

The predatory behavior of wintering *Accipiter* hawks: temporal patterns in activity of predators and prey

Timothy C. Roth II · Steven L. Lima

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Abstract Studies focused on how prey trade-off predation and starvation risk are prevalent in behavioral ecology. However, our current understanding of these trade-offs is limited in one key respect: we know little about the behavior of predators. In this study, we provide some of the first detailed information on temporal patterns in the daily hunting behavior of bird-eating *Accipiter* hawks and relate that to their prey. During the winters of 1999–2004, twenty-one sharp-shinned hawks (*A. striatus*) and ten Cooper’s hawks (*A. cooperii*) were intensively radio tracked in rural and urban habitats in western Indiana, USA. Cooper’s hawks left roost before sunrise and usually returned to roost around sunset, while sharp-shinned hawks left roost at sunrise or later and returned to roost well before sunset. An overall measure of Cooper’s-hawk-induced risk (a composite variable of attack rate and activity patterns) generally reflected the timing of prey activity, with peaks occurring around sunrise and sunset. In contrast, risk induced by the smaller sharp-shinned hawk did not strongly reflect the activity of their prey. Specifically, an early morning peak in prey activity did not correspond to a period with intense hawk activity. The lack of early morning hunting by sharp-shinned hawks may reflect the high risk of owl-induced predation experienced by these hawks. The net effect of this intraguild predation may be to “free” small birds from much hawk-induced predation risk prior to sunrise.

This realization presents an alternative to energetics as an explanation for the early morning peak in small bird activity during the winter.

Keywords Activity patterns · Cooper’s hawk · Foraging game · Predator–prey interactions · Sharp-shinned hawk

Introduction

Decisions made by key species under the risk of predation can affect the dynamics of an entire community (Peacor and Werner 2000; Schmitz et al. 2004; Fortin et al. 2005). A better understanding of the broader impacts of predator/prey interactions requires knowledge of the behaviors that produce these interactions from the perspectives of both predator and prey. However, most studies that focus on how animals make decisions under the risk of predation typically focus on the behavior of prey, while making assumptions about the behavior of the predator (Lima 2002). As a result, predators are often treated as a generalized source of risk rather than active participants in a predator–prey interaction (Lima 2002). Such treatment leaves us with little conceptual understanding of predator behavior and promotes further conceptual simplification of their behaviors (e.g., Lima 1985), which often results in generalizing risk based on habitat type or some other easily measured environmental feature (see Caro 2005). Consequently, we frequently neglect the fact that predators also make decisions, respond to their prey and their own predators, and manage trade-offs, and thus participate in a complex foraging game with prey (Brown et al. 1999).

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T. C. Roth II (✉) · S. L. Lima
Department of Ecology & Organismal Biology,
Indiana State University, Terre Haute, IN 47809, USA
e-mail: TRoth@indstate.edu

In this paper, we examine temporal patterns of predator/prey interactions. The timing of activity is one aspect of predator/prey interaction that can be flexible and dependent upon the activity of one's own predator or prey (Sih 1992; Hugie 2003). The activity of prey relative to predation risk has been studied in a number of different taxa (see Lima 1998; Kronfeld-Schor and Dayan 2003 for review). For example, zooplankton undergo diel vertical migration to avoid visual predators during the day. In doing so, they trade-off the availability of food at the surface where visual predators are common against a lower risk of predation in the deeper water (Lampert 1989; Fiksen and Giske 1995). Similarly, desert rodents reduce foraging activity during periods of bright moonlight, when they would be under a greater risk of predation from owls (Kotler et al. 1991, 1994; Bouskila 1995). Such studies highlight the importance of temporal patterns in vulnerability to predators for prey behavior, but they do not fully consider the behavior of predators per se.

In fact, relatively few studies have examined the activity patterns of both predators and prey. Such studies that have done so report that prey avoid predators by shifting their activity to times when the predator is temporally restricted and cannot follow. For example, Fenn and MacDonald (1995) documented a population of Norway rats (*Rattus norvegicus*) that seemed to become diurnal to escape predation pressures from their nocturnal predators, foxes (*Vulpes vulpes*). In the absence of foxes, the rats reverted back to their normal nocturnal behavior, suggesting that predation pressure was the key to their switch in activity patterns. Such work, however, has been focused mainly on animals that can be both nocturnal and diurnal, such as mammals and fish (Kronfeld-Schor and Dayan 2003), so the possibility of temporal escape from predators is relatively high. Less work has been dedicated to the more subtle shifts in activity by animals that are relatively temporally restricted, such as diurnal birds (but see Van der Veen 2000).

We focus on the temporal interactions between wintering *Accipiter* hawks and their avian prey under the "small-bird-in-winter" research paradigm. The small bird in winter is one of the principal conceptual paradigms in behavioral ecology, in which small wintering birds maximize their fitness by avoiding both starvation and predation by *Accipiter* hawks. Behavioral options that lessen one of these two risks often increase the other. Thus, small birds must trade-off the risk of starvation against the risk of predation when making behavioral decisions. Understanding this sort of trade-off has had a great impact on our present understanding of sociality (Bertram 1978; Pulliam and Caraco

1984), foraging behavior (Lima 1985; Stephens and Krebs 1986; Cuthill and Houston 1997; Giraldeau and Caraco 2000), energy management (Pravosudov and Grubb 1997; Lind et al. 1999), and behavioral theory in general (Mangel and Clark 1988; Houston and McNamara 1999). A trade-off between starvation and predation may be the driving factor behind the bimodal pattern of activity in small birds (McNamara et al. 1994). However, this explanation for small bird activity does not consider a behaviorally responsive predator.

Despite its prominence in the conceptual foundations of behavioral ecology, however, our present view of the small-bird-in-winter paradigm is lacking in one key respect: we know very little about the hawks. We have some insights into the diet and attack behavior of European sparrowhawks (*A. nisus*; e.g., Newton 1986; Cresswell 1996; Cresswell et al. 2003), Cooper's hawks (*A. cooperii*; e.g., Roth and Lima 2003, 2006a), and sharp-shinned hawks (*A. striatus*; e.g., Roth et al. 2006). However, we know very little about how these hawks move across a landscape (see Roth and Lima 2006b) and know even less about the timing of their activity and how they might influence the activity of prey. As a result, we have a poor understanding of the large-scale interactions between these hawks and their prey. A better understanding of such interactions is important not only for the small-bird-in-winter paradigm, but also for predator/prey ecology in general (Lima 2002; see also Lind and Cresswell 2005).

Thus, we examined the temporal aspects of the predatory behavior of wintering sharp-shinned hawks (*A. striatus*) and Cooper's hawks (*A. cooperii*) and compared their activity to that of their prey. We found that Cooper's hawk hunting activity peaked before sunrise and then again slightly before sunset and largely coincided with the activity of their prey. In contrast, sharp-shinned hawks generally avoided hunting in the crepuscular periods. Consequently, small avian prey typically taken by sharp-shinned hawks may have been free to forage at relatively low risk during a brief period prior to sunrise when these hawks were largely inactive.

Materials and methods

Study sites

Our study site was centered in Vigo County in west-central Indiana and adjacent Clark County in eastern Illinois, USA. The area was divided into two distinct habitats: urban and rural. Our approximately 40-km² urban study site was the city of Terre Haute, Indiana

(population 60,000; 39°27.1'N, 087°18.5'W). We focused on Cooper's hawks in this urban habitat mainly during the winter seasons of 1999–2001 (see also Roth and Lima 2003), although one Cooper's hawk was tracked into the city during the winter of 2003–2004. Approximately 30% of this urban site consisted of high density residential and commercial areas (>14 buildings/block), while the remaining 70% was lower density residential areas (<14 buildings/block; topologically integrated geographic encoding and referencing data, U.S. Census Bureau, Geography Division 2000). We attempted to study sharp-shinned hawks in this urban setting, but none were trapped in the city and few were observed (Roth and Lima 2003).

We focused on sharp-shinned hawks in our rural study site, which included all areas to the immediate southwest of the urban site. The rural study site covered approximately 1,000 km² although most of the tracking was done within a 100-km² core area. This site consisted of a mixture of small clusters of houses or sparse city suburbs, agricultural land, and fragmented forest. The habitat composition of this area was approximately 4% residential, 48% agricultural field (bare in winter), 18% grass/fallow field, 25% upland forest, 4% bottomland forest, and 1% water (lakes, ponds, river, or wetland).

Hawk capture and tracking

Trapping was conducted from late November through late January during each winter using constantly monitored bal chatri traps (Berger and Mueller 1959) and bow nets. Traps were baited with European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*), which were later released unharmed. These traps were positioned in open areas, potential hawk travel paths, and potential roost locations. Areas such as parking lots, cemeteries, and recreational parks were commonly used for trapping in the city, whereas forest edges, roadsides, power lines, and long-established bird feeders were used in the rural site.

Hawks were tracked using radio telemetry. Hawks were fitted with 2.4- to 11.0-g position-sensitive transmitters (Holohil; male sharp-shinned hawks, 2.4 g; female sharp-shinned hawks, 3.5–4.5 g; male Cooper's hawks, 4.2–5.8 g; female Cooper's hawks, 6.9–11.0 g) using the pelvic harness of Rappole and Tipton (1994; see also Roth and Lima 2003). These position-sensitive transmitters provided information on posture and were instrumental in observing attacks, determining their success, and finding the remains of prey. A horizontal (rapid) signal was an indication that the hawk was in flight whereas a slow signal indicated a perched hawk.

Frequent fluctuations in pulse rate of a stationary signal, the result of repeated bouts of plucking/feeding (head down) and vigilance (head up), was a reliable indication of prey consumption (Roth et al. 2006).

Tracking was conducted intensively from the day of capture. All hawks were tracked no less than 2 h daily (although frequently up to 10 h depending upon the number of hawks and trackers available) from vehicles using yagi and whip antennae. The first and last hawk tracked each day was determined systematically, and all hawk roosts were verified each night. In addition, activity was monitored at roosts 0.5–1 h before sunrise and up to 0.5–1 h after sunset to determine, respectively, the time of morning roost departures and evening arrivals. In the unusual event that a hawk switched roost trees between nights, the new roost was verified by remaining at the new site until at least 30 min after sunset.

Temporal patterns in hawk activity

For our temporal analyses, the day was divided into bins with sunrise referenced at 0.0 and sunset referenced at 1.0 to standardize day length (i.e., photoperiod) during the study. Given that the typical day length during the study was approximately 10 h, our 0.10 day time bins represents approximately 1.0-h intervals. The absolute interval of time bins was slightly shorter around the winter solstice and longer late in the winter.

As repeated observations of the same individual may not be statistically independent, we avoided the pooling of data across hawks whenever possible. Instead, we characterized the average activity of individual hawks and then used each hawk-specific point as an independent datum. To characterize roosting behavior, the proportion of roost departures and arrivals that occurred in each time bin was calculated for each hawk. The data were then summarized as the mean hawk-specific proportion of departures and arrivals in each time bin for each species. In addition, the general activity of hawks was categorized broadly as "out-of-roost" and "active-when-out". Hawks were considered to be out-of-roost when they had moved at least 50 m (spatial resolution based on the estimation of telemetry error; White and Garrott 1990; T. C. Roth and S. L. Lima, unpublished data) from their roost tree and until they returned to roost. Actively hunting hawks (active-when-out) were defined as those hawks that were out-of-roost, not handling prey, and not in a digestive pause (defined as the period after prey consumption up to the next movement >50 m). The proportion of time spent out-of-roost and actively hunting

was calculated for each individual during each time bin. For both measures of activity, these proportions were calculated as the number of points out-of-roost or active-when-out divided by the total time tracked. We report proportions as means \pm SE calculated over all tracked hawks.

When calculating attack rates, we were forced to pool data across hawks because we did not have sufficient data to examine individuals. Attack rates were estimated as the total number of attacks observed divided by the total amount of time spent tracking for each bin. For these pooled analyses, sample sizes (both the number of individual hawks and the total number of points) are given for each analysis in the text and figure legends.

Prey activity and abundance

We collected data on the daily temporal activity of prey across the winter. In the rural site, a long-established feeder in the center of the site was monitored with video cameras during the winter periods of 1999–2000 and 2002–2003. The feeder was stocked continuously with millet to attract small, sparrow-sized species that are typical prey of sharp-shinned hawks, such as dark-eyed juncos (*Junco hyemalis*), white-throated sparrows (*Zonotrichia albicollis*), American tree sparrows (*Spizella arborea*), and northern cardinals (*Cardinalis cardinalis*; Roth et al. 2006). We recorded all activity at the site from 1 h before sunrise to 1 h after sunset daily for the entire winter (mid December through early March) using time-lapsed video (1 frame/s). Abundance was estimated as the mean number of birds at the feeder over a 1-min period every 3 min.

We estimated the abundance and activity of prey feeding in the urban site using 5-min unlimited-distance point counts (Bibby et al. 1992), since our urban Cooper's hawks did not hunt birds that typically visit bird feeders (Roth and Lima 2003). All counts were performed 3 times weekly at eight locations during the winter of 2005. The point counts were positioned near the center of the urban study site and were representative of major urban feeding areas for the main prey of Cooper's hawks (Roth and Lima 2003): European starlings (*S. vulgaris*), mourning doves (*Zenaidura macroura*), and rock pigeons (*Columba livia*). Points were located in the parking lots of fast-food restaurants or other businesses in clear sight of multiple trash dumpsters (three), in open areas dominated by large buildings and businesses (three), and in city parks (two). Prey abundance was recorded as the mean sum of feeding prey at each count location throughout the winter.

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 for a given cycle were completed within the same day.

Comparison of predator and prey activity

To compare the activity of predators to that of prey, we fit both predator and prey activity to the same scale and determined the statistical significance of the difference in values for each time interval. We first independently standardized each set of prey and predator data ($n = 12$ time bins for each group, mean = 0, variance = 1), and then calculated the difference between predator and prey z -scores within each time bin. We then bootstrapped z -score differences without replacement ($n = 1,000$ replicates) from the distribution of predator and prey values observed throughout the entire day. We compared the observed difference values in each time bin to their respective bootstrapped distribution to estimate a P -value for each observed difference (Bonferroni adjusted $\alpha = 0.004$). All statistical analyses were performed using SYSTAT 10.0 (SPSS 1998).

Results

A total of 40 sharp-shinned hawks (rural site) and 13 Cooper's hawks (urban site) were captured and tracked during the study. Of these hawks, 21 sharp-shinned and ten Cooper's hawks were tracked for at least 4 weeks (range = 4–20 weeks) and considered in the following analyses, although not all hawks had usable data in all analyses. Hawks not included were lost due to transmitter failure, mortality, or a quick departure from the study area (Roth et al. 2005). Overall, we present data from 6,976 h of radio tracking (Cooper's hawks = 1,667 h; sharp-shinned hawks = 5,309 h).

Hawk roost departure and arrival

Cooper's hawks tended to leave the roost early and arrive at the roost late. Over 80% of Cooper's hawk roost departures occurred before sunrise and about 60% of arrivals occurred after sunset (Fig. 1). In fact, several individuals were occasionally observed hunting by moonlight and flushing prey from their roosts (see also Newton 1986). Surprisingly, there was no significant effect of having made a kill on the timing of roost entry. The proportion of Cooper's hawks returning to

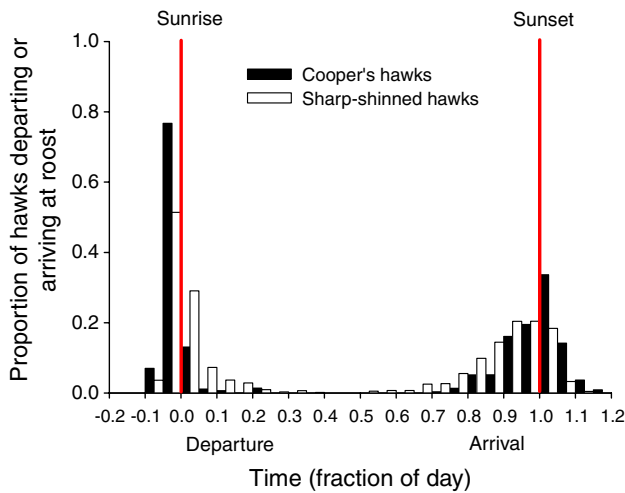


Fig. 1 Mean proportion of roost departure (before time 0.5) and arrival (after time 0.5) times of Cooper’s hawks (*Accipiter cooperii*; dark bars; $n = 8$ hawks, 248 departures and arrivals) and sharp-shinned hawks (*A. striatus*; light bars; $n = 21$ hawks, 1,185 departures and arrivals) in each time bin. The resulting approximate distributions are not true distributions in that they do not sum to 1.0. Time 0.0 represents sunrise, time 1.0 represents sunset, and time bins represent approximately 0.5-h intervals

roost after a kill, either during the time bin of the kill or the next bin, was not significantly different from those that had not made a kill (Wilcoxon signed rank test, $t = 0.944$, $n = 12$, $P = 0.345$; Fig. 2a). These results suggest that even after having consumed a meal, the Cooper’s hawks did not have a strong incentive to return to roost.

Sharp-shinned hawks tended to leave the roost later than Cooper’s hawks (Fig. 1). The mean standardized individual departure time of sharp-shinned hawks ($X \pm SE = -0.012 \pm 0.006$) was significantly later than that of Cooper’s hawks (-0.044 ± 0.004 ; $t_{29} = -3.244$, $P = 0.003$). Approximately 50% of sharp-shinned hawks left the roost after sunrise with many of those departures occurring well after sunrise (Fig. 1). Sharp-shinned hawks arrived at the roost relatively early (Fig. 1), with nearly 80% of hawks arriving at the roost before sunset, and 95% arriving by approximately 30 min after sunset (standardized time 1.05, Fig. 1). The mean individual arrival time of sharp-shinned hawks (0.891 ± 0.012) was significantly earlier than that of Cooper’s hawks (0.961 ± 0.011 ; $t_{29} = 3.184$, $P = 0.003$). Unlike Cooper’s hawks, sharp-shinned hawks tended to return to roost after an afternoon kill. The proportion of sharp-shinned hawks returning to roost during the same time bin in which they made a kill or the following bin was significantly different from those that had not made a kill (Wilcoxon signed rank test, $t = 2.201$, $n = 12$, $P = 0.028$; Fig. 2b). However, as sunset approached (standardized time of approxi-

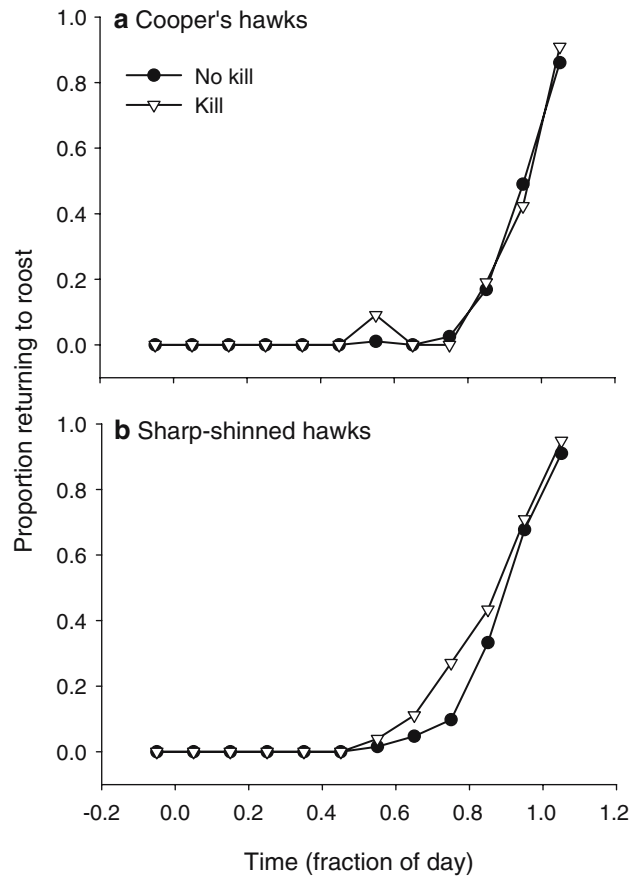


Fig. 2 The proportion of **a** Cooper’s hawks and **b** sharp-shinned hawks returning to roost after no kill (filled circle) or making a kill (downward triangle) in the current or previous time interval. Cooper’s hawk data were pooled across eight individual hawks and consisted of 1,547 returns to roost with no kill and 176 returns after having made a kill. Sharp-shinned hawk data were pooled across 21 hawks and consisted of 6,548 returns without a kill and 1,102 returns after having made a kill. For explanation of x-axis, see Fig. 1

mately 0.90, Fig. 2b), all out-of-roost sharp-shinned hawks were returning to roost regardless of whether they had recently eaten (Fig. 2b).

Proportion active

The mean proportion of hawks out-of-roost generally followed the trends of roost arrivals and departures. Cooper’s hawks tended to be more active earlier and later than sharp-shinned hawks. The proportion of Cooper’s hawks out-of-roost was significantly higher ($t_{29} = -2.973$, $P = 0.006$) than that of sharp-shinned hawks during the first time bin but only marginally so during the last time bin ($t_{29} = -1.887$, $P = 0.069$; Fig. 3a and b). The proportion of hawks out-of-roost for both species for most of the day was >0.90 . The proportion of hawks that were active-when-out of roost peaked

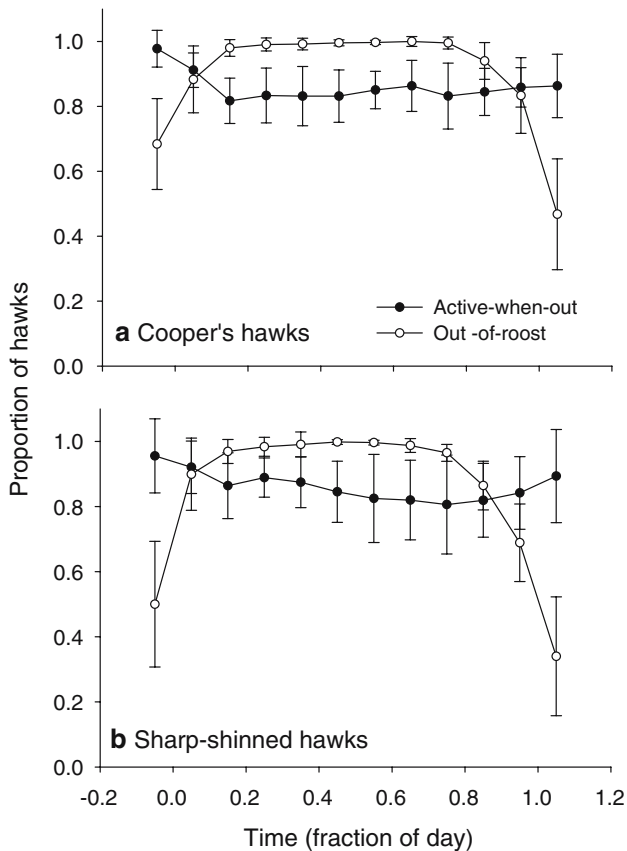


Fig. 3 The proportion of **a** Cooper's hawks ($n = 10$ hawks, 10,003 points) and sharp-shinned hawks ($n = 20$ hawks, 31,855 points) actively hunting (filled circle) and out-of-roost (not including hunting; open circle). Hawks out-of-roost but not actively hunting are those that were feeding or in a digestive pause (see text for details). Points represent the mean percent out for all hawks in that time bin ± 1 SD. For explanation of x -axis, see Fig. 1

early and remained relatively constant at approximately 0.80–0.85 for most of the day in both species. In other words, about 15–20% of hawks were “inactive” at most points in the day due to ongoing prey consumption or digestive pauses.

Composite measure of overall risk

To estimate the overall risk of predation that may be experienced by small wintering birds over the course of the average day, we calculated the standardized, time-bin-specific product of three measures of hunting activity: proportion out-of-roost, proportion actively hunting, and attack rate. Independently, these measures do not fully reflect the hunting patterns of *Accipiter* hawks. However, when combined as a product, we get a better estimate of the average temporal pattern in the risk of attack experience by feeding birds.

Overall, we observed 253 attacks by sharp-shinned hawks and 211 attacks by Cooper's hawks. Considered

alone, attack rate was not constant during the day. Cooper's hawk attack rate peaked just before sunrise and then remained relatively constant throughout the day with a small increase around sunset (Fig. 4a). The sharp-shinned hawk attack rate was largely constant throughout most of the day, with a noticeably low rate just before sunrise and a marked peak around sunset (Fig. 4b).

For both sharp-shinned and Cooper's hawks, the pattern of overall risk throughout the day (Fig. 5) broadly reflected the temporal patterns of attack rates (Fig. 4). Since the proportions active and out-of-roost were generally constant during the bulk of the day, the main influences of these two variables on overall risk occurred at the beginning and the end of the day. Overall risk induced by Cooper's hawks peaked before sunrise, fell in the middle of the day, and remained relatively constant with a small increase just before sunset, after which it dropped to its lowest point (Fig. 5a). The post sunset drop in overall risk was largely the result of fewer hawks hunting around sunset. Risk induced by sharp-shinned hawks was low before sunrise, increased just after sunrise and remained relatively constant during the day, peaked just before sunset, and then fell back to a low level after sunset (Fig. 5b).

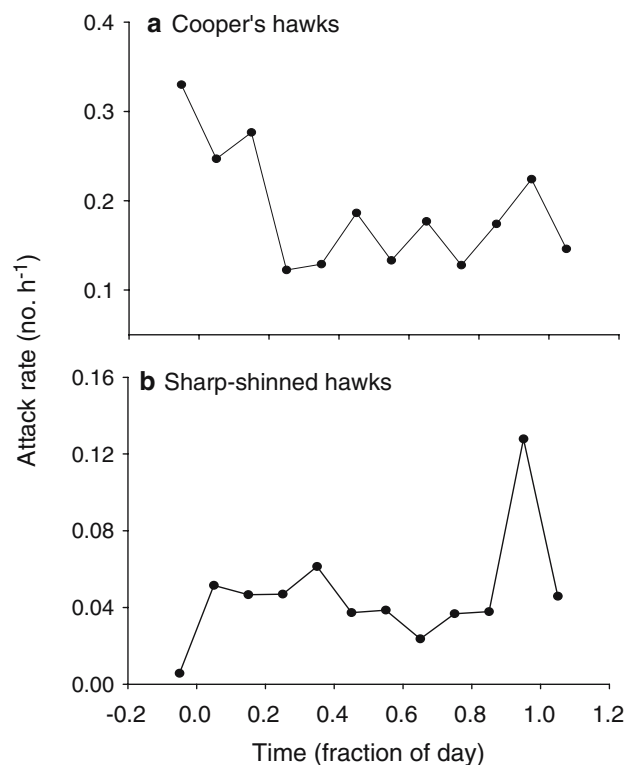


Fig. 4 Attack rates (no. attacks per hour tracked) for **a** Cooper's hawks ($n = 9$ hawks, 211 attacks, 11–30 range per bin) and **b** sharp-shinned hawks ($n = 21$ hawks, 253 attacks, 1–44 range per bin). For explanation of x -axis, see Fig. 1

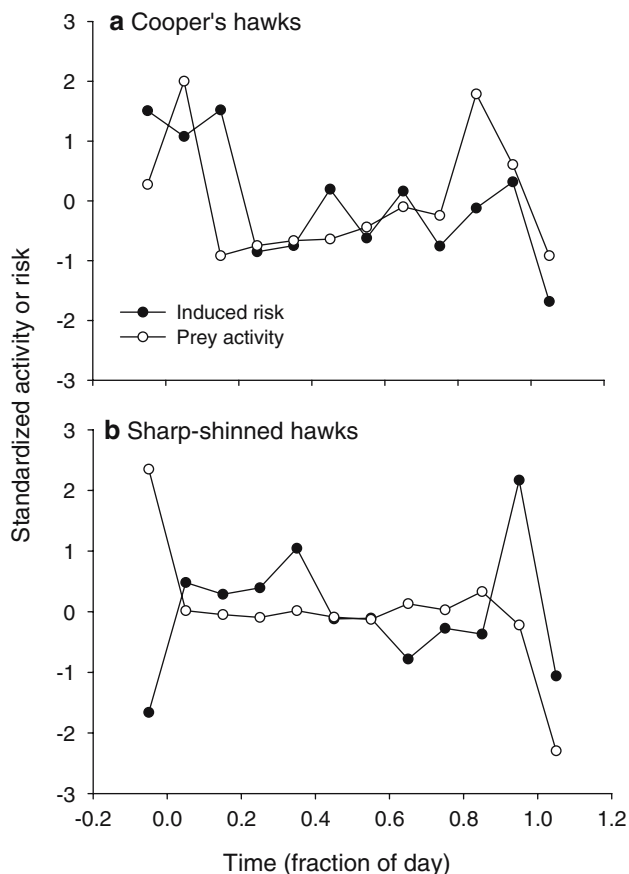


Fig. 5 A comparison of the standardized activity of prey (*open circle*) and hawk-induced risk (*filled circle*) in **a** urban point counts ($n = 25$ count replications at eight locations) and **b** a rural feeder ($n = 165$ days of observation, 33,839 points counted). Estimates of hawk-induced risk for **a** Cooper's hawk and **b** sharp-shinned hawks were calculated as the proportion out-of-roost \times proportion actively hunting \times attack rate (see text for details). For explanation of x-axis, see Fig. 1

Prey activity

In the urban site, prey activity (mostly European starlings, mourning doves, and rock pigeons) peaked just after sunrise and again just before sunset, but was low during the middle of the day (Fig. 5a). Similarly, urban Cooper's-hawk-induced risk peaked in the morning (Fig. 5a), although the evening increase in risk was not as marked as that observed in prey activity (Fig. 4a). None of the differences between the standardized time-bin-specific (z -score) values for Cooper's-hawk-induced risk and urban prey activity were significant as determined by bootstrapping randomization procedure (see Materials and methods; all P s > 0.13).

Small bird abundance (mostly dark-eyed juncos, American tree sparrows, white-throated sparrows, and northern cardinals) at the rural feeder site peaked before sunrise, fell after sunrise and remained rela-

tively constant throughout most of the day. There was a small increase in feeding during the late afternoon, which was followed by a substantial decrease towards sunset (Fig. 5b). The early pulse of activity in these prey corresponded to the lowest rate of observed sharp-shinned-hawk-induced risk, while the evening decline in prey activity corresponded temporally to the highest estimates of risk (Fig. 5b). Between these temporal extremes, hawk-induced risk generally dropped slowly over the day, whereas prey activity was largely constant. The absolute difference in the standardized sharp-shinned-hawk-induced risk and rural prey scores in this first time bin was 4.01, and significantly different from those observed in the bootstrapped data ($P = 0.004$). The large difference in evening z -score (2.39) value was not significant at $P = 0.08$. The differences in all other time bins were more clearly not significantly different (P s > 0.284).

Discussion

Overall, we found that hawk activity varied throughout the day with significant differences in activity occurring between the two species. Cooper's hawks left the roost earlier and returned to roost later than sharp-shinned hawks, although about 80–85% of hawks of both species were hunting during most of the time between sunrise and sunset. Those not hunting were actively consuming prey or in a digestive pause. Attack rate peaked in the morning and again somewhat just before sunset in urban Cooper's hawks, but were generally constant in sharp-shinned hawks until the end of the day when they peaked markedly. Towards the end of the day, it appears that the out-of-roost sharp-shinned hawks were making more attacks, which caused the overall risk to small prey to a peak just prior to sunrise. The overall kill rate generally followed that of attacks in both hawk species (T. C. Roth and S. L. Lima, unpublished data), suggesting that there was no major change in success rate over the day.

The activity patterns of Cooper's and sharp-shinned hawks have several implications for the behavior of their prey. The activity patterns of small wintering birds tend to be bimodal or unimodal with a single peak in the morning (McNamara et al. 1994). In general, these patterns were observed in the birds at our rural feeder (peak in the morning with a minor increase in activity towards the latter part of the day) and in our urban point counts (with a bimodal pattern). McNamara et al. (1994) suggest a mechanism for bimodality in prey activity where early activity replenishes energy stores and later activity "tops off" those stores

while minimizing mass-driven predation risk; unimodal patterns are also expected when resources are high and stable such as at our feeder. These sorts of patterns can be achieved with a constant attack rate over time and may even be maintained if attack rates are higher in the morning (McNamara et al. 1994).

Our observations of sharp-shinned hawk activity, however, suggest an alternative explanation for the patterns of small bird activity. Sharp-shinned hawk predatory risk started out low, was roughly constant throughout the day, and peaked somewhat before sunset. The activity of their prey showed a significantly different trend during the morning by peaking sharply early and then remaining relatively constant throughout the day. This difference between hawk and prey activities suggests that the prey of sharp-shinned hawks take advantage of “free time” early in the morning when the risk of predation is low. This sort of low-risk period for prey was unexpected and is not predicted by predator–prey game theory (Kotler et al. 2002). In fact, the Kotler et al. (2002) model suggests that predator activity should match that of their prey activity rather closely, and that prey will largely drive the temporal dynamics of the game: when prey are most active, so too should the predators. In our study, however, this was not the case for our rural sharp-shinned hawks. Our urban Cooper’s hawks, on the other hand, tended to match their activity to that of their prey.

Intraguild predation may help explain the observed disparity between sharp-shinned hawk activity and that of their prey. Predation risk from owls was high for sharp-shinned hawks around sunrise and sunset (Roth et al. 2005). Twelve of 23 sharp-shinned hawks with known fates at the end of our study were killed by predators; one of these hawks was killed by a Cooper’s hawk, the remainder were killed by owls (Roth et al. 2005). Perhaps an explanation for the late departures of sharp-shinned hawks from the roost is that they stay in the roost longer to avoid interactions with owls and possibly intensely hunting Cooper’s hawks. This idea is further supported by the observation that sharp-shinned hawks are likely to return to roost shortly after a mid-afternoon meal (Fig. 2b), since spending time in the roost is probably safer than being out of the roost (see Beauchamp 1999 and references therein). This scenario suggests that instances in which a sharp-shinned hawk stays out late perhaps are due to energetically stressed hawks that are willing to accept more risk (B. Kotler and J. Brown, personal communication), although we cannot fully access this idea beyond Fig. 2. The behavior of the much larger Cooper’s hawks was not consistent with the avoidance of crepuscular activity. Cooper’s hawks

almost always started hunting prior to sunrise and stayed out significantly longer than sharp-shinned hawks, even after having made a kill, suggesting that their risks associated with crepuscular activity may not be great. The safety of Cooper’s hawks is supported by the fact that we observed no predation on these hawks in our urban site (Roth et al. 2005), where owls were largely absent (T. C. Roth and S. L. Lima, unpublished data).

By limiting the early morning activity of sharp-shinned hawks, owls may release small birds from risk just before sunrise. Although small birds generally tend to avoid activity during crepuscular periods (Lahti et al. 1997), the reduced threat of predation by hawks in this system may make this period a favorable time for small birds to forage. While owls themselves may kill small birds on occasion, the most abundant species in our study site (barred owls, *Strix varia*, and great horned owls, *Bubo virginianus*) are large and pose little threat to small birds. Especially in the winter, the diets of barred and great horned owls generally include less than 5% avian material (Earhart and Johnson 1970; Marks et al. 1984; Cromrich et al. 2002), most of which includes species much larger than those taken by sharp-shinned hawks (Roth et al. 2006). Even the single small owl species in the area (eastern screech owl, *Otus asio*) usually take few avian prey (Earhart and Johnson 1970). Therefore, small birds in our rural habitat probably were relatively safe during their early morning burst of feeding activity. The possibility of predators avoiding their own predators has not been considered theoretically in activity games between predators and prey (Kotler et al. 2002), but is clearly a possibility in our system and probably many others (e.g., Rydell et al. 1996).

Our study illustrates the importance of understanding the behavior of predators when attempting to understand that of their prey (see also Brown et al. 1999). When predators are removed from their conceptual “black boxes” (Lima 2002), new explanations for prey behavior may be revealed (e.g., Creel and Winnie 2005) and the behavioral mechanisms underlying predator–prey dynamics can be better understood (Fortin et al. 2005). A major impediment here, however, is that work with wide-ranging and elusive predators such as *Accipiter* hawks often presents many more challenges than does work on their prey. We nevertheless believe that further work on such predators will inevitably lead to many new insights into prey behavior and predator–prey interactions in general.

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