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Determinants of predation risk in small wintering birds: the hawk's perspective

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Abstract The small-bird-in-winter paradigm is prominent in the field of behavioral ecology. However, our conceptual understanding of this paradigm is limited by our lack of knowledge about *Accipiter* hawks. Although Accipiters are the major predators of small wintering birds, we know little about their behavior during the winter. In this paper, we present the first description of the predatory behavior of wintering sharp-shinned hawks (*Accipiter striatus*), focusing on their selection of prey and attack strategies. We also relate basic prey behavior to the risk of death during an attack. During the winters of 2000–2004, we observed 255 attacks and recovered 112 prey items from 21 intensively radio-tracked hawks. The diet of sharp-shinned hawks in the study was composed primarily of sparrow-sized prey, intermediate-sized starlings (*Sturnus vulgaris*), American robins (*Turdus migratorius*), and the occasional larger prey such as mourning doves (*Zenaida macroura*). Both sexes killed all sizes of prey, although female hawks took significantly more large prey than did males. Small preys under 20 g, such as parids, were largely ignored. This lack of very small prey in the diet of sharp-shinned hawks suggests that we might focus the small-bird-in-winter paradigm on sparrows and intermediate-sized prey, such as robins, as the main prey base of Accipiters at least in North America. In addition, solitary and feeding prey were significantly more likely to be captured during an attack than prey in groups and those not feeding. Our hawk-driven observations provide rare empirical support for the concept that flocking birds are safer than solitary birds and alert birds experience less risk than those preoccupied with feeding.

Keywords *Accipiter striatus* · Foraging · Group size effect · Hunting behavior · Predator–prey interactions · Vigilance

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Introduction

The small-bird-in-winter paradigm is a prominent conceptual idea in behavioral ecology. Under this paradigm, small birds must avoid predation from hawks, such as those in the genus *Accipiter*, and avoid starvation during a period of harsh environmental conditions. A small bird cannot maximally avoid both predation and starvation because any behavior that reduces risk from one source of mortality may increase risk from the other. Hence, optimal behavior involves some sort of trade-off between the two risks of mortality. This predation–starvation trade-off is the essence of the small-bird-in-winter paradigm, which has been influential in understanding many aspects of behavior, including sociality (Bertram 1978; Pulliam and Caraco 1984; Sullivan 1984; Dolby and Grubb 2000), foraging behavior (Lima 1985; Stephens and Krebs 1986; Giraldeau and Caraco 2000), body mass regulation and energy management (Cuthill and Houston 1997, Pravosudov and Grubb 1997), and predator–prey theory in general (Mangel and Clark 1988, Houston and McNamara 1999).

Despite its prominence in behavioral ecology, our conceptual understanding of the small-bird-in-winter paradigm is limited. Although much is known about the antipredator behavior of small birds, the behavior of wintering *Accipiter* hawks has seldom been studied. Even basic natural history information such as home range use, prey (but see Roth and Lima 2003), activity patterns, and the propensity to use bird feeders as hunting sites is largely unknown for wintering *Accipiter* hawks (Rosenfield and Bielefeldt 1993; Bildstein and Meyer 2000, but see Dunn and Tessaglia 1994). An exception to this dearth of knowledge on wintering Accipiters is unique work on the behavior of the European sparrowhawk, *Accipter nisus* (Newton 1986; Cresswell 1994a,b, 1996; Whitfield et al. 1999). These studies found that sparrowhawks were most successful when attacking small groups of shorebirds using the tactic of surprise (see also Hilton et al. 1999). While important to the understanding of *Accipiter* behavior, many of these studies dealt with the unusual situation of an *Accipiter* attacking shorebirds on mudflats and do not address the more typical hunting situation of Accipiters (but see Newton 1986 and Selas 1993).

A better understanding of *Accipiter* behavior is clearly necessary for a more complete understanding of the small-bird-in-winter paradigm (Lima 2002). For example, information about *Accipiter* diets may yield an understanding of the degree of risk perceived by different prey. Some species may be prominent in the hawks' diet and, thus, experience high levels of risk, while others may be largely ignored and so experience relatively low risk. For example, Roth and Lima (2003) found that house sparrows (*Passer domesticus*) and other small birds are nearly absent in the diet of wintering urban Cooper's hawks (*Accipiter cooperii*). This fact, combined with a lack of urban sharp-shinned hawks (*Accipiter striatus*), suggests that small birds may suffer very little risk from hawks in urban habitats (Roth and Lima 2003). As another example, an examination of *Accipiter* activity patterns may help to explain the daily activity patterns of small birds. The bimodal activity pattern observed in small birds at feeders can be explained as a compromise between starvation and predation assuming a constant risk of attack over time (McNamara et al. 1994). However, the temporal aspects of *Accipiter* hunting behavior that may affect prey activity patterns have not been assessed. Furthermore, a hawk may focus on prey engaged in risky activities, such as foraging, and ignore prey engaged in nonforaging activities, during which the latter can devote more attention to vigilance. Finally, knowledge of the large-scale movement patterns of hawks may yield a better understanding of the dynamic spatial games between predators and prey, such as the "shell game" (Mitchell and Lima 2002).

A long-term objective of our research is to better understand the small-bird-in-winter paradigm from the hawk's perspective. In this paper, we focus on the determinants of risk in a community of wintering birds in a rural habitat in western Indiana, USA. We specifically examine (1) the types and species of prey attacked and those captured, (2) the general types of attacks used and the relative success of each, and (3) attack success as a function of general prey behavior at the time of attack. Our results suggest that certain prey species are much more at risk than others and that solitary and actively feeding birds are much more likely to be killed than birds in other situations.

Materials and methods

Our study site consisted of a mixture of small residential clusters and peripheral city suburbs, agricultural land, and fragmented forest located mainly in Vigo County, Indiana, USA, immediately southwest of the city of Terre Haute. The site covered approximately 1,000 km^2, as determined by the movement of tracked hawks, although most hawks were tracked in a core area of approximately 100 km^2. The habitat composition of the site was approximately 4% residential, 48% agricultural field (bare earth or stubble in winter), 18% grass/fallow field, 29% forest, and 1% water, as determined by Landsat thematic mapping imagery (30 m resolution) and ArcView 3.2.

Sharp-shinned hawks were trapped during the winters of 2000–2004 from late November to late January using constantly monitored bal chatri traps (Berger and Mueller 1959) and bow nets baited with European starlings (*Sturnusvulgaris*) or house sparrows (*P. domesticus*, Roth and Lima 2003). Traps were positioned conspicuously in open areas or flight corridors, such as edges of open fields, roadsides, power line corridors, bird feeders, and potential roost sites.

Hawks were tracked using radio telemetry. Each hawk was fitted with an appropriately sized, position-sensitive radio transmitter (Holohil, Ontario, Canada; <3% total body mass; males, 2.4 g; females, 3.5–4.5 g) using the pelvic harness of Rappole and Tipton (1994). The position-sensitive transmitters provided information on the activity of the hawks. A slow pulse indicated a perched, stationary hawk. A stationary, rapid pulse rate or fluctuations in pulse rate was indicative of prey consumption where hawks were in a prey consumption posture with alternating bouts of feeding and vigilance. A sustained and mobile rapid pulse rate indicated flight. A sudden switch to the flight signal prompted our attention to a possible attack.

All hawks were tracked by vehicles using yagi and whip antennas. Each hawk was tracked for at least 2 h daily, although tracking times were frequently higher (up to 10 h) depending upon the availability of trackers. Tracking began 0.5–1.0 h before sunrise and ended 0.5–1.0 h after sunset or until all hawks were verified at roost. The hawks tracked first and last each day were rotated systematically to ensure no temporal biases in tracking data. During tracking, we attempted to maintain visual contact from vehicles to more accurately describe hawk behavior. Hawks did not appear to be disturbed in any way by the presence of our tracking vehicles; vehicles were common in the area, even on many of the rural roads.

The location and predatory behavior of hawks were recorded according to Roth and Lima (2003). Hawk 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 other nonflying activities. When an attack was observed, trackers recorded when possible (1) the behavior of the hawk and prey before the attack, (2) attack type, (3) prey flock size, (4) species attacked, and (5) the result of the attack. Prey behavior at the beginning of attacks was categorized as feeding (on ground or in vegetation), flying, or perched (all other nonflying activities). Observed attacks were classified as "open" if they were made where prey could have detected the approaching hawk at 15 m or more, and "surprise" attacks if they were made using visual obstructions, ambush, or contour-hugging flight where prey could not readily detect the hawk during the final leg of the attack. Unlike in Roth and Lima (2003), we could not divide open and surprise attacks into finer subcategories because complete attack sequences were difficult to observe in the relatively dense rural vegetation.

After the hawk had finished consuming its prey and moved well away from the site, trackers would (if possible) intensively search the area for prey remains for at least 30 min. Such searches were conducted only when a precise fix on the location of the feeding site could be determined. All remains were compared to specimens in the Indiana State University Vertebrates Collection to verify species.

During the winters of 2002–2004 (the period during which most hawks were tracked), we estimated the relative abundance of avian prey within the study site. Unlimited-distance 5-min point counts (Bibby et al. 1992) were performed weekly from late December through early March at 48 sites. The point counts were positioned in the center of the study site (covering approximately 30 km^2) and were representative of all major habitat types: forest, forest edge, open fields, and riparian. Edge points (26) were located within 50 m of forest edge; open points (7) were in large, bare or fallow fields >250 m from edge; forest points (9) were located in forested habitat >100 m from edge, and riparian points (6) were within 50 m of a permanent stream. As our hawks rarely hunted in open habitat (Roth and Lima, unpublished data), prey abundance data from such points were excluded. During counts, the distance to each bird was estimated and categorized as 0–49 m, 50–100 m, or >100 m. To reduce observational bias of conspicuous species, observations >100 m from the observer were excluded from our analyses. The relative abundances of species between categories 0–49 m and 50–100 m were virtually identical; thus, we pooled observations across the 0–100 m range. In addition, we pooled all observations for all years in our analysis, as species abundances were highly correlated between years (Pearson Correlation, r=0.934, n=47, p<0.001). All counts were performed in good weather (no precipitation, no strong winds). The order of counts was systematically rotated to avoid temporal biases, and all points were usually completed within the same day (whenever the weather permitted so).

All statistical analyses were performed with Systat 9.0 (SPSS Inc. 1998) using parametric and nonparametric tests as appropriate. We did not have enough observations to make statistical statements about individual hawks, so we report data pooled over all hawks tracked for most analyses. However, individual hawks were broadly similar in hunting tactics and diet (see "Results").

Results

Forty sharp-shinned hawks were trapped during the winters of 2000–2004. Of the hawks captured, 21 were tracked for more than 3 weeks. Many of the hawks tracked for fewer than 3 weeks were depredated or were itinerant and left the study site (Roth et al. 2005). There were no significant differences between the capture rates of either sex, and the age ratio was biased toward immatures (Roth et al. 2005). The average tracking time per hawk was 39.3±6.4 days (mean±SE).

Who is attacked and killed?

We observed a total of 255 attacks and recorded 112 kills by sharp-shinned hawks during the course of the study. The position-sensitive transmitters made it possible to find kills even when the attack was not observed. Thus, the number of kills recorded is not directly related to the number of attacks observed. We initially report results pooled among hawks and then consider sex and individual-level variation. The scientific names of all avian species are listed in Table 1.

Sharp-shinned hawks attacked a wide range of birds, but had a distinct preference for certain species of birds (Table 1). Of the 255 attacks observed for sharp-shinned hawks, prey species was identified in 160 cases, unknown in 68 cases, and identified to unknown sparrow in the remaining 27 cases. Over 75% of the 160 identified attacks involved just five species: house sparrows (21.3%), northern cardinals (15.0%), European starlings (13.8%), American robins (12.5%), and dark-eyed juncos (11.9%) (Table 1). Four of these species were attacked more frequently than expected by their abundance in the environment: house sparrows [attack index (AI)=proportion attacked/proportion in environment=6.5], starlings (AI=2.1), American robins (AI=4.6), and juncos (AI=1.7). Attacks on cardinals largely reflected abundance (AI=0.94). Smaller species such as Carolina chickadees, *Carolina wrens*, American goldfinches, and white-breasted nuthatches were only rarely attacked although they were quite common in the study site (Table 1). Large birds over about 120 g, such as rock pigeons and pileated woodpeckers, were largely ignored.

We retrieved 112 identifiable prey remains over the course of the study (Table 1). In general, the same species that were commonly attacked were those commonly killed (n=23, r=0.685, p<0.001; see also below). The species overrepresented the most in the diet relative to their abundance in the environment were starlings [vulnerability index (VI)= proportion in diet/proportion in environment=2.0], *Zonotrichia* sparrows (VI=5.8), house sparrows (VI=3.6), juncos (VI=1.7), and American robins (VI=4.3) (Table 1). Generally speaking, small birds under about 20 g were commonly observed, but largely absent from the diet. Species such as Carolina chickadees (VI=0.15) and tufted titmice (VI=0.14*)* were greatly underrepresented relative to their availability (Table 1). Hawks neither attacked nor killed any bird species over 120 g. Also greatly underrepresented in the diet were two common intermediate-sized prey, blue jays (VI=0.07) and red-bellied woodpeckers (VI=0.15). Cardinals were also somewhat underrepresented (VI=0.62), even though they were frequent prey (11 cases; Table 1). This

Table 1 Prey, attack success, vulnerability and attack indexes, and relative abundance of prey of sharp-shinned hawks

Prey Species		Mass (g)[a]	Relative abundance			Individuals attacked				Individuals eaten[b]			Vulnerability index[c]	Attack index[c]
			Rank	Number of samples	Percentage	Rank	Number of samples (f, m)[d]	Percentage	Success (%)	Rank	Number of samples (f, m)[d]	Percentage		
Rock pigeon	*Columba livia*	355	25	59	0.8	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Pileated woodpecker	*Dryocopus pileatus*	287	26	33	0.4	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Northern bobwhite	*Colinus virginianus*	178	35	3	<0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Belted kingfisher	*Megaceryle alcyon*	148	32	10	0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Northern flicker	*Colaptes auratus*	133	20	116	1.5	17.5	1 (1, 0)	0.6	0	30.5	0 (0, 0)	0	0	0.4
Mourning dove	*Zenaida macroura*	119	16	172	2.3	6.5	7 (6, 1)	4.4	14.3	9	4 (3, 1)	3.6	1.6	1.9
Common grackle	*Quiscalus quiscula*	114	21	111	1.5	6.5	7 (7, 0)	4.4	14.3	11	3 (2, 1)	2.7	1.8	3
Killdeer	*Charadrius vociferus*	96.6	22	81	1.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Eastern meadowlark	*Sturnella neglecta*	89	33	7	<0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Blue jay	*Cyano cittacristata*	87	2	982	12.9	17.5	1 (1, 0)	0.6	0	18	1 (1, 0)	0.9	0.1	0.1
European starling	*Sturnus vulgaris*	82	4	499	6.6	3	22 (18, 4)	13.8	31.8	1	15 (13, 2)	13.4	2.0	2.1
American robin	*Turdus migratorius*	77	12	205	2.7	4	20 (20, 0)	12.5	20	3	13 (11, 2)	11.6	4.3	4.6
Red-headed woodpecker	*Melanerpes erythrocephalus*	72	23	77	1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Hairy woodpecker	*Picoides villosus*	66.3	31	11	0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Red-bellied woodpecker	*Melanerpes carolinus*	62	6	445	5.8	17.5	1 (1, 0)	0.6	0	18	1 (0, 1)	0.9	0.2	0.1
Cedar waxwing	*Bombycilla cedrorum*	56	29	15	0.2	31.5	0 (0, 0)	0	–	18	1 (0, 1)	0.9	4.5	0
Red-winged blackbird	*Agelaius phoeniceus*	53	10	229	3	9	4 (3, 1)	2.5	25	11	3 (2, 1)	2.7	0.9	0.8
Yellow-bellied sapsucker	*Sphyrapicus varius*	50.3	36.5	2	<0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0

Table 1 (continued)

Prey Species		Mass (g)[a]	Relative abundance			Individuals attacked				Individuals eaten[b]			Vulnerability index[c]	Attack index[c]
			Rank	Number of samples	Percentage	Rank	Number of samples (f, m)[d]	Percentage	Success (%)	Rank	Number of samples (f, m)[d]	Percentage		
Brown-headed cowbird	*Molothrus ater*	49	39.5	1	<0.1	31.5	0 (0, 0)	0	–	13.5	2 (0, 2)	1.8	–	0
Northern mockingbird	*Mimus polyglottos*	48.5	27	22	0.3	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Northern cardinal	*Cardinalis cardinalis*	45	1	1211	15.9	2	24 (21, 3)	15	4.2	5.5	11 (3, 8)	9.8	0.6	0.9
Eastern towhee	*Pipilo erythrophthalmus*	41	28	16	0.2	31.5	0 (0, 0)	0	–	18	1 (0, 1)	0.9	4.2	0
Gray catbird	*Dumetella carolinensis*	36.9	34	5	0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Eastern bluebird	*Sialia sialis*	32	14	199	2.6	10.5	3 (1, 2)	1.9	0	30.5	0 (0, 0)	0	0	0.7
Horned lark	*Eremophila alpestris*	31.4	36.5	2	<0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
House sparrow	*Passer domesticus*	28	8	241	3.2	1	34 (30, 4)	21.3	35.3	3	13 (12, 1)	11.6	3.7	6.6
Downy woodpecker	*Picoide pubescens*	27	9	238	3.1	12.5	2 (2, 0)	1.3	50	8	5 (3, 2)	4.5	1.4	0.4
Zonotrichia sparrows	*Zonotrichia sp.*	26	18	129	1.7	10.5	3 (1, 2)	1.9	33.3	5.5	11 (1, 10)	9.8	5.8	1.1
Purple finch	*Carpodacus purpureus*	24.9	39.5	1	0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Tufted titmouse	*Baeolophus bicolor*	22	5	471	6.2	17.5	1 (0, 1)	0.6	0	18	1 (0, 1)	0.9	0.1	0.1
House finch	*Carpodacus mexicanus*	21	24	67	0.9	8	5 (2, 3)	3.1	20	11	3 (3, 0)	2.7	3.0	3.5
Song sparrow	*Melospiza melodia*	21	15	197	2.6	12.5	2 (1, 1)	1.3	100	7	6 (1, 5)	5.4	2.1	0.5
White-breasted nuthatch	*Sitta carolinensis*	21	13	200	2.6	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
American tree sparrow	*Spizella aborea*	20	19	125	1.6	17.5	1 (0, 1)	0.6	0	13.5	2 (0, 2)	1.8	1.1	0.4
Dark-eyed junco	*Junco hyemalis*	20	3	536	7	5	19 (16, 0)	11.9	21.1	3	13 (3, 10)	11.6	1.6	1.7
Eastern phoebe	*Sayornis phoebe*	19.8	39.5	1	<0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0
Carolina wren	*Thryothorus ludovicianus*	19	17	146	1.9	17.5	1 (0, 1)	0.6	0	30.5	0 (0, 0)	0	0	0.3
Swamp sparrow	*Melospiza georgiana*	17	39.5	1	<0.1	31.5	0 (0, 0)	0	–	30.5	0 (0, 0)	0	0	0

Table 1 (continued)

Prey Species		Mass (g)[a]	Relative abundance			Individuals attacked				Individuals eaten[b]			Vulnerability index[c]	Attack index[c]
			Rank	Number of samples	Percentage	Rank	Number of samples (f, m)[d]	Percentage	Success (%)	Rank	Number of samples (f, m)[d]	Percentage		
American goldfinch	*Carduelis tristis*	13	11	215	2.8	17.5	1 (0, 1)	0.6	0	30.5	0 (0, 0)	0	0	0.2
Field sparrow	*Spizella pusilla*	12.5	30	12	0.2	31.5	0 (0, 0)	0	–	18	1 (1,0)	0.9	5.7	0
Carolina chickadee	*Poecile carolinensis*	10	7	443	5.8	17.5	1 (0, 1)	0.6	0	18	1 (0, 1)	0.9	0.2	0.1
Unknown sparrow		–		71	0.9	–	–	–	–	–	–	–		
Unknown mammal		–		–	–	–	–	–	–	–	1 (0,1)	0.9		
Total					7607		160 (131, 29)		22.8		112 (60, 53)			

Species are listed in decreasing order of body mass
[a]Body mass data are taken from Dunning (1993)
[b]Includes cases located without observation of the attack and cases resulting from observed successful attacks
[c]See text for calculations
[d]*f* Females, *m* males

result may be the due to observational bias, i.e., cardinals may have been overcounted due to their conspicuous coloration. Still, cardinals were the second most frequently attacked species and the third (tied with *Zonotrichia* sparrows) most frequent species in the diet (Table 1).

While the number of prey collected for each individual varied, individual hawks did not specialize on any particular prey species or size. The number of prey collected for any given hawk ranged from 1 to 22 with a mean of 5.1±1.22 (mean±SE). Hawks, for which we collected four or more prey (n=9), killed from four to eight species, suggesting no evidence of individual specialization. Much of the variation in the number of retrieval of kills was due to hawk activity in areas to which we had limited or no access. Note, however, that access to kills was generally a function of land ownership and not of vegetation type or terrain. Thus, we do not believe that individuals in particular habitats were overrepresented in the data set or prey choice by hawks in "low access" areas differed systematically from that of other hawks.

One case of prey specialization in our data set was apparent when comparing hawks by sex. Male and female sharp-shinned hawks differ substantially in size [males, n=18, 101.46±2.3 g, (mean±SE); females, n=22, 171.06±2.4 g]; thus, they may attack or kill different-sized prey (Mueller et al. 2000; see Table 1). To examine the effect of sex on prey size selection, we calculated the mean prey size taken for each individual hawk and compared these values between the sexes. Male sharp-shinned hawks attacked significantly more small prey (e.g., sparrows) than did females (Mann–Whitney U test, U=109, n=21, p=0.008) and likewise killed significantly smaller prey (U=90, n=21, p=0.006). Interestingly, however, the species killed by each sex overlapped almost completely (Table 1). Even the largest species in the diet (mourning dove, 119 g) was killed by a male, while one of the smallest species (field sparrow, 12.5 g) was killed by a female.

Attack success and prey behavior

Sharp-shinned hawk capture success (22.5%, 36 of 160 identified attacks, sexes pooled) did not vary systematically across prey species. The rank of prey species killed was strongly correlated with that of prey attacked (Spearman rank correlation, r = 0.796, n = 41, p<0.001), indicating no major differences in prey catchability across species. When species that were neither attacked nor killed were excluded from the analysis, the relationship was similarly strong and significant (r = 0.751, n = 25, p<0.001).

Prey behavior at the point of attack, however, had a significant effect on success. Combining across all prey species (as suggested by a nonsignificant effect of species on attack success, Yates corrected χ^2=13.5, df=17, p=0.702), solitary birds were more likely to be captured during an attack than those in a group (Fig. 1a; χ^2=9.73, df=1, p=0.002). The relative vulnerability of solitary prey held for large prey (>70 g; Fig. 1b; χ^2=6.52, df=1, p=0.011) and smaller prey (<70 g; Fig. 1c; χ^2=4.07, df=1, p=0.044). This effect of sociality also held in specific prey types for which we had many observed attacks, such as sparrows (emberizids and house sparrows combined; Fig. 1d; χ^2=5.22, *df*=1, *p*=0.022). Furthermore, actively feeding prey were much more likely to be killed during an attack than were prey that were perched or in flight (Fig. 2; χ^2=8.206, *df*=2, *p*=0.016). Preys that were feeding were over four times more likely to be killed during an attack than prey that were not feeding.Despite this effect, hawks made numerous attempts to capture perched prey. We performed independent analyses on group size and behavior as solitary prey were not more likely to be feeding than groups of prey (χ^2=3.60, *df*=2, *p* = 0.166).

Basic predatory behavior

Most attacks made by sharp-shinned hawks were surprise attacks at close quarters. We were able to classify 137 attacks as surprise or open; of these, the great majority (117 or 85.4%) was surprise attacks. However, we observed no significant difference in the success rates between the attack strategies (open: 11.1%, 2 of 18 attacks successful; surprise: 13.6%, 14 of 103 attacks successful; χ^2=0.064, *df*=1, *p*=0.800).

After a successful attack, sharp-shinned hawks consumed their prey in secure areas. Nearly 90% of prey (33 of 37 known cover locations) were consumed in dense cover on the ground or on a perch <1 m above ground; the remaining prey (4) were consumed in trees >1 m above the ground. Most preys were completely consumed with the exception of the larger flight feathers, a smaller proportion of contour feathers, and occasionally the skull, bill, and legs. In eight cases, hawks cached the carcass and returned to it the following day. Catched preys were mainly larger birds (e.g., mourning doves) that were captured late in the day leaving insufficient time for complete consumption.

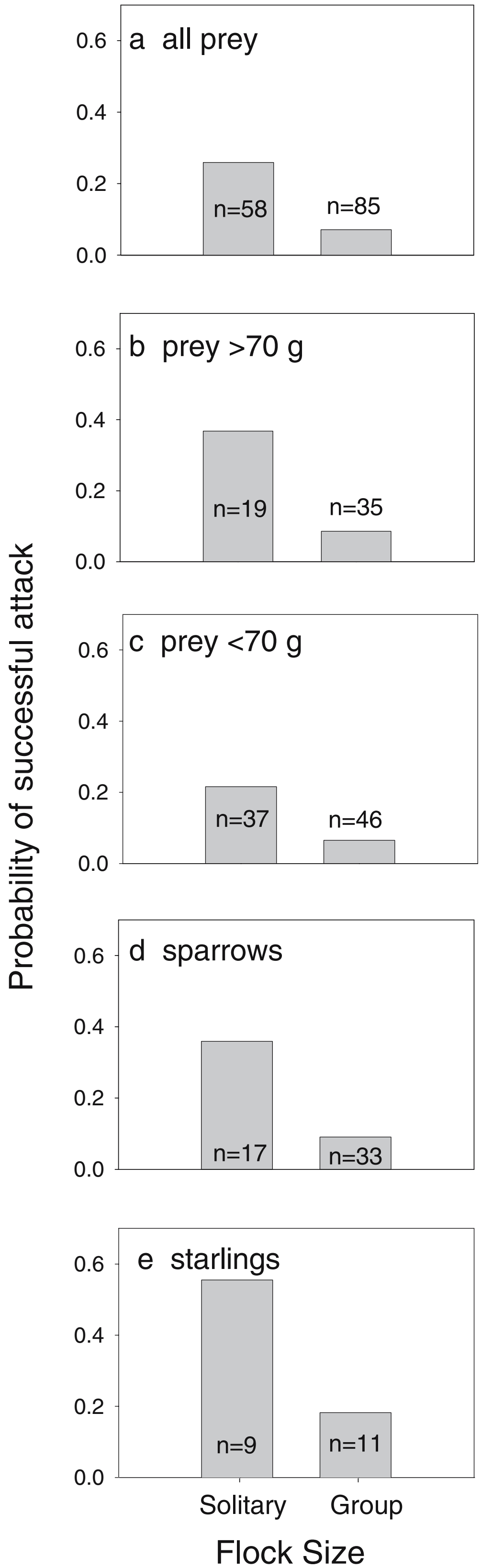

Fig. 1 The effect of flock size on attack success for wintering sharp-shinned hawks. Attacks are pooled over **a** all prey species, *n*=143, **b** large prey (>70 g), *n*=54, **c** small prey (<70 g), *n*=83, **d** sparrows

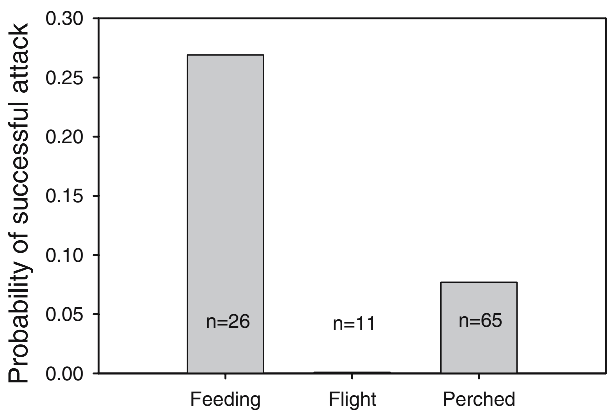

Fig. 2 Attack success of wintering sharp-shinned hawks as a function of prey behavior at the time of attack. Feeding prey were those foraging on the ground or in a tree, and flight denotes a prey attacked in flight. All other nonfeeding behaviors are categorized as perched

Discussion

While many studies focus on the behavior of small wintering birds, few consider the behavior of their predators. As a result, our understanding of the small-bird-in-winter paradigm is quite “one-sided.” We present, to our knowledge, the first description of the predatory behavior of wintering sharp-shinned hawks, focusing on their prey and attack success. In addition, we consider the success of hawk attacks relative to the behavior of their prey, a rare result in empirical studies of predator–prey interactions (Lima 2002).

The wintering sharp-shinned hawks at our study site attacked primarily sparrow-sized prey, intermediate-sized starlings and American robins, and the occasional larger prey, such as mourning doves (see also Mueller and Berger 1970.) These hawks focused virtually exclusively on birds, as did the Cooper’s hawks in our site (Roth and Lima 2003). Female hawks took significantly larger prey than males, although both males and females were capable of killing the same range of prey items. Aside from the northern cardinal, the prey species most abundant in the diet were also those overrepresented relative to their availability in the environment (Table 1). House sparrows and American robins were particularly abundant in the diet representing nearly seven- and fivefold increases, respectively, in the diet relative to the environment (Table 1). The hunting behavior of sharp-shinned hawks was based on surprise and the use of visual obstructions, which appears to be typical of Accipiters (Newton 1986; Cresswell 1996; Roth and Lima 2003). Furthermore, solitary prey (Fig. 1) and those that were feeding (Fig. 2) were especially vulnerable during an attack by sharp-shinned hawks.

Small bird species such as chickadees and their mixed-flock associates have played a prominent role in the small-bird-in-winter paradigm (e.g., Lima 1985; Smith 1991; Dolby and Grubb 1998), but such species were largely avoided as prey by the sharp-shinned hawks at our site. We observed a few attacks on parids and other small species (Table 1), so they are not entirely without risk of death. However, generally speaking, small prey under 20 g may simply not be worth including in the diet as per optimal foraging theory (Stephens and Krebs 1986). Additionally, some of these small species may be difficult for sharp-shinned hawks to capture. Carolina chickadees, tufted titmice, and white-breasted nuthatches, for example, typically form mixed-species flocks during the winter and feed primarily in the mid- to upper tree canopy. Due to the increased vigilance benefits of these flocks (Dolby and Grubb 1998; Greenberg 2000) facilitated in part by open canopy, these preys may be difficult to approach. Furthermore, many of these species, as well as blue jays (*Cyanocitta cristata*), conspicuously respond to predators with mobbing or alarm calling, which may further make a stealthy approach by a hawk difficult. Thus, the small energetic return of these species may not outweigh the additional hunting costs necessary to catch them, both in terms of time spent exposed to predators and lost opportunities to hunt other prey.

What then is an appropriate small bird in the small-bird-in-winter paradigm? While parids and the like were generally avoided, relatively small dark-eyed juncos (20 g), zonotrichid sparrows (26 g), and house sparrows (28 g) were frequently killed by sharp-shinned hawks. These sparrows tend to feed on the ground in edge habitat and, thus, may be easily attacked using visual obstructions and surprise, the most common hunting strategy of hawks observed in this study. Intermediate-sized prey, such as robins (77 g) and starlings (82 g), were also among the top species killed, particularly by females. Thus, at our site, it seems that preys in the range between 20 and 85 g are the typical size of prey taken by sharp-shinned hawks. Surprisingly, even some larger prey such as common grackles (114 g) and mourning doves (119 g) were killed by hawks in this study, including males. Although conducted in the breeding season, Selas (1993) found nearly the same result in southern Norway. Sparrowhawks focused on ground-dwelling prey 51–80 g and avoided prey <15 g and >250 g. Thus, the apparent lack of parids and other very small prey in the diet of sharp-shinned hawks suggests that we might reconsider the conceptual prey in the paradigm and focus on ground-feeding, sparrowlike, and larger birds as the main prey base of Accipiters. We do, however, accept the idea that predation is still a major factor shaping the behavior of small birds such as parids.

One of the tenets of the small-bird-in-winter paradigm is that flocking birds are safer than solitary birds (Elgar 1989; Beauchamp 2003; Lima et al. 1999; Greenberg 2000). There are literally hundreds of studies on vigilance and sociality in birds, but very few demonstrations that social birds are actually safer. In this study, solitary prey were considerably more likely to be captured during an attack. Without the benefit of collective detection, it appears that hawks can approach solitary prey more closely before being detected and thus are more successful. These results are consistent with previous studies on the effects of flock size on predatory success in European sparrowhawks hunting shorebirds (Whitfield 1985; Wilson and Weir 1989; Cresswell 1994a; Cresswell and Whitfield 1994; Cresswell 1996) and finches (Lindstrom 1989), and urban Cooper’s hawks hunting larger prey such as mourning doves and starlings (Roth and Lima 2003).

Another assumption of the small-bird-in-winter paradigm is that feeding birds should be more at risk than prey engaging in nonfeeding activities (e.g., Kaby and Lind 2003). This idea, however, has rarely been addressed in birds (but see Gotmark and Post 1996) and is limited elsewhere (e.g., Krause and Godin 1996). We observed that preoccupied prey, i.e., those that were feeding, had a significantly greater probability of being killed during an attack relative to those perched or those engaged in other nonfeeding activities (Fig. 2). These observations represent some of the first evidence of the foraging costs paid by prey as demonstrated from the perspective of their predator (see also Cresswell et al. 2003) and support the assumption of Bednekoff (1997) that alert animals or those acting as sentinels experience a relatively low risk of predation.

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