The Condor 105:474–483

HUNTING BEHAVIOR AND DIET OF COOPER'S HAWKS: AN URBAN VIEW OF THE SMALL-BIRD-IN-WINTER PARADIGM

TIMOTHY C. ROTH II[1] AND STEVEN L. LIMA
Department of Life Sciences, Indiana State University, Terre Haute, IN 47809

Abstract. We examined the predatory behavior of wintering urban Cooper's Hawks (*Accipiter cooperii*). Eight Cooper's Hawks (7 female, 1 male) were radio-tracked intensively during two winter periods from 1999–2001. We observed 179 attacks, 35 of which were successful, for an overall attack success rate of 20%. We recorded an additional 44 kills resulting from unobserved attacks. European Starlings (*Sturnus vulgaris*), Mourning Doves (*Zenaida macroura*), and Rock Doves (*Columba livia*) made up 95% of the prey attacked and 91% of the diet. Smaller birds (<70 g), such as House Sparrows (*Passer domesticus*), were numerous in the study area but were rarely attacked. Mammals were not included in the diet. Surprise attacks (initiated at close range, often from behind an obstruction), were more successful than ''open'' attacks, although the latter were more frequent. In addition, attacks on single individuals were significantly more successful than those on flocks. Nonetheless, many attacks were attempted on large flocks. Our results suggest that the smaller bird species (<70 g) in our urban study area were at low risk of predation from Cooper's Hawks.

Key words: Accipiter, *hawks, hunting behavior, predator-prey interactions, safety in groups, urban environment, wintering birds.*

Comportamiento de Caza y Dieta de *Accipiter cooperii*: Una Visión Urbana del Paradigma de Aves Pequeñas durante el Invierno

Resumen. Examinamos el comportamiento de depredación de individuos urbanos de la especie *Accipiter cooperii* durante el período de invernada. Ocho individuos (siete hembras y un macho) fueron seguidos intensamente mediante radio telemetría durante dos períodos invernales desde 1999 hasta 2001. Observamos 179 ataques, de los cuales 35 fueron exitosos, con una tasa general de éxito de ataque del 20%. Adicionalmente, registramos 44 muertes que resultaron de ataques no observados. *Sturnus vulgaris*, *Zenaida macroura* y *Columba livia* compusieron el 95% de las presas atacadas y el 91% de la dieta. Aves pequeñas (<70 g), como *Passer domesticus*, fueron muy abundantes en el área de estudio pero fueron raramente atacadas. La dieta no incluyó mamíferos. Los ataques sorpresivos (iniciados a una corta distancia, generalmente desde detrás de algún objeto) fueron más exitosos que ataques ''abiertos,'' aunque estos últimos fueron más frecuentes. Además, los ataques sobre individuos que se encontraban solos fueron significativamente más exitosos que aquellos sobre bandadas. Sin embargo, muchos ataques fueron intentados sobre bandadas grandes. Nuestros resultados sugieren que en nuestra área de estudio urbana las especies de aves más pequeñas (<70 g) tenían un menor riesgo de ser depredadas por *A. cooperii*.

INTRODUCTION

A prominent conceptual paradigm in behavioral ecology is that of the small bird in winter. In this paradigm, small wintering birds maximize their fitness by avoiding both starvation and predation by bird-eating *Accipiter* hawks. Behavioral options that lessen one of these two risks often increase the other. Thus, small wintering birds must trade off the risk of starvation against the risk of predation when making behavioral decisions. This conceptual paradigm has had a great impact on our present understanding of sociality (Bertram 1978, Pulliam and Caraco 1984, Sullivan 1984), foraging behavior (Lima 1985, Stephens and Krebs 1986, Cuthill and Houston 1997, Giraldeau and Caraco 2000), and predator-prey theory (Mangel and Clark 1988, Houston and McNamara 1999).

Despite its prominence in behavioral ecology, our present view of the small-bird-in-winter paradigm is lacking in one key respect: we know very little about the behavior of wintering *Accipiter* hawks. Even the basic behaviors of these hawks, such as their diet, hunting behavior, gen-

Manuscript received 18 October 2002; accepted 22 March 2003.
[1] E-mail: lsroth@scifac.indstate.edu

eral movements, home range, and activity period, are largely unknown during the winter. The exception to this generalization is some pioneering work by Newton (1986) and Cresswell and colleagues (Cresswell 1994a, 1996, Whitfield et al. 1999) on Sparrowhawks (*A. nisus*) in the United Kingdom. The winter behavior and ecology of the main small-bird predators in North America, the Cooper's Hawk (*A. cooperii*) and the Sharp-shinned Hawk (*A. striatus*), however, are almost entirely unknown. As a result of this general lack of knowledge, students of the small-bird-in-winter paradigm have tended to treat hawks merely as a source of risk rather than as active participants in behavioral predator-prey interactions (Lima 2002). This simplistic abstraction of predators is pervasive in the study of behavioral predator-prey interactions in general (Lima 2002).

There are many conceptual gains to be made from a better understanding of *Accipiter* behavior. For instance, some small bird species may be prominent in the hawks' diet while others may be largely ignored. The latter prey may then be freed from some of the behavioral constraints imposed by predators. Insights into the temporal hunting activity of *Accipiter* may shed light on the daily activity routines (McNamara et al. 1994) and patterns in weight gain (Pravosudov and Grubb 1997, Lind et al. 2003) in small birds. The hunting tactics of these hawks may also influence small and large-scale patterns in habitat choice by birds (Lima 1993, Cresswell 1994a). Furthermore, an understanding of *Accipiter* movement patterns could shed light on the movements of their prey (Greenberg 2000, Mitchell and Lima 2002).

Our long-term goal is thus to reconsider the small-bird-in-winter paradigm from the perspective of an interaction that involves both predator and prey. However, with so little known about accipiters, we must first establish an understanding of their basic predatory behavior. Hence, the objective of this paper is to present information on the predatory behavior of wintering Cooper's Hawks. We focus here on the processes of attack and capture of prey in an urban habitat. We examine (1) the species of prey attacked and the success of attacks, (2) how the attacks are carried out, and (3) events after the attack. We also consider the implications of our results for the small-bird-in-winter paradigm.

METHODS

STUDY SITE

Our study site was centered on the city of Terre Haute, Indiana (population 60 000) and covered approximately 40 km^2. This urban site is approximately 30% high-density residential and commercial land (>14 buildings per block) and 70% low-density residential areas (<14 buildings per block). Streets are arranged in a rectangular grid with an interstreet spacing of about 125 m. The area surrounding the study site is a mixture of city suburbs, agricultural land, and fragmented forest.

HAWK CAPTURE

We trapped 13 Cooper's Hawks during November–January of 1999–2000 and 2000–2001. Constantly monitored bal-chatri traps (Berger and Mueller 1959) and bow nets were used during trapping. Bal-chatri traps were enlarged from the standard design to a barrel-shaped trap 0.75 m in diameter and 0.75 m in height. The larger traps provided more volume in which lure birds could move, which made them more conspicuous to passing hawks. Standard monofilament line slipknots were included on the top, sides, and base of the trap. The bow nets were 2.1 m in diameter with a lure bird in a cage (25 × 25 × 60 cm) at the center of the trap. All traps used European Starlings (*Sturnus vulgaris*) as lures, since House Sparrows (*Passer domesticus*) proved to be too small to interest hawks, and Rock Doves (*Columba livia*) were not active in traps. Traps were positioned in open areas such as parking lots, cemeteries, and parks to maximize exposure to passing hawks.

RADIO-TRACKING

Hawks were tracked using radio-telemetry. We used position-sensitive transmitters on all hawks. Mercury switches in these transmitters provided information on hawk posture (body vertical vs. horizontal), which allowed us to determine whether a given hawk was perched (vertical), flying (horizontal and moving), or consuming prey (horizontal and stationary). These transmitters allowed us to maintain close contact with the hawks. During 1999–2000, 5.0–11.0 g radio-transmitters (AVM Instrument Company, Ltd., Colfax, California, and Advanced Telemetry Systems, Inc., Isanti, Minnesota) were attached to hawks via tail mounts (Kenward 1978,

TABLE 1. Cooper's Hawks captured in Terre Haute, Indiana, during the winters of 1999–2000 and 2000–2001, including number of days tracked and number of attacks observed for each hawk.

Winter Hawk	Sex	Age	No. of attacks	Days tracked
1999–2000				
520	Female	Immature	4	14
620[a]	Female	Adult	0	59
640[b]	Female	Adult	0	1
660[b]	Male	Adult	0	1
680	Female	Immature	28	30
2000–2001				
015	Male	Immature	40	101
063[a]	Female	Adult	0	10
089[a]	Female	Adult	0	1
635	Female	Adult	27	85
672	Female	Adult	21	95
720	Female	Adult	28	85
728	Female	Immature	28	90
758	Female	Adult	3	23

[a] These hawks were tracked out of the city and were not included in the analyses.

[b] These hawks removed their transmitters less than one day after capture and were not included in the analyses.

2001). However, the tail mount attachment was not successful for our hawks. Only three hawks (of five captured) were tracked for any length of time due to the loss of tail feathers and transmitters (Table 1). During the second season, 4–7 g radio transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) were attached to hawks using the synsacral mount described by Rappole and Tipton (1991). Transmitters were sewn onto a harness made from 1.5-mm polyester cord. This method was much more successful; of the eight hawks captured during the second season, six were tracked intensively for ≥23 days. The remaining two hawks quickly moved south of the study site and disappeared shortly after capture.

Hawks were tracked intensively on a daily basis from the time of capture through early March. Each hawk was tracked by vehicle using Yagi and whip antennas for a period of no less than 2 hr per day. Depending upon the number of hawks and trackers available, the period of tracking for a given hawk ranged from 2 hr to 12 hr. Tracking began approximately 0.5–1 hr before sunrise at the last known roost of a particular hawk and then rotated systematically among hawks until all hawks returned to roost. The starting and ending hawk was rotated each day, and each hawk's roost was verified every night. During a tracking period, the tracker stayed as close as possible to the hawk, attempting to maintain visual contact without disturbing it. These urban hawks were unperturbed by the presence of humans in vehicles or other urban disturbances (e.g., moving vehicles, trains, loud noises, etc.).

HUNTING BEHAVIOR AND DIET

Trackers recorded the location and the general behavior of the hawks. Hawk locations were recorded in the field as distances and bearings from street and alley intersections. These positions were then logged into a geographical information system. For present purposes, behaviors were categorized as attacks, consumption of prey, and perching. Attacks included all attempts to capture prey. Prey consumption included any point that the hawk was in contact with prey after its capture. Perching included all nonflying activities except prey consumption. When an attack was observed, trackers recorded when possible (1) the hawk and prey height above ground at the point of attack, (2) the distance between the hawk and prey at attack initiation, (3) prey flock size, (4) species attacked, (5) the result of the attack, and (6) weather variables such as temperature, wind, cloud cover, and precipitation. Trackers would occasionally begin tracking a hawk that was in the process of consuming prey. Under such circumstances, the tracker would seek permission to enter the property in question and search the area for at least 30 min for prey remains (after the hawk finished eating and left the area). Prey identified in this manner were included in the total sample and analyzed in the same way as prey from observed attacks.

Each attack was also categorized as surprise or open (Newton 1986, Cresswell 1996). The final (i.e., detectable) stage of surprise attacks occurred close to prey, either as a result of maneuvering to a point close to prey or by ambush from a concealed location (Cresswell 1996). The final stage of open attacks did not begin close to prey, but occurred within view of prey, typically when prey were perched or feeding in open areas (i.e., where prey could have detected the hawk's approach at a distance of about 15 m or more; Cresswell 1996).

The category of surprise was divided into contour-hugging and ambush attacks (Newton

1986). A typical contour-hugging attack began with a hawk in dense or high vegetation well away from the attack site. During the attack, the hawk flew within one meter of the ground, following the contours of the terrain, apparently to avoid detection. The hawk then accelerated to a high speed over or around the final obstruction, often only a few meters from the attack site, and flew directly toward the prey. Hawks appeared to attack any bird (in a flock) that was slow to escape. During contour-hugging attacks, hawks often maneuvered well ''off course'' in order to stay out of sight. Such attack deviations were often many tens of meters away from the most direct path to prey, wherein hawks lost any possibility of maintaining visual contact with prey. In contrast, ambush attacks occurred when hawks were perched in dense vegetation and a prey bird flew close by (usually within about 3 m). During the prey's approach, a hawk would often defecate, stretch, and otherwise prepare for flight, suggesting anticipation of the approaching attack.

During the second season (in which more hawks were tracked), we estimated the relative abundance of prey within the study site. Unlimited-distance point counts (5 min) were performed twice at 36 random points (at least 500 m apart) within the main hawk activity area (approx. 20 km^2) during early to mid February. As these points were established within the city, the detection of birds was greatly limited by obstructions such as buildings. As such, our detection of birds was likely similar to that experienced by Cooper's Hawks. We report the sum of all birds observed on all point counts and both visits. All point counts were performed during mornings in good weather conditions.

STATISTICAL ANALYSES

All statistical analyses were performed with Systat 9.0 (SPSS Inc. 1998) using parametric and nonparametric tests as appropriate. We pooled data from all hawks and treated attacks as independent estimates of the interaction between Cooper's Hawks and their prey. We did not obtain enough data from most hawks to make statistical statements about individual variation in hunting behavior. We note, however, that the hawks in this study were broadly similar in hunting tactics and diet.

RESULTS

Five Cooper's Hawks were trapped during 1999–2000, and eight were trapped in 2000–2001 for a total of 13 hawks (Table 1). Of those captured, the sex ratio was highly skewed toward females (11 females, 2 males). This significant bias ($\chi^2_1 = 6.2$, $P = 0.01$) appeared to reflect a true lack of males in our study area; we rarely encountered unmarked male Cooper's Hawks while tracking, but often encountered unmarked females. The age distribution of the captured hawks was moderately skewed toward adults (4 immatures, 9 adults). Of the 13 hawks captured, one adult female and one adult male were lost quickly due to the transmitter loss discussed above. In addition, three adult females left the study site but were still tracked outside of the city. We did not track these hawks as closely as those within the city and thus could not readily observe their attacks or kills. As a result, these hawks effectively were not included in these analyses. Our analyses thus included data from seven females (3 immatures, 4 adults) and one male (immature). These eight hawks were tracked on average 65 days (range 14–101 days; Table 1). During the study period, 179 attacks were observed during 982 hr of tracking.

Of 179 observed attacks, we identified the prey species involved in 144 (80%) attacks. In the cases where prey were not identified, we observed attack initiation but could not observe most other aspects of the attack. Note that the position-sensitive transmitters allowed us to determine the success or failure of an attack (a stationary signal in the horizontal position for an extended period indicated prey consumption), even if we could not precisely locate the feeding site. Our tracking technique was unlikely to bias our assessment of prey consumption. The ability to detect and find successful attacks was usually a function of gaining access to private property, not prey type.

Three avian species were attacked frequently (Table 2). European Starlings (52%), Mourning Doves (*Zenaida macroura*; 24%) and Rock Doves (*Columba livia*; 19%) made up 95% of prey attacked (Table 2). The one male hawk occasionally attacked other species such as a Red-bellied Woodpecker (*Melanerpes carolinus*), a House Sparrow, and a Northern Cardinal (*Cardinalis cardinalis*), but also focused attacks largely on starlings, Mourning Doves, and Rock

TABLE 2. Attack success, diet, and relative abundance of prey for Cooper's Hawks in Terre Haute, Indiana, 1999–2001. Prey species are listed in decreasing order of occurrence in point count surveys conducted during the 2000–2001 tracking period.

Species		Mass (g)	Individuals attacked[a]		Success (%)	Individuals eaten[b]		Relative abundance	
			n	%		*n*	%	*n*[c]	%
European Starling	*Sturnus vulgaris*	82	75	52	23	32	56	1296	60
Rock Dove	*Columba livia*	355	27	19	26	12	21	357	17
House Sparrow	*Passer domesticus*	28	2	1	0	1	2	287	13
Mourning Dove	*Zenaida macroura*	119	34	24	15	8	14	75	3
Blue Jay	*Cyanocitta cristata*	87	0	0	0	1	2	37	2
House Finch	*Carpodacus mexicanus*	21	0	0	0	0	0	25	1
Dark-eyed Junco	*Junco hyemalis*	20	0	0	0	0	0	19	1
Northern Cardinal	*Cardinalis cardinalis*	45	1	1	0	1	2	17	1
American Robin	*Turdus migratorius*	77	1	1	0	0	0	8	<1
Carolina Chickadee	*Poecile carolinensis*	10	0	0	0	0	0	8	<1
Red-winged Blackbird	*Agelaius phoeniceus*	62	1	1	0	0	0	7	<1
Northern Flicker	*Colaptes auratus*	133	0	0	0	0	0	3	<1
Common Grackle	*Quiscalus quiscula*	114	1	1	0	0	0	2	<1
White-throated Sparrow	*Zonotrichia albicollis*	26	0	0	0	0	0	2	<1
American Tree Sparrow	*Spizella arborea*	20	0	0	0	0	0	2	<1
Downy Woodpecker	*Picoides pubescens*	27	0	0	0	0	0	1	<1
Unidentified			2[d]	1	—	2[d]	4	9	<1
Total			144	100	20	57	100	2146	100

[a] 35 unknowns were not included in the analysis of attacks. The species under attack could not always be observed.
[b] 22 unknowns were not included in the analysis of diet. Kills for which attacks were not observed were included when found.
[c] The sum of all birds observed during two visits to 36 point count stations in the tracking area.
[d] One woodpecker, one small mammal.

Doves (83% of observed attacks). Overall, the success rate of attacks was 20% (35 of 179 attacks), and success rate among species (grouped as starlings, Mourning Doves, Rock Doves, and all other species) did not differ significantly ($\chi^2_3 = 2.5$, $P = 0.47$; Table 2). Of the 79 kills recorded (including 44 prey captures for which the actual attack was not observed), 22 were not identifiable to species (we could not precisely locate or gain access to these kill sites), and thus 57 kills were included in our dietary analysis. Starlings, Mourning Doves, and Rock Doves made up 91% of the hawks' diet (Table 2). Only one attack occurred on a mammal, which was a small (mouse-sized) species.

Prey choice was apparent in our urban Cooper's Hawks. European Starlings, House Sparrows, and Rock Doves were the three most common species in the study site (Table 2), as one would expect in an urban environment. Mourning Doves were a distant fourth in frequency (Table 2). These four species made up 93% of prey surveyed and 93% of prey in the diet (Table 2). However, the occurrence of these four species in the diet differed significantly from their occurrence in our survey ($\chi^2_3 = 50.8$, $P < 0.001$). (We used our raw survey data as a coarse index of prey availability to hawks.) Both starlings and Rock Doves were attacked roughly in proportion to their occurrence in our surveys (Table 2). Mourning Doves appeared to be attacked more often than expected based on occurrence. House Sparrows were seldom attacked although they were relatively common. In fact, small birds in general (<70 g) seemed to be under very little risk of attack even though collectively such birds made up 18% of those counted. Removing the few small birds attacked by the (smaller) male hawk, the trend was even more apparent: birds <70 g were virtually never attacked by female Cooper's Hawks.

The hawks' diet (frequency by species) closely reflected the frequency of prey attacked ($r = 0.97$; $P < 0.001$; $n = 16$ species, Table 2). This correlation suggests no major differences in ''catchability'' across species; that is, species were captured in proportion to their frequency of attack. However, flock size had a significant effect on attack success (Fig. 1; $\chi^2_2 = 7.6$, $P = 0.02$). Attacks on solitary individuals were most likely to be successful. Attacks on larger flocks (5 or more birds) were about one-third as successful as those on solitary individuals (Fig. 1).

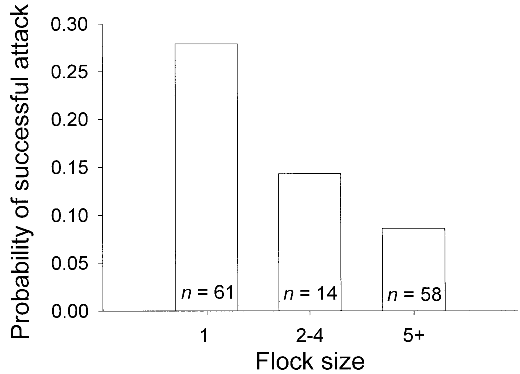

FIGURE 1. The probability of a successful attack by Cooper's Hawks on three categories of flock size: solitary individuals, small flocks (2–4 individuals) and large flocks (5 or more individuals). Cooper's Hawks were tracked during two winters in Terre Haute, Indiana; all attacks with known prey species are included ($n = 133$).

Nevertheless, we observed many attacks on large flocks. Prey choice by hawks was not greatly affected by flock size because solitary individuals of all three main prey species were often observed. Attack success was also not significantly associated with prey height (grouped as above or below median) at the point of attack ($\chi^2_1 = 0.9$, $P = 0.33$) or weather variables (temperature grouped as above or below 0°C: $\chi^2_1 = 1.0$, $P = 0.33$; snow cover grouped as presence or absence: $\chi^2_1 = 0.1$, $P = 0.81$).

We classified 59 of 120 attacks as surprise attacks and 61 of 120 attacks as open attacks. (Only 120 of our total 179 attacks were observed in sufficient detail to be categorized as open or surprise.) Contour-hugging attacks (40 of 59 surprise attacks, 68%) usually employed visual obstructions such as buildings, vegetation, and fences in an effort to get very close to prey before the final stage of an attack (see methods). Hawks also planned surprise attacks on prey that were not present. On four occasions, hawks maneuvered into a surprise attack upon a feeder only to attack a nonexistent flock at an empty feeder (see also Wilson and Weir 1989). Ambush attacks accounted for 19 of 59 (32%) surprise attacks. Ambush attacks were most successful when prey unknowingly entered the clump of vegetation concealing the hawk itself (all five such attacks were successful).

Surprise attacks were more successful than open attacks ($\chi^2_1 = 10.3$, $P < 0.01$). Of the 61

TABLE 3. Attack types used by Cooper's Hawks on their three main prey species during winter in Terre Haute, Indiana.

Species	Open	Surprise	Total
European Starling	27	24	51
Mourning Dove	16	7	23
Rock Dove	6	16	22
Total	49	47	96

open attacks, only four (7%) were successful. However, of the 59 surprise attacks, 17 (30%) were successful. Prey species had a significant effect on the type of attack used ($\chi^2_2 = 8.2$, $P = 0.02$; Table 3). Open attacks were more frequently used on starlings and Mourning Doves, while surprise attacks were more frequent on Rock Doves. Being large and fast, Rock Doves may require surprise for successful capture. Flock size (as defined in Fig. 1) was not significantly associated with the type of attack ($\chi^2_2 = 1.8$, $P = 0.41$).

After a successful attack, hawks usually consumed prey within 50 m of the attack site (23 of 29 successful attacks for which we determined both the attack and plucking site). Only when a successful attack was made in a dangerous or exposed area (e.g., middle of a street or parking lot) did the hawk carry its prey more than 50 m away (6 of 29 cases). Hawks usually ate on the ground in dense vegetation (40 of 75 kills for which we could determine plucking site; this sum includes 44 kills for which the attack itself was not observed). This tendency to eat in dense vegetation was particularly true when American Crows (*Corvus brachyrhynchos*) were present (see also Newton 1986, Cresswell and Whitfield 1994), probably in an attempt to hide prey. Hawks usually mantled (covered prey with wings) when crows were in the area, even if the latter were just flying overhead. The remaining prey (35 of 75 kills) were consumed in trees or on buildings. In such places, hawks were relatively conspicuous, but removed from terrestrial disturbances.

We recorded four cases of kleptoparasitism by crows. Overall, crows were much more likely to harass immature hawks than adults. We observed 70 cases of crows harassing immature Cooper's Hawks, but only 9 cases involving adult (female) hawks. This ratio differed greatly from the ratio of 4 immatures:4 adults of our eight focal hawks ($\chi^2_1 = 60.8$, $P < 0.001$). Kleptoparasitism by other Cooper's Hawks or raptors was not observed.

DISCUSSION

Our urban Cooper's Hawks focused nearly exclusively (95% of prey attacked) on three common species of relatively large prey: European Starlings, Mourning Doves, and Rock Doves. In our urban study, smaller prey such as House Sparrows were completely ignored by adult females and seldom attacked by the male even though collectively such prey were common. Attacks were more successful when hawks could get close to their prey, either by simple ambush or by using visual obstructions during surprise attacks. Even though surprise attacks using visual obstructions were more successful, open attacks (without the immediate use of such obstructions) made up about one-half of observed attacks.

The hunting behavior of our Cooper's Hawks was similar to that seen in the European Sparrowhawk (Newton 1986, Wilson and Weir 1989, Cresswell 1996). Like Cooper's Hawks, Sparrowhawks attempt (when possible) to conceal themselves in order to get close to prey before the final stage of an attack. The main distinctions between our study and those of Cresswell (1994a, 1994b, 1996) are the landscapes and associated changes in hawk hunting strategies. Cresswell studied Sparrowhawks hunting shorebirds in an open estuary, where ambush attacks were very difficult to achieve. Thus, the vast majority of Sparrowhawk attacks involved flight and the use of visual obstructions where possible. In contrast, our urban residential habitat facilitated many more ambush attacks.

Our observations suggest that the three main prey species (Starlings, Mourning Doves, and Rock Doves) could have been most safe from Cooper's Hawks by occupying open habitats well away from visual obstructions (e.g., out in large lawns; Lima 1993, Cresswell 1994b). All three species were observed in such open areas, but they nonetheless occurred routinely in visually obstructed areas where they were at maximal risk to these hawks. Furthermore, none of the three main prey species required vegetation or other structures to escape attack, hence open habitats were exploited (Lima 1993). Perhaps these species were attracted to the more dangerous habitats by better feeding opportunities or thermal advantages (especially shelter from wind, Bakken 1990, Dolby and Grubb 1999). Although we did not observe a significant effect of weather on hunting success (but see Hilton et al. 1999), avoidance of wind or cold microclimates in the open may have made prey more vulnerable to attacks.

Our observations also suggest a considerable advantage to feeding in flocks (Fig. 1) and represent a relatively rare empirical example of the benefits of avian flocking obtained from free-living avian predators. Cresswell (1994a) also found lower attack success on large flocks of Redshanks (*Tringa totanus*) for Sparrowhawks and Peregrine Falcons (*Falco peregrinus*). Similarly, Page and Whitacre (1975) found that attacks on solitary shorebirds by Merlins (*Falco columbarius*) were more successful than attacks on larger groups. Despite the clear advantages of sociality that we documented, our Cooper's Hawks found many opportunities to attack solitary prey. Intraspecific competition for food may explain why many prey birds fed alone or in small groups (cf. Caraco 1979, Pulliam and Caraco 1984).

Why were small prey ($<$70 g) not attacked? Small birds were probably not worth the effort given the abundance of larger prey. Cooper's Hawks require much effort to capture avian prey, if for no other reason than waiting for the appropriate time to attack. Following optimal diet theory (Stephens and Krebs 1986), we suspect that the abundance of large prey made it energetically favorable to simply ignore smaller prey. Even when we used House Sparrows as lures in our traps, Cooper's Hawks did not attack them (see also Mueller and Berger 1970), although hawks clearly noticed the sparrows' inability to flee. While it is possible that our point counts were biased in favor of detecting larger birds, accounting for such a bias would only strengthen our conclusion that small birds were largely ignored by Cooper's Hawks.

Nevertheless, if larger prey were the target of attacks, why were Blue Jays (*Cyanocitta cristata*) rarely attacked? Blue Jays are the appropriate size (approx. 90 g, see also Bielefeldt et al. 1998) for Cooper's Hawks and were fairly common, but we recorded only one kill (for which the attack was not observed; Table 2). Blue Jays may have been relatively safe due to their constant sociality and frequent, noisy harassment of Cooper's Hawks (we observed 35 cases of jays harassing focal hawks). Cooper's Hawks may have also avoided jays because such harassment could make hunting more difficult by alerting other prey to the presence of the hawk.

Our results suggest that smaller bird species are at low risk of predation from our urban Cooper's Hawks. The question then is: Did these smaller birds ''know'' that they were safer than their larger counterparts? The answer is unclear. Small birds at feeders in the city showed typical antipredatory behavior such as vigilance and flocking. They responded strongly to the appearance of Cooper's Hawks, despite the fact that our Cooper's Hawks rarely attacked them. While smaller bird species may be unable to distinguish between Cooper's Hawks and Sharp-shinned Hawks, which are nearly identical except for size, Curio (1993) suggests that birds can make many subtle distinctions in predator recognition. It seems more likely that these small birds responded to all *Accipiter* appearances as a precaution. Even if small prey were not the primary targets of the Cooper's Hawk attacks, capture is still possible (Table 2; Kennedy and Johnson 1986). Furthermore, the cost of such antipredator responses by small birds may not be very large unless encounters with accipiters are frequent.

Of course, predators other than Cooper's Hawks could have maintained antipredator behaviors in these smaller bird species. However, other serious avian predators such as Sharp-shinned Hawks were observed only six times in our urban study site, predominantly around the outskirts of the city (although they were abundant in the surrounding country side; Roth and Lima, unpubl. data). It is conceivable that small prey were not abundant enough to attract Sharp-shinned Hawks to the city, but this is unlikely. We suggest that the presence of many large female Cooper's Hawks deterred Sharp-shinned Hawks from establishing home ranges in urban areas. Sharp-shinned Hawks are an appropriate size (100–170 g) to be prey for female Cooper's Hawks and are frequently taken as prey (Roth and Lima, unpubl. data; see also Klem et al. 1985, George 1989). In any case, smaller urban birds probably experience a genuinely low risk of predation by accipiters when the habitat is dominated by female Cooper's Hawks.

ACKNOWLEDGMENTS

We thank Brian Thomas and William ''Trey'' Franklin, III, for help with hawk tracking. Peter Scott, Chris Ritzi, and Trey Franklin assisted with point counts. We would also like to thank local businesses, landowners, and the Terre Haute Parks Department for their cooperation. Doug Bensinger and Don Garvin assisted in trapping hawks. John Castrale and two anonymous reviewers provided helpful comments on drafts of this manuscript. This research was supported in part by the National Science Foundation (Grant IBN-0130758 to SLL), the Indiana Academy of Sciences, and the Indiana State University Department of Life Sciences and School of Graduate Studies.

LITERATURE CITED

BAKKEN, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. Auk 107:587–594.

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

BERTRAM, B. C. R. 1978. Living in groups: predators and prey, p. 279–309. *In* J. R. Krebs and N. B. Davies [EDS.], Behavioral ecology: an evolutionary approach. Blackwell Science Ltd. Oxford, UK.

BIELEFELDT, J., R. N. ROSENFIELD, W. E. STOUT, AND S. M. VOS. 1998. The Cooper's Hawk in Wisconsin: a review of its breeding biology and status. Passenger Pigeon 60:111–121.

CARACO, T. 1979. Time budgeting and group size: a theory. Ecology 60:611–617.

CRESSWELL, W. 1994a. Flocking as an effective antipredation strategy in Redshanks, *Tringa totanus*. Animal Behavior 47:433–442.

CRESSWELL, W. 1994b. Age-dependent choice of Redshank (*Tringa totanus*) feeding location—profitability or risk. Journal of Animal Ecology 63: 589–600.

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., AND P. WHITFIELD. 1994. The effects of raptor predation on wintering wader populations at the Tyninghame estuary, southeast Scotland. Ibis 136:223–232.

CURIO, E. 1993. Proximate and developmental aspects of antipredator behavior. Advanced Studies in Behavior 22:135–238.

CUTHILL, I. C., AND A. I. HOUSTON. 1997. Managing time and energy, p. 97–120. *In* J. R. Krebs and N. B. Davies [EDS.], Behavioral ecology: an evolutionary approach. 4th ed. Blackwell Science Ltd. Oxford, UK.

DOLBY, A. S., AND T. C. GRUBB JR. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. Condor 101:408–412.

GEORGE, J. R. 1989. Bald eagle kills Sharp-shinned Hawk. Journal of Raptor Research 23:55–56.

GIRALDEAU, L.-A., AND T. CARACO. 2000. Social foraging theory. Princeton University Press, Princeton, NJ.

GREENBERG, R. 2000. Birds of many feathers: the formation and structure of mixed-species flocks of forest birds, p. 521–558. *In* S. Boinski and P. A. Garber [EDS.], On the move: how and why animals travel in groups. University of Chicago Press, Chicago, IL.

HILTON, G. M., G. D. RUXTON, AND W. CRESSWELL. 1999. Choice of foraging area with respect to predation risk in Redshanks: the effects of weather and predator activity. Oikos 87:295–302.

HOUSTON, A., AND J. MCNAMARA. 1999. Models of adaptive behavior. Cambridge University Press, Cambridge, UK.

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. E. 1978. Radio transmitters tail-mounted on hawks. Ornis Scandinavica 9:220–223.

KENWARD, R. E. 2001. A manual for wildlife radio tagging. Academic Press, London, UK.

KLEM, D., JR., B. S. HILLEGASS, AND D. A. PETERS. 1985. Raptors killing raptors. Wilson Bulletin 97: 230–231.

LIMA, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the Black-capped Chickadee. Oecologia 66:60–67.

LIMA, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack—a survey of North American birds. Wilson Bulletin 105:1–47.

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

LIND, J., S. JAKOBSSON, AND C. KULLBERG. 2003. Impaired predator evasion in the life-history of birds; behavioral and physiological adaptations to reduced flight ability. Current Ornithology, in press.

MANGEL, M., AND C. W. CLARK. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, NJ.

MCNAMARA, J. M., A. I. HOUSTON, AND S. L. LIMA. 1994. Foraging routines of small birds in winter—a theoretical investigation. Journal of Avian Biology 25:287–302.

MITCHELL, W. A., AND S. L. LIMA. 2002. Predator-prey shell games: large-scale movement and its implications for decision-making by prey. Oikos 99: 249–260.

MUELLER, H. C., AND D. D. BERGER. 1970. Prey preferences in the Sharp-shinned Hawk: the roles of sex, experience, and motivation. Auk 87:452–457.

NEWTON, I. 1986. The Sparrowhawk. T & AD Poyser, Calton, UK.

PAGE, G., AND D. F. WHITACRE. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

PRAVOSUDOV, V. V., AND T. C. GRUBB JR. 1997. Energy management in passerine birds during the nonbreeding season: a review. Current Ornithology 14:189–234.

PULLIAM, H. R., AND T. CARACO. 1984. Living in groups: is there an optimal group size?, p. 127–147. *In* J. R. Krebs and N. B. Davies [EDS.], Behavioral ecology: an evolutionary approach. 2nd. ed. Blackwell, Oxford, UK.

RAPPOLE, J. H., AND A. R. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62: 335–337.

SPSS INC. 1998. SYSTAT 9.0 for Windows. SPSS Inc., Chicago.

STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton University Press, Princeton, NJ.

SULLIVAN, K. A. 1984. The advantages of social foraging in Downy Woodpeckers. Animal Behavior 32:16–22.

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

WILSON, J. D., AND A. G. WEIR. 1989. Hunting behavior and attack success of a female Sparrowhawk between October 1987 and April 1988. Scottish Birds 15:126–130.