Ethology

The Effect of Feeder Hotspots on the Predictability and Home Range Use of a Small Bird in Winter

Timothy C. Roth II & William E. Vetter

Department of Ecology and Organismal Biology, Indiana State University, Terre Haute, IN, USA

Correspondence
Timothy C. Roth II, Department of Biology,
University of Nevada, Reno, NV 89557, USA.
E-mail: tcroth@unr.edu

Received: August 14, 2007
Initial acceptance: November 6, 2007
Final acceptance: December 14, 2007
(S. Forbes)

doi: 10.1111/j.1439-0310.2008.01477.x

Abstract

Few studies address how resources and predation risk affect movement patterns and the overall spatial use of prey species. Although movement is generally considered to be dangerous, at large scales, movement may be important for predator avoidance and the predictability of such movement may be key. We examine the movement patterns of a small bird (*Junco hyemalis*) in winter to better understand how these birds might respond to the trade-off of unpredictable movements for predator avoidance with the foraging benefits of visiting large, predictable food sources. We manipulated resources by adding feeders to junco home ranges and compared the movement patterns of these flocks to those without access to feeders. Juncos with access to feeders were more spatially and temporally predictable, had reduced movement rates and smaller home range sizes. Our results suggest that the influence of resource distribution on junco movements is high. Juncos with highly productive and predictable resource hotspots may place more value on resources than remaining unpredictable. Consequently, they may be employing non-movement methods of anti-predator behavior, such as vigilance, at feeders, although this requires further investigation.

Introduction

Resource distributions may be important for spatial use in animals. There appears to be a negative relationship between resource quality or density and home range size (McNab 1963; e.g. Dussault et al. 2005), and moreover, the distribution of resources within a home range may also affect its overall shape (Mitchell & Powell 2004). All else equal, the more resources that are available, the less area an animal may need to use to access a suitable number of those resources. Territoriality, however, may complicate this effect (Maher & Lott 2000), making spatial use more a function of individual interactions than resources *per se* (Adams 2001). Few, however, have considered how predation risk and resource distribution might interact to affect animal movement patterns and overall spatial use (e.g. Jensen et al. 2005), especially in non-territorial species.

Recent theory predicts that predators should use resource hotspots (point sources of abundant resources), whereas prey should avoid areas where predators are abundant (Hugie & Dill 1994; Sih 1998). This perspective, however, does not fully consider movement as a behavioral strategy (Sih 2005; but see Hammond et al. 2007), but rather considers movement to be dangerous for prey (e.g. Werner & Anholt 1993; Lima 1998). While this may be the case at a small scale (Lima 1998), the wholesale application of this idea to larger spatial scales reduces risk to a constant probability in homogeneous space. As behavioral interactions between predators and prey can be dynamic (reviewed by Lima 2002 and Sih 2005), the movement patterns of both predators and prey, the predictability of that movement may be important (Mitchell & Lima 2002).

In a situation where both predators and prey can learn and move among different patches, a shell game may potentially emerge (Mitchell & Lima 2002). In such a game, movement by prey is considered optimal as stationary prey can quickly be found and consumed by the learning predator (Mitchell & Lima 2002). The forager then can face a trade-off between predation risk and access to resources – the predation costs of being predictable vs. the foraging benefits of utilizing a predictable food source.

For birds, feeders are obvious resource hotspots. Bird feeders typically represent resource densities that can be orders of magnitude higher than the surrounding landscape and consequently, attract large numbers of birds (Wilson 1994). The large-scale effect of bird feeders on bird movement and home range use, however, is unknown. The spatial ecology of wintering birds under the risk of predation in general is poorly studied despite its importance for studies of small bird behavior. Indeed, most studies that consider the anti-predator behavior of small birds during the winter focus on activity at a single location, typically a feeder. Consequently, we do not know whether and how the behavior of these birds changes when they do not have access to a feeder and if our observation of behaviors at feeders is representative of behavior away from a feeder.

Thus, we studied the movements of small birds in conjunction with our previous hawk research (e.g. Roth and Lima 2003, 2007a,b). We focused on the dark-eyed junco (*Junco hyemalis*), which is an abundant small bird species frequently included in the diet of *Accipiter* hawks (Roth et al. 2006). Juncos at our study site have figured prominently in recent studies of anti-predator behavior (e.g. Lima & Bednekoff 1999; Franklin & Lima 2001). In addition, this species is particularly appropriate for use in a movement study as they travel in groups of 15–20 individuals, flock stability is relatively high (approx. 75% of the members remain in the same flock throughout the winter; Vetter and Roth, unpubl. data) and they frequent birds feeders.

We tested the hypothesis that access to a hotspot resource would affect the movement patterns of juncos. We manipulated junco resources by adding feeders and compared the movement, predictability and home range use of birds with and without access to these hotspots. We expected that juncos with access to feeders would have reduced movement and home range sizes, as predicted by resource theory. In addition, shell game theory predicts unpredictable movement patterns of prey, so we expected juncos without feeders to have unpredictable spatial patterns. However, as hotspots restrict activity somewhat, we expected the spatial patterns of juncos with feeders to be more predictable, but independent of home range size.

Methods

Study Site

Our study site was located in west-central Indiana, USA, approx. 7 km southwest of the city of Terre Haute (population approx. 60 000). The landscape was composed of small residential clusters, fragmented forest and, grassland and agricultural areas (Fig. 1; see also Roth & Lima 2007a). The total site covered approx. 45 km^2.

Trapping and Tracking

Juncos were studied from early December through early March of 2000–2004. All juncos were trapped in mist nets either at feeders (with-feeder groups) or

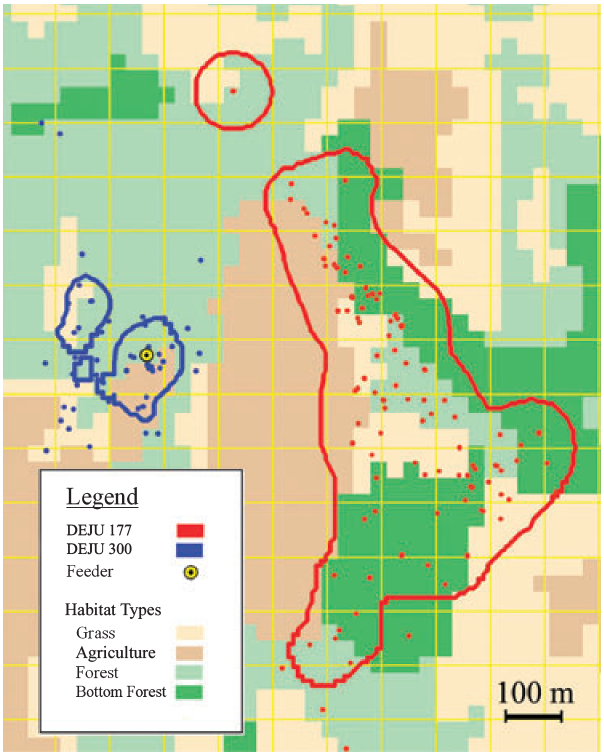

Fig. 1: A representative example of two dark-eyed junco (*Junco hyemalis*) home ranges during the winters of 2000–2004. The home range in blue (2.80 ha) contained a feeder. Note that 29% and 56% of observed points fell within 5 and 50 m of the feeder, respectively. The home range in red (27.92 ha) contained no feeder. The yellow lines represent the cells used in the predictability analysis (see text for details).

in movement paths (without-feeder groups). Our objective was to monitor the activity of entire groups of juncos over the course of the winter. During the initial trapping event for each flock, we attempted to capture and color band as many members of the flock as possible in order to determine flock membership. In addition, we attached 0.56 g (<3% total body mass) radio transmitters (Holohil, Inc., Holohil Systems Ltd., Carp, Ontario, Canada) to one to three members of each flock. These transmitters were glued to the backs of birds with cyanoacrylate glue (Raim 1978). We chose to track several individuals of a flock to ensure that we had continuous data from that flock as transmitters can sometimes fail or can be removed by the birds. The life of our transmitters was approx. 20 d, well less than the duration of the entire winter. In order to maintain continuous data collection throughout the winter, we recaptured and tagged members of the same flock every three wk. Recapture did not seem to influence subsequent movement patterns of the birds.

During radio tracking, each junco was located at least four times daily and at roost. Locations were recorded on detailed aerial photographs of the study site and transferred by hand into ArcView GIS 3.2. As these birds can easily fly across their home range in minutes, the time between successive points (mean = 156 min) is adequate to avoid the statistical problems of autocorrelation (Otis & White 1999).

Feeders

Ten long-term feeders were created in the study site. Each feeder was at least 1 km away from the other and except for a few cases did not share birds. Feeders consisted of an approx. 3 × 2 m area cleared of vegetation to bare ground, upon which concrete board was placed. Feeders were constantly stocked with white millet (*Panicum miliaceum*) and corn meal (*Zea mays* ssp.) and replenished about twice weekly. It is important to note that our feeders represented a food resource far greater than any available in the natural environment and any other residential feeder in the landscape.

Our feeders were the only non-natural source of food available to juncos in this study and feeder-less juncos did not have access to any feeders within their home range. The exception to this was a residential feeder nearby one of our feeder sites. Although birds occasionally visited that residential feeder, the feeder was not a reliable source of food and was not likely to have a detectible impact on our results.

Statistical Analysis

We measured home range size, total distance moved during the winter and total distance moved per day. Home ranges were estimated using 95% least-squares cross-validated kernel estimates (Worton 1989) in the Animal Movements extension (Hooge & Eichenlaub 1997) for ArcView. Total distances and daily distances moved were calculated in ArcView.

We also created two measures of predictability: temporal and spatial. Temporal predictability was measured as the time required to return to a given area (as did Roth & Lima 2007a). Using ArcView, we created a grid consisting of one ha cells across the entire study site and then measured the time required to return to a given cell. We could not compare the observed distribution to that of a theoretically random distribution as did Roth & Lima (2007a), because radio transmitter life was too short to track the juncos for an adequate period of time. Instead, we calculated a single measure of the probability of return as 1/(mean return time) and compared this value across juncos. Only cells visited 10 or more times were used in this analysis.

For the analysis of spatial predictability, we chose a statistical procedure that was independent of home range size. Rather than determining the amount of space within a particular utilization distribution (e.g. a 10% kernel), we created a spatially randomized set of small buffers and quantified the overlap of observed junco locations within these buffers. As this technique is independent of home range size, it should detect non-random patterns of movement regardless of the overall amount of space used by the animal. The alternative of using home range kernels could produce erroneous results due to a dependence upon home range size. For example, a smaller 10% kernel area would be more likely produced in a smaller 95% kernel home range.

Our estimate of spatial predictability was based on the likelihood of points falling into buffers within the home range. For birds with a feeder, we determined the proportion of all observed points that fell into 10, 50, and 100 m buffers around the feeder. The 10 m buffer represented activity at the feeder itself, while the 50, and 100 m buffers represented activity in the feeder area, but not on the feeder itself. For birds without feeders, we generated 10, 50 and 100 m buffers in the 95% kernel home range. We then determined the mean and maximum proportion of observed points that overlapped each buffer size (buffers independent; 1000 replicates). This technique allowed us to identify the average and most frequently used area in the home range of juncos without access to feeders. In addition, we calculated the average overlap of our three buffers with a random distribution of points within each 95% kernel home range. We then compared these proportions of use for juncos without feeders to the observed proportion of use for juncos with feeders using a Bonferroni corrected alpha of 0.017. It is important to note that our comparison of the maximum overlap buffers (i.e. the sites most frequently used areas in the home ranges) of feeder-less juncos with those of a junco home range containing one of our supplemental feeders was used as a conservative test of the difference in the predictability of the maximum hotspot use between feeder and non-feeder areas.

Although multiple birds were tracked in each flock, all analyses were performed at the level of the flock. Data from birds tracked simultaneously within the same flock were averaged to a flock mean. Data were log transformed when necessary to meet the assumptions of parametric analysis. When those assumptions could not be met with transformation, non-parametric statistics were used. All statistical tests were performed in SYSTAT 10.0 (SYSTAT 10.0, San Jose, California, USA).

Results

Overall Spatial Use

Over the course of the study, we radio tracked 79 juncos from 34 flocks (16 flocks without feeder, 18 flocks with feeders). Feeders had a large effect on home range size and movement (e.g. Fig. 1). The home range size of junco flocks with access to our feeders was significantly smaller than those without feeders ($t = 6.736$, $df = 32$, $p < 0.0001$; Fig. 2). The total distance moved was greater by juncos without a feeder ($U = 207.0$, $n = 31$; $\chi^2 = 12.981$, $df = 1$; $p < 0.001$). Moreover, the mean daily movement was also significantly greater for birds without a feeder ($t = 6.506$, $df = 32$, $p < 0.001$). The grand mean distance for the junco flocks without feeders (1206.5 ± 95.75 m) was more than twice that of those flocks with feeders (540.4 ± 45.74 m). Year had no effect on our estimates of spatial use (all ps > 0.400).

Predictability

Juncos with access to feeders were temporally more predictable than those without feeders. The probability of returning to frequently used cells was significantly higher when flocks had feeders in their home range ($U = 1029.0$, $n = 83$ cells; $\chi^2 = 7.046$, $df = 1$; $p = 0.008$). Of the 1136 possible cells available in all junco home ranges, 83 cells contained enough data to be included. Data from these cells represented 68 of 79 radio tracked birds. Interestingly, though, 10 of the 11 birds that could not be included in this analysis were from the non-feeder treatment. While we cannot measure the temporal predictability of these 11 birds, *per se*, the fact that these individuals did not return to any cell more than 10 times when they were tracked for the same length of time as all other groups suggests that they were spreading their activity across their home range and thus were not likely predictable.

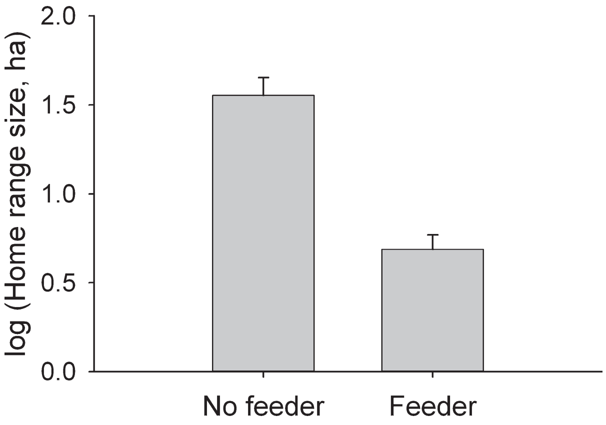

Fig. 2: Mean home range size of dark-eyed juncos with and without supplemental feeder. Error bars are standard errors.

Furthermore, feeders had the effect of concentrating spatial activity and thus making birds more spatially predictable. Juncos with feeders spent significantly more time localized within a single area (i.e. the feeder) than did juncos without feeder (Fig. 3, see also Fig. 1). This was the case at all three scales of analysis when controlling for flock (10 m: $F_{3,30} = 50.176$, $p < 0.001$; 50 m: $F_{3,30} = 106.338$, $p < 0.001$; 100 m: $F_{3,30} = 143.192$, $p < 0.001$). In fact, juncos with feeders spent nearly twice as much time in 50 and 100 m buffers around the feeder than the maximum time spent by any feeder-less junco in any other area of equal size and over three times as much time at the feeder itself than any non-feeder bird did at any 10 m buffer location. Furthermore, Tukey *post hoc* analysis suggests that at all three spatial scales, the mean buffer overlap (of 1000 replicates) did not differ significantly from overlap with a random distribution of points (10 m: $p > 0.999$; 50 m: $p > 0.999$; 100 m: $p = 0.995$; Fig. 3).

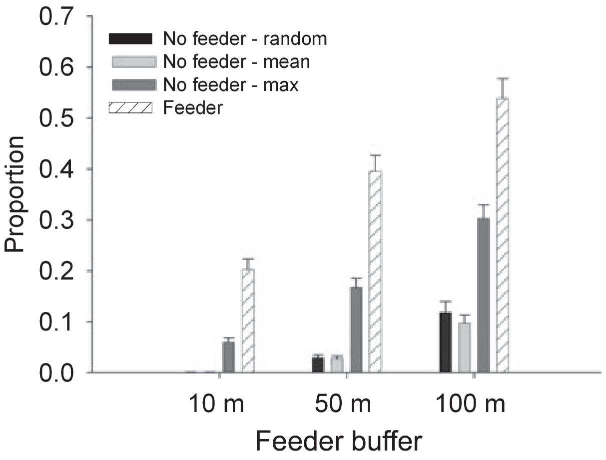

Fig. 3: The proportion of dark-eyed junco points within 10 m, 50 and 100 m buffers of feeders (hatched bars) and randomized non-feeder locations (solid bars). Within the non-feeder treatment, the proportion of overlap is considered relative to a random distribution of points (black bars), the mean (of 1000 randomized replicates) overlap of observed junco points (light gray) and the maximum (of 1000 randomized replicates) of observed junco points (dark gray bars). See text for detail. Error bars represent standard errors.

Discussion

Access to reliable food resources (i.e. a feeder) reduced small bird movement and increased the predictability of those movements. Small bird activity was obviously focused on these feeder hotspots, suggesting that the influence of resource distribution on junco movements was high. Juncos with access to our highly productive and predictable resource hotspots seem to have placed more value on those resources than on remaining unpredictable.

With no feeder, junco flocks moved more, maintained larger home ranges, and were significantly less spatially and temporally predictable than juncos with access to our supplemental feeders. For birds without feeders, there was no spatial anchor, or what hotspots were available were not important enough to act as anchors. These birds were forced to use more space in order to find an adequate amount of food and may have moved more in order to avoid being found by predators. These birds were indeed more difficult to find within their home range than birds with feeders. This was certainly true for us while tracking and was likely true for hawks as well. In the situation without feeders, maintaining unpredictability might be important and thus a shell game, i.e. movement by prey to avoid predators and movement by predators to find prey, might potentially occur (e.g. Mitchell & Lima 2002).

It is possible that the distribution of resources alone was responsible for the observed effect on junco spatial patterns. Indeed, animals with access to high-density resources tend to use smaller areas in which to obtain those resources and the distribution of resources can influence home range size and shape (Mitchell & Powell 2004). However, the key prediction for our results is the difference in predictability between the treatment groups. It is conceivable that randomly distributed resources might produce seemingly random movements and so our results might be the product of resource distribution alone. However, we are unaware of any hypotheses that predicts independent of spatial scale a reduction in the spatial or temporal predictability of movement based on a scattered resource distribution. In fact, two alternative movement strategies that could be used with a scattered resource are to focus predictably on several feeding locations (e.g. Ohashi & Thomson 2005) or to systematically move throughout an area completely depleting the resources before moving on to the next location. These two hypothetical movement patterns, however, were not observed in our case.

When prey are spatially anchored, such as at a feeder, they may instead drive the predator/prey system (*sensu* Sih 2005). Accipiter hawks use unpredictability as a hunting strategy (Roth & Lima 2007a), which is probably the result of the prey's behavior at feeders (Roth & Lima 2007a). As our feeders were such high-density resources, juncos may have been inclined to spend a great deal of time there rather than moving in a shell game. The differences between feeder and non-feeder junco movements was stark. This may have forced the juncos to use non-movement types of anti-predator behaviors such as vigilance and retreat to cover at feeders. Consequently, feeder hotspots might then have become less valuable for hawks, as increased activity at feeders may prompt prey to become more vigilant and more difficult to catch (Roth & Lima 2007a). In response to this behavior, hawks might reduce their use of feeders and visited them in a temporally unpredictable manner. Do hawks hunt the same way without feeders? Possibly not, although we really cannot know for certain from this study. While we tracked five hawks without feeders in previous work (Roth et al., unpubl. data), those hawks still moved unpredictably on a daily scale (Roth & Lima 2007a).

Unfortunately, we cannot determine from our study the full relationship between predation and resources, as we could not reliably measure perceived risk (i.e. vigilance) in the birds without feeders. Determining the cost of being predictable is a key step in fully understanding the movement patterns of prey. We see this as an important next step in this line of research that would allow for the separation of the predation and resources hypotheses. Group sizes equal, we would expect higher rates of vigilance in birds at the feeders, as they could be using increased vigilance to compensate for their predictability. Still, our results are consistent with our predictions based on the strategy of moving to avoid predation risk.

In addition to measuring vigilance, a reasonable next step in this research is to determine how the quality of hotspot resources affect prey movement. Hotspots certainly occur in natural systems (e.g. fruit trees, a patch of seeding grass, etc.), but available natural hotspots in this study were not nearly as valuable as our feeders. At more modest levels, hotspots may become periodic locations worth visiting and may elicit more lingering by prey, but in effect may still not anchor their movements. Another important factor could be the number of hotspots in the home range. In our case, we offered a single, highly valuable location. If several highly valuable locations existed in the home range of prey, we might expect to see less spatial anchoring and more movement between patches, e.g. traplining.

A final point of consideration is the effect of feeders on the predatory dynamics of the small bird/hawk system. From a conservation standpoint, human-initiated feeders may have such large impacts on the distribution of resources that they change the way that predators and prey interact. Feeders may be in part responsible for the rebound in Accipiter populations since the ban of DDT and other forms of persecution and may be changing the way in which accipiters migrate by reducing the length of migration (Viverette et al. 1996). Whether through changes in behavioral strategy or resources distributions alone, our data clearly show that feeders have a strong impact on small bird activity. Thus, they might have an effect on small bird predators as well. This topic deserves more study both from a behavioral and a conservation standpoint.

Acknowledgements

We are indebted to Steven Lima for his intellectual and financial contributions to this study. We also thank Steven Jenkins, Vladimir Pravosudov and two anonymous reviewers for helpful comments on drafts of this manuscript. The National Science Foundation (Grant IBN-0130758 to Steven Lima) and the Department of Ecology and Organismal Biology provided financial support. We would also like to thank our field technicians for their help and local landowners for allowing us access to their properties during our study.

Literature Cited

Adams, E. S. 2001: Approaches to the study of territory size and shape. Annu. Rev. Ecol. Syst. **32**, 277—303.

Dussault, C., Courtois, R., Ouellet, J. P. & Girard, I. 2005: Space use of moose in relation to food availability. Can. J. Zool. **83**, 1431—1437.

Franklin, W. E. & Lima, S. L. 2001: Laterality in avian vigilance: do sparrows have a favourite eye?. Anim. Behav. **62**, 879—885.

Hammond, J. I., Luttbeg, B. & Sih, A. 2007: Predator and prey space use: Dragonflies and tadpoles in an interactive game. Ecology **88**, 1525—1535.

Hooge, P. N. & Eichenlaub, B. 1997: Animal Movement Extension to Arcview, ver. 1.1. Alaska Biological Science Center, U.S.G.S., Anchorage, AK.

Hugie, D. M. & Dill, L. M. 1994: Fish and game – a game-theoretic approach to habitat selection by predators and prey. J. Fish Biol. **45**, 151—169.

Jensen, S. P., Gray, S. J. & Hurst, J. L. 2005: Excluding neighbours from territories: effects of habitat structure and resource distribution. Anim. Behav. **69**, 785—795.

Lima, S. L. 1998: Stress and decision making under the risk of predation: recent developments from behavioral, reproductive and ecological perspectives. Adv. Study Behav. **27**, 215—290.

Lima, S. L. 2002: Putting predators back into behavioral predator–prey interactions. Trends Ecol. Evol. **17**, 70—75.

Lima, S. L. & Bednekoff, P. A. 1999: Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? Anim. Behav. **58**, 537—543.

Maher, C. R. & Lott, D. F. 2000: A review of ecological determinants of territoriality within vertebrate species. Am. Midl. Nat. **143**, 1—29.

McNab, B. K. 1963: Bioenergetics and determination of home range size. Am. Nat. **97**, 133—140.

Mitchell, W. A. & Lima, S. L. 2002: Predator–prey shell games: large-scale movement and its implications for decision-making by prey. Oikos **99**, 249—260.

Mitchell, M. S. & Powell, R. A. 2004: A mechanistic home range model for optimal use of spatially distributed resources. Ecol. Model. **177**, 209—232.

Ohashi, K. & Thomson, J. D. 2005: Efficient harvesting of renewing resources. Behav. Ecol. **16**, 592—605.

Otis, D. L. & White, G. C. 1999: Autocorrelation of location estimates and the analysis of radiotracking data. Biometrics **63**, 1039—1044.

Raim, A. 1978: A radio transmitter attachment for small passerine birds. J. Exp. Biol. **49**, 326—332.

Roth, T. C. & Lima, S. L. 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. & Lima, S. L. 2007a: Use of prey hotspots by an avian predator: purposeful unpredictability? Am. Nat. **169**, 264—273.

Roth, T. C. & Lima, S. L. 2007b: The predatory behavior of wintering Accipiter hawks: temporal patterns in activity of predators and prey. Oecologia **152**, 169—178.

Roth, T. C., Lima, S. L. & Vetter, W. E. 2006: Determinants of predation risk in small wintering birds: the hawk's perspective. Behav. Ecol. Sociobiol. **60**, 195—204.

Sih, A. 1998: Three trophic level ideal free distributions: a game–theory approach to understanding the predator–prey behavioral response race. In: Advances in Game Theory and the Study of Animal Behavior (Dugatkin, L. A. & Reeve, H. K., eds). Oxford University Press, London, pp. 221—238.

Sih, A. 2005: Predator–prey space use as an emergent outcome of a behavioral response race. In: Ecology of Predator–Prey interactions (Barbosa, P. & Castellanos, I., eds). Oxford University Press, London, pp. 241—255.

Viverette, C. B., Struve, S., Goodrick, L. J. & Bildstein, K. L. 1996: Decrease in migrating sharp-shinned hawks (*Accipiter striatus*) at traditional raptor-migration watch sites in eastern North America. Auk **113**, 32—40.

Werner, E. E. & Anholt, B. R. 1993: Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. Am. Nat. **142**, 242—272.

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

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