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Predicting the location of northern goshawk nests: modeling the spatial dependency between nest locations and forest structure

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Abstract

Northern goshawks interact with each other and their environment in a spatially dependent manner. However, finding the location of active goshawk nests (e.g. where eggs are laid) in a given year is difficult due to the secretive nature of the hawks in their forest environment, their annually variable attempts at nesting, and the extent of the area within a home range where they will nest. We used a Gibbsian pairwise potential model to describe the spatial dependency (1) among nest locations influenced by territoriality and (2) between nest locations and the environment for a large population of goshawks on the Kaibab National Forest's (NNF) North Kaibab Ranger District (NKRD). Nest locations in a given year were regularly distributed at a minimum distance of 1.6 km between active nests; however, as the spatial scale increased (i.e. as distance between the nests increased), the degree of regularity decreased. Important forest predictors for nest locations included canopy closure, total basal area, proportion of basal area in ponderosa pine, spruce, fir, and aspen, maximum height of the understory vegetation, and presence/absence of seedlings and saplings. The probability of an occurrence of an active nest within a 10-m × 10-m area was modeled using logistic regression. Spatial analysis, using nest spacing and habitat variables, indicated that potential active nest locations were abundant and randomly distributed throughout the NKRD. This supports the supposition that the availability of locations with high potential for nests is not limiting the goshawk population on the study area. Instead, territoriality, and what appear to be non-compressible territories, sets the upper limit to the nesting population. Ultimate choice of nest location was probably constrained by the availability of high potential locations within spaces defined by neighboring territories. Overall territory density, on the other hand, may reflect the abundance, quality, and accessibility of prey on the study area. This model can be used to evaluate the influence of forest management activities on the nesting goshawk population on the NKRD. The modeling technique described in this paper may be applied to other study areas, where vertebrate densities and the spatial resolution of habitat data may be less or greater than on this study, provided that new point process and pairwise potential models are developed for each area.
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1. Introduction

The northern goshawk (*Accipiter gentilis*; hereafter goshawk) has been the focus of intensive research for the past decade (Block et al., 1994; Kennedy, 1997; Peck, 2000) because of suspected population declines

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due to loss of habitat (Reynolds, 1983, 1989; Kenward and Widén, 1989; Speiser and Bosakowski, 1984; Crocker-Bedford, 1990; Widén, 1997) and changes in forest structure (Reynolds et al., 1992), both resulting from forest management. Many goshawk studies in North America and Europe have focused on the hawks' habitat use, food habits, movements, distribution, demographics, and diets (Block et al., 1994); however, no studies have attempted to use spatially explicit models to describe simultaneously the spatial dynamics among goshawks and between goshawks and their environment. Although some researchers (Clark et al., 1993; Baker et al., 1995; Augustin et al., 1996; Ripple et al., 1997; van Manen and Pelton, 1997; Carroll et al., 1999; Dettmers and Bart, 1999; Mladenoff et al., 1999; Swindle et al., 1999; Thome et al., 1999; Pearce and Ferrier, 2000; Mitchell et al., 2001; Finn et al., 2002) have used spatial modeling to explore wildlife-habitat relationships, few (Reich et al., 2000; Peres-Neto et al., 2001; Austin, 2002) have recognized their value in exploring these manifold spatial dependencies.

Goshawks interact with conspecifics (members of the same species) and their habitat in a spatially dependent manner (Widén, 1985; Selås, 1997; Reynolds and Joy, 1998). By first describing the spatial distribution among active goshawk nests (i.e. nests in which eggs are laid) within a goshawk population and then modeling the interaction between nest locations and forest structure, it may be possible to predict the location of active nests in a given year. Locating active nests is extremely difficult due to the secretive nature of the birds and their annually variable attempts at nesting (Reynolds and Joy, 1998), nest concealment, and the size of the area within their home ranges where they will nest.

Many bird species, such as the goshawk, attempt to exclude conspecifics from all or a part of their territory. Territoriality, in most cases, is an effort to secure resources, such as food and a mate, against their use by others, thereby increasing an individual bird's fitness (Ricklefs, 1973). Such behavior tends to space nests evenly throughout their habitat. Thus, the size of an individual territory tends to vary from species to species, and within species from habitat to habitat depending on the availability of resources. Spatial point process models that are commonly used to model such patterns include the Markov point process and Gibbs distribution. Ripley and Kelly (1977) first introduced the Markov point process model, while the Gibbs model has a longer history in statistical physics (Preston, 1977). These models provide the basis for describing complex spatial patterns and have been used widely for modeling regular spatial patterns (Ripley, 1977; Ogata and Tanemura, 1981, 1984). Taking into consideration a species' spatial pattern incorporates both biologically and ecologically meaningful information into the modeling process, as a close relationship exists between the abundance of an individual species and its spatial distribution.

Intra-specific competition (i.e. territoriality) is a complex biological phenomenon. Therefore, any spatial point process model developed to describe this spatial relationship is necessarily an approximation of the true process. Such models are limited by the availability of sufficient data to estimate reliably all the parameters required by the models. Even if such models could be developed, they may be of limited value unless (1) the corresponding data required to implement the model were available and (2) the model was based on variables that were easily obtained in the field. However, models such as the Markov point processes and Gibbs distributions have been found to perform adequately in such situations. These models are based on simple assumptions relating to how points interact in a pairwise fashion (such as, the influence between pairs of points depends on their relative, not the absolute, positions) and are relatively easy to fit.

Since their introduction, much attention has focused on a special case of the Markov and Gibbs models, the pairwise interaction model, in which a set of points (e.g. nests) are considered to interact in a pairwise fashion (Strauss, 1975; Besag et al., 1982; Diggle et al., 1987; Ripley, 1990; Cressie, 1991, pp. 674–678; Diggle et al., 1992). "Competitive" intra-specific interactions may therefore be described by the pairwise potential function of either model. In addition, the Gibbsian pairwise potential model may be expanded by including environmental variables to identify potential habitat for a species in a landscape (Reich et al., 1997). As a result, the model performs similarly to other habitat predicting techniques (e.g. generalized linear model (GLM), generalized additive models (GAM), classification and regression tree models). The model's advantage, however, is in its ability to simulate dynamic

and interactive ecological processes to achieve greater ecological "reality" in predicting species occurrences.

In this paper, we fit a Gibbsian pairwise potential model to describe the spatial variability among goshawk nests and their association with forest structure on the Kaibab National Forest's (KNF) North Kaibab Ranger District (NKRD) in northern Arizona. We also identify habitat that is more likely to have nests by correlating the location of known nests with environmental variables that account for the coarse-scale variability (gradients) across the landscape. Finally, we explain how this modeling effort may be applied to other vertebrate studies and study areas.

2. Study area

The study area (1285 km^2) included forests on the NKRD above 2182 m in elevation. This elevation was chosen because it represented the lower elevation of the distribution of forest; below this elevation forests were dominated by shorter pinyon (*Pinus edulis*)–juniper (*Juniperus* spp.) woodlands where goshawks rarely nest (Squires and Reynolds, 1997; S.M. Joy, personal observation). The study area comprises the northern two-thirds of the Kaibab Plateau in northern Arizona and is bounded by the Grand Canyon National Park to the south, steep slopes to the east, and gentle slopes to the north and west that descend to a shrub-steppe plain. Six vegetation classes dominate the study area (Fig. 1; Joy et al., 2003): (1) pinyon–juniper woodlands (106 km^2, 8% of study area) occur at lower elevations (2182–2250 m) and mix with ponderosa pine (*Pinus ponderosa*) at transitional zones; (2) ponderosa pine (704 km^2, 55%) occurs between 2250 and 2550 m; (3) mixed-conifer, comprised of ponderosa pine, white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga mensiesii*), and quaking aspen (*Populus tremuloies*) (145 km^2, 11%), occurs between 2550 and 2650 m elevation; (4) spruce (*Picea pungens*, *Picea englemannii*)-dominated mixes (130 km^2, 10%), primarily with subalpine fir (*Abies lasiocarpa*), occurs above 2650 m elevation; (5) deciduous (quaking aspen, Gamble's oak (*Quercus gambeli*))-dominated mixes (112 km^2, 9%) occur throughout the forest and are common where extensive disturbance has occurred (Fig. 1); and (6) openings (90 km^2, 7%) that contain grasses and herbaceous vegetation include a series of long, narrow meadows and various smaller gaps in the canopy which are scattered throughout the forest.

Nearly all of the KNF has been altered by some form of management during the past 100 years (Pearson, 1950; Burnett, 1991). By the early-1900s livestock grazing was common and fire suppression had been established. A long-term policy of fire exclusion has resulted in large numbers of shade-tolerant seedlings and saplings throughout the forest creating fuels and a closing-in of the historically more-open understory (Weaver, 1951). Organized tree harvests in the form of sanitation cuts and single-tree selection began in the 1920s. These harvest regimes continued, along with occasional, small (0.1 km^2) clearcuts in the mixed-conifer zone, until the late-1970s. Intensive forest management at the stand level (shelterwood, seed, salvage, removal, and thinning cuts) began in the 1980s and continued until 1991, when the NKRD implemented forest management prescriptions designed to enhance the habitat of goshawks and their prey (Reynolds et al., 1992).

The NKRD receives about 67.5 cm of precipitation annually, with winter snowpacks of 2.5–3.0 m (White and Vankat, 1993). A drought period typically occurs in May and June, followed by mid- to late-summer thunderstorms and heavy showers.

3. Methods

3.1. The data

The data layers used to model spatial dependencies among goshawks and their environment included the location of active nests, field measurement, Landsat Thematic Mapper (TM) imagery, and GIS-derived topographic variables. Nest locations were used to describe the spatial distribution of nests; whereas, the field measurements, Landsat imagery, and topographic variables were used to model forest composition and structure to a 10-m spatial resolution.

3.1.1. Goshawk nest locations

Searches for active goshawk nests began in 1991 and continued through 1998. Nest searches began in April and ended after the post-fledging period (mid-August). Each year, the overall search area on
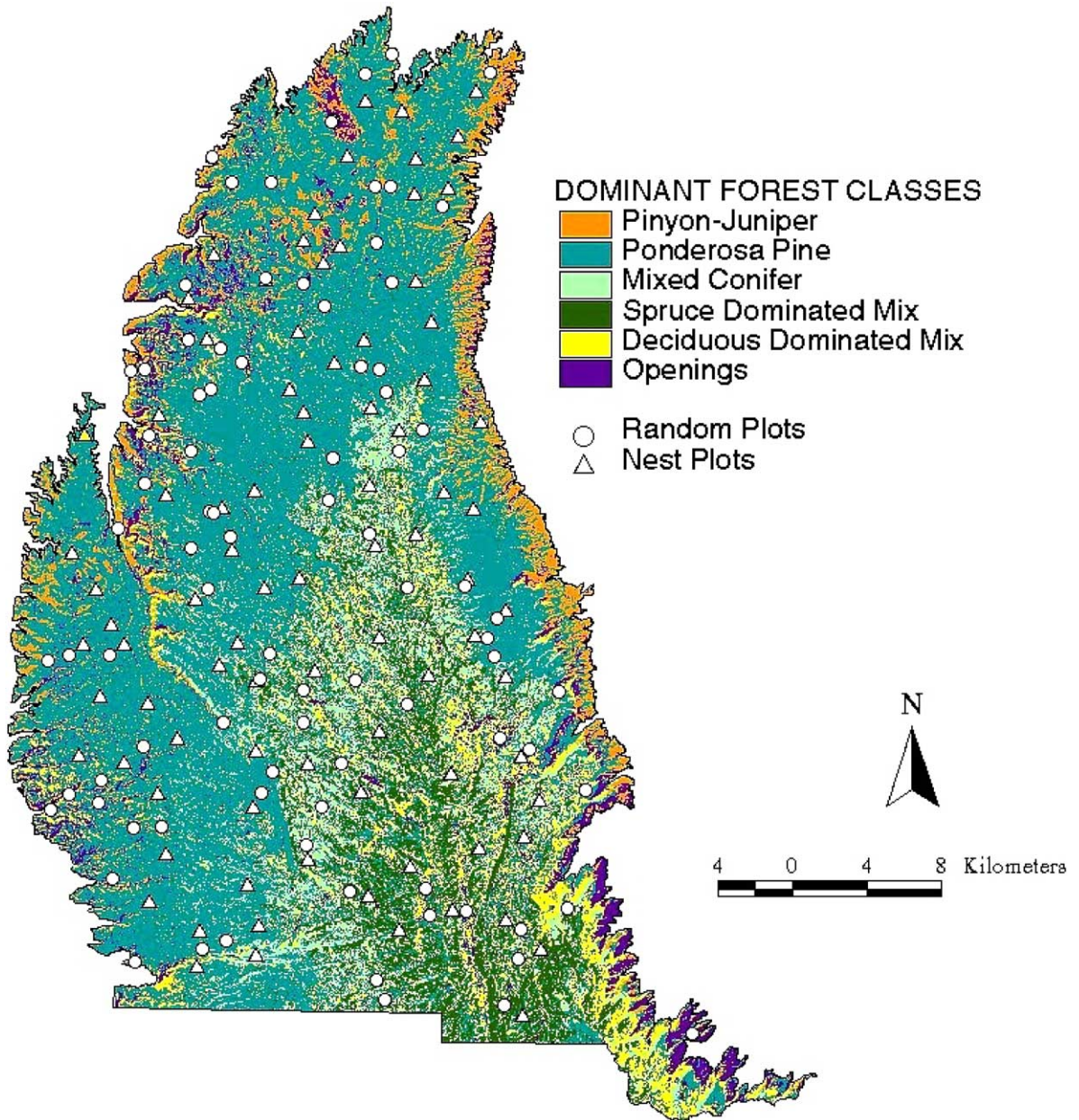
Fig. 1. Distribution and arrangement of nest plots (△) and random plots (○) used to model forest structure displayed among dominant vegetation classes on the North Kaibab Ranger District, Kaibab National Forest, Arizona.

the NKRD was expanded to include more territories. Nests were found by (1) searching on foot (Reynolds, 1982), (2) systematically broadcasting goshawk vocalizations from predetermined stations on transects (Kennedy and Stahlecker, 1993; Joy et al., 1994),

and (3) visiting active nests found in prior years of the study. When the status of a previously-active nest remained unknown, searches of 16 and 24 km^2 areas around that nest were carried out on foot or by broadcasting, respectively, to locate an alternate

active nest within the territory. Goshawks may use more than one nest within their territories among breeding years (Reynolds and Wight, 1978; Reynolds et al., 1994; Reynolds and Joy, 1998). A "territory" (approximately 1.5 km radius) is the area used and defended by a single pair of goshawks during the nesting season and may contain one or more alternate nest trees (Reynolds et al., 1994). At each active nest, adults and juveniles were captured and banded with a USDI Fish and Wildlife Service aluminum leg band and an anodized aluminum colored leg band, the latter marked with unique two-character alpha-numeric codes readable at up to 50–80 m with 20–40 power spotting scopes. Identifying the individual goshawks allowed us to correctly associate new nests with individual territories. On the study area, territoriality is maintained even in non-breeding years by marked individuals who continue to defend their territory (Reynolds et al., 1994).

3.1.2. Field data

Models of forest structure were based on the spatial interpolation of habitat attributes at both active nests sites and randomly selected sites (Fig. 1):

- *Goshawk nest plots*. We measured the forest vegetation immediately surrounding the nest tree at one nest within each of 92 goshawk territories studied through 1998. In territories containing multiple active alternate nests that had been active since 1991, we randomly selected one alternate at which to measure the forest characteristics. At single-nest territories, we measured the vegetation at that nest tree.
- *Randomly located plots*. To describe the spatial/structural variability on the NKRD, we located 85 random plots throughout the study area. We placed no constraints on the location of random plots (i.e. they were placed irrespective of territories and nests), because we considered all habitat to be potentially available to goshawks for nest site use.

3.1.3. GIS and Landsat TM data

The GIS database consisted of four topographic variables (elevation, slope, aspect, and landform), six bands (1–5, and 7) of Landsat TM data (1997; 22 June; Path 37, Row 35), and seven variables representing stand structure (percent canopy closure; total basal area; proportions of (a) ponderosa pine, (b)

spruce/fir, and (c) aspen in the total basal area; maximum height of the understory vegetation; and the presence of seedlings or saplings). All habitat-related variables were believed to be important to goshawk nest tree selection. Elevation was obtained from USGS digital elevation models (DEM) and used to derive aspect and slope. The DEM was also used to calculate a landform index (McNab, 1989), which expresses surface shape as a measure of surface concavity or convexity (computed as the mean slope gradient from the original cell to adjacent cells in 4 directions), as a continuous variable. Grid coverages for elevation, slope, aspect, and landform were resampled to 10 m, corresponding to the spatial resolution of the field data (below). Grid coverages representing forest structure were developed by spatially interpolating the random and nest-based field data to a 10-m spatial resolution using trend surface models and regression trees (Joy, 2002, pp. 46–95). Landsat bands 1–5 and 7, and topographic data were used as predictor variables. All grid manipulations were performed in ArcView® (ESRI, 1998).

3.2. Field measurements

Because the spatial variability in forest structure can vary at scales smaller than those determined by the spatial resolution of Landsat TM imagery (i.e. <30 m), we designed our field sampling to classify forest structure to a 10-m spatial resolution. Sample plots consisted of a cluster of nine 10-m × 10-m subplots that corresponded to a 30-m × 30-m pixel on our Landsat TM imagery, the location of which was verified using a Trimble Navigation Pathfinder™ Asset Surveyor Global Positioning System (estimated accuracy = 1–3 m). Field measurements were collected during August and September of 1997. Each plot was established in a north–south, east–west fashion with the coordinate systematically assigned to either the center (nest tree plot) or lower left corner (random plots) of the plot. Vegetative characteristics were recorded on each of the nine 10-m × 10-m subplots and included canopy closure (measured with a concave, spherical densiometer; Lemmon, 1956, 1957), overstory species, total basal area by species (measured with a 20 factor prism), height of the understory vegetation, and the presence of seedlings and saplings.

3.3. Spatial distribution of active goshawk nests

Territoriality (i.e. behavior related to the defense of a specified area against intruders) is assumed to strongly influence the spatial distribution of nests among breeding pairs of goshawks across the landscape. Therefore, intra-specific behavior such as this is a necessary component of any habitat model involving breeding birds. To model the distribution of active goshawk nests, we selected a large (528 km^2) rectangular region within the NKRD. A rectangular region was selected to simplify the algorithm required to adjust for edge effects, while the shape of the rectangular was selected to include as many nests as possible. The spatial location of all active nests in 1998 within the rectangular region B (Fig. 2) was assumed to represent the spatial relationship between active goshawk nests and forest structure when the population is at or near full occupancy because, in 1998, active nests attained the most continuous spacing (i.e. fewest gaps due to non-nesting territorial pairs or individuals) among all the breeding years studied (Fig. 3).

Using the spatial location of each nest in the rectangular region B, a Monte Carlo test (Besag and Diggle, 1977) based on the Cramér–von Mises type statistic (Cressie, 1991, p. 642)

$$k = \int_0^H [\hat{K}(h)^{1/2} - \pi^{1/2}h]^2 \, dh \qquad (1)$$

was used to test the null hypothesis of complete spatial randomness (CSR); i.e. whether the arrangement of nests within a circular region of radius H does not differ significantly from that expected under the assumption of CSR. This was done at 14 spatial scales ranging from 2 to 16 km in increments of 1 km by simulating values of the test statistic under CSR and comparing them to the corresponding statistic calculated from the observed pattern of active goshawk nests. For each simulation, we calculated the empirical K-function, $\hat{K}_i(h)$ (Ripley, 1977), corrected for edge effect (Cressie, 1991, p. 616), and the Cramér–von Mises statistic k. The significance (P-value) of the test was calculated as $\hat{p} = (R + 1 - r)/R$, where R is the number of simulations, and r is the rank of the test statistic associated with the observed point pattern. A small P-value supports the alternative hypothesis of a non-random spatial pattern. All tests were based on 200 realizations of a spatial Poisson process to allow for the calculation of a P-value to the nearest 1%.

Traditional nearest neighbor statistics, which are often used to test nest spacing (e.g. Newton et al., 1977), assume that the nearest neighbors are independent (Cressie, 1991, pp. 603–606). If applied to mapped data sets such as nests, however, the nearest neighbor measurements are not independent, and one would tend to reject the null hypothesis of CSR too often (Cressie, 1991, p. 610). In contrast, the K-function and the Cramer–von Mises goodness-of-fit test do not assume that distance measurements are independent. Furthermore, they use information on many spatial scales because they are based on squared distances to the first, . . . , kth nearest neighbors.
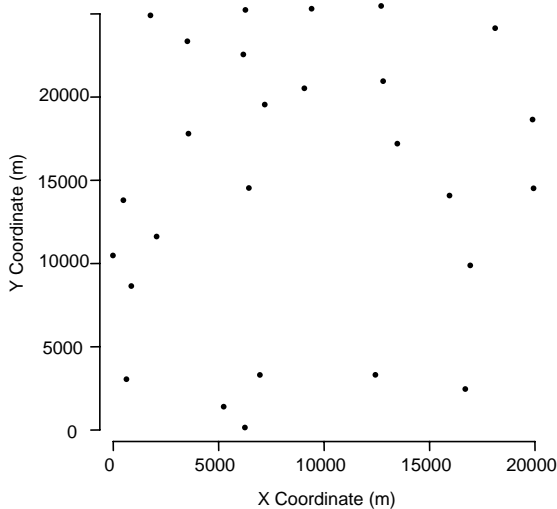

Fig. 2. Bounded region (B) showing the relative location of 27 active northern goshawk nests from 1998 used to model the spatial relationship between active nests and forest structure.

3.4. Gibbsian pairwise potential model

The Gibbsian pairwise potential model is a Markov point process, a flexible class of models in that they simulate both regular (inhibition) and aggregated (contagious) patterns. The primary use of such models has been in the study of regular point patterns, such as those exhibited by the goshawk (Reynolds and Joy, 1998; Widén, 1985), other accipiters (Newton et al.,

Fig. 3. The location of active northern goshawk nests between 1991 and 1998 on the North Kaibab Ranger District, Kaibab National Forest, Arizona.

1977), as well as other raptors (Cade, 1960; Ratcliffe, 1962; Newton, 1979).

The most extreme form of spatial regularity results from the direct exclusion from a given area, whether by complete occupancy, allelopathy, or territoriality. Models that describe such phenomenon are termed hard-core models. Every individual in the population has a circular neighborhood within which no other individual can exist. For biological populations that display plasticity of size and shape, the hard-core model may be too extreme. As an alternative, a soft-core model with fixed-range interactions may be used. Soft-core models are less extreme, in that within a given neighborhood of radius R, inhibition is not complete, and a competitive effect (i.e. territoriality) is experienced. The degree of territoriality

may or may not be a function of the distance between individual pairs (h).

3.4.1. Potential energy of goshawk nests

The location of all N goshawk nests within the bounded region B were assigned coordinates $X = \{X_i = (x_i, y_i) \in B, i = 1, \ldots, N\}$. To model the spatial distribution and association of individual territorial goshawk pairs (i.e. nests), we assumed that the territorial influence between pairs depended on the relative, and not the absolute position of nests. This assumption implies a homogeneous environment. The territorial interaction, or potential energy, Ψ, can be modeled as a function of the Euclidean distance $h_{ij} = ||X_i - X_j||$ between pairs of nests in which the territorial influence between individual pairs decreases with increas-

ing distance. Thus, the total potential energy for the point process is defined as (Cressie, 1991, p. 677):

$$U_N(X) = \sum_{i<j}^{N} \Psi(h_{ij}), \tag{2}$$

where $U_N(X)$ can be thought of as the total energy required to add a nest to the point pattern. The observed point pattern of goshawk nests, therefore, can be regarded as being distributed according to a Gibbs canonical distribution:

$$f(x) = \frac{\exp[-U_N(X)]}{Z(\Psi; N)}, \tag{3}$$

where $Z(\Psi; N)$ is a normalizing constant where the joint probability density integrates to 1. If the normalizing constant exists, the point pattern is said to be stable. The sign and shape of the potential functions are determined by whether there is inhibition or attraction between nests. Positive values indicate inhibition, while negative values represent attraction. If no interactions exist between nests, the value of the potential function is zero. A strictly positive pairwise potential (i.e. inhibition process) always yields a stable process, while those with negative potential energy at some specified distances (i.e. contagious process) are generally unstable (Cressie, 1991, p. 678).

3.4.2. Model parameter estimation

Consider a family of parameterized pairwise potential functions $[\Psi_\theta(h); \theta \in \Theta]$. Given a finite set of points in a bounded region, B, the likelihood of the potential function $\Psi_\theta(h)$ is given by the Gibbs canonical distribution (Eq. (3)). The maximum likelihood estimate of θ is obtained by finding a $\hat{\theta}$ that maximizes Eq. (3). Maximization requires computing the normalizing constant $Z(\Psi; N)$, which is not usually available in closed form (i.e. where an explicit solution exists). Ogata and Tanemura (1981) use the cluster-expansion method of statistical mechanics (Ogata and Tanemura, 1981; Cressie, 1991, p. 682) to obtain an approximation of the normalizing constant, conditioned on the number of points in B:

$$Z(\Psi; N) = |B|^N \left(\frac{1 - a(\theta)}{|B|} \right)^{N(N-1)/2}, \tag{4}$$

where

$$a(\theta) = 2\pi \int_0^{\infty} h[1 - \exp(-\psi_\theta(h))]\,\mathrm{d}h \tag{5}$$

is the second cluster integral, and $|B|$ is the area of the bounded region B. In their approximation, only pairwise interactions were considered; higher order interactions were assumed to be negligible. Cressie (1991, p. 683) points out that this approximation holds only for stable pair-potentials, and may not be valid for unstable pair-potentials that require higher-order interactions such as a Markov cluster process. Combining Eqs. (3) and (4) leads to the approximate log likelihood function:

$$\log L(\theta|X) = \sum_{i<j}^{N} \Psi_\theta(||X_i - X_j||)$$
$$- \frac{1}{2}N(N-1)\log\left(1 - \frac{a(\theta)}{|B|}\right), \tag{6}$$

which can be solved using nonlinear optimization procedures.

To use this relationship in describing the spatial distribution and association of individual nests, one must be able to mathematically describe the interaction potentials of a spatial point pattern. Three parameterized potential functions proposed by Ogata and Tanemura (1981, 1985) are available to describe the interactions observed in the distribution of the goshawk nests:

$$\text{PF1}: \quad \Psi_\theta(h) = -\log[1 + (\alpha h - 1)\,\mathrm{e}^{-\beta h^2}],$$
$$\theta = (\alpha, \beta), \alpha \geq 0, \beta > 0 \tag{7}$$

$$\text{PF2}: \quad \Psi_\theta(h) = -\log[1 + (\alpha - 1)\,\mathrm{e}^{-\beta h^2}],$$
$$\theta = (\alpha, \beta), \alpha \geq 0, \beta > 0 \tag{8}$$

$$\text{PF3}: \quad \Psi_\theta(h) = \beta \left(\frac{\sigma}{h}\right)^{12} - \alpha \left(\frac{\sigma}{h}\right)^{6},$$
$$\theta = (\alpha, \beta, \sigma), \beta > 0. \tag{9}$$

All three potential functions can model both repulsive and attractive forces. The parameter, α, controls the type of force between a pair of points, while β and σ are scaling parameters. The potential function PF1 represents a purely repulsive potential when $\alpha = 0$, and has both repulsive and attractive potentials when $\alpha > 0$. The potential function PF2 is repulsive when

$0 \leq \alpha < 1$, independent when $\alpha = 1$, and attractive when $\alpha > 1$. The potential for PF3 is purely repulsive when $\alpha < 0$, and attractive when $\alpha > 0$. The second cluster integral, $a(\theta)$, for the three potential functions are given by

$$\text{PF1}: \quad a(\alpha, \beta) = \left(\frac{\pi}{\beta}\right)\left(\frac{1 - \alpha\sqrt{\pi/\beta}}{2}\right) \quad (10)$$

$$\text{PF2}: \quad a(\alpha, \beta) = \frac{\pi(1 - \alpha)}{\beta} \quad (11)$$

$$\text{PF3}: \quad a(\alpha, \beta, \sigma)$$
$$= -\frac{\pi}{6}\beta^{1/6}\sigma^2\sum_{k=0}^{\infty}\frac{1}{k!}\Gamma\left(\frac{6k - 2}{12}\right)\alpha^k\beta^{-k/2}. \quad (12)$$

The pairwise potential models PF1–PF3 were fit to the point data of the individual nests using a nonlinear least squares procedure to obtain an estimate of the parameter vector $\theta = (\alpha, \beta)$ or $\theta = (\alpha, \beta, \sigma)$ that maximized the approximate log likelihood (Eq. (6)). Akaike's (1977) AIC, was used to select the best model among the three possible models (PF1–PF3).

3.5. Potential energy between nests and forest structure

To include environmental heterogeneity in the model, the total potential energy was redefined as follows:

$$U_N(X) = \sum_{i<j}^{N}\Psi(h_{ij}) + \sum_{i=1}^{N}\phi(z_i), \quad (13)$$

where $\phi(z_i)$ is a measure of the interaction of individual nests with the environment (i.e. forest structure). If we assume that the presence, or absence, of a nest is correlated to a set of known environmental variables we can, for example, define the probability of observing a goshawk nest at a given location as π. The potential energy associated with this location can be expressed as (Reich et al., 1997):

$$\phi(z) = \frac{1}{\pi} - 1 = f(\text{environmental variables}). \quad (14)$$

Large positive values indicate "poor" nest locations while small values indicate "good" nest locations. We define "good" nest locations as those with higher probabilities of observing an active nest (see above).

"Good" locations as defined by forest structure, however, do not necessarily confer greater fitness on the birds using those sites (Van Horne, 1983; Vickery et al., 1992) because fitness (measured directly or indirectly by survival and reproductive success) is a function of, not only, habitat characteristics, but also food resources and life history strategies used throughout the home range (Newton et al., 1977; Reynolds et al., 1992; Kostrzewa, 1996). Furthermore, the presence of good habitat alone does not guarantee that a nest will be present because the value of an area as a nest location is dependent upon the arrangement of both fine- and coarse-scale (i.e. landscape scale) variability in the landscape (Ricklefs, 1987), territoriality, and population density.

3.6. Modeling nest site suitability

To model the potential energy associated with forest structure we used a multiple logistic regression model (Hosmer and Lemeshow, 1989; Manly et al., 1993):

$$\pi = \frac{e^{\beta_0 + \beta_1 z_1 + \cdots + \beta_k z_k}}{1 + e^{\beta_0 + \beta_1 z_1 + \cdots + \beta_k z_k}}, \quad (15)$$

where π is the probability of observing a goshawk nest, $z_1, \ldots, z_k$ are independent predictor variables, and $\beta_1, \ldots, \beta_k$ are logistic coefficients. Independent variables considered in the model included topographic data (elevation, slope, aspect, landform) and forest structure (total basal area, proportion of pine, aspen, spruce-fir basal area, height of understory vegetation, and presence of seedlings). The final form of the model was based on a forward selection process that eliminated independent variables with high P-values. Coefficients from the logistic regression model indicate the direction of change (positive—increase, negative—decrease) required by an independent variable to maximize the probability of an occurrence of an active nest, given the topographic and environmental constraints imposed by other independent variables.

Preliminary analysis indicated that the functional form of the logistic regression model differed among vegetation classes in that not all of the independent variables were important in all vegetation classes. To account for these differences, we added dummy variables to the model. After fitting the logistic regression, a final model, composed of significant variables and

coefficients, was used to create a map of the probability distribution of nest locations. We standardized (Neter et al., 1985, p. 262) the regression coefficients for the logistic model to compare the relative strength of individual variables within each model, as well as across vegetation classes.

We used classification error rates to evaluate the fit of the model. To calculate classification rates, we compared the probability from the logistic regression models, a continuous variable, to a cutoff value. Each 10-m × 10-m pixel of the NKRD was categorized into a dichotomous variable with a value of 1 or 0, representing good and poor nest locations, respectively. To determine the optimal cutoff value, we compared model results to those that would be obtained from a random process. The optimal cutoff value was selected by maximizing the improvement of model predictions over a null model of random habitat selection (i.e. maximizing the difference between the proportion of nest pixels correctly classified and the proportion of the NKRD classified as good nest habitat; Pierera and Itami, 1991; Ozesmi and Mitsch, 1997). This process considered the trade off between maximizing the correct classification of good nest habitat by selecting a lower cutoff value, and minimizing the area classified as good habitat by selecting a higher cutoff value.

Leave-one-out cross-validation (Efron and Tibshirani, 1993, p. 240) was used to generate the mean cutoff value and its associated standard deviation. This mean optimal cutoff value was used to create a grid surface showing the location of good and poor nest locations. All grid cell values over the optimal cutoff value were assigned a value of 1, while cell values less than the optimal cutoff were assigned a value of 0. The logistic regression model was also used to generate a grid surface of potential energy associated with forest structure (Eq. (14)).

3.7. Simulating the spatial distribution of goshawk nests

To simulate a point pattern of goshawk nests in a given year, the point process was conditioned on N, the total number of nests observed in the bounded region, B. Using an algorithm proposed by Ogata and Tanemura (1989), the following steps were used to simulate the two components (spatial interactions

among nests and forest structure) of the spatial distribution of goshawk nests:

- *Step 1*. Randomly locate the first nest ($t = 1$) within the bounded region B. If forest structure is taken into consideration, the location ($X_t = \{x_t, y_t \in B; t = 1\}$) of the first nest is selected proportional to $\exp[-U_1(X)]$, where $U_1(X)$ is the potential energy associated with forest structure (Eq. (14)). The nest site is selected with probability proportional to the suitability of the site, which is based on the logistic regression model (Eq. (15)). A low potential energy would indicate a good site, while a high potential energy would indicate a poor site for a nest. If forest structure in not considered in the location of nest sites, the location of the nest is chosen from a uniform distribution on the bounded region B.

- *Step 2*. For the second and successive steps (t, $t = 2, \ldots, N$), two additional locations are chosen: $X'_t = \{x'_t, y'_t \in B; t = 2, \ldots, N\}$ and $X^*_t = \{x^*_t, y^*_t \in B; t = 2, \ldots, N\}$ using the procedures outlined in *Step 1*.

- *Step 3A*. If the spatial interaction between nests is not being considered, the total potential energies, $U'_t(X)$ and $U^*_t(X)$, associated with the two locations obtained in *Step 2* are computed (Eq. (14)) and compared. The location, X'_t or X^*_t, that minimizes the total potential energy is selected as the new location to add to the point pattern.

- *Step 3B*. If the spatial interaction between nests is taken into consideration, the total potential energies, $U'_t(X)$ and $U^*_t(X)$, associated with the two locations obtained in *Step 2* are computed using Eq. (13). If $\min\{U'_t(X), U^*_t(X)\} < U_{t-1}(X)$, the new location, X_{t+1} is taken as $\min\{U'_t(X), U^*_t(X)\}$. If $\min\{U'_t(X), U^*_t(X)\} \geq U_{n-1}(t)$, a uniform random number, ξ, on the interval $(0, 1)$ is computed. If ξ is less than $\exp[U_{t-1}(X) - \min\{U'_t(X), U^*_t(X)\}]$, location X_{t+1} is taken to be $\min\{U'_t(X), U^*_t(X)\}$. Otherwise, no new nest is added to the point pattern in this step.

  Steps 2 and 3 are repeated until all N nests have been located within the bounds of the population.

- *Step 4*. The last step in the simulation was to apply the Metropolis algorithm (Cressie, 1991, p. 679; Ogata and Tanemura, 1989) to adjust the initial point pattern to a state of equilibrium. This is ac-

complished by randomly selecting one of the N simulated nest locations $X'_t = \{x'_t, y'_t \in B; t = 1, \ldots, N\}$. Next, a new location is randomly selected in such a way that the coordinates $\{x^*_t, y^*_t\}$ lie in a square with vertices at the point $x'_t \pm \delta$ and $y'_t \pm \delta$, while all other $N - 1$ nests have the same position. The total potential energies associated with the two point patterns are computed and compared using the procedures described in Step 3B. If the total potential energy for the point pattern with one of the nest moved slightly is less than the potential energy for the original point pattern, the nest is moved to this new location. This process is repeated until the point pattern converges to a state of equilibrium. To ensure this convergence, δ, the maximum single step displacement allowed in passing from one state to the next, was selected so as to reject one-half of the trial states (Cressie, 1991, p. 680). Other than this recommendation, no information is available in the literature on how many steps are required for convergence (Cressie, 1991, p. 680). In simulating the spatial distribution of the nests we used 78×200 Monte Carlo steps and a $\delta = 30 \, \text{m}$.

Ogata and Tanemura (1985) suggest one way to evaluate the equilibrium assumption is to examine the stationarity of the time series (t) of the total potential energy of the simulated point pattern. If we graph the change in total potential energy as a function of time, one would expect the sample mean of the time series to equal zero (Ogata and Tanemura, 1985). If a significant bias exists, this would indicate the point process is non-stationary and alternative models should be considered.

The goodness-of-fit of the point process model was assessed by comparing the transformed empirical K-function ($\hat{L}(h) = \{\hat{K}(h)/\pi\}^{1/2}$) (Ripley, 1977), corrected for edge effect (Cressie, 1991, pp. 615–618), to the transformed K-functions from 200 simulated realizations of the model. The simulations were used in constructing confidence envelopes based on the minimum and maximum transformed K-function to test the null hypothesis of no significant differences at the $\alpha = 0.05$ level. If, for any distance, the observed transformed K-function falls above or below the confidence envelopes the null hypothesis is rejected at the appropriate level of significance.

We first evaluated the point process model describing the spatial interaction between individual northern goshawk nests. Next, we evaluated the component describing the spatial relationship between individual nests and forest structure. Finally, we combined the two components together to simulate the spatial distribution of goshawk nests based on the spatial interaction between individual nests and forest structure. To assess the degree of agreement between the distribution of predicted nest points and that of active nests, we used a chi-square goodness-of-fit to test for differences in the probabilities of locating a nest between the predicted points and active nests in 1998.

To identify potential nest site locations, the point process model was used to simulate the locations and spatial distribution of 92 nests on the study area, representing the number of territories studied between 1991 and 1998. This process was repeated 50 times to generate a total of 4600 potential nest locations based on the interactions between nests and forest structure. Using a bandwidth of 1.5 km, a kernel estimator (Cressie, 1991, pp. 597–601) was used to estimate the density of points representing potential nest locations. The resulting surface was standardized to a maximum value of one.

4. Results

4.1. Modeling nest site suitability

The mean optimum probability cut off from the logistic regression used to distinguish good from poor nest locations was $48 \pm 1.5\%$ (95% confidence intervals; S.D. = 0.008). Based on this threshold, approximately one-third ($410 \, \text{km}^2$, 33%) of the NKRD was classified as good nest habitat (Fig. 4). None of the pinyon–juniper vegetation class was classified as a good nest habitat (Table 1), while 38% ($274 \, \text{km}^2$) and 35% ($36 \, \text{km}^2$) of pure ponderosa pine and spruce-dominated sites were classified as good, respectively. Only 24% ($35 \, \text{km}^2$) of mixed-conifer sites were classified as good nest locations; whereas, 48% ($54 \, \text{km}^2$) of deciduous sites provided good nest locations. Open areas obviously do not contain trees for nesting, however, in our model 14% ($11 \, \text{km}^2$) of openings (Table 1) were classified as good nest locations.
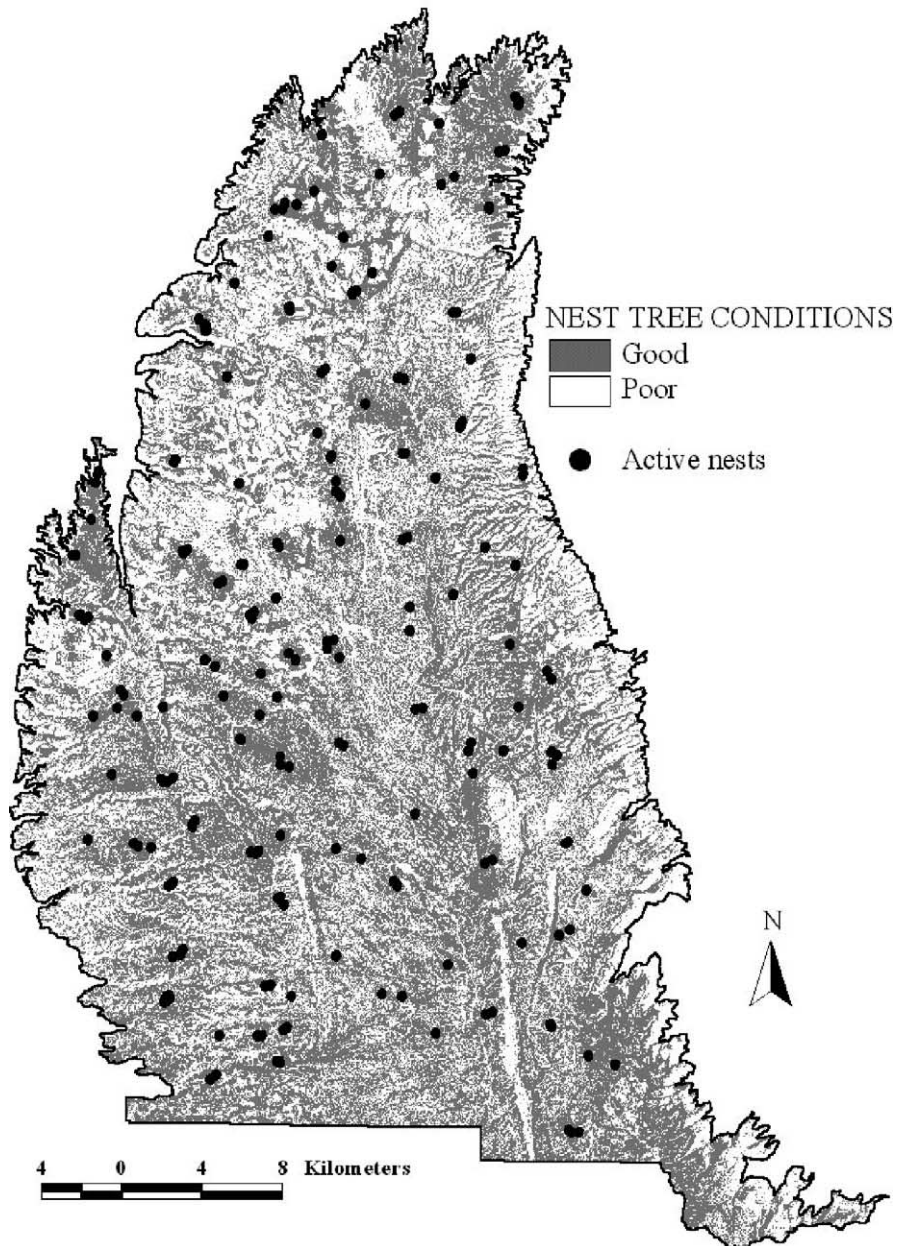
Fig. 4. Spatial distribution of estimated "good" and "poor" locations for northern goshawk nests on the North Kaibab Ranger District, Kaibab National Forest, Arizona, and all nests active between 1991 and 1998.

4.2. Trends in nest habitat use

Between 1991 and 1998, the number of active nests on the study area ranged from a low of 19 (1994) to a high of 55 (1993), representing 204 unique nest lo-cations (out of 344 nest attempts) on 94 unique terri-tories (Table 2). The majority (147; 72%) of nest lo-cations, representing 51 territories, were in good nest habitat, while 57 nests (28%), representing 43 territo-ries, were in poor nest habitat (Table 3; Fig. 4). The

Table 1
Distribution of estimated good and poor northern goshawk nest habitat by vegetative class on the North Kaibab Ranger District, Arizona

Vegetation class	Good (%)	Poor (%)
Pinyon–juniper	0	100
Ponderosa pine	38	62
Mixed-conifer	24	76
Spruce-dominated mix	35	65
Deciduous-dominated mix	48	52
Opening	14	86
All vegetation classes	33	66

largest proportion (79%) of nests in good habitat was in the ponderosa pine class. The fewest ($\leq$5%) nests in good habitat were found in deciduous-dominated and mixed-conifer forests. Of the 57 nests in poor habitat, over half (54%) were also in ponderosa pine, while almost a third (30%) were in the mixed-conifer class. Regardless of vegetation class, however, nearly 80% (45 of 57) of nests in poor sites were found within 10 m of a good site.

4.3. Nest habitat

Important variables from the logistic regression model and their standardized coefficients (Table 4), which discriminated between good and poor nest site locations, varied with vegetation class (Table 5). In ponderosa pine, the likelihood that a stand contained a nest improved with increasing total basal area (above 29 m^2/ha), but smaller proportions of spruce-fir basal area (<5.5%) and, especially, aspen basal area (<7.9%). Denser canopy closures, flatter slopes, and understory vegetation taller than 0.5 m also improved the probability of a nest location. In the mixed-conifer zone, the likelihood of observing a nest was greater on steeper (>8%) slopes with easterly exposure, and in drainages, particularly where smaller proportions of spruce and fir, but greater proportions of aspen basal area, occur. Elevations lower than approximately 2600 m, understory vegetation taller than 0.5 m, dense canopy closures and, in particular, seedlings and saplings also improved the likelihood for nest habitat in the mixed-conifer forest type. In

Table 2
Total number of territories and active northern goshawk nests between 1991 and 1998 above 2182 m in elevation on the North Kaibab Ranger District, Arizona

	Year								Total
	1991	1992	1993	1994	1995	1996	1997	1998	
Total territories monitored	36	58	72	87	95	102	105	105	660
New territories with active nests	36	21	13	3	10	8	0	4	94
Active nests	35	52	55	19	48	42	30	53	344
New active alternate nests	35	37	33	9	29	21	15	25	204

Table 3
Number of active nests between 1991 and 1998 by estimated suitability (good, poor) of nest locations and vegetative class on the North Kaibab Ranger District, Arizona

Vegetation class	Good		Poor		Total number of nests
	Number of nests	%	Number of nests	%	
Pinyon–juniper	0	0	0	0	0
Ponderosa pine	116	79	31	54	147
Mixed-conifer	8	5	17	30	25
Spruce-dominated mix	17	12	5	9	22
Deciduous-dominated mix	6	4	4	7	10
Openings	0	0	0	0	0
Total	147	100	57	100	204

Table 4

Standardized regression coefficients for variables that maximize the likelihood of a northern goshawk nest occurring in a vegetative class on the North Kaibab Ranger District, Arizona

Variable	Vegetation class					
	Pinyon–juniper	Ponderosa pine	Mixed-conifer	Spruce-dominated mix	Deciduous-dominated mix	Openings
Aspect	–	–	−0.082	−0.172	0.570	–
Slope (%)	−0.373	−0.044	0.041	0.007	0.653	−0.001
Elevation (m)	–	–	−0.016	0.077	–	−0.052
Landform	–	–	0.067	−0.083	−0.324	–
Total BA[a] (m^2/ha)	0.050	0.102	0.116	−0.040	0.112	0.032
Ponderosa pine BA[b]	–	–	–	0.689	–	–
Spruce-fir BA[b]	−0.051	−0.042	−0.096	–	0.639	−0.067
Aspen BA[b]	0.000	−0.109	0.076	–	−0.236	0.020
Canopy[c]	−0.004	0.003	0.002	0.002	−0.002	−0.001
Understory height (m)	0.053	0.046	0.039	−0.192	−0.486	0.062
Seedlings[d]	0.062	0.061	0.128	0.091	0.039	0.053

The magnitude and direction of the coefficients (positive—increase, negative—decrease) are comparable within and between models.

[a] Basal area.
[b] Proportion of total BA (m^2/ha).
[c] Proportion of canopy closure.
[d] Presence or absence.

spruce-dominated areas, higher nest-use was associated with less total basal area—although proportions of ponderosa pine greater than 23%, particularly concurrent with shorter (<7 m) understory heights—and somewhat greater canopy closure. Flatter, east-facing slopes, higher elevations than approximately 2680 m, and gradual ridges on the landscape also increase the likelihood for locating a nest in spruce-dominated landscapes. In deciduous-dominated forests, nest site use was enhanced by the presence of ridges and, espe-

Table 5

Means for variables that maximize the likelihood of a northern goshawk nest occurring in a vegetative class on the North Kaibab Ranger District, Arizona

Variable	Vegetation class					
	Pinyon–juniper	Ponderosa pine	Mixed-conifer	Spruce-dominated mix	Deciduous-dominated mix	Openings
Aspect	–	–	181	155	129	–
Slope (%)	18	6	8	7	9	7
Elevation (m)	–	–	2605	2682	–	2490
Landform	–	–	0.002	−0.046	0.327	–
Total BA[a] (m^2/ha)	17	29	39	36	30	2
Ponderosa pine BA[b]	–	–	–	0.228	–	–
Spruce-fir BA[b]	0.068	0.055	0.706	–	0.442	0.052
Aspen BA[b]	0.000	0.079	0.138	–	0.825	0.087
Canopy[c]	0.800	0.931	1.035	1.038	1.057	0.267
Understory height (m)	0.947	0.506	0.499	0.682	0.592	0.772
Seedlings[d]	0.371	0.639	0.887	0.944	0.897	0.222

[a] Basal area.
[b] Proportion of total BA (m^2/ha).
[c] Proportion of canopy closure.
[d] Presence or absence.

cially, steeper (>9%) slopes with south or south-west facing aspects, shorter (<6 m) understory vegetation, and greater amounts of total basal area, including larger proportions (>44%) of spruce-fir basal area, but lower proportions (<82%) of aspen basal area. Lower canopy closures, more typical of spruce-fir than of aspen, also improve the potential for nesting. It follows that openings, which are devoid of trees, require greater amounts of total basal area than 2 m^2/ha to improve their potential for nest site use. Greater amounts of aspen, which is generally a seral species in openings following a disturbance, increase nest use potential in particular. Seedlings, saplings, and taller understory vegetation are also favored. According to our logistic model, none of the pinyon–juniper vegetation class was considered "good" nest habitat. Nonetheless, we derived coefficients for the variables that would maximize the likelihood of a nest occurrence in this forest type. These conditions included flatter slopes (<18%) and the presence of seedlings and saplings, greater total basal area (>17 m^2/ha), but smaller proportions (<7%) of spruce-fir basal area, and a slightly more open (<80%) canopy. Overall, our model suggests that the presence of seedlings and/or saplings improves nest habitat in all vegetation classes.

4.4. Simulating the spatial distribution of nests

The transformed *K*-function (Fig. 5) of the spatial distribution of individual goshawk nests ($N = 27$) in the rectangular region *B* shows some territoriality as the empirical *K*-function extends below the lower simulation envelope for distances less than 2 km. The minimum distance observed between active nests in 1998 was 1.6 km. This indicates that there are fewer pairs of nests within a 2-km distance than expected if the nests were randomly distributed, and that those nests were regularly distributed. At distances greater than 2 km, the empirical *K*-function is contained within the simulation envelopes, indicating that the spatial distribution of goshawk nests does not differ significantly from a random spatial pattern. The Cramér–von Mises goodness-of-fit statistic also indicated some non-randomness in the spatial distribution of goshawk nests (Table 6). The *P*-value associated with this test was ≤0.14 for all distances ≤16 km. The strongest degree of non-randomness ($P < 0.05$) was observed for distances less than 6 km.

When the Gibbsian pairwise potential model was fit to the nest point data, model PF2 ($\hat{\alpha} = 0.005204$, $\hat{\beta} = 0.005923$) (Fig. 6) was selected as the best fit-
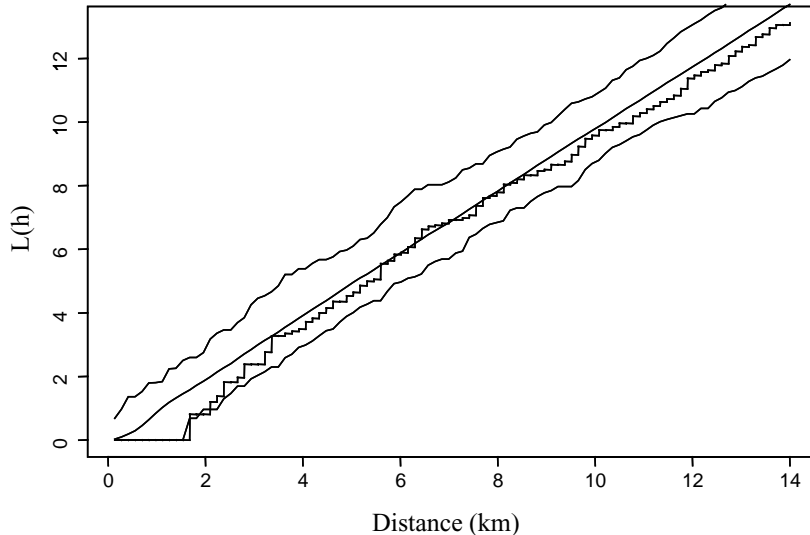

Fig. 5. Plot of the transformed *K*-function, $L(h) = [K(h)/\pi]^{1/2}$, against distance *h*, used to model the spatial arrangement of individual northern goshawk nests on the bounded region (*B*) on the North Kaibab Ranger District, Kaibab National Forest, Arizona. The stair-step line represents the empirical *K*-function calculated from the data; continuous lines represent the upper, average, and lower 99% simulation envelopes for 200 realizations of a spatial Poisson process.

Table 6
Results of the Cramér–von Mises goodness-of-fit test used to test the null hypothesis that northern goshawk nests in 1998 were randomly distributed on the North Kaibab Ranger District, Arizona

Distance (km)	Test statistic	P-value
2	282.25	0.00
3	238.38	0.03
4	195.17	0.00
5	163.32	0.01
6	136.43	0.02
7	117.68	0.06
8	109.72	0.13
9	95.31	0.13
10	98.55	0.10
11	96.42	0.09
12	101.12	0.03
13	104.97	0.13
14	107.94	0.11
15	110.31	0.14
16	119.35	0.08

ting model based on the AIC. The shape of the potential function suggests that individual nesting pairs of goshawks have a repulsive tendency toward one another and that the territorial effects between individual pairs decrease with increasing distance between nests (i.e. soft-core model). The point at which the potential energy approaches zero (≈ 20 km) provides an estimate of the maximum zone (circular area) of territoriality around individual nests. This result corroborates the above-mentioned results.

The transformed empirical K-function for the component of the point process model that describes the spatial interaction between individual nests (Fig. 7a) is contained within the bounds of the simulation intervals indicating the model provides a good fit to the data. In the range of 5.5–9.5 km, the point process model shows a more regular pattern than observed in the data. Territories defended by goshawks may be irregular in shape, especially in years when neighboring pairs are not breeding, and their nests may be located near the edge of their territories. Thus, at coarser scales there may be a tendency for some type of clustering of nests. In contrast, the model assumes the nests are at the center of their territories and exhibit an equal territorial force in all directions, resulting in a more regular pattern at all scales. The fact that the empirical K-function is contained within the simulation envelopes suggest the following two hypotheses: (1) the distribution of goshawk nests are spatially independent of forest structure; and (2) there is enough available habitat for nests on the study area as to not limit the spatial distribution of individual goshawk nests.

Except for distances less than 2 km, the transformed empirical K-function for the forest structure component of the point process model (Fig. 7b) is contained within the bounds of the simulation intervals. This graph looks similar to the one obtained when we tested for CSR (Fig. 5), suggesting that
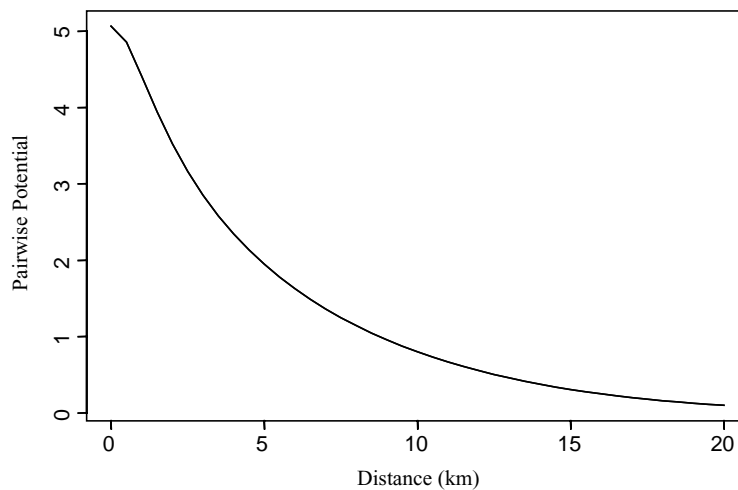

Fig. 6. Plot of the fitted pairwise potential model (PF2) for individual northern goshawk nests on the bounded region (*B*) on the North Kaibab Ranger District, Kaibab National Forest, Arizona.
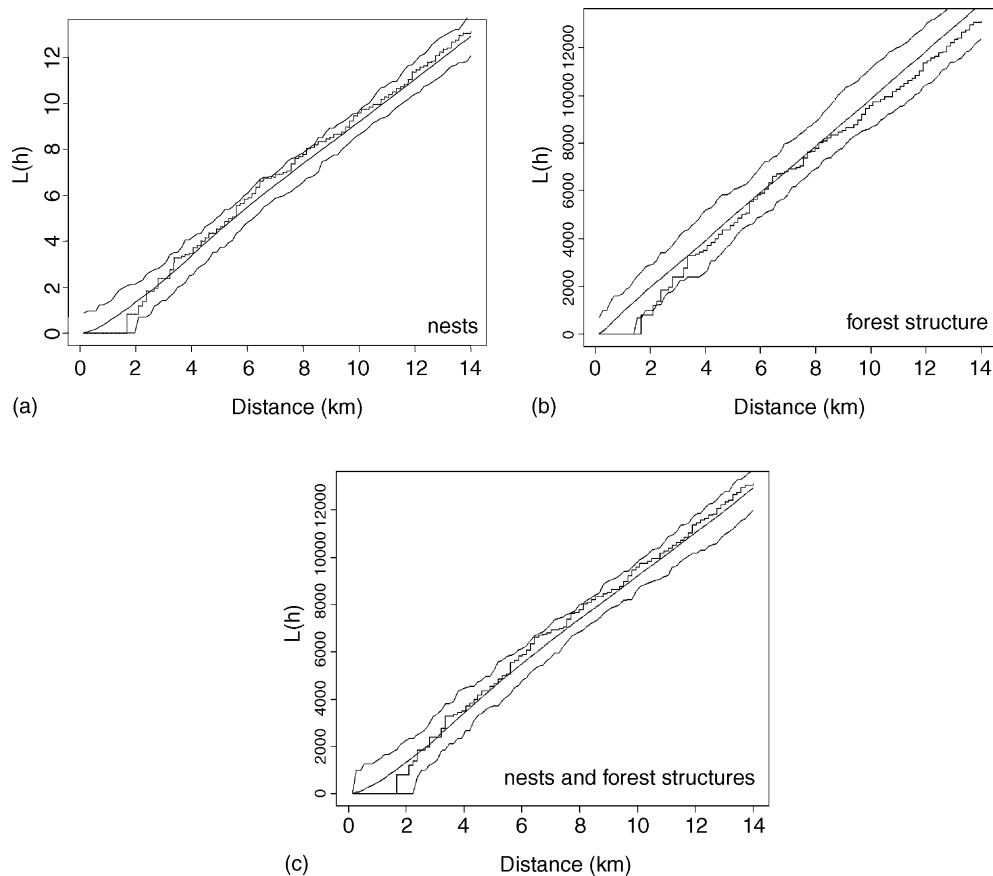
Fig. 7. Plot of the transformed *K*-function, $L(h) = [K(h)/\pi]^{1/2}$, against distance *h*, used to model the spatial arrangement of individual northern goshawk nests on the study area on the North Kaibab Ranger District, Kaibab National Forest, Arizona. The stair-step line represents the empirical *K*-function calculated from the data and the continuous lines represent the upper, average, and lower 99% simulation envelopes for 200 realizations of the (a) nest component of the point process model, (b) forest component of the point process model, (c) point process model that takes into consideration the territoriality between individual active nests and forest structure.

if we allocate nests using the potential energy associated with forest structure we generate a pattern similar to that of a random one. This result supports the second hypothesis that the current availability of good nest locations on the study area is not a factor limiting the spatial distribution of active goshawk nests.

The transformed empirical *K*-function for the complete model (Fig. 7c) is contained within the bounds of the simulation intervals indicating that the spatial model is capable of describing the distribution of nests on the study area, and in turn, provides a measure of the spatial dependency among individual nests and forest structure. Realization of the final model allows

us to predict the location of 27 nest points within the bounded region *B* (Fig. 8) and 96 nest points on the entire KNF (Fig. 9). The distribution of nest site probabilities associated with the predicted points depicted in Fig. 9 did not differ ($\chi^2 = 11.14$, d.f. = 9, *P*-value = 0.266) from the nest site probabilities associated with active nests in 1998 on the study area (Table 7).

The estimated density of potential nest locations based on 50 simulations of the point process model and a kernel bandwidth of 1.5 km (Fig. 10) suggests that the spatial distribution of nest sites is non-stationary (i.e. densities shift with the number of simulations). Consequently, there is a trend of increasing poten-
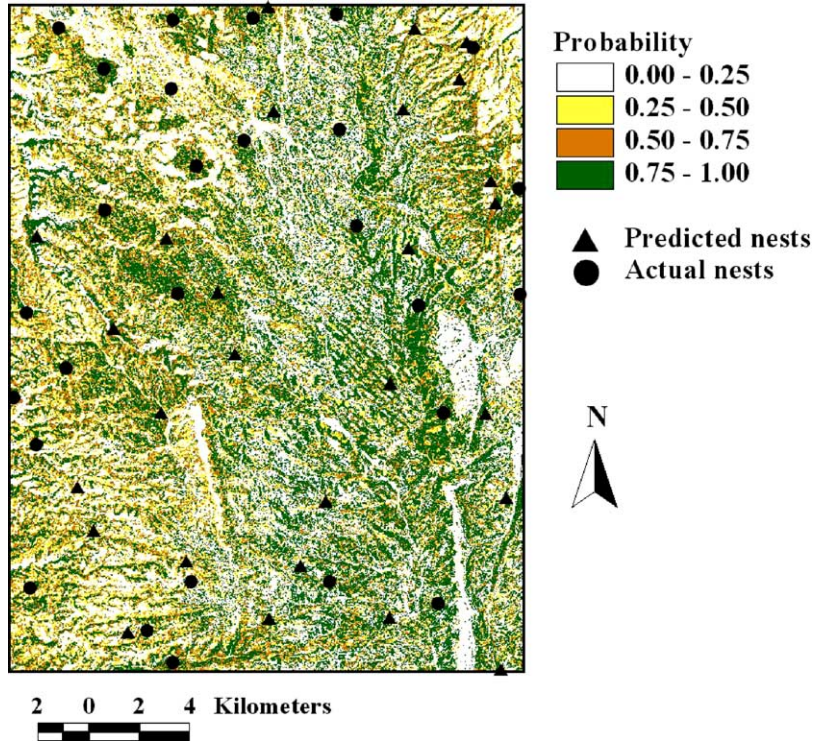
Fig. 8. Realization of the point process model (▲) that takes into consideration the territoriality between individual northern goshawk nests and forest structure on the North Kaibab Ranger District, Kaibab National Forest, Arizona. The locations of 27 active northern goshawk nests (●) used in fitting the model are plotted for comparison. The point patterns are overlaid on a surface showing the probability of finding a northern goshawk nest within the bounded region (*B*) on the study area associated with forest structure. Areas with a low probability (poor net areas) are lighter in color and areas with a high probability (good nest areas) are darker in color.

tial nest site density from the center of the study area outward. The edges of the study area tend to have a higher likelihood of nest sites than the interior portion, in part, due to the nonexistence of territories (i.e. territorial influence) outside the study area boundary to the north, east, and west, and to the exclusion of territories in the Grand Canyon National Park. Notably, the model suggests that there should be nests in the southeastern part of the study area. However, this area is dominated by dense aspen habitat unlikely to support nesting goshawk, as well as a closed understory that would most likely prohibit foraging goshawks from accessing prey (R.T. Reynolds, personal observation). Overall, though, an overlay of the locations of all active nests observed from 1991 to 2002, shows a high degree of correspondence between the potential nest site density plot and active nests.

5. Discussion

Spatial statistics have not been used to their fullest potential in animal ecology due to a generally poor understanding of these statistical methods. Recent ecological models that predict the distribution and abundance of wildlife species are derived from GLM or GAM that relate spatially-explicit response variables (distribution or density) to spatially referenced covariates (habitat measurements) (James and McCulloch, 2002; Lehmann et al., 2002). For example, logistic regression is used to predict the suitability of habitat or the probability of a species' occurrence (Pearce and Ferrier, 2000; Guisan and Zimmermann, 2000). Autologistic models, on the other hand, are used to account for spatial autocorrelation among sampled populations of species that respond in a clustered or aggregated manner (Augustin et al., 1996; Austin,
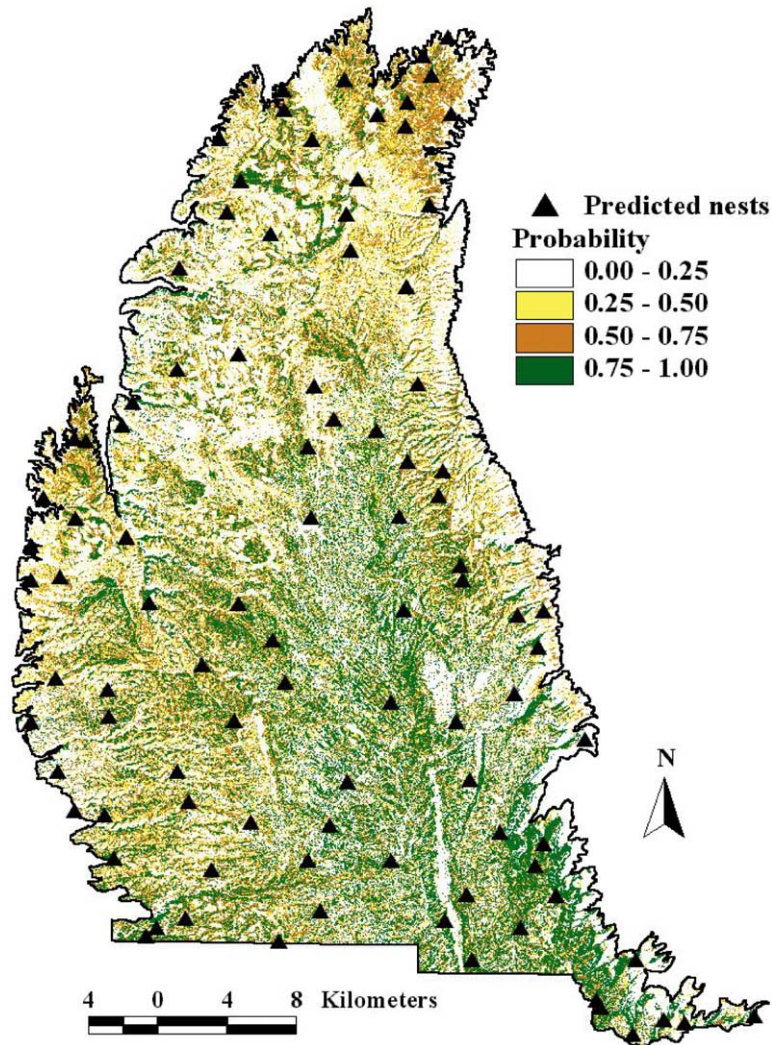
Fig. 9. Realization of the point process model (▲) that takes into consideration the territoriality between northern goshawk nests and forest structure on the North Kaibab Ranger District, Kaibab National Forest, Arizona. The predicted point pattern of nests is overlaid on a surface showing the probability associated with forest structure of finding a northern goshawk nest within the study area. Areas with a low probability (poor nest areas) are lighter in color and areas with a high probability (good nest areas) are darker in color. The probabilities associated with each simulated point do not differ ($\chi^2 = 11.14$, d.f. = 9, P-value = 0.266) from those of actual nests.

2002). Spatial covariates (typically habitat attributes) used in these models are assumed to be biologically meaningful. However, model prediction errors are generated, in part, by a failure to incorporate behavioral aspects (such as competition) into the model (Austin, 2002; Pearce et al., 2002). While these techniques represent significant progress in modeling the distribution and abundance of wildlife species, they do not account for inter- or intra-specific competition. These models, therefore, may not provide accurate representations of the biological factors governing aspects of abundance (Keitt et al., 2002).

We present a flexible point process model that describes the spatial dependency between the location of active goshawk nests and forest structure. The model assumes that individual nests are distributed accord-
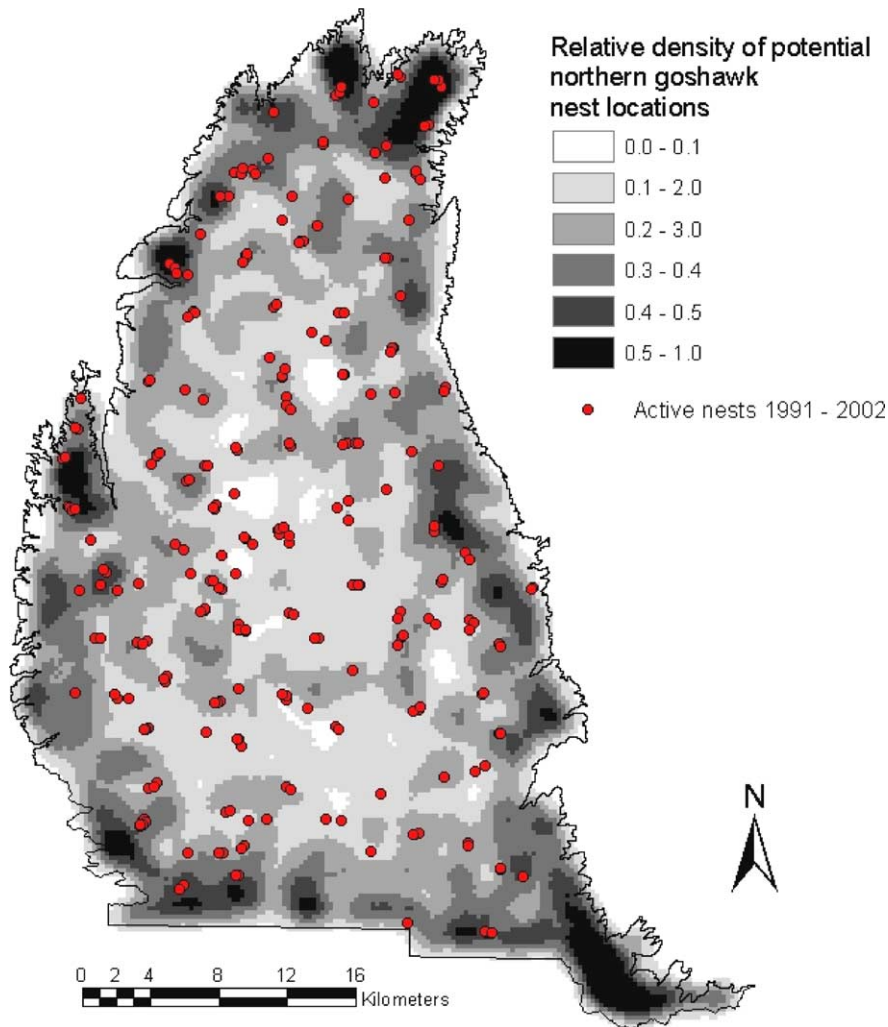
Fig. 10. Standardized nonparametric kernel estimate of the density of potential northern goshawk nests on the North Kaibab Ranger District, Kaibab National Forest, Arizona using a 1.5 km kernel. Density estimates were based on 50 realizations of the point process model that take into consideration the territoriality between individual northern goshawk nests and forest structure. Overlaid on the figure are the locations (●) of all goshawk nests observed from 1991 to 2002.

ing to the potential energy associated with the structure of the forest and a conspecific-competitive effect (territoriality).

In our goshawk study, it appeared that suitable nest habitat was not limiting the distribution and abundance of goshawks on the NKRD. Instead, territoriality, and what appeared to be non-compressible territories, limited the distribution and abundance of the nesting population. Within territories, choices of nest locations appeared to be limited by the availability of sites with "good" nest habitat (suitable forest structures and topography; see Reynolds et al., 1992). Territory size and ultimately density, on the other hand, probably reflected the amount of suitable goshawk foraging habitat and the abundance, distribution, and accessibility of prey within territories (Newton et al., 1977; Nilsson et al., 1982; Kenward and Widén, 1989; Widén, 1997; Kenward et al., 2001).

Annual nest locations were regularly distributed with a minimum of 1.6 km between active nests.

Table 7
Distribution of probabilities of finding a northern goshawk nest associated with predicted and observed (1998) nest points on the North Kaibab Ranger District, Arizona

Observed nests		Predicted nests	
Probability	Frequency	Probability	Frequency
0.0–0.1	9	0.0–0.1	11
0.1–0.2	5	0.1–0.2	3
0.2–0.3	5	0.2–0.3	6
0.3–0.4	11	0.3–0.4	8
0.4–0.5	12	0.4–0.5	9
0.5–0.6	12	0.5–0.6	11
0.6–0.7	7	0.6–0.7	13
0.7–0.8	7	0.7–0.8	11
0.8–0.9	11	0.8–0.9	12
0.9–1.0	17	0.9–1.0	14

Although goshawks need only a small patch (about 0.01–$0.10 \, km^2$) of suitable habitat to nest, the "quality" of those sites (judged by annual rate of egg laying and number of young produced) should, in part, be determined by the suitability of surrounding habitat for supporting populations of diverse prey species and providing foraging opportunities for goshawks (Reynolds et al., 1992; Widén, 1997). Although the "quality" of nest sites was not used in this study, nest site quality varied across the study area (Joy, 2002, pp. 153–219). Nevertheless, degradation of forest structure in large areas by forest management or natural disturbances may reduce the quality of nest habitat, thereby affecting the distribution of goshawk territories in our model.

In our final model, the locations of active goshawk nests appeared to be the result of territoriality. However, the distribution of good and poor potential habitat, based on forest structure, played an important role in nest location within territories. The within-territory relationship to forest structure may reflects past forest management on the NKRD. While many forests in the southwest received heavy railroad logging in the late-1800 and early 1990s, the Kaibab Plateau, because of its isolation by the Grand Canyon, was not railroad-logged during this period (Pearson, 1950). Management on the NKRD since the 1960s has been variable; some areas have been heavily harvested (i.e. seed tree, shelterwood cuts, clearcuts), while others received less tree cutting (i.e. thinning, individual tree selection). Areas heavily harvested between 1958 and

1998 generally contain more low quality nest habitat (74% of $114 \, km^2$). In contrast, areas within 1200-m radii of active nests, which contain lesser amounts of low quality nest habitat (62% of $114 \, km^2$). With the implementation of management to enhance goshawk nest and foraging habitats (Reynolds et al., 1992), the structure of the forest should become more suitable for both goshawks and their prey species.

The varying importance and direction (increase, decrease) of forest structural components based on logistic regression coefficients within each vegetation class (Table 4) predict identified structural conditions that increased a site's potential to contain a goshawk nest. Increased total basal area in all vegetation classes, except the spruce-dominated type, improved nest habitat. Less spruce-fir and aspen in ponderosa pine forests, greater proportions of ponderosa pine trees in spruce-dominated forests, less spruce and fir trees and more aspen in the mixed-conifer forest, and less aspen, but more spruce and fir trees in the deciduous-dominated forest increase a site's potential. In ponderosa pine forests, more spruce and/or fir trees increases the density of smaller trees, restricting a goshawk's access to its nest; whereas, more aspen (which typically have high, thin crowns) might decrease the vegetation cover at or near nests, especially prior to leaf-out. In spruce-dominated habitat, ponderosa pine crowns provide large branches for nest substrate, easier access to the nest, and would provide more cover above a nest. Because mixed-conifer forest is typically dense in both overstory and understory (S.M. Joy, personal observation), increased amounts of aspen basal area in a mixed-conifer site improves nest site habitat quality by opening the understories, providing large open crowns for nest placement and easier access to nests. In large openings created by management or natural disturbance, our model suggests the obvious—regenerating these areas restores the potential of these sites to contain nests.

Nest habitat is enhanced by greater canopy closure and less steep slopes in ponderosa pine forests. In the deciduous-dominated forest type, less canopy closure, greater basal area of ponderosa pine, and steeper, southeast-facing slopes associated with increasing gradient of convexity improves nest habitat. Steeper slopes associated with drainages at elevations below 2600 m, easterly-facing exposures, and dense canopy closure, improve nest habitat within the mixed-conifer

forest. Nests in mixed-conifer forests are typically found in trees (usually ponderosa pine) on steep slopes. At lower elevations, east-facing slopes in drainages have more ponderosa pine trees or aspen, which provides greater canopy coverage as well as a greater number of useable nest trees and perhaps limits the amount of fir regeneration. The habitat characteristics that create good nest sites in spruce-dominated forests—east-facing exposures with a slightly convex landscape—would most likely enhance the growth of more spruce and fir. Pinyon–juniper, which tends to grow on steep, dry, west-facing slopes above 2182 m on NKRD improved nest habitat only on flatter slopes and on sites with less canopy closure. Although goshawk nests are not found in pinyon–juniper forests on the study area, they do occur in narrow stands (stringers) of ponderosa pine in drainages that extend into the pinyon–juniper zone (S.M. Joy, personal observation). These stringers of ponderosa pine can provide cooler sites for nesting.

Our model suggests that the presence of seedlings and/or saplings "improves" nest habitat in all vegetation classes. However, the nature of tree regeneration in actual nest areas varied widely. In some areas, seedlings/saplings were small and few, and did not impose a physical or visual barrier for nesting hawks. However, as saplings increase in size and density, they likely hinder goshawk movements to and from nest trees. Regardless, the presence or absence of seedlings and saplings alone is insufficient to provide a biologically meaningful index of nest site potential. Shrubs and herbaceous understory height may also be a poor predictor for similar reasons.

Although the majority (86%) of openings on the study area were classified as poor nesting habitat, some openings (14%) were classified as good habitat. Within ponderosa pine and mixed-conifer forests on the NKRD, small (10-m × 10-m) openings are common. These small openings may represent some of the 14% that fell in good nest habitat; whereas, some openings classified as good nest habitat may be classification errors attributed to the "open" vegetation class. Openings contained the highest (23%) classification error rate of all vegetation classes (Joy et al., 2003).

Between 1991 and 1998, 57 out of 204 active nests were in "poor" nest habitat. Of the 80% (45) were found within 10 m of a "good" nest site, regardless of vegetation class. The classification of these nest locations as poor might have been due to errors in the mapping of nest trees or registration of the Landsat information. Mapping errors lower the significance of the logistic regression model, indicating that good nest locations are more randomly distributed (Stoms et al., 1992) and decrease our ability to discriminate nest sites from random sites. However, we believe the majority of our nests were mapped to within 3 m of their actual locations. Alternatively, if the spatial resolution of our models did not capture the geographic scale at which goshawks choose nest trees (e.g. if nest trees were selected based on local prey availability), we might also expect more nests to be in poor sites. Furthermore, adult territorial goshawks not nesting in one or more years likely introduced spaces into the distribution of territories and nests, and errors in our classification of good and poor nesting habitat. We believe that territorial interactions (Ozesmi and Mitsch, 1997) among breeding goshawks, as well as potential interactions with other raptors (Janes, 1984) and the lack of good sites in some territories, explain why not all of the active nests were located in good sites.

Treating forest structural components as one continuous variable in the model allowed the introduction of environmental heterogeneity into the point process model. Including environmental heterogeneity, in turn, allowed the spatial interaction between goshawk pairs at nests, both locally and regionally, to be modeled. Such a model is useful in simulating the effects that changes in a forest have on the spatial dynamics of a goshawk population. This is accomplished by systematically changing the potential energy associated with forest structure and observing how change influences the spatial distribution of goshawk nests. As some nest sites become unsuitable because of disturbance, goshawks may move to an alternate nest within their territory. The location of alternate nests within territories depends on the availability of sites. Our model also provided information on the potential of goshawk occupancy of a forest area. Moreover, when the demography of a goshawk population is incorporated into the point process model, it should be possible to study the spatio-temporal behavior of the goshawk population as influenced by forest management activities.

Such a model should benefit researchers and managers interested in ecosystem processes by providing a better understanding of the influence that coarse- and fine-scale spatial variability have on the abundance and

productivity of goshawk populations. The Gibbsian pairwise potential model used here accounted for the response of northern goshawks to their environment, as well as the effects of conspecific-competitive interactions (territoriality). Knowledge of nest locations based on territorial spacing, as well as environmental variables, should be a priority for habitat managers because managers need to know more than the probability of a nest being in a particular location—they also need to know how individuals or species interact behaviorally to influence those locations.

While our specific model may not be applicable to all forests because it was based on population-level data, models can be developed for alternate areas using sample data (i.e. incomplete data on a population). The Takacs–Fiksel method could be used to estimate the parameters of the pair-potential functions using data collected through sample field observations (Tomppo, 1986). Apart from the Takacs–Fiksel method (based on a step function), no other estimation methods have been applied to field observations. Also, the pseudo-likelihood estimation methods, employed in this paper, coincide with the Takacs–Fiksel method depending on the pair-potential function used (Diggle et al., 1992). Hence, one can assume that the pseudo-likelihood method is also applicable to field observations. It is possible, therefore, to develop models similar to the one presented in this paper for other forests using sample data. Such models could be used to identify potential nest site locations, as well as identify areas that should have a high priority for management under the goshawk management recommendations (Reynolds et al., 1992).

Austin (2002) suggested that ecological processes be incorporated into statistical models to produce more robust predictions and equations with more explanatory power. Austin (2002, p. 103) states that, "Current (analytical) techniques need not be limited to static equilibrium situations . . . " Our approach to modeling the spatial dynamics of an individual species with their habitat is at the leading edge of ecological modeling. Furthermore, our modeling approach can be used in a variety of applications and study areas once inter- or intra-specific interactions and species–environment interactions have been modeled. Inferences from the model generated here, however, should not be made beyond the scope of our study area. In areas where goshawks may occur at lower densities than on the NKRD, where nest spacing might be irregular, or where habitat data are at a coarser resolution, a new point process model should be developed.

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