The Condor 110(2):260–268

SPATIAL ECOLOGY OF WINTING *ACCIPITER* HAWKS: HOME RANGE, HABITAT USE, AND THE INFLUENCE OF BIRD FEEDERS

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Abstract. Despite their likely ecological importance, the basic biology of Cooper's (*Accipiter cooperii*) and Sharp-shinned (*A. striatus*) Hawks remains poorly understood. This is particularly true during the winter, when even basic information on the spatial ecology of these species is largely unknown. Thus, we characterized the home range size and habitat chosen by these species as part of a larger study on wintering *Accipiter* hawks. We also compared our findings of bird feeder use by Cooper's Hawks to our previously published study on Sharp-shinned Hawks. During the winters of 1999–2004, we intensively radio-tracked 21 Sharp-shinned Hawks and six Cooper's Hawks in rural areas, and eight Cooper's Hawks in urban areas. We found that Sharp-shinned Hawks and Cooper's Hawks in rural areas used significantly larger areas than did Cooper's Hawks in urban areas, and that adult hawks generally used smaller areas than immature individuals. Habitat use by Cooper's Hawks and Sharp-shinned Hawks in rural areas was nearly identical and focused mostly on forested and grass habitat types. Cooper's Hawks in urban areas focused disproportionately on grassy areas such as parks in addition to residential areas. All hawks avoided very open areas such as fallow agricultural fields. We observed no systematic use of bird feeders by Cooper's Hawks. In fact, visits by Cooper's Hawks to feeders were not statistically different from that expected by a null model based on random feeder visitations, a result consistent with our work on Sharp-shinned Hawks and the idea of "prey management" by *Accipiter* hawks.

Key words: bird feeders, Cooper's Hawks, home range, predator-prey interactions, radio-tracking, raptors, Sharp-shinned Hawks.

Ecología Espacial de los Halcones *Accipiter* Durante el Invierno: Ámbito de Hogar, Uso de Hábitat e Influencia de los Comederos de Aves

Resumen. La biología básica de los halcones *Accipiter cooperii* y *A. striatus* permanece aún escasamente conocida, a pesar de su probable importancia ecológica. Ésta es especialmente desconocida durante el invierno, cuando inclusive información tan básica como la ecología espacial de estas especies no se conoce en gran medida. Por esta razón, caracterizamos el tamaño del ámbito de hogar y el tipo de hábitat escogido por estas especies como parte de un estudio mayor sobre halcones del género *Accipiter* durante el invierno. También comparamos nuestros resultados sobre el uso de comederos de aves por parte de *A. cooperii* con nuestro estudio publicado anteriormente sobre *A. striatus*. Durante los inviernos de 1999 a 2004, utilizando radio-telemetría seguimos intensamente a 21 individuos de *A. striatus* y 6 de *A. cooperii* en áreas rurales y 8 individuos de *A. cooperii* en áreas urbanas. Encontramos que *A. striatus* y *A. cooperii* utilizaron áreas significativamente mayores que *A. cooperii* en las áreas urbanas, y que los individuos adultos utilizaron generalmente áreas de menor tamaño que los individuos inmaduros. El uso de hábitat por *A. striatus* y *A. cooperii* en áreas rurales fue casi idéntico, concentrándose en los tipos de hábitat de bosque y pastizal. En las áreas urbanas, *A. cooperii* se concentró desproporcionadamente en las áreas con césped como parques o áreas residenciales. Todos los halcones evitaron áreas muy abiertas, como campos agrícolas no plantados. No observamos un uso sistemático de los comederos por parte de *A. cooperii*. De hecho, las visitas de *A. cooperii* a los comederos no fueron estadísticamente diferentes de lo esperado por un modelo nulo basado en visitas al azar a los comederos. Este resultado es consistente con nuestro trabajo sobre *A. striatus* y con la idea de "manejo de presas" por parte de los halcones del género *Accipiter*.

INTRODUCTION

Cooper's (*Accipiter cooperii*) and Sharp-shinned (*A. striatus*) Hawks are key avian predators in the North American landscape. As two of the primary predators of small birds, these hawks play an important role in many studies of behavioral ecology (Lima 2002). In addition, they are considered to be threatened or species of special concern in many areas (Rosenfield and Bielefeldt 1993, Bildstein and Meyer 2000). However, despite their ecological importance and conservation status, we still know relatively little about these species.

Manuscript received 24 September 2007; accepted 6 June 2008.

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The Condor, Vol. 110, Number 2, pages 260–268. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2008.8489

Our understanding of basic *Accipiter* biology has, however, increased considerably in recent years, with several studies having focused on the long-term breeding success and population trends of these hawks. For example, work in Wisconsin (Rosenfield et al. 1995, 2000, Rosenfield and Bielefeldt 1999), Arizona (Boal 1997, Boal et al. 1998, Boal and Mannan 1999, Mannan et al. 2004), and elsewhere in North America (Reynolds and Meslow 1984, Kennedy and Johnson 1986) has added much to our understanding of reproduction, migration, and diet of Cooper's Hawks during the breeding season. In addition, many behaviorally oriented studies in Europe have focused on the Sparrowhawk (*A. nisus*), both during the breeding (Newton 1986), but particularly during the nonbreeding, season (Cresswell 1994, 1996, Whitfield et al. 1999, Cresswell et al. 2003, Cresswell and Quinn 2004, Quinn and Cresswell 2004). In accordance with these behavioral studies, we have recently examined several behavioral aspects of wintering Cooper's and Sharp-shinned Hawks, including diet (Roth and Lima 2003, 2006, Roth et al. 2006), predatory behavior (Roth and Lima 2003, 2007a, 2007b, Roth et al. 2006), and survival (Roth et al. 2005). However, there is still little general information on the spatial ecology of these species, especially during the winter.

One component of the spatial ecology of wintering *Accipiter* hawks that has received some attention is the use of bird feeders. Both Cooper's and Sharp-shinned Hawks are thought to focus their hunting around feeders (Dunn and Tessaglia 1994), giving a new connotation to the term "bird feeder." It has been hypothesized that the increase in feeders in the northeastern United States may partially be responsible for the observed decrease in migration counts of these species at banding stations farther south (Viverette et al. 1996). The apparent importance of feeders, however, may reflect the fact that humans are most likely to see these hawks at bird feeders. In a previous study (Roth and Lima 2007a), we found that Sharp-shinned Hawks did not hunt at bird feeders more often than what would be expected by a random null model, possibly the consequence of hunting behaviorally responsive prey. However, similar analyses of Cooper's Hawk behavior have not yet been published.

Here, we further characterize the spatial ecology of wintering Sharp-shinned and Cooper's Hawks to expand upon our previous work with these hawks. We report the home range size and habitat use of these species, which have not yet been examined during the winter. In addition, we examined the use of bird feeders by Cooper's Hawks, for comparison with our previous work on Sharp-shinned Hawks.

METHODS

STUDY SITE

Our study site comprised Vigo County, Indiana, and adjacent Clark County, Illinois, and contained both rural and urban areas. The urban area was centered on the city of Terre Haute, Indiana (population ~60 000), and covered approximately 100 km^2. The composition of the urban study site was approximately 30% high-density residential and commercial (>14 buildings per block) and 70% low-density residential areas (<14 buildings per block; Topologically Integrated Geographic Encoding and Referencing data, U.S. Census Bureau, Geography Division, data for the year 2000). Here, we focused on Cooper's Hawks during the winters (late November through early March) of 1999–2001, although an additional Cooper's Hawk was followed in the city during the 2003–2004 season. While we attempted to study Sharp-shinned Hawks in the urban area, very few were seen there and none were captured.

The rural area of our study site was immediately to the southwest of the urban site. This landscape consisted of residential clusters, agricultural land, and fragmented forest. The rural area covered approximately 1000 km^2, although most hawks were radio-tracked in a core area of about 100 km^2. Here, we focused mainly on Sharp-shinned Hawks during the winters (late November through early March) of 2001–2004, but we also radio-tracked a smaller number of Cooper's Hawks during the winters of 1999–2004.

CAPTURE AND RADIO-TRACKING

Trapping was conducted from late November to late January in all years (1999–2004). Constantly monitored bal-chatri traps (Berger and Mueller 1959) and bow nets were baited with European Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*; Roth and Lima 2003). Traps were positioned in potential roost locations as well as in high-visibility areas such as fields, roadsides, and power line corridors in the rural site, and parking lots, cemeteries, and recreational parks in the city.

All hawks were observed using radio-telemetry. Upon capture, hawks were fitted with aluminum U.S. Fish and Wildlife Service bands and appropriately sized position-sensitive transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) using the pelvic harness of Rappole and Tipton (1994), modified by Roth and Lima (2003). Transmitters and harnesses were usually <2% and always <3% of the total body mass of the hawk. Hawks were radio-tracked daily for at least 2 hr (but frequently for up to 10 hr) using vehicles and yagi antennae. Due to the frequent vehicular traffic associated with the moderate to intense level of human activity throughout the study site, it is unlikely that the presence of our vehicles disturbed the hawks.

One of the main goals of our radio-tracking was to observe hawk behavior, so we attempted to maintain visual contact with the hawks as much as possible. As such, we recorded the locations of hawks in 10 min intervals, thus creating a standardized time between observations ("step distances"; Turchin 1998). This data collection technique gave us an accurate view of spatial use (Kenward 1997, De Solla et al. 1999) that was not biased due to detectability. Repeated observations of an individual may raise the level of pseudoreplication of points (Swihart and Slade 1985); however, all

of our analyses are based on the statistical unit of the individual hawk, thus alleviating the problems with point pseudoreplication. Our spatial resolution (when hawks were not in view), based on the calculation of tracking and mapping errors (White and Garrott 1990), was 50 m (TCR, unpubl. data).

SPATIAL ANALYSES

Home range estimates. We used ArcView 3.2 and the Animal Movements extension (Hooge and Eichenlaub 1997) to calculate 95% least squares cross-validated kernel home range estimates (Worton 1989). These estimates were log transformed and analyzed with a general linear model to determine the effect of statistical group (see below), age, and sex on home range size. Fisher's LSD post-hoc tests were used to distinguish significance between the different groups. Since there were very few Sharp-shinned Hawks in our urban study area (Roth et al. 2005), we could not run a full model of species and habitat preferences; instead, we compared statistical groups as Sharp-shinned Hawks, Cooper's Hawks observed predominantly in the rural study area (hereafter, rural Cooper's Hawks), and Cooper's Hawks observed predominantly in the urban area (hereafter, urban Cooper's Hawks). The number of days that hawks were radio-tracked was used as a covariate, although only hawks followed for >27 days were included in this analysis. Although migratory status (migratory or resident) may influence spatial use, we were unable to examine this factor in Cooper's Hawks, since we could determine the status of only seven of the 14 hawks fitted with transmitters (two migratory, five resident; Roth et al. 2005). All of the Sharp-shinned Hawks in our study were migratory as they do not breed in our study area (Bildstein and Meyer 2000), hence no resident vs. migrant comparison could be made.

Habitat analysis. Basic habitat use was determined by the overlap of points at which hawks were observed ("hawk points") with five habitat categorizations based on vegetation cover from the Indiana Gap Analysis Program as derived from Landsat images. We use the term 'habitat' as a broad categorization of many possible vegetation types that are generally found in a particular area. Habitat was classified as: 1) residential: houses, industry, and other developed areas; 2) forest: trees with a closed canopy; 3) grass: pasture and fallow fields; 4) agriculture: bare earth or agricultural field >50 m from a transition with another habitat type; and 5) edge: a 50 m border around an agricultural field. We included agricultural edge as a distinct category because it is an abundant and distinct habitat type consisting of transitional grasses and thickets that is frequently used by species taken as prey by *Accipiter* hawks (Roth et al. 2006). Other transition zones (e.g., forest to grass) are far less abundant and not commonly used by the prey of *Accipiter* hawks.

We compared the percentage of observed hawk points in each habitat type with the percentage of available habitat using a compositional analysis (Aebischer et al. 1993). To assess broad habitat preferences at a landscape scale, we used the entire study site as our area of interest to calculate available habitat. Since urban Cooper's Hawks had already chosen urban habitat (by definition), we also performed this analysis at a smaller scale (within the city of Terre Haute, Indiana) for these hawks. In both cases, the study site for comparison was arbitrarily designated as a square that enclosed all hawk points and 97% of urban hawks, respectively. The focal square for the entire study site contained all hawk home ranges and covered an area roughly the size of Vigo County (approximately 1300 km^2), while the focal square for the urban area covered most of the city of Terre Haute and its southern suburbs (approximately 120 km^2). The hawks' positions and the percentage of available habitat were determined using ArcView 3.2. The compositional analysis was performed using the 'adehabitat' package (Calenge 2006, 2008) for R (R Development Core Team 2008).

Bird feeder use. We used only stable, long-term feeders (active over an entire winter season) in our analysis determining the level of hawk activity at bird feeders in both the rural and urban areas. We documented feeders during our observations of hawks. We compared observed feeder use to that of randomized feeder locations using ArcView GIS software as per methods in Roth and Lima (2007a). This method involved creating buffers of 300 m radius around each feeder location. Given our spatial resolution, 300 m buffers were large enough to detect shifts in hawk location, yet small enough to see detailed changes in spatial use. In addition, as hawks can take prey in transit to feeders, we chose the size of the buffer as a representation of the "area of influence" around a feeder, rather than focusing on the point location of the feeder itself (Roth and Lima 2007a). The results were the same if we used a 100 m buffer.

For each individual hawk, we used the number of hawk points that overlapped the 300 m feeder buffers as a measure of feeder visitation. We compared this observed overlap to the overlap of the same hawk points with the same number of feeders when feeders were randomly repositioned (using ArcView) within the 95% kernel home range; these randomizations were repeated 100 times for each hawk to estimate a *P*-value using a two-tailed design and significance determined using a Bonferroni-adjusted $\alpha = 0.005$. For this analysis we pooled urban and rural Cooper's Hawks, as the distributions of their feeder use values overlapped almost entirely. We also used a Pearson correlation to determine the relationship between the number of feeders within a home range and home range size.

Prey density. Home range size can be highly influenced by the density and distribution of resources available (McNab 1963, Jetz et al. 2004). To address the issue of resource density, we used data collected from point count surveys to estimate the density of prey species in both rural and urban habitats. Eight urban sites were sampled three times weekly during the

winter of 2004–2005 and 45 rural points were sampled weekly (Roth et al. 2006, Roth and Lima 2007b) during the winters of 2002–2004. At each point count site, we conducted 5 min unlimited-distance counts of all birds (Bibby et al. 1992). We limited our analysis to species that would reasonably be potential prey for Sharp-shinned or Cooper's Hawks (Roth and Lima 2003, 2006, Roth et al. 2006). The species included in the analysis covered a broad range of body sizes, from the smallest species noted in our counts, the Carolina Chickadee (*Poecile carolinensis*; 10 g), to species over 150 g (e.g., the Northern Flicker [*Colaptes auratus*]). We excluded species that were unlikely to ever be *Accipiter* prey, such as the American Crow (*Corvus brachyrhynchos*), Pileated Woodpecker (*Dryocopus pileatus*), and Canada Goose (*Branta canadensis*). To reduce the possibility of overrepresenting large or conspicuous species in our analysis, we only included observations within 100 m of the observer (Roth et al. 2006). The mean sum of prey birds observed at each point count was used in our analyses, and we present prey density as mean ± SE.

RESULTS

Over five winter seasons, 40 Sharp-shinned Hawks (all rural), 14 rural Cooper's Hawks, and 13 urban Cooper's Hawks were captured. Of these, 21 Sharp-shinned Hawks (nine male, 12 female; 13 immature, eight adult), six rural Cooper's Hawks (five male, one female; four immature, two adult) and eight urban Cooper's Hawks (one male, seven female; four immature, four adult) were tracked for >27 days and thus included in the analyses, with the exception of one particularly wide-ranging immature Sharp-shinned Hawk that was removed from the home range analysis as an outlier (studentized residual = –3.003).

HOME RANGE ESTIMATES

Age and statistical group (Sharp-shinned Hawks, rural Cooper's Hawks, or urban Cooper's Hawks) had significant effects on home range size (Fig. 1, Table 1). Immature hawks had significantly larger 95% kernel estimates than adult hawks within

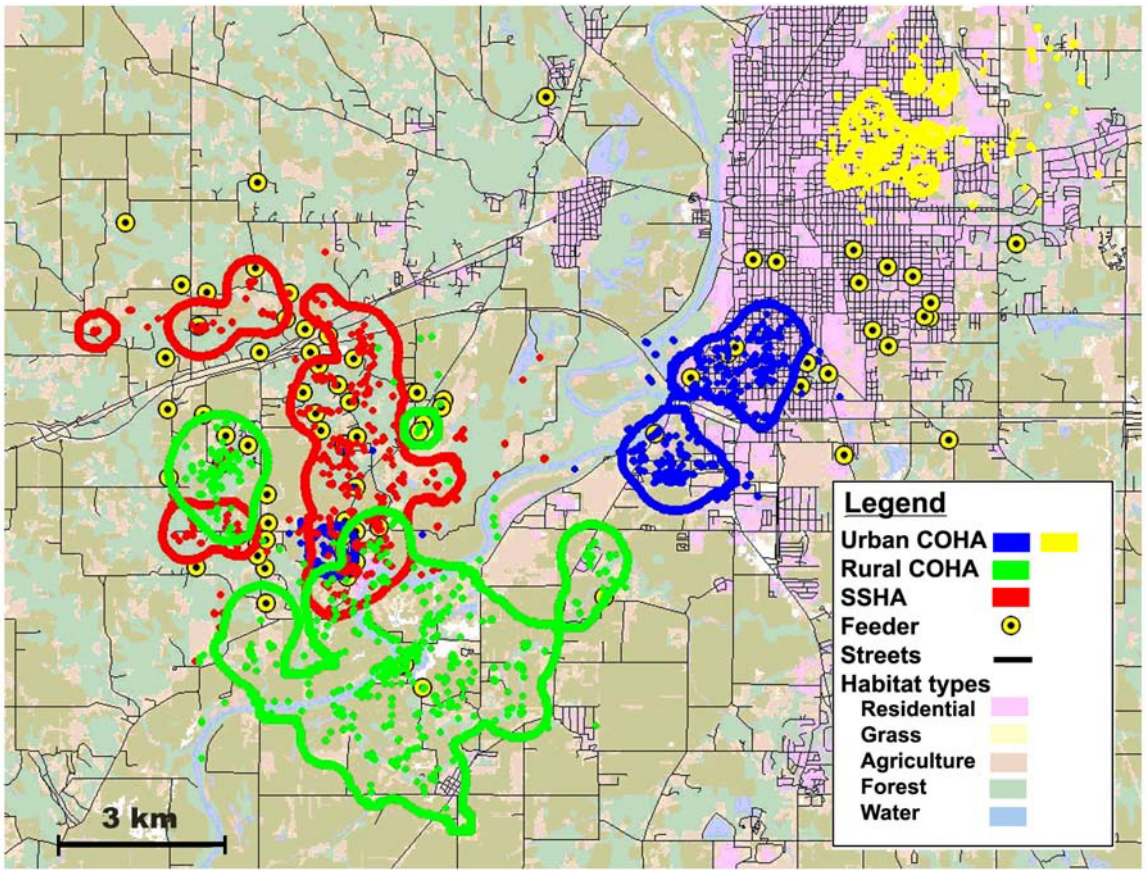

FIGURE 1. Representative examples of home range size, habitat use, and bird feeder use for wintering *Accipiter* hawks radio-tracked during 1999–2004. Two hawks that inhabited rural areas (Sharp-shinned Hawk: red [home range = 14.1 km^2]; Cooper's Hawk: green [home range = 24.6 km^2]) and two hawks using urban areas (both Cooper's Hawks: blue and yellow [home ranges = 6.4 and 2.0 km^2, respectively]) are represented both with and without several feeders in the home range. COHA = Cooper's Hawk; SSHA = Sharp-shinned Hawk.

TABLE 1. General linear model ($r^2 = 0.40$) of the effect of age, sex, group (Sharp-shinned Hawk, rural or urban Cooper's Hawk), and days radio-tracked on the 95% kernel estimates of home range size of wintering *Accipiter* hawks ($n = 34$) in west-central Indiana from 1999 to 2004. SS = sums of squares, df = degrees of freedom, and MS = mean square.

	SS	df	MS	*F*	*P*
Age	8.5	1	8.5	9.3	0.005
Sex	1.0	1	1.0	1.0	0.32
Group	7.0	2	3.5	3.8	0.03
Days radio-tracked	0.4	1	0.4	0.4	0.53
Error	25.7	28	0.9		

TABLE 2. Mean 95% kernel home range size (km^2) and standard error of adult and immature wintering *Accipiter* hawks in west-central Indiana.

	Adult home range ± SE (*n*)	Immature home range ± SE (*n*)
Sharp-shinned Hawk	12.8 ± 4.6 (8)	33.0 ± 11.5 (13)
Cooper's Hawk (urban)	3.9 ± 1.6 (4)	10.1 ± 2.9 (4)
Cooper's Hawk (rural)	14.2 ± 0.9 (2)	14.9 ± 4.1 (4)

the context of the model ($P = 0.005$; Table 2), although this difference was driven by Sharp-shinned and urban Cooper's Hawks (Table 2). Similarly, within the context of the full model, there was a significant difference in home range size among groups ($P = 0.03$). Fisher's LSD post-hoc tests showed a significant difference between urban Cooper's and Sharp-shinned Hawks ($P = 0.01$) and a nearly significant difference between urban and rural Cooper's Hawks ($P = 0.06$). There was no significant difference in home range size between rural Cooper's Hawks and Sharp-shinned Hawks ($P = 0.87$). Sex and the number of days radio-tracked did not significantly affect home range size (Table 1).

HABITAT ANALYSIS

Habitat use by all hawk groups as determined with compositional analysis was significantly different from habitat available (Sharp-shinned Hawks: $\lambda_4 = 0.2$, $P < 0.001$; rural Cooper's Hawks: $\lambda_4 = 0.2$, $P = 0.02$; urban Cooper's Hawks: $\lambda_4 = 0.1$, $P = 0.003$). In general, habitat use by rural Cooper's Hawks and Sharp-shinned Hawks was virtually identical. Sharp-shinned Hawks preferred (in descending order) forests, grass, residential areas, and edge to agricultural fields, and rural Cooper's hawks preferred (in descending order) forests, grass, edge, and residential areas to agricultural fields (Table 3). These two groups differed from urban Cooper's Hawks in one key way: both Sharp-shinned Hawks and rural Cooper's Hawks tended to focus on forested areas, while their urban counterparts did not (Fig. 2).

Urban Cooper's hawks preferred (in descending order) residential areas, grass, forest, and edge to agricultural fields in both scales of analysis (Table 3). Urban Cooper's hawks used forested habitat less often than expected, focusing instead on residential habitat. Urban hawks spent on average 26% of their time in open areas such as parks, compared to 18% and 19% for Sharp-shinned Hawks and rural Cooper's Hawks, respectively. In all other respects, urban and rural hawks were similar in habitat use. All groups used similar amounts of edge habitat, and all hawks shared a nearly equal avoidance of bare agricultural fields (Fig. 2). In fact, all hawk groups used bare fields significantly less often than expected based on their availability (Fig. 2), and, on average, <5% of hawk points fell within the bare field habitat. This low value is probably an overestimate, since our habitat maps (based on 30 × 30 m pixels) often could not resolve fences or hedge rows within the agricultural fields; hawks occasionally hunted along such hedgerows, and the resulting points were assigned to the agricultural field habitat.

BIRD FEEDER USE

Bird feeders were not major focal points of hunting activity for Cooper's Hawks. We documented 78 long-term feeders in the study site (including both urban and rural areas; Fig. 1), of which 58 were known to occur for more than one season. Cooper's Hawks (combining both urban and rural) did not hunt around feeders more often than expected under our random null model ($z = -1.3$, $P = 0.18$). This result held for individual

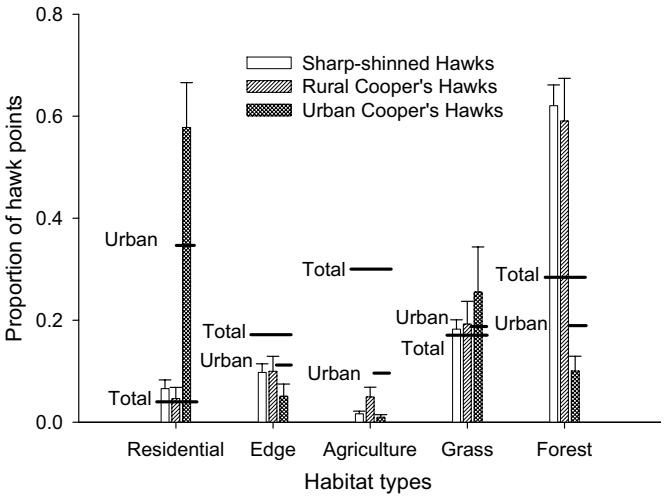

FIGURE 2. Habitat use by wintering Sharp-shinned ($n = 21$) and Cooper's Hawks ($n = 14$). All hawks avoided agricultural areas, focusing on more complex habitat. Bars represent the mean ± SE value of the proportion of hawk points within each habitat type (hawks treated as individual data points). Horizontal lines represent the proportion of each habitat type available in the entire study site (Total) and urban site alone (Urban; for Cooper's Hawks in this habitat only).

TABLE 3. Habitat ranking profile of Sharp-shinned and Cooper's Hawks during the winters of 1999–2004 in west-central Indiana. Habitats are shown in rank order (preferred to avoided) as determined by compositional analysis. Bars represent no significant difference ($\alpha = 0.05$) between habitat types. Sharp-shinned and rural Cooper's Hawk habitat use was compared to habitat available in the entire study site. Urban Cooper's Hawk habitat use was compared to habitat available in both the entire study site and the urban site alone.

Species					
Habitat type	Habitat type				
Sharp-shinned Hawk					
	Forest	Grass	Residential	Edge	Agriculture
Forest	———				
Grass		———	———		
Residential		———	———	———	
Edge			———	———	
Agriculture					———
Rural Cooper's Hawk					
	Forest	Grass	Edge	Residential	Agriculture
Forest	———	———		———	
Grass	———	———		———	
Edge			———	———	
Residential	———	———	———	———	———
Agriculture				———	———
Urban Cooper's Hawk (entire study site)					
	Residential	Grass	Forest	Edge	Agriculture
Residential	———				
Grass		———			
Forest			———	———	
Edge			———	———	
Agriculture					———
Urban Cooper's Hawk (urban site only)					
	Residential	Grass	Forest	Edge	Agriculture
Residential	———	———			
Grass	———	———	———		
Forest		———	———	———	
Edge			———	———	———
Agriculture				———	———

hawks, none of which differed significantly from the random mean (Bonferroni-adjusted $\alpha = 0.005$). If anything, these hawks showed a tendency to avoid feeders (Fig. 3), and three Cooper's Hawks (two urban, one rural) established home ranges in areas without known feeders. Furthermore, if feeders were particularly important resources, then we would have expected hawks to have had smaller home ranges when their home ranges contained more feeders. However, we observed a strong positive correlation between the number of feeders in a home range and home range size ($r = 0.7$, $n = 33$, $P < 0.001$), again suggesting that feeders were no more important than other foraging locations without feeders in the home range.

PREY DENSITY

Prey density was higher in the urban study site. On average, prey were nearly eight times more abundant at urban than rural point count sites (urban: 42.7 ± 8.5; rural: 7.6 ± 0.5), representing a significant difference in the density of prey between the rural and urban sites ($t_{52} = 10.8$, $P < 0.001$).

DISCUSSION

This study represents the first large-scale analysis of the spatial ecology of wintering Cooper's and Sharp-shinned Hawks. Overall, the use of space by these wintering hawks varied by age and location (rural vs. urban). Immature hawks tended to have larger home ranges than adults (except rural Cooper's Hawks), which is common in many taxa (Thogmartin 2001, Romanach et al. 2005, Borger et al. 2006). The size of Sharp-shinned Hawk home ranges was, on average, over three times larger than that of urban Cooper's Hawks, although it was comparable to that of rural Cooper's Hawks. The smaller home range size of urban hawks is consistent with a recent study on the effects of urbanization on Cooper's Hawks in California (S. Chiang et al., Western Foundation of Vertebrate Zoology, unpubl. data). Although the rural Cooper's Hawks that we studied were mostly male and the urban hawks mostly female, there was no significant effect of sex on home range size.

All of the wintering hawks that we studied avoided hunting in open (bare earth or stubble) agricultural fields. Instead,

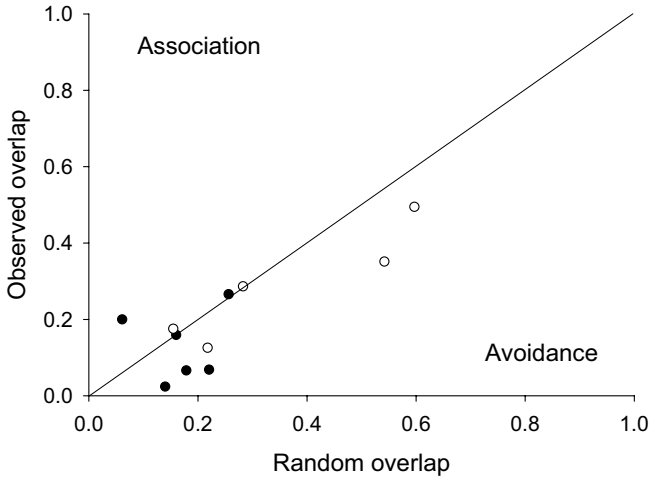

FIGURE 3. Bird feeder use by wintering Cooper's Hawks (rural, unfilled circles, $n = 5$; urban, filled circles, $n = 6$) was not significantly different from random. Three hawks (one rural and two urban) were without known feeders in their home ranges, and thus are not included here. Shown is the proportion of observed hawk locations that overlapped 300 m radius buffers around feeders plotted against the mean overlap of 100 replicated feeder location randomizations. In the randomizations, observed hawk points remained stationary, while the feeders within the home range of individual hawks were randomly relocated to estimate random use of feeders. The area above the diagonal line represents a tendency for hawks to hunt at or near feeders, while the area below the line represents the tendency to avoid feeders. Feeder use by individual hawks was in no case significantly different from the expected random mean (adjusted $\alpha = 0.005$).

hawks focused most of their activity on forested and edge habitats (rural hawks) and residential habitat (urban hawks), as these areas tended to harbor their prey. Furthermore, hawks probably avoided open agricultural fields because their hunting tactics rely on surprise, which is difficult to achieve in such areas (Roth and Lima 2003, Roth et al. 2006; but see Cresswell 1994, 1996). Urban Cooper's Hawks overutilized residential habitat. Since we caught these hawks in the urban habitat, this result is not surprising. What is enlightening, however, is that the use of residential areas was significantly different from all other habitat types and the secondary use of grass habitat was significantly different from forest and edge habitat. Simply because they were caught in the city and spent a great deal of time there does not mean that they spent all of their time in the residential habitat. Within the urban landscape, open areas such parks and areas with mixed vegetation were important hunting locations. In fact, urban Cooper's Hawks showed a tendency to avoid forested areas even in and around the residential habitat, likely because their main prey, Mourning Doves (*Zenaida macroura*) and European Starlings (Roth and Lima 2003), were more easily accessible in urban residential habitat. However, the vertical structure of many urban areas, including our study site, is somewhat forest-like and grassy areas such as parks were important for Cooper's Hawks in the urban study site. This result is consistent with the findings of S. Chiang et al. (Western Foundation of Vertebrate Zoology, unpubl. data) and may apply to the breeding season as well.

In general, we observed no systematic use of bird feeders by Cooper's Hawks, which is consistent with our work on Sharp-shinned Hawks (Roth and Lima 2007a). Although a few hawks visited feeders more often than expected, just as many avoided them, as was the case for Sharp-shinned Hawks (Roth and Lima 2007a). These results suggest that feeders are simply locations where humans are most likely to observe hawk attacks, not locations where hawks are necessarily most likely to hunt. Furthermore, the lack of a strong tendency to hunt around feeders is consistent with the idea of prey management by hawks, whereby hawks avoid repeated attacks at areas (feeders) frequently visited by behaviorally responsive prey, thus ensuring a usable source of prey over the long term (Roth and Lima 2007a). Alternatively, bird feeders may simply not be particularly good places for hawks to hunt prey.

Differences between groups in home range size and feeder use are possibly due to differences in diet and habitat. The typically larger prey of the larger, mainly female urban Cooper's Hawks tend not to be attracted to feeders and are more common in urban than rural areas (Roth and Lima 2003, 2007b, Roth et al. 2006). As a result, urban Cooper's Hawks would not be expected to hunt at feeders. While we cannot measure the impact of atypical urban feeders that might attract such prey (e.g., dumpsters, dog food bowls), these prey resources are relatively small and sporadic, and thus probably do not represent a predictable resource for prey. In addition, urban prey density was greater than rural prey density (Beissinger and Osborne 1982). As a result, urban Cooper's Hawks probably needed less space than rural hawks to obtain an adequate prey base, and thus had smaller home ranges (McNab 1963, Mannan and Boal 2000, Jetz et al. 2004) than rural Cooper's Hawks and Sharp-shinned Hawks.

Another possible explanation for the smaller home ranges of urban hawks may be noise. Relative to rural environments, human-induced noise levels are quite high in urban settings. Such high levels of background noise might limit the perceptual abilities of prey and thus might produce compensatory changes in their antipredator behavior. Following the results of Quinn et al. (2006), it is possible that hawks hunting in noisy environments might have an easier time surprising prey and consequently may not need as much space in which to hunt (W. Cresswell, University of St. Andrews, pers. comm.). While the mechanism of this alternative explanation is speculative, the influence of urbanization on predator-prey systems is undoubtedly important and will be a fruitful direction for future study (S. Chiang et al., Western Foundation of Vertebrate Zoology, unpubl. data).

Although the popular impression of *Accipiter* hawks is that they frequently hunt around bird feeders, our research

suggests otherwise for both Sharp-shinned and Cooper's Hawks. In fact, in our study area, both species maintained relatively large home ranges during the winter and were just as likely to visit areas with or without feeders. It is conceivable that these patterns in the use of space by *Accipiter* hawks apply only to our particular study site, but we suspect that our results apply throughout the geographical ranges of these two species. Further work on the biology of these elusive hawks will shed more light on this matter and many other aspects of this important predator-prey system.

ACKNOWLEDGMENTS

We thank our many field assistants for their assistance with radio-tracking. We are grateful to local businesses, land owners, and the city of Terre Haute for their cooperation. Will Cresswell, Per Widen, and an anonymous reviewer provided helpful comments on earlier drafts of this manuscript. This research was funded in part by the National Science Foundation (Grant IBN-0130758), the Indiana Academy of Sciences, and the Indiana State University Department of Biology and School of Graduate Studies.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Beissinger, S. R., and D. R. Osborne. 1982. Effects of urbanization on avian community organization. Condor 84:75–83.

Berger, D. D., and H. C. Mueller. 1959. The bal-chatri: a trap for the birds of prey. Bird- Banding 30:18–26.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird census techniques. Academic Press, London, UK.

Bildstein, K. L., and K. Meyer. 2000. Sharp-shinned Hawk (*Accipiter striatus*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 482. The Birds of North America, Inc., Philadelphia, PA.

Boal, C. W. 1997. An urban environment as an ecological trap for Cooper's Hawks. Ph.D. dissertation, The University of Arizona, Tucson, AZ.

Boal, C. W., and R. W. Mannan. 1999. Comparative breeding ecology of Cooper's Hawks in urban and exurban areas of southeastern Arizona. Journal of Wildlife Management 63:77–84.

Boal, C. W., R. W. Mannan, and K. S. Hudelson. 1998. Trichomoniasis in Cooper's Hawks from Arizona. Journal of Wildlife Diseases 34:590–593.

Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz, and T. Coulson. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. American Naturalist 168:471–485.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Calenge, C. [online] 2008. adehabitat: analysis of habitat selection by animals. Version 1.7.1. <http://cran.univ-lyon1.fr/web/packages/adehabitat/index.html> (11 April 2008).

Cresswell, W. 1994. Flocking as an effective anti-predation strategy in Redshanks, *Tringa totanus*. Animal Behaviour 47:433–442.

Cresswell, W. 1996. Surprise as a winter hunting strategy in Sparrowhawks *Accipiter nisus*, Peregrines *Falco peregrinus*, and Merlins *F. columbarius*. Ibis 138:684–692.

Cresswell, W., J. Lind, U. Kaby, J. L. Quinn, and S. Jakobsson. 2003. Does an opportunistic predator preferentially attack non-vigilant prey? Animal Behaviour 66:643–648.

Cresswell, W., and J. L. Quinn. 2004. Faced with a choice, Sparrowhawks more often attack the more vulnerable prey group. Oikos 104:71–76.

De Solla, S. R., R. Bonduriansky, and R. J. Brooks. 1999. Eliminating autocorrelation reduces relevance of home range estimates. Journal of Animal Ecology 68:221–234.

Dunn, E. H., and D. L. Tessaglia. 1994. Predation of birds at feeders in winter. Journal of Field Ornithology 65:8–16.

Hooge, P. N., and B. Eichenlaub. 1997. Animal Movement extension to ArcView. Version 1.1. Alaska Biological Science Center, U. S. Geological Survey, Anchorage, AK.

Jetz, W., C. Carbone, J. Fulford, and J. H. Brown. 2004. The scaling of animal space use. Science 306:266–268.

Kennedy, P. L., and D. R. Johnson. 1986. Prey-size selection in nesting male and female Cooper's Hawks. Wilson Bulletin 98:110–115.

Kenward, R. 1997. Wildlife radio tagging: equipment, field techniques, and data analysis. Academic Press, London, UK.

Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology & Evolution 17:70–75.

Mannan, R. W., and C. W. Boal. 2000. Home range characteristics of male Cooper's Hawks in an urban environment. Wilson Bulletin 112:21–27.

Mannan, R. W., W. A. Estes, and W. J. Matter. 2004. Movements and survival of fledgling Cooper's Hawks in an urban environment. Journal of Raptor Research 38:26–34.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97:133–140.

Newton, I. 1986. The Sparrowhawk. T & A.D. Poyser, Calton, UK.

Quinn, J. L., and W. Cresswell. 2004. Predator hunting behavior and prey vulnerability. Journal of Animal Ecology 73:143–154.

Quinn, J. L., M. J. Whittingham, S. J. Butler, and W. Cresswell. 2006. Noise, predation risk compensation and vigilance in the Chaffinch *Fringilla coelebs*. Journal of Avian Biology 37:601–608.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http:\www.R-project.org> (11 April 2008).

Rappole, J. H., and A. R. Tipton. 1994. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Reynolds, R. T., and E. C. Meslow. 1984. Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. Auk 101:761–779.

Romanach, S. S., E. W. Seabloom, O. J. Reichman, W. E. Rogers, and G. N. Cameron. 2005. Effects of species, sex, age, and habitat on geometry of pocket gopher foraging tunnels. Journal of Mammalogy 86:750–756.

Rosenfield, R. N., and J. Bielefeldt. 1993. Cooper's Hawk (*Accipiter cooperii*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 75. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Rosenfield, R. N., and J. Bielefeldt. 1999. Mass, reproductive biology, and nonrandom pairing in Cooper's Hawks. Auk 116: 830–835.

ROSENFIELD, R. N., J. BIELEFELDT, AND J. L. AFFELDT. 1995. Nesting density, nest area reoccupancy, and monitoring implications for Cooper's Hawks in Wisconsin. Journal of Raptor Research 29:1–4.

ROSENFIELD, R. N., J. BIELEFELDT, S. A. SONSTHAGEN, AND T. L. BOOMS. 2000. Comparable reproductive success at conifer plantation and non-plantation nest sites for Cooper's Hawks in Wisconsin. Wilson Bulletin 112:417–421.

ROTH, T. C., II, AND S. L. LIMA. 2003. Hunting behavior and diet of Cooper's Hawks: an urban view of the small-bird-in-winter paradigm. Condor 105:474–483.

ROTH, T. C., II, AND S. L. LIMA. 2006. Predatory behavior and diet of wintering male Cooper's Hawks in a rural habitat. Journal of Raptor Research 40:287–290.

ROTH, T. C., II, AND S. L. LIMA. 2007a. Use of predictable prey hotspots by an avian predator: purposeful randomness? American Naturalist 169:264–273.

ROTH, T. C., II, AND S. L. LIMA. 2007b. The predatory behavior of wintering *Accipiter* hawks: temporal patterns in activity of predators and prey. Oecologia 152:169–178.

ROTH, T. C., II, S. L. LIMA, AND W. E. VETTER. 2005. Survival and causes of mortality in wintering Sharp-shinned and Cooper's Hawks. Wilson Bulletin 117: 237–244.

ROTH, T. C., II, S. L. LIMA, AND W. E. VETTER. 2006. Determinants of predation risk in small wintering birds: the hawk's perspective. Behavioral Ecology and Sociobiology 60:195–204.

SWIHART, R. K., AND N. A. SLADE. 1985. Testing for independence of observations in animal movements. Ecology 66:1176–1184.

THOGMARTIN, W. E. 2001. Home-range size and habitat selection of female Wild Turkeys (*Meleagris gallopavo*) in Arkansas. American Midland Naturalist 145:247–260.

TURCHIN, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer and Associates, Sunderland, MA.

VIVERETTE, C. B., S. STRUVE, L. J. GOODRICK, AND K. L. BILDSTEIN. 1996. Decrease in migrating Sharp-shinned Hawks (*Accipiter striatus*) at traditional raptor-migration watch sites in eastern North America. Auk 113:32–40.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, London, UK.

WHITFIELD, D. P., W. CRESSWELL, N. P. ASHMOLE, N. CLARK, AND A. D. EVANS. 1999. No evidence for Sparrowhawk selecting Redshanks according to size or condition. Journal of Avian Biology 30:31–39.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.