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Cassandra L. Mehls
South Dakota State University, casey.heimerl@state.sd.us

Kent C. Jensen
South Dakota State University

Mark A. Rumble
U.S. Forest Service, Rocky Mountain Research Station

Michael C. Wimberly
South Dakota State University

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Multi-scale Habitat Use of Male Ruffed Grouse in the Black Hills National Forest

CASSANDRA L. MEHLS[1], KENT C. JENSEN, MARK A. RUMBLE, AND MICHAEL C. WIMBERLY

Department of Natural Resource Management, South Dakota State University, Brookings, SD 57006, USA (CLM, KCJ)
U.S. Forest Service, Rocky Mountain Research Station, 8221 S. Highway 16, Rapid City, SD 57701, USA (MAR)
GIS Center of Excellence, South Dakota State University, Brookings, SD 57006, USA (MCW)

ABSTRACT Ruffed grouse (*Bonasa umbellus*) are native upland game birds and a management indicator species (MIS) for aspen (*Populus tremuloides*) in the Black Hills National Forest (Black Hills). Our objective was to assess resource selection of male ruffed grouse to identify the most appropriate scale to manage for aspen and ruffed grouse in the Black Hills. During spring 2007 and 2008, we conducted drumming surveys throughout the central and northern Black Hills to locate used and unused sites from which we compared habitat characteristics at increasing spatial scales. Aspen with >70% overstory canopy cover (OCC) was important to the occurrence of ruffed grouse across all spatial scales, but was most influential within 1600 m of drumming sites. Probability of a site being used was maximized when 20% of the 1600-m scale (~804 ha) had aspen with >70% OCC. Ruffed grouse also selected for areas with many small, regular shaped patches of aspen over those with few large patches. At the smallest scale evaluated of 200 m (~12.5 ha), ruffed grouse selected drumming logs in close proximity to high stem densities of aspen with a minimal presence of roads. Ponderosa pine (*Pinus ponderosa*) had a negative influence on site selection at the 400-m (~50 ha), 1600-m (~804 ha), and 4800-m (~7200 ha) scales. Management for ruffed grouse in the Black Hills as the MIS for aspen should focus on increasing the extent of aspen with a goal of at least 20% occurrence on the landscape. Management efforts also should incorporate multiple age and size classes of aspen with an emphasis on enhancing early successional habitat to provide valuable cover through increased stem densities.

KEY WORDS aspen, Black Hills National Forest, *Bonasa umbellus,* display areas, habitat use, *Populus tremuloides,* ruffed grouse, scale

Ruffed grouse (*Bonasa umbellus*) are the most widely distributed upland game bird in North America (Johnsgard 1973) whose geographic range closely corresponds to *Populus* species, primarily quaking aspen (*Populus tremuloides*; Johnsgard 1989). Many studies have provided evidence that ruffed grouse and aspen populations are integrally linked (Gullion and Svoboda 1972, Gullion 1977, Stauffer and Peterson 1985). Ruffed grouse use all successional stages of aspen; sapling to pole-sized trees of early successional stands provides optimal cover from predators and inclement weather due to associated high stem densities, while catkins of mature aspen provides a valuable food resource during the winter (Svoboda and Gullion 1972, Gullion 1977, Gullion and Alm 1983, McCaffery et al. 1997). This close connection with aspen influenced the 1997 Forest Plan Revision for the Black Hills National Forest (Black Hills) in the selection of ruffed grouse as a management indicator species (MIS) for aspen communities (USDA Forest Service 1997). As a MIS species, ruffed grouse populations should indicate the health and abundance of aspen stands.

Landscapes of the Black Hills where aspen stands were once prolific are now in late successional stages often dominated by mixed conifer communities (Bartos 2001). Since European settlement in the Black Hills region, fire suppression, forest management, and ungulate browsing have favored the expansion and dominance of ponderosa pine (*Pinus ponderosa*) and have reduced the extent of aspen (Parrish et al. 1996, Bartos and Shepperd 2003). In response to these landscape vegetation changes, the U.S. Forest Service identified aspen as a management issue and a priority to increase forest diversity in the Black Hills (K. Burns, USDA Forest Service Black Hills National Forest, personal communication). Although ruffed grouse occupancy is currently low in the Black Hills (Hansen et al. 2011*a*), it should increase if the extent and health of aspen is increased.

During spring and fall, male ruffed grouse "drum" on elevated structures, typically logs, to attract females and establish or maintain territories (McBurney 1989). Because our study design was based on drumming sites, our results are primarily focused on habitat requirements of males during spring. However broader inferences can be made to ruffed grouse habitat use. Although male ruffed grouse show strong site fidelity to their drumming logs (Chambers and Sharp 1958, Craven 1989), typically remaining associated with the site throughout their lives (Boag and Sumanik 1969), female ruffed grouse require the same vegetative features during the critical period of winter and early spring (Brander 1965). Forest stands used year-round by drumming males provide protection from weather and predators through high stem densities and overstory canopy cover, which also provides suitable habitat for non-breeding and brood rearing females (Boag and Sumanik 1969, Haulton et al 2003). Consequent-

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[1] Corresponding author email address: casey.heimerl@state.sd.us

ly, male drumming sites are often used to assess ruffed grouse habitat use (Rusch et al. 2000, Zimmerman et al. 2007).

Given the status of ruffed grouse as a MIS and an upland game bird, the South Dakota Department of Game, Fish and Parks also had interest in assessing their status and habitat requirements in the Black Hills. Little is known about ruffed grouse resource selection in the Black Hills. Because landscape and local habitat features drive resource selection (Doherty et al. 2010), we examined the influence of habitat features at multiple spatial scales on male ruffed grouse occurrence. Thus, our objective was to evaluate vegetative features associated with male ruffed grouse habitat use at multiple spatial scales to facilitate an understanding of the appropriate scale to focus management.

STUDY AREA

Our study was located in the Black Hills National Forest of western South Dakota and northeastern Wyoming (Severson and Thilenius 1976). Elevation ranged from 975 m to 2,207 m. Average annual precipitation varied from 46 cm at low elevations to 66 cm at higher elevations in the northern regions (Orr 1959). The climate was continental, averaging 6º C in winter and 22º C in summer (Orr 1959). The dominant vegetation type was ponderosa pine (84%), which had a common understory of white coral berry (*Symphoricarpos albus*), bearberry (*Arctostaphylos uva-ursi*), western snowberry (*S. occidentalis*), and common juniper (*Juniperus communis*; Hoffman and Alexander 1987, Larson and Johnson 2007). White spruce (*Picea glauca*) occupied approximately two percent of the forest and was dominant in cooler, wetter sites at mid to high elevations. Quaking aspen occurred with paper birch (*Betula papyrifera*) on about four percent of the forest as small inclusions within ponderosa pine and white spruce stands or more pure vegetation types on some mountain slopes, drainages, or adjacent to grasslands and streams (Severson and Thilenius 1976, Hoffman and Alexander 1987). Bur oak (*Quercus macrocarpa*), green ash (*Fraxinus pennsylvanica*), and hop-hornbeam (*Ostrya virginiana*) also occurred in isolated patches at low elevations (Hoffman and Alexander 1987, Larson and Johnson 2007). Our study area encompassed the northern two thirds of the Black Hills, north of SD Highway 16. The area of the Black Hills south of SD Highway 16 had limited quantities of aspen and was not incorporated in our study because it included a low probability of locating ruffed grouse drumming sites (Hansen et al. 2011*a*). The study area was separated into three regions of low, medium, or high densities of aspen patches (Fig. 1) based on the ratio of aspen area to total vegetation area.

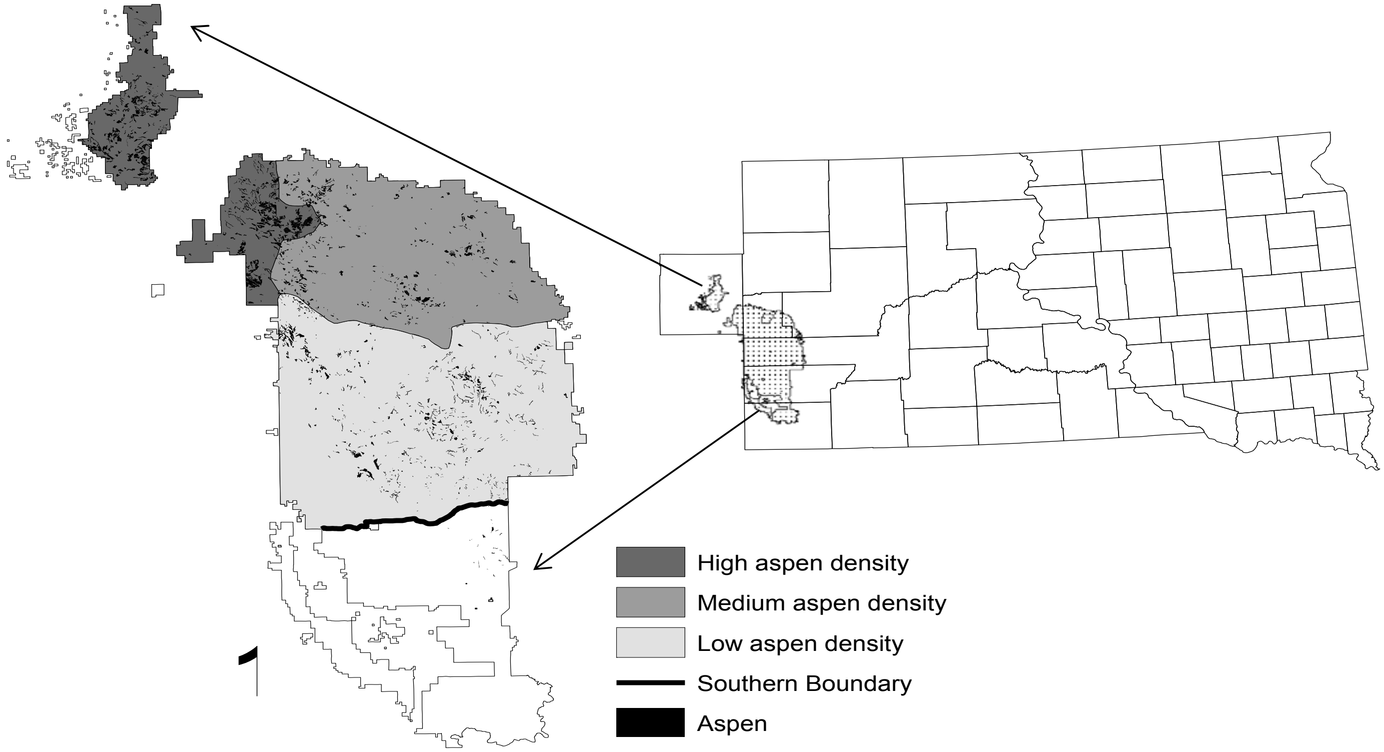

Figure 1. The Black Hills National Forest of western South Dakota and northeastern Wyoming, USA, showing physiographic strata of high, medium and low aspen stem densities.

METHODS

Scales of Study

We based all spatial scales considered on increasing radii centered on used and unused male ruffed grouse drumming sites from the occupancy study of Hansen et al. (2011*a*). Hansen et al. (2011*a*) combined ruffed grouse drumming surveys with occupancy modeling to develop a monitoring protocol which indicates the status, trends, and general habitat associations of ruffed grouse in the Black Hills. In contrast, we utilized similar data but addressed the question of how scale size influences resource selection of male ruffed grouse.

The smallest scale of 200 m radius around a drumming log (~12.5 ha) is approximately the average size of a ruffed grouse activity center or drumming territory (e.g., Gullion 1967). An activity center is the area of the forest most often used by male ruffed grouse during the breeding season and contain the drumming logs (Gullion 1967). The 400-m scale (~50 ha) is the range that males will typically range around the drumming site (Barber et al. 1989). The largest scale extended out to 4,800 m (~7,200 ha) and encompassed movements of female ruffed grouse from an active drumming log to a nest site (Brander 1967) and the approximate distance young ruffed grouse can travel during natal dispersal (e.g., Small and Rusch 1989). In addition, we selected a scale at 1600 m (~804 ha) which represented an intermediate level between the 400-m and 4800-m scales.

Selection of Study Sites

We conducted ruffed grouse breeding surveys of drumming males during spring 2007 and 2008 to estimate occupancy of ruffed grouse and develop a monitoring protocol for the Black Hills (Hansen et al. 2010, 2011*a*). Hansen et al. (2011*a*) calculated the number of survey points and survey frequency using MacKenzie and Royle's (2005) formulas for occupancy models. We selected locations for drumming survey points along secondary and primitive roads (minimal maintenance roads with limited vehicular traffic) using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA), and a stratified random sampling design with aspen patch density (see above) as strata. Hansen et al. (2011*a*) found the farthest distance ruffed grouse could be heard drumming from a survey point was 550 m in the Black Hills. We selected survey points >1.6 km apart to ensure independence and no overlap between points.

We conducted drumming surveys at 402 points three to five times each from 2 April through 31 May in spring 2007 and from 14 April through 7 June in spring 2008 (see Hansen et al. 2011*a*). During surveying, we recorded the detection of a drumming grouse or the lack of a drumming grouse. When drumming was heard at a survey point, we attempted to locate the drumming log by following the sound and either obtaining an observation of the grouse on its log or finding a log with an accumulation of fresh droppings (Hansen et al. 2011*b*). When the location of a used log was confirmed, we recorded the coordinates of the center of the log on a hand held geographic position system (GPS) unit. We used these coordinates as the center point for our used sample sites. When multiple drumming logs were located in close proximity (<100 m) to one another at an individual survey point, we randomly selected one of the logs to use as the center point for the used site.

Across the two-year sampling period, we documented a total of 32 independent used sites (Hansen et al. 2011*a*). We randomly selected 32 unused sites from the remaining 370 road survey points where drumming ruffed grouse were not detected to compare habitat features between used and unused ruffed grouse drumming locations. At the 200-m and 400-m scales we selected sites within three strata reflecting the extent of aspen. Within each region, we paired a used site with the nearest unused survey point. If used sites shared a nearest unused survey point, we selected the second or third nearest location. To limit the amount of scale overlap at the larger 1600-m and 4800-m scales, we used a random number generator to randomly select 32 unused sites from all road survey points in the study area where ruffed grouse were not detected.

Field Methods

200-m scale.—We measured vegetation features surrounding used and unused drumming sites at the smallest scale of 200 m. The average distance between the center of the used drumming logs and their associated survey point along secondary and primitive roads was approximately 100 m. At each unused road survey point, we randomly selected a compass bearing and traveled 100 m along the bearing. We then identified the first fallen log that was ≥10 cm in diameter (Hansen et al. 2011*a*) that was unused (no fecal droppings of ruffed grouse). We recorded a GPS coordinate at the center of the unused log, which we then used as the center point for our unused site. If the compass bearing led through impassable terrain or private property, we selected a new bearing in the same random manner.

We measured vegetation features along eight, 200-m transects which radiated outward in 45º increments from the center point on the used or unused drumming log. We located one 10-m fixed-radius plot (Mannel et al. 2006) at the center point and three additional 10-m plots at 67 m intervals along each 200-m transect (n = 25 for each site). Beginning at the center of each 10-m fixed-radius plot we had four, 10-m transects placed in each cardinal direction (n = 40 for each site). We measured overstory canopy cover along these transects at 1-m intervals using a moose horn (Garrison 1949). We calculated percent canopy cover for each plot and averaged the values across the 25 plots to obtain percent canopy cover for the entire site. Within each plot we also recorded species and diameter at breast height (dbh) of all trees with a dbh ≥12.7 cm and tallied all saplings (dbh 2.54 cm to 12.7 cm).

GIS Analysis

Stem density at 200-m scale.—We calculated total stem density at each of the 25 sample plots for ponderosa pine saplings and for combined aspen sapling and trees. We included ponderosa pine sapling stem density as a variable to determine if ruffed grouse were utilizing the close spacing of trees in young ponderosa pine stands as an additional source of cover. We interpolated the values for both species across the 200-m scale using inverse distance weighting (IDW) using the Spatial Analyst tool in ArcGIS 9.3. Inverse distance weighting estimates stem densities of pine saplings and aspen continuously for intervals between measured plots by weighting the average of the values recorded at sampled points within the same region. Weighted means are inversely related to the distance between unsampled locations and sampled plots. They are based on the assumption that a sampled plot closer to the unsampled locations better represents the value to be estimated then plots located farther away (Lu and Wong 2008). We used a natural breaks classification scheme previously developed by Jenks (1967), with a designated value of ≥1,000 stems/ha which included the top 10% of stem density values for both ponderosa pine saplings and aspen. This defined the boundaries of what we termed "high" stem density patches for both species, relative to what was available around the sites. We then calculated percent coverage in the high stem density class for ponderosa pine saplings and aspen.

Vegetation composition at 200-m, 400-m, 1600-m, and 4800-m scales.—We obtained information for vegetation composition in the Black Hills using the Resource Information System (RIS) GIS layer obtained from the U.S. Forest Service. This database classifies vegetation types into patches using a hierarchical system based on dominant vegetation type, dbh, and overstory canopy coverage (Buttery and Gillam 1983). At the 200-m, 400-m, and 1600-m scales we modified the RIS database by delineating and digitizing aspen patches that were not included in the original layer using 1:24,000 color aerial photos of the Black Hills taken in August and September of 2007. During these months, stands of aspen appeared either light green or yellow in color and were discernible from the surrounding forest stand. If a polygon (a delineated aspen patch greater than 0.02 ha) was composed of ≥50% aspen we assigned it the attribute of "aspen". We delineated "mixed aspen" patches if estimated composition was <50% aspen in the polygon. We compared the newly digitized polygons with adjacent previously mapped Forest Service lands to determine the overstory canopy cover (OCC) as 0–40% OCC, 40–70% OCC, or >70% OCC (Buttery and Gillam 1983). The RIS database only covered Black Hills National Forest lands, so we also mapped vegetation composition of private lands using the 1:24,000 aerial photos and identified patches to vegetation type and overstory canopy cover. We did not map aspen inclusions at the 4800-m scale because we assumed this spatial extent was too large for small patches of aspen to influence resource selection.

Using the edited RIS database we calculated percent area of the 200-m, 400-m, 1600-m, and 4800-m scales in aspen, ponderosa pine, white spruce, and aspen/ponderosa pine mixed vegetation types. We further categorized the aspen, ponderosa pine, and mixed vegetation types by percent area of each in 0–40% OCC, 40–70% OCC, and >70% OCC at each scale. We used percent of area to standardize values for variables across spatial scales. We calculated average patch size using the 2009 GIS roads coverage for the Black Hills and split polygons by the roads layer. We recalculated the area of each polygon and summarized average patch size for aspen, ponderosa pine, and mixed vegetation types.

Vegetation configuration at 200-m, 400-m, 1600-m, and 4800-m scales.—Using GIS we measured the distance from the center of used drumming logs and randomly selected logs at unused sites to the nearest patch of aspen. We calculated the average distance between each patch of aspen using the average nearest neighbor tool (Spatial Statistics) in ArcGIS, and tallied the number of aspen patches at each scale size. We calculated a mean shape index (MSI) for aspen patches by dividing the sum of aspen patch perimeters by the square root of the patch areas adjusted for a circular standard. Mean shape index equaled one when all patches were circular and increased as average patch shape became increasingly irregular (McGarigal and Marks 1994). We intersected a GIS roads layer obtained from the U.S. Forest Service with vegetation coverage to establish polygons created by roads to consider the influence of roads on patch shape. We also used the roads layer to tabulate the total length of roads at 200-m, 400-m, and 1600-m scales.

Data Analyses

We conducted all statistical analyses using SPSS version 11.5 for Windows (SPSS Incorporated 2002; SPSS Inc., Chicago, IL, USA). We reduced many initial variables by examining univariate likelihood ratio test statistics with a critical value of $\alpha \leq 0.15$ to identify the important predictors between used and unused sites (Hosmer and Lemeshow 2000, Guthery et al. 2005, Stephens et al. 2005). We also evaluated collinearity among variables using Pearson's correlation coefficients and eliminated one variable when $r \geq 0.70$, keeping the variable with the lowest α value from the univariate likelihood ratio test.

We assumed that not all variables would have a linear influence on site selection, therefore, we determined the best supported structural form for each variable from four possible options: linear, quadratic, exponential, and pseudothreshold.

The linear form assumes the effect of the variable on selection increases or decreases at a constant rate, $\Theta=\beta_1(x)$, where Θ is selection and x is the covariate. The quadratic form assumes the effect of the variable on selection reaches a peak or valley, $\Theta=\beta_1(x) + \beta_2(x^2)$, the exponential form assumes the variable has an exponential effect on selection, $\Theta=\beta_1 e^{(x)}$, and the pseudothreshold form assumes the effect of the variable on selection stabilizes at some point, $\Theta=\beta_1 log_e(x+1$; Franklin et al. 2000). We used Akaike's Information Criterion corrected for small sample size (AIC_c) to compare relative support of each structural form for each individual variable and retained the form with the lowest AIC_c value (Burnham and Anderson 2002).

Model development.—Using the most supported structural form of each variable after the variable screening process, we developed linear additive models for each scale size to evaluate resource selection at multiple spatial scales. The 200-m scale included 20 candidate models that incorporated vegetation features from field data such as percent canopy cover, percent area in high aspen stem density and percent area in high ponderosa pine sapling stem density. Geographic information system variables at the 200-m scale included percent aspen, percent aspen >70% OCC, percent ponderosa pine <40% OCC, number of aspen patches, distance to nearest patch of aspen, and total road length.

The 400-m, 1600-m, and 4800-m scale candidate models included variables from the GIS analysis. The 20 candidate models at the 400-m scale included the GIS variables at the 200-m scale, and percent ponderosa pine, percent ponderosa pine >70% OCC, and aspen mean shape index (MSI). The 20 candidate models at the 1600-m scale included variables from the 400-m scale and added aspen <40% OCC, ponderosa pine 40–70% OCC and average distance between aspen patches. There were only eight candidate models at the 4800-m scale due to the few variables for use after the variable screening process. The models included aspen cover, aspen 40–70% OCC, ponderosa pine cover, and number of aspen patches.

We evaluated all models using logistic regression and an information theoretic approach (Burnham and Anderson 2002). We ranked the candidate models using AIC_c and considered models within 2 ΔAIC_c units to be supported. Our models were developed to explore habitat relations opposed to predicting ruffed grouse occurrence on the landscape; therefore we did not conduct any model averaging for competitive models. We evaluated model strength of support for each model using Akaike weights (w_i; Burnham and Anderson 2002) and receiver operating characteristic (ROC) curve with values between 0.7 and 0.8 considered acceptable discrimination and values greater than 0.8 considered excellent discrimination (Hosmer and Lemeshow 2000).

Post hoc analysis.—To determine the most appropriate scale to manage for ruffed grouse, we constructed 25 additional models that incorporated the covariates from the top ranked candidate models from each scale. If covariates were represented across multiple scales (e.g., aspen >70% OCC was included at both 400-m and 1600-m and pine cover was included at 1600-m and 4800-m) we included them individually at each scale with a suite of other variables. We also ran the models using logistic regression, and used the same methods as previously described to rank and assess model fit.

RESULTS

200-m Scale

The model with the greatest support ($w_i = 0.42$) predicting used from unused sites included the variables of high aspen stem density (positive exponential relationship), distance from the drumming log to the nearest patch of aspen (negative pseudothreshold relationship), and total length of roads (negative pseudothreshold relationship; Tables 2, 3). Used sites on average had 20.03/3.89 = 5.15 times more coverage in high aspen stem densities than unused sites (Table 1). When the proportion of the 200-m scale in high aspen stem density was greater than 60% the probability of a site being used was maximized (Fig. 2). Aspen patches were on average three times closer to used sites than unused (Table 1), although the confidence intervals for the parameter estimate overlapped zero suggesting that this variable had little effect on predicting site use by ruffed grouse. The probability of a site being used declined as total length of roads increased and reached a minimum when total road length exceeded 1 km (Fig. 3). The model had a ROC value of 0.91, indicating excellent discrimination.

400-m Scale

The top ranked model ($w_i = 0.44$) predicting used from unused sites included the variables of percent aspen >70% OCC (positive pseudothreshold relationship), percent ponderosa pine <40% OCC (negative exponential relationship), and aspen MSI (negative linear relationship; Tables 2, 3). The percentage of coverage in aspen with >70% OCC was 10.87/4.59 = 2.37 times greater for used versus unused sites (Table 1). When the proportion of the 400-m scale in aspen with >70% OCC exceeded 50%, probability of a site being used was maximized (Fig. 4A). Used sites also on average had 21.98/11.45= 1.92 times less coverage in pine with <40% OCC than unused sites (Table 1). Male ruffed grouse selected sites with an aspen MSI close to one, or circular in shape. Probability of a site being used declined as MSI increased and patch shape became increasingly irregular. Model discrimination for the top model was acceptable with a ROC value of 0.79.

There was one competing model ($w_i = 0.18$) that exchanged number of aspen patches (positive pseudothreshold relationship) for percent aspen >70% OCC. Unconditional means estimates indicated the number of aspen patches had a

Table 1. Mean and SE of vegetation characteristics at used and unused male ruffed grouse drumming sites in the Black Hills, South Dakota, USA, 2007–2008, used in logistic regression models after variable screening processes.

		Used		Unused		
Scale	Variable	$\bar{x}$	S.E.	$\bar{x}$	S.E.	*P*-value[a]
200 m	aspen (%)	18.59	3.35	7.94	1.99	0.014
	aspen >70% OCC[b] (%)	14.23	2.90	4.99	1.66	0.015
	pine <40% OCC (%)	9.45	2.59	22.26	5.01	0.029
	number of aspen patches	2.88	0.35	1.72	0.35	0.023
	distance to nearest aspen patch (m)	68.64	18.25	199.76	38.10	0.003
	canopy cover (%)	38.87	2.23	30.48	1.93	0.007
	high aspen density (%)	20.03	4.42	3.89	1.55	0.001
	high pine sapling density (%)	14.02	3.25	6.73	1.86	0.055
	road length (km)	0.35	0.03	0.60	0.04	≤ 0.001
400 m	aspen (%)	15.35	2.55	8.70	1.72	0.034
	aspen >70% OCC (%)	10.87	2.13	4.59	1.28	0.014
	pine (%)	37.94	4.38	52.31	4.37	0.024
	pine <40% OCC (%)	11.45	2.07	21.98	3.72	0.017
	pine >70% OCC (%)	2.91	1.12	8.27	1.86	0.017
	number of aspen patches	10.31	1.03	5.31	0.80	≤0.001
	aspen MSI[c]	1.41	0.03	1.52	0.04	0.048
	distance to nearest aspen patch (m)	68.64	18.25	199.76	38.10	0.003
1600 m	aspen (%)	13.20	1.88	8.02	1.61	0.04
	aspen <40% OCC (%)	0.86	0.19	1.82	0.38	0.026
	aspen >70% OCC (%)	8.78	1.30	2.56	0.70	≤0.001
	pine cover (%)	43.56	3.00	68.84	3.11	≤0.001
	pine <40% OCC (%)	14.11	2.06	22.44	2.17	0.008
	pine 40-70% OCC (%)	20.71	1.86	26.77	2.28	0.043
	pine >70% OCC (%)	6.96	1.57	12.55	2.04	0.034
	aspen patch size (ha)	1.13	0.11	1.54	0.19	0.066
	aspen MSI[c]	1.40	0.01	1.48	0.03	0.031
	number of aspen patches	82.72	9.05	39.75	6.06	≤0.001
	distance between aspen patches (m)	180.28	14.14	257.06	28.38	0.017
4800 m	aspen (%)	11.72	2.41	4.46	0.86	0.007
	aspen 40-70% OCC (%)	3.06	0.55	1.43	0.33	0.014
	pine (%)	75.96	1.45	82.76	1.95	0.007
	number of aspen patches	69.66	7.53	43.5	6.85	0.013

[a] Probability of significant differences between used and unused sites from log ratio test; [b] Overstory Canopy Cover; [c] Mean Shape Index (sum of aspen patch perimeters divided by the square root of the patch areas adjusted for a circular standard. MSI equals one when all patches are circular and increases as average patch shape became increasingly irregular [McGarigal and Marks 1994]).

positive influence on the probability of a site being used with used sites having two times the number of aspen patches occurring within 400 m than at unused sites (Table 1). Model discrimination also was acceptable (ROC = 0.78).

1600-m Scale

The model with the greatest support ($w_i = 0.50$) predicting used from unused sites included the variables of percent aspen >70% OCC (positive pseudothreshold relationship), pine cover (negative exponential relationship), and aspen patch size (negative linear relationship) (Tables 2, 3). The percentage of coverage in aspen with >70% OCC was 8.78/2.56 = 3.4 times greater at used sites than unused (Table 1). When the proportion in aspen with >70% OCC exceeded only 20%, the probability of a site being used was maximized (Fig. 4B). Used sites also on average had 68.84/43.52 = 1.58 times less ponderosa pine cover than unused sites at the 1600-m scale

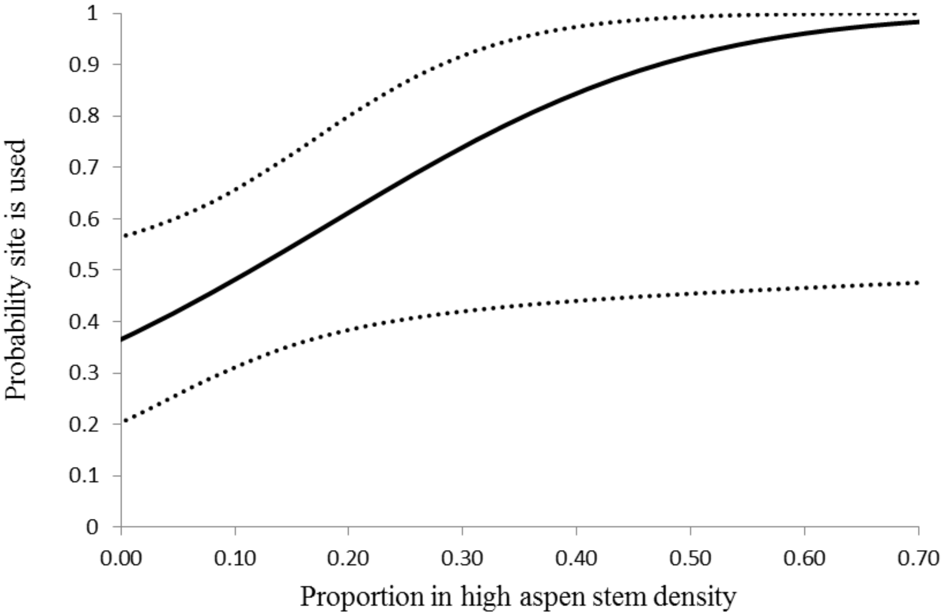

Figure 2. Probability of a site being used by male ruffed grouse with the proportion of the 200-m scale in high aspen stems densities (≥1,000 stems/ha) in the Black Hills, South Dakota, USA, 2007–2008. Dashed lines represent the upper and lower 95% confidence limits.

Table 2. Top ranked logistic regression models predicting male ruffed grouse used versus unused drumming sites at the 200-m, 400-m, 1600-m, 4800-m scales, and across all spatial scales in the Black Hills, South Dakota, USA, 2007–2008. Only models within 2 ΔAIC_c are shown.

Scale	Model covariates[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]
200 m	high aspen stem density_E + distance to aspen_P + road length_P	5	58.23	0.00	0.42
400 m	aspen >70%OCC_P + pine <40%OCC_E + aspen MSI_L	5	74.64	0.00	0.44
	aspen patch #_P + pine <40%OCC_E + aspen MSI_L	5	76.44	1.80	0.18
1600 m	aspen>70% OCC_P + pine_E + aspen patch size_L	5	57.13	0.00	0.50
4800 m	aspen_P + pine_Q	5	81.76	0.00	0.49
Multiscale	high aspen stem density 200_E + road length 200_P + aspen MSI 400_L + aspen >70% OCC 1600_P + aspen patch size 1600_L	7	38.53	0.00	0.63

[a] The structural form of each covariate (Linear [L], quadratic [Q], pseudothreshold [P], exponential [E]) was determined individually using univariate logistic regression and AIC_c; [b] Number of parameters including intercept and SE; [c] Akaike's information criterion corrected for small sample size; [d] Change in AIC_c relative to minimum AIC_c; [e] Akaike weight (Burnham and Anderson 2002).

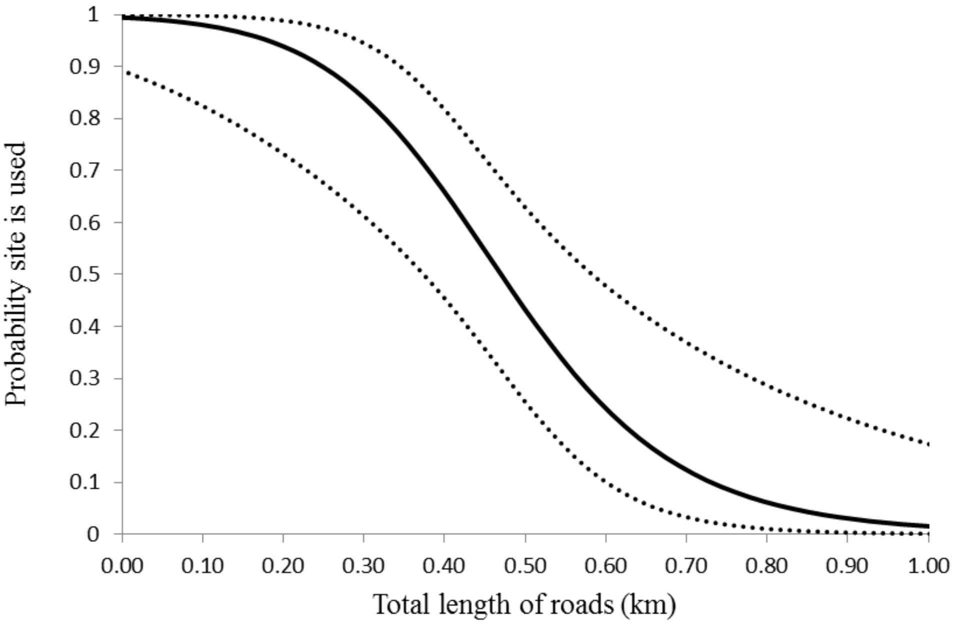

Figure 3. Probability of a site being used by male ruffed grouse with the total length of roads within the 200-m scale in the Black Hills, South Dakota, 2007–2008. Dashed lines represent the upper and lower 95% confidence limits.

Table 3. Regression coefficients, SE, and 95% confidence intervals of covariates from the best approximating models at the 200-m, 400-m, 1600-m, and 4800-m scales predicting male ruffed grouse used versus unused sites in the Black Hills, South Dakota, 2007–2008.

Scale	Covariate		β-estimate	SE	Lower 95% CI	Upper 95%CI
200 m	high aspen stem density_E		4.56	2.26	0.12	9.00
	road length_P		−13.47	4.01	−21.33	−5.61
	distance to aspen_P		−5.73	3.16	−11.93	0.47
400 m	aspen >70% OCC_P		10.30	4.23	2.02	18.59
	pine <40% OCC_E		−3.51	1.63	−6.72	−0.32
	aspen MSI_L		−5.07	2.04	−9.07	−1.08
1600 m	aspen >70% OCC_P		32.61	12.83	7.47	57.75
	pine_E		−3.09	1.37	−5.77	−0.41
	aspen patch size_L		−2.25	0.88	−3.97	−0.53
4800 m	aspen_P		10.18	5.88	−1.35	21.71
	pine_Q[a]	x	87.25	49.79	−10.33	184.83
		x^2	−58.88	32.07	−121.73	3.98

[a] The quadratic form of the equation is a polynomial including the linear (x) and nonlinear (x^2) form.

(Table 1). The probability of a site being used decreased by almost half as the proportion of the 1600-m scale in ponderosa pine cover increased from 0 to 60% (Fig. 5). Sites used by drumming male grouse had aspen patches that averaged 0.40 ha smaller then unused sites (Table 1). The model had a ROC value of 0.92 indicating excellent discrimination.

4800-m Scale

The most supported model (w_i = 0.49) predicting used from unused sites included the variables of aspen cover (positive pseudothreshold relationship) and pine cover (quadratic relationship; Tables 2, 3). Estimates for regression coefficients had wide confidence intervals that overlapped zero,

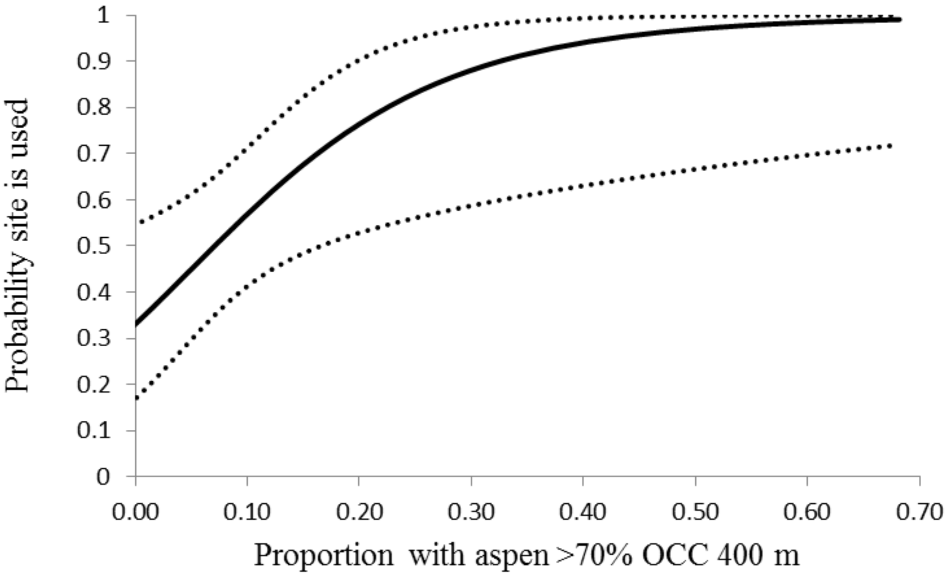

Figure 4A. Probability of a site being used by male ruffed grouse with the proportion of aspen with >70% OCC within the 400-m scale in the Black Hills, South Dakota, 2007–2008. Dashed lines represent the upper and lower 95% confidence limits.

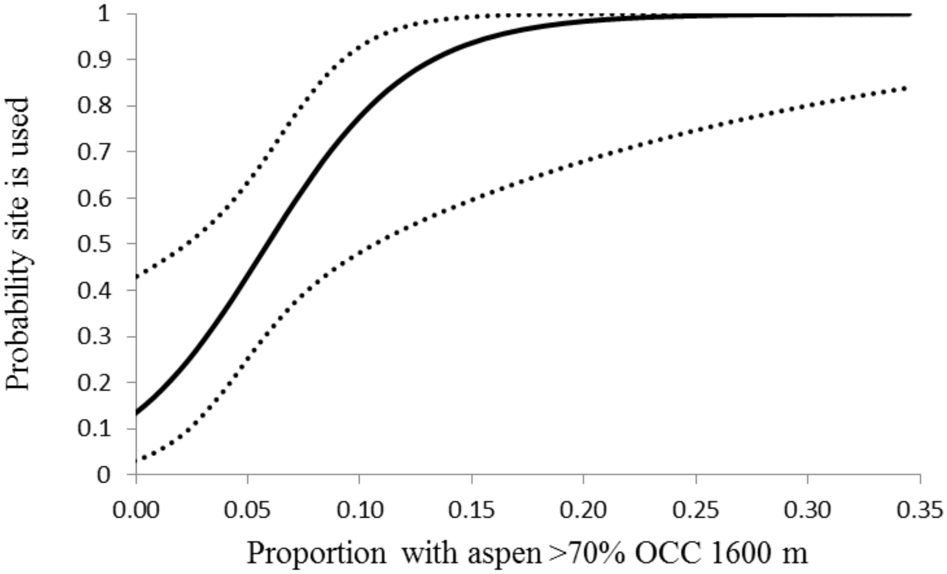

Figure 4B. Probability of a site being used by male ruffed grouse with the proportion of aspen with >70% OCC within the 1600-m scale in the Black Hills, South Dakota, 2007–2008. Dashed lines represent the upper and lower 95% confidence limits.

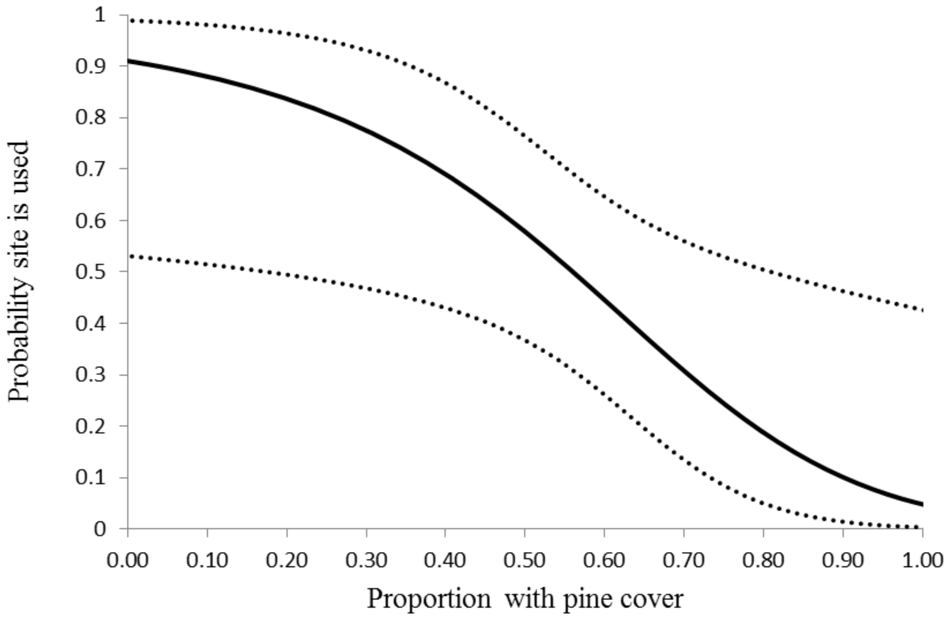

Figure 5. Probability of a site being used by male ruffed grouse with the proportion of ponderosa pine cover within the 1600-m scale in the Black Hills, South Dakota, USA, 2007–2008. Dashed lines represent the upper and lower 95% confidence limits.

suggesting these covariates had little effect on site use by ruffed grouse. Model discrimination was acceptable (ROC = 0.78).

Multi-scale Evaluation

The combined evaluation of individual scale models showed that across all spatial scales the most supported model ($w_i = 0.63$) included variables of aspen in high stem densities at 200 m, total length of roads at 200 m, aspen MSI at 400 m, aspen with >70% OCC at 1600 m, and aspen patch size at 1600 m. The model had a ROC value of 0.98 indicating excellent discrimination.

DISCUSSION

Recent studies of avian resource selection have recognized that species select habitats at multiple spatial scales (Bergin 1992, Saab 1999, Sodhi et al. 1999, Bakermans and Rodewald 2006, Doherty et al. 2010). We found variations in selected vegetation structure and composition as the spatial scale changed, but the primary factors that remained consistent across all scales were a positive influence of aspen and a negative influence of ponderosa pine cover. As the spatial scale decreased in size, selection occurred for finer scale vegetation attributes of the two cover types.

The largest scale at which an organism responds to the surrounding environment is the extent of an ecological system and it forms the uppermost boundary for hierarchal selection (Kotliar and Wiens 1990). The largest scale at 4800 m covered almost 60% of the study area and indicated male ruffed grouse site use was connected to the extent of aspen and was negatively associated with ponderosa pine cover throughout the Black Hills. Both variables of aspen and pine cover had a high degree of variability in the individual scale modeling and neither was included in the top multiscale model, suggesting this spatial extent is likely too large to be perceived by ruffed grouse and is not applicable for management efforts.

While greater aspen cover was important at both the 400-m and 1600-m scales, our combined modeling showed that it had the most influence on site occupancy at the 1600-m scale, suggesting this was a more appropriate spatial extent to direct management for increasing aspen. This scale incorporates the typical home range or territory size for several individual ruffed grouse and managing at this size increases the likelihood of a site being used. At the 1600-m scale, male ruffed grouse also selected areas with an interspersion of many small patches of aspen over few large patches. Aspen patches were on average 0.40 ha smaller at used sites but the total area of aspen was greater than at unused sites. Landscapes that contain a high density of relatively small aspen patches opposed to those with few large patches could potentially have a greater diversity of aspen size classes.

Due to fire suppression, forest management practices, and ungulate browsing, aspen in the Black Hills occurs in fragmented small patches (Parrish et al. 1996, Bartos and Shepperd 2003). Ponderosa pine and white spruce also are encroaching into aspen stands, consequently leading to the decline of aspen (Parrish et al. 1996). Conifer encroachment into aspen stands may have reduced aspen by 60% in the Black Hills from pre-European conditions (D. Bartos, Rocky Mountain Research Station, personal communication). This ecological trend was likely reflected in the negative relation between probability of use and ponderosa pine cover in the model at the 1600-m level. The landscapes selected by male ruffed grouse with many fragmented small patches of aspen may be the most suitable remaining habitat in the Black Hills.

The negative relationship of the aspen MSI at the 400-m scale suggested that male ruffed grouse preferentially selected more regularly shaped patches of aspen over those with more irregular and linear shape often occurring in draws in the Black Hills. Fearer and Stauffer (2003) also found that ruffed grouse home range size increased with the irregularity of the shape of patches in the landscape, suggesting that irregular shaped aspen patches provided lower quality habitat. Compact, circular patches often contain higher plant species richness then elongated irregular patches (Forman 1995). Aspen patches with an irregular shape are more likely to be impacted by temporal and spatial encroachment of ponderosa pine and the effects of the surrounding environment (Hamazaki 1996). Considering two patches of the same area (e.g., one circular in shape and the other irregular), ponderosa pine encroaching on the perimeter of a patch would cause a proportionally greater decline in area of the irregular patch due to the increased amount of edge. Conifer encroachment into aspen can greatly suppress the understory biomass production of aspen stands (Stam et al. 2008), which could reduce cover and food resources for ruffed grouse.

At the 200-m scale, male ruffed grouse selected for the location and structure of vegetation within patches of aspen. The region within 200 m of a drumming log is the activity center of male ruffed grouse where drumming and breeding activities are concentrated (Gullion 1967). Male ruffed grouse are more conspicuous while drumming, therefore drumming sites need to provide cover surrounding the log to avoid predation (McBurney 1989). Hansen et al. (2011*b*) found ruffed grouse in the Black Hills selected drumming sites with low visibility between 0.9 m and 1.8 m and high density of herbaceous and woody stems >1 m in height to avoid predation. In our study, male ruffed grouse selected activity centers with high stem densities of aspen surrounding drumming logs. The regular, dense spacing associated with young aspen stands with high stem densities provides protective cover from avian and terrestrial predators of ruffed grouse (Gullion 1977, Barber et al. 1989). In northern Minnesota, where aspen is prevalent across the landscape, Gullion (1977) recommended a stem density of aspen for breeding ruffed grouse of approximately 12,000 to 20,000 stems/ha. In our study, stem density of aspen at used sites averaged approximately 600 stems/ha (compared to 50 stems/ha at unused sites), far below this recommendation.

MANAGEMENT IMPLICATIONS

The combined multiscale model suggests the largest spatial scale appropriate for aspen management in the Black Hills to benefit male ruffed grouse was at 1600-m radius area (256 ha). We believe the greatest benefit of restoring aspen would occur in areas where it occurred historically with a goal of comprising 20% of the landscape. Management techniques for aspen such as cutting, burning and spraying should also create regular shaped patches to increase and maintain understory diversity. As a MIS for the health and abundance of aspen communities in the Black Hills, the presence of ruffed grouse should be an indication of the success of our management recommendations.

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