VOL. 169, NO. 2 THE AMERICAN NATURALIST FEBRUARY 2007

Natural History Miscellany

Use of Prey Hotspots by an Avian Predator: Purposeful Unpredictability?

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Submitted June 5, 2006; Accepted August 22, 2006;
Electronically published December 20, 2006

ABSTRACT: The use of space by predators in relation to their prey is a poorly understood aspect of predator-prey interactions. Classic theory suggests that predators should focus their efforts on areas of abundant prey, that is, prey hotspots, whereas game-theoretical models of predator and prey movement suggest that the distribution of predators should match that of their prey's resources. If, however, prey are spatially anchored to one location and these prey have particularly strong antipredator responses that make them difficult to capture with frequent attacks, then predators may be forced to adopt alternative movement strategies to hunt behaviorally responsive prey. We examined the movement patterns of bird-eating sharp-shinned hawks (*Accipiter striatus*) in an attempt to shed light on hotspot use by predators. Our results suggest that these hawks do not focus on prey hotspots such as bird feeders but instead maintain much spatial and temporal unpredictability in their movements. Hawks seldom revisited the same area, and the few frequently used areas were revisited in a manner consistent with unpredictable returns, giving prey little additional information about risk.

Keywords: Accipiter, hotspot use, movement, predator-prey interactions, predictability, use of space.

The use of space is an important aspect of predator-prey interactions (Holt 1984; Sih 1984; Orrock et al. 2003). Particularly for quickly moving predators with highly responsive and potentially mobile prey, movement dynamics may dictate how frequently predators come into contact with their prey and how prey assess risk. However, studies of the use of space typically focus on the movement of either predators or prey to the exclusion of the other (Fryxell et al. 2004; Luttbeg and Sih 2004). For instance, classic optimal foraging theory (see Stephens and Krebs 1986) suggests that predators should focus their efforts on areas where prey are most abundant, that is, at prey hotspots. Although factors such as random movements cause deviations from the hotspot expectation (Ruxton and Humphries 2003), hotspot use is still an intuitive expectation for predator hunting strategies. Such ideas, however, seldom consider the response of the prey and are generally based on prey that are behaviorally inert, such as seeds. On the other hand, behavioral models focused on prey movement and habitat selection typically envision predators as fixed in space (see Lima 2002). As a result of these two orthogonal approaches, we are left with a limited understanding of the behavioral interplay between predator and prey across an ecological landscape.

Only recently has effort been dedicated to understanding the dynamics of space use by both predators and behaviorally responsive prey. Models that incorporate active and simultaneous patch choice by both predators and prey find that the intuitive expectation of hotspot use by predators may no longer hold (see Sih 2005). These models predict that predator distributions should match their prey's resources while prey distributions should reflect habitat riskiness (Hugie and Dill 1994; Sih 1998; see also Heithaus 2001). If, however, prey resources are fixed in space and heterogeneously distributed, then both predators and prey may match the resource (Sih 2005), the end result being that predators focus on prey hotspots. Alternatively, if both predators and prey have several patches in which to forage, then prey might move between these patches with a degree of unpredictability in a sort of "shell game" of predator avoidance (Mitchell and Lima 2002); even in this situation, predators should still focus their activity on likely prey hotspots. A potential complication in most models of this dynamic interplay between predator and prey, however, is the existence of nonmovement types of antipredator defenses such as vigilance and refuge use. If prey have particularly effective (nonmovement) antipredator responses, then prey may become very difficult to capture once the predator's presence in a patch has been detected (see, e.g., Lima et al. 2003). Assuming that

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Am. Nat. 2007. Vol. 169, pp. 264–273.

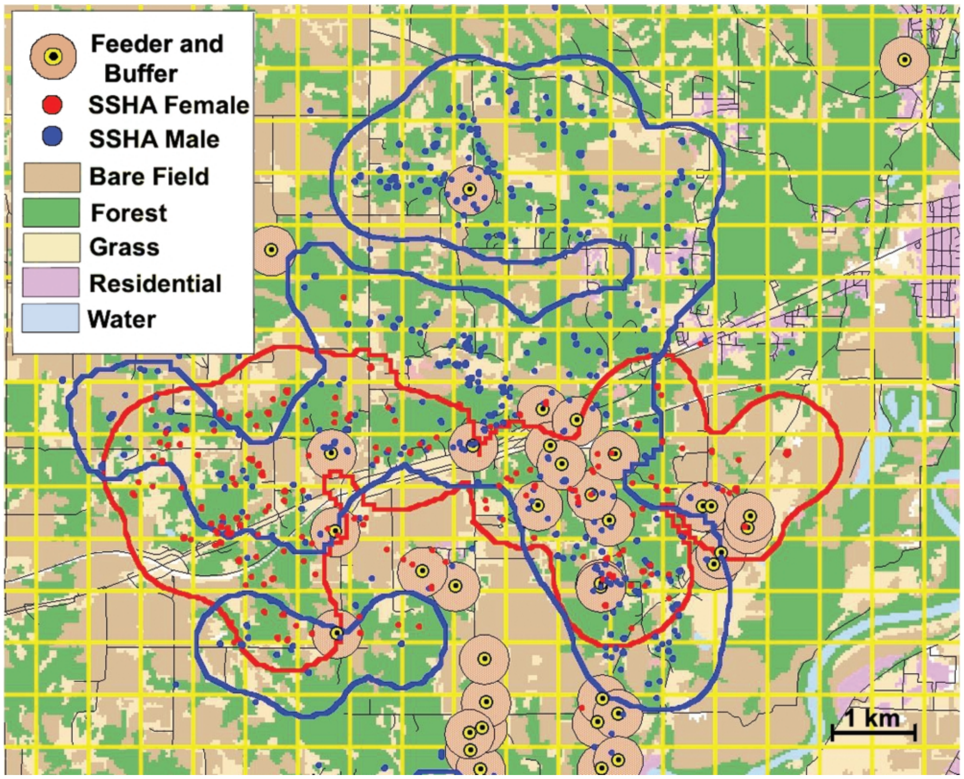

Figure 1: A representative example of the use of space by two sharp-shinned hawks during the winter of 2001–2002. The two hawks are distinguished by red (female) and blue (male) points/lines within their 95% kernel home ranges (as outlined). Feeders (*yellow points*) are shown surrounded by 300-m buffers. The 40-ha cells used in the return-time analysis are outlined in yellow.

the predator has access to other patches, then such antipredator behavior might favor predators that incorporate a degree of restraint and unpredictability in their use of specific prey locations (cf. Hugie 2003). In a sense, predators may be restrained in their use of hotspots in order to reduce their effect on the antipredator behavior of their prey (see Brown et al. 1999; Lima 2002).

Here, we describe work on a poorly studied but conceptually important predator, bird-eating *Accipiter* hawks, in an attempt to shed light on hotspot use by predators. *Accipiter* hawks are an important component of the "small-bird-in-winter" research paradigm, in which small wintering birds are seen as trading off the risk of predation from hawks against the risk of starvation during harsh environmental conditions. This research paradigm is historically important in behavioral ecology, having had a major influence on our understanding of many aspects of prey behavior, such as sociality (Bertram 1978; Pulliam and Caraco 1984), foraging behavior (Stephens and Krebs 1986), and behavioral trade-offs in general (Mangel and Clark 1988; Houston and McNamara 1999). However, the small-bird-in-winter paradigm is lacking in one key respect: we know relatively little about wintering *Accipiter* hawks. We do have some insights into the diet and attack behavior of European sparrow hawks (*A. nisus*; see, e.g., Newton 1986; Cresswell 1996; Cresswell et al. 2003), Cooper's hawks (*A. cooperii*; see, e.g., Roth and Lima 2003), and sharp-shinned hawks (*A. striatus*; see, e.g., Roth et al. 2006), but we know almost nothing about the larger-scale interactions between these hawks and their prey.

We thus examined the movement patterns of wintering sharp-shinned hawks, specifically focusing on their use of prey hotspots such as bird feeders. Bird feeders are point sources of abundant, predictable prey for *Accipiter* hawks and in many ways represent the ultimate prey hotspot for these predators. In fact, during the winter, the most common species included in the diet of sharp-shinned hawks (house sparrows, *Passer domesticus*; northern cardinals, *Cardinalis cardinalis*; and dark-eyed juncos, *Junco hyemalis*; Roth et al. 2006) are those species most likely to visit feeders (Wilson 1994; T. C. Roth and S. L. Lima, unpublished data). These feeders are exceptional foraging sites for such prey and may act as a spatial anchor (sensu Sih 2005) for a large number of birds. Accordingly, one would expect that hawks should routinely focus on areas of abundant prey such as feeders (see Dunn and Tessaglia 1994). Our results, however, suggest that sharp-shinned hawks do not focus on feeders but instead move so as to maintain spatial and temporal unpredictability.

Methods

Study Site

Our study site was the rural area immediately to the southwest of Terre Haute, Indiana. The general landscape was a mixture of agricultural land, fragmented forests, and small residential clusters (fig. 1; see also Roth et al. 2006). Here, we studied sharp-shinned hawks during the winters of 2000–2004 in an area of approximately 1,000 km^2, although most of our results focus on a 100-km^2 core area.

The study site contained several prey hotspots in the form of stable, long-term bird feeders that were maintained regularly throughout the winter season. We included private feeders that we discovered during our tracking activities as well as our own feeding stations, many of which were used in multiple years. Many of these feeders were typically visited by up to several hundred birds per day and attracted birds from a distance of 300 m or more (T. C. Roth and S. L. Lima, unpublished data; see also Wilson 1994). These known feeders were certainly the largest and most important feeder hotspots in our study site, although a few lesser feeders may have been undetected.

Capture and Tracking

Hawks were tracked using radio telemetry. Hawk trapping was conducted from late November to late January in all years in accordance with Roth et al. (2005, 2006). Upon capture, 2.4–4.5-g transmitters (Holohil) were attached to hawks using the synsacral harness of Rappole and Tipton (1991). All transmitters were <3% of the body mass of the hawk and were equipped with position-sensitive switches that provided information on hawk behavior (Roth et al. 2005, 2006).

Hawks were radio tracked intensively on a daily basis from the day of capture. Tracking was done from vehicles using yagi and whip antennae beginning 0.5–1 h before sunrise and ending 0.5–1 h after sunset. The first and last hawks tracked each day were determined systematically, and each hawk was tracked for at least 2 h/day but frequently up to 10 h/day (grand mean ± SE = 4.6 ± 0.4 h/day). Full-day tracking results (12.1% of 1,130 tracking days) suggest that hawks utilize a relatively small portion of their home range during a given day. Thus, we are confident that our tracking data represent a good approximation of a hawk's daily movement, given the large scale of our analysis. We note further that during tracking, hawks were undisturbed by the presence of vehicles, which were common throughout the study site.

Hawk locations were recorded on high-resolution aerial photos for each detectable move made by the hawk and later entered into ArcView 3.2 GIS (geographic information system). The time between points was converted to a standardized time step of 10-min intervals (Turchin 1998), resulting in a maximum of six moves within a 1-h period. Frequent visual contact with hawks minimized our tracking error. Our spatial resolution based on the calculation of tracking and mapping errors (in accordance with White and Garrott 1990) was 50 m (T. C. Roth, unpublished data).

Statistical Analyses

There are few standardized statistics available to analyze the predictability of large-scale animal movements (see also Mane et al. 2005). Thus, we devised two different tests, one focused on feeder use and the other on return times to feeders and other locations, to assess the predictability and patterns of hotspot use. All spatial analyses were performed in ArcView, and the results were analyzed in SYSTAT 10 (SPSS 2000). To estimate the overall area used by an individual hawk (a quantity used in subsequent analyses), we determined 95% least squares cross-validated kernel and minimum convex polygon home ranges using the animal movements extension for ArcView (Hooge and Eichenlaub 1997). Individual hawks were treated as statistically independent units in our analysis.

To quantify the use of bird feeders by hawks, we used ArcView to create buffer areas around each feeder and determined the use of these areas relative to a (computer-generated) random reorganization of feeders in a given home range. A 300-m radius buffer centered on the feeder was used as an estimate of general feeder space; this radius includes birds at the feeder itself as well as birds moving to and from the feeder. For each hawk, we calculated the proportion of observed points that overlapped feeder buffers within the 95% kernel home range (see fig. 1). We then randomized the locations of those feeders within suitable habitat (agricultural fields and water excluded) in its home range and calculated the proportion of observed hawk points that overlapped these randomly chosen locations. This randomization procedure was replicated 100 times for each hawk. We then compared the observed mean to the distribution of random means using a two-tailed design to estimate a P value. In addition, observed and mean randomized overlaps were compared across hawks using a Wilcoxon signed-rank test. If hawks were attracted to feeder hotspots within their home ranges, then the observed overlap of feeder buffers should be consistently greater than predicted, given the randomization of feeder locations. If hawks avoided feeders, then the observed overlap should be less than that predicted after the randomization of feeders.

We also examined the timing of returns to specific areas within a hawk's home range. We focused on returns to both feeders and standardized cell grids. For each hawk, we first determined the temporal pattern of visits to a given 300-m feeder buffer and then determined the time (in days) between each visit (return times). To obtain a reasonably accurate estimate of the distribution of return times, we limited our analysis to buffers that were known to be revisited at least 20 times. Using a Kolmogorov-Smirnov (K-S) test, we compared the observed distribution of return times (in days) to a geometric distribution with a mean equal to that of the observed distribution. The geometric distribution (Ross 2003) follows from an assumption that the daily probability of revisiting a given feeder buffer is constant and independent of the time elapsed since the last visit; such a pattern of visitation imparts no information to prey regarding return times. All expected geometric distributions have a mode of 1 day between returns and thus no central tendency. It is not necessary to have a complete record of daily movement to apply this analysis, but since we were not able to track each hawk all day every day, the observed mean return time will be somewhat greater than the true return time. We also used an autocorrelation test to detect temporal predictability in the sequence of return times, which should not be observed in a geometric random variable.

There were relatively few revisits to feeder buffers (see "Return Times"); hence, we also examined the temporal predictability of revisits to general areas throughout the home ranges of hawks. This analysis was done as described for feeder buffers, but here the analysis focused on returns to 40-ha cells superimposed over the entire study site (fig. 1). This cell size was chosen to reflect the area used by typical sharp-shinned hawk prey (Roth et al. 2006; T. C. Roth, W. E. Vetter, and S. L. Lima, unpublished data; see also Gaddis 1980; Smith 1991) and is comparable to the area of a feeder buffer. As before, this analysis was restricted to cells with at least 20 returns. We excluded all data recorded at hawk roost sites since these locations were necessarily revisited each day. However, points that were recorded while a hawk was hunting near its roost were included in the analysis.

Results

We captured a total of 40 sharp-shinned hawks over the course of the 4-year study (see Roth et al. 2005). Of these hawks, 21 (12 females, 9 males) provided long-term data (over 4 weeks of tracking) and were included in the analyses. Not all hawks produced data that could be used in all analyses. A few hawks could not be included in the feeder analysis as they did not have any known feeders within their home ranges. Likewise, some hawks did not revisit any 40-ha cell or 300-m feeder buffer frequently enough to be included in our return-time analysis. Thus, sample sizes vary somewhat between analyses.

The amount of space used by sharp-shinned hawks was large and variable, ranging over two orders of magnitude (95% kernel home range: mean $\pm$ SE $= 25.33 \pm 7.54$ km^2, range $= 1.19$–153.08 km^2). While sharp-shinned hawks maintained relatively stable home ranges, they were not territorial, having home ranges that overlapped considerably with those of other hawks (fig. 1). On average, only 28.5% ± 6.8% of a hawk's home range did not overlap the home range of another hawk tracked during the same winter. Surprisingly, even with this large amount of spatial overlap, we observed no obvious behavioral interactions between hawks during 5,424 tracking hours, even though several hawks roosted in the same areas and sometimes hunted in clear sight of each other.

Feeder Use

Overall, we documented 78 feeders in the main study site. Of these, 58 were known to occur for more than one winter season. Contrary to intuitive expectations, hawks in this study did not focus their activity on these feeder hotspots. Of 19 hawks that had feeders in their home ranges, the use of feeders did not differ significantly from that expected by randomly reorganizing the feeder locations (Bonferroni-corrected $\alpha = 0.003$; range of P values from .01 to .89). As a group, hawks showed no tendency to be above or below expected random overlap (fig. 2; Wilcoxon $Z = -1.167$, $n = 19$, $P = .243$). These results suggest little overall bias in the use or avoidance of feeder buffers by these hawks. The success rate of attacks at feeders (22 of 109, 20.2%) did not differ significantly from that away from feeders (38 of 139 attacks, 27.3%; $\chi^2 = 1.705$, df $= 1$, $P = .192$).

Return Times

The return times to feeder buffers suggest that they were visited with temporal unpredictability. Of 19 hawks that visited a possible 78 feeders, only eight hawks (at 11 feeders) had 20 or more returns to a feeder buffer. In all cases, the modal revisitation period was 1 day. Of these 11 feeder buffers, only two (involving different hawks) had return-time distributions that differed from the expected geometric distribution (Bonferroni-corrected $\alpha = 0.005$; K-S $D = 0.404$, $P < .001$ and K-S $D = 0.317$, $P = .001$; all other P values $> .50$; see fig. 3*A* for representative exam-

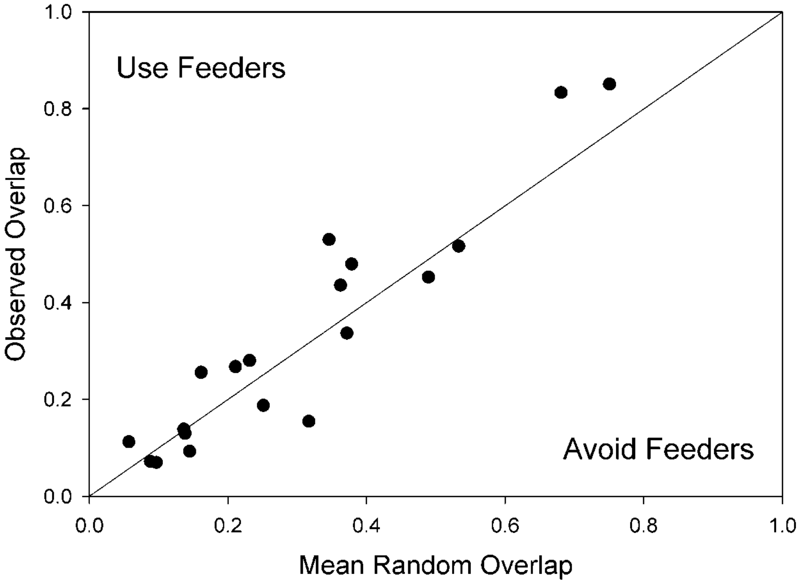

Figure 2: Feeder use by wintering sharp-shinned hawks. The proportion of observed points that overlapped 300-m feeder buffers is plotted against the mean proportion that overlapped the same number of buffers randomly positioned within the home range ($n = 19$ hawks). The area above the diagonal line represents a tendency for feeder use, while the area below the line represents feeder avoidance. No cases were significantly different from the random mean based on bootstrap analysis (100 replicates; Bonferroni-corrected $\alpha = 0.003$).

ples). Both of these hawks also had significant autocorrelations in their return sequence at a time lag of 1 day ($r = 0.678$, $n = 132$, $P < .001$; $r = 0.756$, $n = 100$, $P < .001$). Autocorrelation in returns to only one of the remaining feeder buffers was significant, although relatively small ($r = 0.473$, $n = 119$, $P < .001$; all other P values $> .05$), and also occurred at a time lag of 1 day.

Most of the 40-ha cells in hawk home ranges were also infrequently revisited, even though home ranges were stable. Hawks, on average, had 237.5 ± 31.0 (mean ± SE) cells of usable (nonagricultural) habitat in their minimum convex polygon home ranges. Of these cells, 35.9% ± 2.5% were known to be visited at least once during the winter. Of the cells actually visited, 60.8% ± 3.0% were revisited only once, 45.1% ± 3.7% were revisited at least twice, and 7.2% ± 2.2% were revisited 10 or more times; only 0.9% ± 0.3% (15 overall) were revisited 20 or more times and thus are used in our analysis.

These frequently visited 40-ha cells were also used in a manner consistent with unpredictable return times. All return-time distributions had a mode of 1 day, and in all of the 15 possible cases, the observed distribution was not significantly different from the expectation based on the geometric distribution (Bonferroni-corrected $\alpha = 0.003$; one P value $= .030$, all other P values $> .498$; see fig. 3*B* for representative examples). In addition, only two cells showed significant autocorrelations in return times, both of which were relatively weak ($r = 0.45$, $n = 120$, $P < .001$; $r = 0.53$, $n = 99$, $P < .001$) and at a time lag of 1 day.

The location of frequently visited cells varied by hawk. Five of 15 such cells included a bird feeder, while many of the others contained, or were adjacent to, hawk roosts. Such near-roost cells may be frequently visited mainly out of simple convenience. We emphasize, however, that hawks did not hunt at these near-roost locations every time they left or returned to roost. On most days, hawks quickly moved well away from their roosts before hunting.

Discussion

Sharp-shinned hawks exhibited a substantial degree of spatial and temporal unpredictability in their use of space. Our radio-tracked hawks did not strongly focus their activities on prey hotspots as represented by bird feeders. In fact, on average the hawks showed no bias in their tendency to avoid or use the area around bird feeders relative to that expected by randomly repositioning the feeders within their home ranges. In addition, most areas in a given home range were visited only a few times, and the few areas that were frequently revisited were visited in a pattern largely consistent with unpredictable return times. To our knowledge, this is the first demonstration of such a pattern in the use of space by predators.

One possible explanation for this general randomness and unpredictability is that sharp-shinned hawks lack the cognitive or spatial abilities to respond to large-scale patterns in prey hotspots. Based on our observations, however, this seems unlikely. Hawks seemed to know exactly where feeders were located. On several occasions, we observed hawks stealthily approach a visually obstructed feeder (e.g., on the opposite side of a building) only to make an attack on a feeder that happened to have no birds present; such attacks clearly suggest prior knowledge of the feeder's location. We also observed several instances of hawks going well out of their way to visit a particular feeder. In addition, after finishing a meal in the afternoon, sharp-shinned hawks generally flew straight back to their roost (T. C. Roth and S. L. Lima, unpublished data) regardless of their location. Thus, our observations suggest that hawks possess a well-developed sense of location within their home ranges.

Alternatively, hawks may be moving randomly as a strategy to find randomly moving or unpredictable prey (see, e.g., Ramos-Fernandez et al. 2004). Sharp-shinned hawk prey, however, do not move randomly but instead tend to focus most of their activity on a single, high-quality feeder source (T. C. Roth, W. E. Vetter, and S. L. Lima, unpublished data). Moreover, because hawks move on a much larger spatial scale than their prey (2,500 vs. 40 ha, respectively), random-movement strategies are unlikely to be useful. Furthermore, the absence of hotspot use by sharp-shinned hawks was probably not the result of direct mutual social interference, as found by Rohner and Krebs (1998) in territorial great-horned owls (*Bubo virginianus*). Our wintering sharp-shinned hawks were not territorial, and we observed no apparent interactions among them, although this does not rule out the possibility of indirect interference among hawks.

A more likely possibility is that behaviorally responsive prey diminish the "hotspot" quality of feeders. While feeder hotspots are sources of abundant prey, the individuals at such feeders generally benefit from group vigilance as a result of these higher densities (Elgar 1989; Roberts 1996). As a result, the vulnerability of the prey may actually be lower at feeders than at other locations. Some recent work suggests that sparrow hawks target more vulnerable prey groups (Cresswell and Quinn 2004; Quinn and Cresswell 2004). Thus, if the vulnerability of prey at feeders drops below that of prey elsewhere, then hawks might forgo hunting at feeders even though they are sources of abundant prey. Feeder hotspots may become even less valuable when multiple hawks make attacks at a given site (a form of interference competition). We note, however, that there was no significant difference in capture success between feeder and nonfeeder sites even with the considerable overlap in hawk home ranges.

We suggest that our observations of unpredictable movement reflect a sort of "prey management" by predators (Lima 2002), whereby predators spread their hunting activity over multiple areas in an effort to avoid inflating the antipredator behavior of their prey (see also Brown et al. 1999). This hunting strategy may be effective when prey are anchored (sensu Sih 2005) to high-resource areas such as feeders and utilize antipredator behaviors, such as high vigilance, that reduce a predator's attack success if it attacks frequently and predictably. This situation seems possible in our system because prey at feeders generally do not move among multiple feeders (T. C. Roth, W. E. Vetter, and S. L. Lima, unpublished data), and the few instances of persistent feeder attacks that we did observe caused prey to become very vigilant and difficult to catch. Under such circumstances, and when hawks have access to several alternative hunting locations, they may benefit from limiting their visits to any particular location (e.g., not using feeders more often than expected by chance) and being unpredictable in when they return, thereby giving their prey little information about impending attacks (see also Hugie 2003). Prey unable to predict predator movement or arrival patterns must simply assess risk at a general or baseline level for a given area. Accordingly, the idea of a constant probability of attack at a given location, an assumption made in behavioral models for mathematical convenience (see, e.g., Lima 1985; McNamara et al. 1994), may be realistic for small wintering birds.

We did not explicitly examine and cannot comment on the mechanisms that generate this unpredictable behavior, nor do we wish to imply that hawk movements are truly random. No animal can be truly random in its behavior, and claims of randomness reflect mainly a limitation of the statistical power of the analysis (Wimsatt 1980). We argue, however, that the movements of the hawks would likely approximate randomness from the perspective of the prey; hawks need only be unpredictable enough to limit imparting information about risk to their prey.

The idea of purposeful restraint in visiting feeders as a strategy of prey management invokes the possibility of evolutionarily unstable "prudent" predation, but this is not likely a problem in our system. Even if a "cheater" (i.e., a predictable predator that repeatedly attacks at a given area) were to occur in the system, subsequent prey capture would likely be more difficult for that cheater than for other predators. Thus, the cheater would not benefit from such activities. That is not to say that variation in behavior does not exist (see also Morales and Ellner 2002). For example, we observed a particular female sharp-shinned hawk repeatedly attack a feeder (without success) within a short time frame. Such behaviors were, however, not typical of this or other hawks.

Might other predators show the same lack of predict-

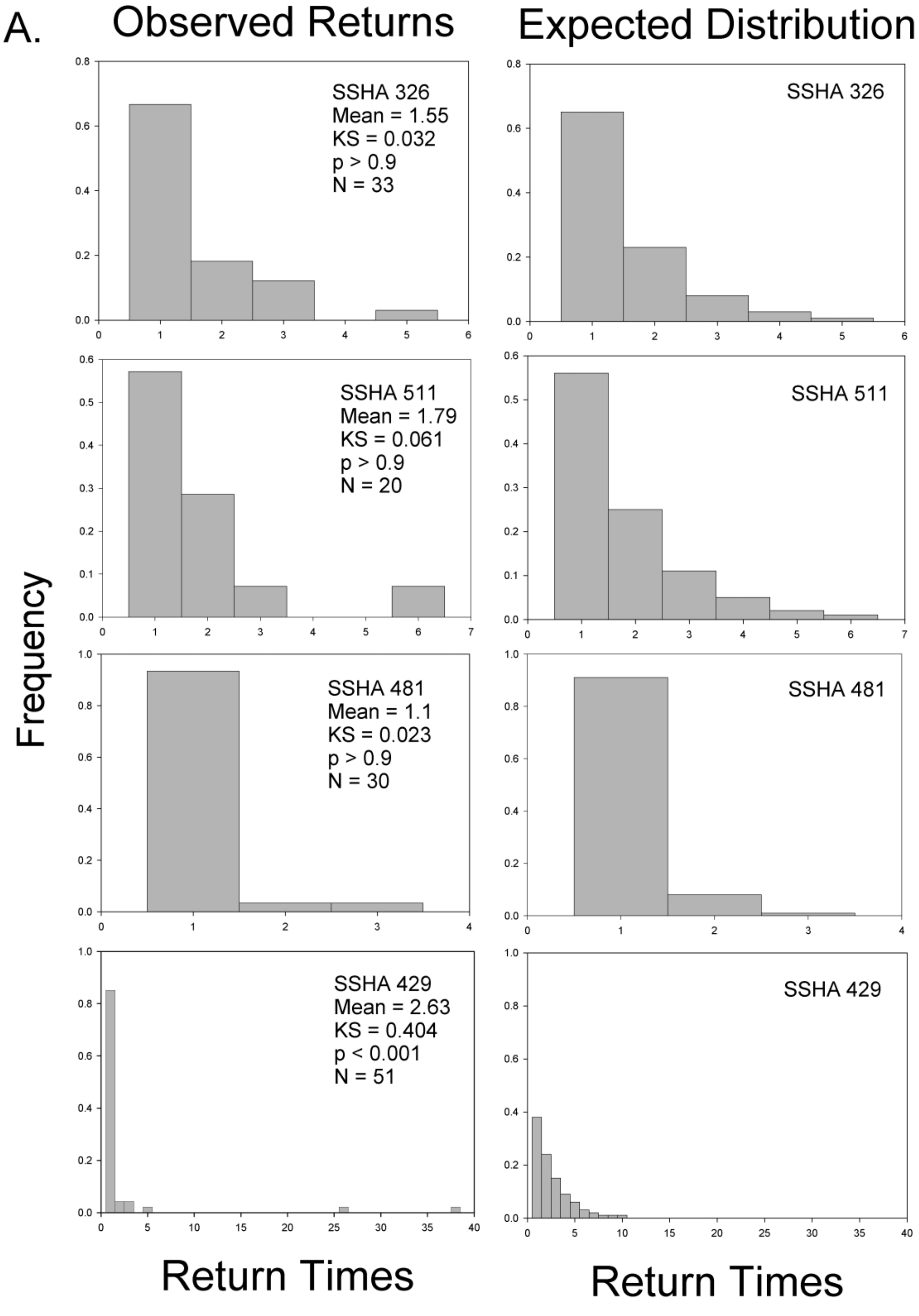

Figure 3: Distribution of representative sharp-shinned hawk return times to frequently visited (*A*) 300-m feeder buffers and (*B*) 40-ha cells. The distribution of observed return times (*left column*) was compared to an expected random distribution (geometric distribution with the same mean; *right column*) using a Kolmorgorov-Smirnov test. The observed return-time distributions in the top three graphs in *A* and all graphs in *B* are not significantly different from the expected geometric distribution (Bonferroni-corrected $\alpha = 0.003$).

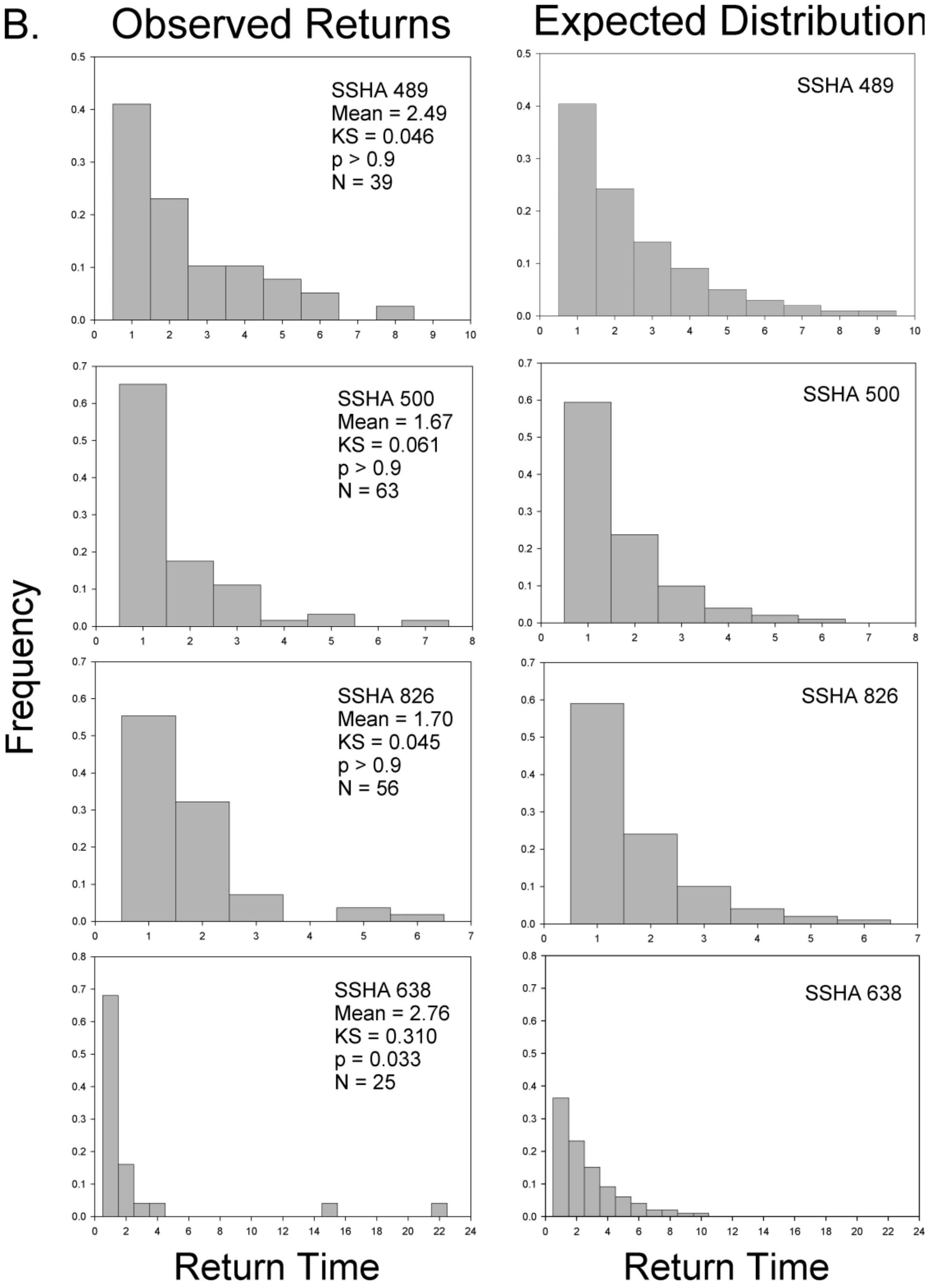

Figure 3 (*Continued*)

ability? Perhaps large mammal systems, such as an ungulate/canid system, may be good candidates for similar large-scale behavioral patterns. However, most studies of such systems do not consider the antipredator aspects of movement dynamics. An exception is recent work by Creel and colleagues (e.g., Creel and Winnie 2005; Creel et al. 2005) that explicitly considers the movement and behavior of elk in the context of wolf movement. However, given that wolves cannot possibly cover their territory as quickly as a hawk, they may only be able to manage ungulate herds on relatively small spatial and short-term temporal scales by limiting direct contact with prey herds. Other mammalian systems, such as the lion/ungulate (see, e.g., Hopcraft et al. 2005) or mustelid/rodent (see, e.g., Hanski et al. 2001) system, might also be worth investigating. In addition, arthropod systems, such as those involving bark beetles (see, e.g., Cronin et al. 2000) or spiders (e.g., Hoefler and Jakob 2006), might be fruitful areas for such research. In any case, studies on the large-scale movement of predators with behaviorally responsive prey promise to provide valuable insights into the dynamic nature of predator-prey interactions across ecological landscapes.

Acknowledgments

We thank our many field technicians for their assistance in tracking hawks. We would also like to thank local landowners (especially M. Evrard, J. Irwin, C. Martin, and C. Miller) for their cooperation. We thank J. Cox, V. Formica, J. Lesku, and T. Steury for discussions about statistical analysis. We also thank W. Cresswell and one anonymous reviewer for their comments, which greatly enhanced the quality of this manuscript. This research was supported in part by the National Science Foundation (grant IBN-0130758 to S.L.L.), the Indiana Academy of Sciences, and the Department of Ecology and Organismal Biology and School of Graduate Studies at Indiana State University. This research conformed to the guidelines of the Institutional Animal Care and Use Committee at Indiana State University (protocols 00-19:TR/SL and 08-21-2003:TR/SL).

Literature Cited

Bertram, B. C. R. 1978. Living in groups: predators and prey. Pages 279–309 *in* J. R. Krebs and N. B. Davies, eds. Behavioral ecology: an evolutionary approach. Blackwell Science, Oxford.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385–399.

Creel, S., and J. A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour 69:1181–1189.

Creel, S., J. A. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

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

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

Cronin, J. T., J. D. Reeve, R. Wilkens, and P. Turchin. 2000. The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. Oikos 90:127–138.

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

Elgar, M. A. 1989. Predator vigilance and group-size in mammals and birds: a critical review of the empirical evidence. Biological Reviews 64:13–33.

Fryxell, J. M., J. F. Wilmshurst, and A. R. E. Sinclair. 2004. Predictive models of movement by Serengeti grazers. Ecology 85:2429–2435.

Gaddis, P. 1980. Mixed flocks, accipiters and anti-predator behavior. Condor 2:348–349.

Hanski, I., H. Henttonen, E. Korpimaki, L. Oksanen, and P. Turchin. 2001. Small-rodent dynamics and predation. Ecology 82:1505–1520.

Heithaus, M. R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92: 542–554.

Hoefler, C. D., and E. M. Jakob. 2006. Jumping spiders in space: movement patterns, nest site fidelity and the use of beacons. Animal Behaviour 71:109–116.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124:377–406.

Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to Arcview, ver. 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559–566.

Houston, A., and J. McNamara. 1999. Models of adaptive behavior. Cambridge University Press, Cambridge.

Hugie, D. M. 2003. The waiting game: a "battle of waits" between predator and prey. Behavioral Ecology 14:807–817.

Hugie, D. M., and L. M. Dill. 1994. Fish and game: a game-theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45:151–169.

Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. Oecologia (Berlin) 66:60–67.

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

Lima, S. L., W. A. Mitchell, and T. C. Roth II. 2003. Predators feeding on behaviorally responsive prey: some implications for classical models of optimal diet choice. Evolutionary Ecology Research 5: 1083–1102.

Luttbeg, B., and A. Sih. 2004. Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk. Israel Journal of Zoology 50:233–254.

Mane, S., C. Murray, S. Shekhar, J. Srivastava, and A. Pusey. 2005.

Spatial clustering of chimpanzee locations for neighborhood identification. Technical Report to the Department of Computer Science and Engineering, University of Minnesota, Minneapolis.

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 99:249–259.

Morales, J. M., and S. P. Ellner. 2002. Scaling up animal movement in heterogeneous landscapes: the importance of behavior. Ecology 83:2240–2247.

Newton, I. 1986. The sparrowhawk. T & AD, Poyser, UK.

Orrock, J. L., B. J. Danielson, M. J. Burns, and D. J. Levey. 2003. Spatial ecology of predator-prey interactions: corridors and patch shape influence seed predation. Ecology 84:2589–2599.

Pulliam, H. R., and T. Caraco. 1984. Living in groups: is there an optimal group size? Pages 127–147 *in* J. R. Krebs and N. B. Davies, eds. Behavioral ecology: an evolutionary approach. 2nd ed. Sinauer, Sunderland, MA.

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

Ramos-Fernandez, G., J. L. Mateos, O. Miramontes, G. Cocho, H. Larralde, and B. Ayala-Orozco. 2004. Levy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). Behavioral Ecology and Sociobiology 55:223–230.

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.

Roberts, G. 1996. Why individual vigilance declines as group size increases. Animal Behaviour 51:1077–1086.

Rohner, C., and C. J. Krebs. 1998. Response of great horned owls to experimental "hot spots" of snowshoe hare density. Auk 115:694–705.

Ross, S. M. 2003. Introduction to probability models. 8th ed. Academic Press, San Diego, CA.

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

Roth, T. C., II, S. L. Lima, and W. E. Vetter. 2005. Survival and causes of mortality in wintering sharp-shinned hawks and Cooper's hawks. Wilson Bulletin 117:237–244.

———. 2006. Determinants of predation risk in small wintering birds: the hawk's perspective. Behavioral Ecology and Sociobiology 60:195–204.

Ruxton, G. D., and S. Humphries. 2003. Non-IFD movements: reflections on past work and prospects for future developments. Evolutionary Ecology Research 5:155–157.

Sih, A. 1984. The behavioral-response race between predator and prey. American Naturalist 123:143–150.

———. 1998. Three trophic level ideal free distributions: a game-theory approach to understanding the predator-prey behavioral response race. Pages 221–238 *in* L. A. Dugatkin and H. K. Reeve, eds. Advances in game theory and the study of animal behavior. Oxford University Press, London.

———. 2005. Predator-prey space use as an emergent outcome of a behavioral response race. Pages 241–255 *in* P. Barbosa and I. Castellanos, eds. Ecology of predator-prey interactions. Oxford University Press, London.

Smith, S. M. 1991. The black-capped chickadee: behavioral ecology and natural history. Comstock, Ithaca, NY.

SPSS. 2000. SYSTAT 10.0 for Windows. SPSS, Chicago.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, NJ.

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

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tagging data. Academic Press, London.

Wilson, W. H. 1994. The distribution of wintering birds in central Maine: the interactive effects of landscape and bird feeders. Journal of Field Ornithology 65:512–519.

Wimsatt, W. C. 1980. Randomness and perceived randomness in evolutionary biology. Synthese 43:287–329.

Natural History Editor: Henry M. Wilbur