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COMPARATIVE NEST SITE HABITATS IN SHARP-SHINNED AND COOPER'S HAWKS IN WISCONSIN

DALE R. TREXEL,[1] ROBERT N. ROSENFIELD,[2,5] JOHN BIELEFELDT[3], AND EUGENE A. JACOBS[4]

ABSTRACT.—From an analysis of nest site habitat data at 24 Sharp-shinned Hawk (*Accipiter striatus*) and 52 Cooper's Hawk (*A. cooperii*) nests in Wisconsin, we conclude that Cooper's Hawks tend to nest in stands with lower densities of taller and larger trees than do Sharp-shinned Hawks, and that Cooper's Hawks also tend to nest in sites with a greater proportion of hardwood cover than Sharp-shinned Hawks. Significant interspecific differences were found in combined habitat types (hardwoods, mixed conifer-hardwoods, and conifer plantations) for nest tree height and nest tree DBH (diameter at breast height); nest height; nest height relative to tree height; canopy height; canopy cover; tall shrub density; tree density; and mean DBH. Nest sites of the two species were similar in terms of understory canopy cover, ground cover, low shrub index, understory tree density, basal area, distance to nearest forest opening, and distance to water. We detected few significant intraspecific differences in nest site habitat, and these only in the Cooper's Hawk. *Received 23 Oct. 1997, accepted 4 Nov. 1998.*

Although the Sharp-shinned Hawk (*Accipiter striatus*) and the Cooper's Hawk (*A. cooperii*) breed sympatrically in many parts of the United States and southern Canada, their nest site habitats have been compared in only four published quantitative studies. These congeners are sometimes assumed to partition nesting habitat by way of interspecific competition and/or predation (Siders and Kennedy 1996). With one exception in Missouri (Wiggers and Kritz 1991), these studies were conducted in the western United States (Oregon: Reynolds et al. 1982, Moore and Henny 1983; New Mexico: Siders and Kennedy 1996).

Such geographically restricted results may be difficult to extrapolate to other areas of sympatry because of regional differences in vegetational composition and structure. Each of the previously published comparisons of these hawks' nest site habitats was derived from upland forests with relatively homogeneous vegetation, principally montane conifer forests in New Mexico and Oregon, and conifer plantations or oak-hickory forests in Missouri. Our study area (Fig. 1) was the state of Wisconsin (145,000 km^2). The ecologically diverse set of available woodland nesting habitats on this statewide scale includes boreal conifer forests (plus conifer swamps of boreal affinity over much of the state), conifer plantations, mixed conifer-hardwood forests, purely deciduous woodlands on upland and lowland sites, and highly fragmented or urban woodlands (Rosenfield et al. 1996) as well as extensive forests. For further details on Wisconsin forests see Curtis (1959).

Potentially conflicting results among past studies may also limit their utility in unstudied areas of sympatry. In New Mexico, for example, Siders and Kennedy (1996) found significant differences between Sharp-shinned Hawks and Cooper's Hawks in the majority of nest site variables tested, while in Oregon, both Reynolds and coworkers (1982) and Moore and Henny (1983) found few discernible differences in nest site characterisitics between these accipiters. Furthermore, Siders and Kennedy (1996) have suggested that interpretations of previous results may be hampered by small sample sizes, especially for Sharp-shinned Hawks ($n < 18$ nests in prior studies), and by possible biases in nest search methods or methods of selecting search areas.

We compare habitat at 24 Sharp-shinned Hawk nests and 52 Cooper's Hawk nests in Wisconsin, 1980–1994, all discovered by unbiased means. Previous comparative work on nest site habitats of these two hawks has emphasized interspecific differences within relatively uniform habitat types. We expand this

[1] Dept. of Ecology, Evolution, and Behavior, 100 Ecology Building, 1987 Upper Buford Circle, Univ. of Minnesota, St. Paul, MN 55108.

[2] Dept. of Biology, Univ. of Wisconsin, Stevens Point, WI 54481.

[3] Park Planning, Racine County Public Works Division, Sturtevant, WI 53177.

[4] Linwood Springs Research Station, 1601 Brown Deer Lane, Stevens Point, WI 54481.

[5] Corresponding author; E-mail: rrosenfi@uwsp.edu

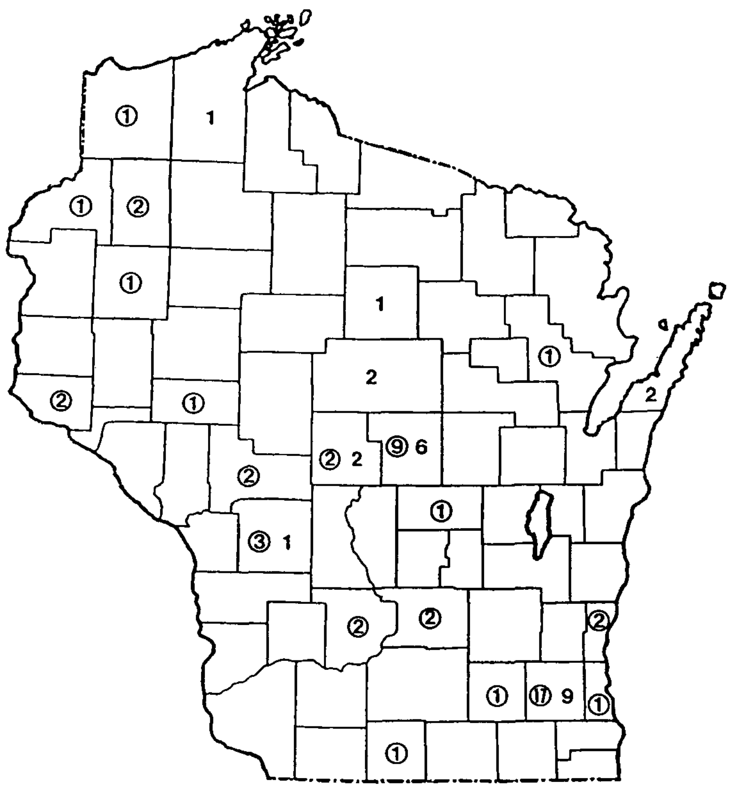

FIG. 1. Distribution by county of nest sites sampled for *Accipiter cooperii* (circled) and *A. striatus* (not circled) in Wisconsin.

emphasis to include intraspecific similarities as well as interspecific differences across habitat types (i.e., combined habitats) at a landscape scale. Intraspecific nest site features held in common across habitat types may aid land management agencies in assessing and conserving a range of usable breeding habitats for Sharp-shinned and Cooper's hawks. Our results seem timely and pertinent to the recent Birds in Forested Landscape project for North America (Cornell Lab of Ornithology), which focuses in part on the nesting habitats of these two hawks, and is designed to develop management and conservation strategies on their behalf (Anonymous 1997).

METHODS

Nest locations.—Nest site locations were considered unbiased if they were discovered by one of two methods: (1) incidental or random locations obtained by cooperators during any activity other than searching for accipiter nests, and (2) locations resulting from Cooper's Hawk density studies in which objectively drawn study areas were completely searched regardless of their perceived suitability for nesting and without foreknowledge of current or historical nest sites on these areas. By these methods, we located Cooper's Hawk nests in Wisconsin (see Fig. 1) on 52 widely separated, independent nesting areas, as defined in Rosenfield and Bielefeldt (1992, 1996). All 24 Sharp-shinned Hawk nests occurred in independent nesting areas; therefore each was included in our analyses.

Data collection and analyses.—Habitat measurements (Table 1) were made postfledging at each nest site within a 0.04 ha circular plot centered on the nest tree following the technique of James and Shugart (1970) as modified by Titus and Mosher (1981).

All variables were tested for normality with Lilliefors test; further statistical analyses were performed on SYSTAT (Wilkinson 1992). *t*-tests were used exclusively to examine interspecific differences among seven habitat varables that exhibited normal distributions in combined habitats (i.e., tree height, tree DBH, nest height, nest percent, canopy height, total canopy, and mean DBH; Table 2). We used the Mann-Whitney *U*-test for all other inferential comparisons because all other variables were not normally distributed.

To examine inter- and intraspecific differences and

TABLE 1. Habitat variables and measurement techniques at *Accipiter striatus* and *A. cooperii* nest sites in Wisconsin.

Variable	Description
Tree height	Height (m) of nest tree (Haga altimeter)
Tree DBH	Diameter (cm) at breast height of nest tree
Nest height	Height (m) of nest (meter tape or Haga altimeter)
Nest percent	(Nest height/Tree height) × 100
Canopy height	Mean height (m) of five canopy trees in study plot (Haga altimeter)
Total canopy	Percent of area over study plot occluded by overstory foliage[a]
Deciduous can.	Percent of area over plot (*not* of total canopy) occluded by deciduous overstory foliage[a]
Coniferous can.	Percent of area over plot occluded by evergreen overstory foliage[a]
Understory can.	Percent of area over plot occluded by understory foliage[a]
Ground cover	Percent of ground in plot covered by ground-layer foliage[a]
Shrub density	Index of tall shrubs < 3 cm DBH and ≥ shoulder height[b]
Shrub index	Index of low shrubs < 3 cm DBH between knee and shoulder height[b]
Tree density	Number of canopy trees ≥ 9 cm DBH per hectare
Under. dens.	Number of understory trees ≥ 9 cm DBH per hectare
Basal area	m^2/ ha of canopy trees
Mean DBH	Mean DBH (cm) of canopy trees in study plot
Dist. to water	Distance (m) to nearest permanent water source (pacing or USGS 7.5 min. quadrangles)
Dist. to open.	Distance (m) to nearest forest opening ≥ 5 ha (pacing or USGS 7.5 min. quadrangles)

[a] 40 ocular tube readings.
[b] Sum of four plot radii.

similarities among habitat types, we separated our nest site samples into three categories based on trees present within the 0.04 ha plot. We first divided nest site samples between those occurring within conifer plantations and those not in plantation habitats. (While deciduous trees occurred in some conifer plantations, no nest sites occurred in hardwood plantations.) We then divided non-plantation nest sites into those situated in pure hardwood stands (where no trees within the study plot were conifers) and those in mixed conifer-hardwood stands. In keeping with our statewide sample, these three habitat categories should be construed as physiognomic types that do not necessarily exhibit other internal similarities in vegetational attributes. In hardwood stands, for example, dominant or prominent tree species might include oaks (*Quercus* spp.), maples (*Acer* spp.), aspen (*Populus* spp.), and other species of varied ages, management histories, and moisture regimes. Mixed woodlands might include lowland conifers such as tamarack (*Larix larcina*) and black spruce (*Picea mariana*) or upland conifers such as pines (*Pinus* spp.) as well as deciduous species. For compositional variety among nest tree species (and scientific names) see Table 3.

Because there was only one pure hardwood site used by Sharp-shinned Hawks, we examined interspecific differences only within conifer plantations and mixed conifer-hardwood habitats. Likewise, we could only test for intraspecific differences between mixed and plantation habitats among Sharp-shinned Hawk nest sites. We used the nonparametric Kruskall-Wallis test to examine interspecific differences among the three habitat types used by Cooper's Hawks. Because of the number of multiple univariate comparisons (Table 2), we calculated that an alpha of 0.001 was the appropriate level of significance for both inter- and intraspecific inferences (Sokal and Rohlf 1981).

RESULTS

The majority of the 18 nest site variables compared for Sharp-shinned and Cooper's hawks in combined habitats showed statistically significant interspecific differences (Table 2). Nest tree DBH in conifer plantations, and nest height and canopy height in mixed conifer-hardwood stands were significantly different between species across uncombined habitat types (Table 2).

Of the 18 variables examined only four exhibited significant intraspecific differences across habitat types, and only in Cooper's Hawk (Table 2). Although intraspecific nest site selection itself might vary among habitats, we speculate that these statistical differences instead are attributable to inherent vegetational contrasts among habitat types as circumscribed here. In the most transparent example, cross-habitat intraspecific differences in percentages of coniferous and deciduous canopy covers at Cooper's Hawk nest sites in hardwood stands versus pine plantations (Table 2) are a predictable outcome of our habitat categories. The more interesting result of intra-

TABLE 2. Mean values of habitat variables measured at *Accipiter striatus* and *A. cooperii* nest sites in Wisconsin.

Variable	*A. striatus* (mean ± SE) Combined	Mixed	Plantation
	(n = 24)[a]	(n = 11)	(n = 12)
Tree height (m)	15.1 ± 0.6	14.8 ± 0.6	15.8 ± 1.0
Tree DBH (cm)	23.8 ± 1.4	26.2 ± 2.3	21.4 ± 1.6
Nest height (m)	9.1 ± 0.6[b]	7.9 ± 0.7[b]	10.4 ± 0.8
Nest percent (%)	59.7 ± 2.7[b]	54.1 ± 4.3[b]	65.5 ± 2.7
Canopy height (m)	15.2 ± 0.6	15.0 ± 0.6	15.8 ± 0.9
Total canopy (%)	76.5 ± 2.3	74.3 ± 2.5	80.4 ± 3.3
Deciduous can. (%)	15.2 ± 4.4	24.3 ± 7.7	3.8 ± 1.7
Coniferous can. (%)	61.3 ± 5.6	50.0 ± 8.1	76.7 ± 3.6
Understory can. (%)	32.7 ± 5.8	42.7 ± 8.7	19.8 ± 6.2
Ground cover (%)	39.0 ± 6.2	53.4 ± 8.0	22.9 ± 7.8
Shrub density	61.6 ± 9.3	73.4 ± 17.5	50.3 ± 9.2
Shrub index	90.3 ± 13.7	79.0 ± 18.4	98.1 ± 21.9
Tree density (trees/ha)	1071 ± 95[c]	914 ± 96	1037 ± 131[c]
Under. dens. (trees/ha)	334 ± 71[b]	375 ± 120[b]	231 ± 57
Basal area (m^2/ha)	28.9 ± 3.0[c]	22.7 ± 2.7	37.5 ± 3.9[c]
Mean DBH (cm)	17.6 ± 0.9[c]	16.9 ± 1.2	19.1 ± 1.3[c]
Dist. to water (m)	260 ± 71	88 ± 28	440 ± 120
Dist. to open. (m)	58.9 ± 16.2	72.7 ± 26.2	50.8 ± 21.8

* $P \leq 0.001$.
** $P \leq 0.0005$.
[a] Combined data for *A. striatus* includes one hardwood nest site in addition to mixed and plantation nest sites.
[b] Missing data at one nest site (n = 23 combined, n = 10 mixed).
[c] Missing data at one nest site (n = 23 combined, n = 11 plantation).

specific analyses may lie in the variables that did not differ significantly across habitats, such as nest tree height, nest height, canopy height, and mean tree DBH—each of which differed between species (see Discussion).

For combined habitats, Cooper's Hawks nested in a wider array of tree species than Sharp-shinned Hawks (Table 3). This variation however, occurred mostly within hardwood sites; within mixed stands and conifer plantations Sharp-shinned Hawks used a greater variety of tree species. Of the coniferous nest trees used by Cooper's Hawks (n = 29), only *Pinus* was represented in this sample, while Sharp-shinnned Hawks (n = 23) used five genera. With only one exception [a Cooper's Hawk nest in a white ash (*Fraxinus americana*)], both species consistently used conifers for nesting in mixed sites where both hardwoods and conifers were present in the canopy. For both species, nest trees in conifer plantations were all conifers, despite the presence of canopy-level hardwoods in 60% of Cooper's Hawk and 42% of Sharp-shinned Hawk plantation sites.

DISCUSSION

Our comparative analyses of nest site habitat at 52 Cooper's Hawk and 24 Sharp-shinned Hawk nests in Wisconsin did not provide data on nest site use relative to availability, and we cannot contend that numbers of nests in our three habitat categories are necessarily proportional to use of these habitat types. Nevertheless, our sample involves independent nests discovered by unbiased means on a statewide scale in compositionally diverse woodland habitats: upland and lowland sites; coniferous, hardwood, and mixed forests; urban and rural woodlands of varied sizes; and both managed and unmanaged forests including conifer plantations. Thus we suggest that our data set provides a reasonably thorough and representative sample of the range of nest site habitats used by these hawks in Wisconsin.

If interspecific differences in nest site characteristics of these congeners occur on a finer within-habitat scale, as some prior work has indicated (Siders and Kennedy 1996), then

TABLE 2. Extended.

A. cooperii (mean ± SE)				Interspecific differences			Intraspecific differences	
Combined	Hardwood	Mixed	Plantation	Combined	Mixed	Plantation	*A. striatus*	*A. cooperii*
(n = 52)	(n = 22)	(n = 10)	(n = 20)					
19.1 ± 0.6	20.5 ± 1.0	17.5 ± 0.8	18.1 ± 0.8	**				
32.6 ± 1.2	36.2 ± 1.6	29.7 ± 3.1	30.0 ± 1.6	**		*		
13.1 ± 0.4	13.3 ± 0.7	13.2 ± 0.7	12.9 ± 0.5	**	*			
69.8 ± 1.4	66.1 ± 2.9	75.0 ± 1.9	72.3 ± 2.1	*				
19.5 ± 0.5	20.9 ± 0.9	18.6 ± 0.6	18.3 ± 0.7	**	*			
84.9 ± 1.3	86.3 ± 2.1	79.3 ± 3.4	86.3 ± 1.8	*				
54.9 ± 4.8	86.1 ± 2.1	46.3 ± 7.3	24.8 ± 5.9	**				**
30.0 ± 4.5	0.1 ± 0.1	33.0 ± 6.2	61.5 ± 5.5	**				**
37.8 ± 3.6	48.8 ± 5.1	30.3 ± 6.0	29.5 ± 6.1					
47.8 ± 3.0	53.6 ± 4.2	54.5 ± 5.7	38.1 ± 5.2					
30.0 ± 4.4	26.2 ± 5.4	38.6 ± 15.8	29.9 ± 6.4	*				
71.5 ± 8.4	65.5 ± 10.7	60.0 ± 15.2	84.0 ± 16.8					
623 ± 48	438 ± 38	623 ± 103	826 ± 87	**				*
307 ± 28	340 ± 40	383 ± 68	233 ± 44					
31.6 ± 2.8	27.4 ± 3.4	24.0 ± 2.0	39.9 ± 5.8					*
25.6 ± 0.9	27.4 ± 1.5	22.4 ± 1.7	25.2 ± 1.4	**				
320 ± 56	412 ± 87	277 ± 111	468 ± 115					
56.7 ± 8.6	86.8 ±17.4	33.9 ± 9.6	39.1 ± 7.3					

differences might also exist on a coarser scale among more broadly defined and heterogeneous habitat types. Such differences might furthermore emerge on a landscape scale among woodland habitats in general.

The variables we measured are not independent indicators of interspecific differences in nest site habitat; many of them seem to be related to stand age or successional stage. Tree age was not measured in this study, but it appears that Cooper's Hawks tended to use older stands with a lower density of taller and larger trees. Sharp-shinned Hawks, on the other hand, tended to use younger stands with a higher density of smaller, shorter trees. Reynolds and coworkers (1982) and Moore and Henny (1983) also have suggested that differences in accipiter nest site habitat are correlated with stand age or successional stage, with Cooper's Hawks using older stands than Sharp-shinned Hawks.

Interspecific differences in combined habitats seldom seem the result of contrasting proportions of habitats used on the intraspecific level. The lower percent coniferous canopy in combined Cooper's Hawk habitats versus Sharp-shinned Hawk habitats (30% vs 61%, $P < 0.0005$; Table 2) appears to be the result of the disproportionate number of Cooper's Hawk sites in hardwoods (42% of 52 nests) compared to the one Sharp-shinned Hawk at a hardwood site (4% of 24 nests). The difference in deciduous canopy cover between Cooper's Hawks versus Sharp-shinned Hawks in combined habitats (55% vs 15%, $P < 0.0005$; Table 2) also seems to be a result of contrasting proportions of habitat use.

In addition to having proportionally more nests in hardwood stands, Cooper's Hawks nested in conifer plantations that had substantially greater deciduous canopies than those used by Sharp-shinned Hawks (25% vs 4%; Table 2). In mixed conifer-hardwood habitats the deciduous canopy cover percentage again was greater for Cooper's Hawks than for Sharp-shinned Hawks (46% vs 24%; Table 2). Although neither of these within-habitat differences was statistically significant, they are clearly consistent with a significant difference in deciduous canopy in combined habitats. On a landscape-scale continuum from Wisconsin's northern coniferous forests (plus conifer plantations) to mixed and southern deciduous woodlands (see Curtis 1959), nest habitat thus appears to be comprised more of deciduous sites or elements for the Cooper's Hawk and coniferous elements for the Sharp-shinned Hawk, albeit with considerable overlap in

TABLE 3. Nest tree species used by *Accipiter striatus* and *A. cooperii* in Wisconsin.

Tree species	*A. striatus*				*A. cooperii*			
	Hardwood	Mixed	Plantation	Total	Hardwood	Mixed	Plantation	Total
Red Oak *Quercus rubra*					7			7 (13%)
Black/Hill's Oak *Q. velutina/ellipsoidalis*	1			1 (4%)	5			5 (10%)
White Oak *Q. alba*					1			1 (2%)
Red Maple *Acer rubrum*					2			2 (4%)
Sugar Maple *A. saccharum*					2			2 (4%)
Basswood *Tilia americana*					1			1 (2%)
Paper/White Birch *Betula papyrifera*					1			1 (2%)
American Elm *Ulmus americana*					1			1 (2%)
Big Tooth Aspen *Populus grandidentata*					1			1 (2%)
White Ash *Fraxinus americana*						1		1 (2%)
White Pine *Pinus strobus*		2		2 (8%)		6	16	22 (42%)
Jack Pine *Pinus banksiana*		1	3	4 (17%)		3	1	4 (8%)
Red Pine *Pinus resinosa*			3	3 (13%)			2	2 (4%)
Scotch Pine *Pinus sylvestris*			1	1 (4%)			1	1 (2%)
Norway Spruce *Picea abies*			4	4 (17%)				
Black Spruce *P. mariana*		1	1	2 (8%)				
Balsam Fir *Abies balsamea*		3		3 (13%)				
White Cedar *Thuja occidentalis*		2		2 (8%)				
Tamarack *Larix laricina*		2		2 (8%)				
Snag					1			1 (2%)
Total	1 (4%)	11 (46%)	12 (50%)	24	22 (42%)	10 (19%)	20 (38%)	52

mixed forests. This divergence seems unapparent in western montane environments (Reynolds 1983, Fischer 1986).

Siders and Kennedy (1996) also found that Cooper's Hawks used significantly taller nest trees with greater diameters and nest sites with lower tree densities than did Sharp-shinned Hawks. However, they reported that Sharp-shinned Hawk nest sites had significantly higher basal areas and canopy closures than did those of Cooper's Hawks. Reynolds and coworkers (1982) found, as we did that Cooper's Hawks had greater nest heights in eastern Oregon, and used habitats at lower tree densities in northwestern Oregon than did Sharp-shinned Hawks. As did Siders and Kennedy (1996), they found that Sharp-shinned Hawk nest sites had greater canopy closure than those of Cooper's Hawks. Moore and Henny (1983) noted that Cooper's Hawk nests were significantly higher than those of Sharp-shinned Hawks, but again in contrast to our results they found that Sharp-shinned Hawk nest sites had significantly higher canopy closure than sites used by Cooper's Hawks.

It seems that significantly higher tree densities at Sharp-shinned Hawk nest sites would usually lead to significantly greater canopy closure, as reported for mostly coniferous habitats in New Mexico and Oregon, but this was not the case for combined habitats in Wisconsin. Our results show lesser canopy closure in association with greater tree densities at nest sites of Sharp-shinned versus Cooper's hawks (Table 2). This seeming contradiction is probably the result of disproportional use of broadleaved hardwood forests (vs needle-leaved conifer forests) by Cooper's Hawks and consequent effects of leaf surface on measures of canopy closure. Overstory canopy measures might also be influenced by lower foliage densities (e.g., tamarack) or strongly conical growth forms (e.g., black spruce) in some nest tree species used by Sharp-shinned Hawks (Table 3).

In Missouri, Wiggers and Kritz (1991) used the most similar set of habitat measures and techniques for analyzing those measures, yet they reported no significant differences in nest site characteristics for these two accipiters. However, they divided their nest sites into habitat types differently than we did and were able to make interspecific comparisons only for pine dominated habitat ("> 50% of overstory trees were pines"). Still, with small data sets (Table 2) and the same alpha level (0.001) we detected significant differences in nest height and average canopy height for nest sites in mixed conifer-hardwoods, and in nest tree DBH in conifer plantations. Wiggers and Kritz (1991) reported significant intraspecific differences between pine habitat and hardwood habitat for Cooper's Hawks; had they combined these habitats they might have found overall interspecific differences as we did. Their ability to detect significant differences may also have been hampered by the fact that 87% of their nests were located by searching habitat (especially coniferous habitat) that was assumed *a priori* to be suitable for one or both species (Siders and Kennedy 1996). Consequently, 92% of nests in conifers (n = 50) and 77% of all nests (n = 60) were situated in pine plantations of similar age and vegetational structure.

In Wisconsin there appear to be numerous interspecific differences in nest site habitats of Cooper's and Sharp-shinned hawks. Such interspecific differences, within and across divergent habitat types, may provide guidance in identifying and managing the respective nesting habitats of these birds, one or both of which have been listed as species of conservation concern in several midwestern states (Rosenfield et al. 1991, Rosenfield and Bielefeldt 1993). Many of the nest tree and nest site variables differing significantly between species (tree heights, densities, diameters, and coniferous components) are routinely and easily estimated measures of woodland habitats among resource managers.

Intraspecific analyses of nest site variables across habitat types may also be useful to management and conservation. Significant intraspecific differences among habitats in the Cooper's Hawk would seem to portray the breadth of acceptable nesting habitat(s). Variables that do not differ intraspecifically across habitat types (e.g., nest tree height or mean DBH of nest site trees) may serve as focal points for managers in identifying potentially usable nesting habitats, whether or not these features actually provide proximate cues to nest site use for the birds themselves.

We examined habitat characteristics only at the nest tree level and in a small area (0.04

ha) immediately surrounding the nest. We did not deal with other habitats used by these accipiters such as hunting areas or non-breeding habitats. Recent studies of nest site habitat in the Cooper's Hawk in North Dakota (M. Nenneman, pers. comm.) suggest that existing analyses of breeding habitats from disparate areas and woodland types may not be generalizable to other regions. Management implications drawn from our Wisconsin data should therefore be cautious.

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