

HABITAT ASSOCIATIONS OF SYMPATRIC RED-TAILED HAWKS AND NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU

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Abstract: We investigated habitat association of sympatric red-tailed hawks (*Buteo jamaicensis*) and northern goshawks (*Accipiter gentilis*) at 2 spatial scales centered on nest sites: (1) fine-scale patterns of forest structure and topography within 16-m radius circles (0.08 ha), and (2) midscale patterns of forested and nonforested areas, forest fragmentation, and topography within 2,085-m-radius circles (1,367 ha). Nonforested areas were defined as any area lacking >20% canopy closure within a 30 × 30-m cell. At both scales, red-tailed hawk associations were more variable and goshawk associations less variable. At the fine scale, goshawks were consistently associated with open understories, tall trees, and gentle slopes (\bar{x} = 9.6°, SD = 6.9) while red-tailed hawks were associated, on average, with steep, north-facing slopes (\bar{x} = 17.4°, SD = 8.1) and dense understories. At the midscale, goshawks were consistently associated with patches of continuous forest and level terrain within 645 m of nest sites. Red-tailed hawks were associated with nonforested areas located within 105–645 m of nest sites and steep slopes within 105 m of nest sites. Forest fragmentation was greater around red-tailed hawk nest sites, and forested regions were more aggregated around goshawk nest sites when compared with the other species. These patterns indicate that on the Kaibab Plateau, red-tailed hawks will gain habitat at the mid-scale and goshawks will lose habitat at both scales if forests are fragmented and mature forest structure is lost.

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Northern goshawks (hereafter referred to as goshawk) in North America breed in a variety of forest types with nest sites typically found in association with mature to old-growth forest structure; foraging and winter habitat are poorly studied but appear to be more diverse and not as strongly dependent on mature forest structure (Squires and Reynolds 1997). The U.S. Forest Service designated goshawks as a “sensitive species” throughout the species’ western range based on concerns related to the impact of forest management practices on goshawk breeding habitat. The status of goshawk populations in the western United States remains the subject of concern and debate (Kennedy 1997, DeStefano 1998, Smallwood 1998). In North America, red-tailed hawks are abundant, ubiquitous, and typically associated with nonforested areas in various environments including coniferous and deciduous forests (Preston and Beane 1993). Several investigators have suggested that red-tailed hawks may be replacing goshawks as

forests are cleared and fragmented (Crocker-Bedford 1990, Kenward 1996, Erdman et al. 1998). The relationship and habitat associations for sympatric *Accipiter* species (Reynolds et al. 1982, Reynolds and Meslow 1984, Bosakowski et al. 1992), sympatric *Buteo* species (Schmutz et al. 1980, Janes 1994, Bosakowski et al. 1996), and sympatric *Buteo* and *Accipiter* species (Titus and Mosher 1981, Selås 1997, Sánchez-Zapata and Calvo 1999) have been the subject of numerous investigations; yet the relationship and habitat associations of sympatric red-tailed hawks and goshawks has not been studied.

Our objective was to provide descriptive information on the habitat associations of sympatric red-tailed hawks and goshawks during the breeding season. We focused our investigation on forest structure at nest sites and forest fragmentation and the presence of nonforested areas around nest sites to clarify how these species will be impacted by forest alterations in the western United States.

STUDY AREA

Red-tailed hawks and goshawks occur sympatrically on the Kaibab Plateau in northern Arizona, USA. Vegetation within our study area on the plateau consisted of ponderosa pine (*Pinus pon-*

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derosa) forest between elevations of 2,075 and 2,500, mixed-conifer forest (*Pinus ponderosa*, *Pseudotsuga menziesii*, *Abies concolor*, *Picea pungens*, *Populus tremuloides*) between elevations of 2,500 and 2,650 m, and spruce (*Picea engelmannii*)–fir (*Abies lasiocarpa*) forest between elevations of 2,650 and 2,800 m (Rasmussen 1941, Merkle 1962, White and Vankat 1993). Transition zones between forest types are relatively broad, following the gradual change in elevation across the plateau. Nonforested areas with herbaceous vegetation originating from natural and anthropogenic causes are located throughout the plateau. The North Kaibab Ranger District (NKR D) of the Kaibab National Forest administers the northern two-thirds of the plateau, and the National Park Service administers the southern one-third bordering the Grand Canyon. Our study area (139,437 ha) was located within NKR D boundaries and confined to elevations above 2,075 m on the west side and elevations above 2,140 m on the north and east sides of the plateau to exclude pinyon (*Pinus edulis*)–juniper (*Juniperus* spp.) woodlands.

METHODS

Sampling and Scale

Approximately 120 goshawk territories and associated nest sites on the Kaibab Plateau have been studied since 1991 as part of a long-term study of the demography and ecology of the goshawk population (Reynolds et al. 1994). In addition, goshawk project personnel documented all red-tailed hawk nest sites and territories discovered during goshawk surveys. We used this information as the basis for red-tailed hawk surveys and monitoring initiated in 1998. Forty-one red-tailed hawk territories were identified within our study area by the summer of 2000; 32 of these were last active during the summer of 2000, 7 in 1999, and 2 in 1998. Of the 120 goshawk territories, 62 were active within our study area during the summer of 2000.

To examine habitat associations, we selected 2 spatial scales corresponding to Johnson's (1980) second- and third-order of selection and Block and Brennan's (1993) recommended spatial scales for avian habitat analysis. We labeled the scales "fine scale" and "midscale" following Morrison et al. (1998:240–243). We defined fine-scale habitat associations as the vegetation structure and topographic features in 16-m-radius circles (0.08 ha) centered at nest trees. We defined midscale habitat associations as the spatial pattern of landscape features contained within 2,085-m-

radius circles (1,367 ha) centered at nest sites and random sites. These features included characteristics of nonforested areas and forested patches as well as the spatial pattern of nonforested areas and topography. We selected a 1,367-ha circle for analysis because it encompassed the estimated home range for red-tailed hawks nesting in forested environments (\bar{x} = 687.5 ha, SD = 228.4, n = 4; Mindell and Samuel 1984, Andersen et al. 1986, Andersen and Rongstad 1989,) and the estimated territory size (1,134 ha) of goshawks on the Kaibab Plateau based on a mean 3.8 km nearest-neighbor spacing of 120 territories (R. T. Reynolds, unpublished data).

Fine Scale

Habitat Variables.—We measured 19 variables within the 16-m-radius plots. Two variables described topography, 8 described nests and nest-tree structures, and 9 described vegetation structure (see Tables 1, 2). We used a clinometer to measure tree and crown heights and a diameter-at-breast-height (dbh) tape to measure tree diameters. Trees were defined as any vegetation with dbh >10 cm and height >2 m; shrubs were defined as any vegetation that did not meet these criteria. To estimate tree and shrub canopy cover, we used a self-righting sighting tube (James and Shugart 1970) with measurements taken at 2-m intervals along 4 line transects radiating from the nest tree at 90° intervals based on an initial random bearing. The first reading for each transect was taken 2 m from the trunk of the nest tree to reduce over-representing the crown cover of the nest tree. Vigor of individual trees was categorized on a 5-point scale based on the proportion of dead branches: (1) entire tree is dead, (2) >75% of the tree is dead, (3) 25–75% of the tree is dead, (4) <25% of the tree is dead, and (5) 0% of the tree is dead. We used a standard Global Positioning System receiver to estimate the Universal Transverse Mercator (UTM) position and elevation of the nest site.

Statistical Analysis.—For the univariate tests, we used multiresponse permutation procedure (MRPP) to examine differences in central tendency (median) and dispersion between the 2 species (Biondini et al. 1988, Mielke and Berry 2001:12–64) with the program BLOSSOM (Cade and Richards 2001). We obtained approximate P -values from moment approximation tests and reported the standardized test statistic as T . For aspect, we used Rayleigh uniformity tests to determine whether aspect was distributed in a non-

Table 1. Means (\bar{x}), standard deviations (SD), and tests with associated *P*-values for 10 nest-site variables measured within 0.08-ha circular plots (fine scale) centered on red-tailed hawk and goshawk nests on the Kaibab Plateau, Arizona, USA, in 2000 (heights reported in meters).

Variable	Red-tailed hawk			Goshawk			<i>T</i> ^a	<i>P</i>
	<i>n</i>	\bar{x}	SD	<i>n</i>	\bar{x}	SD		
Slope (degrees)	41	17.4	8.06	41	9.6	6.91	-11.31	≤0.001
Slope position ^b	40	0.36	0.292	39	0.37	0.369	0.05	0.358
Nest height	39	21.3	4.54	39	19.4	4.13	-2.56	0.030
Nest-tree height	41	28.9	4.94	41	29.4	4.51	0.52	0.609
Nest-tree height difference ^c	41	13.8	6.05	41	10.8	4.58	-3.12	0.018
Nest-tree crown height ^d	38	7.5	4.05	41	11.5	5.55	-6.00	0.001
Nest-tree crown depth ^e	38	21.6	4.92	41	17.9	6.00	-5.78	0.002
Nest-tree dbh ^f (cm)	41	72.5	14.19	41	68.3	13.00	-0.47	0.217
Nest-tree vigor ^g	41	3.9	0.94	41	4.0	0.08	0.15	0.449
Nest % canopy cover ^h	39	58.1	36.93	39	84.2	21.81	-7.41	≤0.001

^a Multiresponse permutation procedure (MRPP) standardized test statistic from moment approximation tests (Mielke and Berry 2001:12–64).

^b Continuous value between zero (bottom of slope) and 1 (top of slope).

^c Difference in height of the nest tree from the average height of trees in plot.

^d Height of the first branch with green foliage in nest tree.

^e Difference between tree height and crown height for the nest tree.

^f Diameter at breast height.

^g 1 = dead; 2 = >75% dead; 3 = 25–75% dead; 4 = <25% dead; 5 = no dead branches.

^h Ocular estimate of the percent canopy cover directly above nest.

uniform pattern thereby indicating a preferred direction (Kovach 1994).

We performed 2 investigations for the multivariate analysis: (1) an analysis of the degree of habitat specialization by species, and (2) an analysis of the linear combination of habitat variables that discriminated nest sites of the 2 species. Initially, we excluded 2 variables (nest height and nest percent canopy cover; Table 1) from the multivariate analysis because they did not represent habitat features but features determined by the species during nest construction. Aspect was

divided into 8 45° intervals for inclusion in the analysis. We evaluated variables for multicollinearity and singularity by examining the variance inflation factors (VIF) from the inverse correlation matrix and values from the partial correlation matrix (PC). When variables were correlated or redundant (VIF ≥ 10 and |PC| ≥ 0.9), we retained the variable judged to be management oriented and ecologically interpretable. From the remaining continuous variables (excluding the categorical variables aspect, nest-tree vigor, and mean tree vigor), we estimated the

Table 2. Means (\bar{x}), standard deviations (SD), and tests with associated *P*-values for 9 shrub and tree variables measured within 0.08-ha plots (fine scale) centered on nests of red-tailed hawks and goshawks on the Kaibab Plateau, Arizona, USA, in 2000 (heights reported in meters).

Variable	Red-tailed hawk (<i>n</i> = 41)		Goshawk (<i>n</i> = 41)		<i>T</i> ^a	<i>P</i>
	\bar{x}	SD	\bar{x}	SD		
Mean tree height	15.1	3.91	18.6	3.59	-9.05	≤0.001
Mean crown height ^b	5.6	3.86	7.2	2.63	-6.25	≤0.001
Mean crown depth ^c	10.2	2.53	10.4	2.49	0.78	0.893
Mean dbh ^d (cm)	32.4	8.25	35.2	7.00	-1.61	0.073
Mean tree vigor ^e	3.7	0.61	3.6	0.24	-7.92	≤0.001
Mean basal area (cm ²)	1,122.4	563.88	1,250.0	462.05	-0.79	0.156
Total no. of shrubs	272.3	280.34	129.1	83.15	-6.33	≤0.001
Percent canopy cover shrubs	15.2	12.78	10.7	9.21	-0.95	0.136
Percent canopy cover trees	41.9	14.54	45.9	12.46	-1.92	0.331

^a Multiresponse permutation procedure (MRPP) standardized test statistic from moment approximation tests (Mielke and Berry 2001:12–64).

^b Height of the first branch with green foliage in nest tree.

^c Difference between tree height and crown height.

^d Diameter at breast height.

^e 1 = dead; 2 = >75% dead; 3 = 25–75% dead; 4 = <25% dead; 5 = no dead branches.

degree of specialization by species with the determinant of the covariance matrix ($\ln|\Sigma|$); this is a measure of generalized variance for the selected variables in which smaller values indicate lower dispersion and more uniform habitat associations (Sakai and Noon 1991). We assessed the equality of the covariance matrices with a 1-sided randomization test where the difference between determinates was the test value and the observation vectors were resampled 100,000 times between the 2 groups without replacement (Good 2001).

For the second component of the multivariate analysis, we used a stepwise logistic regression procedure to select the combination of variables that discriminated nest sites of the 2 species. We eliminated problematic variables (nest-tree vigor and mean tree vigor) that produced extremely high coefficient and standard error values within the direct logistic regression procedure. We then entered the remaining variables into a stepwise logistic regression procedure with a *P*-value to enter of 0.15 and a *P*-value to stay of 0.15. The strength of association for the model was assessed with the square of the area under the receiver operating characteristic curve (c^2); we interpreted this metric as the probability of correctly classifying a randomly selected pair of observations from each species with values of 1.0 indicating perfect prediction and 0.5 indicating prediction no better than chance (Tabachnick and Fidell 2001:546).

Midscale

Landsat Classification.—We acquired a Landsat 7 ETM+ image of the Kaibab Plateau (10 Oct 1999; Path 37, Row 35; Processing Level 1G) to map nonforested areas within the study area. An October date was chosen because the difference in spectral reflectance was more pronounced between evergreen forests and dead and senesced vegetation in nonforested areas. We selected 6 bands from the Landsat image for use in the classification (1–5 and 7) and retained the original cell resolution

of 30 × 30 m throughout the analysis. To delineate elevational boundaries and calculate slope within the study area, we acquired a U.S. Geological Survey digital elevational model (DEM) of the Kaibab Plateau at 30 × 30-m resolution.

Within the Landsat image, we distinguished 2 classes defined as (1) forested, containing >20% canopy closure in the 30 × 30-m cells; and (2) nonforested, containing <20% canopy closure in the 30 × 30-m cells. Twenty-percent canopy cover was selected as a demarcation by examining multiple cells across the classified grid to determine what percentage of canopy cover best distinguished the 2 classes. The classified grid contained 128,360 ha classified as forested and 11,077 ha classified as nonforested. We used the programs IMAGINE (ERDAS 1999) in conjunction with ARC/INFO (Environmental Systems Research Institute 1995) to prepare and classify the Landsat image (see La Sorte 2001 for details on the classification methods).

We estimated the accuracy of the Landsat classification with 240 random locations divided equally between the 2 classes using, as reference images, digital orthophoto quarter quads (DOQQs) taken in 1991–1992 with a resolution of 1 × 1 m. Overall accuracy of the classified image was estimated at 86.3% (Table 3). The 7- and 8-year time lag between the DOQQs and Landsat image introduced a negative bias into the accuracy assessment. This was particularly true in the case of 2 large fires occurring in 1993 (Point fire) and 1996 (Bridger fire) that were classified as nonforested in the Landsat image and appeared as forested in the DOQQs. We made no attempt to compensate for these inconsistencies in the accuracy assessment.

Spatial Analysis.—We conducted 2 spatial analyses at the midscale to examine (1) patterns of forested and nonforested patches around nest sites and (2) patterns of topography around nest sites. We mapped 41 red-tailed hawk and 62 goshawk nest sites on the classified Landsat image

Table 3. Accuracy assessment of the classified Landsat image (10 Oct 1999) of the Kaibab Plateau, Arizona, USA, with 2 classes distinguished: forested (>20% canopy closure), and nonforested (<20% canopy closure). A total of 240 reference points, 120 for each class, were randomly located on the image.

Class	Reference total	Classified total	Total correct	Producers accuracy	Users accuracy	Conditional Kappa
Forested	115	120	101	87.8%	84.2%	0.696
Nonforested	125	120	106	84.8%	88.3%	0.757
Total	240	240	207			

Overall Kappa = 0.725 (95% CI: 0.599 to 0.851)

Overall accuracy = 86.3% (95% CI: 81.9% to 90.6%)

and on a grid of slope values calculated from the DEM. We randomly selected 62 forested cells >2,085 m from the border of the study area. We then placed 23 concentric ring plots around nest sites and random sites and measured the proportion of area classified as nonforested within each plot based on the classified Landsat image and the average slope within each plot based on the slope values estimated from the DEM. The 30 × 30-m cell containing the nest site or random site served as the center of the plots and contributed 15 m to the radius with each concentric plot adding 90 m to the radius, or 3 30 × 30-m cells. The 23 ring plots were defined by inner radii from zero to 1,995 m at 90-m intervals and outer radii from 105 to 2,085 m at 90-m intervals. The first plot was a circle with a radius of 105 m, the second plot was a ring with an inner radius of 105 m and outer radius of 195 m, and the final plot was a ring with an inner radius of 1,995 m and outer radius of 2,085 m.

We used logistic regression to estimate odds ratios for each concentric plot using a case-control retrospective study design to provide a probabilistic framework for interpretation (Ramsey et al. 1994, Swindle et al. 1999). The cases were red-tailed hawk and goshawk nest sites and they were contrasted with random sites. Odds ratios are multiplicative factors in which values of 1 indicate no change in odds, values above 1 indicate increasing odds, and values below 1 indicate decreasing odds. We defined the odds ratio within the classified Landsat image as the change in odds that a site was a nest site after increasing the area classified as nonforested in the plot by 1.0% and within the slope grid generated from the DEM as the change in odds that a site was a nest site after increasing the average slope in the plot by 1°.

Patch Analysis.—We calculated 6 landscape indices to quantify patch characteristics of nonforested and forested patches within the largest circular plot (radius = 2,085 m) defined within the classified Landsat image at red-tailed hawk and goshawk nest sites and random sites. Plot borders were excluded in the calculations except for average patch area (Krummel et al. 1987). We used the 8-neighbor rule, in which each cell has 8 possible neighboring cells, to determine patch extent in calculating all indices. The program APACK 2.21 (Mladenoff and DeZonia 2001) was used to calculate the indices, and MRPP was employed to examine the equality of indices among the 3 groups.

We calculated average area (AVG AREA) and average perimeter (AVG PER) of patches classified as nonforested to examine differences in size

and shape of nonforested areas. Edge density (ED) was calculated to provide a measure of the quantity of edge for each site. This index has a near-linear relationship when the proportion classified as nonforested in a plot has a range from zero to approximately 0.5 (Hargis et al. 1997). All plots had proportions at or below 0.25, except for 1 red-tailed hawk site with a proportion of 0.46, allowing ED to be interpreted as a measure of forest fragmentation. Connectivity between patch centroids (CCE), a gravity-based metric, was calculated as a measure of the spatial pattern of patches. This is a unitless metric with values ≥0; larger values indicate a mosaic of larger patches whose centers are relatively close together, and smaller values indicate a mosaic of smaller patches whose centers are relatively far apart. We calculated AGGREGATION (He et al. 2000) for both classes independently as a measure of patch shape and aggregation. This index ranges from zero to 1; values approaching 1 indicate patches with more cells sharing edges and tending toward a square shape, and values approaching zero indicate patches with fewer cells sharing edges and tending to be long and narrow in shape. To provide a representation of central tendency and range for the indices, we identified the site with the minimum and maximum values for the 6 indices and the site that differed least from the average of the 6 indices for each group.

RESULTS

At the fine scale, we measured vegetation and topographic features at the most recently active nest site in 41 red-tailed hawk territories. We randomly chose 41 goshawk territories from the 62 that were active during the summer of 2000 and measured fine-scale vegetation and topographic features at the active nest site in each territory. At the midscale, we assessed patterns around the same 41 red-tailed hawk nest sites measured at the fine scale, the patterns around all 62 goshawk nest sites that were active during the summer of 2000, and the patterns around 62 random locations.

Fine Scale

The univariate analysis indicated that red-tailed hawk nest sites, on average, were located on steep, north-facing slopes ($n = 40$; $\bar{x} = 19.7^\circ$, 95% CI: 356.8° to 42.6°; Rayleigh test $P \leq 0.001$) containing abundant shrubs (Tables 1, 2). For goshawks, nest sites were located on gentle slopes with few shrubs and no aspect directionality ($n = 41$; Rayleigh test $P = 0.81$; Tables 1, 2). Red-tailed

Table 4. Five variables selected from 9 by the stepwise logistic regression procedure with associated coefficients, standard errors (SE), tests with associated *P*-values, and odds ratios with 95% confidence intervals that differentiated red-tailed hawk (*n* = 37) and goshawk (*n* = 39) nest sites (fine scale) on the Kaibab Plateau, Arizona, USA, in 2000.

Variable	Coefficient	SE	Wald χ^2	<i>P</i>	Odds ratio (95% CI)
Intercept	2.250	1.793	1.58	0.210	
Mean tree height	-0.166	0.092	3.27	0.070	0.847 (0.699 to 1.007)
Slope	0.124	0.045	7.57	0.006	1.132 (1.042 to 1.247)
Nest-tree crown height	-0.135	0.075	3.21	0.073	0.874 (0.746 to 1.004)
Total no. of shrubs	0.005	0.002	2.91	0.088	1.005 (1.000 to 1.011)
Aspect	-0.195	0.119	2.68	0.102	0.823 (0.643 to 1.032)

hawk nests, when contrasted with goshawk nests, were higher in nest trees and had less canopy cover above the nest (Table 1). Red-tailed hawk nests trees, when contrasted with goshawk nest trees, were taller than the surrounding trees and had thicker crowns that were closer to the ground (Table 1). Trees at goshawk nest sites were less vigorous, were taller, had greater dbh, and contained crowns that were farther from the ground than red-tailed hawk nest sites (Table 2).

We selected 9 variables that were not correlated or redundant for the multivariate analysis. These included aspect, slope, slope position, nest-tree height, nest-tree crown height, mean tree height, mean crown depth, total number of shrubs, and percent tree canopy cover. Six nest sites containing missing values were deleted from the analysis, leaving 37 red-tailed hawk and 39 goshawk nest sites available for analysis. The difference in generalized variance between red-tailed hawks ($1n|\Sigma| = 28.8$) and goshawks ($1n|\Sigma| = 26.4$) was greater than expected by chance ($P = 0.029$), indicating more uniform habitat associations for goshawks. The linear combination of variables, in order of descending strength according to odds ratio values, that distinguished nest sites of red-tailed hawks and goshawks were aspect, mean tree height, slope, nest-tree crown height, and total number of shrubs (Table 4). These 5 variables reliably distinguished nest sites between species when contrasted with a reduced model ($\chi^2 = 37.84$, $df = 5$, $P \leq 0.001$) and when contrasted with a saturated model (lack-of-fit $\chi^2 = 67.47$, $df = 70$, $P = 0.56$). The prediction strength for the model was high ($c^2 = 0.77$). Slope was the most reliable predictor in the model; the remaining 4 variables were marginal predictors according to the Wald criteria and the odds ratio 95% confidence intervals (Table 4).

Midscale

With the features examined at the midscale, the central tendency for random sites typically occurred between the central tendencies of the 2

species. Red-tailed hawks had a positive difference from random with greater variance, and goshawks a negative difference from random with lower variance. For the concentric ring analysis of the classified Landsat image (Figs. 1, 2), the mean proportion of area classified as non-

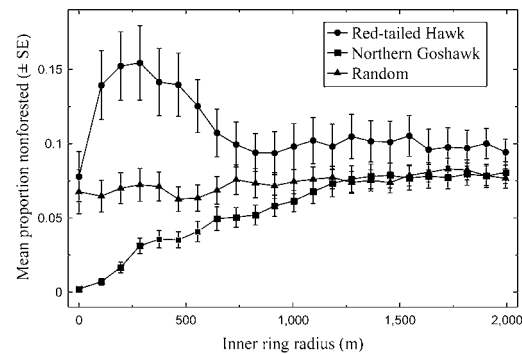


Fig. 1. Mean proportion (\pm SE) of area classified as nonforested in 23 concentric ring plots (midscale) at 90-m intervals centered on nests of red-tailed hawks (*n* = 41) and northern goshawks (*n* = 62) and at random sites (*n* = 62) on the Kaibab Plateau, Arizona, USA, in 2000.

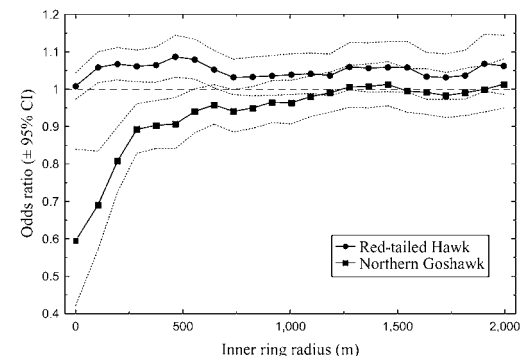


Fig. 2. Estimated change in odds and 95% confidence intervals associated with a 1.0% increase in the area classified as nonforested in 23 concentric ring plots (midscale) at 90-m intervals centered on red-tailed hawk (*n* = 41) and goshawk (*n* = 62) nests and random sites (*n* = 62) on the Kaibab Plateau, Arizona, USA, in 2000.

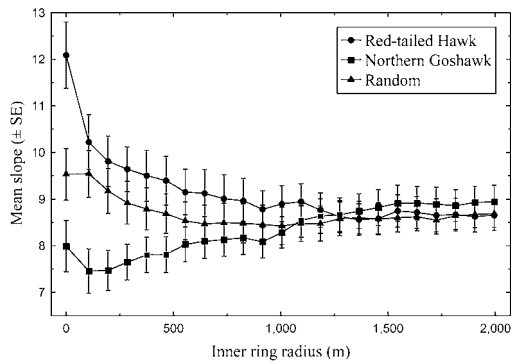


Fig. 3. Average slope (\pm SE) within 23 concentric ring plots (midscale) at 90-m intervals centered on nest of red-tailed hawks ($n = 41$) and goshawks ($n = 62$) and at random sites ($n = 62$) on the Kaibab Plateau, Arizona, USA, in 2000.

forested for the first plot (circle with a radius = 105 m) was similar for red-tailed hawks and random sites. For rings with radii from 105 to 555 m, the variance increased and the mean proportion remained significantly greater for red-tailed hawks. For rings with radii >555 m, red-tailed hawk mean values remained greater than random with greater variance but were not significantly different. In contrast, the mean proportion of area classified as nonforested in the first plot (circle with a radius = 105 m) at goshawk nest sites was significantly lower than random sites with very little variation. For the remaining ring plots, the variance increased and the mean proportion approached random with significant negative differences from random occurring to 555 m. The mean proportion for goshawk nest sites merged with random at approximately 1,275 m.

For the concentric ring analysis of slope (Figs. 3, 4), red-tailed hawks had a significantly greater mean slope with the first plot (circle with a radius = 105 m) and mean values that did not differ from random for the remaining plots eventually merging with random at approximately 1,275 m. Goshawks had mean slope values that were significantly different from random for all plots out to 555 m from the nest site. Beyond 555 m, the mean values approach random and eventually merge with random at approximately 1,005 m.

The central tendencies for the 6 landscape indices for random sites were either between the central tendencies of the 2 species or more similar to goshawk values (Table 5). The standard deviation for red-tailed hawk indices was greater except for the 2 aggregation indices in which the values tended to be similar (Table 5). Red-tailed hawks showed moderate differences ($\alpha = 0.10$) from random with edge density ($P = 0.061$), connectivity between patch centroids ($P = 0.089$), and aggregation of forested patches ($P = 0.083$); goshawks presented no differences from random for any of the indices. Contrasting the 2 species, average perimeter ($P = 0.069$) and connectivity between patch centroids ($P = 0.063$) showed moderate differences, and edge density ($P = 0.008$) and aggregation of forested patches ($P = 0.008$) showed strong differences. Sites representing the minimum and maximum values for the 6 indices showed high variation in landscape pattern for red-tailed hawks and the consistent forested area centered at goshawk nest sites (Fig. 5A–C). The average red-tailed hawk nest site was characterized by a large, centrally located, nonforested area with small nonforested areas dispersed throughout the plot (Fig. 5B). The aver-

Table 5. Means (\bar{x}), standard deviations (SD), and tests with associated P -values for 6 landscape indices measured in 2,085-m radius circles (midscale) centered on red-tailed hawk and goshawk nests and random sites within a classified Landsat image (10 October 1999; 30 \times 30-m cells) of the Kaibab Plateau, Arizona, USA, in 2000.

Index ^a	Red-tailed hawk ($n = 41$)		Northern goshawk ($n = 62$)		Random ($n = 62$)		T^b	P
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD		
AVG AREA	1.00	1.41	0.69	0.77	0.70	0.61	-0.36	0.279
AVG PER	423	186.0	356	158.0	372	139.2	-0.74	0.186
ED	54	23.8	41	21.9	46	2.6	-2.24	0.037
CCE	0.100	0.195	0.049	0.058	0.049	0.049	-1.24	0.110
AGGREGATION								
Nonforested	0.540	0.166	0.476	0.174	0.497	0.170	-0.24	0.309
Forested	0.954	0.023	0.960	0.019	0.962	0.024	-2.15	0.041

^a Indices: AVG AREA = average area of nonforested patches (ha); AVG PER = average perimeter of nonforested patches (m); ED = edge density (m/ha); CCE = connectivity between patch centroids (unitless); AGGREGATION = index of patch shape and aggregation, measured independently for each patch type, that ranges from zero to 1.

^b Multiresponse permutation procedure (MRPP) version of 1-way ANOVA with standardized test statistic from moment approximation tests (Mielke and Berry 2001:12–64).

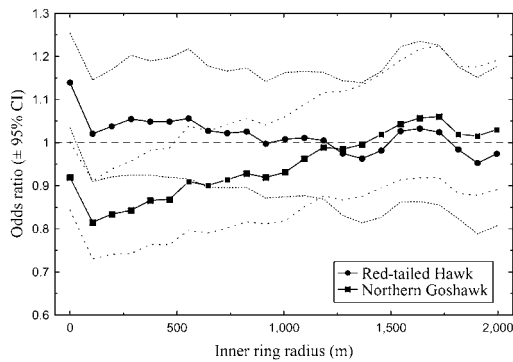


Fig. 4. Estimated change in odds and 95% confidence intervals associated with a 1° increase in slope within 23 concentric ring plots (midscale) at 90-m intervals centered on red-tailed hawk ($n = 41$) and goshawk ($n = 62$) nests and random sites ($n = 62$) on the Kaibab Plateau, Arizona, USA, in 2000.

age goshawk nest site contained a forested area centered at the nest site with small nonforested areas dispersed around the perimeter of the plot (Fig. 5B).

DISCUSSION

The associations at the fine scale can be interpreted based on behaviors unique to the 2 species. Typically, red-tailed hawks enter nests from above the canopy and goshawks enter nests from below the canopy. Researchers have argued that open and unobstructed access to nests from above the canopy is an important factor in red-tailed hawk nest-site habitat selection (Orians and Kuhlman 1956, Titus and Mosher 1981, Bednarz and Dinsmore 1982). Therefore, forest structure below red-tailed hawk nests is secondary, and features related to the nest tree and topography are primary. Nests located high in tall trees on steep, north-facing slopes would presumably allow easy access to nests, a favorable microclimate within the nest with reduced solar radiation, and a clear view of the surrounding area. In contrast, goshawk nest sites were associated with characteristics of mature forest structure. This result is consistent with numerous investigations documenting high canopy closure, mature trees, and open understories at goshawk nest sites (Reynolds et al. 1982, Speiser and Bosakowski 1987, Hayward and Escano 1989, Squires and Ruggiero 1996). These features presumably would allow easier access to nests, unhindered movement through the surrounding forest, a clear view of the forest floor, and a suitable microclimate within the nest.

At the midscale, red-tailed hawks displayed more variation overall and were associated with nonforested areas between 105 and 645 m of the nest site and steeper slopes within 105 m of the nest site. At the midscale, patterns documented within 105 m of the nest site mirrored patterns documented at the fine scale, thus supporting the conclusion that steep slopes are an important factor and forest structure is secondary at, and immediately surrounding, the nest site. Studies examining red-tailed hawk habitat associations have documented both a strong association (Mindell and Samuel 1984, Speiser and Bosakowski 1988, Moorman and Chapman 1996) and no apparent association with nonforested areas (Titus and Mosher 1981). These discrepancies likely result from differences in forest structure and landscape pattern among study areas. Our results support the conclusion that red-tailed hawks nesting in forested environments are capable of tolerating a broad array of forest structures and that fragmented forest structure and nonforested areas appear to play a central role in these associations.

Goshawks were consistently associated at the midscale with regions of continuous forest centered at the nest site. The negative association with nonforested areas extended to 645 m and was strongest within 375 m of the nest site. This forested area corresponds to the post-fledging family area (PFA; Reynolds et al. 1992) estimated at 168 ha or a circle with a radius of 732 m (Kennedy et al. 1994). The PFA, characterized by mature forest structure, is the area where adults forage during the breeding season and young develop their hunting skills. In addition, our results indicate an association with gentle slopes that extend to 555 m from goshawk nest sites. This pattern is consistent across the fine scale and midscale but is not consistent with findings of other investigations (Squires and Reynolds 1997). The predominance of gentle terrain on the Kaibab Plateau and the presence of mature forest structure with open understories in regions with gentle slopes might explain this pattern.

In summary, the patterns of goshawk and red-tailed hawk habitat associations were distinctly different at both the fine and midscale. Goshawks were considerably more specialized at both scales and presented consistent patterns of continuous forest structure on level terrain at both scales. Red-tailed hawks presented greater variation at both scales, with differing central tendencies from goshawks. The pattern at the fine scale suggested that habitat selection for red-tailed hawks

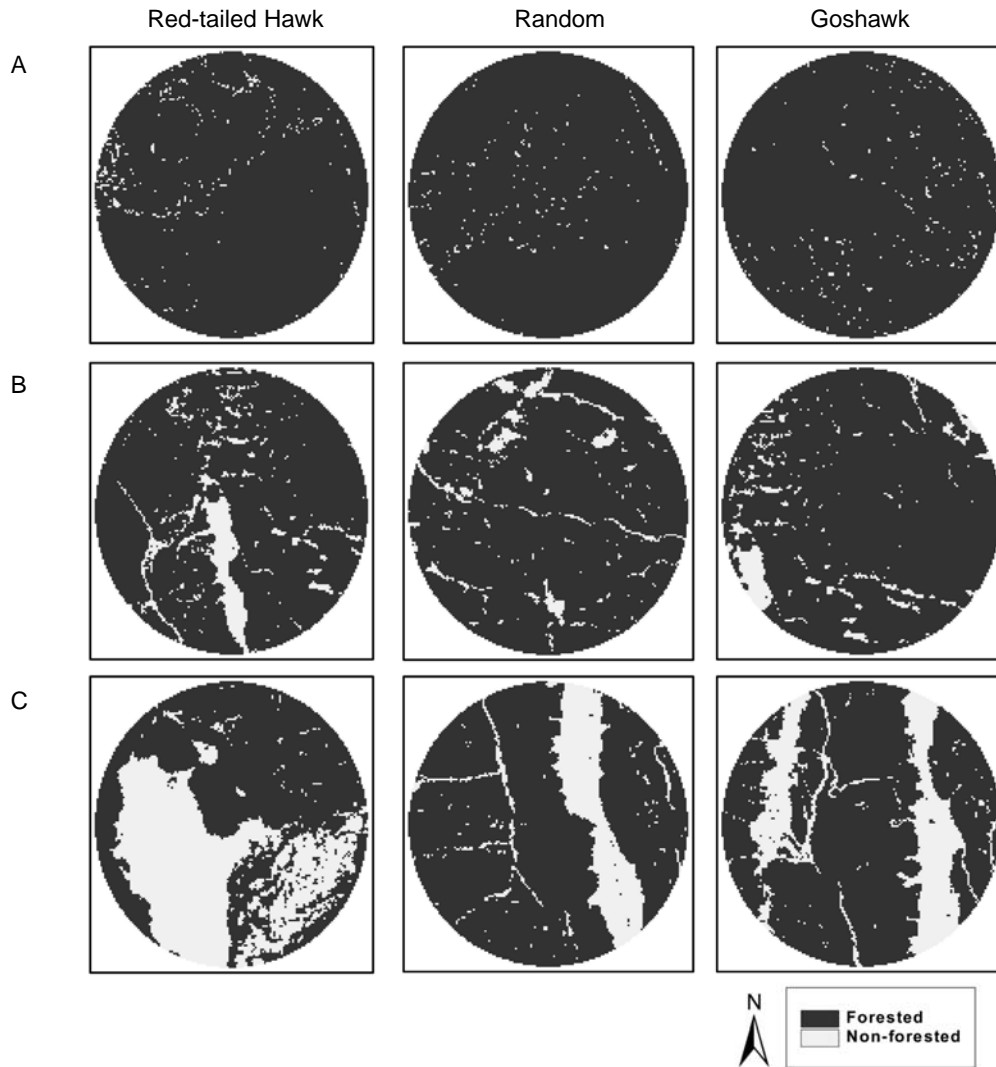


Fig. 5. Classified Landsat images (10 Oct 1999; 30 × 30-m cells) of sites that represented the (A) minimum, (B) that most closely approximated the mean, and (C) represented the maximum for 6 landscape indices measured in 2,085-m radius circles (mid-scale) centered on red-tailed hawk ($n = 41$) and goshawk ($n = 62$) nests and random sites ($n = 62$) on the Kaibab Plateau, Arizona, USA, in 2000.

was not based on consistent patterns of forest structure, as was found at goshawk nest sites, but with features related to nest position and access. Thus, selection was occurring primarily for the nest tree and its relationship to the surrounding topography for red-tailed hawks and for features within and below the canopy for goshawks. Patterns at the mid-scale suggested that habitat selection for red-tailed hawks was based on the presence of nonforested areas and fragmented forest structure around the nest site and steep slopes at the nest site. For goshawks, patterns at the mid-

scale suggested that selection was occurring exclusively for regions of continuous forest on level terrain centered at the nest site.

MANAGEMENT IMPLICATIONS

Our study reaffirms that the habitat associations of goshawks during the breeding season are regionally consistent within a particular environment. This allows resource managers to identify areas containing goshawk breeding habitat and develop management guidelines to protect them (e.g., Reynolds et al. 1992). However, successfully

managing for a species' unique habitat requirements is becoming more difficult in the western United States due to a variety of economic, political, ecological, and social pressures placed on forests and forest managers. An ecological factor that we examined is the presence of a very successful generalist, the red-tailed hawk, which introduces a variety of concerns for goshawk management. One is the possibility of competition for habitat or prey between the 2 species. Another is the encroachment of red-tailed hawks into goshawk territories. If goshawk habitat is altered beyond the range of association documented in our study, it could transition into red-tailed hawk habitat. Both factors could reduce the number of goshawk breeding territories within a region and potentially negatively impact the goshawk population. Our study did not attempt to examine the consequences of competition or habitat alteration; nevertheless, when sympatric, these 2 species coexist in a relationship defined in large part by available habitat. Red-tailed hawks, or any other bird-of-prey, are not likely to represent a serious competitive threat to goshawk populations because of the goshawk's unique habitat associations and highly aggressive behavior. The real issue is one of habitat; if the habitat requirements of a species are not available, that species will have difficulty fulfilling its ecological role. In this case, the threats to goshawk breeding habitat are more severe because of the goshawk's specialization on features that have economic value and features that are threatened by catastrophic wildfires. Thus, to increase the likelihood that goshawk populations persist in the western United States, an important management goal should be to retain goshawk breeding habitat within the goshawk's range of association. This study and many others have attempted to document these associations for particular regions and environments. In addition, an understanding of the forces that are acting to alter forests in the western United States and the potential long-term outcomes of these processes to forest ecosystems need to be incorporated into management strategies.

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