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Foraging ecology of North American tree squirrels on cacheable and less cacheable foods: a comparison of two urban habitats

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ABSTRACT

Hypotheses: Animals often thrive in a variety of habitats where they face very different challenges and opportunities. We hypothesized: (1) As a consequence of higher squirrel density, the squirrels in an urban residential habitat (Oak Park, Illinois) experience greater food limitation than tree squirrels occupying a semi-natural habitat (Morton Arboretum in Lisle, Illinois). (2) Due to higher densities of natural predators, squirrels experience a higher foraging cost of predation at the Morton Arboretum than squirrels inhabiting Oak Park. Furthermore, (3) we expected the residential squirrels to place a higher premium on cacheable foods as a consequence of few oak and nut-producing trees in Oak Park compared with the much higher availability of acorns and nuts at the Arboretum.

Methods and predictions: By measuring giving-up densities in depletable food patches, we anticipated that at the Arboretum: (1) overall giving-up densities should be higher, (2) the difference in giving-up densities between risky and safe microhabitats should be higher, and (3) the difference in giving-up densities between cacheable food (hazelnuts in their shell) and less cacheable food (hazelnuts with shells removed) should be lower.

Results: Interestingly, the first prediction depended on the interaction between site and season. In Oak Park, giving-up densities were highest in summer and lowest in winter, the exact opposite of the Arboretum. Our second hypothesis was refuted, and the third supported.

Conclusions: A lack of cacheable food and an abundance of less cacheable human-derived summer food likely result in easy summers but hard winters for Oak Park squirrels. An abundance of cacheable foods and a summer lull in natural foods produces the opposite situation for the Arboretum squirrels. Less lethal, but more persistent, harassment by pets and people probably explain the higher cost of predation in Oak Park.

Keywords: food caching, foraging ecology, predation risk, *Sciurus*, urban ecology.

INTRODUCTION

Urban environments offer a range of biotopes, from heavily urbanized city centres to semi-natural habitats common along riverbanks and city edges. Frequently, urban areas

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contain a diversity of plants and animals, ranging from robust pioneering species to relatively sensitive species surviving in out-of-the-way corners where human disturbance is minimal. For animals living in and moving through this varied environment, an ability to respond appropriately to different conditions can have important effects on their urban distribution and ecological prospects. A lack of natural predators, an ability to exploit human habits, garbage, and structures allow many species to survive, and often thrive, in urban environments. For many others, urban pollution, automobiles, lack of suitable food and shelter, and the threatening presence of people and pets can make city survival hard or impossible. Recent interest in urban ecology seeks a better understanding of urban wildlife and its relationship to urban land use practices (e.g. papers published in journals such as *Urban Ecosystems* and *Landscape and Urban Planning*). We can expect animal distribution and behaviour to be contingent on many landscape features that vary in time and space. Revealing these contingencies becomes the challenge of the urban ecologist.

Tree squirrels in the urban areas of North America illustrate many of the challenges faced by urban wildlife. Abundant and thriving in some areas, they are totally absent from others. Where thriving, population turnover rates may vary with the level of exploitation (Hansen *et al.*, 1986) or food availability (Gorman and Roth, 1989; Gurnell, 1996). The Chicago Greater Metropolitan Area (CGMA) is a case in point and, as a general rule, squirrels are common in areas with extensive tree cover that provide food, safety, and shelter, but absent or rare in areas with little or no tree cover (van der Merwe *et al.*, 2005). Human refuse, bird feeders, and hand-outs are convenient sources of food, in addition to nuts, acorns, fungi, tree bark, and new plant growth that squirrels encounter in gardens, parks, and preserves. Attics, garden sheds, and other structures often provide convenient nesting sites. Predatory regimes in urbanized areas are typically very different from those in less disturbed habitats. For an animal like a tree squirrel, we expect encounters with natural predators in less urbanized environments to be highly lethal, but pulsed, and encounters with pets and people in urban areas to be less lethal, but more common and continuous.

Both fox (*Sciurus niger*) and grey (*S. caroliniensis*) squirrels occur in the CGMA, are easily observed, and have often been subjects for foraging studies (e.g. Smith and Follmer, 1972; Lewis, 1980; Lima and Valone, 1986; Smallwood and Peters, 1986; Brown and Morgan, 1995; Hadj-Chikh *et al.*, 1996; Schmidt and Brown, 1996; Morgan *et al.*, 1997; Steele and Koprowski, 2001). Foraging and caching are integral to a tree squirrel's existence. In Maryland, grey squirrels spend 80% of their daily activity budget on foraging (Hougart and Flyger, 1981), with the exception of mid-summer (June to August), when they spend 67% of their time foraging. Other activities include resting, moving through trees, and grooming. Tree squirrels generally live in environments where food availability varies seasonally: abundant in fall and spring, and scarce in winter and summer (Montgomery *et al.*, 1975; Steele and Koprowski, 2001). Squirrels cope with periods of scarcity by scatter-hoarding spoil-resistant food mostly during fall, in the form of nuts and acorns. Their well-developed long-term spatial memory and sense of smell allow them to retrieve stored food months after the caching events (MacDonald, 1997). Tree squirrels do not hibernate, and they forage throughout winter. The added cost of thermoregulation in colder temperatures and scarcity of food make foraging during winter an energetically expensive activity. A squirrel's ability to survive harsh winter months may be dependent on the presence of nut-bearing trees (Gurnell, 1996).

While foraging, animals balance benefits and costs. Previous studies have highlighted the importance of predation risk as a cost of foraging to tree squirrels (Brown, 1992, 1999; Brown *et al.*, 1992; Thorson *et al.*, 1998). While depleting a food patch in which the squirrel experiences

diminishing returns, an optimal forager will balance energetic gains with predation risk, metabolic costs, and the missed opportunity cost of foraging. A giving-up density is the density of resources in a patch at which a forager ceases using a patch (Brown, 1988). Giving-up densities are often easy to measure and can be used as indices of the quitting harvest rate (i.e. the harvest rate that balances costs and gains). The gain from harvesting a cacheable food can be realized immediately by consuming the food upon discovery or at some time in the future by caching the food (Gendron and Reichman, 1995). The immediate value of food may be different from its future value. Food can spoil (Janzen, 1977) or ripen (Herrera and McDonald, 1997), affecting future value. Future food scarcity can also increase future value compared with present value. The difference between present and future food value should be reflected in the value that caching animals place on cacheable versus less cacheable food (Kotler *et al.*, 1999).

In this study, we compared two sites in the Chicago area that differ markedly in urbanization, predatory regimes, and food types. The first site, the village of Oak Park, is a residential area and much more urbanized than the second, situated in the park and forested landscape of the Morton Arboretum in the village of Lisle, Illinois. The residential nature of Oak Park results in different major food sources and different types of predators for squirrels. Importantly for squirrels, and despite its name, Oak Park also differs from the Morton Arboretum in having a very low density of acorn and nut-bearing trees (Lanham, 1998).

We addressed the following questions: (1) How do giving-up densities (and therefore quitting harvest rates) on hazelnuts compare for squirrels in habitats that differ in their degree of urbanization? A study by Bowers and Breland (1996) found giving-up densities to be lower in more urbanized areas. However, they covered only the summer season, and we asked whether (2) season has a possible effect on this foraging pattern. Previous studies at both our study sites found that predation risk affects giving-up densities (Tuen and Brown, 1996; Thorson *et al.*, 1998), and we asked (3) if our two study sites, with their different urban and non-urban predatory regimes, differ in the strength of this effect on hazelnut giving-up densities. Our two sites differed markedly in the availability of cacheable food, and we asked (4) if squirrels at the two sites differ in their relative preference for cacheable versus less cacheable hazelnuts. The presence or absence of cacheable food is highly seasonal, which leads to the question of whether (5) there are any interaction effects between food cacheability, season, and site.

METHODS

Study areas and study animals

The residential area of Oak Park is located on the western border of the city limits of Chicago. Single-family dwellings predominate, with interspersed apartment buildings. Large trees line the streets and occupy front yards. Common tree species include elm and maple with some ash and oak (Lanham, 1998). We established feeding stations within the back yards of six single-family homes. The yards chosen for our study measured approximately 10×40 m, which is representative of yards in Oak Park. Most back yards in Oak Park are fenced, nestled between the house and the garage or alley, and, with one exception, back yards used for this study contained at least one tree. The smallest distance between selected back yards was approximately 0.6 km, and we considered stations to be independent from each other with respect to the individual squirrels inhabiting the yards.

Our second study site, the Morton Arboretum, is situated about 40 km west of Oak Park in the village of Lisle. It comprises 660 ha of managed parkland, coniferous forest, deciduous forest, grassy meadow, and prairie habitat. We chose three parkland areas within the Arboretum for study. The parkland areas house the Arboretum's special tree collections, and the grass between trees is mowed regularly. The shortest distance between the three different areas is approximately 0.6 km. Oak trees dominate at two of the study areas, whereas black walnut dominate at the third. Compared with Oak Park, the Arboretum offers squirrels a much higher density of oak and other nut-bearing trees, while Oak Park offers a greater input of food from humans, either from intentional handouts or unintentional access to refuse. (Two of the authors have been residents of Oak Park for several years, and can corroborate the above statement based on long-term personal observation.).

At the Morton Arboretum, fox squirrels predominated at all the study areas, with only transient grey squirrels. In Oak Park, both fox and grey squirrels are abundant, with fox squirrels tending to dominate in the south (where our study yards were located), and grey squirrels tending to dominate in the north (van der Merwe *et al.*, 2005). Ecologically, fox and grey squirrels are remarkably similar. At the level of scale at which we asked our questions for this study, the two species of tree squirrels were considered to be ecological equivalents.

Experimental set-up

In Oak Park, a feeding station was established in each of the six yards. At the Morton Arboretum, three feeding stations were established at each of three areas, for a total of nine feeding stations. At each study area of the Arboretum, the feeding stations were 40–50 m apart and were generally foraged by different individuals (see Morgan *et al.*, 1997). At both sites, each feeding station consisted of four 14-litre plastic containers. Each container/food patch contained 14 hazelnuts thoroughly mixed into 12 litres of pea gravel. To gain access to the hazelnuts, squirrels dug through the pea gravel, resulting in an artificial food patch yielding diminishing returns as food becomes removed from the patch. Two microhabitats were distinguished for each station. Two food patches were placed near a tree (safe microhabitat) and the two remaining food patches were placed approximately 5 m from the tree to represent the risky microhabitat. In Oak Park, in the one back yard that did not have any trees, the fence was used in place of a tree (based on casual observation, the fence was used as an avenue of escape by the squirrels.). Two food types were tested: cacheable hazelnuts with their shells intact and less cacheable hazelnuts with their shells removed. Each microhabitat contained a food patch with cacheable food and a food patch with less cacheable food.

Data collection and analysis

Data were collected opportunistically spanning the three seasons of fall (six days between 7 and 14 November 2002), winter (13 days between 1 December 2002 and 8 February 2003), and summer (eight days between 9 and 29 July 2002). Food patches were opened in the morning (at 07.00 h) and giving-up densities were measured in the afternoon (between 15.00 and 17.00 h), giving the squirrels about 8 h of foraging opportunity. A partially hierarchical analysis of variance (ANOVA) was used to test for the effects of season (Season), food type

(Food), locality (Site), microhabitat (Microhabitat), and station (Station), which was nested within site and date (Date), which was nested within Season, on giving-up densities, using the computer package SYSTAT. Results were considered to be statistically significant at $P < 0.05$.

RESULTS

Table 1 summarizes the statistical results. For the analysis, the independent variables Food, Microhabitat, Date, and Station had significant main effects on giving-up densities. There were significant two-way interactions between the variables Site and Season, Site and Microhabitat, and Site and Food. There was a significant three-way interaction between Site, Food, and Season.

Of all measured effects, food cacheability was the most pronounced. Cacheable nuts (with their shells) were strongly favoured (mean = 4.5) over less cacheable nuts (with their shells removed) (mean = 6.2). Giving-up densities in the open microhabitat were higher (mean = 5.6) than those in the microhabitat close to cover (mean = 5.0). The Site × Food interaction showed that the preference for cacheable over less cacheable nuts was more extreme in Oak Park than at the Morton Arboretum (Fig. 1). This effect varied with season, and there was a significant three-way interaction between Food, Season, and Site (Fig. 1). In Oak Park, the preference for cacheable over less cacheable was most pronounced in the fall. Being less cacheable raised giving-up densities on hazelnuts by an average of 2.9 nuts. At the Arboretum, the preference for cacheable over less cacheable nuts was greatest in the winter, with a difference in giving-up densities of 1.8 nuts. Both sites saw the lowest preference for cacheability during the summer, with differences in giving-up density between less cacheable and cacheable hazelnuts of 1.7 and 0.8 in Oak Park and the Arboretum, respectively. In

Table 1. Results of partially hierarchical analysis of variance

Source	SS	d.f.	MS	*F*-ratio	*P*
Site	80.130	1	80.130	0.94	N.S.
Season	94.229	2	47.114	0.66	N.S.
Food	851.868	1	851.868	119.202	<0.000
Microhabitat	78.298	1	78.298	10.956	0.001
Season × Site	545.681	2	272.841	38.179	<0.000
Food × Site	40.053	1	40.053	5.605	0.018
Microhabitat × Site	30.987	1	30.987	4.336	0.038
Food × Season	31.613	2	15.807	2.212	0.110
Microhabitat × Season	2.271	2	1.136	0.159	0.853
Microhabitat × Food	6.011	1	6.011	0.841	0.359
Food × Season × Site	46.617	2	23.308	3.262	0.039
Date (Season)	1701.877	24	70.912	9.923	<0.000
Station (Site)	1968.408	23	85.583	11.976	<0.000
Error	9147.398	1280	7.146		

Note: The dependent variable is giving-up density. Multiple $R = 0.639$ and multiple $R^2 = 0.409$. The independent variables Site, Season, Food, and Microhabitat were crossed to test for interaction effects. The variables Date and Station are nested into the variables Season and Site, respectively.

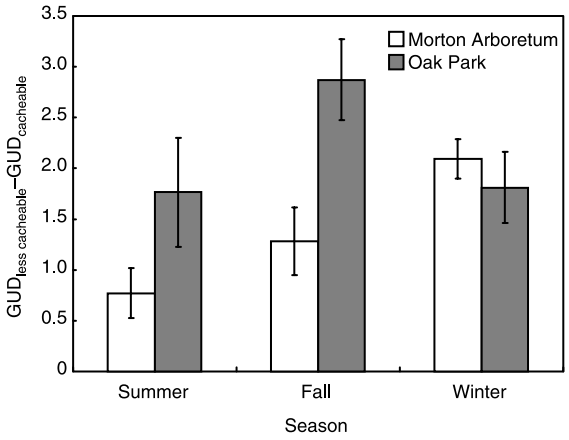

Fig. 1. The difference in giving-up densities between less cacheable hazelnuts and cacheable hazelnuts for the three different seasons in Oak Park and the Morton Arboretum. Bars represent standard errors around means. GUD = giving-up density.

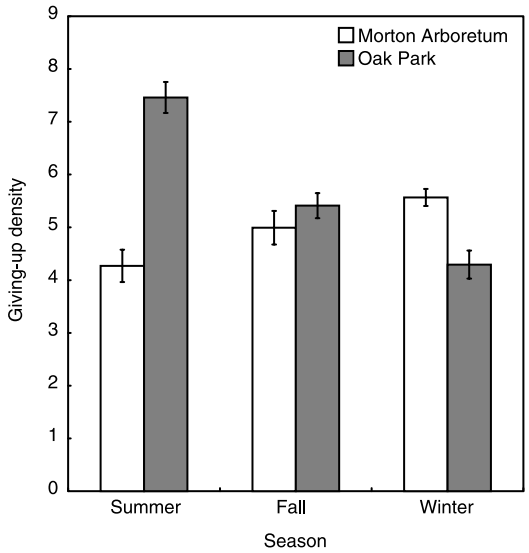

Fig. 2. The effects of the independent variables Site and Season on the least squares means of the dependent variable giving-up density. Bars represent standard errors around means.

terms of differences between the sites, the higher preference for cacheability at Oak Park was most extreme in the fall, and essentially absent in the winter.

The interaction of Site and Season revealed that Oak Park exhibited greater seasonal variation in giving-up densities than did the Arboretum (Fig. 2). Furthermore, squirrels in Oak Park had their highest giving-up densities in the summer, while those at the Arboretum had their highest giving-up densities in the winter. In the summer, giving-up densities were higher in Oak Park than at the Morton Arboretum. During fall, giving-up densities were higher in Oak Park, though the difference was less pronounced (mean = 5.4 vs. 5.0 for

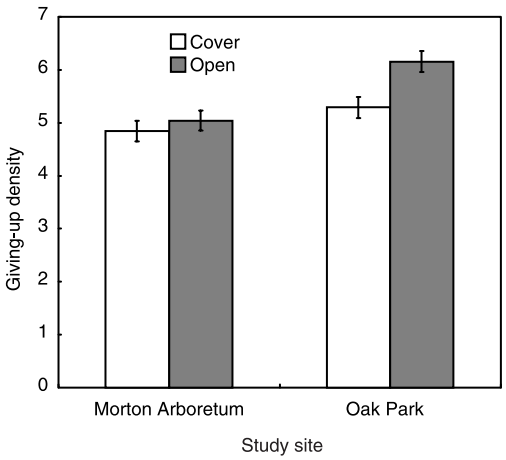

Fig. 3. The interaction effect of the independent variables Site and Microhabitat on the least squares means of the dependent variable giving-up density. Bars represent standard errors around means.

the Morton Arboretum). In winter, this pattern was reversed, and giving-up densities were higher at the Morton Arboretum than in Oak Park. The interaction between Site and Microhabitat showed that the lower giving-up densities near trees relative to away from trees were significantly greater in Oak Park (a difference of 0.9) than at the Morton Arboretum (a difference of 0.2) (Fig. 3). Similarly, the differences in giving-up densities between Oak Park and the Morton Arboretum were generally more pronounced in the open microhabitat than the microhabitat near cover. The interactions of Site × Food × Season and Site × Microhabitat did not reverse for sites, but merely dampened or expanded the main effects of food type and microhabitat.

DISCUSSION

Examples abound of animals having to confront different habitats, urban or otherwise. The introduction of grey squirrels into Europe and the resulting niche shifts and impacts on local wildlife is a well-known concern (summarized in Laidler, 1980; more recent studies include Wauters *et al.*, 2001, 2002). Similarly, Oak Park and the Morton Arboretum provide different opportunities and challenges to their respective tree squirrel populations, resulting in different foraging patterns across sites and seasons. As possible factors driving these differences, different kinds of predators and different food types and food sources are the most obvious candidates for investigation.

The strongest pattern in our data emerged from food cacheability. Food caching is a powerful foraging strategy (Smith and Reichman, 1984; Vander Wall, 1990) that extends food availability into lean periods that might otherwise prove fatal (Wauters *et al.*, 1995). Small animals, in particular, are limited in the amounts of food that can be eaten and stored as body fat. During periods when cacheable food is plentiful, more food can be harvested than can be eaten and food storage becomes advantageous. For tree squirrels, a food item that stores well will often have a higher future than present value, and results in a greater preference for cacheable food.

Food cacheability is clearly important both to squirrels in Oak Park and the Morton Arboretum, but our results indicate that during summer and fall, this difference in preference for cacheable versus less cacheable food in artificial food patches was more pronounced for the squirrels in Oak Park (Fig. 1). During winter, the preference for cacheable food was similar at both sites. Due to the relative scarcity of oak and nut-bearing trees in Oak Park (Lanham, 1998), it would seem that cacheable food there is at a premium, increasing its value relative to less cacheable food. (Note, however, that in winter, there was an equally strong preference for more cacheable food at the Arboretum.). In contrast, the Morton Arboretum has a much higher density of oaks and walnuts, and a much lower density of squirrels, than Oak Park. Oak trees dominate at two of our Arboretum study sites, and walnut trees at the third. This relative abundance of highly cacheable food items at the Arboretum was supported by our data, and resulted in a less pronounced preference for nuts in their shell. However, it is interesting that during winter, when food availability at the Arboretum is severely reduced, more cacheable food becomes as highly valued as in Oak Park.

Though site or season strengthened or weakened the difference in giving-up densities between hazelnuts with their shells intact as opposed to hazelnuts with their shells removed, the pattern never reversed, again emphasizing the importance of food cacheability to tree squirrels. In another Morton Arboretum study, Kotler *et al.* (1999) measured squirrel giving-up densities on sunflower seeds, which is a less-cacheable food, while supplementing the squirrels with different regimes of cacheable and less cacheable hazelnuts. Sunflower seed giving-up densities were highest when less cacheable food was augmented and lowest without any food augmentation. When augmented with cacheable food, giving-up densities were intermediate, demonstrating a clear foraging response to cacheable versus less cacheable food augmentation.

Several studies have demonstrated that the importance of acorn cacheability for squirrels differs between different species of acorns (summarized in Smallwood *et al.*, 2001; Steele *et al.*, 2001). Acorns belonging to the white oak group germinate in fall, while those belonging to the red oak group germinate the following spring. Due to these different germination schedules, acorns belonging to the red oak group are generally more cacheable than acorns belonging to the white oak group and are preferred by squirrels. In the present study, the pattern of preference for cacheable food stands out regardless of season, site or microhabitat. That cacheable food is strongly preferred even during summer months suggests that not only is long-term caching (over a period of months) important, but also short-term caching (over periods of days or weeks).

In some ways our results contrast with those of the earlier study by Bowers and Breland (1996). Bowers and Breland used giving-up densities on sunflower seeds to investigate squirrel foraging along an urban–rural gradient in northern Virginia. By making use of public volunteers, they measured giving-up densities at 78 different sites representing different levels of urban impact. All data were collected in summer (throughout July and the first few days of August). They found that giving-up densities were lower near or at human habitation than giving-up densities from more rural or agricultural areas. Bowers and Breland (1996) cite several studies (Flyger, 1959, 1970; Shuler, 1969; Havera and Nixon, 1980; Gorman and Roth, 1989) in support for urban habitats maintaining higher densities of squirrels than more rural habitats. They suggest that lower giving-up densities in urban areas may either be a result of food limitation (due to high squirrel densities) or decreased predation risk (thus lowering the cost of foraging). In contrast, using the same logic for our study and comparing

our summer results with the data from Bowers and Breland (1996), our results suggest the opposite for our more urban site, where summer giving-up densities were higher. Summer squirrels in Oak Park either have access to abundant food supplies (and population sizes are likely to be more restricted by available nest sites than by food), or foraging costs (e.g. due to predation/harassment) in Oak Park are higher, or a combination of these two factors are important. Also, note that in our study this pattern flip-flopped between summer and winter (discussed below). The different results for these two studies illustrate the potential danger of extrapolating results from one urban context to another. Patterns can be highly contingent on local factors, and careful observation and experimentation are typically required to reveal these contingencies.

Not only did our study yield a different pattern of giving-up densities from that of Bowers and Breland (1996), but the pattern of higher giving-up densities in Oak Park than at the Morton Arboretum depended on season. The highest giving-up densities measured were in Oak Park during summer. Summer is thought to be a time of scarcity for squirrels in natural habitats (together with winter), but our results suggest that summer is a time of exceptional food abundance (or perhaps foraging costs) to urban squirrels. Whereas giving-up densities in Oak Park are highest during summer and lowest during winter, this pattern is completely reversed at the Morton Arboretum, which had higher giving-up densities during the winter and lower giving-up densities during the summer. At both sites, giving-up densities were intermediate during the fall. Our results provide clear support for the importance of summer food sources to urban squirrels, compared with squirrels in less urban habitats. In the Chicago area, people spend their time outdoors mainly during spring, summer, and fall, and much less so during winter. Human outdoor activity, via hand-outs, bird feeders, garden work leading to overflowing garbage bins, and so on, seems to be a relatively constant and easy source of summer food for urban squirrels (personal observation). However, few of these types of foods will be cacheable, and their future value is therefore minimal, conforming to the results discussed earlier. The relative scarcity of acorns and nuts in Oak Park means that winter food caches will be relatively small. This explains why giving-up densities drop so dramatically during winter in Oak Park, when human handouts and bird feeders are a less reliable food source. At the Arboretum, feeding of wildlife is discouraged, access to garbage is minimal, and squirrels have to rely much more on natural food sources. During summer, these natural food sources are limited, and the low summer giving-up densities of the Arboretum reflect this. However, Arboretum squirrels have easier access to more cacheable acorns and nuts, and winter giving-up densities are not as low as in Oak Park.

The Site $\times$ Microhabitat interaction is interesting. Tuen and Brown (1996) recorded a significant effect of microhabitat (near tree and away from tree), and thus predation risk, on giving-up densities for Oak Park squirrels, and Thorson *et al.* (1998) recorded the same pattern for the Morton Arboretum. Our study confirms these results, as food patches in the open yielded higher giving-up densities at both sites than food patches close to cover. Interestingly, this effect was significantly stronger in Oak Park than at the Morton Arboretum, suggesting that the cost of predation is higher in Oak Park. At the Arboretum, there is a variety of natural squirrel predators that are not generally found in Chicago's more urbanized areas. Especially common are red tailed hawks and coyotes. In Oak Park, natural squirrel predators are rare, and the nearest equivalent would be the potential predatory threat of dogs and cats. The effect of pets as predators on small mammals has been documented before (George, 1974; Liberg, 1984), but our expectation was that the prevalence

of natural predators at the Arboretum would result in a greater predation risk than at Oak Park. It was therefore surprising to discover that the unnatural predators in Oak Park may have a greater effect on squirrel foraging than their natural counterparts at the Morton Arboretum. Dogs and cats in urban habitats are more abundant and predictably present than their natural counterparts in more undisturbed areas. It is possible that squirrels are better equipped to deal with their natural predators, whose presence will typically be more lethal, but pulsed. Even if dogs and cats do not kill large numbers of squirrels, the continuous harassment from pets may be a significant foraging cost. Humans themselves may also be still perceived as predators. Although there is no squirrel hunting in residential areas, humans have certainly been important squirrel predators in the past. Future investigation of squirrel predation and/or harassment under natural and urban conditions, and its relative effects on squirrel behaviour, will be an interesting avenue of research.

Our study compared only one urban area with one semi-natural area, and extrapolation of our results to other urban areas should be treated with caution. However, our results do suggest some very interesting patterns and avenues for future study. Based on our results, habitat qualities such as types of trees and food sources, differences in seasonality and cacheability of food sources, and different predatory regimes all seem to be important factors in determining squirrel foraging and caching behaviour. An extension of our methods to a variety of additional sites, a closer look at the different types of food sources associated with different levels of urbanization, and a more detailed evaluation of the different types of urban and rural predators will all greatly enhance our understanding of the different challenges faced by urban (and not so urban) squirrels.

A species may appear to thrive in two different places and under different circumstances, but the combination of environmental factors supporting the species may vary, and revealing the relative importance of these factors is a challenge for the urban ecologist. As demonstrated in this study, foraging behaviour, and patch use in particular, allows the animal to reveal the mix of factors that make a particular place suitable or unsuitable.

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