FOREST STRUCTURAL CHARACTERISTICS OF ACCIPITER NESTING HABITAT: IS THERE AN ALLOMETRIC RELATIONSHIP?¹

MELISSA S. SIDERS² AND PATRICIA L. KENNEDY
Department of Fishery and Wildlife Biology, Colorado State University, Ft. Collins, CO 80523

Abstract. In montane forests of the western United States, a general correlation of accipiter body size and scaling of the vegetation component of nesting sites and nest trees used by sympatric Accipiter species has been reported. We evaluated this pattern with vegetation data collected at Northern Goshawk (Accipiter gentilis), Cooper's Hawk (A. cooperii), and Sharp-shinned Hawk (A. striatus) nest sites in the Jemez Mountains and Pajarito Plateau of north-central New Mexico. We selected habitat variables at the nest tree and nest site scale that would allow us to evaluate the prediction that accipiters use nesting habitat in which their body size is positively correlated with tree size and tree spacing, and inversely correlated with tree density, basal area, and percent canopy closure. At the nest-site level, density of larger diameter trees should be positively correlated with body size, and density of smaller diameter trees should be inversely correlated with body size. Our results suggest that nest tree height and diameter support body size predictions about nesting habitat for accipiter hawks. None of the nest-site parameters measured in this study supported the body size predictions due to a large amount of intra-specific variation. As a result of this variation, it was difficult to differentiate between Cooper's Hawk and Northern Goshawk nest sites for most site variables. These results suggest there is a correlation between accipiter size and nest tree size, but that a correlation between nest site structural size and accipiter body size may not be a widespread phenomenon for all vegetation variables for all three species. Many commonly measured forest stand structural characteristics such as basal area and total tree densities may not be adequate for predicting suitable accipiter nesting habitat in all areas, particularly in the absence of comparisons with available habitat.

Key words: Accipiter gentilis; Accipiter cooperii; Accipiter striatus; nesting habitat; body size; New Mexico; niche partitioning.

INTRODUCTION

The three North American Accipiter species, Northern Goshawk (A. gentilis; hereafter referred to as goshawk), Cooper's Hawk (A. cooperii), and Sharp-shinned Hawk (A. striatus), are sympatric predators that nest in many forested areas in North America (Palmer 1988, Reynolds 1989). In western forests, Reynolds et al. (1982), Moore and Henny (1983), and Fischer (1986) reported a general correlation of accipiter size and tree size (used as an index of stand age or successional stage) of nest sites used by sympatric Accipiter species. Recently, Siders and Kennedy (1994) reviewed the literature to determine if accipiter hawks consistently use nesting habitat in which their body size is (1) positively correlated with nest tree height and average tree diameter of the nest site, and (2) inversely correlated with average tree density of the nest site and average percent canopy closure of the nest site. Their analysis focused on these four parameters because they are commonly measured indices of forest structural characteristics. Siders and Kennedy concluded that average tree density and tree diameter of nest sites consistently supported the body size predictions but that site percent canopy closure and nest tree height did not consistently follow the expected pattern. They also noted that among studies there was much variation in mean parameter values and ranges in mean values overlap among species. As a result of this variation, Cooper's Hawk and goshawk nest sites were difficult to separate vegetatively (Sharp-shinned Hawk sites were more distinct vegetatively). Siders and Kennedy suggested that these equivocal results are a result of both habitat variation among study areas and low power to detect differences due to small sample sizes (n < 20 for each species; exceptions are Moore and Henny 1983 and Wiggers and Kritz 1991).

¹ Received 19 June 1995. Accepted 11 October 1995.
² Present address: USDA Forest Service, North Kaibab Ranger District, P.O. Box 248, Fredonia, AZ 86022.
Efforts to separate accipiter nesting habitat have been further hampered by investigators using nest sites that may not have been located in an unbiased manner (but see Moore and Henny 1983, Fischer 1986, Bosakowski et al. 1992). In general, previous investigators (1) did not document their nest search method (Reynolds et al. 1982, Kennedy 1988), (2) used historical nests located with unknown search techniques (Hayward and Escano 1989) or (3) searched areas that they assumed a priori contained suitable nesting habitat (Joy 1990, Wiggers and Kritz 1991).

We reevaluated this relationship between accipiter size and the structural size of their nest trees and sites by conducting a nesting habitat study in north-central New Mexico in 1992 and 1993. Our primary study objective was to test the prediction that accipiters use nesting habitat in which their body size is positively correlated with tree size and tree spacing, and inversely correlated with tree density, basal area (BA), and percent canopy closure. This study was conducted in the same area studied by Kennedy (1988). We more than doubled sample sizes of goshawk and Cooper’s Hawk nest sites used in her study and include Sharp-shinned Hawk nest sites. This is the largest sample size of accipiter nests to be used in a study of this type. In addition, nest sites were located primarily with broadcast surveys (Kennedy and Stahlecker 1993) conducted in all forest types. This procedure gives an unbiased sample of the nesting habitat of the accipiter population in this area.

METHODS

STUDY AREA

The study area was in the Jemez Mountains and adjacent Pajarito Plateau in north-central New Mexico and is 645,265 ha in size. The Jemez Mountains were formed by volcanic activity and are dissected by steep-walled canyons formed by erosion of volcanic tuff. The Pajarito Plateau is an eastern, table-like extension of the Jemez Mountains. Elevations range from 1,645 m to 3,200 m. Mean annual precipitation is 45 cm, 75% of which occurs from May through October. Ponderosa pine (Pinus ponderosa), Douglas fir (Pseudotsuga menziesii), and white fir (Abies concolor) are the most prevalent forest cover types (SAF 1980) found over the study area. Subalpine grassland, Engelmann spruce-subalpine fir (Picea engelmannii-Abies lasiocarpa), pinyon-juniper (Pinus edulis-Juniperus sp.), juniper-grassland, and riparian habitats are also present. USDA Forest Service (USFS), Santa Fe National Forest, National Park Service, Bandelier National Monument, and Los Alamos National Laboratory manage most of the land in this area.

The study population consisted of 45 goshawk nest trees, 56 Cooper’s Hawk nest trees, and 16 Sharp-shinned Hawk nest trees located during surveys conducted from 1984–1993. Most nests (68.2% of goshawk, 89.3% of Cooper’s Hawk and 66.7% of Sharp-shinned Hawk nests) were located with search techniques that would not result in a habitat bias. This included nests that were located while conducting broadcast surveys in all forest types throughout the study area (Kennedy and Stahlecker 1993), or while conducting other investigations at random points throughout the study area. The remaining nests were located with unknown techniques, e.g., historic sites or sites located by the public (9.1% of goshawk and 4.3% of Cooper’s Hawk nests) or by searching areas that we assumed a priori contained suitable nesting habitat (22.7% of goshawk, 6.4% of Cooper’s Hawk and 33.3% of Sharp-shinned Hawk nests).

During the 1992 and 1993 field seasons, we visited nest sites at least once in late May–June to determine occupancy, and to locate any new alternate nest trees. A “nest site” was defined as the area surrounding a nest tree, including vegetation and topographic features used by a nesting pair during the entire nesting season exclusive of foraging areas (Reynolds et al. 1982). We defined a “nesting area” as a defended area that may contain a cluster of nest sites that accipiters used during the breeding season (Reynolds et al. 1992). Data analysis was not conducted by year due to sample size limitations. To avoid pseudoreplication, alternate nest trees within a nesting area were identified. We had limited numbers of banded birds so associating nest trees with individual birds was difficult. To estimate which nests belonged to the same nesting area, distances between active nest trees were calculated by year and by species. This was done using Universal Transverse Mercator (UTM) nest tree locations:

\[ \text{inter-site distance} = \sqrt{(\Delta UTM_e)^2 + (\Delta UTM_n)^2} \]

where UTM_e is the easting coordinate and UTM_n is the northing coordinate. The shortest distance between two active nest trees was 2,631 m for
FIGURE 1. Plot layout for determining inter-tree distances between overstory trees (≥ 15.2 cm dbh). Distance of nearest neighbor trees was measured A) from the nest tree in each of four quadrants, and B) to each of their nearest neighbors in each of four quadrants.

goshawk, 1,176 m for Cooper's Hawk, and 790 m for Sharp-shinned Hawk. All nest trees were considered to be within the same nesting area if their separation was less than the above distances, resulting in 24 goshawk, 47 Cooper's Hawk and 12 Sharp-shinned Hawk nesting areas.

NESTING HABITAT

With the exception of one goshawk nest site and four Cooper's Hawk nest sites, habitat data were collected at all nest sites that had been located in the study area since 1984 (42 goshawk, 52 Cooper's Hawk, and 16 Sharp-shinned Hawk nest sites). We excluded the one goshawk nest site because it was harvested after it was located (1984) and has not been occupied since the harvest. Four Cooper's Hawk and two goshawk sites were excluded because of their inaccessibility. All nest tree locations were determined using a Trimble Navigation Pathfinder Basic Global Positioning System (GPS) and differentially corrected (Trimble Navigation Ltd. 1992).

We evaluated habitat variables at two scales: nest tree and nest site. Tree size and percent canopy closure were evaluated at both nest tree and nest site scales. All other variables were evaluated at the nest site scale.

Circular plots (0.08 ha corrected for slope [see Siders 1995, Appendix 4 for slope correction methodology]) were established around nest trees. Within each plot, nest tree height and diameter at breast height (dbh) of all trees (≥ 2.5 cm dbh) were measured using standard forest measurement techniques (Wenger 1984). To determine percent canopy closure and inter-tree distance, the plot was divided into four quadrants using four cardinal directions for quadrant boundaries. Percent canopy closure was measured using a convex spherical densiometer (Lemmon 1956, 1957). Four canopy closure measurements were taken (facing to NE, SE, SW, NW) at each of five locations (nest tree, and one-half radius of plot to NE, SE, SW, and NW) and averaged for each plot. Inter-tree distances were determined at two levels to determine spacing between overstory trees (≥ 15.2 cm dbh). Using the same four quadrants as for percent canopy closure, a point-centered quarter method was used to measure distance (corrected for slope) to the tree nearest the nest tree in each quadrant (Greig-Smith 1983, Fig. 1A). Similar quadrants were established around each nearest neighbor and distance to its nearest neighbor in each quadrant was measured (Fig. 1B). Site tree density was determined by counting all trees (≥ 2.5 cm dbh) within the 0.08 ha plot. Trees were also placed into size classes: sapling (2.5–12.6 cm dbh), pole (12.7–30.4 cm dbh), large (30.5–45.6 cm dbh), and mature (> 45.6 cm dbh). Density of trees (no/ha) was calculated for each size class. These size classes were selected to be compatible with USFS size classes for the southwestern region (Reynolds et al. 1992). Basal area (BA) for each individual tree in the plot was calculated from dbh (Wenger 1984), then summed over all trees for the plot (m²/ha).

DATA ANALYSIS

To avoid pseudoreplication, alternate nest sites within a nest area were treated as the same ex-
Experimental unit. We did not select alternate nest sites randomly by nesting area for analysis because there was a great deal of intra-nesting area variability and we wanted to examine this variability in our analysis. Therefore, an unbalanced two-stage nested analysis of variance (ANOVA; PROC GLM (SAS Institute 1985)) was conducted to compare means of variables by species including species as a fixed effect and nesting area as a random effect (Sokal and Rohlf 1981). Using this approach we were able to include all nest sites in the analysis, and account for potential pseudoreplication that could result from including multiple nest sites selected by the same birds. Means were calculated for each species using the least squares means option (PROC GLM, LSMEANS option, SAS Institute, 1985), also including nesting area as an effect. For this type of model, PROC GLM does not correctly calculate standard deviations for the variables. Standard deviations were estimated independently using a method described by Steel and Torrie (1980, details are presented in Siders 1995). The model was first used to compare all three species, testing the null hypothesis that all three means for a variable were equal. Those variables that were found to be significantly different were then compared by pairs to determine which species were significantly different. Means were ranked by variable, determining largest to smallest by species, then the model was run comparing the two species with the largest ranks. This was repeated for the species with the smallest ranks. For each pairwise ANOVA, we constructed a 95% confidence interval to estimate the magnitude of the difference between means (see Siders 1995 for details) which is a post hoc evaluation of the statistical power of comparisons (Journal of Wildlife Management 1995).

All vegetation variables were tested for normality using PROC UNIVARIATE NORMAL (SAS Institute 1985) and all were found to be non-normal and skewed. Non-normality and/or skewness was not consistent among species within a variable. Normality tests were rerun on transformed data: arcsine and arcsine square root transformations for percent canopy closure data, and log and squared transformations for all other variables. Transformations did not result in normal distributions for all of the variables. Since the normality assumption of parametric tests was violated by this data set, the non-parametric equivalent model (Kruskal-Wallis, PROC NPAR1WAY WILCOXON (SAS Institute 1985)) was also conducted on the data for both three-way and two-way comparisons using means for nesting areas.

RESULTS

Nest tree and nest site measurements are summarized in Tables 1, 2 and Figs. 2, 3. In the full model means were significantly different (P < 0.05; df = 2 ANOVA and Kruskal-Wallis) among species for all habitat variables except for sapling density (2.4–12.6 cm dbh; P = 0.08 df = 2 ANOVA; P = 0.17 df = 2 Kruskal-Wallis) and density of large trees (30.5–45.6 cm dbh; P = 0.69 df = 2 ANOVA; P = 0.75 df = 2 Kruskal-Wallis) (Table 2, Figs. 2, 3). The results of the pairwise comparisons of significant full model variables are presented in Table 3 and discussed below.

---

### Table 1. Forest cover type of Accipiter nest sites by species.

<table>
<thead>
<tr>
<th>Forest cover type</th>
<th>Goshawk</th>
<th>Cooper's Hawk</th>
<th>Sharp-shinned Hawk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa Pine</td>
<td>17 (40%)</td>
<td>36 (70%)</td>
<td>3 (19%)</td>
</tr>
<tr>
<td>Douglas Fir–</td>
<td>8 (19%)</td>
<td>13 (25%)</td>
<td>7 (44%)</td>
</tr>
<tr>
<td>White Fir</td>
<td>2 (5%)</td>
<td>0 (0%)</td>
<td>2 (12%)</td>
</tr>
<tr>
<td>Spruce–Fir</td>
<td>12 (29%)</td>
<td>3 (6%)</td>
<td>4 (25%)</td>
</tr>
<tr>
<td>Aspen/Mixed Cone</td>
<td>3 (7%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
</tr>
</tbody>
</table>

* Cover type was determined by calculating BA by size class and forest cover for each nest site. The forest cover type with the greatest overstory BA was designated the site cover type.

### Table 2. Summary of nest tree variables measured at accipiter nest trees and sites in north-central New Mexico. For each variable, species are listed in descending order of means.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Species</th>
<th>N (nest site)</th>
<th>N (nest area)</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest tree ht (m)</td>
<td>NOGO</td>
<td>42</td>
<td>21</td>
<td>28.4</td>
<td>2.6</td>
</tr>
<tr>
<td></td>
<td>COHA</td>
<td>51</td>
<td>43</td>
<td>20.9</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>SSHA</td>
<td>16</td>
<td>12</td>
<td>15.7</td>
<td>3.6</td>
</tr>
<tr>
<td>Nest tree dbh (cm)</td>
<td>NOGO</td>
<td>42</td>
<td>21</td>
<td>50.0</td>
<td>6.7</td>
</tr>
<tr>
<td></td>
<td>COHA</td>
<td>52</td>
<td>43</td>
<td>39.6</td>
<td>9.8</td>
</tr>
<tr>
<td></td>
<td>SSHA</td>
<td>16</td>
<td>12</td>
<td>26.5</td>
<td>9.2</td>
</tr>
<tr>
<td>Nest % canopy closure</td>
<td>SSHA</td>
<td>16</td>
<td>12</td>
<td>78.8</td>
<td>10.3</td>
</tr>
<tr>
<td></td>
<td>NOGO</td>
<td>42</td>
<td>21</td>
<td>66.3</td>
<td>7.5</td>
</tr>
<tr>
<td></td>
<td>COHA</td>
<td>52</td>
<td>43</td>
<td>66.2</td>
<td>11.2</td>
</tr>
</tbody>
</table>

1. NOGO—Goshawk; COHA—Cooper's Hawk; SSHA—Sharp-shinned Hawk.
2. N = 52 due to a missing tree height measurement.
FIGURE 2. Box plots of vegetation parameters at accipiter nest sites in the Jemez Mountains, New Mexico. Each box contains 50% of the data (25% quartile to 75% quartile). Vertical lines range from 1% quartile to 99% quartile and + indicates the mean. NOGO is Northern Goshawk, COHA is Cooper’s Hawk and SSHA is Sharp-shinned Hawk.

TABLE 3. Summary of pairwise comparisons of means for all habitat variables measured at accipiter nest trees and sites in north-central New Mexico.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Species</th>
<th>P Value</th>
<th>df</th>
<th>ANOVA</th>
<th>Kruskal-Wallis</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest tree ht (m)</td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>7.5 ± 1.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SSHA vs. COHA</td>
<td>1</td>
<td>0.003</td>
<td>0.001</td>
<td>5.2 ± 2.5</td>
<td></td>
</tr>
<tr>
<td>Nest tree dbh (cm)</td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>0.003</td>
<td>0.003</td>
<td>13.1 ± 3.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SSHA vs. COHA</td>
<td>1</td>
<td>0.002</td>
<td>&lt;0.001</td>
<td>10.4 ± 5.7</td>
<td></td>
</tr>
<tr>
<td>Nest tree % canopy closure</td>
<td>SSHA vs. NOGO</td>
<td>1</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>12.5 ± 6.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>0.969</td>
<td>0.732</td>
<td>0.1 ± 3.9</td>
<td></td>
</tr>
<tr>
<td>Site % canopy closure</td>
<td>SSHA vs. NOGO</td>
<td>1</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>11.7 ± 4.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>0.298</td>
<td>0.379</td>
<td>3.1 ± 2.8</td>
<td></td>
</tr>
<tr>
<td>BA (m²/ha⁻¹)</td>
<td>NOGO vs. SSHA</td>
<td>1</td>
<td>0.914</td>
<td>0.901</td>
<td>0.4 ± 4.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SSHA vs. COHA</td>
<td>1</td>
<td>0.031</td>
<td>0.008</td>
<td>6.3 ± 4.4</td>
<td></td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>SSHA vs. NOGO</td>
<td>1</td>
<td>0.211</td>
<td>0.125</td>
<td>83.4 ± 37.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>0.006</td>
<td>0.016</td>
<td>156.8 ± 16.5</td>
<td></td>
</tr>
<tr>
<td>Inter-tree distance (m)</td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>0.679</td>
<td>0.327</td>
<td>0.2 ± 0.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>COHA vs. SSHA</td>
<td>1</td>
<td>0.005</td>
<td>0.004</td>
<td>1.7 ± 0.9</td>
<td></td>
</tr>
<tr>
<td>Total site density (trees ha⁻¹)</td>
<td>SSHA vs. COHA</td>
<td>1</td>
<td>0.008</td>
<td>0.008</td>
<td>633.2 ± 288.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>0.583</td>
<td>0.943</td>
<td>89.0 ± 157.9</td>
<td></td>
</tr>
<tr>
<td>Pole density (trees ha⁻¹)</td>
<td>SSHA vs. COHA</td>
<td>1</td>
<td>&lt;0.001</td>
<td>0.001</td>
<td>392.5 ± 18.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>0.054</td>
<td>0.139</td>
<td>36.3 ± 10.3</td>
<td></td>
</tr>
<tr>
<td>Mature tree density (trees ha⁻¹)</td>
<td>NOGO vs. COHA</td>
<td>1</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>35.0 ± 0.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SSHA vs. COHA</td>
<td>1</td>
<td>0.993</td>
<td>0.729</td>
<td>0.0 ± 1.4</td>
<td></td>
</tr>
</tbody>
</table>

¹ NOGO—Goshawk; COHA—Cooper’s Hawk; SSHA—Sharp-shinned Hawk.

This is a 95% CI on the difference between the means (See Siders 1995, Appendix 6 for calculational details) which is a post hoc evaluation of the statistical power of the comparison.

Poles (12.7-30.4 cm dbh) and mature (>45.6 cm dbh). Sapling and large size classes were not included in the pairwise comparison because these variables were not significantly different in the three-way comparison.
FIGURE 3. Box plots of tree density by diameter size class (sapling 2.5–12.6 cm dbh; pole 12.7–30.4 cm dbh; large 30.5–45.6 cm dbh; mature >45.6 cm dbh) in accipiter nest sites in the Jemez Mountains, New Mexico. Each box contains 50% of the data (25% quartile to 75% quartile). Vertical lines range from 1% quartile to 99% quartile and + indicates the mean. NOGO is Northern Goshawk, COHA is Cooper’s Hawk and SSHA is Sharp-shinned Hawk.

NEST TREE CHARACTERISTICS

Results of pairwise comparisons indicated that the only vegetation variables that follow body size predictions were nest tree height and nest tree dbh. Goshawk nest trees were taller and had greater diameters than Cooper’s Hawk nest trees which were taller and had greater diameters than Sharp-shinned Hawk nest trees (Tables 2, 3). Mean nest tree percent canopy closure did not follow the general trend predicted from body size for all three species (Table 2). Percent canopy closure of Sharp-shinned Hawk nest trees was significantly higher than percent canopy closure of goshawk nest trees. However, percent canopy closure of goshawk and Cooper’s Hawk nest trees were not significantly different (Table 3).

NEST SITE CHARACTERISTICS

All three species used conifer and conifer/aspen forest for nesting habitat (Table 1). Goshawks also nested in aspen stands and Cooper’s Hawks were not found in spruce-fir forests. Although elevation is not a characteristic that has been related to accipiter body size, it is interesting that elevation of goshawk sites (2,495 m ± 37) was significantly greater than Cooper’s Hawk nest sites (2,338 m ± 42) but was not significantly different from Sharp-shinned Hawk nest sites (2,578 m ± 57) (Table 3).

Pairwise comparisons indicated that none of the nest site variables followed predictions from body size for all three species. Vegetation variables that followed the predicted trend were: (1) mean total density of trees ≥2.5 cm dbh (Fig. 2, Table 3) which decreased with increasing accipiter size, mean inter-tree distance of overstory trees (Fig. 2, Table 3) which increased with increasing accipiter size and density of pole size trees (Fig. 3, Table 3) which decreased with increasing accipiter size. However, means of the above variables were not significantly different for one of the pairs of comparisons due to large amounts of intra-specific variation in these variables.

Mean site percent canopy closure (Fig. 2, Table 3) was greatest for Sharp-shinned Hawk nest sites, and was significantly higher than mean percent canopy closure of goshawk sites as expected. However, percent canopy closures of goshawk and Cooper’s Hawk sites were not significantly different. Mean BA (Fig. 2, Table 3) was higher for Sharp-shinned Hawk sites than for Cooper’s Hawk sites as expected. However, mean BA for goshawk sites was not significantly different from mean BA of Sharp-shinned Hawk sites. From this relationship we assumed that mean nest site
BA for goshawks was significantly higher than Cooper’s Hawk site BA, which does not support body size predictions.

Mean total tree density (Fig. 2, Table 3) of Sharp-shinned Hawk sites was significantly greater than mean total tree density of Cooper’s Hawk sites as expected. Mean total tree density of Cooper’s Hawk sites was greater than the mean total tree density of goshawk sites, but the difference was not significant. From this relationship we assumed that total tree densities on Sharp-shinned Hawk sites were significantly greater than total tree densities on goshawk sites. These similarities in overall tree densities are also reflected in the densities within tree size classes (Fig. 3, Table 3). Mean density of pole size trees (12.7–30.4 cm dbh) was significantly greater in Sharp-shinned Hawk nest sites than in Cooper’s Hawk nest sites. Mean density of mature size trees (>45.6 cm dbh) was significantly greater in goshawk nest sites than in Cooper’s Hawk nest sites. However, densities of pole size trees in Cooper’s Hawk nest sites were not significantly different from pole densities in goshawk sites and Cooper’s Hawk and Sharp-shinned Hawk nest sites had equal mean densities of trees in the mature size class. As indicated previously in the three-way analysis, mean densities of trees in the sapling and large size classes were similar for all three species.

Mean inter-tree distance for overstory trees (≥15.2 cm dbh) in Sharp-shinned Hawk sites were less than for Cooper’s Hawk sites as predicted. Trees in Cooper’s Hawk sites were more closely spaced than trees in goshawk nest sites, but differences were not significant. From this relationship we assume that mean inter-tree distance was significantly greater in goshawk sites than it was in Sharp-shinned Hawk sites, as predicted.

DISCUSSION
DESCRIPTION OF ACCIPITER NESTING HABITAT
Based on our results (± 1 SD) nesting habitat of the three Accipiter species in the Jemez Mountains in north-central New Mexico can be described as follows. Goshawks nest in ponderosa pine, aspen/mixed conifer, and mixed conifer stands at 2,460–2,530 m in elevation. They use nest trees 25–31 m tall and 43.3–56.7 cm dbh with 58–74% canopy closure at the nest tree. Nest sites have 60–71% canopy closure, 31–40 m² ha⁻¹ BA, overall site density of 800–1,400 trees ha⁻¹, and overstory trees are spaced 4.8–6.8 m apart. Nest sites are composed of 2.8–8.0% mature, 2.1–11.1% large, 5.2–32.8% pole and 16.8–83.6% sapling trees. Site tree densities by size class are 460–970 sapling trees ha⁻¹, 130–370 pole trees ha⁻¹, 55–115 large trees ha⁻¹, and 53–90 mature trees ha⁻¹.

Cooper’s Hawks nest in habitat that is more diverse, but is more similar to goshawk habitat than to Sharp-shinned Hawk habitat. Only nest tree height, elevation, and density of mature trees were significantly different between goshawk and Cooper’s Hawk nest sites, whereas Cooper’s Hawk nest sites were significantly different from Sharp-shinned Hawk sites in all variables except elevation and density of sapling, large, and mature trees. Cooper’s Hawks nest predominantly in ponderosa pine and mixed conifer stands at 2,300–2,380 m in elevation. They use nest trees 17–25 m tall and 29.8–49.4 cm dbh with 55–78% canopy closure at the nest tree. Nest sites have 58–74% canopy closure, 29–42 m² ha⁻¹ BA, overall site density of 750–1,650 trees ha⁻¹, and overstory trees are spaced 4.2–7.0 m apart. Nest sites are composed of a mixture of trees from all size classes: 1.3–4.1% mature-, 2.5–9.9% large-, 8.8–41.6% pole- and 7.4–99.4% sapling-sized trees. Nest site tree densities by size class are 390–1,115 sapling trees ha⁻¹, 170–520 pole trees ha⁻¹, 40–130 large trees ha⁻¹, and 10–60 mature trees ha⁻¹.

Sharp-shinned Hawks nest predominantly in mixed conifer stands at 2,500–2,640 m in elevation. They use nest trees 12–19 m tall and 17.3–35.7 cm dbh with 68–90% canopy closure at the nest tree. Nest sites have 70–85% canopy closure, 22–36 m²/ha⁻¹ BA, overall site density of 1,410–2,260 trees ha⁻¹, and overstory trees are spaced 2.6–5.2 m apart. Nest sites contain 0.8–4.4% mature-, 1.3–9.5% large-, 27.4–64.6% pole- and 28.2–100.0% sapling-sized trees. Nest site tree densities by size class are 790–1,500 sapling trees ha⁻¹, 435–760 pole trees ha⁻¹, 30–110 large trees ha⁻¹, and 12–58 mature trees ha⁻¹.

EVALUATION OF forest STRUCTURAL CHARACTERISTICS AS PREDICTORS OF NESTING HABITAT
Our results suggest that nest tree height and diameter support body size predictions about nesting habitat for accipiter hawks. We concur with
earlier studies that larger accipiters apparently use larger trees to support their nest structures. However, none of the nest site parameters measured in this study supported the body size predictions due to a large amount of intra-specific variation. As a result of this variation, it was difficult to differentiate between Cooper’s Hawk and goshawk nest sites for most site variables. No nest site variable measured by other investigators consistently support body size predictions among study areas (see review in Siders and Kennedy 1994). These results suggest there is a correlation between accipiter size and nest tree size but that a correlation between nest site structural size and accipiter body size may not be a widespread phenomenon for all vegetation variables for all three species. Many commonly measured forest structural characteristics such as basal area and tree densities may not be adequate for predicting suitable accipiter nesting habitat in all areas, particularly in the absence of comparisons with available habitat. Siders and Kennedy (1994) suggested that differences in habitat variables at accipiter nest sites might exist but they have not been detected due to small sample sizes (low power to detect differences). Although we did not estimate power a priori, we did calculate 95% confidence intervals on the difference between the means of each variable used in the pairwise comparisons (Table 3). The width of the confidence interval provides qualitative information on the power of our analyses (Journal of Wildlife Management 1995). The width of the 95% confidence interval for each nonsignificant comparison was similar to the interval width for the equivalent significant comparison for all variables (e.g., site percent canopy closure — SSHA vs. NOGO = 6.9—16.5%, \( P < 0.001 \), 1 df; NOGO vs. COHA 0.3—5.9%, \( P = 0.38 \), 1 df [Kruskal-Wallis] and \( P = 0.38 \), 1 df [ANOVA]) (Table 3). This suggests that the analyses in our study had sufficient power to detect differences if they existed.

It is also possible that differences exist among the Accipiter nest sites but the measurements and analyses commonly used in habitat studies do not do a good job of discriminating among nest sites of the three species. For example, interspecific differences may be masked by analyzing forest structural characteristics across all forest types. There is a great difference in vegetation structure between, for example, ponderosa pine, and Douglas fir-white fir forest cover types, and both are used by the accipiters for nest sites to varying degrees (Table 1). Vegetation variables such as percent canopy closure, BA, density of trees, distribution of size classes and inter-tree distance may be related to forest cover type, and thus result in confounding effects.

Similar to other accipiter habitat studies (see review in Siders and Kennedy 1994), we did not stratify by forest species composition because bird distributions and abundances are more closely correlated with habitat physiognomy (Anderson and Shugart 1974, Roth 1976, Cody 1981) and stratifying by forest type would reduce sample sizes (Table 1) and thus, the power of the analyses. However, to address this possibility we reanalyzed the goshawk and Cooper’s Hawk nest site data from the ponderosa pine type. We chose this subset because our largest number of nest sites were located in this forest type (Table 1). Sharp-shinned Hawks were not included in this analysis because (1) of their small sample size in this type and (2) Cooper’s Hawks and goshawks had the most similar nest sites when data were pooled over forest type. All site variables were analyzed using the pairwise comparisons described earlier.

The results of the ponderosa pine site analysis were similar to the results of the site analysis with data pooled over forest type. The only variables that were significantly different between Cooper’s Hawk and goshawk ponderosa pine sites were BA (Cooper’s Hawk \( \bar{x} = 26.5 \text{ m}^2/\text{ha} \); goshawk \( \bar{x} = 33.4 \text{ m}^2/\text{ha} \); \( P = 0.02 \), 1 df [Kruskal-Wallis] and \( P = 0.02 \), 1 df [ANOVA]) and mature tree density (Cooper’s Hawk \( \bar{x} = 26.5 \text{ trees/ha} \); goshawk \( \bar{x} = 33.4 \text{ trees/ha} \); \( P = 0.001 \), 1 df [Kruskal-Wallis] and \( P < 0.001 \), 1 df [ANOVA]). These results support our conclusions that accipiter nests sites cannot be discriminated by forest structural characteristics even if sites are stratified by forest type. However, we interpret these data cautiously because this is a post-hoc analysis of one forest type with limited sample sizes and two species.

Body size predictions are based on the assumption that habitat niche partitioning occurs as a result of interspecific competition for nesting habitat (Moore and Henny 1983, Fischer 1986) or avoidance of larger congenerics which are potential predators (Reynolds et al. 1982, Moore and Henny 1983, Reynolds 1983). This is based on the widespread assumption that coexistence of similar species depends on their partitioning resources. Thus, variation in the degree of over-
lap in Accipiter nesting habitat documented by different investigators may reflect variation in rates of interspecific competition and/or congeneric predation rates among study areas. Conversely, Accipiter species may exhibit high levels of interspecific competition for nesting habitat throughout their range but this competition may not result in partitioning of nesting habitat. Basset (1995) recently demonstrated theoretically that when competition occurs asymmetrically with a superiority of the larger species, differences in size between individuals of competing species can result in stable coexistence independent of resource partitioning. Although we cannot evaluate the degree of interspecific competition in this population with our data, Basset's results suggest that complete overlap in Accipiter nesting habitat is possible even if there is interspecific competition for this resource.

ACKNOWLEDGMENTS

This project was funded by the USDA Forest Service, Southwestern Region, and the Santa Fe National Forest (SFNF). Dan Lentz, Bill McKinney, and John Peterson of the Jemez Ranger District were especially helpful and supportive of this project. Tim Smith, and Chris Chaves in the Supervisor's Office of the SFNF were invaluable in their assistance with GPS data collection and differential corrections. We received additional support from Los Alamos National Laboratory which provided access to many of the lower elevation Coop-er's Hawk nest sites and provided GPS Community Base Station data. Jeanne Fair, Roger Hoffer, Orrin Myers, Richard Reynolds and Joni Ward were indispensable in their helpful suggestions for this project's design, implementation, and analysis. Roger Hoffer and Richard Reynolds also helped revise the manuscript. Phil Chapman provided invaluable statistical advice. Amber Alexander, Kelly Colfer, Tylan Dean, John DeLong, Vicky Dreitz, Joan Moore, and David Sinton helped find nest sites of all three species, assisted in vegetation data collection, and occasionally climbed trees for GPS locations in dense canopies. Special thanks go to Vicky Dreitz, Tylan Dean, and David Sinton for assistance in all aspects of the research. Chuck Henny and an anonymous reviewer helped improve the manuscript.

LITERATURE CITED


