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Resource Selection Habitat Model for Northern Flying Squirrels in the Black Hills, South Dakota

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Abstract.—Northern flying squirrels (*Glaucomys sabrinus*) of the Black Hills National Forest (BHNF) of South Dakota represent a unique and isolated population, but little is known about the distribution and habitat use of this population. A resource selection function (RSF) habitat model was created for northern flying squirrels (*G. sabrinus*) throughout BHNF. Using methods from Manly *et al.* (2002) and Johnson *et al.* (2006), logistic regression was used to compare habitat variables at used habitat locations (radio-tracking and trapping locations) to a random sample of available habitat locations throughout the study area. Logistic regression coefficient estimates of significant variables were incorporated into a GIS raster layer to produce a map with RSF values for BHNF. The RSF values were transformed to a relative probability of habitat use ranging from 0 to 1. Independent validation data were used to determine model fit based on predictive performance of the RSF. Data used in the model determined that northern flying squirrels in BHNF used habitats with higher precipitation, closer distance to a stream, aspen (*Populus tremuloides*), northwest aspect, higher basal area of snags and a higher density of live trees and snags than randomly available habitats. The RSF map identifies possible high use areas of habitat by northern flying squirrels throughout BHNF and is useful for management purposes, as well as a baseline for future research and monitoring for an isolated population at the southern edge of their range.

Introduction

Data on habitat use, obtained through radiotelemetry, can be integrated into geographic information systems (GIS) to create species-specific resource selection function (RSF) habitat models (Gibson *et al.*, 2004; Posillico *et al.*, 2004). Manly *et al.* (2002) defined RSFs as any function that is proportional to the probability of use by an organism. Mapping the potential distribution based on model predictions identifies possible high use areas that aid resource managers in determining important habitats for management (Fielding and Bell, 1997).

The ecology of northern flying squirrels is as varied as the forest communities in which it occurs (Smith, 2007). Across their range northern flying squirrels use habitats with features typical of mature forest, including large-diameter trees (Holloway, 2006; Lehmkuhl *et al.*, 2006; Smith *et al.*, 2004), large snags (Carey, 1995; Carey *et al.*, 1999; Holloway and Malcolm, 2006; Smith *et al.*, 2004), coarse woody debris (Carey *et al.*, 1999; Smith *et al.*, 2004) and truffle abundance (Lehmkuhl *et al.*, 2006; Waters and Zabel, 1995). Northern flying squirrels typically inhabit mixed-coniferous-hardwood forests or dominant coniferous forests across their range (Weigl, 1978; Wells-Gosling and Heaney, 1984; Carey *et al.*, 1999; Holloway, 2006)

Movements, home range size and use of space appear to be influenced by availability of food resources (Menzel *et al.*, 2006a), primarily truffles (Gomez, 2005), as well as by the availability of suitable den sites (Carey, 1995; Carey *et al.*, 1997). Northern flying squirrel diet primarily consists of mycorrhizal fungus fruiting bodies, truffles, (North *et al.*, 1997; Carey *et al.*, 1999; Ransome and Sullivan, 1997, 2004; Weigl, 2007), but they also consume lichens,

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buds, berries, staminate cones and animal material (Weigl, 2007). For denning, northern flying squirrels use cavities in live hardwoods (Carey *et al.*, 1997; Cotton and Parker, 2000; Hackett and Pagels, 2003; Holloway and Malcolm, 2007; Hough and Dieter, 2009b), cavities in snags (Maser *et al.*, 1981; Bakker and Hastings, 2002; Meyer *et al.*, 2005; Hough and Dieter, 2009b) and conifers for external dray nests (Mowrey and Zasada; 1984; Carey *et al.*, 1997; Cotton and Parker, 2000; Hough and Dieter, 2009b).

In the Black Hills National Forest (BHNF), there is an isolated population of northern flying squirrel, *Glaucomys sabrinus bangsi* (Rhoads) (King, 1951; Wells-Gosling and Heaney, 1984) that is restricted to this region of western South Dakota. Due to its rarity, isolation and population risk because of restricted range, northern flying squirrels within the BHNF are considered a Forest Service Species of Local Concern (USDA Forest Service, 2005) and a Species of Special Concern (S2) by the South Dakota Natural Heritage Program (South Dakota Department of Game Fish and Parks, 2006).

Despite the increase in northern flying squirrel research over the last two decades across their range, disjunct populations at the southern edge of their range, such as the BHNF population, have not been well studied (Weigl, 2007; Smith, 2007). Prior to this study two other studies were conducted in (northern Black Hills; Krueger, 2004) or adjacent to (Wind Cave National Park; Duckwitz, 2001) BHNF, but they were limited in study area extent and duration. Studying the BHNF population is important because there is a threat to disjunct squirrel populations, such as those at the southern edge of their range that may be impacted by human activities (*e.g.*, clear-cutting, development), which destroy extensive tracts of habitat (Koprowski, 2005; Weigl, 2007).

The objectives of this study were to determine probability of habitat selection throughout the Black Hills and potential distribution. Logistic regression was used to compare habitat variables at radio-tracking and trapping locations (used habitats) to characteristics within the Black Hills study area (available habitats). Logistic regression is commonly used in wildlife studies to predict habitat use throughout a study area (Fielding and Haworth, 1995; Mladenoff *et al.*, 1999). The GIS map layer produced from the model will help wildlife managers determine important areas of northern flying squirrel habitats, as well as provide a baseline for future research.

MATERIALS AND METHODS

Study area.—This study was conducted in the BHNF, located in western South Dakota (UTM 13N 574719–641489 E, 4809979–4932866 N) (Fig. 1). The BHNF is a unique ecosystem that consists of forest surrounded by Great Plains grasslands (Froiland, 1990). The ponderosa pine dominated hills extend 900–1200 m above the surrounding Great Plains prairie. The Black Hills were formed by mountain uplift, extend 200 km north to south and 100 km east to west and encompass 486,000 ha. Topography varies from steep ridges, rock outcrops, canyonlands and gulches to upland prairie, rolling hills and tablelands. Their elevation range is approximately 1200 to 2207 m, with the forested region extending to 2102 m (Froiland, 1990).

The southern Black Hills, has a warmer (9.3 C) and drier (45–51 cm/y) annual climate than the northern portion of the range (7.2 C and 61–66 cm/y; Shepperd and Battaglia, 2002). Ponderosa pine is found throughout the BHNF and is the most abundant tree species, dominating 83% of the landscape (USDA Forest Service, 2005). In the central to southern hills quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) are interspersed with pine in the bottomlands and along water sources, spruce occurs sporadically and is commonly found along streams, and there is little to no understory. In

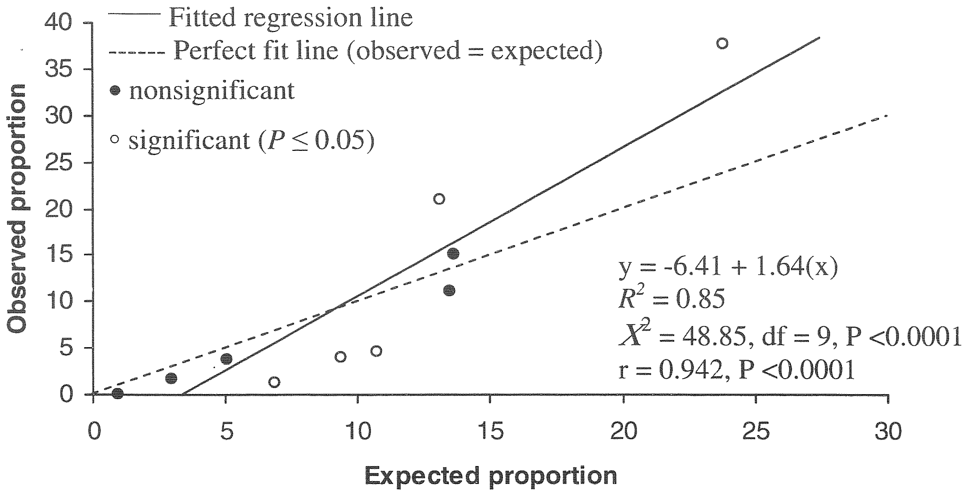

FIG. 1.—Fitted regression of 10 resource selection function (RSF) bins (categories) for proportion of expected versus observed validating data locations (n = 300) for a RSF habitat model for northern flying squirrels studied in the Black Hills National Forest (May–Aug., 2005–2007). Black circles are bin observations not significantly different from expected. Hollow circles are bin observations significantly different from expected. Spearman rank correlation ® and overall goodness-of-fit (χ^2) test results are provided

the northern hills white spruce is more abundant, comprising 2% of the vegetation (USDA Forest Service, 2005). The northern hills has an understory component, primarily bur oak (*Quercus macrocarpa*), but may also include American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*) and eastern hop-horn-beam (*Ostrya virginiana*) (Hoffman and Alexander, 1987). Quaking aspen and paper birch dominate moister environments, particularly in disturbed areas, of the central to northern BHNF (Hoffman and Alexander, 1987).

Habitat model.—To create a RSF habitat model for northern flying squirrels, we downloaded digital databases from the Black Hills National Forest Service website (USDA Forest Service, 2006). The databases included a vegetation polygon layer, digital line graph of streams and digital elevation model (10 m resolution). Precipitation databases for South Dakota and Wyoming were downloaded from the Water and Climate Center of the Natural Resources Conservation Service website (USDA Natural Resources Conservation Service, 2007).

The vegetation layer provided vegetation composition and structure variables along with landscape features for a site. Variables taken from the vegetation layer were habitat types (grass-shrub, aspen-birch, bur oak, pine and spruce), structural stage (1–2, 3A, 3B, 3C, 4A, 4B, 4C), aspect, # live trees/ha, basal area (m^2) of live trees ≥12.7 cm dbh, basal area (m^2) of dead trees ≥12.7 cm dbh, # dead and down trees ≥12.7 cm dbh and # snags ≥12.7 cm dbh. Descriptions of variables used in the model are provided in Table 1. Structural stage 1–2 is grass-shrub habitat, which was not used by northern flying squirrels; therefore, this variable was not included in the model. Spatial analyst extension (Environmental Systems Research Institute, 2004) was used in ArcGIS 9.1 to convert the vector polygon layer to a

TABLE 1.—Description of variables considered for the resource selection function (RSF) habitat model for northern flying squirrels studied in the Black Hills National Forest (May–Aug., 2005–2007)

Variable	Description
Continuous	
Elev	Elevation in meters.
Precip	Average annual precipitation in centimeters.
DistStrm	Distance to nearest stream in meters.
LiveHa	Total number of live trees per hectare.
LiveBA	Sum of the basal area (m^2/ha) of live trees ≥12.7 cm dbh.
DeadBA	Sum of the basal area (m^2/ha) of dead trees ≥12.7 cm dbh. This includes all salvageable and unsalvageable standing mortality, down mortality, standing sound snags, down sound snags, or standing unsound snags.
DeadDown	The number of dead and down trees with a dbh ≥12.7 cm. This includes salvageable and unsalvageable down mortality, down sound snags, or down unsound snags.
TotalSnags	Total number of standing mortality trees, hard snags and soft snags with a dbh >12.7 cm per hectare.
Categorical	
GRA	Grass-shrub habitat
TAA	Aspen-birch habitat
TBO	Bur oak habitat
TPP	Ponderosa pine habitat
3A	Habitat structural stage with trees 2–23 cm dbh and 11–40% canopy cover.
3B	Habitat structural stage with trees 2–23 cm dbh and 41–70% canopy cover.
3C	Habitat structural stage with trees 2–23 cm dbh and <71% canopy cover.
4A	Habitat structural stage with trees 23–40 cm dbh and 11–40% canopy cover.
4B	Habitat structural stage with trees 23–40 cm dbh and 41–70% canopy cover.
4C	Habitat structural stage with trees 23–40 cm dbh and <71% canopy cover.
NO	North aspect
NE	Northeast aspect
EA	East aspect
SE	Southeast aspect
SO	South aspect
SW	Southwest aspect
WE	West aspect
NW	Northwest aspect

raster dataset with 30 m resolution. Spatial analyst was also used to create a 30-m raster dataset depicting distance from streams. All layers were projected to UTM World Geodetic System 1984 coordinate system. The model was produced for the contiguous national forest land within the Black Hills of South Dakota and Wyoming. JMPIN 4.0 (SAS Institute Inc., Cary, North Carolina) was used to create the model and the model was integrated into ArcGIS 9.1 to produce the RSF habitat suitability map. Where not already stated rejection limit was set to $\alpha = 0.05$. Where applicable, Shapiro-Wilk's test was used to test variables for normality. Nonparametric tests were performed because assumptions of normality and heterogeneity were not always met.

There were 1503 trapping ($n = 223$), tracking ($n = 1255$) and observational ($n = 25$) locations for northern flying squirrels used in producing and validating the RSF habitat model. The locations were collected from 2005–2007 and data were pooled across all study years. Three hundred (20%) random points were removed from the sample of used habitat locations for use in validating the model. A random sample of 1203 points, with replacement, was taken from the study area to describe the available habitat.

Spatial analyst was used to reclassify categorical variables (aspect, tree species and structural stage class) into indicator variables and a separate layer was created for each indicator variable. If the variable was present then the cell was coded '1' and if absent the cell was coded '0'. For example, in the north aspect layer all cells with a north aspect will have a '1' and all other cells will have a '0'. This process was continued for the other seven aspects, as well as dominant tree species and structural stage class.

The used habitat locations and available habitat locations point layers for building the model were intersected with variables considered for inclusion in the RSF model (Table 1) using the intersect point tool in Hawth's Analysis Tools (Beyer, 2007). The resulting attribute tables contained values of each variable at each point. The two attribute tables (used habitat locations and available habitat locations for model building) were exported to JMPIN and combined. In the table with combined data a column was added and all used habitat locations were coded '1', while the available habitat locations were coded '0'.

Within the Black Hills, spruce only dominates approximately 2% of the landscape and northern flying squirrel locations from 2005–2007 did not fall within areas dominated by spruce. Therefore, spruce was not considered as a variable in the logistic regression model. However, spruce has been found to be significant in other northern flying squirrel studies across their range (Connor, 1960; Jackson, 1961; Musser, 1961; Weigl and Osgood, 1974; Mowrey and Zasada, 1984; Urban, 1988; Payne *et al.*, 1989; Loeb *et al.*, 2000; Odom *et al.*, 2001; Hackett and Pagels, 2003; Smith and Nichols, 2003; Ford *et al.*, 2004; Menzel *et al.*, 2006b), therefore, a value of one was added to all cells containing spruce in the RSF model to give weight to spruce habitat.

The model building data were subjected to a series of tests to determine which variables would be incorporated into the final model. Fisher's exact test was used to compare proportions of used habitat locations and available habitat locations categorical (indicator) variables. Wilcoxon rank sums test was used to compare means of continuous variables between used habitat locations (trapping and tracking) and available habitat locations (random points throughout the study area). Any categorical or continuous variables found to be significant at the 10% level were retained for further statistical analysis. A correlation matrix was established with retained variables. When two variables were highly correlated ($r \geq 0.70$), the one deemed to be less significant biologically was removed (Manly *et al.*, 2002).

Logistic regression was used to determine coefficients of remaining variables with the dependent variables being used habitats (1) or available habitats (0). Logistic regression has become the standard method of analysis for discrete response outcome variables (Hosmer and Lemeshow, 2000), including small mammal studies (Carey *et al.*, 1999; Menzel *et al.*, 2006a). In addition, the assumptions for the independent variables are more lenient and continuous and categorical variables can both be included in the model (Hosmer and Lemeshow, 2000). The final RSF model was determined by stepwise backward elimination. In the logistic regression model, likelihood ratio chi square test was used to determine which variables were significant in determining habitat use by northern flying squirrels at the 10% level (Manly *et al.*, 2002). The variable with the highest likelihood ratio chi square p-value was removed and logistic regression was run on the remaining variables. This process continued until all variables in the model had a regression coefficient that was significant at the 10% level. The regression coefficients were included in the logistic regression equation

$$w * (x) = \exp\left(\beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p\right)$$

where β_0 is the estimated constant intercept coefficient, $\beta_{1...p}$ are the significant regression estimated coefficients and $x_{1...p}$ are the corresponding variables (Manly *et al.*, 2002).

RSFs in use-availability studies often take on an exponential form of function (Manly *et al.*, 2002; Johnson *et al.*, 2006). Contamination can occur where used habitat locations are included in the sample of available habitat locations. For use-availability studies, the sampling probabilities of used habitat locations (P_u) and available habitat locations (P_a) are incorporated into the logistic regression model to modify the intercept coefficient (β_0) ($\beta_0 + \log_e[(1 - P_a)P_u/P_a]$) (Manly *et al.*, 2002). If the sampling probabilities of used habitat locations and available habitat locations are not known, then the probabilities along with the constant intercept coefficient are removed from the logistic regression equation, which we did in this study. A RSF is estimated using the estimated coefficients and significant variables from the logistic regression model with the following formula

$$w(x) = \exp\left(\beta_1 x_1 + \ldots + \beta_p x_p\right)$$

where $\beta_{1...p}$ are significant regression coefficients and $x_{1...p}$ are the corresponding significant variables (Manly *et al.*, 2002) The accepted model was then incorporated into ArcGIS 9.1 to produce a RSF value for each 30 m resolution cell in the study area. The resulting RSF values were used to predict relative probability of selection throughout the study area. RSF values are not an absolute probability, therefore, a high probability of use does not define optimal habitat (Manly *et al.*, 2002), because these values are based on used habitat locations and available habitat locations, where sampling probabilities are not known. The raw RSF scores are transformed to scale the predicted values (w) between 0 and 1 using the following formula

$$\hat{w} = \frac{w(x)}{1 + w(x)}$$

where habitat selection probability increases as the transformed RSF value ($\hat{w}$) approaches 1. The RSF probabilities from the resulting map were then classified into 10 quantiles (ordinal bins) which represent categories of increasing habitat selection (Johnson *et al.*, 2006). Where habitats with RSF values falling within bin 1 have the lowest habitat selection or lowest probability of use and habitats with RSF values falling within bin 10 have the highest habitat selection or highest probability of use.

Statistical methods normally used to test validity of a logistic regression model (ROC, Kappa and confusion matrix) are not appropriate for use-availability research designs due to contamination (Boyce *et al.*, 2002). The independent validation data were used to validate the model according to methods suggested by Johnson *et al.* (2006). The utilization $U(x_i)$ value of each of the bins was determined using the formula

$$U(x_i) = w(x_i)A(x_i) \Big/ \sum_j w(x_j)A(x_j)$$

where $w(x_i)$ was the midpoint value of the RSF bin (i) and $A(x_i)$ was the area of bin i (Boyce and McDonald, 1999). The midpoint value $w(x_i)$ for each bin was the midpoint of the RSF probability range for that bin and the area $A(x_i)$ was total number of pixels for each bin (Johnson *et al.*, 2006). The number of validation observation points within each bin were counted. The expected number of validation observations within each bin (N_i) was estimated using

$$N_i = N * U(x_i)$$

where N was the total number validation points and $U(x_i)$ was the utilization function from above (Johnson *et al.*, 2006). The proportion of expected observations was compared to the proportion of observed validation points using linear regression. The regression line was compared to a slope of zero (use = availability). R^2 was also calculated from the linear regression model comparing proportions of expected and observed points, with a high value indicating an acceptable fit of the model. Spearman rank correlation was conducted between observed and expected frequencies to determine degree of correlation. Chi-square goodness-of-fit was calculated and a nonsignificant p-value ($P \geq 0.05$) indicates an acceptable model. Lastly, Pearson chi-square test was used to determine which bins have an expected value different from observed value.

RESULTS

Habitats used by northern flying squirrels were at higher elevations, higher precipitation, closer to streams, had a higher basal area of live trees >12.7 cm dbh and a higher basal area of dead trees >12.7 cm dbh, contained more live trees per hectare, more dead down trees per hectare and more snags per hectare than randomly available habitats (Table 2). Used habitats were comprised of less grass-shrub habitat, more aspen-birch, less structural classes 3A and 3B and more structural class 4A and 4B than randomly available habitats (Table 3). Structural class 4C was marginal ($P = 0.1008$), therefore, 4C was considered for the logistic model (Table 3). Used habitats were also more likely to be on east and northwest slopes, but less likely to be on southeast and west slopes than randomly available habitats (Table 3).

Two variables found to be significant were removed because they were highly correlated ($r \geq 0.70$) with another significant variable. Elevation and precipitation were correlated ($r = 0.75$). Elevation was removed because moisture levels can influence fungus abundance and distribution and therefore, northern flying squirrel abundance and distribution. The variable estimating the number of dead and down trees (DeadDown) was correlated with dead basal area (DeadBA) ($r = 0.81$). The variable estimating dead and down trees was removed because the dead basal area variable includes down mortality and down sound snags.

The final estimated RSF was

$$\hat{w} = \exp\{0.0983(\text{Precip}) - 0.0009(\text{DistStrm}) - 0.5634(\text{GRA}) + 1.3875(\text{TAA}) - 2.0695(3\text{A}) - 1.8418(3\text{B}) - 0.9112(\text{WE}) + 0.3129(\text{NW}) + 0.0005(\text{LiveHa}) + 0.0387(\text{DeadBA}) + 0.0372(\text{TotSnags}) + 1(\text{TWS})\}$$

The final RSF indicated that habitats used by northern flying squirrels had higher precipitation and were closer to streams than randomly available habitats. Northern flying squirrels used aspen-birch habitat, but not grass-shrub habitat (Table 4). Structural classes 3A and 3B were used less than expected based on availability (Table 4). Northwest aspect was used more than expected, while west aspect was used less than expected based on availability (Table 4). Northern flying squirrels used habitats with a higher density of live trees and snags, as well as a higher basal area of dead trees >12.7 cm dbh (Table 4) than randomly available habitat.

The linear regression model comparing the proportion of expected to observed frequencies for each bin indicated a good model fit ($R^2 = 0.85$) (Fig. 1). The regression line was significantly different from zero (use ≠ availability) ($P = 0.0002$). Spearman rank correlation value was 0.9423 ($P < 0.001$). The goodness of fit chi-square test indicated expected and observed values were significantly different ($\chi^2 = 48.85$, df = 9, $P < 0.0001$). Individual bin Pearson chi-square tests found that five of the ten bins had observed frequencies similar to expected frequencies (Table 5). Even though the goodness of fit chi-square test was significant, all other tests indicate a good model performance between

TABLE 2.—Chi-square tests comparing means of trapping and tracking locations (used habitat) (n = 1203) and random locations throughout the study area (available habitat) (n = 1203) to determine continuous variables retained for resource selection function (RSF) habitat model of northern flying squirrels studied in the Black Hills National Forest (May–Aug., 2005–2007). See table 1 for description of variables

Variable	Used mean ± SE	Available mean ± SE	Z	p-value[a]
Elev[b]	1755.11 ± *5.89*	1669.74 ± *7.07*	8.14	0.0000
Precip	25.14 ± *0.09*	23.58 ± *0.14*	10.36	0.0000
DistStrm	269.14 ± *7.03*	292.34 ± *7.30*	−3.36	0.008
LiveHa	1048.89 ± *33.70*	471.50 ± *20.49*	15.87	0.0000
LiveBA	28.57 ± *0.47*	24.64 ± *0.58*	5.81	<0.0001
DeadBA	7.22 ± *0.22*	4.07 ± *0.20*	16.21	0.0000
DeadDown[b]	9.97 ± *0.41*	5.93 ± *0.42*	8.94	0.0000
TotalSnags	7.46 ± *0.26*	3.36 ± *0.19*	15.99	0.0000

[a] Means tested with Wilcoxon rank sums ($P \leq 0.10$)
[b] Removed due to correlation ($r \geq 0.70$)

observed and expected frequencies. Therefore, the model was accepted based on validation data. Our decision to accept the current model is based on two anomalies (Jasper Burn and Black Elk Wilderness Area) within the BHNF vegetation layer, which may have affected the validation data and are furthered explained in the discussion. A 30 m resolution map of transformed RSF values ranging from 0–1 probability of habitat selection is depicted in

TABLE 3.—Fisher's exact test comparing proportion of trapping and tracking locations (used habitat) (n = 1203) and random locations throughout the study area (available habitat) (n = 1203) to determine categorical variables retained for resource selection function (RSF) habitat model of northern flying squirrels studied in the Black Hills National Forest (May–Aug., 2005–2007). *See* Table 1 for description of variables

Variable	Used (%)	Available (%)	p-value[a]
GRA	4.82	22.36	<0.0001
TAA	12.14	2.58	<0.0001
TBO	0.17	0.25	1.0000
TPP	82.88	72.74	<0.0001
3A	1.16	4.82	<0.0001
3B	1.16	6.98	<0.0001
3C	4.16	3.41	0.3927
4A	36.41	28.01	<0.0001
4B	30.67	23.69	0.0001
4C	12.97	10.72	0.1008
NO	10.81	9.39	0.2790
NE	18.12	16.63	0.3603
EA	17.87	14.63	0.0356
SE	8.06	10.31	0.0663
SO	6.65	8.40	0.1219
SW	16.87	19.29	0.1379
WE	3.24	12.64	<0.0001
NW	18.37	8.73	<0.0001

[a] Means tested with Fisher's exact test ($P \leq 0.10$)

TABLE 4.—Estimated coefficients for the resource selection function (RSF) habitat model for northern flying squirrels studied in the Black Hills National Forest (May–Aug., 2005–2007). *See* Table 1 for description of variables

Coefficient	Estimate	SE	χ^2	p-value[a]	Odds ratio
Precip	0.0983	*0.0129*	59.80	<0.0001	1.10
DistStrm	−0.0009	*0.0002*	17.13	<0.0001	1.00
GRA	−0.5634	*0.0838*	50.27	<0.0001	0.32
TAA	1.3875	*0.1642*	118.03	<0.0001	16.04
3A	−2.0695	*0.2657*	88.28	<0.0001	0.02
3B	−1.8418	*0.2421*	97.70	<0.0001	0.03
NW	0.3129	*0.0741*	18.48	<0.0001	1.87
WE	−0.9112	*0.1118*	81.55	<0.0001	0.16
LiveHa	0.0005	*0.0001*	93.72	<0.0001	1.00
DeadBA	0.0387	*0.0097*	16.77	<0.0001	1.04
TotSnags	0.0372	*0.0086*	20.98	<0.0001	1.04

[a] Coefficients tested with likelihood ratio chi square ($P \leq 0.10$)

Figure 2. The RSF habitat model was compared to a GIS habitat layer for the Black Hills and areas of low, medium and high probability of use were delineated (Fig. 3).

DISCUSSION

Habitat suitability models are an important management tool for nocturnal and elusive species that are difficult to study. The RSF habitat model for northern flying squirrels in BHNF does not give an indication of presence or absence based on habitat characteristics at

TABLE 5.—Comparison of observed and expected frequencies for the 10 quantiles, which represent ordinal resource selection function (RSF) bins (categories) with increasing habitat selection to determine validity of RSF model. RSF values ($w(x)$) are habitat selection probabilities for northern flying squirrels in the Black Hills National Forest (May–Aug., 2005–2007). RSF bin midpoint $w(x_i)$ is the midpoint RSF value for the range of the RSF bin (i) and $A(x_i)$ is the number of 30-m pixels within the study area for bin (i). The observed frequency is the number of independent validation data points within each bin range. The expected frequency of each bin ($n_{i;i}$) was estimated using $N_i = N * \left[w(x_i)A(x_i)/\sum_j w(x_j)A(x_j)\right]$ where N is the total number of validation points (N = 300)

RSF Bin (i)	RSF Bin range	RSF Bin midpoint $w(x_i)$	# pixels $A(x_i)$	Observed n	Observed %	Expected n	Expected %	p-value[a]
1	0.044–0.690	0.367	512895	0	0.00	3	0.99	0.08
2	0.690–0.795	0.743	510101	5	1.67	9	2.95	0.29
3	0.795–0.866	0.831	525449	11	3.67	15	5.06	0.43
4	0.866–0.903	0.885	507894	4	1.33	21	6.84	0.00
5	0.903–0.933	0.918	541661	12	4.00	28	9.38	0.01
6	0.933–0.955	0.944	505975	14	4.67	32	10.71	0.01
7	0.955–0.974	0.965	544236	45	15.00	41	13.62	0.67
8	0.974–0.985	0.980	467932	33	11.00	41	13.51	0.35
9	0.985–0.993	0.989	401043	63	21.00	39	13.12	0.02
10	0.993–1.000	0.997	651218	113	37.67	71	23.82	0.00

[a] Observed versus expected frequencies tested with Pearson chi square ($P \leq 0.05$)

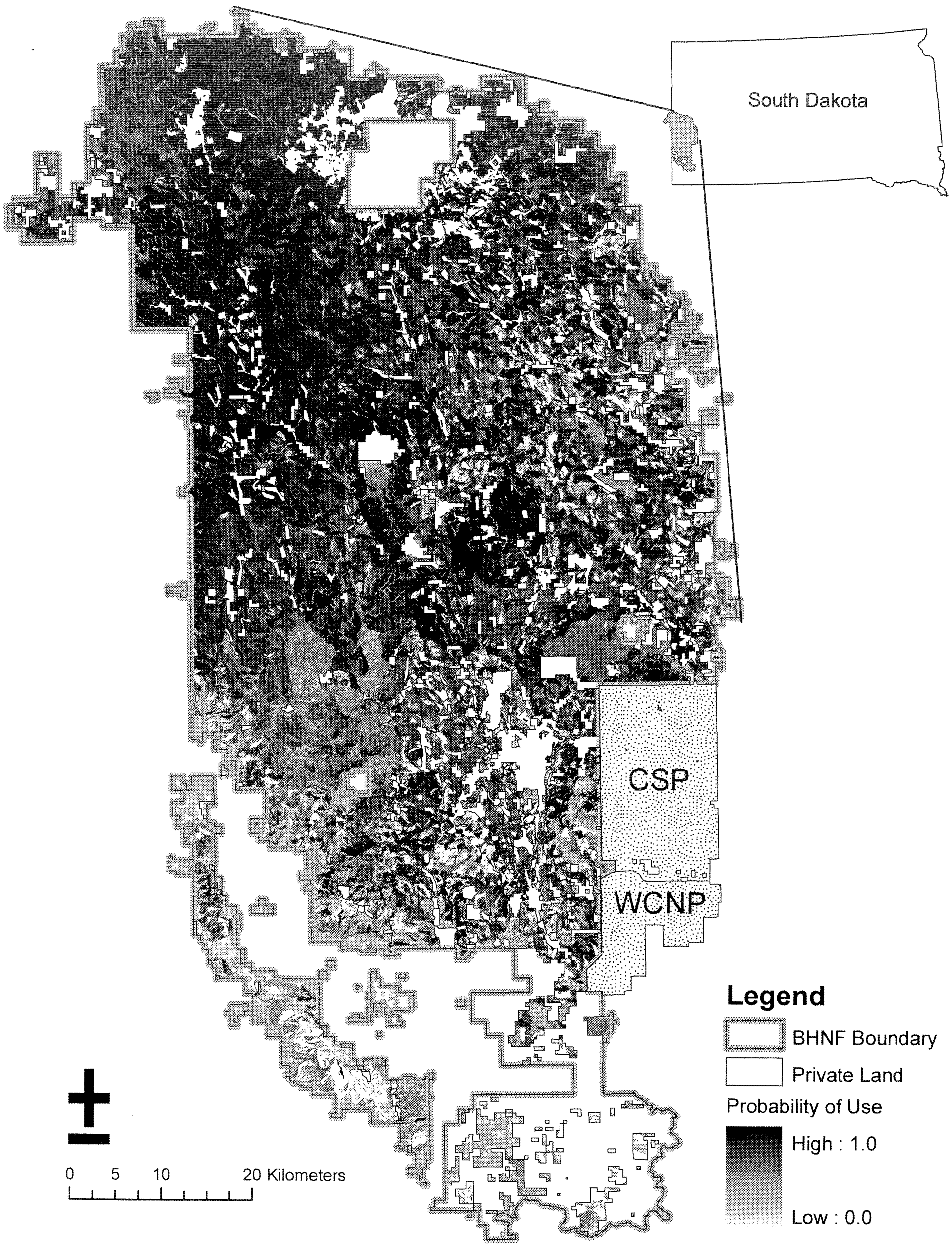

FIG. 2.—Map depicting relative probability of habitat use (30-m) by northern flying squirrels in the Black Hills National Forest (BHNF) (May–Aug., 2005–2007). Logistics regression was used to compare trapping and tracking locations (used habitats) and random locations (available habitats) throughout the BHNF to determine probability of use. CSP = Custer State Park; WCNP = Wind Cave National Park

a site, but instead provides a management tool to identify areas of habitat suitability based on known locations. Trapping results suggest northern flying squirrels are distributed throughout the Black Hills at varying densities across the landscape (Hough, 2008). These densities are presumably related to habitat suitability, which is depicted in the habitat model. One caution in using RSF habitat models is that maps that predict a high probability of use for certain areas do not define optimal habitat (Manly *et al.*, 2002). However, Rosenberg and Anthony (1992) suggested that because of the distribution of northern flying squirrels throughout their range, this species is highly adaptable and is a habitat generalist. Across their range, there is no single variable or group of variables that explained variation in abundance (Smith *et al.*, 2004). Abundance has been found to be correlated with a range of variables, including density of large trees and snags, shrub and canopy cover, prevalence of old-forest features (*e.g.*, coarse woody debris) and abundance of hypogeous mycorrhizal fungi (Smith, 2007).

We believe the population of northern flying squirrels in the Black Hills is stable, because northern flying squirrels were caught throughout the Black Hills and were found in less than optimal habitats (edge of harvested and burned areas) (Hough, 2008). Also, northern flying squirrels are breeding successfully and rearing young. During all three study years juveniles were captured while trapping and observed while radio-tracking.

Northern flying squirrels used aspen and birch habitat, however, grass-shrub habitat does not provide essential resources. Aspen-birch (2% of the landscape) was found to be important denning habitat for northern flying squirrels in BHNF (Hough, 2008). Aspen and birch trees are important for den sites, because cavities are readily created by primary cavity users in live trees and snags (Carey and Gill, 1983; Shepperd and Battaglia, 2002; Menzel *et al.*, 2004; Holloway, 2006). Aspen and birch do not provide optimal foraging habitats because hypogeous fungi are associated with conifers (Weigl, 1978; Maser *et al.*, 1985; U.S. Fish and Wildlife Service, 1990, Loeb *et al.*, 2000). Menzel *et al.* (2006b) found that several of the squirrels they tracked denned during the day in hardwood patches and foraged during the evening in conifers patches, in mixed conifer-hardwood patches. The same pattern was found in BHNF, with squirrels tracked to bottomlands of aspen and birch during the day and ponderosa pine dominated slopes and ridges during the night (Hough, 2008). Grass-shrub was not selected due to the species' dependence on trees. Grass-shrub habitat would not provide optimal foraging habitat for northern flying squirrels, because this habitat does not provide hosts for fungal growth or other favored food sources, in addition there is a lack of nest sites and protection from predators.

Studies in the Appalachians have found spruce to be the primary predictor in northern flying squirrel presence (Weigl and Osgood, 1974; Weigl, 1978; Urban, 1988; Payne *et al.*, 1989; Loeb *et al.*, 2000; Odom *et al.*, 2001; Hackett and Pagels, 2003; Ford *et al.*, 2004; Menzel *et al.*, 2006a, 2006b). Northern flying squirrels are also found in spruce forests across other parts of their range including, southeastern New York (Connor, 1960), Great Lakes region (Jackson, 1961), Alaska (Mowrey and Zasada, 1984; Smith and Nichols, 2003) and Utah (Musser, 1961). Across northern flying squirrel distribution range, spruce is an important component of habitat use because they are used for dray nests (Menzel *et al.*, 2004; Mowrey and Zasada, 1984; Hough, 2008). Spruce seeds also provide a potential food source (Smith, 2007). Also, hypogeous fungi are associated with spruce (Luoma *et al.*, 1991; Loeb *et al.*, 2000; Pyare and Longland, 2001). Future research should determine northern flying squirrel abundance in spruce dominated areas of the Black Hills which were inadvertently neglected in this study, due to the small extent of spruce dominated habitat across the landscape.

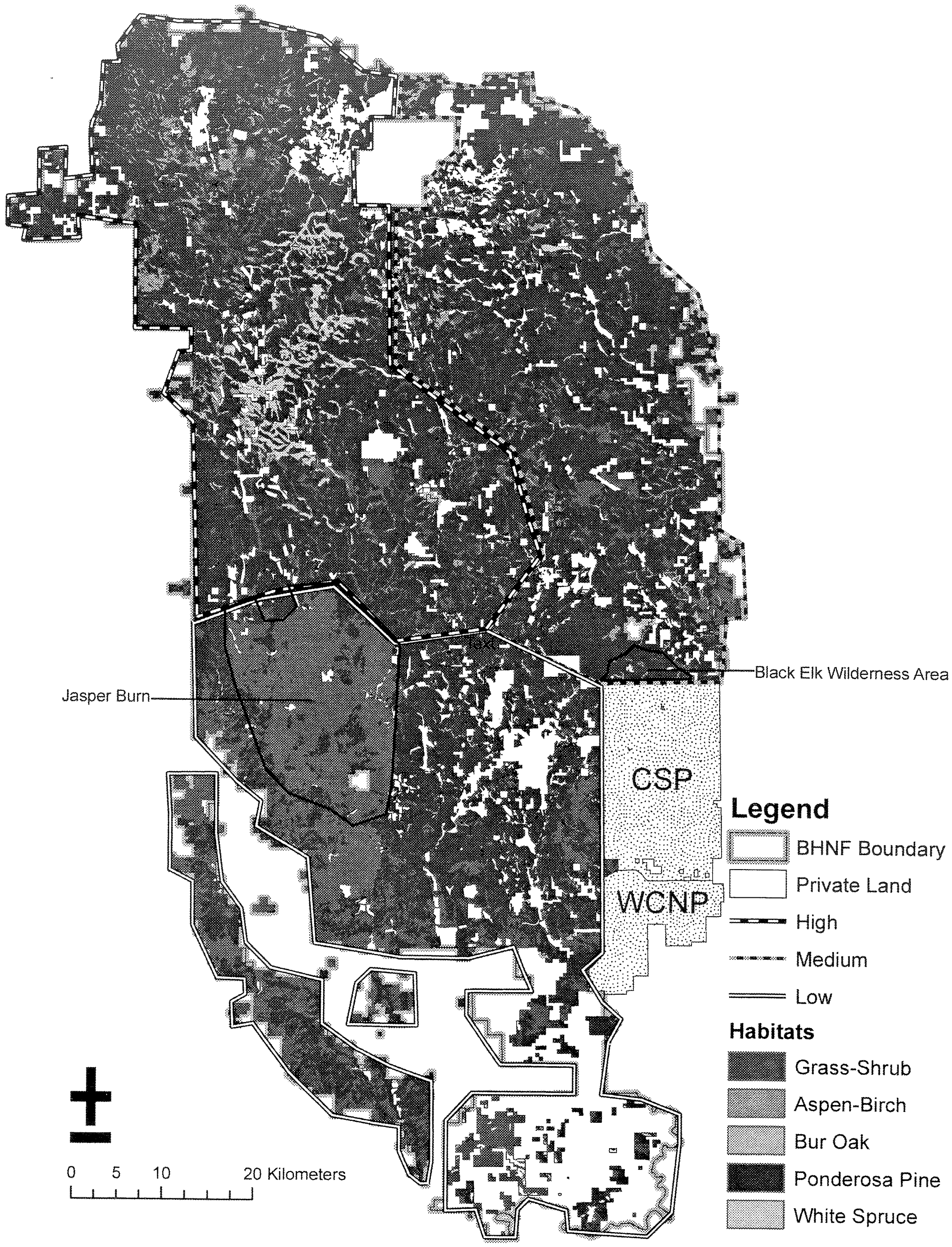

FIG. 3.—Logistics regression was used to produce a resource selection function habitat model based on a study of northern flying squirrels in the Black Hills National Forest (BHNF) (May–Aug., 2005–2007). The model compared trapping and tracking locations (used habitats) and random locations (available habitats) throughout the BHNF to determine probability of use through BHNF. Three probability categories (high, medium and low) were delineated based on the habitat selection map probabilities and overlaid on a map of dominant vegetation for BHNF. CSP = Custer State Park; WCNP = Wind Cave National Park

Northern flying squirrel abundance increases with forest complexity (Weigl *et al.*, 1992; Carey *et al.*, 1999; Carey, 2001). The model results suggest that not only was density of live trees important as a predictor of northern flying squirrel presence, but so was the basal area of dead trees and total number of snags. Live trees provide food sources, such as mycorrhizal fungi and seeds, and canopy cover for protection from predators. In the Pacific Northwest, habitat features that consistently explain significant variation in northern flying squirrel abundance are forest characteristics associated with snags and down, dead wood or decay (Carey *et al.*, 1999). Cavities in snags provide den sites and fungal diversity has been found to be positively correlated with the abundance of coarse woody debris (Carey *et al.*, 1999). In Oregon, the highest density of northern flying squirrels occurred in stands with the highest coarse woody debris (Carey *et al.*, 1999) and southeastern Alaska (Smith *et al.*, 2004). Northern flying squirrels in BHNF also used habitats with larger trees, but not canopy cover (structural stages 4A, 4B and 4C). Large trees serve as den sites and an indication of food availability. Northern flying squirrels select larger trees for dray nests (Hough, 2008) and larger trees are presumed to indicate a mature stand, which has an established mycorrhizal community and more seed production (Fisher and Wilkinson, 2005). Also, mycorrhizal fungus is often clumped and short-lived, therefore relatively dense canopies, large tall trees, and open midstories are important for squirrels to move through their home range efficiently and safely (Vernes, 2001).

Northern flying squirrels used habitats with higher precipitation and closer distances to streams compared to available habitat locations throughout the study area. Hypogeous fungi fruiting bodies require moist, nutrient-rich and cool environments to grow (Pyare and Longland, 2001). Northern flying squirrel population distribution may be heterogeneous across landscapes because of the heterogeneous spatial distribution of truffles (Pyare and Longland, 2002). In drier sites in the west, squirrels appear to be associated with riparian areas with cooler and wetter conditions (Meyer *et al.*, 2005, 2007), because fungus composition and abundance may be related to moisture levels (Rillig *et al.*, 2002). Southern BHNF is classified as Dry Coniferous Forest (Marriott *et al.*, 1999); therefore, squirrels in the southern hills may be limited to riparian areas where fungus grows. The northern BHNF, is a Mesic Coniferous Forest (Marriott *et al.*, 1999), which typically support higher population densities of northern flying squirrels than xeric forests (Lehmkuhl *et al.*, 2006; Hough, 2008). Microhabitat use in mesic forests is not restricted to riparian areas (Carey *et al.*, 1999). An increase in moisture results in an increase in fungal community diversity (Carey and Johnson, 1995) and abundance (Luoma *et al.*, 1991). This in turn, results in an increase in northern flying squirrel abundance (North *et al.*, 1997; Ransome and Sullivan, 1997; Carey *et al.*, 1999; Pyare and Longland, 2001).

One problem with the model is the degree of habitat selection in the Black Elk Wilderness Area [located just north of Custer State Park (Fig. 2 and 3)], which is reserved as a wildlife refuge where timber harvest is restricted. The Black Elk Wilderness area covers about 4080 ha and is a category 1 management area. The area is managed to protect and perpetuate natural ecological processes with little human interference (USDA Forest Service, 1996). Late successional vegetation occurs in the area. The area consists of a diversity of species composition and structure. We predicted the Black Elk Wilderness area to have a high probability of use because in the Pacific Northwest northern flying squirrel abundance was higher in old-growth and complex young forests than managed coniferous stands (Carey *et al.*, 1992; Witt, 1992; Carey, 1995; Waters and Zabel, 1995). The model suggests that this area is not as highly selected as we predicted. We believe three of the habitat variables (number of live trees, dead basal area and number of snags) found to be significant in the model are not accurate for the Black Elk Wilderness area in the GIS database. All three variables had low values; therefore, indicating this area was not suitable as northern flying squirrel habitat. However, during 2005, which had a low trapping success overall, we trapped on the edge of the wilderness area. We captured five adult flying squirrels and four juvenile flying squirrels, indicating that not only are the squirrels in the area, but they are successfully reproducing.

Another problem with the model is the high probability of selection indicated in the northern portion of the Jasper burn [located in the southwest contiguous portion of BHNF (Fig. 2 and 3)]. The burn area has a high number of snags and, therefore, a high dead basal area. These high values resulted in a high probability of use for this area. In other studies, northern flying squirrels did not use areas with stand replacing fires, such as the Jasper burn, and edges of the burn area were sink habitat (Fisher and Wilkinson, 2005).

This study contributes to the knowledge of northern flying squirrels for an isolated population at the southern edge of their range, where information is lacking for this species (Smith, 2007; Weigl, 2007). The RSF habitat model could be used by land managers for determining areas and habitat characteristics important to northern flying squirrels. Understanding resources requirements is important for isolated populations in intensively managed forests, because across their range northern flying squirrels play an important role in improving forest health through dispersal of mycorrhizal fungus and management decisions can greatly impact the population. The map shows the predicted spatial distribution of northern flying squirrel habitat (and presumably population) throughout the Black Hills. Future research and monitoring will also benefit from the model and map, because northern flying squirrels are secretive and elusive and trapping success is low, therefore, the RSF habitat map can be used to determine where to focus research efforts.

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