SPATIAL ANALYSIS OF NORTHERN GOSHAWK TERRITORIES IN THE BLACK HILLS, SOUTH DAKOTA

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Abstract. The Northern Goshawk (*Accipiter gentilis*) is the largest of the three North American species of *Accipiter* and is more closely associated with older forests than are the other species. Its reliance on older forests has resulted in concerns about its status, extensive research into its habitat relationships, and litigation. Our objective was to model the spatial patterns of goshawk territories in the Black Hills, South Dakota, to make inferences about the underlying processes. We used a modification of Ripley's *K* function that accounts for inhomogeneous intensity to determine whether territoriality or habitat determined the spacing of goshawks in the Black Hills, finding that habitat conditions rather than territoriality were the determining factor. A spatial model incorporating basal area of trees in a stand of forest, canopy cover, age of trees >23 cm in diameter, number of trees per hectare, and geographic coordinates provided good fit to the spatial patterns of territories. There was no indication of repulsion at close distances that would imply spacing was determined by territoriality. These findings contrast with those for the Kaibab Plateau, Arizona, where territoriality is an important limiting factor. Forest stands where the goshawk nested historically are now younger and have trees of smaller diameter, probably having been modified by logging, fire, and insects. These results have important implications for the goshawk's ecology in the Black Hills with respect to mortality, competition, forest fragmentation, and nest-territory protection.

Key words: Accipiter gentilis, *Black Hills, South Dakota, forest management, Northern Goshawk, Ripley's* K *function, spatial statistics.*

Análisis Espacial de los Territorios de *Accipiter gentilis* en Black Hills, Dakota del Sur

Resumen. *Accipiter gentilis* es la más grande de las tres especies de *Accipiter* de América del Norte y es la que está más asociada con los bosques maduros. Su dependencia de los bosques maduros ha traído aparejada preocupaciones sobre su estatus, numerosas investigaciones sobre sus relaciones de hábitat y pleitos judiciales. Nuestro objetivo fue modelar los patrones espaciales de sus territorios en Black Hills, Dakota del Sur, para hacer inferencias sobre los procesos subyacentes. Empleamos una modificación de la función *K* de Ripley que considera la intensidad homogénea para establecer si la territorialidad o el hábitat determinó el espaciado de los individuos de *A. gentilis* en Black Hills, encontrando que los factores determinantes fueron las condiciones de hábitat más que la territorialidad. Un modelo espacial que incorpora el área basal de los árboles del bosque, la cobertura del dosel y la edad de los árboles >23 cm de diámetro, el número de árboles por hectárea y las coordenadas geográficas brindó un buen ajuste a los patrones espaciales de los territorios. No se encontró evidencia de repulsión a distancias cercanas, indicando que el espaciado estuvo determinado por la territorialidad. Estos resultados contrastan con aquellos para la Meseta de Kaibab, Arizona, donde la territorialidad es un factor limitante importante. Los bosques donde *A. gentilis* nidificó históricamente son ahora más jóvenes y tienen árboles de menor diámetro, habiendo sido modificados probablemente por aprovechamiento maderero, fuego e insectos. Estos resultados tienen importantes implicancias para la ecología de *A. gentilis* en Black Hills con relación a mortalidad, competencia, fragmentación del bosque y protección del territorio de nidificación.

INTRODUCTION

The Northern Goshawk (*Accipiter gentilis*) is the largest of the three North American species of *Accipiter* and is more closely associated with older forests than are the other species (Reynolds et al. 1982). This relationship to older forest has resulted in concern about the species, extensive research into habitat relationships, and litigation (Squires and Kennedy 2006). The goshawk is listed as a species of concern and a sensitive species in all administrative regions of the U.S. Fish and Wildlife Service and the U.S. Forest Service, respectively.

In South Dakota, it is listed as a species of greatest concern in the state's Wildlife Action Plan (South Dakota Department of Game, Fish and Parks 2006).

At large spatial scales on a year-long basis, the goshawk is a habitat generalist and uses a wide variety of forest types; however, during the nesting season at a local scale, it is a habitat specialist nesting in a relatively narrow range of forest structures (Squires and Reynolds 1997, Squires and Kennedy 2006). The nest area consistently includes a high density of large trees, with canopy cover 50–90%, tree diameter at breast height (DBH) >50 cm, basal area >29 m^2 ha^{-1}, and tree density >425 trees ha^{-1} (Squires and Reynolds 1997, Daw et al. 1998, Penteriani 2002, Reynolds et al. 2006, Squires and Kennedy 2006). There are limited data suggesting that forest structure may be more important in nest-site selection than is prey abundance (Penteriani 2002, Squires and Kennedy 2006, Beier et al. 2008). Forest structure may be important in reducing predation by the Great Horned Owl (*Bubo virginianus*) and competition with the Red-tailed (*Buteo jamaicensis*) and Red-shouldered (*B. lineatus*) hawks (Kenward 1996, Penteriani and Faivre 2001). For nesting, stands may be selected for the suitable microclimate they provide for eggs and nestlings (Penteriani 2002). Some evidence suggests that alteration of habitat may reduce nesting by goshawks (Crocker-Bedford 1990, Patla 2005). For example, in Idaho, occupancy of nesting areas was lower in previously harvested forests than in less disturbed areas (Patla 2005). In their review, Squires and Kennedy (2006) concluded that forest management—cutting, thinning, fire management—is the primary anthropogenic effect on goshawk populations, these practices either enhancing or degrading habitat depending on their nature and extent.

To test the importance of habitat quality on nesting, Reich and co-workers (Reich et al. 2004, Reynolds and Joy 2006) made an extensive spatial analysis of nest territories of the well-studied Kaibab Plateau population. They concluded that the availability of suitable nest sites was not limiting but rather that territoriality set the upper limit to the population. The choice of nest location was constrained by the availability of high-quality habitat within spaces defined by neighboring territories.

The goshawks of the Black Hills of South Dakota and Wyoming are isolated from other populations (Squires and Kennedy 2006). Additionally, the forests of the Black Hills have been intensively managed for over a century and have a high density of roads (Baker and Knight 2000, Shepperd and Battaglia 2002). Thus the species' spatial ecology in the Black Hills likely differs from that on the Kaibab Plateau. The goshawk's nesting ecology in the Black Hills was studied by Bartelt (1977) from 1975 to 1976, Erickson (1987) from 1980 to 1981, and the South Dakota Department of Game, Fish, and Parks from 2003 to 2009 (Knowles and Knowles 2007, 2008, 2009). In addition, between 1981 and 2009, U.S. Forest Service personnel made localized nest surveys to evaluate the effects of forest management and mining.

We used the data of Bartelt (1977), Erickson (1987), and Knowles and Knowles (2007, 2008, 2009) to investigate the spatial relationship of goshawks to each other and to characteristics of vegetation. Our objective was to examine the spatial patterns of goshawk territories in the Black Hills to make inferences about the underlying processes to see if they are the same as on the Kaibab Plateau, where the goshawk population is not isolated. We used a modification of Ripley's *K* function (Ripley 1977, 1981), which accounts for inhomogeneous intensity, to investigate whether territoriality or habitat determined spacing of goshawks in the Black Hills. Our hypotheses were that goshawks used vegetation types similar to those described elsewhere and that territoriality determined the spacing of goshawk nests. If tests showed evidence of significant repulsion after vegetation characteristics were taken into account, we would conclude that territoriality determined the birds' spacing. Otherwise, we would conclude that vegetation characteristics were the primary influence on the goshawk's distribution. Finally, we explored whether forest stands with goshawk territories in the 1970s and 1980s still had structure suitable for nesting.

METHODS

STUDY AREA

Our study took place on public lands in the Black Hills National Forest, within Pennington and Lawrence counties in western South Dakota and Crook and Weston counties in Wyoming (43° 30′ N to 44° 30′ N and 103° 20′ W to 104° 20′ W). Elevations range from 1370 to 2207 m (Froiland 1990). The climate is continental; mean annual temperatures range from 5 to 9 °C with extremes of −40 and 44 °C (South Dakota Office of Climatology 2005).

The Black Hills extend approximately 190 km north–south and 80 km east–west and are isolated from other forested regions by grassland. The geology consists of a Precambrian granitic and metamorphic core with an overburden of younger sedimentary layers (e.g., Paleozoic Paha Sapa Limestone; Froiland 1990). The limestone plateau is a high, relatively flat escarpment and forms the main hydrological divide. Surface water is limited because of the high porosity of the rocks (Froiland 1990). Forests are dominated by ponderosa pine (*Pinus ponderosa*), along with bur oak (*Quercus macrocarpa*) on drier sites and trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) at higher elevations.

The Black Hills National Forest administers approximately 80% of the Black Hills. Predominant land uses include timber production, cattle grazing, second-home development, recreation, sport hunting, and as winter range for big game. The Black Hills National Forest has the highest densities of roads of any national forest in Colorado, South Dakota, or Wyoming (Baker and Knight 2000). Major natural disturbances include wildfire and infestation by the mountain pine beetle (*Dendroctonus ponderosae*). Since the early 20th century the region has been logged extensively, and the majority of forests in the Black Hills are now second growth. The predominant

silvicultural treatment has been even-aged management: mainly shelterwood and seed tree systems (Shepperd and Battaglia 2002). In contrast, before settlement, frequent surface fires created multi-aged stands with heterogeneous structure (Brown 2006). Fire suppression and forest management have reduced structural diversity, resulting in more homogeneous forests dominated by smaller trees (Brown and Cook 2006).

NEST SEARCHES

We used data from surveys for goshawk nests in three periods: 1975–1976, 1980–1981, and 2007–2009. During the first two periods, we located nests by searching locations of previous nests and intensively from the ground in suitable forest (dense growth of mature conifers with basal area >29 m^2 ha^{-1} and height >10 m), broadcasting calls. From 2007 to 2009, we located nests by searching previously known nesting territories both visually and by using broadcast calls (Kennedy and Stahlecker 1993, Joy et al. 1994). Additionally, we made systematic surveys at 1450 stations in suitable goshawk habitat throughout the Black Hills by walking and driving trails and roads, stopping at 0.8-km intervals, and broadcasting the goshawk's alarm calls. Known territories were visited ≥3 times during the nesting season. Points of broadcast calls were not consistent from year to year. Rather we tried to systematically cover as many areas as possible each year where we thought there was potential for nest territories. Generally, we did not survey areas of intensive logging nor did we survey the area of the large Jasper fire. Within known nesting territories, if we did not find an adult on a known nest during our May visit, we often used the same specific points for call surveys. If we found a bird at a known nest on our first visit, we omitted call surveys in that territory that year. Call surveys consisted of playing six to eight recorded alarm calls interspersed with periods of listening over about a 10-min period.

VEGETATION MEASUREMENTS

The methods we used for quantifying vegetation varied by study. During the 1975–1976 surveys, basal area (m^2 ha^{-1}) of trees at nest sites was measured with a 10-factor angle gauge (Hovind and Reick 1970). During the 1980–1981 surveys, Erickson (1987) measured trees' basal area at nest sites in fixed plots of 15 by 25 m. During the 1975–1976 surveys, Bartelt (1977) estimated canopy cover by photo-interpreting stereographic photographs. During the 1980–1981 surveys, Erickson (1987) measured canopy cover by using a moose-horn periscope at 5-m intervals along the inner sides of the 15-by-25-m fixed plot.

For vegetation conditions for the 2007-2009 survey, we used the 2008 vegetation data from the Black Hills National Forest geographic information system (http://www.fs.usda.gov/detail/blackhills/landmanagement/gis, accessed 5 August 2008). For information on the vegetation characteristics of stands we used the U.S. Forest Service's R2VEG data base. On the basis of previous studies of the goshawk's nest sites (Squires and Reynolds 1997, Daw et al. 1998, Penteriani 2002, Reynolds et al. 2006, Squires and Kennedy 2006), we chose percent total canopy cover of trees, the number of all live trees per hectare in the territory, the number of live trees per hectare with a DBH ≥12.7 cm, total basal area for all live trees with DBH >12.7 cm, quadratic mean diameter of live trees ≥2.54 cm in diameter (i.e., their weighted average diameter), quadratic mean diameter of live trees ≥12.7 cm in diameter, and average age and average height of all live trees ≥23 cm in diameter.

The forest stands that contained active nests 1975–1976 and 1980–1981 no longer do; they have changed substantially from logging and other management. While forest stands containing nests have changed over time, we hypothesized that goshawks have not changed their habitat preference and that habitat quality determines the distribution of nests in the Black Hills. We used analysis of variance to compare basal area and canopy cover for all nest stands with data collected during the time nests were occupied (1975–1976, 1980–1981, or 2007–2009). Additionally, for nests occupied 1975–1976, we determined the basal area and canopy cover in 2008 from the data in Black Hills National Forest's geographic information system. We adjusted pairwise comparisons with a Bonferroni correction.

Furthermore, we compared the current condition of forest stands used by goshawks 1975–1976 and 2007–2009 with the existing vegetation data in the Black Hills National Forest's geographic information system. In this comparison, using Welch's two-sample t-tests, we assessed the number of trees per hectare, quadratic mean diameter, stand age, and total height.

SPATIAL STATISTICAL ANALYSES

If territoriality determines the distribution of nests in the Black Hills, then we would expect to find regularity in their spacing, regardless of any spatial patterns of habitats within territories. To measure these distributions, we used a modification of Ripley's K function (Baddeley et al. 2000) to test whether the point process of the nest territories departed from randomness and approached aggregation or regularity (Ripley 1977, 1981). Ripley's K function models second-order processes and assumes stationarity (i.e., spatial homogeneity where aspects of the ecosystem do not vary significantly from location to location; Cressie 1993, Pélissier and Goreaud 2001, Baddeley and Turner 2005). For Ripley's K to be used, any spatial trends (first-order effects such as habitat characteristics) must be removed to avoid spurious results (Pélissier and Goreaud 2001, Cornulier and Bretagnolle 2006). Inferences from Ripley's K analysis are robust to missing data, provided that the missing data are not spatially biased (Baddeley et al. 2000, Møller and Waagepetersen 2002).

Many real point patterns cannot be described as stationary, and the naïve use of Ripley's K would be invalid (Pélissier and Goreaud 2001, Baddeley and Turner 2006, Cornulier and Bretagnolle 2006). The homogeneous Ripley's K function overstates departure from complete spatial randomness (Hering et al. 2009), requiring the use of the inhomogeneous K function of Baddeley et al. (2000). Intuitively, the inhomogeneous K function has the same interpretation as the homogeneous

K function, except that the intensity of nests is no longer constant but depends on location (Hering et al. 2009). Compared to the homogeneous K function, the inhomogeneous K function has wider critical envelopes that would support the null hypothesis (Hering et al. 2009). We used the inhomogeneous L function, $L(r) = [K_{inhom}(r)/\pi]^{1/2} - r$, which is a linearized form of the K function and is more convenient to interpret because it has an expectation of zero (Cressie 1993).

We evaluated the presence of spatial trends in the point process by residual analysis (Baddeley et al. 2005). We initially fit the null model (intercept only, i.e., stationary model) and used lurking-variable plots to test if the point process depended on the spatial covariates. These lurking-variable plots incorporate Pearson residuals compared to a spatial covariate (or Cartesian coordinate), which are comparable to usual Pearson residuals for linear models. We modeled the point process by generalized linear models with Cartesian coordinates and spatial covariates (Baddeley and Turner 2000). We considered as spatial covariates basal area, trees ha^{-1}, canopy cover, and average age of all live trees ≥23 cm in diameter. We used a quadratic function of trees ha^{-1} because we hypothesized that there could be too few or too many trees for suitable habitat. We also considered the quadratic function of the Cartesian coordinates because most goshawk territories recorded by Bartelt (1977) and Erickson (1987) were in the central plateau of the Black Hills.

To determine the most appropriate models of the first-order trends, we developed a priori a set of plausible models combining one or more forest-structure variables and Cartesian coordinates and compared the models by the Akaike information criterion (AIC) and Akaike weights (Akaike 1973, Burnham and Anderson 2002). To determine whether there was evidence of clustering or repulsion after accounting for the spatial covariates, we generated simulation envelopes of K_{inhom} from 999 Monte-Carlo simulations of the null model (either a homogeneous or inhomogeneous Poisson process) with an α level of 0.05. If there was evidence of significant repulsion (observed values lower than the confidence envelopes) or attraction (observed values higher than the confidence envelopes) after spatial covariates were taken into account, we would conclude that there was territory-to-territory interaction. Significant repulsion would imply that territoriality determines spacing of goshawk territories. Otherwise, we would conclude that the spatial covariates were the primary determinant of the distribution of goshawk territories and that territoriality had a negligible influence.

Additionally, we tested if there was spatial dependence between the locations of territories identified in the 1975–1976 and 2007–2009 surveys by comparing the spatial patterns of the two sets of territories (Baddeley and Turner 2006). We computed the bivariate version of the L function along with 999 simulations of the territories under a null model of random relabeling, in which locations remained fixed and were randomly assigned to one of the two time periods by sampling without replacement (Baddeley and Turner 2005, 2006). These simulation envelopes were calculated with an α level of 0.05.
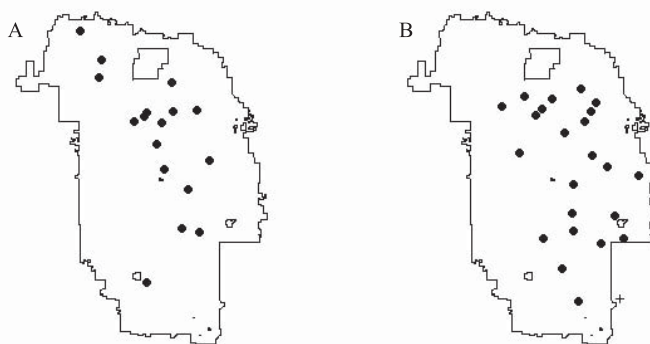

FIGURE 1. Locations of Northern Goshawk territories in the Black Hills, South Dakota. A, 17 territories found during 1975–1976 surveys; B, 25 territories found during 2007–2009 surveys.

Statistical analyses were run in R 2.10.1 (R Development Core Team 2011). For all spatial analyses and models we used the functions of the Spatstat 1.17-5 add-on package (Baddeley and Turner 2005). Our observation window was the irregular boundary of federal lands in the Black Hills (Fig. 1).

RESULTS

We located 28 goshawk nests representing 17 territories during the 1975–1976 surveys (Fig. 1a) and 52 nests representing 25 territories during the 2007–2009 surveys (Fig 1b). Territories contained clusters of two to five nests. We considered each cluster a single territory, and we used the cluster's geographic center as the location of the territory. The mean nearest-neighbor distance between territories was 7.39 km (range 1.12–20.85 km) in the earlier survey and 6.99 km (range 2.80–13.46 km) in the later survey; there was no statistical difference between these distances ($t_{25.755} = 0.315$, $p = 0.755$). For 1975–1976, we measured basal area at 24 nests and canopy cover at 4 territories. We determined vegetation characteristics for all nests located 2007–2009 from the Black Hills National Forest vegetation map. During the 1980–1981 surveys, we located 45 nests, of which we had measurement of basal area and canopy cover at 14. At the time of our current analysis the data set of locations for these nests was lost, so spatial analyses for 1980–1981 were not possible.

SPATIAL ANALYSIS

2007–2009 Data set. We plotted cumulative Pearson residuals against the four continuous spatial covariates (basal area, canopy cover, age, and trees per hectare; Fig. 2). For all four covariates, the curves are less than the –2σ limit of error bounds, indicating the null model overestimated the intensity of nest territories for spatial locations with low values of these covariates and underestimated territories located in forest stands with higher values of these covariates. For basal area (Fig. 2a), there was a sharp increase in cumulative residuals after the nadir point (25 m^2 ha^{-1} basal area), indicating that territories were associated with stands with basal area >25 m^2 ha^{-1}. For canopy cover (Fig. 2b), the increase
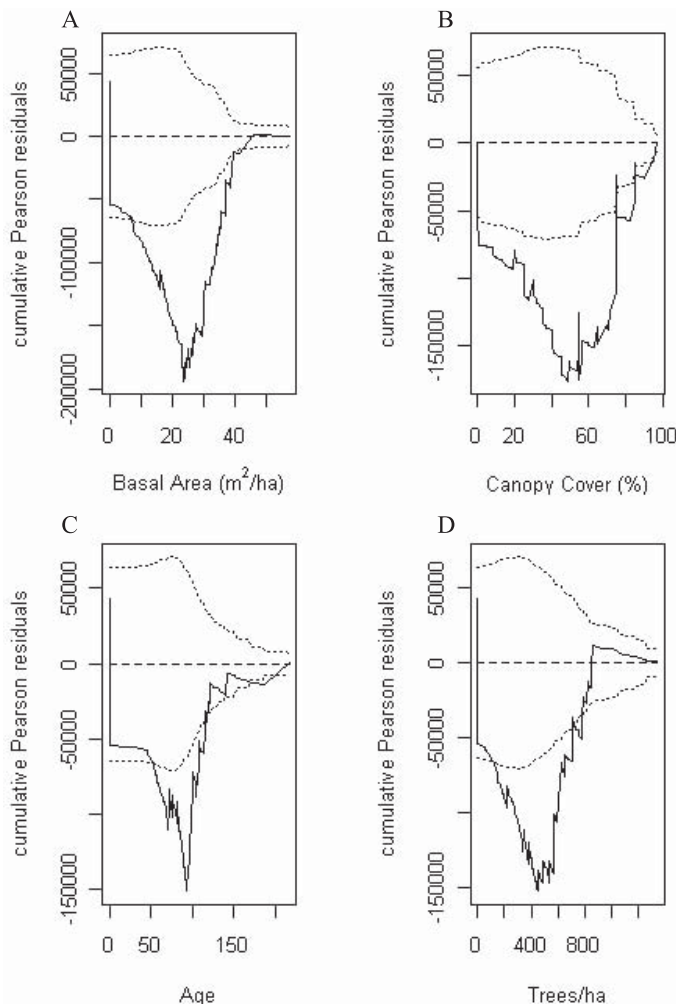
FIGURE 2. Lurking-variable plots of standardized Pearson residuals for Northern Goshawk territories found during the 2007–2009 surveys in the Black Hills, South Dakota, with vegetative covariates derived from the 2008 vegetation data in the Black Hills National Forest's geographic information system. A, basal area of trees (m^2 ha^{-1}); B, forest canopy cover (%); C, age of the forest stand (years); D, number of trees per hectare. The solid line represents observed values; the horizontal dashed line with dotted lines represents complete spatial randomness and the critical envelope at the 0.05 significance level.

in cumulative Pearson residuals occurred after 50% cover and remained below -2σ throughout the range to 100% canopy cover, indicating that territories were associated with high values of canopy cover. For stand age, cumulative Pearson residuals increased sharply (Fig. 2c) from the nadir point (90 years), indicating territories were associated with stands between 90 and 125 years old. For trees per hectare, cumulative Pearson residuals (Fig. 2d) increased rapidly from the nadir point (450 trees ha^{-1}), indicating that nest territories were more likely in stands with 470–750 trees ha^{-1}.

We fit 14 heterogeneous Poisson models to the 2007–2009 nest territories (Table 1). Under the assumption of a stationary

(constant-intensity) Poisson process (i.e., a null model with no spatial covariates), the observed values of the K function were higher (more clustered) than expected under a null model of complete spatial randomness at distances larger than 6 km and fell outside the 95% simulation envelope at distances larger than 11 km. We eliminated this trend by modeling the second power of the Cartesian coordinates using a heterogeneous Poisson model. The addition of basal area, canopy cover, stand age, quadratic form of the Cartesian coordinates with either linear or quadratic forms of trees per hectare improved the model's fit further (Fig. 3). There was a clear choice of the best model (Akaike weight 0.6825 with 2.7 times more support than the next supported model), which included basal area, canopy cover, age, trees per hectare, and the second power of the Cartesian coordinates. Under this model, the observed values of the inhomogeneous L statistic were less than zero at all distances but did not exceed the 95% simulated envelope under the heterogeneous Poisson model. The value of AIC for the model with the linear form of trees per hectare was approximately 2 greater than that with the quadratic form, indicating that the more parsimonious model balanced bias and uncertainty (Table 1).

1975–1976 Data set. We fit the 1975–1976 nest territories by using the current forest vegetation map to determine if these territories were in stands that remained suitable over the years. In contrast to the 2007–2009 data set, the plots of cumulative Pearson residuals for the four continuous covariates generally remained in the $\pm2\sigma$ error bounds, indicating that little variation was explained by these vegetation variables (Fig. 4).

TABLE 1. Model selection of Poisson point process models for Northern Goshawk nest territories in the Black Hills, South Dakota, 2007–2008.

Model[a]	ΔAIC[b]	w_i[c]
BA + canopy + age + TPH + $(x + y)^2$	0.0000[d]	0.6825
BA + canopy + age + TPH^2 + $(x + y)^2$	1.9955	0.2517
BA + canopy + age + TPH^2 + $x + y$	5.2300	0.0500
BA + canopy	8.9134	0.0079
BA + canopy + age + TPH	10.2907	0.0040
Canopy	11.6393	0.0020
BA + canopy + age + TPH^2	12.2484	0.0015
BA	17.4071	0.0001
$(x + y)^2$	29.0171	0.0000
TPH^2	29.6821	0.0000
Age	31.1027	0.0000
TPH	31.7668	0.0000
$x + y$	37.5980	0.0000
Intercept only	40.6979	0.0000

[a] Model parameters: basal area (BA), canopy cover (canopy), age of trees with diameter at breast height >23 cm (age), trees ha^{-1} and quadratic (TPH and TPH^2), Cartesian coordinates and quadratic ($x + y$ and $[x + y]^2$)
[b] Difference between the "best model" and other models.
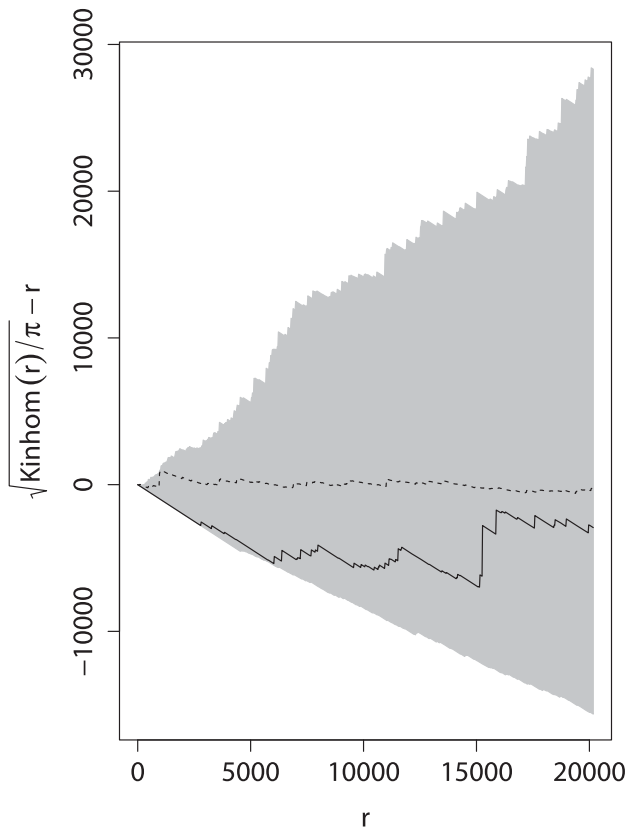[c] Akaike weight.
[d] Lowest value of AIC = 890.4417.

FIGURE 3. L functions of heterogeneous Poisson generalized linear models of Northern Goshawk territories in the Black Hills, South Dakota, located 2007–2009 with Cartesian coordinates and spatial covariates derived from the 2008 vegetation data in the Black Hills National Forest's geographic information system. The model included basal area, canopy cover, stand age, trees per hectare, and quadratic form of Cartesian coordinates. The solid line represents observed values; the horizontal dotted line represents complete spatial randomness. The shaded area represents the critical envelope at the 0.05 significance level.
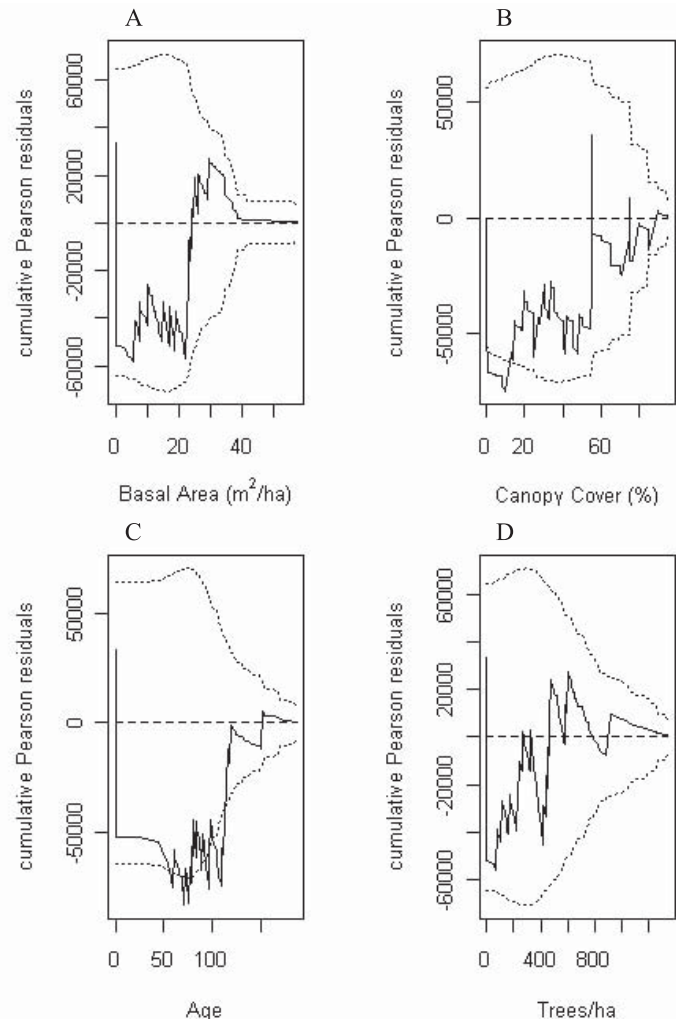

FIGURE 4.   Lurking-variable plots of standardized Pearson residuals for Northern Goshawk territories found during the 1975–1976 surveys in the Black Hills, South Dakota, with vegetative covariates derived from the 2008 vegetation data in the Black Hills National Forest's geographic information system. A, basal area of trees (m^2 ha^{-1}); B, canopy cover (%); C, age of forest stand (years); D, number of trees per hectare. The solid line represents observed values; the horizontal dotted line with dashed lines represents complete spatial randomness and the critical envelope at the 0.05 significance level.

We fit the same 14 Poisson point process models to these data as we fit the 2007–2009 data (Table 2). As with the 2007–2009 data set, the inhomogeneous L statistics computed under assumption of a stationary Poisson process clustered more than expected under complete spatial randomness, with observed inhomogeneous L statistics falling outside the 95% simulation envelopes at distances greater than 15 km. The best model included only the second power of the Cartesian coordinates. This model had >4.25 times the Akaike weight of the next-ranked model that included habitat variables. The model with Cartesian coordinates alone appeared to fit the data adequately. The addition of the spatial covariates basal area, canopy cover, stand age, or the linear or quadratic forms of trees per hectare did not improve the model's fit over that of the model based on the second power of the Cartesian coordinates (Table 2, Fig. 5).

Finally, we compared the spatial relationship between goshawk territories located 1975–1976 and 2007–2009 (Fig. 6). The observed bivariate L statistic was at or above the upper bound of the 95% simulation envelope up to approximately 8 km, indicating that the 2007–2009 territories were more likely to occur close to the 1975–1976 territories than under the null model of random relabeling. This result suggested that goshawks typically moved to areas close to previously suitable habitat.

VEGETATION ANALYSIS

Basal area was greater for nests when occupied than for the same nest sites measured currently (Fig. 7a). There were no significant differences in basal area among the occupied nests, except between nests found 1980–1981 and those found 2007–2009 (mean

TABLE 2.   Model selection of Poisson point process models for Northern Goshawk nest territories in the Black Hills, South Dakota, 1975–1976.

Model[a]	ΔAIC[b]	w[c]
$(x + y)^2$	0.0000[d]	0.6609
BA + canopy + age + TPA + $(x + y)^2$	2.8963	0.1553
BA + canopy + age + TPA^2 + $(x + y)^2$	4.8526	0.0584
Age	4.9419	0.0559
Canopy	7.1755	0.0183
Intercept only	8.3924	0.0099
BA + canopy + age + TPA	8.4669	0.0096
BA + canopy	9.1638	0.0068
BA	9.2071	0.0066
$x + y$	9.8240	0.0049
TPA	10.0653	0.0043
TPA^2	10.1524	0.0041
BA + canopy + age + TPA^2	10.4617	0.0035
BA + canopy + age + TPA^2 + $x + y$	12.2122	0.0015

[a] Model parameters: basal area (BA), canopy cover (canopy), age of trees with diameter of breast height >23 cm (age), trees ha^{-1} and quadratic (TPH and TPH^2), Cartesian coordinates and quadratic ($x + y$ and $[x + y]^2$).
[b] Difference between the "best model" and other models.
[c] Akaike weight.
[d] Lowest value of AIC = 690.6405.

± SD: 1975–1976 occupied, 35.5 ± 10.3 m^2 m^{-1}; 1975–1976 current, 22.2 ± 8.3 m^2 m^{-1}; 1980–1981 current, 22.0 ± 9.1 m^2 m^{-1}; 2007–2008, 30.4 ± 5.6 m^2 m^{-1}). Canopy cover was higher at nests occupied 1975–1976 than at those sites currently. There were no significant differences within those occupied (Fig 7b; 1975–1976 occupied, 88.4 ± 9.7%; 1975–1976 current, 47.0 ± 18.9%; 1980–1981 occupied, 70.0 ± 7.6%; 2007–2008, 64.1 ± 16.1%).

All values of trees per hectare were marginally higher at the sites currently than when the sites were occupied ($t_{36.0} = 1.73$, $P = 0.0914$, Fig. 8a); however, occupied sites had significantly more trees per hectare with DBH >12.7 cm ($t_{37.7} = -3.80$, $P = 0.0005$, Fig. 8b). There was no difference in quadratic mean diameter for either trees >2.54 cm DBH ($t_{38.9} = -0.621$, $P = 0.538$, Fig. 8c) or trees >12.7 cm DBH ($t_{36.8} = 1.622$, $P = 0.113$, Fig. 8d). Stand age was greater at sites when occupied sites than at those sites currently ($t_{66.3} = -2.761$, $P = 0.0074$, Fig. 8e), and there was no difference in stand height ($t_{36.6} = 0.168$, $P = 0.867$, Fig. 8f).

DISCUSSION

Our analysis indicated that locations of goshawk territories in the Black Hills were determined more by habitat conditions than by territoriality because there was no statistically significant repulsion at close distances that would have indicated territoriality determined spacing. These findings contrast with those for spacing of goshawk territories on the Kaibab Plateau (Reich et al. 2004, Reynolds and Joy 2006), where territories
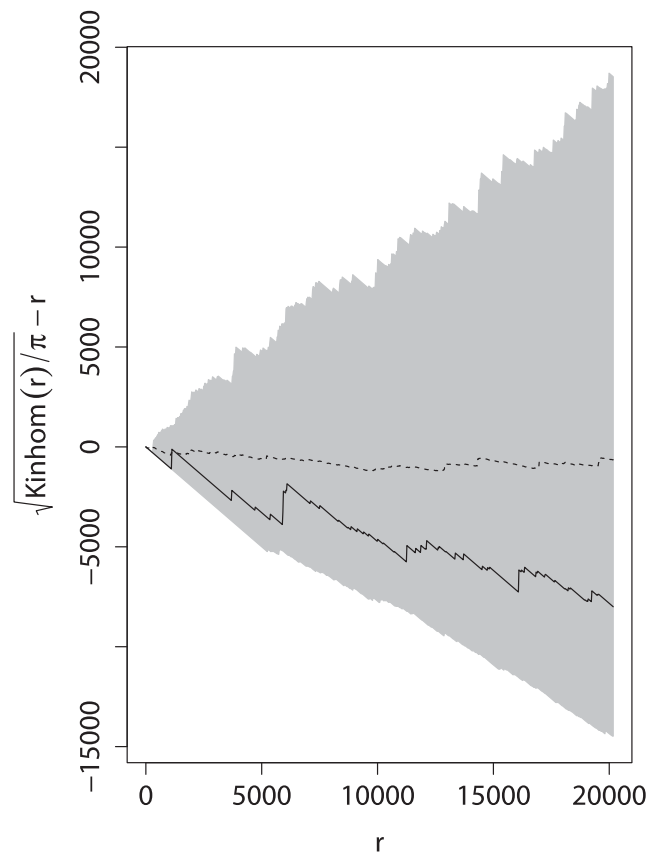

FIGURE 5. L functions of heterogeneous Poisson generalized linear models of Northern Goshawk territories in the Black Hills, South Dakota, located 1975–1976 with Cartesian coordinates and spatial covariates derived from the 2008 vegetation data in the Black Hills National Forest's geographic information system. The model included basal area, canopy cover, stand age, trees per hectare, and quadratic form of Cartesian coordinates. The solid line represents observed values; the horizontal dotted line represents complete spatial randomness. The shaded area represents the critical envelope at the 0.05 significance level.

were constrained by the availability of high-potential habitat within spaces defined by neighboring territories. In agreement with our results, however, important predictors for preferred nesting habitat on the Kaibab Plateau included basal area of trees and canopy cover.

We acknowledge that the number of territories in the Black Hills is much smaller than that on the Kaibab Plateau. In recent years, however, few territories additional to those found in our initial surveys have been located. Our mean nearest-neighbor distance (approximately 7 km) between territories is greater than those reported by Squires and Reynolds (1997) for Arizona (3 km, range 1.6–6.4 km) and California (3.3 km, range 1.3–6.1 km) but more similar to those they reported for Oregon (5.6 km) and Sweden (5.9 km). This may indicate that we missed territories. Because of private land ownership and forest management, however, the Black Hills have large meadows
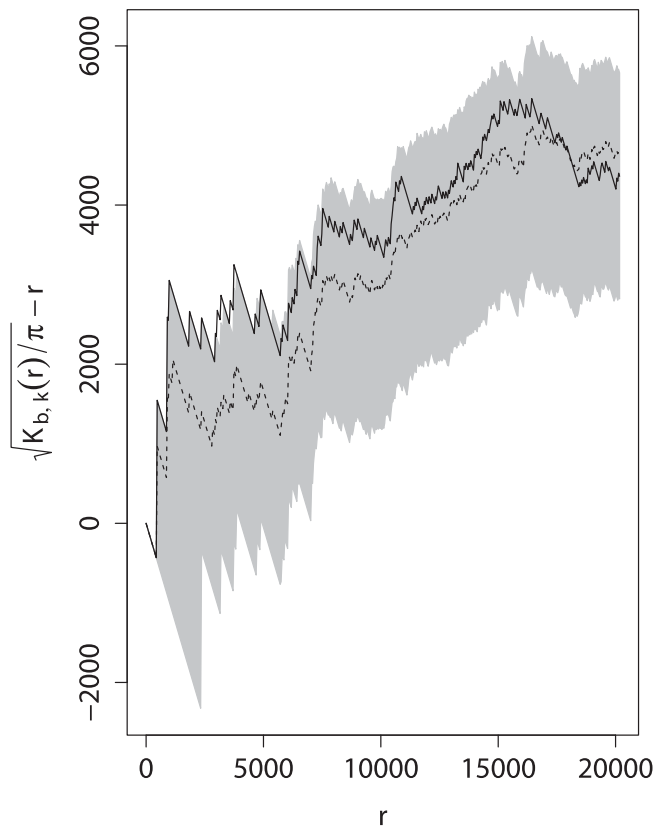
FIGURE 6.   Plot of the bivariate *L* function for Northern Goshawk territories located during the 1975–1976 and 2007–2009 surveys in the Black Hills, South Dakota. The solid line represents observed values; the dashed line represents the values expected under the null model. The shaded area represents the critical envelope at the 0.05 significance level.

FIGURE 7.   Box plots comparing (A) basal area of trees (m^2 ha^{-1}) and (B) canopy cover at Northern Goshawk nest trees in the Black Hills, South Dakota. Letters above boxes indicate common groups.

and extensive areas of sparse forest canopy less suitable for goshawks. While we do not know all goshawk territories in the Black Hills, we believe that we have discovered the majority of territories and our survey effort has been sufficient for these analyses. However, if we missed territories nonrandomly (as in regions of dense vegetation), this would affect our results.

Our best spatial model (incorporating forest stands' basal area, canopy cover, age of trees >23 cm, trees per hectare, and geographic coordinates) provided good prediction of territories. Our goal was to explain environmental variation. The geographic coordinates not only accounted for the observations of Bartelt (1977) and Erickson (1987) that territories were concentrated on the central plateau, they accounted for unexplained spatial variation that reflects spatial variability in elevation and topography. In the Black Hills, goshawks were consistent in their use of habitat through time; they used different stands, but with similar habitat characteristics. Despite differences over time in methods of measurement, there was little difference in basal area and canopy cover for nest sites occupied 1975–1976, 1980–1981, and 2007–2009. However, nest sites that were occupied 1975–1976 and 1980–1981 but are currently unoccupied lie within forests with reduced basal area and canopy cover. By
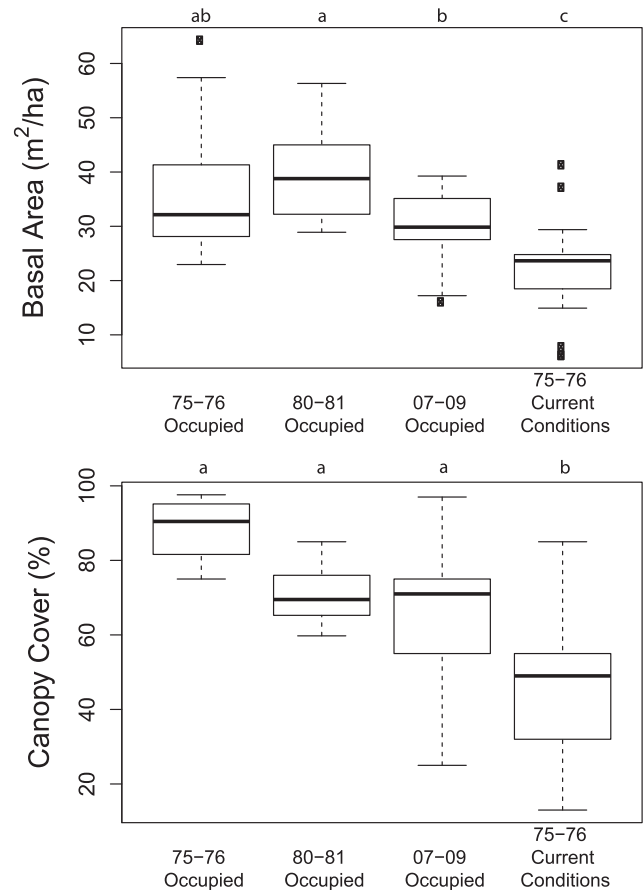
2008, forest stands containing nest sites studied 1975–1976 had more trees per hectare but a lower density of larger trees and the trees' average age was younger. These stands had probably been modified through logging, fire, or insects and are no longer suitable for nesting. These results have important implications for the goshawk's ecology with respect to mortality, competition, forest fragmentation, and nest-territory protection.

Younger, fragmented forests have a physical structure that provides poor-quality habitat for the goshawk but benefits the Red-tailed Hawk and Great Horned Owl, important competitors and predators of the goshawk (Kenward 1996, Penteriani and Faivre 2001). The Great Horned Owl is the dominant predator of the goshawk in North America (Kenward 1996, Squires and Kennedy 2006). From 2007 to 2009, Great Horned Owls nested in goshawk nests eight times (Knowles and Knowles 2009). Additionally, predation by Great Horned Owls and Red-tailed Hawks was suspected in four nest failures (Knowles and Knowles 2009). This intraguild predation (the killing of species that use similar resources) is an extreme form of interference competition (Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997, Sergio and Hiraldo 2008) and
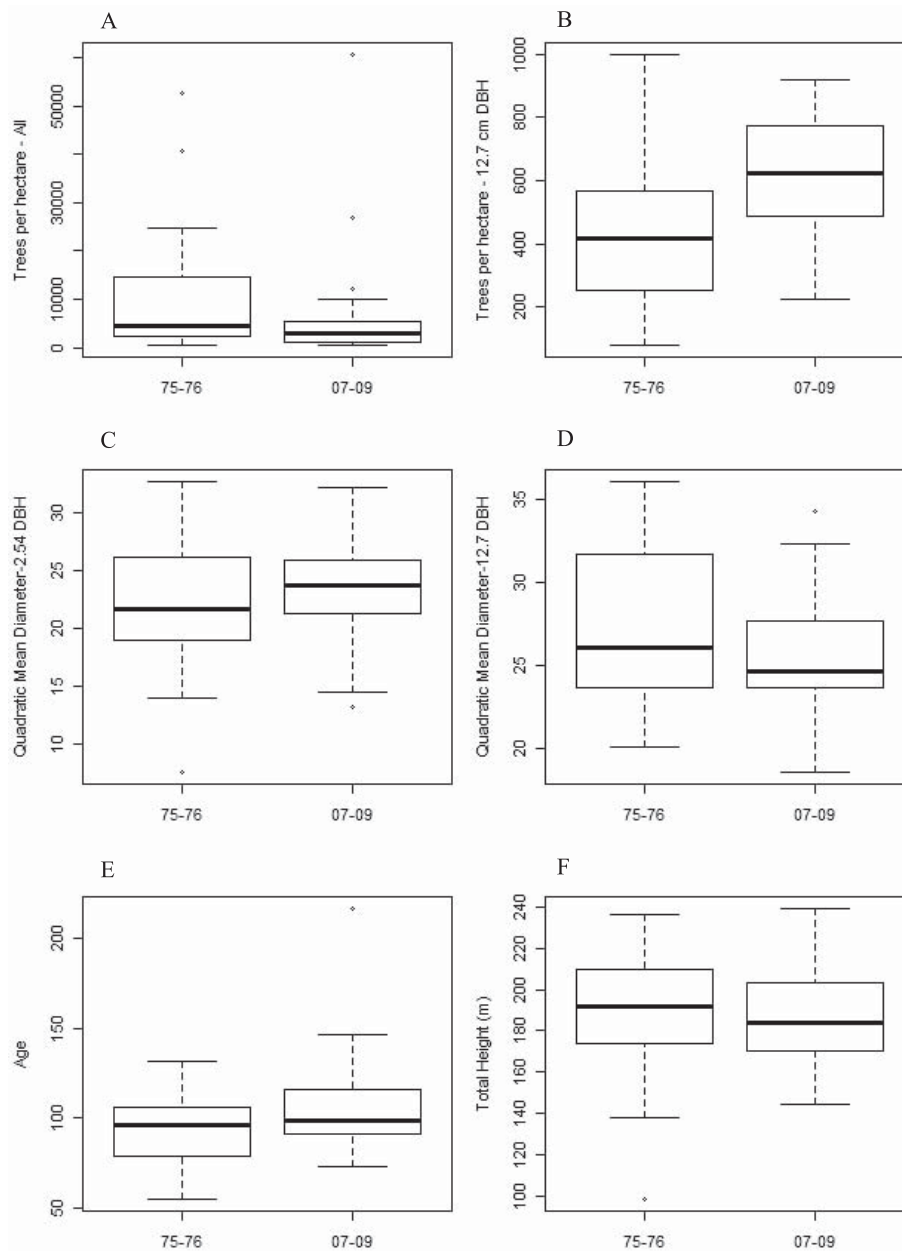
FIGURE 8.   Box plots comparing (A) density of all trees (ha^{-1}), B) density of trees ≥12.7 cm in DBH, (C) quadratic mean diameter of trees ≥2.54 cm in DBH, (D) quadratic mean diameter of trees ≥12.7 cm in DBH, (E) stand age (years), and (F) height of trees (m) at Northern Goshawk nest trees located during the 1975–1976 and 2007–2009 surveys in the Black Hills, South Dakota, according to the 2008 vegetation data in the Black Hills National Forest's geographic information system.

may represent a trade-off between maximizing survival in the presence of predators and acquiring resources for long-term survival (Cresswell 2008). Incidental predation of one raptor on another also may affect behavior, population dynamics, and community structure (Cresswell 2008, Sergio and Hiraldo 2008), with nonlethal effects being more important than the direct effect of predation (Cresswell 2008).

Other serious, nonlethal effects include the displacement of goshawks by Red-tailed Hawks and Great Horned Owls. As forests are fragmented and mature forest is lost, Red-tailed Hawks gain and goshawks lose habitat (La Sorte et al. 2004). Because Red-tailed Hawks typically enter nests from above the canopy, open and unobstructed access from above is an important factor in their nest-site selection (Orians and Kuhlman 1956, Titus and Mosher 1981, Bednarz and Dinsmore 1982, La Sorte et al. 2004). In contrast, goshawks enter nests from below the canopy, explaining the importance at goshawk nest sites of mature trees and open

understory, which provide easier access to nests, unhindered movements through the forest, and suitable microclimate within the nest (Hayward and Escano 1989, La Sorte et al. 2004, Reynolds et al. 2006, Squires and Kennedy 2006). In addition, both the Red-tailed Hawk and Great Horned Owl nest before the goshawk (Kenward 1996, Squires and Kennedy 2006), providing additional competition by forcing goshawks to construct or use alternative nests (Reynolds et al. 1994, Squires and Kennedy 2006).

Evidence suggests that the degree of habitat fragmentation in the Black Hills, relative to the goshawk's needs, is extensive. For example, in an individual-based modeling exercise, Smith (2007) found that there was not 24 ha of contiguous suitable habitat surrounding any nest site in the Black Hills. Smith (2007) and Knowles and Knowles (2009) concluded that the goshawk population in the Black Hills was a sink because recruitment of juveniles did not compensate for mortality of adults. For other goshawk populations in the Rocky Mountains, on the basis of an analysis of sensitivity and elasticity (Kennedy 2003), adult survival was the variable with greatest influence on the finite rate of population growth.

The forests of the Black Hills are dynamic because of natural causes (e.g., fire and insects); logging magnifies their dynamism, and this can have implications for the future of the goshawk in the Black Hills. In dynamic landscapes, species' critical behavior is more pronounced than in static landscapes (Wimberly 2006). Wimberly (2006) found that habitat occupancy always declines more rapidly with decreasing habitat and a declining population reaches extinction more quickly in dynamic landscapes than in static landscapes. Highly mobile species are less sensitive to landscape dynamics than are species of low and restricted mobility (Wimberly 2006). However, because the Black Hills are isolated from other forested ecoregions, rescue of the goshawk population by high levels of immigration is unlikely (Bartelt 1977, Smith 2007).

Goshawk territories in the Black Hills have been affected by logging since at least the 1970s (Bartelt 1977, Erickson 1987, Knowles and Knowles 2009). Between 2003 and 2009, 16 of 30 territories have been negatively affected by logging (Knowles and Knowles 2009). Territories consistently occupied from year to year have high conservation priority (Korpimäki 1988, Krüger and Lindström 2001, Sergio and Newton 2003). A relatively small number of territories may sustain a much larger population through source–sink dynamics (Newton 1991, Hanski 1999, Sergio and Newton 2003). For example, the best-quality individuals (older, dominant, or first to arrive) should monopolize the best-quality sites (Fretwell and Lucas 1970); territorial behavior then minimizes access to these high-quality sites by lower-quality birds, which are relegated to progressively inferior territories. At the population level, habitat heterogeneity and this ideal despotic process of settlement results in the percentage of low-quality territories that are occupied increasing with population density. Increasing use of low-quality territories causes a decline in per capita productivity, which may

regulate the population (Rodenhouse et al. 1997, Newton 1998, Sergio and Newton 2003). So to sustain the population in the Black Hills, territories occupied consistently should receive additional consideration and protection.

Our analysis indicates that when a forest stand is adversely modified, the goshawks using it may move to suitable stands nearby (Fig. 6). This suggests that landscape-scale management is appropriate for goshawk habitat. Preliminary analysis with the Forest Vegetation Simulator (Wykoff et al. 1982) of even-age silviculture prescribed for the Black Hills National Forest (available from http://www.fs.fed.us/fmsc/fvs/software/addfiles.php) suggests that such management does not sustain goshawk habitat (R.W. Klaver, unpubl. data). Perhaps silvicultural methods of group selection or free selection (Graham et al. 2007, Youtz et al. 2008) would be better suited for managing the goshawk in the Black Hills, because these methods would help to maintain forest diversity and more older, mature forest.

Finally, because they are more vulnerable to extinction from both demographic (e.g., Allee effect) and genetic factors (e.g, inbreeding depression, Noss and Cooperrider 1994), disjunct populations in isolated habitats present special conservation concerns. The Black Hills are a relatively small area to maintain a viable population of a species of the size and vagility of the goshawk, much less a sink population. In addition, the considerable effects of human activities (e.g., logging, development, grazing) and natural changes (e.g., fire and insect outbreaks) greatly limit the habitat and area available to this large, reclusive hawk in the Black Hills. Even in a species whose territoriality influences its density and distribution across a landscape (e.g., the Kaibab population, Reich et al. 2004), habitat quality and availability may be more important for determining the density and distribution of individuals in disjunct populations. Results from our study suggest this. Hence identifying the importance of habitat quality and availability for maintaining a disjunct population is critical for its conservation.

Adaptive management and structured decision (Walters and Holling 1990, Lancia et al. 1996, Nichols and Williams 2006, Lindenmayer and Likens 2009) might be appropriate for managing this species of special concern, considering the uncertainty of management, recurrent decisions, and diverse, multijurisdictional stakeholders. Adaptive management should be helpful in balancing the often conflicting land-management decisions of goshawk requirements with management for timber, mountain pine beetles, roads, and fire. Effectively incorporating the biological needs of the goshawks into the management of the Black Hills National Forest should provide increased biodiversity for the entire ecosystem (Sergio et al. 2005, 2006, 2008a, b).

ACKNOWLEDGMENTS

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