NEST SITE CHARACTERISTICS OF THREE COEXISTING ACCIPITER HAWKS IN NORTHEASTERN OREGON

by
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Abstract

Habitat data were evaluated at 34 Goshawk (*Accipiter gentilis*), 31 Cooper's Hawk (*A. cooperii*), and 15 Sharp-shinned Hawk (*A. striatus*) nest sites in coniferous forests of northeastern Oregon. Crown volume profiles indicate a strong similarity in vegetative structure at nest sites of *cooperii* and *striatus*; both commonly nest in younger successional stands than *gentilis*. Habitat separation of nest sites among the three species was illustrated using a stepwise discriminant analysis; 88% of all *gentilis* sites were correctly classified. Interspecific overlap in nest site habitat was further demonstrated using a canonical analysis of habitat variables. Nest site habitat space of *gentilis* is distinct and is less variable in structure than that of the other species. *Cooperii* preferred nesting sites with northern aspects, whereas *striatus* and *gentilis* showed no preference. The use of mistletoe (*Arceuthobium* sp.) growth by *cooperii* for nest platforms (64% of all nests) may explain its preference for Douglas fir (*Pseudotsuga menziesii*) as a nesting tree. Douglas fir is most commonly parasitized by mistletoe.

Introduction

Populations of the Goshawk, Cooper's Hawk, and Sharp-shinned Hawk are sympatric in the coniferous forests of northeastern Oregon. These congeneric predators may coexist by partitioning the resources available to them, thus avoiding competition when resources are limited. It has been demonstrated that partitioning of food resources occurs among these three accipiters by the selection of prey which is optimal for the size and behavior of each species (Reynolds 1979). *Gentilis* takes larger prey and a greater proportion of mammals, while *striatus* takes primarily small song birds. Prey items of *cooperii* fall on the gradient between these two (Storer 1966, Snyder and Wiley 1976, Reynolds 1979). In this study our objective was to determine whether each species located its nest in a unique type of habitat. Previous *Accipiter* nest site studies were limited by the paucity of sites investigated (generally < 10 per species for a locality, usually considerably fewer). In this study, 80 nest sites were investigated in the coniferous forests of northeastern Oregon.

Several studies of avian species provide evidence that birds respond to vegetational features in selecting their habitats (Pitelka 1941, Sturman 1968, Wiens 1969, Reynolds et al. 1982).

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Vegetation height, amount at particular levels, density, and life form were found to be important factors affecting passerine diversity (MacArthur et al. 1962). Sturman (1968) found that the breeding densities of the Black-capped Chickadee (*Parus atricapillus*) were significantly correlated with canopy volume of trees and shrubs. The physiognomy and some aspects of the vegetative structure of North American *Accipiter* nest sites was described in Utah by Hennessy (1978) and in Oregon by Reynolds et al. (1982). Both authors found that differences in *Accipiter* nest sites were primarily related to vegetative structure immediately surrounding the nest site which reflected the successional stage of the forest stand. Newton et al. (1977) found that the European Sparrowhawk (*Accipiter nisus*) nested only in woodlands of a certain vegetational structure equated with the growth stage. They also suggested that availability of nesting habitat along with spacing of nesting territories, which was a function of prey availability, limited overall densities of nesting territories.

Multivariate techniques were useful for analysis of the vegetative structure of habitat and description of the n-dimensional species niche (Green 1971). Several authors have used these methods to describe habitat selected and niche separation by analysis of vegetative structure associated with each species within the community (James 1971, Anderson and Shugart 1974, Cody 1978, Holmes et al. 1979, Reynolds et al. 1982). Multivariate techniques used in this study were chosen because of their power in describing multi-dimensional habitat spaces. N-space habitat vectors can easily be reduced to fewer dimensions by linear combinations of the original variables.

Methods

Study Area

The study area was located within and around the Wallowa-Whitman National Forest in northeastern Oregon between 45° and 46° North Latitude at elevations between 500 and 1600 m. The Wallowa-Whitman Forest, in the Blue Mountains province of Oregon, consists primarily of montane forest with moderate to steep relief. A detailed description of the physiognomy of this province and climatic conditions of various forest types are given by Franklin and Dyrness (1973). Hall (1973) recognized several climax forest plant communities in this area: ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), grand fir (*Abies grandis*), subalpine fir (*A. lasiocarpa*), and mixed conifer stands, e.g., ponderosa pine, Douglas fir, grand fir, and western larch (*Larix occidentalis*). Many stands are on a gradient between these communities. Vegetation of natural open areas consists of grass and forbs. A mosaic of forest stands of various age class and species composition is present.

Since searches for the three species were conducted, all habitat types within the forests were checked. Nest searches were concentrated in areas where repeated sightings or trapping of *Accipiters* occurred. Information provided by U.S. Forest Service personnel and loggers often led to nest discoveries.

Vegetative Sampling

Occupied and unoccupied nests at undisturbed sites which had been located between 1975 and 1979 were examined. Unoccupied nests were generally sampled the year following occupancy, but in a few cases 2 years intervened before measurement. This delay resulted from habitat data not being recorded during the first 2 years of the nesting study. Each nest site was examined only once; nesting adults were captured and banded when possible. If a known pair (i.e., both previously banded and recaptured) was located during more than 1 year, only the first nest site was used in this analysis. Vegetation was sampled within 0.08 ha circular plots (16.03 m radius) centered on the nest tree. Vertical distribution of tree crown volume was measured using the technique of Mawson et al. (1976) with the program HTVOL. Each tree within the plot was considered in relation to 15 possible crown shapes and relegated to the best fit. Dimensions of these shapes were measured using a clinometer and steel tape. The program HTVOL calculated total crown volume within 3 m height classes up to 36 m to develop a crown profile for each plot. Diameter at breast height (dbh) and species were recorded for each tree in the plot. All plants greater than 0.3 m and less than or equal to 3 m in height were measured as shrubs. Shrub crown volume was calculated by fitting shrubs or groups of shrubs into the smallest possible cube and measuring the dimensions of that cube. Shrub and tree crown volumes were combined to develop a total crown profile for each plot, since shrub crown volumes contribute to the vertical structure of the site. Ground cover was measured by point sampling along transects in four cardinal directions from the nest tree (James and Shugart 1970). Slope and aspect of each site were recorded.

The following nest tree characteristics were recorded: species, condition (alive, dead), dbh, height, and crown height. The following nest characteristics were measured: height, exposure, nest substrate and canopy coverage at the nest (measured with a spherical densiometer).

Analysis

Tree crown profiles and stand composition variables were tested for differences among *Accipiter* species using multivariate analysis of variance (MANOVA). Orthogonal multiple comparisons were used to identify significantly different variables (Morrison 1967). Stepwise discriminant analysis was used to select those variables which were most important in discriminating among nest sites of the species. A canonical analysis of nest site variables was used to identify variables which were the most powerful discriminators of each species' nesting habitat.

Univariate data were tested with one-way analysis of variance and Chi-square tests (Snedecor and Cochran 1967). Nest tree selection was examined using Bonferroni normal statistics in conjunction with Chi-square (Neu et al. 1974). Nest site aspect and nest directional exposure were tested for significant mean direction with Rayleighs R statistics (Zar 1974). Computer analyses utilized the Statistical Analysis System (SAS) (Helwig and Council 1979) and the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975).

Results

Nest Site Habitat Structure

Crown volume was calculated for the plots surrounding 34 *gentilis* nests, 31 *cooperii* nests and 15 *striatus* nests to yield mean crown profiles of the nest stands of each species (Fig. 1). Crown profiles indicate a strong similarity in vegetative structure of *cooperii* and *striatus* nest sites. Both commonly nest in younger successional stands with highest density of foliage in layers from 3 to 15 m. Nests of *gentilis* are found in older growth coniferous stands at the opposite end of the successional spectrum. Crown volumes at lower levels, 0 to 12 m, are generally low while the majority of foliage is in strata from 12 to 24 m. This profile is produced by stands of larger coniferous trees ($\geq$ 16.5 cm dbh), with relatively low understory crown volumes.

MANOVA of crown profiles of the three species indicates a significant difference among species of strata from 0 to 36 m ($P < 0.05$). This significance results from lower crown volumes in the sites of *gentilis* from 6 to 12 m and larger crown volumes in the 18 to 24 m strata when compared to these strata of *cooperii* and *striatus* nest sites. No significant difference between crown profiles of *cooperii* and *striatus* were detected.

Frequency of various dbh classes, number of trees per 0.08-ha, basal area of the plot, and mean tree dbh (Table 1) provide further information on the vegetative structure of nest sites. Trees less than 16.5 cm dbh made up 77% and 80% of the total tree density of *cooperii* and *striatus* sites respectively, while only 51% of the total tree density of *gentilis* sites. Nests of *gentilis* were located on sites with fewer and larger trees than those of *cooperii* and *striatus*. The tree dbh classes, basal area, and mean dbh were used in a MANOVA to test for differences among species. Tree density was omitted since the sum of size class frequencies equal the total tree density, reducing the rank of the model. No significant differences were detected between *cooperii* and *striatus*, but *gentilis* sites were significantly different ($P < 0.05$) in frequency of the two smallest dbh size classes and average dbh.

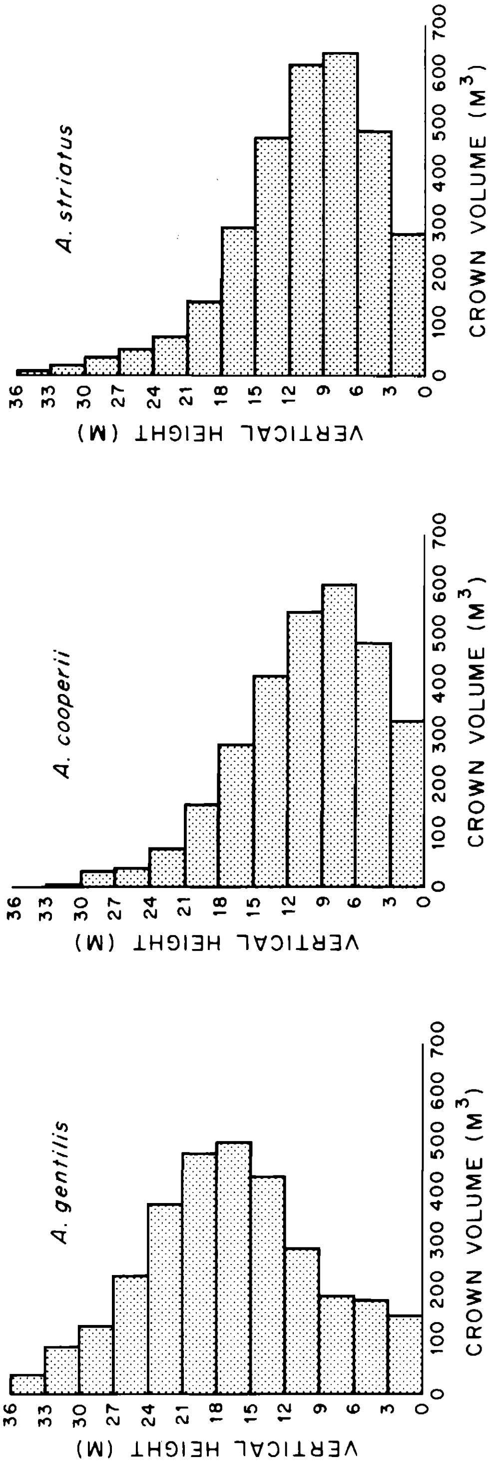

Figure 1. Crown profiles for the plots surrounding the nest sites of three species of *Accipiters* using mean crown volumes for each stratum.

Table 1. Structural characteristics of plots surrounding nest sites

Variable	*A. gentilis* (N = 34) Mean frequency	*A. gentilis* (N = 34) S.D.	*A. cooperii* (N = 31) Mean frequency	*A. cooperii* (N = 31) S.D.	*A. striatus* (N = 15) Mean frequency	*A. striatus* (N = 15) S.D.
Tree size dbh						
2.5-8.9 cm	22.4*	19.8	74.7	69.9	92.5	73.6
8.9-16.5 cm	19.0*	12.6	38.2	21.9	56.6	42.4
16.5-31.7 cm	23.4	13.3	24.7	12.1	30.1	11.9
31.7-41.9 cm	10.8	6.2	6.8	4.3	5.8	4.9
>42 cm	5.9	4.5	2.8	3.6	2.3	2.4
Stems/0.081 ha	81.6	34.2	146.0	86.7	187.3	117.8
Basal area (m^2) (0.081 ha)	4.2	1.4	3.2	1.4	3.5	1.2
Mean dbh (cm)	22.1*	5.8	15.0	5.6	12.9	3.0
Slope (%)	14.0	10.6	17.2	10.3	24.6	18.8
Ground cover forbs (%)	46.7	18.2	25.3	16.3	29.5	13.5
Ground cover grasses (%)	12.6	11.1	16.9	12.9	10.1	7.7
Ground cover absent (%)	40.4	20.5	56.5	18.7	59.8	16.1

* ($P < 0.05$).

Nest site habitat separation among the three species can be illustrated using the crown volume variables, tree dbh classes, basal area, and mean dbh variables in a stepwise discriminant analysis. The discriminant functions also provide a means of classifying each observation according to *a posteriori* probabilities that an observation classified as one particular habitat is in fact occupied by that species. The classification results given in Table 2 show that 88% of all *gentilis* sites were correctly classified. Sites of *cooperii* and *striatus* were misclassified most often by the lack of discriminating power between these two species rather than similarities with *gentilis* sites.

Interspecific overlap in nest site habitat can be graphically demonstrated using a canonical analysis of habitat variables in the same manner as Cody (1978). Canonical analysis generates new variables which are linear combinations of original variables, each weighted according to their power to discriminate. The position of individual observations can be plotted along the canonical functions to get a graphical interpretation of the nature and extent of species separation. Nest site habitat space of *gentilis* is distinct from the other two species and appears to be less variable in structure (Fig. 2).

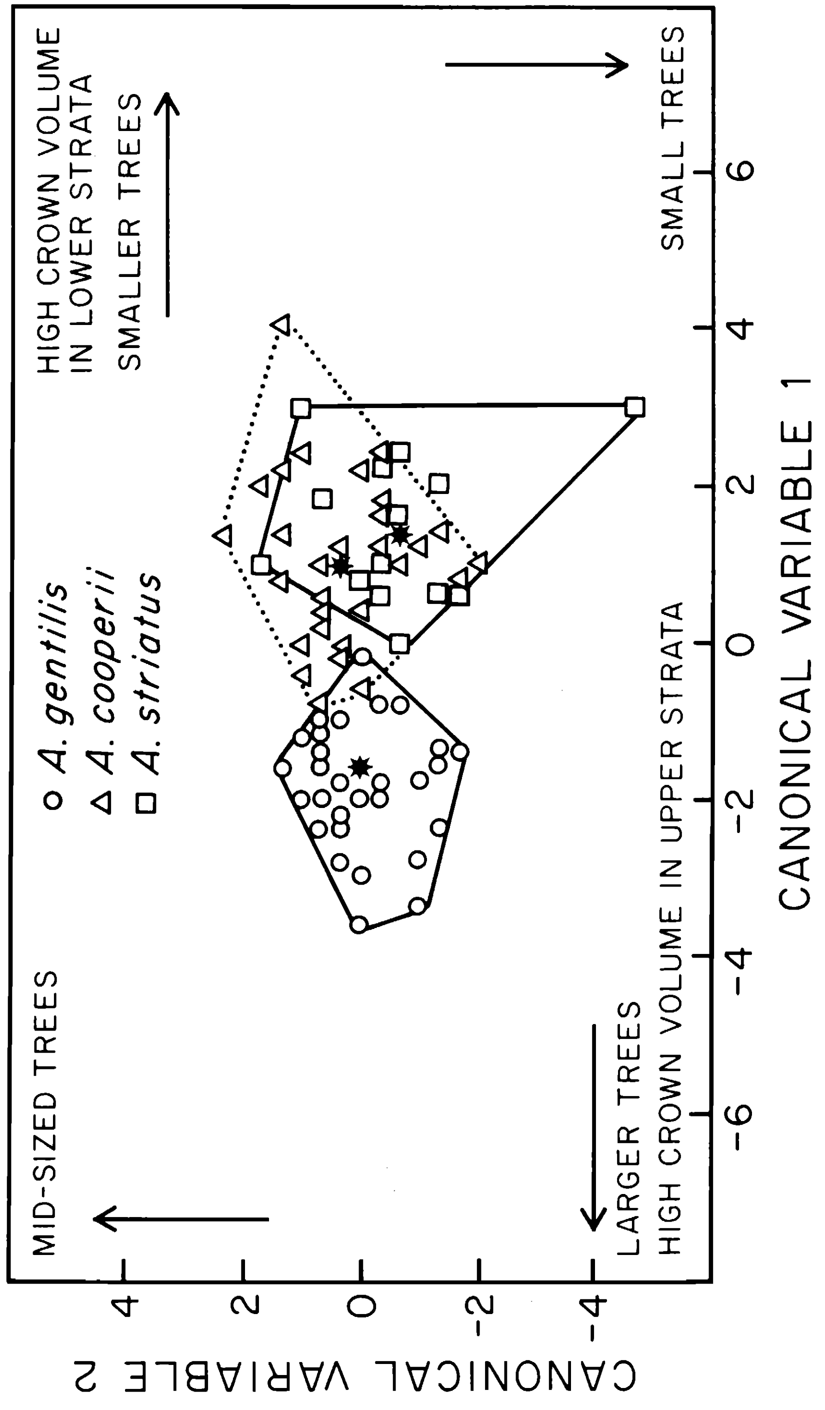

Figure 2. Distributions of nest site habitat for three species of *Accipiters*. Axes represent canonical variables from canonical analysis of original nest site variables (star represents group means).

Table 2. Classification results of discriminant analysis of nest site characteristics

		Predicted group membership		
Group	N	*A. gentilis*	*A. cooperii*	*A. striatus*
A. gentilis	34	30	3	1
		88.2%	8.8%	2.9%
A. cooperii	31	2	19	10
		6.5%	61.3%	32.3%
A. striatus	15	0	7	8
		0.0%	46.7%	53.3%
		[71% of grouped cases were correctly classified]		

Nest Site Aspect

The nest site aspect (assuming equal availability) was tested for significant mean directional preference (Fig. 3). Nests on flat terrain (< 3% slope) were excluded. *Gentilis* nest sites showed a mean angle of 24° (0° =north) with an angular diviation of ± 87°. However, no preference of site aspect was indicated (P < 0.20). *Gentilis* also showed greater variability in the predominant tree species at the nest sites and a greater frequency of nests on flat terrain.

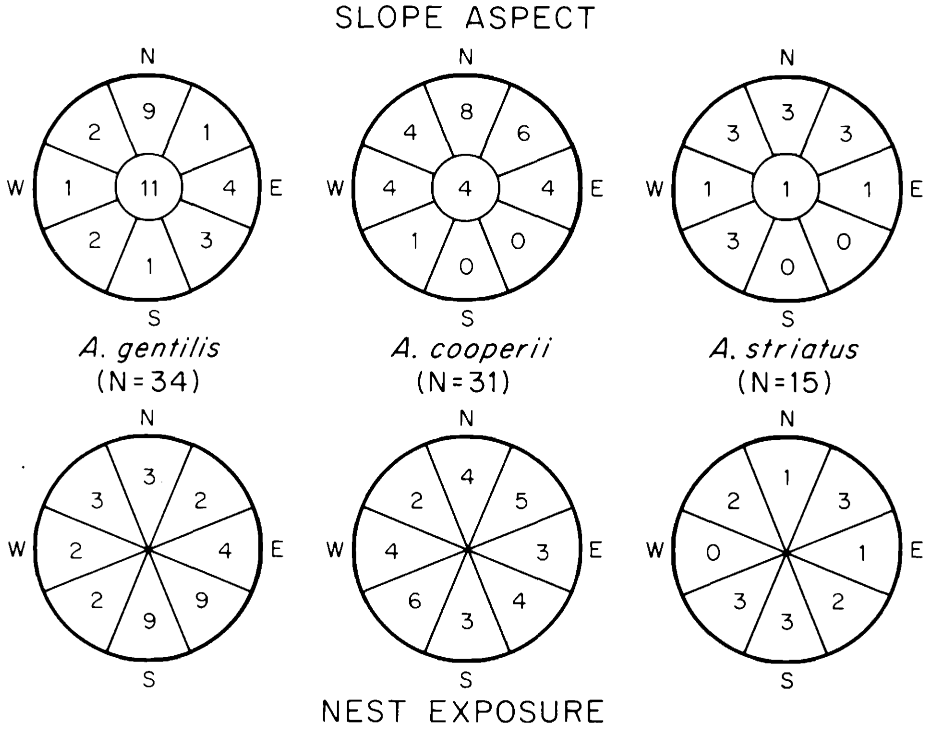

Figure 3. Nest site aspects and nest exposures relative to the bole of the nest for each species. Number in each cell is the frequency of sites on that aspect or nests with that exposure.

The nest sites of *cooperii* showed a significant preference for northern (3° ± 64°) aspects ($P < 0.001$). No directional preference (338° ± 78°) was indicated for *striatus* ($P < 0.20$), although 60% of nest sites were on northern aspects.

Nest Tree Characteristics

To evaluate the tree species preferred by each of the accipiters for nesting, we first pooled the number of trees of adequate size (*gentilis* 20-76 cm dbh, *cooperii* 18-76 cm dbh, *striatus* 10-50 cm dbh) within the plots for each *Accipiters* species. The proportion of each tree species is shown in Figure 4. Grand fir and Douglas fir were the predominant tree species at most nest sites for all three accipiters. Nest tree selection was examined by comparing the proportion of each tree species available with the proportion used as a nest tree. None of the accipiters nested in tree species in proportion to their availability (*gentilis* $P < 0.005$, *cooperii* $P < 0.005$, *striatus* $P < 0.01$). *Gentilis* showed preference for Douglas fir and western larch, while *cooperii* showed a preference for Douglas fir. Lodgepole pine was avoided by all species.

Selection of avoidance of a tree species for nesting is probably due to growth form and foliage patterns unique to each tree species. Structural characteristics of nest trees are given in Table 3. A negative value for the nest-crown relationship represents nests below the canopy. Nest heights of *striatus* were significantly lower than those for the other two species. Nest-crown relationship was significantly different only between *gentilis* and the other two species. A correlation was indicated between nest height and the nest-crown relationship ($R^2 = 0.53$, $N = 80$, $P < 0.0001$). Position of the nest in the nest tree may be strongly affected by the height of the nest tree canopy. *Gentilis* prefers to build below the crown in more exposed positions, while the other two species build up in the canopy.

Significant differences were found in canopy coverage over the nest for all three species ($P < 0.0001$) using ANOVA on arcsine-converted-percentage-data (Table 3). *Gentilis* nested in

Table 3. Nest tree characteristics of three species of *Accipiters*

	A. gentilis (N = 34)		*A. cooperii* (N = 31)		*A. striatus* (N =15)	
Variable	Mean	S.D.	Mean	S.D.	Mean	S.D.
Dbh (cm)	51.6*	14.9	43.7	15.2	28.7	13.7
Nest height (m)	14.5	4.4	12.1	3.2	7.6*	3.2
Nest-crown relationship (m)	−1.7*	4.8	2.0	4.0	1.0	3.9
Nest canopy coverage (%)	88.1**	8.8	95.2	4.1	97.9	1.5
Frequency of use of mistletoe for nest substrate	14.7%		64.5%		20.0%	
Frequency of use of dead trees for nest trees	17.6%		0		0	

* ($P < 0.05$).
** ($P < 0.0001$).

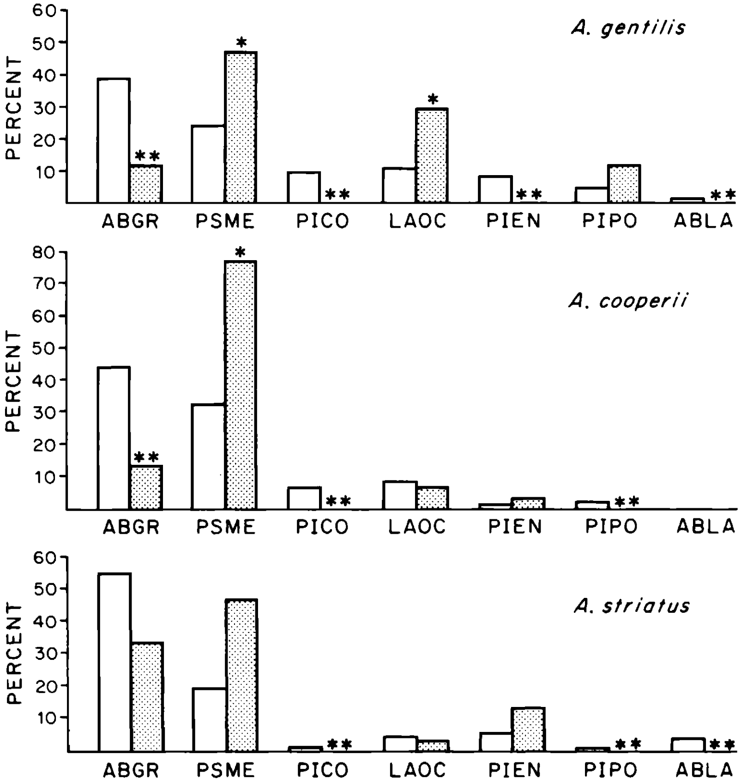

Figure 4. Stand composition and nest tree selection for three species of *Accipiters*. Open bars represent proportions of each tree species from the pooled species composition of nest sites. Shaded bars represent the proportion of each tree species used as nest trees. ** = significant avoidance using 90% confidence intervals; * significant selection; no asterisk indicates proportional use. (ABGR = grand fir, PSME = Douglas fir, PICO = lodgepole pine, LAOC = western larch, PIEN = Englemann spruce [*Picea engelmannii*], PIPO = ponderosa pine, ABLA = subalpine fir).

larger trees at a greater height, but below the canopy of the nest tree and with less canopy coverage over the nest. The higher degree of exposure and the greater accessability to *gentilis* nests was further illustrated by the use of dead trees for nesting (Table 3). Dead trees supporting occupied nests ranged from those still retaining needles to snags. Accipiters often use masses of mistletoe-affected growth as a nest substrate (Table 3). These tangles of foliage provide a sturdy and well-concealed nest substrate most often used by *cooperii* (64% of all nests). This preference may explain selection for Douglas fir as a nest tree since this tree is most commonly parasitized by mistletoe.

Nest exposure, in relation to tree bole, was examined to determine whether preferences existed for nest placement (Fig. 3). *Gentilis* preferred the southeast side of the tree (mean 148° ± 83°) for nest placement ($P < 0.02$). Both *cooperii* and *striatus* showed a random distribution of nest placement (*cooperii*, $P = 0.60$; *striatus*, $P = 0.60$). Concealment of nests and shading from sunlight may be more important for those two species than insolation effects. Distance from the nest tree to a permanent water source was significantly farther for *cooperii* (473 m ± 545) than for *gentilis* (199 m ± 239) or *striatus* (200 m ± 242) ($P < 0.02$).

Discussion

The importance of the vegetative structure at accipiter nest sites, as pointed out by several authors (Hennessy 1978, Reynolds et al, 1982), is confirmed by this study. The critical characteristics for nest sites of each species are structural features associated with the successional stage of nesting stands. Intraspecific similarities in structural features of nest sites indicate that some species-specific selection of nesting sites occurs on the basis of vegetative structure.

Perceptual responses to complex habitats by birds are not well known but habitat selection is probably not based on any single environmental cue. Selection may be released by gestalt perception of the environment rather than by a few proximate factors (Lack 1933). James (1971) felt that each species had a characteristic perception of vegetational requirements of its habitat, the niche-gestalt. This was supported by consistent occurrence of a species when certain structural features of the vegetation were present as we found.

The association with certain structural characteristics is apparent even when comparing nest sites of accipiters occurring in other regions. Titus and Mosher (1981) examined *cooperii* nests in the eastern deciduous forests. Vegetative structure there was similar to what we found. Nest heights and nest tree size were also similar. Nest sites of *gentilis* in the Adirondack Mountains of New York also appeared similar in structure to our findings, i.e., Allen (1978) reported nest sites with most of the basal area in larger size classes of trees.

While all three species seem to occupy a single macrohabitat, the vegetative structure associated with each successional stage creates one type of patchiness within the heterogeneous macrohabitat. Differential use of these patches occurs in selection of nest sites. Nests of congeners were sometimes found in close proximity to each other; thus, interspecific spacing of nest sites did not seem to occur. Nest site availability was not determined, but this factor would affect the role that competition plays in nest site selection. Possible interspecific competition for nest sites was observed once; the replacement of a *cooperii* pair by a *gentilis* pair at the same nest site the following year.

Conceivably *gentilis* could exclude the other two species through social dominance or predation; however, evidence indicates that the presence of *gentilis* may not be a factor in excluding *cooperii* and *striatus* from using older age stands for nest sites. Reynolds (1979) indicated that in northwest Oregon, where *gentilis* was not found, *cooperii* and *striatus* did not fully utilize the available sites with vegetative structure similar to those preferred by *gentilis*. The similarity of nest sites of these two species was still evident even in the absence of *gentilis*.

Sites chosen by *cooperii* and *striatus* may provide concealment from avian predators such as the Great Horned Owl (*Bubo virginianus*) or *gentilis*. Use of mistletoe growth for nest sites and placement of nests within the canopy support this idea. *Gentilis* may be able to protect the nest more easily from large avian predators because of its size. However, predation of nests of all three accipiters by Great Horned Owls was recorded.

Thermoregulation may also play a role in nest site selection. Considering placement of nests, those of *gentilis* probably received higher insolation, at least during the early hours of the day. This population generally begins incubation in April with brooding in May. Higher insolation of nests may help mitigate the effects of low temperatures during this period. Canopy coverage directly overhead (88%) would still provide shading during periods of higher temperatures. Nest placement for *striatus* and *cooperii* showed no preference for exposure. Both species had nests in strata with high crown volumes and higher mean canopy coverage. Thus, nest insolation may not be as important as nest concealment or shading during warm temperatures. Both species are migratory in our study area (unpublished band recovery data), and both begin incubation later than *gentilis*.

Nest site selection and nest placement may also be influenced by accessibility. An association between increasing body size and changes in the vegetative structure of nesting habitat is apparent. Spacing of stems and foliage at *gentilis* nest sites provide more open flight lanes. This factor may be important for adults as well as fledglings with inferior flight control. Several factors appear to be operating in the selection of nesting habitat including predation, morphological and physiological adaptations, prey availability (not assessed in this study), and to a lesser extent, social interaction with congeners.

A relatively recent factor which may have influenced the partitioning of nesting habitat, by limiting numbers of nest sites, is logging by man. Effects of logging are difficult to quantify, as reoccupancy of nest sites is not guaranteed even at undisturbed sites. If other suitable sites were available, logging may only cause a relocation of nest sites. However, if nesting sites are limited, logging could result in local reduction in the breeding population. The influence of logging may be especially critical for *gentilis* which is dependent upon older age stands. Logging may benefit populations of other avian predators such as the Red-tailed Hawk (*Buteo jamaicensis*) and Great Horned Owl (Franzeb 1977). Increased competition and predation upon accipiters could result. Logging may also alter the availability or vulnerability of certain prey species.

Acknowledgments

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BALD EAGLE NEST WATCHERS NEEDED

The U.S. forest Service needs volunteers for observation of nesting Bald Eagles in Central Arizona, February through May 1984. Duties involve collection of behavioral and habitat data and protection of nest sites. Back country travel and camping are required. Subsistence living quarters and reimbursement for field expenses are provided. Field experience is desirable. Anyone interested should contact Larry Forbis, Tonto National Forest, Box 29070, Phoenix, Arizona 85038 (602 261-4240), or Terry Grubb, Rocky Mountain Forest & Range Experiment Station, ASU Campus, Tempe, Arizona 85287 (602 261-4365).