

# Ruffed Grouse Selection of Drumming Sites in the Black Hills National Forest

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**ABSTRACT.**—Ruffed grouse (*Bonasa umbellus*) are important game birds that depend on multiple forest age-classes of aspen (*Populus* spp.) for food and cover, which makes them an appropriate management indicator species for the condition of quaking aspen (*Populus tremuloides*) communities in the Black Hills National Forest of western South Dakota and northeastern Wyoming (BHNF). Recent landscape-scale drumming surveys showed that occupancy of ruffed grouse in the BHNF depended primarily on the amount of aspen-dominated vegetation within a 95 ha site. However, an investigation of drumming site characteristics is lacking. To evaluate drumming site selection, we located and measured the drumming structure and surrounding vegetation for 49 primary drumming sites and 147 paired unused sites during 2007 and 2008. We used discrete-choice modeling with an information-theoretic approach to evaluate resource characteristics of drumming sites associated with use. Percent area exposed (visibility) between 0.9 m and 1.8 m in height around the drumming structure had a negative, exponential relationship with drumming site selection and the combined density of woody and herbaceous plants  $\geq 1$ -m tall with a stem diameter  $< 2.54$  cm had a positive, asymptotic relationship with site selection. Reducing the visibility between 0.9 m and 1.8 m around the structure from 40% to 0% increased the relative probability of selection of drumming sites 9-fold. Increasing the density of woody and herbaceous stems from 8000 stems/hectare to 24,000 stems/hectare increased the relative probability of selection 20-fold. The selection of drumming sites with a high density of vegetation  $\geq 1$  m in height and low visibility between 0.9 m and 1.8 m suggests ruffed grouse select drumming sites that might reduce the chances of predation. Thus, management actions to improve ruffed grouse breeding habitat should focus on increasing the density of vegetation cover  $\geq 1$  m in height.

## INTRODUCTION

Ruffed grouse (*Bonasa umbellus*) are the management indicator species for the condition of quaking aspen (*Populus tremuloides*) in the Black Hills National Forest of western South Dakota and northeastern Wyoming (BHNF; U.S. Forest Service, 1997) because of their dependence on multiple age-classes of aspen (*Populus* spp.) for food and cover (Bump *et al.*, 1947; Gullion and Svoboda, 1972; Kubisiak, 1985, 1989). Given their status and popularity as a game bird, 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 Black Hills and develop greater knowledge of the vegetative features that influence ruffed grouse

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occurrence. Recent ruffed grouse drumming surveys showed that the probability of ruffed grouse occupying a sample site (550-m buffer surrounding the survey point) was positively associated with the amount of aspen-dominated vegetation within the site (Hansen, 2009). Results from that study describe ruffed grouse selection of dominant vegetation types at a landscape scale (95 ha), but do not consider micro-site vegetation attributes that might also influence selection.

During the spring, male ruffed grouse “drum” on elevated structures, such as fallen logs, stumps and rocks to attract females and maintain their territory (Bump *et al.*, 1947). Thus, characteristics of the drumming structure (*e.g.*, height, diameter, length) and the adjacent vegetation (*e.g.*, stem density, basal area, visibility, overstory canopy cover) might be important in the selection of drumming sites. Studies investigating the selection of ruffed grouse drumming sites throughout the United States and Canada have found that selection is positively correlated with the amount of understory cover (Stoll *et al.*, 1979; Palmer, 1963; Thompson *et al.*, 1987; Stauffer and Peterson, 1985; Buhler and Anderson, 2001). However, not all studies agree that drumming structure characteristics affect ruffed grouse site selection of drumming sites. No research has been conducted in the BHNF to determine the characteristics associated with ruffed grouse selection of drumming sites and whether factors affecting selection of drumming sites are similar to previously recorded relationships.

Understanding selection of drumming sites is an important complement to landscape-scale investigations of occupancy (Hansen, 2009) because forest management at multiple scales might be necessary to improve the quality of ruffed grouse habitat (*e.g.*, Fearer and Stauffer, 2003) in the BHNF. Our objective was to determine the characteristics associated with ruffed grouse selection of drumming sites in the BHNF and ascertain the relative importance of drumming structure and adjacent vegetation on selection of drumming sites.

## METHODS

### STUDY AREA

The BHNF is located in the western portion of South Dakota and includes the Bear Lodge Mountains of northeastern Wyoming (Fig. 1). Elevation ranges from 1066 m–2207 m. Annual rainfall in the BHNF exceeds 50.8 cm per year and varies with elevation (Ball *et al.*, 1996). The BHNF encompasses 500,000 ha and consists mostly of ponderosa pine (*Pinus ponderosa*, 84%), quaking aspen/paper birch (*Betula papyrifera*, 4%) and white spruce (*Picea glauca*, 2%). Other vegetation types comprise <10% of the BHNF and include bur oak (*Quercus macrocarpa*), hop-hornbeam (*Ostrya virginiana*) and green ash (*Fraxinus pennsylvanica*) (Hoffman and Alexander, 1987; Froiland, 1990). Common shrubs include western snowberry (*Symphoricarpos occidentalis*), white coralberry (*S. albus*), kinnikinnick (*Arctostaphylos uva-ursi*) and common juniper (*Juniperus communis*) (Hoffman and Alexander, 1987; Severson and Thilenius, 1976).

### FIELD METHODS

During spring 2007 and 2008, we completed ruffed grouse drumming surveys on the northern two-thirds of the BHNF (Hansen, 2009). When we heard a grouse drumming during a survey, we completed the 5 min survey (to maintain the monitoring protocol) then immediately located the drumming ruffed grouse. 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 *et al.*, 2000). To determine whether a structure was primary or alternate, we counted the

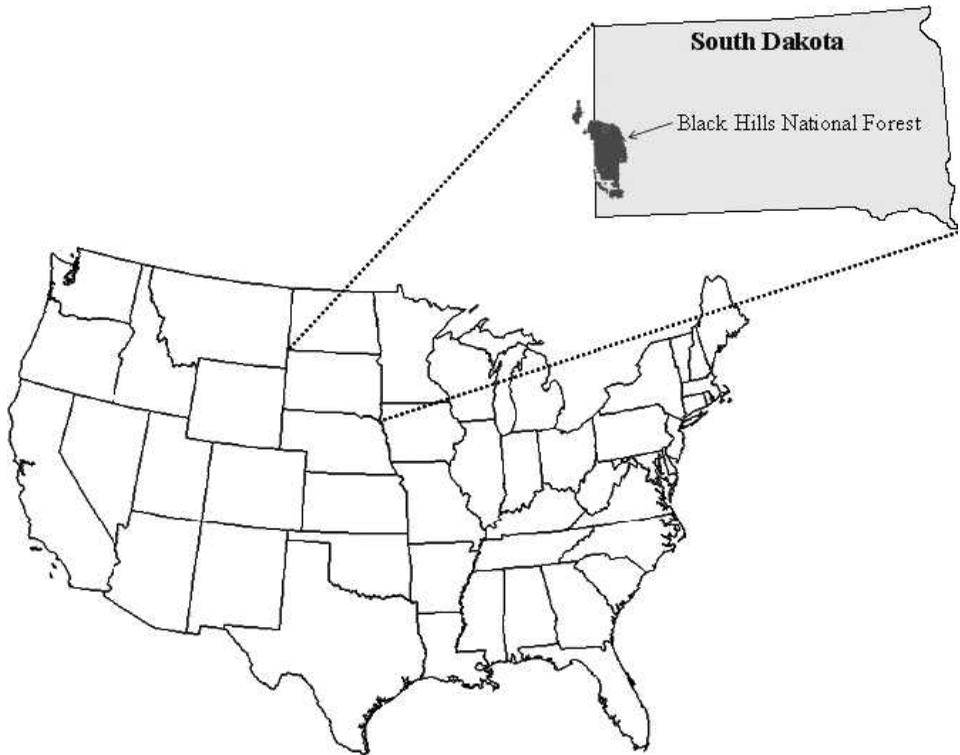


FIG. 1.—View of the location of the Black Hills National Forest, where we evaluated the selection of ruffed grouse drumming sites in 2007 and 2008

number of droppings on the structure. We assumed a structure with  $\geq 20$  droppings was the primary structure because it had been visited for an extended period of time by a ruffed grouse (Gullion, 1967). We only considered primary structures in our analyses.

For each unique drumming site, we characterized the drumming structure and vegetation within 12.5 m of the structure. Ruffed grouse select drumming sites that increase their probability of attracting mates (Johnsgard, 1989; McBurney, 1989). Thus, to characterize the drumming structure, we recorded type, length, diameter, height, number of branches  $>15$  cm in length and percent bark on the structure, if appropriate (McBurney, 1989; Buhler and Anderson, 2001; Zimmerman and Gutiérrez, 2008). We also recorded the azimuth and percent topographic slope the drumming grouse faced, which was determined either visually or by the accumulation of droppings on the structure (Table 1). Finally, we measured distance of the drumming stage (location on the drumming structure where the grouse drummed) to the nearest end of the drumming structure and used that measurement to determine the location of the plot center on random structures.

Ruffed grouse often select drumming sites that have a dense understory 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). Thus, to characterize surrounding vegetation, we recorded visibility (%), stem density (no./ha),

TABLE 1.—Description of the covariates to be used in discrete-choice models which assess the relationship of drumming structure and adjacent vegetative characteristics with selection of ruffed grouse drumming sites in the Black Hills National Forest during spring 2007 and 2008

Covariate	Description
<b>Structure</b>	
Height	Height (cm) of drumming structure at the drumming stage
Diameter	Diameter (cm) of drumming structure at the drumming stage
Slope	Topographic slope (%) that the drumming grouse faced
Bark0	0–20% drumming structure covered by bark
Bark1	21–60% drumming structure covered by bark
Bark2	61–100% drumming structure covered by bark
Length	Length (cm) of drumming structure
Branch	Number of branches >15 cm on the drumming structure
Stage_canopy	Overstory canopy cover (%) directly above drumming stage
<b>Vegetation</b>	
QA_basal	Basal area (m <sup>2</sup> /ha) of quaking aspen ≥10 cm DBH <sup>a</sup>
WS_basal	Basal area (m <sup>2</sup> /ha) of white spruce ≥10 cm DBH <sup>a</sup>
PP_basal	Basal area (m <sup>2</sup> /ha) of ponderosa pine ≥10 cm DBH <sup>a</sup>
Basal_total	Basal area (m <sup>2</sup> /ha) of all vegetation ≥10 cm DBH <sup>a</sup>
Cover1	Visibility (%) from 0–0.9 m in height
Cover2	Visibility (%) from 0.91–1.8 m in height
Cover_total	Visibility (%) from 0–1.8 m in height
QA_sapling	Density (no./ha) of quaking aspen saplings (aspen vegetation ≥ 1.37 m tall and 10 cm > DBH <sup>a</sup> ≥ 2.54 cm)
WS_sapling	Density (no./ha) of white spruce saplings (spruce vegetation ≥ 1.37 m tall and 10 cm > DBH <sup>a</sup> ≥ 2.54 cm)
PP_sapling	Density (no./ha) of ponderosa pine saplings (pine vegetation ≥ 1.37 m tall and 10 cm > DBH <sup>a</sup> ≥ 2.54 cm)
Sapling_total	Density (no./ha) of all saplings (vegetation ≥ 1.37 m tall and 10 cm > DBH <sup>a</sup> ≥ 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
Plot_canopy	Canopy cover (%) throughout the drumming site

<sup>a</sup> Signifies the diameter at breast height (1.37 m)

overstory canopy cover (%) and tree basal area (m<sup>2</sup>/ha). We estimated visibility using a modified cover board partitioned into 6, 1.2 m wide × 0.3 m tall vertical sections, each containing 144 black dots spaced 5 cm apart (Nudds, 1977; Hale *et al.*, 1982). We placed the cover board directly in front of the drumming stage, facing each cardinal direction and counted the number of visible dots in each section from a distance of 5 m and the same height as the section we were counting. We used this count to estimate visibility at multiple heights surrounding the drumming stage.

We counted stems of forbs and woody vegetation with a diameter <2.54 cm in 1-m<sup>2</sup> plots at 2-m intervals along 12-m transects radiating from the drumming structure in each cardinal direction. We tabulated woody vegetation and forbs in two categories: “short

stems" (15 cm to 1 m tall) and "tall stems" ( $\geq 1$  m tall). These were summed for all plots to estimate stem density of both size classes.

We used a moose-horn densiometer to tabulate overstory canopy cover at 1-m intervals along 12-m transects radiating out from the drumming structure in each cardinal direction. From these data we calculated percent overstory canopy cover. We also estimated percent canopy cover immediately above the drumming structure using a spherical densiometer positioned at approximately ruffed grouse height (30 cm) directly above the drumming stage.

Finally, we measured all trees  $>2.54$  cm DBH [diameter at breast height (1.37 m)] within a 12.5 m, fixed-radius plot centered over the drumming structure. For trees  $\geq 10$  cm DBH, we recorded species, DBH and condition (alive or dead). For trees  $<10$  cm DBH (hereafter referred to as saplings), we recorded species and condition. We calculated total basal area and basal area of aspen, spruce and pine for trees  $\geq 10$  cm DBH and calculated total density of saplings and density of aspen, spruce and pine saplings.

After completing measurements at the drumming site, we collected the same measurements at three random locations within a radius of 50 to 300 m of the drumming structure. We assumed a radius of 300 m represented an approximate territory size of male ruffed grouse (Kubisiak, 1989) and because alternate drumming structures are typically located  $<50$  m from the primary structure (Lovallo *et al.*, 2000), we constrained our random locations to be  $>50$  m from the primary structure. Random locations were selected without replacement using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) or a random number generator to determine the random direction and distance from the drumming site. Upon arriving at a random location, we located the nearest elevated structure  $>10$  cm diameter and searched the structure for ruffed grouse droppings to ensure a ruffed grouse was not using the structure. If there was evidence of previous use by ruffed grouse, we selected a different random site. Also, if the structure was  $<10$  cm diameter or the site occurred in a meadow or field, we selected a different random site because these conditions were unsuitable for drumming.

#### MODEL DEVELOPMENT

Preliminary examination of our data suggested that many of the covariate associations with selection of drumming sites might be non-linear. As a result, we determined the most supported structural form of each covariate from four possible forms: linear, quadratic, pseudothreshold (*i.e.*, asymptotic) and exponential (Franklin *et al.*, 2000). We used Akaike's Information Criterion (AIC) to compare relative support for structural forms of each covariate separately, and retained the structural form with the lowest AIC value (Burnham and Anderson, 2002). Using the structural form for each covariate that was most supported, we fit models to evaluate literature-based hypotheses on the relationship of drumming structure and adjacent vegetation characteristics with ruffed grouse selection of drumming sites in the BHNF.

We first hypothesized drumming structure characteristics were correlated with drumming site selection; therefore, we developed eight additive models that included a combination of structure characteristics (Table 1). Second, we hypothesized adjacent vegetation might be related to drumming site selection so we created seven additive models including adjacent vegetation covariates (Table 1). Finally, we predicted both structure and vegetation covariates could be correlated with selection; thus, we developed two models which included both drumming structure and adjacent vegetation covariates. Because ruffed grouse selection of drumming sites might not be influenced by structure or vegetation characteristics, we included one null model which contained no covariates. A detailed

description of each model, hypothesized parameter effects and a rationale for each model is available in Hansen (2009).

#### ANALYTICAL METHODS

We assumed available resources were unique for each individual ruffed grouse, requiring the pairing of used and available (random) sites. Thus, we used discrete-choice models (Cooper and Millsbaugh, 1999) to evaluate hypotheses associated with selection of primary drumming sites by ruffed grouse. 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:

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

We used PROC MDC to fit models and calculate covariate estimates (SAS Institute, 2006).

We ranked our candidate models using an information-theoretic approach (Burnham and Anderson, 2002) and based our model rankings on  $\Delta AIC_c$  and Akaike weights (Burnham and Anderson, 2002) for each model. We calculated odds ratios and 95% confidence intervals for covariate estimates to assess the strength of each covariate's relationship with selection of drumming sites. Finally, we determined goodness-of-fit of our models by calculating the likelihood ratio index ( $\rho$ ) for each model using:

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

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 most supported discrete-choice model for selection of drumming sites, we used a modified  $k$ -fold cross-validation design (Boyce *et al.*, 2002). We randomly extracted 80% of our paired used and available drumming site data and calculated a new discrete-choice model from these data, while incorporating the covariates from the most-supported discrete-choice model. We then evaluated how the discrete-choice model predicted the remaining 20% of the data by comparing the relative probabilities of paired used and available drumming sites (Boyce *et al.*, 2002). We repeated this process five times and calculated the proportion of paired used and available drumming sites in which the selected choice (*i.e.*, the used drumming site) had the highest probability of being selected, compared to the available drumming sites in the surrounding area. We expected a good predictive model to demonstrate a large proportion of used sites with high relative probabilities of selection. We assumed a proportion  $\leq 25\%$  meant the model had no ability to distinguish between used and available sites.

#### RESULTS

We located 56 ruffed grouse drumming sites; 41 in spring 2007 and 15 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%). Seven of these structures (4 fallen logs, 1 stump, 1 dirt mound and 1 rock cliff) were considered alternate structures because they had less than

TABLE 2.—Ranking of drumming site models after considering non-linear relationships of structure and vegetation covariates with ruffed grouse selection of drumming sites during spring 2007 and 2008 in the Black Hills National Forest. The most supported structural form for each covariate [linear (**L**), quadratic (**Q**), asymptotic (**A**), exponential (**E**)] was determined individually using single covariate models and AIC.  $AIC_c$  represents Akaike's information criterion adjusted for small sample size and  $\Delta AIC_c$  is the difference in  $AIC_c$  value from the top model

Model <sup>a</sup>	-2*log-likelihood	No. of covariates	$AIC_c$	$\Delta AIC_c$	Akaike weight	Likelihood ratio index
<b>E_Cover2</b> + <b>A_Stem2</b> + <b>L_QA_sapling</b>	25.84	3	32.37	0.00	0.96	0.81
<b>Q_Height</b> + <b>Q_QA_basal</b> + <b>A_WS_basal</b> + <b>E_Cover2</b> + <b>A_Stem2</b> + <b>L_QA_sapling</b> + <b>A_Plot_canopy</b> + <b>E_Stage_canopy</b>	14.78	10	40.57	8.20	0.02	0.89
<b>E_Cover1</b> + <b>E_Cover2</b> + <b>A_Stem1</b> + <b>A_Stem2</b> + <b>L_QA_sapling</b> + <b>A_WS_sapling</b> + <b>E_PP_sapling</b>	23.87	7	40.60	8.23	0.02	0.82
<b>Q_QA_basal</b> + <b>A_WS_basal</b> + <b>E_Cover1</b> + <b>E_Cover2</b> + <b>A_Stem1</b> + <b>A_Stem2</b> + <b>L_Sapling_total</b> + <b>A_Plot_canopy</b> + <b>E_Stage_canopy</b>	18.33	10	44.12	11.75	0.00	0.86
<b>Q_QA_basal</b> + <b>A_WS_basal</b> + <b>A_Plot_canopy</b> + <b>E_Stage_canopy</b> + <b>E_Cover2</b> + <b>A_Stem2</b> + <b>L_QA_sapling</b> + <b>A_WS_sapling</b> + <b>E_PP_sapling</b>	19.31	10	45.10	12.73	0.00	0.86
<b>L_Slope</b> + <b>Q_Diameter</b> + <b>Bark0</b> + <b>Bark1</b> + <b>Bark2</b> + <b>Q_QA_basal</b> + <b>A_WS_basal</b> + <b>E_Cover2</b> + <b>A_Stem2</b> + <b>L_Sapling_total</b> + <b>A_Plot_canopy</b> + <b>E_Stage_canopy</b>	10.15	14	50.50	18.13	0.00	0.92
<b>Q_Diameter</b> + <b>A_Length</b> + <b>Bark0</b> + <b>Bark1</b> + <b>Bark2</b>	37.37	6	51.37	19.00	0.00	0.72
<b>Q_Height</b> + <b>L_Slope</b> + <b>Q_Diameter</b> + <b>Bark0</b> + <b>Bark1</b> + <b>Bark2</b> + <b>A_Branch</b> + <b>A_Length</b>	26.76	10	52.55	20.18	0.00	0.80
<b>Q_Height</b> + <b>L_Slope</b> + <b>Q_Diameter</b> + <b>Bark0</b> + <b>Bark1</b> + <b>Bark2</b>	33.71	8	53.31	20.94	0.00	0.75
<b>Q_Height</b>	49.11	2	53.37	21.00	0.00	0.64
<b>Q_Diameter</b>	48.94	3	55.47	23.10	0.00	0.64
<b>Q_Diameter</b> + <b>Bark0</b> + <b>Bark1</b> + <b>Bark2</b>	49.92	5	61.32	28.94	0.00	0.63
<b>Q_QA_basal</b> + <b>A_Plot_canopy</b> + <b>E_Stage_canopy</b>	72.79	4	81.70	49.33	0.00	0.46
<b>Q_QA_basal</b> + <b>A_WS_basal</b> + <b>A_Plot_canopy</b> + <b>E_Stage_canopy</b>	72.31	5	83.71	51.33	0.00	0.47
<b>Q_QA_basal</b> + <b>A_WS_basal</b> + <b>L_PP_basal</b> + <b>A_Plot_canopy</b> + <b>E_Stage_canopy</b>	72.26	6	86.26	53.89	0.00	0.47
<b>A_Branch</b>	123.45	1	125.54	93.17	0.00	0.09
Constant	135.28	0	135.28	98.74	0.00	0.00

<sup>a</sup> See Table 1 for definition of covariate symbols

20 droppings. Thus, our analyses were based on 49 independent drumming sites and 147 random sites.

The most supported model contained 96% of the Akaike weight (Table 2); thus, we considered only this model for interpretation. In this model, visibility between 0.9 m and

TABLE 3.—Covariate estimates, standard errors (SE), odds ratios and 95% odds ratio confidence intervals for the most supported discrete-choice model after considering non-linear relationships [linear (L<sub>-</sub>), quadratic (Q<sub>-</sub>), asymptotic (A<sub>-</sub>), exponential (E<sub>-</sub>)] with ruffed grouse selection of drumming sites in the Black Hills National Forest during 2007 and 2008

Covariate <sup>a</sup>	Estimate	SE	Odds ratio	Lower 95% CI	Upper 95% CI
E_Cover2	-4.65	1.41	0.01	0.001	0.15
A_Stem2	5.41	2.06	224.15	3.94	12,751.80
L_QA_sapling	1.38	0.76	3.99	0.90	17.80

<sup>a</sup> See Table 1 for a definition of covariate symbols

1.8 m was related in an exponential form, tall stem density was related in an asymptotic form and aspen sapling density was related in a linear form with drumming site selection. No drumming structure covariates were included. Covariate estimates and odds ratios suggested that visibility between 0.9 m and 1.8 m and the density of tall stems were the most important to drumming site selection, while aspen sapling density was less important (Table 3). Decreasing the visibility between 0.9 m and 1.8 m around the drumming structure from 40% to 0% increased the relative probability a site would be selected for drumming by ruffed grouse 9-fold (Fig. 2). The density of tall stems had a positive relationship with selection of drumming sites. Increasing the density of tall stems from 8000 stems/hectare to 24,000 stems/hectare increased the relative probability of selection 20-fold (Fig. 3).

The *k*-fold validation procedures using the most supported discrete choice model resulted in the observed choice (*i.e.*, the used drumming site) in the test data being ranked as the most probable choice out of the available drumming sites 94% of the time. Thus, our discrete-choice model predicted activity center selection well.

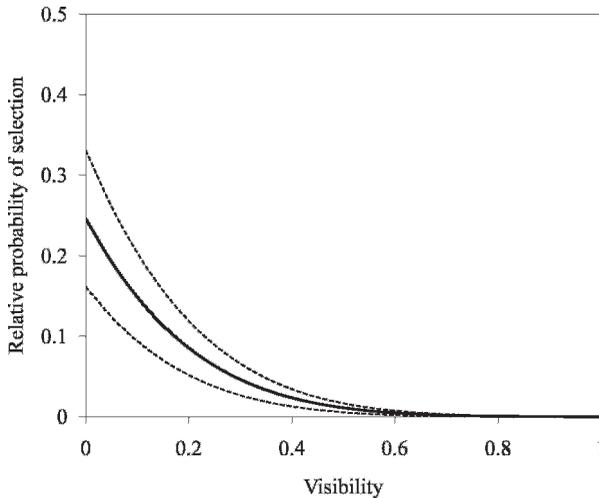


FIG. 2.—Relationship of percent visual obstruction (visibility) with the relative probability of ruffed grouse selection of drumming sites in the Black Hills National Forest. The solid line represents relative probability while dashed lines represent the upper and lower 95% confidence limits. Probabilities were calculated using the most supported discrete-choice model derived from drumming site measurements during 2007 and 2008

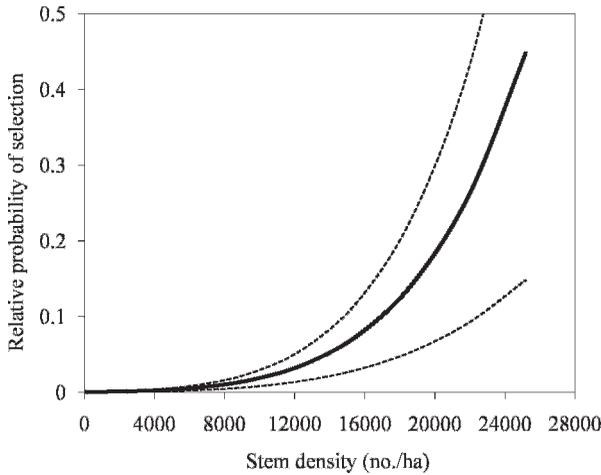


FIG. 3.—Relationship of the density of stems (vegetation with a stem diameter  $<2.54$  cm)  $\geq 1$  m tall with the relative probability of ruffed grouse selection of drumming sites in the Black Hills National Forest. Two outlying data points representing 78,688 and 40,413 stems/ha were excluded from the figure to display the effects of stems  $\geq 1$  m at more representative densities. The solid line represents relative probability while dashed lines represent the upper and lower 95% confidence limits. Probabilities were calculated using the most supported discrete-choice model derived from drumming site measurements during 2007 and 2008

#### DISCUSSION

Ruffed grouse drumming sites were associated with the height of vegetative cover surrounding the drumming structure, suggesting that predator avoidance might potentially be a factor determining selection of sites. During drumming, ruffed grouse are especially susceptible to predation, causing them to select drumming sites with substantial understory vegetative cover  $>1$  m in height to avoid avian predators and less ground-level cover to detect approaching ground predators and potential mates (Johnsgard, 1989; McBurney, 1989; Furtman, 1999). Ruffed grouse in the BHNF selected drumming sites characterized by low visibility between 0.9 m and 1.8 m and tall stem density, which might make it more difficult for avian predators to detect and approach the drumming ruffed grouse. Similar findings were reported in Georgia and northern Michigan, where drumming sites were characterized by shrub thickets that reduced visibility between 0.5 and 4 m (Hale *et al.*, 1982) and high densities of stems  $>2.4$  m tall (Palmer, 1963). However, these studies also found that ruffed grouse avoided drumming sites with high visibility below 0.5 m and high densities of stems  $<60$  cm tall. We did not find a negative relationship with visibility below 0.9 m and short stem density as we hypothesized; however, the absence of these covariates in the most supported model suggests that height of vegetation is important to drumming site selection. These results are consistent with the predation hypothesis and imply that ruffed grouse selection of drumming sites in the BHNF is driven by the height and density of vegetation surrounding the structure. While no research has examined survival and predation rates of drumming ruffed grouse in the BHNF, we hypothesize that avoidance of predation strongly influences ruffed grouse selection of drumming sites.

Ruffed grouse selection of drumming sites in the BHNF was not related to characteristics of the drumming structure. It has been suggested that male ruffed grouse select drumming

structures to increase the distance at which a potential mate can detect their drum (Johnsgard, 1989; McBurney, 1989). However, models that included characteristics associated with the drumming structure had essentially no support in our analysis. In Alberta (Canada) and Ohio (U.S.), the only requirement for a drumming structure was a level drumming stage on a slightly elevated structure (Boag and Sumanik, 1969; Stoll *et al.*, 1979). Similarly, Zimmerman and Gutiérrez (2008) reported that logs were the only drumming structure characteristic important to selection of a drumming site in Minnesota. We did not evaluate the association of drumming structure type with selection of drumming sites. However, every primary drumming structure we evaluated was a log, suggesting that ruffed grouse in the BHNH also prefer to drum on logs. While it is plausible that the absence of logs could limit the occurrence of ruffed grouse, we assume logs are abundant on the forest floor of the BHNH. As a result, type and characteristics of potential drumming structures are probably not the determining factor of ruffed grouse distribution or selection of drumming sites.

Species composition of forest vegetation was not related to selection of sites in our study. In Alberta Canada, drumming sites had high densities of white spruce and aspen vegetation (Boag and Sumanik, 1969). Also, Zimmerman and Gutiérrez (2008) and Felix-Locher and Campa (2010) reported higher densities of aspen vegetation surrounding drumming sites in Minnesota and Michigan, respectively. Aspen sapling density was included in our most supported model, but there was not sufficient evidence to conclude that aspen sapling density was a driving factor in selection of drumming sites within breeding territories. Further, models including aspen or spruce basal area had no support in our analysis. Ruffed grouse drumming sites occurred in quaking aspen, white spruce, paper birch, bur oak and ponderosa pine vegetation types. The diversity of vegetation types might have diluted any relationship between species composition and selection of drumming sites. Alternatively, species composition might not be important to ruffed grouse resource selection at a small scale. Stoll *et al.* (1979) and Hale *et al.* (1982) observed that the physical structure of vegetation was more important to ruffed grouse drumming site selection than species composition in Ohio and Georgia, respectively. Our results corroborate this hypothesis and suggest that species composition might not be as important at local (drumming site) scale as it is at determining landscape-scale (95 ha) distribution (Hansen, 2009). These findings and Hansen (2009) suggest ruffed grouse select early successional structure for drumming sites within aspen-dominated vegetation communities.

Given we tested a large set of models and did not validate our model using independent data, there is potential for spurious results. However, when placed in a biological context, our results were consistent with literature and the biology of ruffed grouse. Thus, management to improve overall ruffed grouse habitat in the BHNH should focus on increasing the extent of aspen vegetation and density of cover >1 m in height within aspen communities.

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