranged from 1,066 m – 2,207 m. Annual rainfall in the BHNF exceeded 50.8 cm per year and varied with elevation (Ball et. al. 1996). The BHNF included 500,000 hectares of a variety of vegetation types, consisting primarily of ponderosa pine (84%), quaking aspen/paper birch (*Betula papyrifera,*4%), and white spruce (2%). Bur oak (*Quercus macrocarpa*), hop-hornbeam (*Ostrya virginiana*), and green ash (*Fraxinus pennsylvanica*) also occupied the BHNF, comprising < 10% (Hoffman and Alexander 1987, Froiland 1990). Common shrubs included western snowberry (*Symphoricarpos occidentalis*), white coralberry (*S. albus*), kinnikinnick (*Arctostaphylos uvaursi*), and common juniper (*Juniperus comunis*) (Severson and Thilenius 1976, Hoffman and Alexander 1987).

The BHNF had one of the highest road densities (3.2 km/km^2) of any national forest (Rumble et al. 2005), consisting primarily of secondary (i.e., gravel) and primitive (i.e., dirt) roads. Our study area encompassed the northern 2/3 of the BHNF, north of Highway 16 (Appendix A). Highway 16 was used as our southern boundary because ruffed grouse are known to occur in extremely low abundance south of Highway 16.

METHODS

A Priori Sample Site Determination

Prior to field work, we estimated the number of sites and the number of repeat surveys required for each site (MacKenzie and Royle 2005). Occupancy and the probability of detecting ruffed grouse were unknown in the BHNF so we used data from Zimmerman (2006) and abundance estimates from previous surveys in the BHNF (SAIC 2005) to guide our *a priori* sample size calculations. We assumed occupancy probabilities would be heterogeneous throughout the BHNF; therefore, we stratified the BHNF into 3 physiographic strata (high, medium, and low aspen density) using the Resource Information System (RIS) data from the BHNF. Physiographic strata were primarily delineated by district (e.g., Bear Lodge, Northern Hills, and Mystic/Hell's Canyon) with slight modification to district boundaries. Areas of high aspen density (Bear Lodge district) had ~ 1 hectare aspen per 11 hectares vegetation, areas of medium aspen density (Northern Hills district) had ~ 1 hectare aspen per 25 hectares vegetation, and areas of low aspen density (Mystic/Hells Canyon district) had ~ 1 hectare aspen per 31 hectares vegetation (Appendix A). Using a standard occupancy design (MacKenzie 2005, MacKenzie and Royle 2005), an assumed detection probability of 0.31 (Zimmerman 2006), and occupancy probabilities of 0.2, 0.3, and 0.4 (for low, medium, and high aspen density, respectively, [SAIC 2005]), we computed the number of sites (s) and the number of surveys at each site (K) to achieve the desired precision (standard error [SE] = 0.05) for occupancy and detection probability (MacKenzie and Royle 2005). Based on these analyses, survey requirements were 90 sites for low aspen strata, 123 sites for medium aspen strata, and 148 sites for high aspen strata. Additionally, MacKenzie and Royle (2005) recommended completing 5 repeat surveys, with a minimum of 3 repeat surveys, at each site. Because of the uncertainty of parameters we used to estimate sample size, and because we anticipated that we could not reach some sites (e.g., impassable road, area closure, private property), we increased the sample size in each strata by 50%.

After estimating sample size, we used ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA), and a simple random sampling design, without replacement, in each stratum to identify the location of survey sites along secondary and primitive roads. We constrained sampling sites to be >1 mile apart to ensure independence among sites. We did not include sites along primary roads (i.e., paved and upgraded gravel roads) because there was considerable traffic on them which could interfere with our ability to hear drumming ruffed grouse.

We assumed that ruffed grouse drumming surveys along secondary and primitive roads would be representative of the entire study area because of the extensive network of roads in the BHNF (3.2 km/km^2; Rumble et al. 2005). During spring 2007, we located drumming grouse and estimated the maximum distance we could hear grouse drum. By using this maximum distance (550 m) and creating a buffer in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) around all secondary and primary roads, we estimated that we could hear a ruffed grouse throughout 91.3% of the study area from this road network. Additionally, we assume we were able to properly evaluate the influence of the amount of aspen vegetation on ruffed grouse occupancy because 96.6% of the aspen vegetation in the BHNF fell within the buffered region. After identifying our survey sites, we organized these sites into routes using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) to improve our sampling efficiency.

Field Methods

From 2 April 2007 through 31 May 2007, 4 September through 27 October 2007, and 14 April 2008 through 7 June 2008, we conducted drumming counts in the BHNF. In spring 2008, our surveys were conducted two weeks later than 2007 because of adverse weather conditions in early April and our estimates of peak drumming the previous year. Because we assumed that we were sampling a closed population (MacKenzie et al. 2002), we did not expect ruffed grouse occupancy probabilities to change during those two weeks.

During spring surveys, we organized our routes into 5 general regions (Northeast, Northwest, Southeast, Southwest, Bear Lodge Mountains) of the BHNF. Technicians and volunteers simultaneously conducted surveys in each region along routes. We began surveys half an hour before sunrise and navigated to the survey sites using Global Positioning Systems (GPS). At each site we listened for drumming ruffed grouse for 5 minutes, then recorded whether drumming grouse were detected or not, time, date, temperature, wind speed (using a hand-held anemometer), weather conditions, azimuth and estimated distance (<50 m, between 50 and 150 m, >150 m) to drumming ruffed grouse. We conducted surveys up to 5 hours after sunrise ($\bar{x} \sim 2.0$ hrs after sunrise), because occurrence and frequency of drumming decreases throughout the day (Archibald 1976, Maxson 1989).

After we completed surveys at all sites in a region, technicians rotated regions so each site was surveyed by different observers to reduce observer bias. On successive surveys in regions, we reversed the order survey sites were visited to reduce bias that might be associated with the time surveys were conducted. We also ensured weather conditions were favorable by following a specific protocol which inhibited us from surveying when wind speed exceeded 16 km/hr or during heavy snow or rain.

Ruffed grouse will drum in the autumn, presumably to claim breeding territories for the following spring (McBurney 1989a). While literature suggests that ruffed grouse are not as active at their drumming sites in the autumn (Bump et al. 1947), the weather in the BHNF is typically more dependable in the autumn, there are fewer animal interferences (e.g., bird vocalizations), and navigating routes is safer because roads are free of snow. Therefore, we evaluated whether autumn drumming surveys were more efficient than spring surveys. During autumn surveys, we surveyed the same sites and collected the same data as in the spring; however, we only surveyed sites in regions where occupancy probabilities were high (e.g., Bear Lodge, Northwest, Northeast, and Southwest regions). This was necessary because we hypothesized that drumming behavior would not be as frequent or consistent in the autumn (Bump et al. 1947). Because inconsistent drumming behavior may cause poor detection probabilities (Zimmerman and Gutiérrez 2007), we allocated more effort to sampling fewer sites more times (MacKenzie et al. 2006). We only sampled during one autumn season due to the poor results of surveys during autumn 2007 (see results).

A Priori Models

To model the influence of sampling and site variables on occupancy, detection, colonization, and local extinction probabilities, we developed *a priori* models based on published literature and evaluated them using an information theory approach (Burnham and Anderson 2002). We chose 15 models (Appendix B) to evaluate the effects of weather (wind, temperature, precipitation), observer (full time technician or volunteer), temporal issues (year, Julian date, time of day), and physiographic strata (high, medium, low densities of aspen) on detection probabilities (Table 1).

Temporal effects (detection).— Temporal variables such as season, date, and time of day can influence the probability of detecting ruffed grouse (Gullion 1966, 1967; Rusch et al. 2000). As a result, we developed 7 models to evaluate the influence of survey date on detection probabilities (Models 2, 3, 11, 12, 13, 14, 15). Because we hypothesized a peak in drumming activity during the season (Gullion 1966, Zimmerman 2006), 6 of the date models assumed a quadratic affect of date on detection probability. We also developed 4 models to evaluate the influence of the time of day on detection probability. We hypothesized time of day would have a slight negative influence on detection probability due to our sampling scheme (see *field methods*) and have an additive effect with other temporal and spatial covariates (Models 4, 12, 14, and 15). Lastly, we included a model to evaluate the affect of year on detection probability (Model 5). We hypothesized detection probability would be constant between years due to similar methods and observer experience.

Weather effects (detection).— Drumming males are more active when temperature rises rapidly in the morning (Gullion 1966, Zimmerman 2006). However, ruffed grouse are less active during poor weather such as rain and snow (McBurney 1989). Assuming temperature would have a slight positive influence on detection probabilities, we developed two models; one assuming temperature alone positively influenced detection probability (Model 8), and one assuming temperature had an additive effect with other variables (Model 15). We also included precipitation and wind in 7 models (Models 6, 7, 11, 12, 13, 14, 15), with the assumption that light precipitation and high winds would have a negative influence on detection probability (Gullion 1966).

Observer effects (detection).— Future monitoring practices will probably solicit volunteers. Therefore, we tested whether there was a difference in detection probabilities between volunteer and full-time technicians. We hypothesized that a difference in observers would have little influence on detection because we trained all observers. Nonetheless, we included observer as a covariate in Models 9 and 15 to test this assumption.

Site effects (detection).— Site variables, such as vegetation type and patch size, can influence the ability to detect ruffed grouse (Zimmerman and Gutiérrez 2007), resulting in heterogeneous detection probabilities due to ruffed grouse density (Aubin 1972, Rodgers 1981, Royle and Nichols 2003, MacKenzie et al. 2006). Consequently, we evaluated the influence of physiographic strata (i.e., high, medium, and low densities of aspen) on detection probability with 3 models (Models 10, 14, and 15).

To test our hypotheses about occupancy, colonization, and extinction probabilities, we developed 16 additional models; 15 were a function of covariates (e.g., seasonal variation, vegetation encompassing the site, and age class of surrounding trees, [Table 1]) and one assumed occupancy, colonization, and extinction probabilities were constant (Model 1, Appendix C). All models used the most supported detection probability model except for Model 16, which evaluated the most supported occupancy, colonization, and extinction models with a constant detection probability model (see *analytical methods*).

Temporal effects (occupancy).— It is assumed that occupancy does not change within a season (MacKenzie et al. 2002); however, occupancy may change between seasons due to colonization and local extinction of sites (MacKenzie et al. 2003). Therefore, we developed a model to test whether occupancy was season (year)-dependent (Model 2).

Vegetative effects (occupancy).— Ruffed grouse select territories based on aspen availability (Gullion and Svoboda 1972). Mixed aspen-conifer stands are favorable to ruffed-grouse in some areas (Zimmerman 2006) but not in others (e.g., Gullion 1989, Kubisiak 1985, Severson 1982). To analyze the influence of vegetation types and patch size on ruffed grouse occupancy, colonization, and extinction probabilities, we developed 11 models (Models 3, 4, 5, 6, 10, 11, 12, 13, 14, 15, and 16) . Ponderosa pine, quaking aspen, and white spruce were the most abundant forest types in the BHNF; therefore, we included these as covariates in most of these models. In addition to vegetative type and size, the age structure of vegetation might influence ruffed grouse occupancy, colonization, and extinction probabilities (Gullion 1967, Gullion 1989, Kubisiak 1985, Severson 1982). To address age structure influences on these metrics, we developed 10 models incorporating vegetation age. 3 models assumed vegetation age alone influenced occupancy, colonization, and extinction probabilities (Models 7, 8, and 9), while 7 other models assumed both the vegetation type and age had an additive influence (Models 10, 11, 12, 13, 14, 15, and 16).

Analytical Methods

We evaluated estimates and influential covariates on occupancy (Ψ) and detection probabilities (p) of ruffed grouse in the BHNF from spring 2007 and 2008 surveys and used the interval between breeding seasons (spring 2007 and 2008) to evaluate colonization (γ) and local extinction probabilities (ε). Because we only detected 2 grouse in autumn 2007, we did not evaluate Ψ and p for autumn 2007 (see results). To quantify site covariate values (i.e., the amount of vegetation encompassing a site), we placed a 550 meter buffer around each survey site (see *a priori sample site determination*) and summed the patch sizes of all analogous vegetation types and ages within the buffered region (using ArcGIS 9.2). We used Program PRESENCE (MacKenzie et al. 2006) and the standard parameterization to estimate Ψ, p, γ, and ε, and compute β values for covariates included in the model (MacKenzie et al. 2006). This parameterization calculates Ψ_t (occupancy during the first season) and uses the dynamic parameters, γ and ε, to derive occupancy during the following season Ψ_{t+1} (Mackenzie et al. 2006) using:

$$\Psi_{t+1} = \Psi_t(1-\varepsilon) + (1-\Psi_t)\gamma \qquad (1)$$

Before evaluating our models, we standardized covariates to Z-scores to reduce the influence of variables that had larger ranges (Donovan and Hines 2007).

We used a two-stage approach in our model selection procedures (e.g., Franklin et al. 2000, Washburn et al. 2004). In the first stage, we compared *a priori* models which evaluated the influence of sampling (e.g., date, observer, wind speed) and site (e.g., physiographic strata) covariates on p, while holding Ψ, γ, and ε constant (i.e., Ψ[.]γ[.]ε[.]p[*covariate*]). In the second stage, we modeled the influence of site covariates on Ψ, γ, and ε simultaneously with the most supported model from stage 1 (i.e., Ψ[*covariate*]γ[*covariate*]ε[*covariate*]p[*best*]; Bailey et al. 2004, Olson et al. 2005, MacKenzie 2006, Kroll et al. 2007). To ensure our most supported p model from stage 1 improved our Ψ, γ, and ε model performance, we evaluated a model which incorporated our most supported Ψ, γ, and ε model from stage 2 with a constant *p* model (i.e., Ψ[*best*]γ[*best*]ε[*best*]*p*[.]) and compared this with the rest of our second stage model set (Bailey et al. 2004). By incorporating a two stage design, we reduced our candidate model set while still evaluating a sufficient set of covariates that might have caused heterogeneity in Ψ, *p*, γ, and ε.

We based our model rankings on Akaike's Information Criterion with an adjustment for small sample size (AIC_c) and Akaike weights (w_i) (Burnham and Anderson 2002). We addressed model selection uncertainty by calculating model-averaged parameter estimates for Ψ, γ, and ε models in the 90% Akaike weight confidence set (Burnham and Anderson 2002). After model averaging, we calculated odds ratios and 95% odds ratio confidence intervals for parameter estimates to assess which parameters in the 90% confidence set influenced Ψ, *p*, γ, and ε.

We determined model goodness-of-fit by applying the Pearson chi-square statistic to our global models for Ψ and *p* each sampling year using:

$$\chi^2 = \sum_{h=1}^{2^T} \frac{(O_h - E_h)^2}{E_h} \tag{2}$$

where O_h is the number of sites that have detection history *h*, E_h is the expected number of sites with history *h* according to the current model (sum of probabilities of observing *h*), and 2^T are the possible detection histories that may be observed (MacKenzie and Bailey 2004). Because we expected to obtain low E_h values, suggesting χ^2 did not have a chi-square distribution, we performed 10,000 parametric bootstraps. Parametric bootstrap methods assessed the overdispersion parameter $\hat{c}$ using:

$$\hat{c} = \frac{\chi^2_{Obs}}{\overline{\chi}^2_B} \tag{3}$$

where $\overline{\chi}^2_B$ is the average of the test statistics obtained from the parametric bootstrap. We assumed models with $\hat{c}$ values ~1 were adequate descriptors of the data (MacKenzie and Bailey 2004).

Model Validation.— We used a *k*-fold cross-validation design (Boyce et at. 2002) to evaluate the predictive ability of our model-averaged logit (occupancy) equation because of its similarity to a resource selection function (Manly et al. 1993). Instead of evaluating rank correlations between bins and area-adjusted frequencies (Boyce et al. 2002), we evaluated correlations between the frequency of observed and expected observations in each occupancy probability bin using Spearman-rank correlations (Boyce et al. 2002, Johnson et al. 2006). We randomly extracted 80% of our original data (training data) and calculated new parameter coefficients from this data, while incorporating the same covariates from our model-averaged occupancy model. We then evaluated how the new occupancy model predicted the remaining 20% of the data (testing data) by creating an occupancy probability map of the BHNF in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) using the new occupancy model. First, we reclassified occupancy probability values on the map into 10 equal interval bins of increasing value. Then, we calculated the expected number of testing observations in each bin (N_i) using:

$$N_i = N \times [w(x_i)A(x_i) / \sum_j w(x_j)A(x_j)] \tag{4}$$

where N is the number of testing data observations, $w(x_i)$ is the midpoint occupancy probability of bin i, and $A(x_i)$ is the area of bin i (Boyce and McDonald 1999, Johnson et al. 2006). Lastly, we counted the actual number of testing observations that fell into each occupancy probability bin. We repeated this process 5 times (evaluating 5 different training and testing data sets) and used the frequencies of observed and expected observations to calculate Spearman-rank correlations for each fold as well as for all folds combined. We expected a good predictive model to demonstrate a large, positive correlation between observed and expected frequencies. We did not evaluate a different occupancy model for each season (i.e., spring 2007 and 2008) because we hypothesized that variables influencing occupancy of ruffed grouse between successive years would not change.

RESULTS

We surveyed 402 sites 3 to 5 times each ($\bar{x}$ = 3.09, SE = 0.014) during spring 2007 and 2008 and surveyed 315 sites between 4 and 5 times each ($\bar{x}$ = 4.48, SE = 0.028) during autumn 2007. Between 2 April and 31 May 2007 we detected ruffed grouse at 30 sites; between 4 September and 27 October 2007 we detected ruffed grouse at 2 sites; and between 14 April and 7 June 2008 we detected ruffed grouse at 33 sites. Between spring 2007 and 2008, 15 sites were colonized and 12 sites either went locally extinct or ruffed grouse went undetected. Because of the infrequency and inconsistency of ruffed grouse drumming in the autumn, we did not calculate Ψ, p, γ, or ε for autumn.

Detection Probability

The global model for p (Model 15, Appendix B) passed goodness-of-fit measures for spring 2007 (P-value = 0.59, $\hat{c}$ = 0.83) and 2008 (P-value = 0.59, $\hat{c}$ = 0.86), implying the detection probability data fit the model well and were not overdispersed. Therefore, we did not adjust AIC$_c$ values or standard errors for model estimates. The most supported model for p included the parameters Julian date and wind (Table 2). Julian date was related to p in a quadratic form while wind was negatively related to p. To examine the effects of the parameters in this model, we plotted the fitted relationship of one parameter with p, while keeping the other parameters constant at their mean values. Predicted values of p were essentially 0 at the beginning of April, gradually increased to a peak on 19 May, and decreased into early June (Figure 1). Additionally, estimated p was highest at low wind speeds and declined towards 0 at wind speeds ≥ 16 km/hr (Figure 2). Based on this model, $p_{2007} = 0.29 \pm 0.052$ and $p_{2008} = 0.27 \pm 0.063$.

Occupancy, Colonization, and Extinction Probability

The global model (Model 14, Appendix C) for Ψ also passed goodness-of-fit measures for spring 2007 (P-value = 0.41, $\hat{c} = 0.99$) and 2008 (P-value = 0.74, $\hat{c} = 0.80$), implying the data were a good fit and not overdispersed. Therefore, we did not adjust standard errors for model estimates. Five occupancy models fell within the 90% Akaike weight confidence set (Table 3). These models suggested that the size of aspen, spruce, and pine patches and the extent of saplings with canopy cover > 70% influenced Ψ, and aspen patch size affected γ and ε (Table 3).

Model-averaged parameter estimates and odds ratios (Table 4) suggested that the amount of aspen vegetation within 550 m of a site had the greatest influence on Ψ. Increasing aspen patch size by 5 hectares simultaneously increased Ψ by an average of 5.0% (Figure 3). The amount of spruce vegetation within 550 m of a site also had a considerable influence on ruffed grouse Ψ; increasing spruce patch size by 5 hectares simultaneously increased Ψ by 3.4% (Figure 3). The extent of ponderosa pine and saplings with > 70% canopy cover within 550 m of a site were not as influential on Ψ; each 5 hectare increase in these variables only increased Ψ by 0.12% and 0.9%, respectively (Figure 3, 4). Finally, model averaged estimates indicated that larger aspen patches increased the odds that a site was colonized by ruffed grouse and, conversely, decreased the odds of a local extinction at a site, although these relationships were minor (Figure 5).

Using the model averaged estimates (Table 4), $\Psi_{2007} = 0.13 \pm 0.029$, $\gamma = 0.005 \pm 0.02$, and $\varepsilon = 0.20 \pm 0.12$ for the interval between the 2007 and 2008 season. Subsequently, applying Ψ_{2007}, γ, and ε estimates to Eq. 1, we estimated that $\Psi_{2008} = 0.11 \pm 0.022$. Our model-averaged occupancy model had a significant (i.e., $\alpha < 0.05$) positive correlation between expected and observed occupancy frequencies across all our validation trials (Table 5), suggesting our model predicted occupancy probabilities well.

DISCUSSION

Our study demonstrated that occupancy estimates of ruffed grouse in the BHNF should account for heterogeneity in detection probabilities caused by date and wind speed. Otherwise, occupancy estimates will be negatively biased (MacKenzie et al. 2002, 2006). Zimmerman and Gutiérrez (2007), who studied ruffed grouse detection probabilities on the Cloquet Forest Research Center in Minnesota, also noted the importance of conducting drumming surveys when detection probabilities were maximized. They and others observed that drumming might be dependent on photoperiod, peaking in late April and early May (Gullion 1966, Zimmerman and Gutiérrez 2007). Additionally, they observed that wind speed negatively affected the probability of detecting ruffed grouse. While wind speed also had a strong negative correlation with detection probability in the BHNF, peak detection rates were slightly different than those observed by Zimmerman and Gutiérrez (2007) and others (e.g., Gullion 1966, Rogers 1981). The peak of detecting ruffed grouse in the BHNF occurred around 19 May, which suggested that photoperiod may not be the determinant. Higher than normal late spring precipitation, including snow, and late snow melt in the BHNF might have delayed drumming activity of the ruffed grouse, or our ability to detect them. At the Cloquet Forest Research Center, the amount of snowfall and the date of snow melt preceding a drumming season influenced the proportion of ruffed grouse participating in drumming activity (i.e., drumming intensity), but snow cover did not influence the peak of drumming activity (Gullion 1966). Therefore, the late peak of detection in the BHNF might not have resulted from a late peak in drumming activity, yet the reduced proportion of drumming ruffed grouse.

The absence of other hypothesized influential variables (e.g., time of survey, precipitation, observer, physiographic strata) on detection probability in our most supported detection probability model might have been a result of our experimental design. Archibald (1976), Maxson (1989), and Rusch et al. (2000) observed that daily drumming activity peaked approximately 0.5 hours before sunrise. Additionally, Gullion (1966) noticed a reduction in drumming activity during moderate and heavy rainfall. We reversed the order of sites in routes on successive surveys and did not sample past five hours after sunrise to account for any influence of time on daily surveys. Also, we did not survey during inclement weather. The influence of these factors on detection probability might have been more evident if we had sampled throughout the day and during inclement weather. While other studies reported effects from observers (Zimmerman and Gutiérrez 2007), and site characteristics (Aubin 1972, Rodgers 1981, Zimmerman and Gutiérrez 2007) on detection rates, none of these factors ranked well among our candidate models. We ensured that technicians and volunteers could hear and distinguish drumming sounds before data collection. As a result, we assume the absence of the observer parameter in our model resulted from our accounting for it in our experimental design. Additionally, the intensity of drumming in Wisconsin is influenced by ruffed grouse density (Rogers 1981). In the BHNF, we doubt that ruffed grouse density had much of an impact on the intensity of drumming or our detection probabilities due to low ruffed grouse occupancy. Consequently, differences in site characteristics which might influence differences in ruffed grouse density did not influence detection rates.

Occupancy probabilities of ruffed grouse were heterogeneous across the BHNF and primarily influenced by vegetation type as we hypothesized. The area of quaking aspen and white spruce within 550 meters had large positive influences on our estimates of ruffed grouse occupancy, corroborating with most ruffed grouse literature throughout the upper Midwest (e.g., Gullion and Svoboda 1972, Kubisiak 1985, Kubisiak 1989). Our occupancy model also suggested ponderosa pine weakly influenced ruffed grouse occupancy. However, we do not believe that ruffed grouse selected territories conditional on area of ponderosa pine given the extensive evidence against that theory (Gullion and Marshall 1968, Gullion 1981, Gullion and Alm 1983). Because aspen, spruce, and pine were the primary forest types throughout the BHNF (Hoffman and Alexander 1987), increasing the extent of one forest type within 550 meters of a site simultaneously decreased one or both of the others. Thus, increasing the extent of pine surrounding a site would not increase the probability of ruffed grouse occupancy at the site because of the associated decrease in the extent of aspen or spruce, which had much stronger positive influences on occupancy. Consequently, we believe our model suggested that ruffed grouse will not select sites consisting exclusively of ponderosa pine over other sites in which aspen and spruce are present. Our data also implied that dense sapling stands had a slight negative influence on ruffed grouse occupancy. In Minnesota and Wisconsin, investigators found younger age classes (< 25 yr) of forest were preferred over mature stands (Gullion 1967, Gullion 1989, Kubisiak 1985, Severson 1982). However, the young age classes evaluated in those studies consisted primarily of aspen. In the BHNF, the majority of dense sapling stands consisted primarily of pine, which may not be suitable for ruffed grouse (Gullion and Alm 1983). Additionally, ruffed grouse utilize mixed-age forest stands which contain both young trees for cover from predators and mature trees for food (Bump et al. 1947, Barber et al. 1989, Sharpe et al. 1997). Thus, evaluating only the presence and size of dense sapling stands may not have been appropriate for ruffed grouse in the BHNF without simultaneously considering vegetation type. Although the factors influencing ruffed grouse occupancy in the BHNF deviated slightly from other ruffed grouse studies throughout the upper Midwest, validation procedures suggested our occupancy model performed well.

Colonization and local extinction rates of ruffed grouse in the BHNF had low precision and were not as strongly influenced by vegetation or age structure as we had hypothesized. The most supported colonization and extinction models included aspen area, suggesting increasing the extent of aspen around a site will increase the probability of ruffed grouse colonization and reduce the probability of local extinction. However, our data suggested that the probability of colonization only increased by 2% and the probability of local extinction only decreased by 3% when maximizing the area of aspen around a site. Yoder (2004) observed that ruffed grouse were less likely to disperse in forested regions with many edges (i.e., superior habitat). Thus, we might not have witnessed ruffed grouse colonization or local extinction to a great extent in the BHNF because the high quality habitats in the BHNF may have already been saturated with ruffed grouse. Alternatively, MacKenzie et al. (2003) suggested inclusion of multiple season intervals to effectively evaluate these processes. We only evaluated one season interval in the BHNF, where occupancy rates of ruffed grouse were low. Therefore, our data prohibit us from making robust inferences on the factors influencing ruffed grouse colonization and local extinction. Nonetheless, our results suggested that occupancy probabilities were relatively stable between the 2 years of our study, exhibiting a stationary Markov process (MacKenzie et al. 2006). Our estimated occupancy rates declined by 2% between spring 2007 and 2008, but the difference was not significant. Future ruffed grouse occupancy surveys will be necessary to assess whether the decrease in occupancy from spring 2007 to 2008 resulted from temporal or spatial stochasticity, or an actual downward trend of ruffed grouse occupancy in the BHNF.

MANAGEMENT IMPLICATIONS

Occupancy rates of ruffed grouse throughout the BHNF were low and related to the occurrence of aspen. Therefore, ruffed grouse occupancy could be increased by increasing the area and extent of aspen communities. For each 10 hectare increase in aspen vegetation within a 550 meter radius (95 ha), managers can expect the probability of ruffed grouse occupancy to increase by 10%. Additionally, increasing the area of aspen patches throughout the BHNF will encourage ruffed grouse to further colonize these patches, thereby reducing the probability of becoming locally extinct. As a result, we encourage managers to continue efforts to increase the amount of aspen in the BHNF.

To assess occupancy trends of ruffed grouse in the BHNF, we recommend continuing drumming surveys between the first and fourth week of May when detection probabilities are highest. We do not recommend the use of autumn surveys of ruffed grouse in the BHNF. Surveys should be completed within 5 hours of sunrise and on rain or snow free days with little or no wind. Last, survey crews should be trained to ensure they can hear and distinguish a ruffed grouse drumming in the field. Maximizing the probability of detecting a ruffed grouse if it is present will improve the efficiency of monitoring ruffed grouse occupancy and dynamic trends in the BHNF.

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Table 1. Description of variables used in *a priori* models which assess factors that influenced the probability of occupancy, colonization, local extinction, and detection of ruffed grouse in the Black Hills National Forest during spring 2007 and 2008 drumming surveys.

Variable	Description
Vegetation	
taa	Quaking aspen (ha)[a]
tbo	Burr oak (ha)[a]
tpb	Paper birch (ha)[a]
tpp	Ponderosa pine (ha)[a]
tws	White spruce (ha)[a]
Low	Delineated physiographic section with low aspen density[b]
Med	Delineated physiographic section with medium aspen density[b]
High	Delineated physiographic section with high aspen density[b]
Age Structure	
3B	Amount of area (ha) with 40-70% sapling cover[a]
3C	Amount of area (ha) with >70% sapling cover[a]
4B	Amount of area (ha) with 40-70% mature tree cover[a]
4C	Amount of area (ha) with >70% mature tree cover[a]
Weather	
Wind	Average wind speed (kmph) during the 5 minute survey

Table 1 continued.

Variable	Description
Weather	
Temp	Average temperature (°C) during the survey
Precip	Precipitation occurred during the survey (e.g., rain, snow)
Observer	
Obs_tech	The observer performing the survey was a full time technician
Temporal	
y	Year of survey
Time	Time of survey
Julian	Julian date of the survey
Julian^2	Squared Julian date of the survey

[a] Calculated within a 550 m buffer around each site

[b] See Appendix A

Table 2. Ranking of candidate models which assess the influence of temporal and spatial variables on detection probability (p), assuming occupancy (Ψ), colonization (γ), and local extinction (ε) probabilities are constant, for ruffed grouse in the Black Hills National Forest during spring 2007 and 2008 surveys. K is the number of parameters in the model, -2LL is -2 * log-likelihood, AIC_c is Akaike's information criterion adjusted for small sample size, Δ AIC_c is the difference in AIC_c value from the top model, and w_i is the Akaike weight.

Model[a]	K	-2LL	AIC_c	Δ AIC_c	w_i
Ψ(.),γ(.),ε(.),p(Julian^2+wind)	7	611.56	627.60	0.00	0.51
Ψ(.),γ(.),ε(.),p(Julian^2+wind+time+precip)	9	607.60	629.00	1.40	0.25
Ψ(.),γ(.),ε(.),p(Julian^2+precip+wind)	8	610.85	629.52	1.92	0.20
Ψ(.),γ(.),ε(.),p(global)	13	602.16	635.59	7.99	0.01
Ψ(.),γ(.),ε(.),p(Julian^2+wind+time+precip +low+med+high)	11	606.42	633.60	6.00	0.03
Ψ(.),γ(.),ε(.),p(Julian^2)	6	629.82	643.32	15.72	0.00
Ψ(.),γ(.),ε(.),p(Julian)	5	643.52	654.57	26.98	0.00
Ψ(.),γ(.),ε(.),p(wind)	5	643.83	654.88	27.29	0.00
Ψ(.),γ(.),ε(.),p(time)	5	653.03	664.08	36.49	0.00
Ψ(.),γ(.),ε(.),p(precip)	5	656.63	667.68	40.09	0.00
Ψ(.),γ(.),ε(.),p(.)	4	660.12	668.81	41.21	0.00
Ψ(.),γ(.),ε(.),p(obs_tech)	5	658.93	669.98	42.39	0.00
Ψ(.),γ(.),ε(.),p(temp)	5	659.96	671.01	43.42	0.00

Table 2 Continued.

Model[a]	K	-2LL	AIC$_c$	Δ AIC$_c$	w_i
$\Psi(.),\gamma(.),\varepsilon(.),p(\mathrm{y})$	5	660.09	671.14	43.55	0.00
$\Psi(.),\gamma(.),\varepsilon(.),p(\mathrm{low + med + high})$	6	659.61	673.11	45.51	0.00

[a] See Table 1 for definition of parameter symbols

Table 3. Ranking of candidate models which assess the influence of temporal and spatial variables on occupancy (Ψ), colonization (γ), and local extinction (ε) (while incorporating the most supported detection (p) model) of ruffed grouse during spring 2007 and 2008 surveys in the Black Hills National Forest. K is the number of parameters in the model, -2LL is -2 * log-likelihood, AIC$_c$ is Akaike's information criterion adjusted for small sample size, Δ AIC$_c$ is the difference in AIC$_c$ value from the top model, and w_i is the Akaike weight.

Model[a]	K	-2LL	AIC$_c$	Δ AIC$_c$	w_i
Ψ(taa+tws+tpp+3C),γ(.),ε(.), *p*(Julian^2+wind)[b]	11	583.18	605.86	0.00	0.48
Ψ(taa+tws+tpp),γ(.),ε(.), *p*(Julian^2+wind)	10	586.95	607.51	1.66	0.21
Ψ(taa+tws+tpp+3C),γ(taa),ε(taa) *p*(Julian^2+wind)	13	581.96	608.90	3.04	0.11
Ψ(taa),γ(.),ε(.), *p*(Julian^2+wind)	8	593.06	609.43	3.57	0.08
Ψ(taa+tws+tpp),γ(taa),ε(taa) *p*(Julian^2+wind)	12	585.09	609.89	4.04	0.06
Ψ(taa+tws+tpp+3C),γ(taa+3C), ε(taa+3C)*p*(Julian^2+wind)	15	580.86	612.10	6.25	0.02
Ψ(taa),γ(taa),ε(taa) *p*(Julian^2+wind)	10	591.67	612.23	6.38	0.02

Table 3 Continued.

Model[a]	K	-2LL	AIC$_c$	Δ AIC$_c$	w_i
Ψ(taa+3C),γ(taa+3C),ε(taa+3C) *p*(Julian^2+wind)	13	587.35	614.29	8.43	0.01
Ψ(taa+3C),γ(.),ε(.) *p*(Julian^2+wind)	9	596.74	615.20	9.34	0.00
Ψ(global),γ(global),ε(global), *p*(Julian^2+wind)	22	569.11	615.78	9.92	0.00
Ψ(3C),γ(.),ε(.) *p*(Julian^2+wind)	8	609.36	625.73	19.87	0.00
Ψ(.),γ(.),ε(.), *p*(Julian^2+wind)	7	611.56	625.84	19.99	0.00
Ψ(y),γ(.),ε(.) *p*(Julian^2+wind)	7	611.56	625.84	19.99	0.00
Ψ(3C+4C),γ(.),ε(.) *p*(Julian^2+wind)	9	607.39	625.85	19.99	0.00
Ψ(3C),γ(3C),ε(3C) *p*(Julian^2+wind)	10	609.10	629.66	23.81	0.00
Ψ(taa+tws+tpp+3C),γ(.),ε(.), *p*(.)	9	631.54	648.00	42.14	0.00

[a] See Table 1 for definition of parameter symbols

[b] Covariates from the most supported detection probability (*p*) model (Table 2)

Table 4. Model-averaged parameter estimates, standard errors (SE), odds ratios, and 95% odds ratio confidence intervals (CI) for occupancy (Ψ), colonization (γ), local extinction (ε), and detection probabilities (*p*) of ruffed grouse in the Black Hills National Forest during spring 2007 and 2008 surveys.

Parameter[a]	Estimate	SE	Odds ratio	95% CI
Occupancy Parameters				
Ψ intercept	-1.90	0.28		
taa	0.82	0.23	2.28	1.44 – 3.60
tws	0.36	0.19	1.43	0.99 – 2.06
tpp	0.34	0.28	1.41	0.81 – 2.45
3C	-0.29	0.31	0.75	0.40 – 1.38
Colonization Parameters				
γ intercept	-4.72	3.11		
taa	0.14	0.25	1.15	0.70 – 1.90
Extinction Parameters				
ε intercept	-1.24	0.68		
taa	-0.02	0.08	0.98	0.83 – 1.16
Detection Parameters				
p intercept	-0.85	0.26		
Julian	0.98	0.26	2.66	1.61 – 4.40
Julian^2	-0.71	0.20	0.49	0.33 – 0.73
wind	-0.79	0.21	0.45	0.30 – 0.68

Table 4. Continued.

[a] See Table 1 for definition of parameter symbols

Table 5. Spearman-rank correlation (r_s) of the model-averaged ruffed grouse occupancy model for each fold from *k*-fold cross-validation. Data was obtained from ruffed grouse drumming surveys throughout the Black Hills National Forest in spring 2007 and 2008.

Fold	r_s	*P*-value
1	0.909	≤ 0.001
2	0.958	≤ 0.001
3	0.748	0.013
4	0.670	0.034
5	0.782	< 0.01
Combined	0.842	≤ 0.001

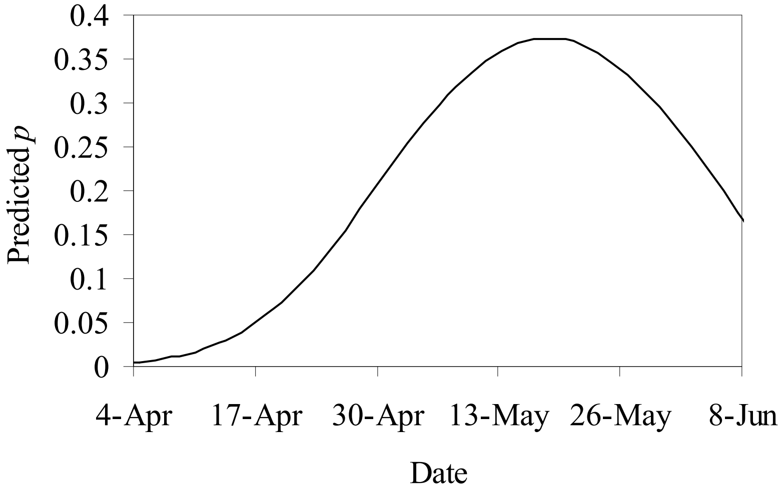


Figure 1. Influence of date on the probability of detecting ruffed grouse (*p*) in the Black Hills National Forest during spring 2007 and 2008 surveys. Probabilities were calculated using parameter estimates from the most supported *p* model.

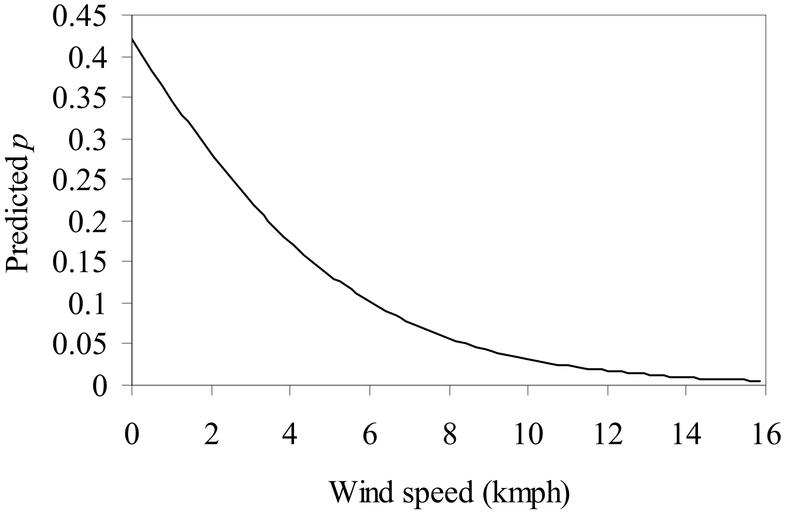


Figure 2. Influence of average wind speed on the probability of detecting ruffed grouse (*p*) in the Black Hills National Forest during spring 2007 and 2008 surveys. Probabilities were calculated using parameter estimates from the most supported *p* model.

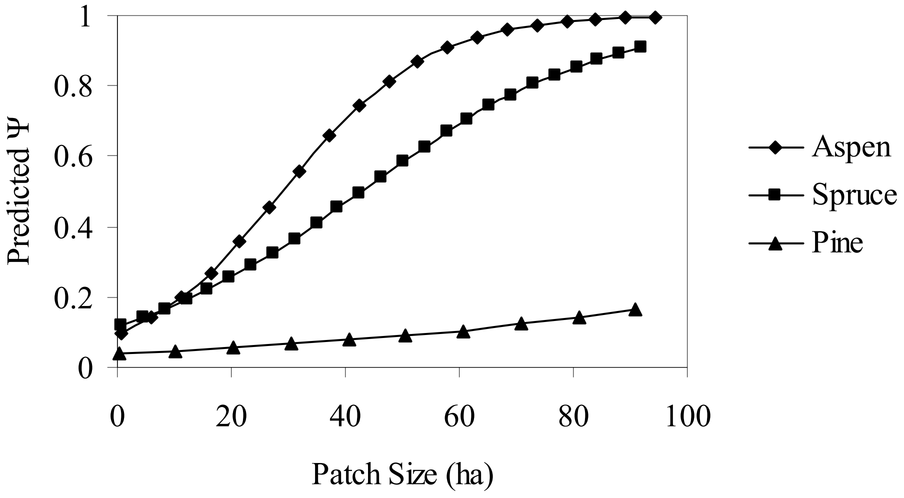


Figure 3. Influence of the area (ha) of quaking aspen (diamonds), white spruce (squares), and ponderosa pine (triangles) within 550 meters of a site on the probability of ruffed grouse occupancy during spring 2007 and 2008 in the Black Hills National Forest. Probabilities were calculated using model-averaged estimates of the top 5 most supported occupancy, colonization, and local extinction models.

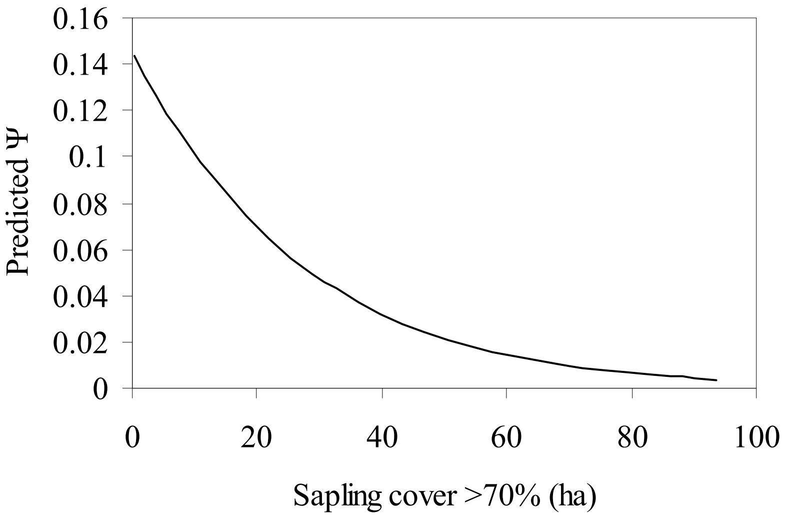


Figure 4. Influence of the amount of area (ha) covered by >70% saplings within 550 meters of a site on the probability of ruffed grouse occupancy during spring 2007 and 2008 in the Black Hills National Forest. Probabilities were calculated using model-averaged estimates of the top 5 most supported occupancy, colonization, and local extinction models.

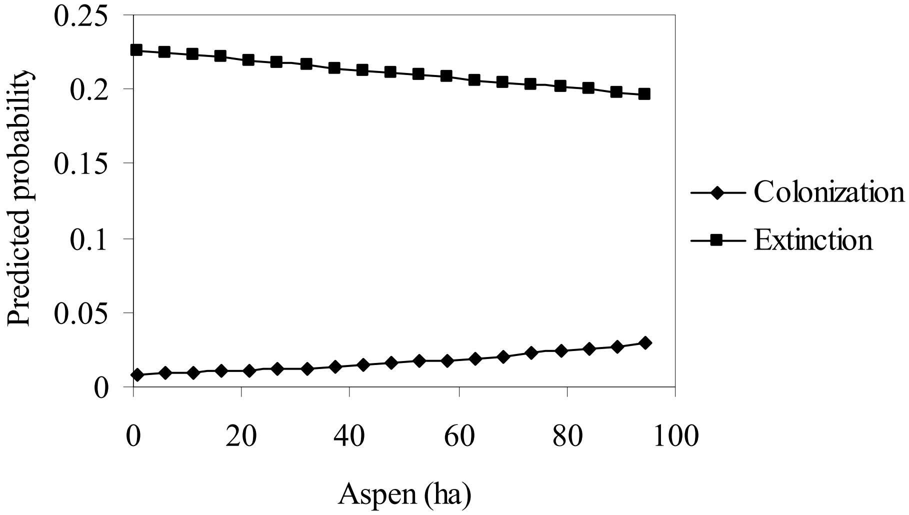
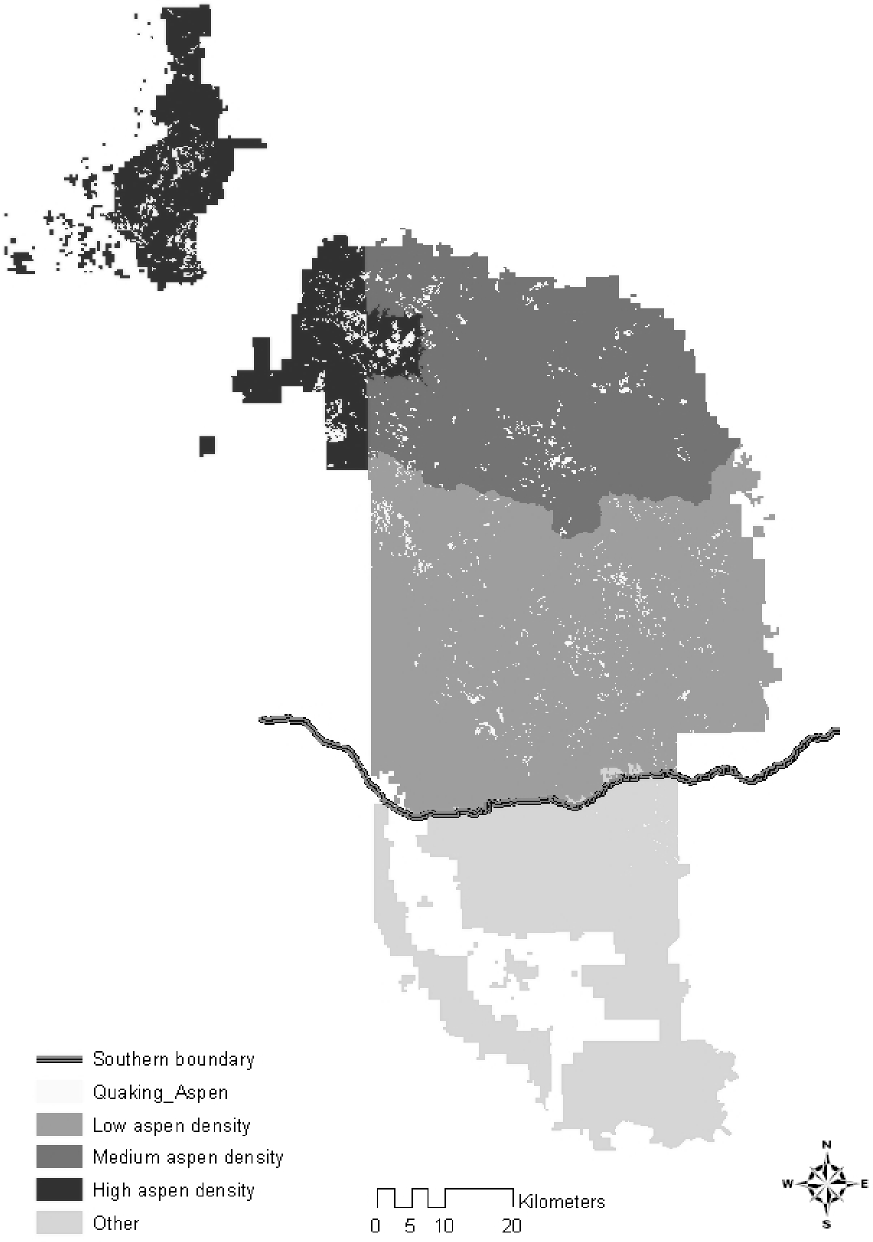


Fig. 5. Influence of quaking aspen area within 550 meters of a site on the probability of ruffed grouse colonization (diamonds) and local extinction (squares) between spring 2007 and 2008 in the Black Hills National Forest. Probabilities were calculated using model-averaged estimates of the top 5 most supported occupancy, colonization, and local extinction models.

APPENDIX A. PHYSIOGRAPHIC STRATA IN THE BLACK HILLS NATIONAL FOREST



APPENDIX B. DETECTION PROBABILITY CANDIDATE MODELS

A priori models assessing factors that influence the probability of detecting ruffed grouse (p), while holding occupancy (Ψ), colonization (γ), and local extinction (ε) constant, in the Black Hills National Forest during spring 2007 and 2008 drumming surveys

Model	Hypothesis	Model[a]	Model Structure	Predicted Parameter Effects
1	Constant: p is constant	$\Psi(.),\gamma(.),\varepsilon(.),p(.)$	β_0	Constant
2	Temporal: p is positively influenced by Julian date	$\Psi(.),\gamma(.),\varepsilon(.),p$ (Julian)	$\beta_0 + \beta_1$(Julian)	$\beta_1>0$
3	Temporal: p is positively influenced by Julian date (quadratic)	$\Psi(.),\gamma(.),\varepsilon(.),p$ (Julian^2)	$\beta_0 + \beta_1$(Julian) + β_2(Julian^2)	$\beta_1>0$, $\beta_2<0$
4	Temporal: p is negatively influenced by the time of day	$\Psi(.),\gamma(.),\varepsilon(.),p$ (time)	$\beta_0 + \beta_1$(time)	$\beta_1<0$
5	Temporal: p is year-dependent	$\Psi(.),\gamma(.),\varepsilon(.),p(y)$	p_1: β_0 p_2: β_0	p_1: Constant p_2: Constant
6	Weather: p is negatively influenced by precipitation	$\Psi(.),\gamma(.),\varepsilon(.),$ p(precip)	$\beta_0 + \beta_1$(precip)	$\beta_1<0$
7	Weather: p is negatively influenced by wind	$\Psi(.),\gamma(.),\varepsilon(.),$ p(wind)	$\beta_0 + \beta_1$(wind)	$\beta_1<0$
8	Weather: p is positively influenced by temperature	$\Psi(.),\gamma(.),\varepsilon(.),$ p(temp)	$\beta_0 + \beta_1$(temp)	$\beta_1>0$

APPENDIX B. CONTINUED

Model	Hypothesis	Model^a	Model Structure	Predicted Parameter Effects
9	Observer: *p* not affected by technician observers	$\Psi(.),\gamma(.),\varepsilon(.)$, *p*(obs)	$\beta_0 + \beta_1$(obs)	B $_1$=0
10	Vegetation: *p* is positively affected by high and medium aspen densities; yet, negatively affected by low aspen densities	$\Psi(.),\gamma(.),\varepsilon(.)$, *p*(section)	$\beta_0 + \beta_1$(high) + β_2(med) + β_3(low)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$
11	Weather + Temporal: *p* is negatively affected by both wind, time, precipitation and positively affected by temp and Julian date (quadratic)	$\Psi(.),\gamma(.),\varepsilon(.)$, *p*(Julian^2 + precip + wind + time)	$\beta_0 + \beta_1$(Julian) + β_2(Julian^2) + β_3(time) + β_4(wind) + β_5(precip)	$\beta_1>0$, $\beta_2<0$, $\beta_3<0$, $\beta_4<0$, $\beta_5<0$
12	Weather + Temporal: *p* is negatively affected by wind and precipitation; yet, positively affected by Julian date (quadratic)	$\Psi(.),\gamma(.),\varepsilon(.)$, *p*(Julian^2 + precip + wind)	β_0+β_1(Julian)+ β_2(Julian^2)+ β_3(precip)+ β_4(wind)	$\beta_1>0$, $\beta_2<0$, $\beta_3<0$, $\beta_4<0$
13	Weather + Temporal: *p* is negatively affected by wind; yet, positively affected by Julian date (quadratic)	$\Psi(.),\gamma(.),\varepsilon(.)$, *p*(Julian^2 + wind)	$\beta_0 + \beta_1$(Julian) + β_2(Julian^2) + β_3(wind)	$\beta_1>0$, $\beta_2<0$, $\beta_3<0$

APPENDIX B. CONTINUED

Model	Hypothesis	Model[a]	Model Structure	Predicted Parameter Effects
14	Weather + Temporal + Vegetaion: *p* is negatively affected by wind, time, precip, and low aspen densities; yet, positively affected by temperature, Julian date (quadratic), high, and medium densities of aspen	$\Psi(.),\gamma(.),\varepsilon(.)$, *p*(Julian^2 + wind + precip + time + section)	$\beta_0 + \beta_1$(Julian) + β_2(Julian^2) + β_3(precip) + β_4(wind) + β_5(time) + β_6(high) + β_7(med) + β_8(low)	$\beta_1>0$, $\beta_2<0$, $\beta_3<0$, $\beta_4<0$, $\beta_5<0$, $\beta_6>0$, $\beta_7>0$, $\beta_8<0$
15	Weather + Observer + Temporal +Vegetation (Global): *p* is influenced negatively by wind, time, precip, and low aspen densities; yet, positively by temperature, Julian date (quadratic), high, and medium aspen densities, observer is constant	$\Psi(.),\gamma(.),\varepsilon(.)$, *p*(global)	$\beta_0 + \beta_1$(Julian) + β_2(Julian^2) + β_3(temp) + β_4(wind) + β_5(precip) + β_6(obs_tech)+ β_7(time) + β_8(high) + β_9(med)+β_{10}(low)	$\beta_1>0$, $\beta2<0$, $\beta_3>0$, $\beta_4<0$, $\beta_5<0$, $\beta_6=0$, $\beta_7<0$, $\beta_8>0$, $\beta_9>0$, $\beta10<0$

[a] See Table 1 for definition of parameter symbols

APPENDIX C. OCCUPANCY AND COLONIZATION CANDIDATE MODELS

A priori models assessing factors that influence the probability of occupancy (Ψ), colonization (γ), and local extinction (ε) of ruffed grouse in the Black Hills National Forest during spring 2007 and 2008 drumming surveys (using the most supported detection probability model p[†])

Model	Hypothesis	Model[a]	Model Structure	Predicted Parameter Effects
1	Constant: Ψ, γ, and ε are constant, most supported *p* model	$\Psi(.),\gamma(.),\varepsilon(.),p(\dagger)$	Ψ: β_0 γ: β_0 ε: β_0 p: †	Ψ: Constant γ: Constant ε: Constant p: †
2	Temporal: Ψ is year-dependent, γ and ε constant, most supported *p* model	$\Psi(y),\gamma(.),\varepsilon(.),p(\dagger)$	Ψ_1: β_0 Ψ_2: β_0 γ: β_0 ε: β_0 p: †	Ψ_1: Constant Ψ_2: Constant γ: Constant ε: Constant p: †
3	Vegetation: Ψ positively affected by aspen patch size, γ and ε constant, most supported *p* model	$\Psi(taa),\gamma(.),\varepsilon(.),$ $p(\dagger)$	Ψ: $\beta_0 + \beta_1(taa)$ γ: β_0 ε: β_0 p: †	Ψ: $\beta_1 > 0$ γ: Constant ε: Constant p: †

APPENDIX C. CONTINUED

Model	Hypothesis	Model[a]	Model Structure	Predicted Parameter Effects
4	Vegetation: Ψ and γ are positively affected by aspen patch size, ε negatively affected by aspen patch size, most supported p model	Ψ(taa),γ(taa),ε(taa), p(†)	Ψ: β_0+ β_1(taa) γ: β_0+ β_1(taa) ε: β_0+ β_1(taa) p: †	Ψ: $\beta_1>0$ γ: $\beta_1>0$ ε: $\beta_1<0$ p: †
5	Vegetation: Ψ is positively affected by aspen and spruce patch size and negatively affected by pine patch size, γ is positively affected by aspen patch size, ε negatively affected by aspen patch size, most supported p model	Ψ(taa + tws + tpp),γ(taa),ε(taa), p(†)	Ψ: β_0+ β_1(taa)+ β_2(tws)+β_3(tpp) γ: β_0+ β_1(taa) ε: β_0+ β_1(taa) p: †	Ψ: $\beta_1>0$, $\beta_2>0$, $\beta_3<0$ γ: $\beta_1>0$ ε: $\beta_1<0$ p: †
6	Vegetation: Ψ is positively affected by aspen and spruce patch size and negatively affected by pine patch size, γ and ε are constant, most supported p model	Ψ(taa + tws + tpp),γ(.)ε(.),p(†)	Ψ: β_0+ β_1(taa)+ β_2(tws)+β_3(tpp) γ: β_0 ε: β_0 p: †	Ψ: $\beta_1>0$, $\beta_2>0$, $\beta_3<0$ γ: Constant ε: Consant p: †
7	Age: Ψ is positively affected by the amount of sapling cover and negatively affected by the amount of mature cover, γ and ε are constant, most supported p model	Ψ(3C + 4C),γ(.), ε(.),p(†)	Ψ: β_0+ β_1(3C)+ β2(4C) γ: β_0 ε: β_0 p: †	Ψ: $\beta_1>0$, $\beta_2<0$ γ: Constant ε: Constant p: †

APPENDIX C. CONTINUED

Model	Hypothesis	Model[a]	Model Structure	Predicted Parameter Effects
8	Age: Ψ is positively affected by the amount of sapling cover, γ and ε are constant, most supported p model	$\Psi(3C)\gamma(.)\varepsilon(.),p(\dagger)$	Ψ: $\beta_0+\beta_1(3C)$ γ: β_0 ε: β_0 p: †	Ψ: $\beta_1>0$ γ: Constant ε: Consant p: †
9	Age: Ψ and γ are positively affected by the amount of sapling cover, ε is negatively affected by sapling cover, most supported p model	$\Psi(3C),\gamma(3C),$ $\varepsilon(3C),p(\dagger)$	Ψ: $\beta_0+\beta_1(3C)$ γ: $\beta_0+\beta_1(3C)$ ε: $\beta_0+\beta_1(3C)$ p: †	Ψ: $\beta_1>0$ γ: $\beta_1>0$ ε: $\beta_1<0$ p: †
10	Vegetation+Age: Ψ is positively affected by the amount aspen and sapling cover, γ and ε are constant, most supported p model	$\Psi(taa + 3C)\gamma(.)$ $\varepsilon(.),p(\dagger)$	Ψ: $\beta_0+\beta_1(taa)+$ $\beta_2(3C)$ γ: β_0 ε: β_0 p: †	Ψ: $\beta_1>0, \beta_2>0$ γ: Constant ε: Constant p: †
11	Vegetation+Age: Ψ and γ positively affected by the amount of aspen and sapling cover, ε is negatively affected by the amount of aspen and sapling cover, most supported p model	$\Psi(taa + 3C),$ $\gamma(taa + 3C),$ $\varepsilon(taa + 3C),p(\dagger)$	Ψ: $\beta_0+\beta_1(taa)+$ $\beta_2(3C)$ γ: $\beta_0+\beta_1(taa)+$ $\beta_2(3C)$ ε: $\beta_0+\beta_1(taa)+$ $\beta_2(3C)$ p: †	Ψ: $\beta_1>0, \beta_2>0$ γ: $\beta_1>0, \beta_2>0$ ε: $\beta_1<0, \beta_2<0$ p: †

APPENDIX C. CONTINUED

Model	Hypothesis	Model[a]	Model Structure	Predicted Parameter Effects
12	Vegetation+Age: Ψ positively affected by aspen and spruce patch size , but negatively affected by pine patch size, γ positively affected by the amount of aspen and sapling cover, ε negatively affected by the amount of aspen and sapling cover, most supported *p* model	Ψ(taa + tws + tpp+ 3C) γ(taa + 3C), ε(taa + 3C),*p*(†)	Ψ: $\beta_0 + \beta_1$(taa)+ β_2(tws) + β_3(tpp) + β_4(3C) γ: $\beta_0 + \beta_1$(taa)+ β_2(3C) ε: $\beta_0 + \beta_1$(taa)+ β_2(3C) *p*: †	Ψ: $\beta_1>0, \beta_2>0, \beta_3<0, \beta_4>0$ γ: $\beta_1>0, \beta_2>0$ ε: $\beta_1<0, \beta_2<0$ *p*: †
13	Vegetation+Age: Ψ positively affected by aspen and spruce patch size, but negatively affected by pine patch size, γ and ε are constant, most supported *p* model	Ψ(taa + tws + tpp + 3C) γ(.)p(†)	Ψ: $\beta_0 + \beta_1$(taa)+ β_2(tws) + β_3(tpp) + β_4(3C) γ: β_0 ε: β_0 *p*: †	Ψ: $\beta_1>0, \beta_2>0, \beta_3<0, \beta_4>0$ γ: Constant ε: Constant *p*: †
14	Vegetation+Age: Ψ positively affected by the amount of aspen, spruce, and sapling cover, but negatively affected by pine patch size, γ positively affected by aspen patch size, ε negatively affected by aspen patch size, most supported *p* model	Ψ(taa + tws + tpp + 3C) γ(taa),ε(taa),*p*(†)	Ψ: $\beta_0 + \beta_1$(taa)+ β_2(tws) + β_3(tpp) + β_4(3C) γ: $\beta_0 + \beta_1$(taa) ε: $\beta_0 + \beta_1$(taa) *p*: †	Ψ: $\beta_1>0, \beta_2>0, \beta_3<0, \beta_4>0$ γ: $\beta_1>0$ ε: $\beta_1<0$ *p*: †

APPENDIX C. CONTINUED

Model	Hypothesis	Model[a]	Model Structure	Predicted Parameter Effects
15	Vegetation + Age (Global): Ψ is positively affected by the amount of aspen, spruce, paper birch, burr oak, sapling cover, but negatively affected by the amount of pine and mature cover, γ positively affected by the amount of aspen and sapling cover, ε negatively affected by the amount of aspen and sapling cover, most supported *p* model	Ψ(taa + tws + tpp + tbo + tpb + 3B + 3C + 4B +4C) γ(taa + 3C) ε(taa + 3C),*p*(†)	Ψ: $\beta_0 + \beta_1$(taa)+ β_2(tws) + β_3(tpp) + β_4(tbo) + β_5(tpb) + β_6(3B) + β_7(3C) + β_8(4B) + β_9(4C) γ: $\beta_0 + \beta_1$(taa)+ β_2(3C) ε: $\beta_0 + \beta_1$(taa)+ β_2(3C) *p*: †	Ψ: $\beta_1>0$, $\beta_2>0$, $\beta_3<0$, $\beta_4>0$, $\beta_5>0$, $\beta_6>0$, $\beta_7>0$, $\beta_8>0$, $\beta_9<0$ γ: $\beta_1>0$, $\beta_2>0$ ε: $\beta_1<0$, $\beta_2<0$ *p*: †
16	Constant *p* model[b]	Ψ(*best*),γ(*best*), ε(*best*),*p*(.)	Ψ: *best* γ: *best* ε: *best* *p*: β_0	Ψ: *best* γ: *best* ε: *best* *p*: Constant

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[a] See Table 1 for definition of parameter symbols

[b] Evaluation of the most supported Ψ, γ, and ε model with a constant *p* model

CHAPTER II

DEVELOPMENT OF A MONITORING PROTOCOL FOR RUFFED GROUSE IN THE BLACK HILLS NATIONAL FOREST

ABSTRACT

Monitoring ruffed grouse (*Bonasa umbellus*) in the Black Hills National Forest (BHNF) is a priority for forest managers due to their status as the management indicator species for quaking aspen (*Populus tremuloides*) vegetation and their popularity as a game bird. Due to time and manpower limitations and the need for robust estimates of ruffed grouse population trends, a protocol which maximizes precision while reducing manpower requirements is needed. We determined the occupancy and detection probability of ruffed grouse in the BHNF during spring 2007 and spring 2008. Using these observed occupancy, detection, colonization, and local extinction probability values, and a range of repeat surveys (2-5), we evaluated site requirements for 3 physiographic strata (low, medium, and high occupancy probability) in the BHNF. We evaluated 2 single-season designs (standard and removal) and 2 multi-season (i.e., year) designs (standard and rotating- panel) over several levels of precision (CV ≤ 0.26 [“rough management”], 0.13 [“accurate management”], and 0.05 [“careful management”]). For single season designs, the standard design required one-fifth the number of sites compared with a removal design. Also, conducting 2 surveys at each site required and average of 48.4%, 43.2%, and 28.3% more effort (no. sites * no. surveys) than conducting 3 surveys when detection probabilities = 0.2, 0.28, and 0.4, respectively. However, conducting 3 repeat surveys required an average of < 2% less effort than conducting 4 surveys at higher detection

probabilities (0.4), but required 27.5% more effort at low detection probabilities (0.2). Survey effort was similar between the standard multi-season design and the rotating-panel design. However, the rotating-panel design required 12.3% more effort over a 4 season period to achieve benchmark precision values for colonization and extinction estimates. Given our results, the standard multi-season design with 3 repeat surveys at each site during each season appears to be the most appropriate monitoring design for ruffed grouse in the BHNF. Using the recommended design for 4 seasons would require 70, 171, and 455 sites to be surveyed each season in high, medium, and low occupancy probability strata, respectively to achieve "rough" management. The "accurate" management benchmark requires > 2.5 times those sample sizes and the "careful" management requires > 15 times the number of sites. The large sample size requirements are associated with the low occupancy rates of ruffed grouse in the BHNF. Because logistic issues will likely prevent investigators from completing the necessary number of sites for each stratum, managers might consider several strategies given trade-offs among personnel requirements, sample size requirements, and low occupancy. For example, monitoring only high and medium strata might offer insight into the general status of ruffed grouse in the BHNF and under a standard multi-season design conducted for 4 seasons would require 70 and 171 sites, respectively to achieve a CV ≤ 0.26. Monitoring ruffed grouse in the strata with low occupancy will require substantially more effort. Thus, managers need to consider whether their objectives dictate monitoring sites in the low occupancy strata. If the extent of aspen in the low strata increases, with a corresponding increase in colonization by ruffed grouse, the sampling requirements to achieve rough management will decrease. As a result, managers may find it appropriate to include low occupancy strata sites in future monitoring practices.

INTRODUCTION

Ruffed grouse (*Bonasa umbellus*) are a valuable resource for hunters and forest managers and their presence is often attributed to a healthy and diverse ecosystem because they generally occupy mixed-age and mixed-forest communities (Madison 1969, Barber et al. 1989b, Zimmerman and Gutiérrez 2007). Ruffed grouse inhabit early successional vegetation that includes interspersed mature trees for food and cover from both avian and mammalian predators (Bump et al. 1947, Gullion and Svoboda 1972, DeStefano et al. 1988, Barber et al. 1989a, Kubisiak 1989). If available, ruffed grouse typically select mixed-age aspen (*Populus* spp.) communities because they provide all the necessary life requirements (Bump et. al. 1947, Gullion and Svoboda 1972, Kubisiak 1985, Kubisiak 1989). In the Black Hills National Forest (BHNF), quaking aspen (*Populus tremuloides*) is essential to ruffed grouse occupancy (Chapter 1). As a result, monitoring ruffed grouse population trends might be valuable for effectively managing both ruffed grouse and aspen in the BHNF.

The 1997 Forest Plan Revision for the BHNF established ruffed grouse as the management indicator species for aspen, making monitoring of ruffed grouse a necessity for the U.S. Forest Service and South Dakota Department of Game, Fish, and Parks. Previous attempts at monitoring ruffed grouse in the BHNF (between 1973 and 1983 [SAIC 2005]) were inconsistent and conducted solely in areas with extensive aspen, which likely biased ruffed grouse population estimates and trends. Additionally, these surveys did not account for imperfect detection (i.e., grouse were present, but not detected), which may also bias population estimates (MacKenzie et al. 2002). Last, because of the high density of roads, and increased vehicular traffic throughout the BHNF, previous transects used for drumming surveys may be inappropriate due to traffic noise.

To improve upon previous survey methods, we integrated occupancy models with spring drumming surveys and estimated occupancy probabilities of ruffed grouse during 2007 and 2008 (Chapter 1). Occupancy models have recently become popular because they account for imperfect detection, only require the investigator to determine the presence or absence of the species from repeated surveys, and can be robust predictors of the proportion of the study area occupied when appropriate predictor variables are considered (MacKenzie et al. 2002, MacKenzie et al. 2006). While occupancy estimates from spring 2007 and 2008 surveys provide crucial information on the current status of ruffed grouse in the BHNF, a long-term monitoring protocol is necessary to evaluate trends in ruffed grouse occupancy and to monitor the implementation of the BHNF Forest Plan.

Selecting a monitoring design that maximizes precision while reducing sampling effort will aid managers in the BHNF to effectively and efficiently monitor occupancy trends of ruffed grouse. Our objectives were to: (1) determine which single season (standard design or removal) and multi-season (standard design or rotating-panel) sampling designs were most efficient in terms of the number of sites required at varying levels of occupancy, detection probability, and repeat surveys, to achieve benchmark levels of precision; (2) estimate the optimal number of surveys to perform at each site to achieve a desired level of precision; and (3) estimate the necessary number of sites to be sampled for each of the previous designs associated with occupancy and detection probability estimates from 2007 and 2008 surveys (Chapter 1).

STUDY AREA

The BHNF was located in the western portion of South Dakota and included the Bear Lodge Mountains of northeastern Wyoming. Elevation ranged from 1,066 m – 2,207 m. Annual rainfall in the BHNF exceeded 50.8 cm per year and varied with elevation (Ball et. al. 1996). The BHNF included 500,000 ha of a variety of vegetation types, consisting primarily of ponderosa pine (*Pinus ponderosa,* 84%), quaking aspen/paper birch (*Betula papyrifera,* 4%), and white spruce (*Picea glauca,* 2%). Bur oak (*Quercus macrocarpa*), hop-hornbeam (*Ostrya virginiana*), and green ash (*Fraxinus pennsylvanica*) also occupied the BHNF, comprising < 10% (Hoffman and Alexander 1987, Froiland 1990). Common shrubs included western snowberry (*Symphoricarpos occidentalis*), white coralberry (*S. albus*), kinnikinnick (*Arctostaphylos uvaursi*), and common juniper (*Juniperus comunis*) (Severson and Thilenius 1976, Hoffman and Alexander 1987).

The BHNF had one of the highest road densities (3.2 km/km^2) of any national forest (Rumble et al. 2005), consisting of secondary (gravel) and primitive (dirt) roads. Our study area encompassed the northern 2/3 of the BHNF; from Highway 16 to the northern boundary of the BHNF (Appendix A). We selected Highway 16 as the southern boundary because there was very little aspen and ruffed grouse occurred in extremely low abundance south of Highway 16.

METHODS

Field Methods for Drumming Surveys

From 2 April 2007 through 31 May 2007, 4 September through 27 October 2007, and 14 April 2008 through 7 June 2008, we conducted drumming counts in the BHNF. We only sampled during one autumn season and given the poor results (Chapter 1), we did not consider autumn surveys further. We assumed occupancy probabilities would be heterogeneous throughout the BHNF; therefore, we stratified the BHNF into 3 physiographic strata (high, medium, and low) based on aspen stand density using the Resource Information System (RIS) data from the BHNF. Physiographic strata were primarily delineated by district (e.g., Bear Lodge, Northern Hills, and Mystic/Hell's Canyon) with slight modification to district boundaries. The Bear Lodge District had ~ 1 ha of aspen/11 ha of forest, the Northern Hills District had ~ 1 ha aspen/25 ha of forest, and the Mystic-Hells Canyon District had ~ 1 ha aspen/31 hectares of forest (Appendix A). Using a standard occupancy design (MacKenzie 2005, MacKenzie and Royle 2005), an assumed detection probability of 0.31 (Zimmerman 2006), occupancy probabilities of 0.2, 0.3, and 0.4 for low, medium, and high aspen density (SAIC 2005), respectively, and 5 repeat surveys, we computed the number of sites to achieve the desired precision (standard error [SE] = 0.05) for occupancy estimates (MacKenzie and Royle 2005). Additionally, because we assumed some sites would not be accessible, we increased the sample size in each stratum by 50%. We used ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) and a stratified random sampling design, without replacement to identify the location of survey sites along secondary and primitive roads. We constrained sampling sites to be > 1 mile apart to ensure independence among sites. We did not include sites along primary roads (i.e., paved and upgraded gravel roads) because there was considerable traffic on them which could interfere with our ability to hear drumming ruffed grouse.

We listened for drumming ruffed grouse for 5 minutes on each survey and recorded whether or not a grouse was detected. Because we assumed occupancy and detection probability would be spatially and temporally heterogeneous, we also recorded date and wind speed during each survey. Later, using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA), we calculated the area of vegetation types and structural stages from RIS data within 550 m around each survey site. We selected 550 m because this was the furthest distance we were able to hear a drumming ruffed grouse during our surveys (Chapter 1).

Analytical Methods

Occupancy, detection, colonization, and extinction probabilities.— We calculated occupancy, detection, colonization, and local extinction probabilities and parameter estimates for covariates using Program PRESENCE (MacKenzie et al. 2006). These estimates served as the basis of our evaluation of survey strategies. We first evaluated sample size estimates for the standard and removal single-season designs, and then evaluated sample size estimates for standard and rotating-panel multi-season designs.

Single season design.— The development of an efficient occupancy modeling protocol requires that the investigator define a period (i.e., "season") in which species occupancy is closed (no immigration or emigration) and allocate effort between the number of sites to sample and the number of repeat surveys to perform at each site (MacKenzie and Royle 2005, MacKenzie et al. 2006, Bailey et al. 2007). As a result, we defined "season" as the ruffed grouse breeding season (i.e., 1st through the 4th week of

May) and the length of time between seasons as one year (i.e., the time between breeding seasons). During a single season, all sites could be surveyed the same number of times (i.e., standard design), or sites could be surveyed only until the presence of the species of interest is determined at the particular site (i.e., removal design; MacKenzie and Royle 2005, MacKenzie et al. 2006). Removal methods may be more efficient than standard designs when detection probabilities are relatively high and constant; however, this design typically provides less flexibility for modeling (MacKenzie et al. 2006).

We evaluated the standard and removal single season sampling designs by calculating the necessary survey effort based upon our estimates of occupancy (Ψ) and detection probability (p) from spring 2007 and 2008 surveys (Chapter 1) and three different estimates of precision suggested by Robson and Regier (1964) and Skalski and Millspaugh (2002). They suggested that a coefficient of variation (CV) of ≤ 0.26 is acceptable for studies which require only "rough" management. However, for studies which require "accurate" or "careful" management, a CV ≤ 0.13 and CV ≤ 0.05 was suggested, respectively (Robson and Regier 1964, Skalski and Millspaugh 2002). We calculated a CV for each level of management using the equation from MacKenzie et al. (2006):

$$CV = \sqrt{\mathrm{var}(\hat{\Psi})} / \Psi \tag{1}$$

Recognizing that ruffed grouse occupancy and detection probabilities will likely change annually, we evaluated the number of sites (s) and amount of effort (E) required to achieve the benchmark precisions described above with varying occupancy probabilities ($\Psi = 0.05, 0.12, 0.25, 0.35$) and detection probabilities ($p = 0.2, 0.28, 0.4$) for both single-season designs. Additionally, MacKenzie and Royle (2005) encourage investigators to complete repeat surveys until $0.85 < (1-[1-p]^K) < 0.95$ (probability that a ruffed grouse is detected at a site after K surveys, if present). Due to low occupancy and detection probability in the BHNF (Chapter 1), this suggestion may not be realistic given time and personnel constraints. Therefore, we also evaluated how changing the number of repeat surveys ($K = 2, 3, 4, 5$) at each site influenced estimates of the number of sites and effort required to achieve the benchmark levels of precision. To evaluate the standard single-season design, we included the parameters described above into the standard equation:

$$s = \frac{\Psi}{\mathrm{var}(\hat{\Psi})}\left[(1-\Psi) + \frac{(1-p^*)}{p^* - Kp(1-p)^{K-1}}\right] \tag{2}$$

where $p^* = 1-(1-p)^K$ is the probability of detecting the species at least once during K surveys of an occupied site (MacKenzie and Royle 2005).

To estimate the number of sites required by the removal design, we incorporated the same parameters above into the removal equation:

$$s = \frac{\Psi}{\mathrm{var}(\hat{\Psi})}\left[(1-\Psi) + \frac{p^*(1-p^*)}{(p^*)^2 - K^2p^2(1-p)^{K-1}}\right] \tag{3}$$

Multi-season design.— Single season designs provide a “snapshot” of the occupancy state of a species and may be completed for multiple seasons to ascertain trends in occupancy over time (i.e., multi-season design; MacKenzie et al. 2006). By conducting surveys for multiple seasons, dynamic properties (e.g., colonization and local extinction) may be evaluated between seasons to determine why some sites are colonized and others are abandoned, thereby offering a more robust view of occupancy. For multi-season designs, the same sites could be surveyed the same number of times each season (i.e.., standard multi-season design), offering investigators a more robust estimate of occupancy, colonization, and local extinction. However, such a design may be logistically difficult for managers because adequate manpower may not be available each season. Conversely, a rotating-panel design could be incorporated, in which a different subset of available sites are sampled each season (MacKenzie et al. 2006, Bailey et al. 2007). Such a design offers a less frequent, yet more logistically achievable estimate of occupancy; however, it provides less inference when evaluating colonization and local extinction probabilities (Bailey et al. 2007).

We evaluated how different multi-season designs influenced estimates of the number of sites required to obtain the levels of precision associated with CV ≤ 0.26, 0.13, and 0.05 for occupancy, colonization, and local extinction estimates, assuming either the same or different sites were surveyed each season for 4 seasons (Bailey et al. 2007). We considered a standard multi-season design (where the same sites were sampled each season) and a "rotating-panel" design that assumed that a subset of sites was sampled each season while the remaining subset was sampled every other season (Table 1).

We incorporated estimates of occupancy probabilities (0.05, 0.12, 0.25, 0.35) and detection probabilities (0.2, 0.28, 0.4) into the standard and rotating panel multi-season designs. Additionally, we included colonization (0.005) and local extinction (0.20) estimates, assuming these values were constant (Chapter 1). Last, we included the optimal number of repeat surveys from single-season analyses ($K = 3$), assuming the same number of repeat surveys would be completed at each site during each season. To obtain estimates of the survey site requirements for benchmark precisions we incorporated the number of surveys, occupancy, detection, colonization, and extinction probabilities into the multi-season design in Program GENPRES (Bailey et al. 2007). We used analytic-numeric approximations within Program GENPRES to assess the precision of occupancy, colonization, and local extinction estimators (Bailey et al. 2007).

RESULTS

Field results

We surveyed 402 sites (137 high, 149 med., 116 low) 3 to 5 times each ($\bar{x}$ = 3.09, SE = 0.014) during spring 2007 and 2008. During spring 2007 and 2008, mean occupancy probability = 0.12 ± 0.026, mean detection probability = 0.28 ± 0.058, colonization probability = 0.005 ± 0.02, and local extinction probability = 0.20 ± 0.12. For high, medium, and low strata, occupancy = 0.24 ± 0.04, 0.12 ± 0.034, and 0.06 ± 0.03, respectively.

Single season

The estimated number of sites and survey effort required to meet benchmark precision values using a standard single season design was lower than the removal design for each occupancy, detection, and survey value. On average, the removal design required 5.6 times the sample size than the standard design (Table 2). Assuming a detection probability of 0.2, 0.28, and 0.4, the removal design required 7.0, 4.2, and 2.2 times the sample size as the standard design, respectively (Table 2). Additionally, for 2, 3, 4, and 5 repeat surveys, the removal design required 7.1, 4.4, 2.9, and 2.0 times the sample size as the standard design, respectively.

As occupancy increased from 0.05 to 0.35, estimates of the sample size necessary to achieve the desired occupancy precision decreased by 86.7% and 85.9% for the standard and removal designs, respectively (Table 2). Also, as detection probability increased from 0.2 to 0.4, estimates of the sample size necessary to achieve the desired occupancy precision decreased by 75.1% and 92.2% for the standard and removal designs, respectively. Last, conducting 2 surveys at each site required and average of 48.4%, 43.2%, and 28.3% more effort (no. sites * no. surveys) than conducting 3 surveys for detection probabilities of 0.2, 0.28, and 0.4, respectively. However, conducting 3 repeat surveys required an average of < 2% less effort than conducting 4 surveys at higher detection probabilities (0.4), but required 27.5% more effort at low detection probabilities (0.2; Figure 1). Given these results, the standard design with at least 3 repeat surveys is the most appropriate of the single season designs for ruffed grouse surveys in the BHNF.

Multi-season

For the range of occupancy and detection probability values we evaluated, the multi-season designs required fewer survey sites and less effort than either of the single-season designs. Increasing the number of seasons from 1 to 4 reduced the estimated sampling effort by 46% and 39% for the standard and rotating-panel design, respectively. Among multi-season designs, the standard and rotating-panel designs had similar estimated survey effort. The estimated survey effort for each design differed by < 2% over the 4-season period to achieve the precision benchmarks for occupancy estimates (Table 3). However, achieving the same levels of precision for occupancy, colonization and local extinction estimates with a standard multi-season design necessitated an average of 12.3% less effort than the rotating-panel design.

While each design had similar effort requirements throughout the range of occupancy estimates, the designs had different effort requirements at varying detection probability values. The standard design required 5.1% less effort over a 4 season period than the rotating-panel design when the detection probability was 0.2. However, the standard design required 15.5% greater sampling effort when detection probability was 0.4. Given these results and the current estimates of occupancy and detection probability for ruffed grouse in the BHNF, the standard multi-season design is currently the most appropriate survey design.

DISCUSSION

Managers have several options for conducting rigorous assessments of ruffed grouse trends in the BHNF. Given occupancy modeling is straightforward, accounts for imperfect detection, and provides useful metrics (e.g., occupancy, colonization, local extinction) for evaluating ruffed grouse trends, we recommend using this approach. The standard multi-season (i.e., year) occupancy modeling design was the most suitable design for monitoring ruffed grouse in the BHNF. This design required similar or less effort than both single season designs and the rotating-panel multi-season design, and provided inference regarding colonization and local extinction probabilities. However, the multi-season design requires a long-term commitment to attain reliable results. Estimated sampling effort to achieve the benchmark precisions recommended by Robson and Regier (1964) and Skalski and Millspaugh (2002) were high, particularly in the low aspen stand density strata, which had a low occupancy probability. Thus, we encourage managers to identify whether it is necessary to sample the low occupancy stratum in the BHNF, what levels of precision are acceptable for their purposes, and what length of time they are willing to continue monitoring. Identifying these objectives will facilitate the selection of an appropriate monitoring approach for ruffed grouse in the BHNF.

Our results demonstrated that a standard single-season design achieved the benchmark levels of precision for occupancy estimates with less survey effort than a removal method. A removal design can provide more precise estimates of occupancy than a standard design with the same number of surveys when occupancy or detection probabilities are > 0.4 (MacKenzie and Royle 2005, MacKenzie et al. 2006). However, given the occupancy and detection probabilities we observed (Chapter 1), the removal design necessitated > 3 times more sites than a standard design in all strata. Additionally, detection probability was highly dependent on date and wind speed (Chapter 1), which necessitates a design which is flexible for modeling detection covariates (MacKenzie and Royle 2005). Therefore, we conclude that the removal design is not currently appropriate for ruffed grouse surveys in the BHNF.

Allocation of effort between the necessary number of sites and number of repeat surveys to achieve a desired precision is important to the development of occupancy studies (MacKenzie and Royle 2005, MacKenzie et al. 2006). MacKenzie and Royle (2005) suggested continuing repeat surveys until the probability of detecting the species at a site after *K* surveys is between 0.85 and 0.95. Given our estimated detection probability, this would necessitate at least 6 repeat surveys at each site. Conversely, Field et al. (2005) observed through simulations that 2 repeat surveys were adequate. Due to low detection probabilities (0.28) of ruffed grouse in the BHNF, achieving the number of repeat surveys suggested by MacKenzie and Royle (2005) was improbable due to the extensive manpower requirements. Our results suggested that completing 2 repeat surveys required > 28% more effort than when completing 3 repeat surveys. However, completing 3 repeat surveys required similar effort compared to completing 4 surveys at high detection probabilities, but required 27.5% more effort at low detection probabilities. Because we assume investigators will survey when detection probability is maximized (Chapter 1), we believe ruffed grouse detection probabilities will increase. Thus, we believe completing at least 3 surveys at each site will be optimal for ruffed grouse surveys in the BHNF.

Occupancy estimates from a single season provide a "snapshot" of the status of ruffed grouse in the BHNF; conversely, occupancy estimates over multiple seasons offer a more robust interpretation of occupancy trends and dynamic processes (e.g., colonization and local extinction; MacKenzie et al. 2006). Our results demonstrated that conducting 4 seasons of surveys reduced the necessary number of sites by 46% and 39% for the standard and rotating-panel designs, respectively. Because of the large prohibitive site requirements for our study under a single season design, it will be important to survey for multiple seasons to achieve more precise estimates of occupancy. However, the manner in which sites are surveyed over multiple seasons may influence the necessary amount of effort. Our results demonstrated that the type of multi-season design did not greatly influence the effort to achieve benchmark precisions for occupancy alone. However, to achieve benchmark precision levels for occupancy, colonization, and local extinction, the standard multi-season design required an average of 12.3% less effort than the rotating panel multi-season design. Because robust estimates of colonization and local extinction may be important when evaluating the status of ruffed grouse in the BHNF, the rotating panel multi-season design might not be an appropriate monitoring design.

Occupancy of ruffed grouse was much lower than we expected in the BHNF during our study, leading to lower precision. Instead of the hypothesized occupancy probabilities of $\Psi = 0.4$, 0.3, and 0.2 for high, medium, and low strata, respectively, we found occupancy probabilities of $\Psi = 0.24 \pm 0.04$, 0.12 ± 0.03, and 0.06 ± 0.03 (Chapter 1). Because of the low occupancy rates, a standard multi-season design with 3 repeat surveys each season for 4 seasons would require 70, 171, and 455 sites in high, medium, and low strata, respectively to achieve a $CV \leq 0.26$. Achieving a $CV \leq 0.13$ would require 413, 762, and 1138 sites in high, medium, and low strata, respectively, and achieving a $CV \leq 0.05$ would require 2597, 4798, and 7166 sites in high, medium, and low strata, respectively. Although our estimates are based on 4 years of surveys, monitoring ruffed grouse in the BHNF will be an ongoing process, thus, estimates of occupancy will become more precise as monitoring practices continue.

Because logistic issues will prevent investigators from completing the necessary number of sites for each stratum, managers might consider several strategies given the numerous trade-offs among personnel requirements, sample size requirements, and low occupancy. For example, annual monitoring in the high and medium strata might offer insight into the general status of ruffed grouse in the BHNF and would require 70 and 171 sites to be monitored. Because monitoring in the low strata would require substantially more effort, managers will need to consider whether their objectives require the inclusion of low strata as it relates to the implementation of the BHNF forest plan (U.S. Forest Service 1997). However, sampling below the recommended benchmarks will result in loss of precision, which should be considered in determining whether strata can be sampled adequately. While site requirements are extremely high to achieve these benchmarks, the requirements should reduce if detection and occupancy probabilities of ruffed grouse throughout the BHNF are increased and a long-term commitment to monitoring is made.

FUTURE RECOMMENDATIONS

We encourage managers to establish their monitoring objectives and identify whether it is necessary to survey ruffed grouse throughout the entire BHNF, what levels of precision are acceptable for their purposes, and the length of time they are willing to continue monitoring. Time and manpower issues will likely hinder the ability of investigators to sample the necessary number of sites in each stratum to meet the highest benchmark precisions. Because ruffed grouse occupancy is so low in the low aspen vegetation strata ($\Psi = 0.06$), it may not currently be appropriate to expend the majority of available resources in this stratum. As a result, managers might desire to focus efforts in high and medium strata, which would require 70 and 171 sites, respectively to achieve "rough" estimates of occupancy. Taking this approach should provide managers with reliable general status and trends of ruffed grouse in the BHNF; however, if this approach is taken, inference towards ruffed grouse expansion into strata of low occupancy would not exist. Alternatively, managers may desire to survey in areas of low occupancy to determine whether timber management (e.g., increasing the extent of aspen) has increased ruffed grouse occupancy in response to specific management activities. Thus, it might be appropriate for managers to also survey sites in strata with low occupancy.

Regardless of the monitoring strategy selected, sites could be randomly selected from the original 402 sites surveyed during spring 2007 and 2008 (Appendix B). If site requirements exceed what was surveyed during 2007 and 2008, additional sites should be placed on secondary (i.e., gravel) or primitive (i.e., dirt) roads at least one mile apart to reduce noise issues from traffic and ensure independence between sites. Each season, these same sites should be surveyed at least 3 times each (i.e., using a standard multi-season design) and proper survey covariates (i.e., date and wind speed) should be recorded for each survey. Additionally, site covariate values (e.g., hectares of aspen, spruce, pine, and sapling canopy cover > 70%) should be included using the same methods described in *Field Methods for Drumming Surveys* to ensure the spatial and temporal heterogeneity in occupancy and detection probability is accounted for (MacKenzie et al. 2006). To increase detection probability of ruffed grouse during surveys, managers should only survey during optimal conditions. These conditions occurred during the month of May and at low wind speeds (Chapter 1).

Occupancy estimates should be evaluated each season to determine whether occupancy rates have changed, thereby requiring the modification of the number of sample sites for the following season. To simplify occupancy, detection, and sample site requirement calculations, we recommend using the ruffed grouse Excel occupancy spreadsheet program which calculates occupancy and detection probability estimates based on the current season's data (Appendix C).

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Table 1. Representation of a standard and rotating-panel multi-season survey design over 4 seasons (i.e., years). “X” represents a survey event, “___” represents a subset of sites that were not surveyed in that particular season, and *s* represents an arbitrary number of sites divided equally into 4 subsets (s_1, s_2, s_3, and s_4).

Standard Design					Rotating-Panel Design				
	Season					Season			
No. of sites	1	2	3	4	No. of sites	1	2	3	4
s_1	XXX	XXX	XXX	XXX	s_1	XXX	XXX	XXX	____
s_2	XXX	XXX	XXX	XXX	s_2	XXX	____	XXX	XXX
s_3	XXX	XXX	XXX	XXX	s_3	XXX	XXX	XXX	____
s_4	XXX	XXX	XXX	XXX	s_4	XXX	____	XXX	XXX

Table 2. Site requirements (*s*) for a standard (S) and removal (R) single season design when CV ≤ 0.26, 0.13, and 0.05, assuming occupancy (Ψ) values range from 0.05 – 0.35, detection probability (*p*) values range from 0.2 – 0.4, and number of repeat surveys (*K*) range from 2 – 5. Occupancy and detection probabilities were estimated from 2007 and 2008 ruffed grouse drumming surveys in the Black Hills National Forest.

			CV ≤ 0.26		CV ≤ 0.13		*CV* ≤ 0.05	
Ψ	*p*	*K*	S (*s*)	R (*s*)	S (*s*)	R (*s*)	S (*s*)	R (*s*)
0.05	0.2	2	5214	44583	20691	176941	130335	1114572
0.05	0.2	3	1807	10216	7170	40545	45161	255398
0.05	0.2	4	990	3853	3926	15290	24726	96310
0.05	0.2	5	676	1890	2683	7501	16896	47245
0.05	0.28	2	2326	12786	9232	50743	58149	319632
0.05	0.28	3	893	2954	3542	11723	22308	73841
0.05	0.28	4	557	1201	2208	4765	13903	30015
0.05	0.28	5	431	681	1709	2700	10763	17004
0.05	0.4	2	985	3061	3907	12146	24606	76510
0.05	0.4	3	481	834	1909	3308	12024	20833
0.05	0.4	4	369	462	1462	1833	9204	11544
0.05	0.4	5	329	359	1303	1424	8207	8966
0.12	0.2	2	2164	18568	8586	73690	54082	464181
0.12	0.2	3	744	4248	2952	16859	18593	106192
0.12	0.2	4	404	1597	1600	6335	10078	39905

Table 2 Continued.

			CV ≤ 0.26		CV ≤ 0.13		CV ≤ 0.05	
Ψ	*p*	*K*	S (*s*)	R (*s*)	S (*s*)	R (*s*)	S (*s*)	R (*s*)
0.12	0.2	5	273	779	1082	3090	6816	19461
0.12	0.28	2	961	5319	3811	21108	24005	132956
0.12	0.28	3	363	1222	1440	4849	9071	30543
0.12	0.28	4	223	492	884	1950	5569	12282
0.12	0.28	5	171	275	677	1090	4261	6861
0.12	0.4	2	402	1267	1593	5026	10029	31655
0.12	0.4	3	192	339	760	1343	4786	8457
0.12	0.4	4	145	184	574	728	3611	4586
0.12	0.4	5	128	141	508	558	3196	3512
0.25	0.2	2	1031	8905	4090	35340	25760	222607
0.25	0.2	3	349	2031	1386	8061	8725	50772
0.25	0.2	4	186	759	737	3010	4638	18955
0.25	0.2	5	123	366	488	1452	3072	9142
0.25	0.28	2	453	2545	1798	10100	11323	63619
0.25	0.28	3	167	579	660	2296	4155	14461
0.25	0.28	4	99	228	393	905	2473	5696
0.25	0.28	5	74	124	293	492	1845	3094
0.25	0.4	2	185	600	733	2381	4614	14995
0.25	0.4	3	84	155	333	613	2098	3859

Table 2 Continued.

			CV ≤ 0.26		CV ≤ 0.13		CV ≤ 0.05	
Ψ	*p*	*K*	S (*s*)	R (*s*)	S (*s*)	R (*s*)	S (*s*)	R (*s*)
0.25	0.4	4	62	81	244	318	1534	2002
0.25	0.4	5	54	60	212	236	1334	1486
0.35	0.2	2	732	6356	2904	25225	18290	158895
0.35	0.2	3	245	1447	972	5740	6122	36156
0.35	0.2	4	129	538	509	2132	3203	13429
0.35	0.2	5	84	257	331	1020	2085	6420
0.35	0.28	2	320	1814	1267	7197	7978	45333
0.35	0.28	3	115	409	454	1623	2858	10220
0.35	0.28	4	67	159	263	629	1657	3959
0.35	0.28	5	49	84	192	334	1208	2100
0.35	0.4	2	128	425	506	1683	3186	10601
0.35	0.4	3	56	106	221	421	1389	2647
0.35	0.4	4	40	53	157	210	986	1320
0.35	0.4	5	34	39	134	152	843	952

Table 3. Effort (*E*) requirements (no. sites * no. surveys * no. seasons) for a standard (S) and rotating-panel (RP) multi-season design when CV ≤ 0.26, 0.13, and 0.05, assuming occupancy (Ψ) values range from 0.05 – 0.35, detection probability (*p*) values range from 0.2 – 0.4, colonization = 0.005, local extinction = 0.2, and number of repeat surveys = 3. Occupancy, detection, colonization, and local extinction probabilities were estimated from 2007 and 2008 ruffed grouse drumming surveys in the Black Hills National Forest.

		CV ≤ 0.26		CV ≤ 0.13		CV ≤ 0.05	
Ψ	*p*	S (*E*)	RP (*E*)	S (*E*)	RP (*E*)	S (*E*)	RP (*E*)
0.05	0.2	7200	8100	48000	42300	240000	243000
0.05	0.28	5700	4950	24000	22500	121200	135000
0.05	0.4	4176	3600	21600	17100	108000	90000
0.12	0.2	3000	3150	14580	18000	72000	85500
0.12	0.28	2100	1944	9600	9000	51000	53100
0.12	0.4	1800	1575	7500	7200	41520	36000
0.25	0.2	1260	1404	7500	8100	36000	38250
0.25	0.28	804	774	3720	4050	21600	19350
0.25	0.4	636	540	3000	2700	16800	13500
0.35	0.2	840	954	3900	4410	27000	31500
0.35	0.28	528	540	2520	2700	14400	15300
0.35	0.4	372	360	2040	1800	10200	9450

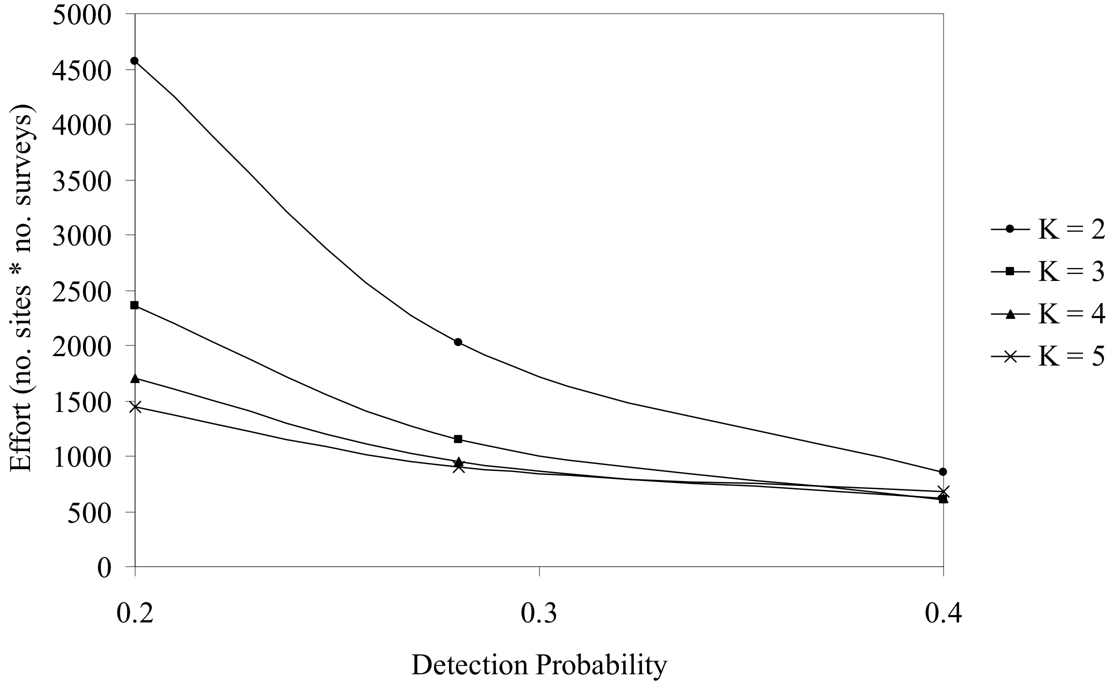
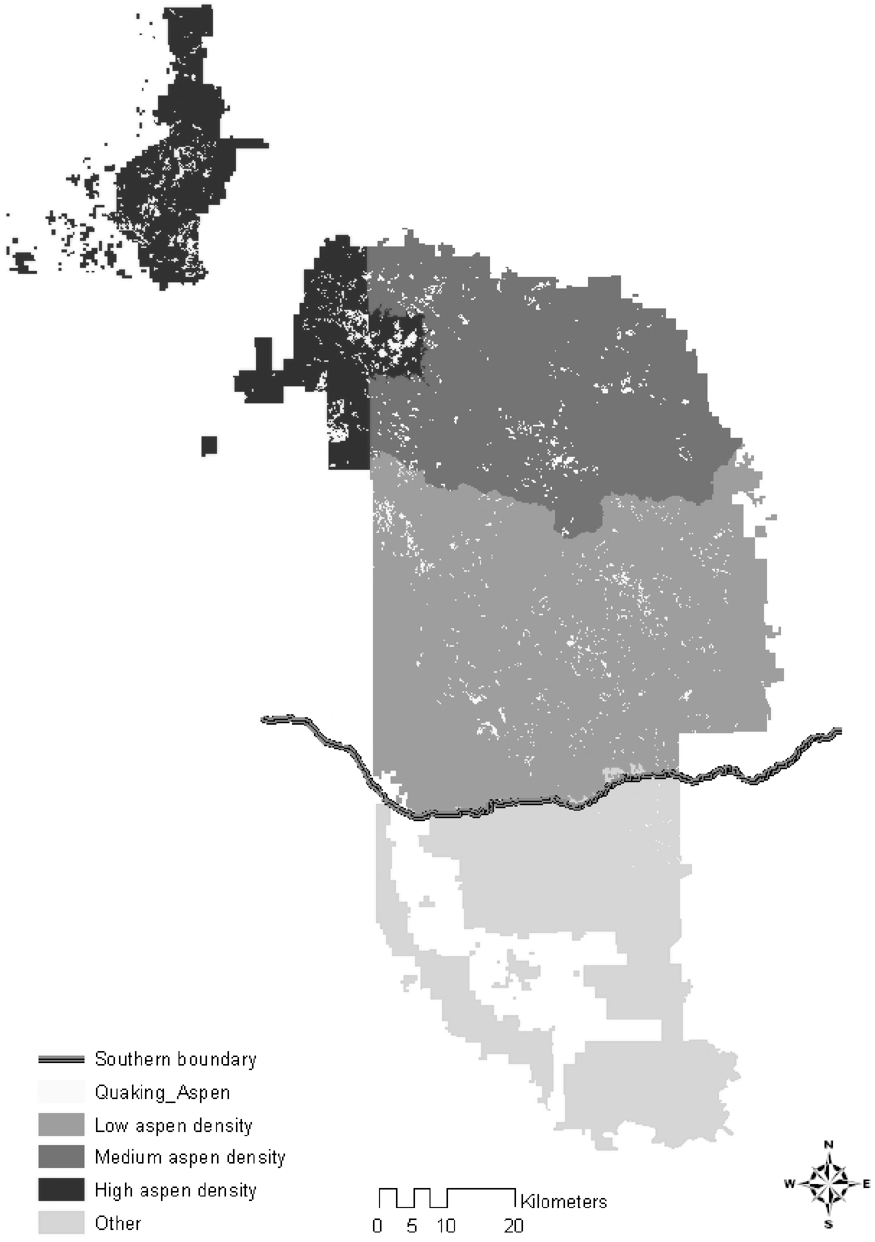


Figure 1. Influence of detection probability and the number of repeat surveys (*K*) on the required effort (no. sites * no. surveys) to achieve ruffed grouse occupancy estimates in the Black Hills National Forest using a standard single-season design, assuming a CV ≤ 0.26. Circles represent *K* = 2, squares represent *K* = 3, triangles represent *K* = 4, and crosses represent *K* = 5.

APPENDIX A. PHYSIOGRAPHIC STRATA IN THE BLACK HILLS NATIONAL FOREST



APPENDIX B. SURVEY SITES

Survey sites that were sampled at least 3 times each during spring 2007 and 2008 ruffed grouse drumming surveys in the Black Hills National Forest.

Strata	Region	Route	Site	UTM_East	UTM_North
High	BL	H17	H_0	546706	4933132
High	BL	H10	H_1	559467	4903268
High	NW	H5	H_10	581629	4909010
High	BL	H7	H_100	571965	4918210
High	NW	H2	H_101	573943	4903874
High	BL	H20	H_102	548454	4950335
High	BL	H14	H_107	541355	4933705
High	BL	H17	H_108	547249	4934825
High	BL	H13	H_109	538334	4930583
High	BL	H14	H_11	541266	4937794
High	BL	H20	H_111	548687	4952679
High	BL	H3	H_114	566831	4906745
High	BL	H10	H_115	559201	4907096
High	BL	H14	H_116	540992	4935831
High	NW	H5	H_117	583424	4914497
High	BL	H7	H_119	567957	4922052
High	BL	H3	H_12	567071	4908465
High	BL	H11	H_121	547417	4923205

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
High	BL	H16	H_122	554847	4935764
High	BL	H20	H_124	550639	4950124
High	NW	H1	H_126	571506	4900597
High	NW	H1	H_128	571753	4896403
High	BL	H18	H_13	553134	4939327
High	BL	H19	H_131	550271	4946512
High	NW	H1	H_134	571170	4892597
High	BL	H18	H_135	555074	4940278
High	BL	H10	H_136	557923	4903959
High	NW	H4	H_137	571832	4908837
High	BL	H6	H_14	573552	4918453
High	BL	H20	H_140	553274	4947585
High	BL	H16	H_141	550821	4937061
High	NW	H5	H_142	578104	4912916
High	BL	H3	H_143	564423	4911387
High	BL	H14	H_145	540304	4931116
High	BL	H9	H_146	573138	4911292
High	BL	H21	H_147	548663	4956769
High	NW	H4	H_148	577064	4911610
High	BL	H3	H_15	568771	4907085

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
High	BL	H7	H_151	568540	4924102
High	BL	H21	H_152	550882	4956559
High	BL	H3	H_153	568095	4905317
High	NW	H4	H_154	573505	4909400
High	BL	H21	H_156	549678	4955264
High	BL	H14	H_158	543608	4939274
High	NW	H4	H_159	579240	4909434
High	NW	H2	H_16	572734	4901993
High	BL	H10	H_160	560036	4911206
High	BL	H3	H_161	564492	4909427
High	BL	H18	H_162	548732	4942577
High	BL	H20	H_164	551911	4948536
High	BL	H15	H_165	546288	4939467
High	BL	H16	H_166	553044	4931407
High	BL	H10	H_168	562309	4905971
High	NW	H5	H_169	577537	4914651
High	BL	H20	H_170	550471	4953330
High	BL	H21	H_171	551993	4958151
High	BL	H11	H_173	541793	4922252
High	BL	H17	H_174	543841	4929345

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
High	BL	H11	H_176	548780	4921557
High	NW	H5	H_177	580937	4914711
High	NW	H2	H_179	573254	4905559
High	BL	H17	H_18	542305	4928268
High	BL	H12	H_180	546037	4928810
High	NW	H1	H_182	569610	4899377
High	NW	H4	H_19	575193	4907502
High	BL	H15	H_20	543696	4936709
High	BL	H10	H_21	560488	4906193
High	NW	H5	H_22	582323	4913029
High	BL	H21	H_23	551280	4960002
High	BL	H10	H_24	559742	4909414
High	BL	H9	H_25	567255	4912017
High	BL	H20	H_26	550249	4948158
High	BL	H14	H_27	542061	4930648
High	NW	H2	H_28	573712	4897311
High	NW	H1	H_3	570972	4894850
High	NW	H4	H_31	572679	4907411
High	NW	H1	H_32	570597	4898398
High	BL	H9	H_33	569668	4909929

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
High	BL	H12	H_35	544921	4925684
High	BL	H18	H_36	550358	4938945
High	BL	H17	H_37	546407	4930570
High	BL	H8	H_38	569010	4915587
High	NW	H1	H_4	575018	4894768
High	BL	H12	H_40	548790	4924575
High	BL	H6	H_42	574911	4916676
High	NW	H2	H_43	573091	4900297
High	BL	H18	H_44	550454	4941373
High	BL	H21	H_45	547367	4954824
High	BL	H16	H_46	547542	4929320
High	NW	H2	H_47	570137	4904080
High	BL	H13	H_48	539864	4928940
High	BL	H10	H_49	557706	4906222
High	BL	H12	H_5	544007	4927278
High	BL	H15	H_50	543133	4934455
High	BL	H3	H_51	564332	4907441
High	BL	H9	H_52	565667	4913363
High	BL	H13	H_53	541526	4925949
High	BL	H11	H_54	545939	4920408

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
High	NW	H5	H_55	583094	4911376
High	BL	H8	H_56	571064	4912207
High	BL	H16	H_58	552839	4933109
High	BL	H21	H_59	549625	4958124
High	BL	H12	H_6	547049	4927322
High	NW	H2	H_60	570527	4906459
High	BL	H6	H_61	574511	4922644
High	BL	H8	H_62	570220	4913686
High	NW	H1	H_63	573372	4893802
High	BL	H14	H_64	543554	4932378
High	BL	H15	H_65	545802	4933828
High	NW	H4	H_67	576423	4908965
High	BL	H16	H_68	552476	4937066
High	BL	H7	H_69	571573	4922398
High	BL	H16	H_70	548924	4930539
High	BL	H8	H_71	568049	4913367
High	BL	H17	H_72	548253	4937685
High	BL	H3	H_73	564697	4905216
High	BL	H7	H_74	570534	4921211
High	NW	H2	H_75	575113	4905531

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
High	BL	H15	H_76	545529	4932055
High	BL	H11	H_77	548687	4919844
High	BL	H6	H_78	575387	4913298
High	NW	H5	H_8	579180	4914359
High	BL	H16	H_80	549742	4934814
High	BL	H16	H_82	550989	4931977
High	NW	H4	H_83	578683	4907888
High	BL	H19	H_84	553777	4945311
High	NW	H1	H_86	570100	4902282
High	BL	H8	H_87	566806	4918398
High	BL	H8	H_88	569350	4911997
High	BL	H12	H_89	545183	4923915
High	NW	H2	H_9	571996	4904258
High	BL	H11	H_92	545158	4922256
High	BL	H19	H_93	552519	4945540
High	BL	H18	H_94	551387	4942917
High	NW	H4	H_96	574790	4910849
High	NW	H5	H_98	580614	4910641
High	BL	H6	H_99	575091	4920947
Low	SW	L10	L_0	582365	4863400

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Low	SW	L8	L_10	580824	4888263
Low	SW	L12	L_100	592716	4874143
Low	SE	L21	L_102	624603	4879583
Low	SW	L30	L_103	594198	4881839
Low	SW	L30	L_104	592012	4879990
Low	SE	L22	L_105	627870	4887619
Low	SE	L23	L_106	630641	4873423
Low	SW	L16	L_107	599933	4858021
Low	SE	L27	L_108	619455	4869585
Low	SE	L1	L_109	617815	4849060
Low	SW	L10	L_11	577059	4861980
Low	SW	L7	L_111	586329	4854511
Low	SW	L3	L_112	602871	4849564
Low	SE	L24	L_113	624835	4866153
Low	SW	L5	L_114	586485	4843873
Low	SW	L13	L_115	596047	4869393
Low	SW	L7	L_116	584740	4857507
Low	SE	L2	L_117	607049	4848700
Low	SE	L28	L_118	609026	4879542
Low	SW	L5	L_119	584359	4844949

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Low	SE	L20	L_12	625702	4886217
Low	SE	L1	L_120	616186	4849890
Low	SE	L23	L_121	631384	4876755
Low	SE	L29	L_122	609763	4867414
Low	SE	L21	L_123	620966	4881839
Low	SE	L19	L_124	612113	4881065
Low	SE	L24	L_125	633316	4865795
Low	SW	L14	L_126	595089	4861300
Low	SW	L17	L_127	601694	4865725
Low	SW	L17	L_128	600648	4863125
Low	SW	L11	L_129	585058	4882972
Low	SW	L10	L_13	578483	4865524
Low	SW	L13	L_130	594740	4872952
Low	SW	L9	L_131	577029	4870470
Low	SW	L7	L_132	586070	4856588
Low	SW	L11	L_133	587324	4882712
Low	SE	L20	L_14	620084	4886202
Low	SE	L24	L_15	628219	4865893
Low	SW	L7	L_16	582621	4858397
Low	SW	L4	L_18	596835	4844717

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Low	SW	L8	L_19	576774	4889438
Low	SE	L23	L_2	629247	4875417
Low	SW	L13	L_20	592913	4868231
Low	SW	L12	L_21	592559	4872493
Low	SW	L8	L_22	577199	4882386
Low	SE	L1	L_23	619993	4848592
Low	SW	L30	L_24	600776	4884552
Low	SE	L18	L_25	600688	4879502
Low	SW	L5	L_26	588722	4842642
Low	SW	L6	L_27	583346	4853882
Low	SE	L21	L_3	622585	4880514
Low	SW	L15	L_30	592228	4857340
Low	SW	L9	L_31	581631	4874667
Low	SW	L10	L_32	577945	4856913
Low	SE	L2	L_33	606547	4846792
Low	SE	L27	L_35	616452	4873825
Low	SE	L24	L_36	629944	4868702
Low	SE	L19	L_37	612746	4886914
Low	SW	L3	L_38	600338	4850252
Low	SW	L15	L_39	595569	4856275

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Low	SW	L8	L_4	584166	4887818
Low	SE	L25	L_40	632705	4853778
Low	SE	L18	L_41	600950	4877333
Low	SW	L9	L_42	582502	4870817
Low	SW	L5	L_43	588826	4848004
Low	SE	L19	L_44	610869	4885419
Low	SE	L2	L_45	609556	4846911
Low	SW	L10	L_46	578403	4868323
Low	SW	L15	L_47	589399	4860631
Low	SE	L2	L_48	609253	4850697
Low	SW	L11	L_49	590558	4883686
Low	SE	L2	L_5	607074	4852705
Low	SW	L9	L_50	579593	4876524
Low	SW	L14	L_51	588843	4863854
Low	SE	L29	L_52	606313	4861000
Low	SW	L16	L_54	597870	4854180
Low	SW	L16	L_55	599309	4855062
Low	SE	L2	L_58	604603	4849448
Low	SE	L29	L_59	610240	4864700
Low	SE	L29	L_6	604842	4866783

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Low	SW	L12	L_60	589123	4871559
Low	SE	L23	L_61	630453	4870474
Low	SW	L13	L_62	597332	4867092
Low	SW	L9	L_64	579895	4872759
Low	SE	L20	L_66	615700	4886616
Low	SW	L9	L_68	577154	4876521
Low	SW	L10	L_69	579249	4858699
Low	SW	L12	L_7	589789	4875759
Low	SW	L4	L_70	599930	4845780
Low	SE	L27	L_71	618763	4871522
Low	SW	L15	L_72	594038	4858579
Low	SW	L6	L_73	581057	4852368
Low	SW	L14	L_74	590622	4863303
Low	SE	L19	L_76	617466	4879615
Low	SW	L15	L_77	594941	4854487
Low	SW	L11	L_78	587212	4886379
Low	SE	L28	L_79	611994	4875295
Low	SW	L5	L_8	587420	4846391
Low	SE	L26	L_80	613734	4862499
Low	SE	L20	L_82	622976	4886248

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Low	SW	L11	L_83	589690	4881821
Low	SE	L19	L_84	611015	4886853
Low	SW	L7	L_86	584495	4859986
Low	SE	L25	L_87	629133	4854779
Low	SE	L19	L_88	612412	4883697
Low	SW	L8	L_89	576739	4887047
Low	SE	L29	L_9	604742	4870069
Low	SE	L25	L_90	630930	4863403
Low	SE	L23	L_91	624641	4874984
Low	SE	L23	L_92	632923	4875103
Low	SW	L3	L_93	603890	4846134
Low	SE	L29	L_94	605439	4864034
Low	SE	L18	L_96	604090	4874787
Low	SW	L14	L_97	592754	4859998
Low	SE	L29	L_99	606403	4865416
Medium	NW	M23	M_1	584182	4910122
Medium	NE	M10	M_10	612551	4891646
Medium	NW	M29	M_100	601562	4916916
Medium	NE	M21	M_101	613824	4913209
Medium	NE	M10	M_102	606282	4893423

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Medium	NE	M31	M_103	620880	4898758
Medium	NW	M2	M_104	589581	4892012
Medium	NE	M14	M_105	607110	4898973
Medium	NE	M14	M_106	611239	4898167
Medium	NE	M11	M_109	620207	4888601
Medium	NW	M23	M_110	583842	4904929
Medium	NW	M1	M_111	581859	4893327
Medium	NE	M16	M_112	622235	4901121
Medium	NE	M12	M_113	619891	4894861
Medium	NW	M30	M_114	593685	4900061
Medium	NE	M18	M_115	616535	4910550
Medium	NW	M6	M_116	590351	4903705
Medium	NE	M12	M_117	612383	4896289
Medium	NE	M21	M_118	613878	4916265
Medium	NE	M16	M_120	618463	4901682
Medium	NW	M2	M_121	587209	4889616
Medium	NE	M15	M_122	618330	4899426
Medium	NW	M26	M_123	579951	4924419
Medium	NW	M2	M_124	590326	4890318
Medium	NE	M10	M_125	612764	4892836

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Medium	NE	M22	M_126	593536	4893739
Medium	NE	M15	M_127	614198	4902680
Medium	NE	M12	M_129	614625	4894519
Medium	NW	M4	M_13	589244	4893840
Medium	NE	M7	M_131	610220	4888938
Medium	NW	M4	M_132	586278	4897660
Medium	NW	M26	M_133	580222	4922260
Medium	NE	M19	M_134	612383	4905721
Medium	NE	M3	M_135	598861	4887557
Medium	NW	M1	M_137	575888	4901028
Medium	NW	M1	M_138	582460	4895329
Medium	NE	M20	M_14	610635	4916403
Medium	NW	M26	M_140	579407	4916391
Medium	NE	M16	M_141	623543	4900459
Medium	NE	M14	M_144	609109	4901542
Medium	NW	M24	M_145	593335	4905924
Medium	NE	M13	M_147	605057	4902936
Medium	NE	M21	M_148	614773	4915104
Medium	NE	M13	M_149	604276	4901092
Medium	NW	M30	M_15	596507	4899227

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Medium	NW	M6	M_150	588419	4902974
Medium	NW	M28	M_151	592043	4914133
Medium	NE	M7	M_152	606326	4885067
Medium	NW	M5	M_153	580368	4904295
Medium	NW	M27	M_154	588321	4919729
Medium	NE	M7	M_156	608973	4885838
Medium	NW	M5	M_157	577239	4906145
Medium	NE	M18	M_16	616451	4912411
Medium	NW	M2	M_160	586237	4892292
Medium	NE	M12	M_161	622227	4895529
Medium	NW	M24	M_162	595305	4902627
Medium	NE	M31	M_164	629360	4896361
Medium	NE	M15	M_165	615720	4901704
Medium	NE	M11	M_166	622875	4892592
Medium	NE	M13	M_167	605799	4897484
Medium	NE	M19	M_168	608187	4909238
Medium	NW	M27	M_169	586331	4923454
Medium	NW	M26	M_17	580182	4920603
Medium	NW	M30	M_170	597331	4901836
Medium	NE	M9	M_171	597078	4896173

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Medium	NW	M30	M_172	598661	4898180
Medium	NE	M19	M_173	608207	4904607
Medium	NE	M17	M_174	618863	4905700
Medium	NW	M27	M_175	584609	4922160
Medium	NW	M4	M_176	586013	4894410
Medium	NW	M29	M_178	599162	4916707
Medium	NW	M1	M_18	579847	4895157
Medium	NW	M25	M_180	581763	4921718
Medium	NE	M31	M_181	622622	4899009
Medium	NW	M4	M_182	585652	4896319
Medium	NE	M11	M_183	619020	4890662
Medium	NE	M11	M_184	625379	4890795
Medium	NE	M18	M_19	621416	4912500
Medium	NE	M9	M_21	603636	4895500
Medium	NE	M9	M_22	601438	4896895
Medium	NE	M19	M_23	606863	4907042
Medium	NW	M24	M_24	600595	4906240
Medium	NE	M12	M_25	618423	4892647
Medium	NE	M10	M_26	610624	4894553
Medium	NE	M17	M_28	615968	4907985

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Medium	NE	M8	M_29	599764	4893472
Medium	NE	M21	M_3	611335	4910292
Medium	NW	M5	M_30	580162	4902159
Medium	NE	M13	M_31	601385	4903176
Medium	NW	M25	M_32	583716	4924280
Medium	NW	M25	M_33	581849	4916572
Medium	NW	M24	M_34	597218	4903811
Medium	NW	M25	M_35	583900	4912927
Medium	NE	M21	M_36	612872	4910774
Medium	NE	M22	M_38	590474	4896347
Medium	NE	M13	M_39	601096	4899879
Medium	NE	M10	M_4	614661	4888902
Medium	NE	M7	M_41	608203	4883176
Medium	NW	M4	M_42	587509	4896420
Medium	NE	M9	M_43	599739	4896006
Medium	NE	M8	M_44	602544	4889012
Medium	NE	M31	M_45	627316	4896994
Medium	NW	M23	M_46	583772	4908124
Medium	NE	M7	M_48	607565	4890375
Medium	NW	M28	M_49	592303	4919916

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Medium	NE	M8	M_5	601557	4890735
Medium	NE	M9	M_50	603264	4897642
Medium	NW	M6	M_51	589696	4901869
Medium	NE	M10	M_52	609147	4892585
Medium	NE	M3	M_53	599065	4890696
Medium	NW	M28	M_55	595909	4915487
Medium	NE	M3	M_56	600949	4886922
Medium	NE	M20	M_57	609657	4919675
Medium	NW	M26	M_58	579646	4918793
Medium	NW	M24	M_59	592737	4904320
Medium	NE	M19	M_6	606261	4904027
Medium	NW	M27	M_60	586589	4918753
Medium	NW	M23	M_61	587656	4904491
Medium	NW	M23	M_62	584655	4906328
Medium	NE	M3	M_64	593014	4889212
Medium	NE	M21	M_65	610290	4907296
Medium	NW	M2	M_66	584502	4892856
Medium	NE	M22	M_67	591840	4894878
Medium	NE	M13	M_68	603711	4903478
Medium	NE	M9	M_69	596123	4894577

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Medium	NE	M15	M_7	615737	4899498
Medium	NE	M22	M_70	591977	4897408
Medium	NE	M7	M_71	609161	4887878
Medium	NE	M14	M_72	615590	4896450
Medium	NE	M10	M_73	610535	4892366
Medium	NE	M17	M_74	623105	4904901
Medium	NE	M17	M_77	621143	4907171
Medium	NE	M10	M_78	609277	4894746
Medium	NW	M29	M_79	602231	4920416
Medium	NW	M6	M_8	587298	4901343
Medium	NE	M14	M_80	613881	4899091
Medium	NE	M14	M_81	608410	4902487
Medium	NE	M11	M_82	621606	4890396
Medium	NE	M18	M_83	615888	4909457
Medium	NE	M12	M_85	616379	4893278
Medium	NW	M1	M_87	575562	4898049
Medium	NW	M4	M_88	587558	4893512
Medium	NE	M7	M_89	603866	4888169
Medium	NE	M8	M_91	603957	4891564
Medium	NW	M24	M_92	599302	4905049

APPENDIX B CONTINUED.

Strata	Region	Route	Site	UTM_East	UTM_North
Medium	NW	M6	M_94	591292	4899643
Medium	NE	M20	M_95	610210	4913550
Medium	NE	M12	M_97	624906	4894096
Medium	NE	M11	M_98	622152	4887960

APPENDIX C. OCCUPANCY EXCEL SPREADSHEET OVERVIEW

The occupancy modeling spreadsheet program uses a maximum likelihood estimation approach and multinomial likelihood framework to calculate single season occupancy and detection probability estimates for ruffed grouse in the Black Hills National Forest (BHNF) using detection histories and covariate values. The model is run through Microsoft Excel 2003 (XP) and the majority of functions are executed using Visual Basic for Applications (VBA) code in modules attached to the Excel workbook. All parameters included in the model (e.g., date, wind speed, amount of aspen, spruce, pine, and saplings with > 70% canopy cover) are the parameters that were most influential on occupancy and detection probability during 2007 and 2008 spring drumming surveys (Chapter 1).

Occupancy models assume the species of interest is detected imperfectly. (MacKenzie et al. 2002). Thus, to estimate occupancy accurately, repeat surveys are necessary at each site to obtain estimates of detection probability (assuming occupancy of the species is "closed" throughout all repeat surveys). Collectively, repeat visits for a site are termed "detection histories." To begin the program, the user must enter the detection histories for each site, entering a "1" if a ruffed grouse was detected at the site during the specific survey, a "0" if a ruffed grouse was not detected, or a "-" if a survey was missed or a site was not surveyed. The program allows the user to visit up to 402 sites and perform 4 repeat surveys at each site.

Next, the user must enter covariate values for each survey and site. For each survey, the user must enter the date (m/d/yyyy) and the average wind speed (km/hr) during the survey. In a separate worksheet, the program automatically changes the date into a Julian date, and then standardizes both the Julian date and wind speed into Z-scores. For each site, the user must enter the hectares of aspen, spruce, pine, and saplings with > 70% canopy cover within 550 meters of the site. This information can be obtained using ArcGIS and BHNF vegetation layers, which are located on the BHNF website (http://www.fs.fed.us/r2/blackhills/projects/gis/index.shtml). Once entered, these data are also automatically standardized into Z-scores.

Once covariate values have been entered, the user may choose whether to calculate a constant occupancy, occupancy as a function of physiographic strata, or occupancy as a function of covariates. Additionally, the user may select to view an occupancy and detection probability trend graph and add the current season's occupancy and detection probability values to the graph. Last, the user may calculate the required number of sites to sample the following season, given the occupancy estimates from the current season and a desired precision. If the user selects "calculate constant occupancy", then occupancy and detection probabilities are calculated, assuming both metrics are constant across the BHNF (i.e., no covariates included). If the user selects "calculate occupancy as a function of strata", then unique occupancy probabilities are calculated for high, medium, and low strata, and detection probabilities are calculated as a function of covariates (e.g., Julian date [quadratic form] and wind speed). If the user selects "calculate occupancy as a function of covariates", then site-specific occupancy probabilities and survey-specific detection probabilities are calculated. Under this option, the user may view detection probability graphs, which display at what dates and wind speeds the probability of detecting a ruffed grouse were maximized. The user may also view the site-specific occupancy values and an occupancy probability distribution graph, which displays the frequency of sites predicted to be in different ranges of occupancy values. Finally, if the user selects “calculate sampling requirements for next season”, the user is given the option to choose between three precisions: CV ≤ 0.26, CV ≤ 0.13, CV ≤ 0.05, representing “rough”, “accurate”, and “precise” management, respectively (Robson and Regier 1964, Skalski and Millspaugh 2002). When one of these options is selected, the user is provided with the necessary number of sites to survey in each physiographic strata, dependent upon the number of repeat surveys completed. Site requirements for the following season are calculated based upon the occupancy and detection probability estimates for the current season.

CHAPTER III

RUFFED GROUSE SELECTION OF ACTIVITY CENTERS IN THE BLACK HILLS NATIONAL FOREST

ABSTRACT

Ruffed grouse (*Bonasa umbellus*) are the management indicator species for quaking aspen (*Populus tremuloides*) in the Black Hills National Forest (BHNF). Given this status and their importance as a game species, there is a vested interest by management agencies to identify resource needs of ruffed grouse in the BHNF. Recent broad-scale surveys demonstrated that ruffed grouse occupancy in the BHNF is primarily dependent on the extent of aspen vegetation; however, a micro-scale investigation of breeding territory selection is lacking. To evaluate ruffed grouse selection of breeding territories, we located primary ruffed grouse drumming structures throughout the BHNF in 2007 and 2008. We located and measured 49 drumming sites (activity centers) and 147 random sites located between 50 and 300 meters from activity center. We then evaluated which resource characteristics of activity centers were related to selection. Visibility above 0.9 m around the drumming structure and the density of stems (i.e., vegetation < 2.54 cm in diameter) ≥ 1 m tall were most correlated with activity center selection. Increasing visibility above 0.9 m around the drumming structure from 15% to 40% decreased the probability of activity center selection by 12%. Although the density of stems ≥ 1 m tall did not have a strong relationship with activity center selection at lower stem densities ($<$ 60,000 stems/hectare), increasing the density of stems from 60,000 stems/hectare to 80,000 stems/hectare increased the probability of selection by 43.8%. Ruffed grouse

breeding territory selection may be correlated with both large-scale and small-scale vegetative attributes. The extent of aspen drove large-scale ruffed grouse occupancy at the population level; however, small-scale selection of activity centers at the individual level was most related to visibility and cover above 1 meter height. Thus, management actions should focus on encouraging ruffed grouse at both the population and individual level by increasing early succession forests of aspen.

INTRODUCTION

Ruffed grouse (*Bonasa umbellus*) are important game birds and the management indicator species for quaking aspen (*Populus tremuloides*) in the Black Hills National Forest (BHNF [U. S. Forest Service 1997]) because of their association with aspen (*Populus* spp.) communities (Bump et. al. 1947, Gullion and Svoboda 1972, Kubisiak 1989, Kubisiak 1985). Due to this status, there has been interest by the U.S. Forest Service and South Dakota Department of Game, Fish, and Parks to assess the status of ruffed grouse in the BHNF, as well as to determine whether ruffed grouse are selecting breeding territories based on aspen availability or other large- or small-scale vegetative attributes. Recent ruffed grouse drumming surveys demonstrated that ruffed grouse occupancy throughout the BHNF was low and primarily dependent on the extent of aspen (Chapter 1). However, results from those surveys also demonstrated that ruffed grouse are not aspen obligates in the BHNF because ruffed grouse occupied vegetation types other than aspen (e.g., white spruce [*Picea glauca*]) (Chapter 1). This finding could be a result of the limited availability of aspen in the BHNF (Hoffman and Alexander 1987) or a more complex form of territory selection that may be dependent on both large-scale vegetative characteristics (e.g., the extent of aspen) and small scale, drumming site attributes (Rusch et al. 2000, Zimmerman and Gutiérrez 2008).

During the spring, male ruffed grouse "drum" on elevated structures (e.g., fallen logs, stumps, rocks) to attract females and maintain their territory (Bump et al. 1947). The male grouse drums consistently on the structure every 3-5 minutes throughout the early morning hours (Bump et al. 1947, Archibald 1976), making it especially susceptible to predation (Rusch et al. 2000). Ruffed grouse are typically faithful to one "primary" structure and, occasionally, use 1-5 "alternate" structures within 100 m of the primary structure (Bump et al. 1947, Gullion 1967, Archibald 1974, Kubisiak 1989, Lovallo 2000). The area around the primary and alternate structures has been termed the "activity center" (Gullion 1967) because it is the central area of intensive drumming and breeding activity of male grouse during spring. Ruffed grouse select activity centers that will increase their probability of attracting a female (Johnsgard 1989, McBurney 1989) and decrease the probability of predation (Boag and Sumanik 1969, Stoll et al. 1979, Hale et al. 1982, Buhler and Anderson 2001, Haulton et. al. 2003). Thus, selection of optimal activity centers may be of primary importance when ruffed grouse establish breeding territories.

Studies have investigated the selection of ruffed grouse activity centers in the east (Stoll et al. 1979, Hale et al. 1982), midwest (Palmer 1963, Gullion 1967, Thompson et al. 1987, Zimmerman and Gutiérrez 2008), and west (Stauffer and Peterson 1985, Buhler and Anderson 2001) United States, as well as Alberta (Boag and Sumanik 1969, Boag 1976). All these studies demonstrated that vegetative characteristics, and predominately those associated with the amount of understory cover around the drumming structure, were correlated with site selection. However, these studies reported differences associated with the importance of several drumming structure characteristics, such as structure height and diameter. No research has been conducted in the BHNF to determine what drumming site characteristics are associated with ruffed grouse selection of activity centers. Because ruffed grouse occupied varying vegetative communities in the BHNF (Chapter 1) and different cover types and vegetative species were available to ruffed grouse than in other regions of their range, it is necessary to determine whether similar patterns of selection hold for ruffed grouse activity center selection in the BHNF.

Our objective was to determine resource selection of ruffed grouse activity centers in the BHNF. Understanding the relationship between activity center selection and micro-site vegetation characteristics are important complements to large-scale investigations of occupancy research (Chapter 1).

STUDY AREA

The BHNF was located in the western portion of South Dakota and included the Bear Lodge Mountains of northeastern Wyoming. Elevation ranged from 1,066 m – 2,207 m. Annual rainfall in the BHNF exceeded 50.8 cm per year and varied with elevation (Ball et. al. 1996). The BHNF included 500,000 ha of a variety of vegetation types, consisting primarily of ponderosa pine (*Pinus ponderosa,* 84%), quaking aspen/paper birch (*Betula papyrifera,* 4%), and white spruce (2%). Bur oak (*Quercus macrocarpa*), hop-hornbeam (*Ostrya virginiana*), and green ash (*Fraxinus pennsylvanica*) also occupied the BHNF, comprising < 10% (Hoffman and Alexander 1987, Froiland 1990). Common shrubs included western snowberry (*Symphoricarpos occidentalis*), white coralberry (*S. albus*), kinnikinnick (*Arctostaphylos uvaursi*), and common juniper (*Juniperus comunis*) (Hoffman and Alexander 1987, Severson and Thilenius 1976).

METHODS

Field Methods

During spring 2007 and 2008, we completed ruffed grouse drumming surveys throughout the northern two-thirds of the BHNF (Chapter 1). When a ruffed grouse drum was heard during a survey, the observer recorded the azimuth and approximate distance to the drumming grouse, completed the 5 minute survey, and began searching for the grouse. As the observer approached the drumming grouse, extreme caution was made not to drive the grouse off its primary drumming structure before the grouse was observed. In addition to locating drumming structures during surveys, we opportunistically located 6 structures. We did not re-measure drumming structures that were used both years, thus we considered each drumming structure an independent sample.

Before we began measuring vegetation around drumming structures, we ensured complete foliar development to prevent incorrectly measuring horizontal or vertical cover because we assumed ruffed grouse established activity centers during autumn, when vegetation had complete foliage (McBurney 1989). The first date we began measurements was 17 May in 2007 and 8 June in 2008. All activity centers were measured during the same season as they were located except for 12, which were located during spring 2007 and measured during autumn 2007. We assumed vegetation would not significantly change until late autumn, thus, the latest we measured an activity center was 11 October 2007, before the deciduous plants lost their foliage.

At each activity center, we measured characteristics of the drumming structure and adjacent vegetation. The majority of activity centers (*n* = 46) and random sites (*n* = 138) were measured by the same observer. We used digital voice recording (DVR) systems to record data to maximize efficiency while measuring vegetation (Rumble et al. 2009). We transcribed data from the DVR into a text file using voice recognition software Dragon Naturally Speaking 7.3 (Nuance Communications, Inc. 2003, 1 Wayside Road, Burlington, MA). We later translated text files into a format compatible with Microsoft Excel using Act Naturally (Thomas M. Juntti 1999, 502 E College Ave, Rapid City, SD 547701).

We began drumming structure measurements by counting the number of droppings on the structure to ensure it was the "primary" structure. We assumed a structure with ≥ 20 droppings had been visited for an extended period of time by a ruffed grouse (Gullion 1967) and was classified as a primary structure. We considered structures with fewer than 20 droppings as alternate structures. Once a structure was classified as primary, we recorded the site number, date, observer name, and universal transverse mercator (UTM) coordinates (using a global positioning system [GPS]) at the drumming stage. We then recorded the type (i.e., log, stump, rock, etc.) and species of the structure, diameter and height (cm) at the drumming stage, length (cm) of the structure, number branches longer than 15 cm on the structure, percent bark on the structure (assuming it was a log or stump), azimuth and percent slope (using a clinometer) the drumming grouse faced, and percent canopy cover (using a spherical densiometer) directly above the drumming stage. We recorded structure type, species, and percent bark as categorical variables, while the other measurements were recorded as continuous variables (Table 1).

We began measuring adjacent vegetative characteristics in the activity center by estimating the “visibility” surrounding the drumming stage. We chose an adaptation of the design described by Nudds (1977) and Hale et al. (1982), creating a cover board that was 1.2 m wide and 1.8 m tall. The board was partitioned into 6 sections, representing vegetation cover from 0-0.3, 0.3-0.6, 0.6-0.9, 0.9-1.2, 1.2-1.5, and 1.5-1.8 meters in height. Each section contained 144 black dots equally spaced 5.0 cm apart. We deviated from the designs presented by Nudds (1977) and Hale et al. (1982) because vegetation around ruffed grouse drumming structures was dense, necessitating the use of a larger, more detailed cover board. To estimate visibility, we placed the cover board directly in front of the drumming stage and counted the number of visible dots at a distance of 5 m from the structure, then repeated these methods for each cardinal direction. We later added the number of dots visible in each unique section across cardinal directions to determine the percent visibility at different heights around the drumming structure.

Second, we estimated stem (i.e., vegetation with a diameter < 2.54 cm) density using 1 m^2 plots spaced 2 m apart in 4 transects around the drumming structure. We measured 6 plots in each transect, which began 2 m away from the drumming structure, in each cardinal direction. Ruffed grouse typically select activity centers with a dense understory and little ground cover (Barber et al. 1989, Haulton et. al. 2003, Tirpak et al. 2006); thus, we separately counted the number of stems (both woody and herbaceous, excluding grasses) 15 cm < height < 1 m and the number of woody and herbaceous stems ≥ 1 m.

Third, we calculated the percent canopy cover within the activity center, using a densiometer. In 4 transects representing the 4 cardinal directions, we recorded a “hit” or “miss” (i.e., whether canopy foliage crossed the center of the densitometer) every meter for 12 m. Later, we counted the number of “hits” throughout the 48 stops within the activity center and divided the number of “hits” by 48 to obtain a canopy cover percent.

Last, we measured vegetation > 2.54 cm diameter at breast height (DBH [1.37 m]) within a 12.5 m, fixed-radius plot with the drumming stage as the center. For each tree ≥ 10 cm DBH, we recorded species, DBH, and condition (i.e., alive or dead). For each tree 2.54 < DBH < 10 cm (hereby referred to as saplings), we recorded only the species and condition. We calculated basal area (only including trees ≥ 10 cm DBH) using the DBH data. We calculated total basal area (i.e., basal area of all trees) and basal area of quaking aspen, white spruce, and ponderosa pine because these were the most abundant tree species in the BHNF (Hoffman and Alexander 1987). Additionally, we calculated both total sapling density (no./ha) and sapling density by species (aspen, spruce, and pine).

After completing measurements in the activity center, we performed measurements at 3 random locations for each used site. We identified random locations, without replacement, using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) or a random number generator to determine the direction and distance from the original structure. All random sites associated with an activity center were placed within “available” habitat. We conservatively estimated that a 300 m territory was available to male ruffed grouse (Kubisiak 1989). Additionally, alternate drumming structures are typically located within 50 m and rarely further than 90 m from the primary structure (Lovallo et al. 2000, Hansen personal observation). To avoid selecting an alternate structure, we constrained our random locations between 50 and 300 m from the primary structure. Upon arriving at a random location, we located the nearest elevated structure (e.g., log or stump) and searched the structure for ruffed grouse droppings to ensure a ruffed grouse was not using the structure. We only selected random structures that were at least 10 cm in diameter because we assumed structures smaller than 10 cm would not be suitable for drumming. Additionally, we did not select any structures without canopy or vegetative cover (e.g., structures in a field) because we also believed these locations were unsuitable. We measured the distance from the drumming stage to the end of the primary structure and used this distance to identify the drumming stage on the random structure. Once the structure and drumming stage were identified, we completed the same structure and vegetative measurements described above.

A Priori **Model Development**

We developed a set of *a priori* hypotheses to evaluate the relationship of drumming structure and adjacent vegetation characteristics on ruffed grouse selection of activity centers in the BHNF. We developed 19 candidate models; 18 which assumed selection was a function of a combination of 20 covariates and 1 which assumed selection was random (Model 1, Appendix).

Structure Covariates.— Ruffed grouse select drumming structures that increase their probability of attracting mates and that provide adequate cover from predators (Johnsgard 1989, McBurney 1989) so we developed models analyzing these hypotheses. To attract female ruffed grouse, male ruffed grouse drum and strut on structures (e.g., logs, stumps, rocks, [Bump et al. 1947, Johnsgard 1989]). The height and slope of the drumming structure might allow the sound of the drum to carry further, thereby attracting females at a greater distance (Buhler and Anderson 2001, Zimmerman and Gutiérrez 2008). Consequently, we developed 4 models (Models 2, 3, 9, 10) to evaluate the relationship of height and slope with drumming log selection, assuming slope had a quadratic relationship. Additionally, the diameter, age, and length of structures possibly correlate with selection. Ruffed grouse prefer wide, old logs because these structures provide a larger drumming stage that is easier to grasp when drumming (McBurney 1989, Rusch et al. 2000, Zimmerman and Gutiérrez 2008). Furthermore, ruffed grouse may select larger structures for strutting purposes (Zimmerman and Gutiérrez 2008). We developed 5 models to evaluate these hypotheses (Models 4, 5, 6, 9, 10). While drumming, ruffed grouse males are increasingly susceptible to predation by avian and mammalian predators (Barber et al. 1989, Haulton et. al. 2003, Tirpak et al. 2006). We hypothesized male ruffed grouse selected structures that had both a sufficient canopy and adequate cover directly surrounding the drumming stage (Gullion 1967) to avoid the risk of predation. Therefore, we developed 4 models (Models 7, 8, 9, 10; Appendix) to evaluate how the number of branches (> 15 cm) emerging from the structure and canopy cover directly above the drumming stage correlated with the selection of an activity centers.

Vegetative covariates.— The characteristics of vegetation adjacent to the drumming structure might also be related to the selection of ruffed grouse activity centers. Therefore, we assessed the relationship of horizontal (i.e., stem and sapling density, visibility, and basal area) and vertical (i.e., canopy cover) cover with the selection of activity centers. Ruffed grouse often select activity centers that have a dense understory (i.e., vegetation > 1.5 m tall) for protection from avian predators, and little ground cover to detect mammalian predators (Boag and Sumanik 1969, Stoll et al. 1979, Hale et al. 1982, Buhler and Anderson 2001, Haulton et. al. 2003). Consequently, we developed 4 models (Models 11, 12, 16, 17) evaluating the visibility at varying heights around the drumming structure and the relationship of small (15 cm < height < 1 m) and large (≥ 1 m tall) stem density (no./ha). Additionally, we assessed the relationship of sapling density (Models 11, 12, 16, 17, 18, 19) around the activity center, assuming sapling density of individual species (e.g., aspen, spruce, and pine) all had a positive relationship with selection (Stoll et al. 1979, Barber et al. 1989, Haulton et. al. 2003, Tirpak et al. 2006).

Ruffed grouse typically inhabit early succession forest communities dominated by pole-sized trees and saplings (Barber et al. 1989, Haulton et. al. 2003, Tirpak et al. 2006); therefore, we hypothesized total basal area of trees with DBH ≥ 10 cm was less around activity centers. Also, ruffed grouse often select these conditions in aspen and spruce communities (Brenner 1989, Gullion and Svoboda 1972, Kubisiak 1985, Chapter 1). We hypothesized that aspen and spruce basal areas were higher around activity centers, while pine basal area was lower. To test these hypotheses, we developed 5 models (Models 13, 14, 15, 16, 17). Last, some studies suggest that canopy cover around an activity center has no relationship with activity center selection (e.g., Hale et al. 1982), while others suggest canopy cover has a positive relationship (e.g., Buhler and Anderson 2001). Therefore, we developed 5 models to test these hypotheses (Models 13, 14, 15, 16, 17). Because we hypothesized drumming structure and adjacent vegetative characteristics both correlated with ruffed grouse selection of activity centers, we developed 2 models (Models 18 and 19) that evaluated a combination of these characteristics.

Analytical Methods

We used discrete-choice modeling to evaluate activity center selection, assuming each ruffed grouse chose 1 primary activity center out of a unique choice set comprised of *n* discrete habitat units (Cooper and Millspaugh 1999). Classic discrete-choice models take the form of the conditional multinomial logit model (McFadden 1974), which estimates the probability (*p*) of an individual selecting the j^{th} unit on the i^{th} choice using:

$$p_{ij} = \frac{\exp(\beta_1 x_{1ij} + \beta_2 x_{2ij} + \ldots + \beta_n x_{nij})}{\sum_{k=1}^{N_i} \exp(\beta_1 x_{1ik} + \beta_2 x_{2ik} + \ldots + \beta_n x_{nik})} \tag{1}$$

By multiplying probabilities across *i* choices, maximum-likelihood estimates (MLEs) of β parameters may be calculated (McDonald et al. 2006). We used PROC REG (SAS Institute 2006) to test explanatory variables for multicolinearity, assuming variables with tolerance values < 0.4 displayed multicolinearity (Allison 1999). If multicolinearity existed, we removed the variable which performed the worst in the model, repeated the analysis, and checked for multicolinearity again. We repeated this procedure until there was no evidence of multicolinearity. To estimate β MLEs, we used PROC MDC (SAS Institute 2006).

We ranked our candidate models using an information-theory approach (Burnham and Anderson 2002) and based our model rankings on the ΔAIC_c and Akaike weights (w_i) (Burnham and Anderson 2002) for each model. We addressed model selection uncertainty by calculating model-averaged parameter estimates from the 90% Akaike weight confidence set (Burnham and Anderson 2002). After model averaging, we calculated odds ratios and 95% odds ratio confidence intervals for parameter estimates to assess which parameters in the 90% set had a stronger relationship with activity center selection. Finally, we determined goodness-of-fit of our models by calculating the likelihood ratio index (ρ) for each model using:

$$\rho = 1 - \frac{LL(\hat{\beta})}{LL(\emptyset)} \tag{2}$$

where $LL(\hat{\beta})$ is the log-likelihood of the parameterized model and $LL(\emptyset)$ is the log-likelihood of the null model (Train 2003). The likelihood ratio index ranges from 0 to 1, with higher values signifying a better performing model compared to the null model (Train 2003). Thus, we assumed a well-fit model should have a likelihood ratio index value close to 1.

Model Validation.— To evaluate the predictive ability of our discrete-choice model for activity center selection, we used a modified *k*-fold cross-validation design (Boyce et at. 2002). We used this design because *k*-fold cross-validation is an effective model validation design for resource selection functions when independent data is unavailable and when used vs. available data are analyzed (Boyce et al. 2002). We randomly extracted 80% of our choice sets (training data) and calculated a new discrete-choice model from this data, while incorporating the same covariates from our model-averaged discrete-choice model. We then evaluated how the discrete-choice model predicted the remaining 20% of choice sets (testing data) by evaluating the selection probability rank of each alternative in every unique choice set. We repeated this process 5 times (calculating new parameter coefficients each time) and calculated the proportion of choice sets in which the selected choice (i.e., the actual activity center) had the highest (rank = 1), second-highest (rank =2), third-highest (rank = 3), and lowest (rank =4) probability of being selected, compared to the available alternatives in the set. We expected a good predictive model to demonstrate a large proportion of selected choices with high probabilities of selection (i.e., lower ranks).

RESULTS

Drumming structure search

We located 41 unique ruffed grouse drumming structures in spring 2007 and 15 unique drumming structures during spring 2008. Drumming structures consisted of 53 fallen logs (94.6%), 1 stump (1.8%), 1 dirt mound (1.8%), and 1 rock cliff (1.8%). We determined that 7 of these structures (4 fallen logs, 1 stump, 1 dirt mound, and 1 rock cliff) were "alternate" structures due to the low amount of ruffed grouse droppings on the structures. Thus, our analyses were conducted on 49 independent activity centers and 147 random plots.

Model analysis

The most supported model included both drumming structure and vegetative characteristics within the activity center (e.g., visibility above 1 meter, density of stems ≥ 1 meter, structure height, canopy cover, aspen and spruce basal area, aspen, spruce, and pine sapling density; Table 2). However, there was some model uncertainty among the top 3 models. Competing models suggested that adjacent vegetation alone (e.g., visibility above 1 meter, stem density, aspen, spruce, and pine sapling density) was correlated with selection of activity centers (Table 2).

Model-averaged estimates and odds ratios demonstrated that percent visibility above 0.9 m and the density of stems ≥ 1 m were significant covariates (Table 3).

Percent visibility had a negative linear relationship on ruffed grouse selection; increasing visibility above 0.9 m around the drumming structure from 15% to 40% decreased the probability of activity center selection by 12% (Figure 1). The density of stems ≥ 1 m had a positive linear relationship with activity center selection. There was not as strong of a relationship with activity center selection at lower stem densities (e.g., < 60,000 stems/hectare); however, increasing the density of stems ≥ 1 m tall from 60,000 stems/hectare to 80,000 stems/hectare increased the probability of selection by 43.8% (Figure 2). Density of small stems (15 cm < height < 1 m), aspen and pine sapling density, aspen and spruce basal area, canopy cover, and height of the drumming structure all had positive relationships while spruce sapling density had a negative relationship on activity center selection (Table 3). However, these model-averaged parameters had odds ratio confidence intervals that included 1; thus, their relationship with activity center selection was insignificant.

The top performing models all had relatively high likelihood ratio values (Table 2). Additionally, *k*-fold validation procedures using the model-averaged discrete choice model resulted in the observed choice (i.e., actual activity center) in the test data being ranked as the most probable choice out of the choice set 86% of the time, while the remaining 14% were ranked the second-most probable choices out of the choice set. Thus, our discrete-choice model predicted activity center selection well.

DISCUSSION

Ruffed grouse selection of activity centers correlated with increasing cover above 1 meter surrounding the drumming site. However, selection was not correlated with tree species, suggesting ruffed grouse select different vegetative attributes at different scales. The visibility above 0.9 meters and the density of stems ≥ 1 meter in height had the strongest relationship with activity center selection, demonstrating that ruffed grouse might select activity centers that reduced the risk of predation (Boag and Sumanik 1969, Stoll et al. 1979, Hale et al. 1982, Buhler and Anderson 2001, Haulton et. al. 2003). Unlike broad-scale ruffed grouse occupancy (Chapter 1), selection of activity centers was not correlated with tree species, suggesting species composition might not be important at the micro-site level. As a result, ruffed grouse selection of breeding territories in the BHNF is likely correlated with vegetative characteristics at multiple scales. At the large scale, tree species might be the overriding feature of general site occupancy, whereas micro-site selection is most related to vegetative features above 1 meter height surrounding an activity center. Thus, management for ruffed grouse should occur at multiple scales.

Throughout the west and upper mid-west, ruffed grouse selection of activity centers was correlated with drumming structure (e.g., log diameter and height) and vegetative characteristics (e.g., shrub and stem density) within the activity center (Stauffer and Peterson 1985, Buhler and Anderson 2001, Zimmerman and Gutiérrez 2008). Our results suggested that ruffed grouse drumming structure characteristics were not significantly correlated with activity center selection; however, adjacent vegetative characteristics were correlated. Rusch et al. (2000) hypothesized that, because there are usually many structures (e.g., logs, stumps, rocks) available to use for drumming, the availability or characteristics of structures would not likely limit the distribution of ruffed grouse. Our results corroborated this hypothesis; ruffed grouse selection of breeding territories was not related to the characteristics of structures within their breeding territory, rather the amount and type of cover within an activity center. As a result, ruffed grouse might be primarily concerned with concealing themselves from predators when selecting activity centers in the BHNF, while selection of drumming structure is a secondary concern. In the Appalachians, ruffed grouse selected activity centers with dense overstory cover and little ground cover to avoid predation from both avian and mammalian species (Haulton et. al. 2003, Tirpak et al. 2006). Our results in the BHNF suggested that ruffed grouse select activity centers for similar reasons because vegetative cover and visibility above 1 meter were correlated with activity center selection, while vegetative cover and visibility below 1 meter were not correlated. As a result, ruffed grouse might have been selecting activity centers in the BHNF where there was sufficient understory cover to avoid avian predators (e.g., northern goshawk [*Accipiter gentiles*]) and less ground cover to avoid mammalian predators (e.g., coyote [*Canis latrans*]).

The species and density of saplings and trees was not significantly correlated with ruffed grouse selection of activity centers in the BHNF, suggesting that species composition is not of primary importance during micro-site selection. In Alberta, activity centers had high densities of white spruce saplings and aspen trees (Boag and Sumanik 1969), while activity centers in northern Minnesota had high densities of aspen saplings (Zimmerman and Gutiérrez 2008). However, these studies were performed in regions where "optimal" ruffed grouse habitat was abundant. Aspen vegetation only comprised 4% of the BHNF (Hoffman and Alexander 1987), thus, because not all ruffed grouse could inhabit aspen communities, the vegetative species composition around ruffed grouse activity centers varied considerably. Hale et al. (1982) observed that the physical structure of vegetation drove ruffed grouse activity center selection preference in Georgia, rather than species composition. Our results corroborate those of Hale et al.

(1982), suggesting that the type and species of cover might not be of utmost importance to activity center selection in the BHNF, rather the quality of cover the adjacent vegetation provided. As a result, ruffed grouse selection of activity centers in the BHNF differed across cover types, basal areas, canopy cover, and vegetative species, but was similar when considering cover attributes above 1 meter in height.

Landscape characteristics at a large scale might correlate with small-scale selection of activity centers or vice versa dependent upon whether selection is top-down or bottom-up (Kristan 2006, Zimmerman and Gutiérrez 2008). The BHNF was composed of a small proportion of early succession aspen communities (Hoffman and Alexander 1987), which are believed to be "optimal" ruffed grouse habitat (Brenner 1989, Gullion and Svoboda 1972, Kubisiak 1985, Rusch et al. 2000). Results from 2007 and 2008 surveys suggested that ruffed grouse not only occupied "optimal" vegetative communities (aspen), but spruce communities as well (Chapter 1). This poses the question: do ruffed grouse select suboptimal vegetative communities, such as white spruce, due to the shortage of optimal vegetation (aspen), or because some aspen vegetative communities lack adequate cover attributes (low density of stems ≥ 1 m) at smaller scales? Chapter 1 demonstrated that species composition is important for ruffed grouse occupancy at the population level. However, results from this micro-site assessment demonstrated that the vegetative cover around an activity center was also correlated with the selection of breeding territories at an individual level. As a result, we believe ruffed grouse are primarily exhibiting a top-down form of selection (Kristan 2006), but might abandon a territory if the small-scale attributes are not satisfactory. Due to these results, all aspen vegetative communities might not be adequate for ruffed grouse because of inadequate micro-scale attributes. Thus, management should not focus solely on increasing the extent and type of preferred vegetation (e.g., aspen), but the micro-scale vegetative characteristics of all vegetative communities as well.

MANAGEMENT IMPLICATIONS

Ruffed grouse occupancy of breeding territories was influenced by broad-scale vegetative attributes (extent and area of aspen) at the population level (Chapter 1) and small-scale vegetative attributes (vegetative cover > 1 meter in height) at an individual level; thus, management actions should occur at both scales. For each hectare increase in aspen vegetation within a 550 meter radius (95 ha), managers can expect the probability of ruffed grouse occupancy to increase by 1% (Chapter 1). Also, by increasing the density of vegetation that is ≥ 1 m tall and < 2.54 cm in diameter (i.e., "stems"; see *Field Methods*) from 60,000 stems/hectare to 80,000 stems/hectare, managers can expect the relative probability of a ruffed grouse selecting an activity center within a breeding territory to increase by at least 43.8%. However, if the density of stems falls below 60,000 stems/hectare, the probability of selection reduces to nearly 0. Thus, to encourage ruffed grouse occupancy in the BHNF at the population and individual level, management should focus primarily on increasing the size and extent of early successional aspen communities characterized by high densities of vegetative cover > 1 m in height and < 2.54 cm in stem diameter. Forest managers must decide what timber management practices (e.g., clear-cutting, prescribed burning) are the most efficient and appropriate for encouraging early successional aspen communities in the BHNF.

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Table 1. Description of the variables to be used in *a priori* models which assess the relationship of drumming structure and adjacent vegetative characteristics with selection of ruffed grouse activity centers in the Black Hills National Forest during spring 2007 and 2008.

Variable	Description
Structure	
Ht	Height (cm) of drumming structure at the drumming stage
Dm	Diameter (cm) of drumming structure at the drumming stage
Slp	Slope (%) that the drumming grouse faced
Bk0	0 – 20% drumming structure covered by bark
Bk1	21 – 60% drumming structure covered by bark
Bk2	61 – 100% drumming structure covered by bark
Lth	Length (cm) of drumming structure
Br	Number of branches > 15 cm on the drumming structure
LCan	Canopy cover (%) directly above drumming stage
Vegetation	
BA_QA	Basal area (m^2/ha) of quaking aspen ≥ 10cm DBH[a]
BA_WS	Basal area (m^2/ha) of white spruce ≥ 10cm DBH[a]
BA_PP	Basal area (m^2/ha) of ponderosa pine ≥ 10cm DBH[a]
BA_tot	Basal area (m^2/ha) of all vegetation ≥ 10cm DBH[a]
Cv1	Visibility (%) from 0 – 0.9 m
Cv2	Visibility (%) from 0.91 – 1.8 m

Table 1 Continued.

Variable	Description
Vegetation	
Cv_tot	Visibility (%) from 0 – 1.8 m
QA_sap	Density (no./ha) of quaking aspen saplings (aspen vegetation ≥ 1.37 m tall and 10 cm > DBH[a] ≥ 2.54 cm)
WS_sap	Density (no./ha) of white spruce saplings (spruce vegetation ≥ 1.37 m tall and 10 cm > DBH[a] ≥ 2.54 cm)
PP_sap	Density (no./ha) of ponderosa pine saplings (pine vegetation ≥ 1.37 m tall and 10 cm > DBH[a] ≥ 2.54 cm)
Sap	Density (no./ha) of all saplings (vegetation ≥ 1.37 m tall and 10 cm > DBH[a] ≥ 2.54 cm)
Stem1	Density (no./ha) of woody and herbaceous stems (excluding grasses) 15 cm < stem height < 1 m
Stem2	Density (no./ha) of woody and herbaceous stems (excluding grasses) ≥ 1 m tall
PCan	Canopy cover (%) in the plot

[a] Signifies the diameter at breast height (1.37 m)

Table 2. Ranking of candidate models which assess the relationship of structure and vegetative characteristics with ruffed grouse activity center selection during spring 2007 and 2008 in the Black Hills National Forest. K is the number of parameters in the model, -2LL is -2 times the log-likelihood estimate, AIC_c is Akaike's information criterion adjusted for small sample size, ΔAIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ρ is the likelihood ratio index value.

Model No.[a]	-2 LL	K	AIC_c	ΔAIC_c	w_i	ρ
19	20.55	8	40.15	0.00	0.573	0.848
11	30.22	5	41.62	1.47	0.274	0.777
12	29.97	6	43.97	3.83	0.084	0.778
16	25.71	8	45.31	5.17	0.043	0.810
17	17.26	11	46.40	6.25	0.025	0.872
2	56.38	1	58.46	18.32	0.000	0.583
3	52.93	3	59.47	19.32	0.000	0.609
18	11.19	16	60.19	20.05	0.000	0.917
9	42.59	8	62.19	22.04	0.000	0.685
10	38.85	10	64.64	24.50	0.000	0.713
6	67.45	5	78.84	38.69	0.000	0.501
4	80.80	1	82.89	42.74	0.000	0.403
5	80.39	4	89.30	49.15	0.000	0.406
7	90.70	1	92.79	52.64	0.000	0.330
8	89.52	2	93.78	53.63	0.000	0.338

Table 2 Continued.

Model No.[a]	-2 LL	K	AIC$_c$	Δ AIC$_c$	w_i	ρ
13	93.06	2	97.33	57.18	0.000	0.312
15	89.57	4	98.48	58.33	0.000	0.338
14	92.96	3	99.49	59.34	0.000	0.313
1	135.28	0	135.28	98.74	0.000	0.000

[a] See Appendix for a full description of each model

Table 3. Model-averaged parameter estimates, standard errors (SE), odds ratios, and 95% odds ratio confidence intervals for the 3 most supported discrete-choice models evaluating ruffed grouse activity center selection in the Black Hills National Forest during 2007 and 2008.

Parameter[a]	Estimate	SE	Odds ratio	Lower 95% CI	Upper 95% CI
Cv2	-6.905	2.853	0.001	0.000	0.269
Stem2	1.976	0.976	7.213	1.065	48.861
Stem1	0.027	0.083	1.028	0.873	1.210
QA_sap	1.117	0.792	3.057	0.647	14.446
WS_sap	-0.047	0.163	0.954	0.693	1.314
PP_sap	0.007	0.210	1.007	0.666	1.521
QA_BA	0.016	0.064	1.016	0.895	1.152
WS_BA	0.044	0.062	1.045	0.926	1.179
PCan	2.008	3.354	7.446	0.010	5337.204
Ht	0.040	0.044	1.041	0.956	1.134
LCan	1.900	2.674	6.685	0.035	1262.045

[a] See Table 1 for a definition of parameter symbols

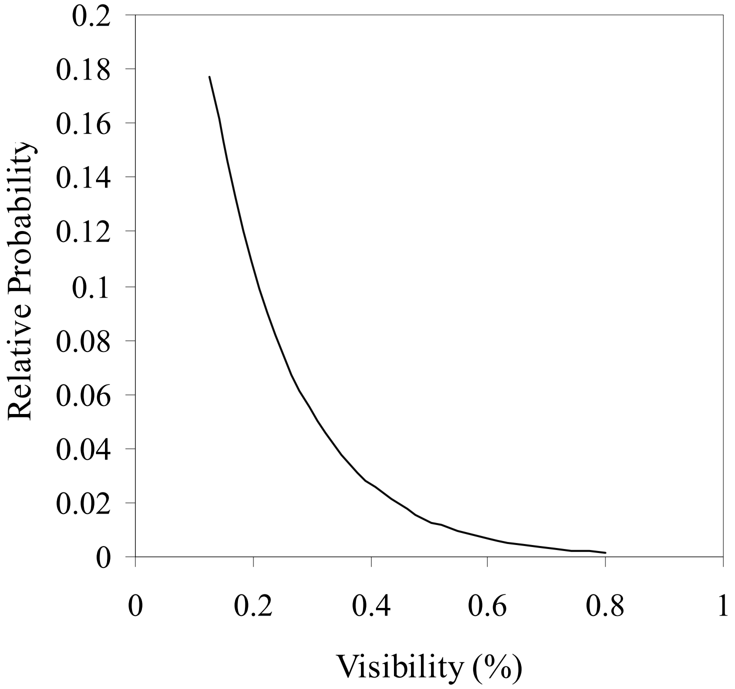

Figure 1. Relationship of percent visibility with the relative probability of ruffed grouse selection of activity centers in the Black Hills National Forest. Probabilities were calculated using the model-averaged discrete-choice model derived from activity center measurements during 2007 and 2008.

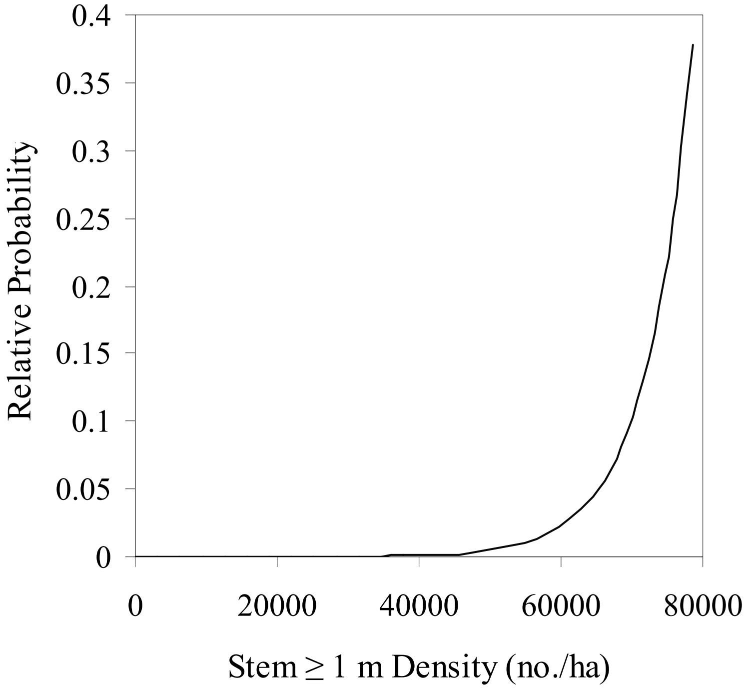

Figure 2. Relationship of stem density ≥ 1 m (no./ha) with the relative probability of ruffed grouse selection of activity centers in the Black Hills National Forest. Probabilities were calculated using the model-averaged discrete-choice model derived from activity center measurements during 2007 and 2008.

APPENDIX A. MODELS INFLUENCING RUFFED GROUSE SELECTION OF ACTIVITY CENTERS

A priori candidate model set and hypotheses assessing the relationship of structure and adjacent vegetative characteristics with the selection of ruffed grouse activity centers in the Black Hills National Forest during spring 2007 and 2008.

Model	Model Description[a]	Model Structure	Hypothesized Parameter Effects
	Constant		
1	Null		Random Selection
	Structure		
2	Ht	β_1(Ht)	$\beta_1>0$
3	Ht + Slp^2	β_1(Slp) + β_2(Slp^2)	$\beta_1>0$, $\beta_2<0$
4	Dm	β_1(Dm)	$\beta_1>0$
5	Dm + Bk0 + Bk1 + Bk2	β_1(Dm) + β_2(Bk0) + β_3(Bk1) + β_4(Bk2)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4<0$
6	Dm + Lth + Bk0 + Bk1 + Bk2	β_1(Dm) + β_2(Lth) + β_3(Bk0) + β_4(Bk1) + β_5(Bk2)	$\beta_1>0$, $\beta_2>0$ or $\beta_2<0$, $\beta_3>0$, $\beta_4>0$, $\beta_5<0$
7	LCan	β_1(LCan)	$\beta_1>0$

APPENDIX A CONTINUED.

Model	Model Description[a]	Model Structure	Hypothesized Parameter Effects
	Structure		
8	LCan + Br	β_1(LCan) + β_2(Br)	$\beta_1>0, \beta_2>0$
9	Ht + Slp^2 + Dm + Bk0 + Bk1 + Bk2 + LCan	β_1(Ht) + β_2(Slp) + β_3(Slp^2) + β_4(Dm) + β_5(Bk0) + β_6(Bk1) + β_7(Bk2) + β_8(LCan)	$\beta_1>0, \beta_2>0, \beta_3<0, \beta_4>0, \beta_5>0, \beta_6>0, \beta_7<0, \beta_8>0$
10	Ht + Slp^2 + Dm + Bk0 + Bk1 + Bk2 + Br + Lth + LCan	β_1(Ht) + β_2(Slp) + β_3(Slp^2) + β_4(Dm) + β_5(Bk0) + β_6(Bk1) + β_7(Bk2) + β_8 (Br) + β_9(Lth) + β_{10}(LCan)	$\beta_1>0, \beta_2>0, \beta_3<0, \beta_4>0, \beta_5>0, \beta_6>0, \beta_7<0, \beta_8>0, \beta_9<0$ or $\beta_9>0, \beta_{10}>0$
	Vegetation		
	Horizontal Cover		
11	Cv2 + Stem2 + QA_sap + WS_sap + PP_sap	β_1(Cv2) + β_2(Stem2) + β_3(QA_sap) + β_4(WS_sap) + β_5(PP_sap)	$\beta_1>0, \beta_2>0, \beta_3>0, \beta_4>0, \beta_5>0$
12	Cv2 + Stem1 + Stem2 + QA_sap + WS_sap + PP_sap	β_1(Cv2) + β_2(Stem1) + β_3(Stem2) + β_4(QA_sap) + β_5(WS_sap) + β_6(PP_sap)	$\beta_1<0, \beta_2<0, \beta_3>0, \beta_4>0, \beta_5>0, \beta_6>0$
	Vertical Cover		
13	BA_QA + PCan	β_1(BA_QA) + β_2(PCan)	$\beta_1>0, \beta_2>0$

APPENDIX A CONTINUED.

Model	Model Description[a]	Model Structure	Hypothesized Parameter Effects
	Vegetation		
	Vertical Cover		
14	BA_QA + BA_WS + Pcan	β_1(BA_QA) + β_2(BA_WS) + β_3(PCan)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$
15	BA_QA + BA_WS + BA_PP + Pcan	β_1(BA_QA) + β_2(BA_WS) + β_3(BA_PP) + β_4(PCan)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$, $\beta_4>0$
	Horizontal + Vertical Cover		
16	BA_QA + BA_WS + PCan + Cv2 + Stem2 + QA_sap + WS_sap + PP_sap	β_1(BA_QA) + β_2(BA_WS) + β_3(PCan) + β_4(Cv2) + β_5(Stem2) + β_6(QA_sap) + β_7(WS_sap) + β_8(PP_sap)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$, $\beta_5>0$, $\beta_6>0$, $\beta_7>0$, $\beta_8>0$
17	BA_QA + BA_WS + BA_PP + BA_tot + Cv1 + Cv2 + Cv_tot + Stem1 + Stem2 + Sap + PCan	β_1(BA_QA) + β_2(BA_WS) + β_3(BA_PP) + β_4(BA_tot) + β_5(Cv1) + β_6(Cv2) + β_7(Cv_tot) + β_8(Stem1) + β_9(Stem2) + β_{10}(Sap) + β_{11}(PCan)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$, $\beta_4<0$, $\beta_5<0$, $\beta_6>0$, $\beta_7>0$, $\beta_8<0$, $\beta_9>0$, $\beta_{10}>0$, $\beta_{11}>0$

APPENDIX A CONTINUED.

Model	Model Description[a]	Model Structure	Hypothesized Parameter Effects
	Structure + Vegetation		
18	Ht + Slp^2 + Dm + Bk0 + Bk1 + Bk2 + LCan + BA_QA + BA_WS + Cv2 + Stem2 + QA_sap + WS_sap + PP_sap + PCan	β_1(Ht) + β_2(Slp) + β_3(Slp^2) + β_4(Dm) + β_5(Bk0) + β_6(Bk1) + β_7(Bk2) + β_8(LCan) + β_9(BA_QA) + β_{10}(BA_WS) + β_{11}(Cv2) + β_{12}(Stem2) + β_{13}(QA_sap) + β_{14}(WS_sap) + β_{15}(PP_sap) + β_{16}(PCan)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$, $\beta_4>0$, $\beta_5>0$, $\beta_6>0$, $\beta_7<0$, $\beta_8>0$, $\beta_9>0$, $\beta_{10}>0$, $\beta_{11}>0$, $\beta_{12}>0$, $\beta_{13}>0$, $\beta_{14}>0$, $\beta_{15}>0$, $\beta_{16}>0$
19	Ht + LCan + BA_QA + BA_WS + Cv2 + Stem2 + QA_sap + PCan	β_1(Ht) + β_2(LCan) + β_3(BA_QA) + β_4(BA_WS) + β_5(Cv2) + β_6(Stem2) + β_7(QA_sap) + β_8(PCan)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$, $\beta_5>0$, $\beta_6>0$, $\beta_7>0$, $\beta_8>0$

[a] See Table 1 for definition of parameter symbols