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FORAGING BEHAVIOR OF URBAN BIRDS: ARE HUMAN COMMENSALS LESS SENSITIVE TO PREDATION RISK THAN THEIR NONURBAN COUNTERPARTS?

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Abstract. We hypothesized that the foraging behavior of urban birds would be less sensitive to variation in the cost of predation than that of nonurban bird species. We predicted that food-patch utilization by House Sparrows (*Passer domesticus*), a widespread human commensal, would be less sensitive to variation in predation risk than that of Spanish Sparrows (*P. hispaniolensis*), its nonurban counterpart. We applied the giving-up density (GUD) method to quantify patch use behavior of the two species with respect to distance from shelter. Our results indicated that Spanish Sparrows perceived a steep gradient of increased predation cost with increasing distance from shelter, while House Sparrows seemed indifferent to distance from shelter. These results support the hypothesis that the cost of predation has less effect on the foraging behavior of urban than nonurban birds, although alternative explanations include differences between species in the degree of neophobia, or variations in their ability to assess predation risk.

Key words: competition, foraging behavior, predation, seed trays, sparrows, urban ecosystem.

Comportamiento de Forrajeo de Aves Urbanas: ¿Son las Comensales de Humanos Menos Sensibles al Riesgo de Depredación que sus Contrapartes No Urbanas?

Resumen. Planteamos la hipótesis de que el comportamiento de forrajeo de las aves urbanas sería menos sensible a la variación en el costo de depredación que el de las especies de aves no urbanas. Predijimos que la utilización de parches de alimentos por parte de *Passer domesticus*, un comensal de los humanos ampliamente distribuido, sería menos sensible a la variación en el riesgo de depredación que la de *P. hispaniolensis*, su contraparte no urbana. Aplicamos el método de densidad de abandono para cuantificar el comportamiento de uso de los parches por parte de las dos especies con respecto a la distancia a los refugios. Nuestros resultados indicaron que *P. hispaniolensis* percibió un gradiente marcado de incremento del costo de la depredación al aumentar la distancia a los refugios, mientras que *P. domesticus* pareció indiferente a la distancia al refugio. Estos resultados avalan la hipótesis de que el costo de depredación tiene menos efecto sobre el comportamiento de forrajeo de las aves urbanas que sobre el de las no urbanas, aunque existen explicaciones alternativas como la existencia de diferencias entre las especies en el grado de neofobia o de variaciones en sus habilidades para evaluar el riesgo de depredación.

Increasingly high rates of urbanization worldwide and rapid replacement of "natural" by urban ecosystems emphasize the importance of understanding the processes that underlie the ecology and evolution of urban animal populations and communities (McIntyre 2000, Marzluff et al. 2001). However, studies in this field are still mostly correlative, and, despite a rapidly increasing body of evidence, our understanding of the underlying evolutionary mechanisms of urban ecosystems is surprisingly limited (Marzluff 2001, Shochat 2004, Shochat et al. 2004).

Compared with the natural ecosystems they replace, urban environments are characterized by increased food abundance, accompanied by high predictability of food and water input (Marzluff 2001, Shochat 2004, Shochat et al. 2004, 2006). The resource matching rule (Parker 1978, Pulliam and Caraco 1984) and the theory of ideal free distribution (Fretwell and Lucas 1969) predict that bird densities will match the distribution of resources among habitats so that individual fitness is equalized across the landscape. The food-enriched urban environment is thus predicted to support proportionally higher bird densities than adjacent wildlands. However, Shochat (2004) and Shochat et al. (2004) suggested that the high level of predictability and continuous input of food and water resources into urban environments may actually result in overmatching (i.e., overexploitation of the richer, urban environments). The result is intense food resource competition in urban environments and scarcity of food at the individual level (Sol et al. 1998, Marzluff 2001). Hence, food input and acquisition may constitute a major determinant of behavior and use of space by foragers in urban ecosystems and in the ecology of urban populations and communities (Fretwell 1972, Mitchell et al. 1990, Bowers and Breland 1996, Shochat et al. 2004, 2006).

The influence of predators on bird abundance and diversity in cities is difficult to assess and is still largely unclear (Shochat et al. 2004). While potential predators may be more abundant than in adjacent wildlands (Sorace 2002), their actual impact on

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bird populations and communities might be reduced or even become negligible (Gering and Blair 1999, Shochat 2004; Bowers and Breland 1996 on urban squirrels). This may occur through changes in the behavior of urban predators, changes in the behavior of their avian prey, or a combination of both (Shochat et al. 2004, 2006).

The cost of predation is directly related to the risk of predation and inversely related to the marginal value of food (Brown 1992). Hence, increased marginal value of energy (food), resulting from intense resource competition, may reduce the overall cost of predation (Charnov 1976, Brown 1988, Kotler and Brown 1988). The impact of predation risk on bird behavior may then be reduced, even if the predation risk itself is unchanged or has even increased (Brown 1992, Bowers and Breland 1996, Shochat 2004, Shochat et al. 2004).

The differences between urban and "natural" environments in the importance of the cost of predation may lead to evolutionary differences in the species that inhabit these environments. In particular, urban species may respond less dramatically to habitat features that in "natural" environments are associated with variation in predation risk. Shelter from predators is one such feature. Indeed, it has been shown that birds perceive a gradient of predation risk around shelters (Lima and Dill 1990, Todd and Cowie 1990, Watts 1990, Beck and Watts 1997, Oyugi and Brown 2003), and it has been suggested that interspecific differences in the perception of this gradient may underlie the structure of bird communities (Davis 1973, Pulliam and Mills 1977, Lima and Valone 1991, Slotow 1996, Beck and Watts 1997). A change in the manner in which birds perceive and respond to the risk of predation may influence selective pressures related to antipredator adaptations and competitive abilities, potentially influencing the morphological, physiological, and behavioral evolution of human commensals. Such changes may also affect the dynamics of urban ecosystems (McKinney 2002).

The goal of this study was to investigate whether a change in the way urban birds perceive and respond to the risk of predation may have occurred. We examined this by studying the way in which foraging House Sparrows (*Passer domesticus*), a common and widely spread human commensal, perceived the distribution of predation risk around structures that provided shelter from predators. We then compared House Sparrow behavior to that of the Spanish Sparrow (*P. hispaniolensis*), a sister taxon (Allende et al. 2001) and a morphologically similar species, which mainly occupies nonurban environments, often in close proximity to urban environments and in parapatry with the House Sparrow.

Optimal foraging theory (Charnov 1976, Stephens and Krebs 1986) can be used to delineate differences in patch use behavior across habitats and microhabitats, and to quantify foraging costs such as those arising from the risk of predation (Brown 1988). For optimal patch use, a forager should exploit a certain portion of the environment as long as the benefits from foraging in it exceed the costs, which include: 1) the energetic costs of activity while searching for and handling food (C), 2) the cost of missed opportunities (MOC), and 3) the cost of predation (P). Optimal patch use should result in a bird ceasing to forage in a food patch when the food harvest rate (H) in the patch balances the sum of the costs, i.e., when $H = C + P + MOC$ (Brown 1988, Kotler and Brown 1988). The giving-up density (GUD) is the corresponding density of patch resources at that time and reflects the individual's costs and its foraging efficiency (Brown 1988). The GUD is expected to rise with an overall increase in foraging costs. When all other costs are controlled for, the GUD can be used to assess the cost of predation (Kotler et al. 1994).

We hypothesized that the behavior of species such as the House Sparrow, which coevolved with urban ecosystems, would be less sensitive to predation risk than the behavior of nonurban species, such as the Spanish Sparrow. As a result, we expected that variation in predation risk across the habitat, such as the variation introduced by proximity to shelter, would affect the patch use behavior of House Sparrows less than it would affect the patch use behavior of Spanish Sparrows. We thus predicted that increasing the distance between a foraging patch and a potential shelter would result in a milder increase in the GUD of House Sparrows in comparison with the GUD of Spanish Sparrows. We also predicted that due to the hypothesized overall decrease in predation cost (P) for human commensals, the overall foraging efficiency of House Sparrows would be higher (i.e., lower overall GUD) than that of Spanish Sparrows (Bowers and Breland 1996, Shochat 2004, Shochat et al. 2004).

METHODS

We used the giving-up density (GUD; the amount of food left by a forager in a resource patch after exploitation) method to assess how proximity to shelter influenced the perception of predation risk by free-ranging House and Spanish Sparrows, both typical ground-foraging granivorous birds. To do this, we used seed trays placed at various distances from a potential shelter as foraging patches. Under experimental settings, differences in GUDs among seed trays reflect the costs of foraging incurred at the level of predation risk (P) experienced by the foragers (Brown 1988, Kotler et al. 1994).

We placed seed trays at increasing distances from large shrubs that were already in use by birds for perching and shelter. In each experimental session there were only a few seed trays and ample numbers of birds (≥150). Seed trays were collected only after the birds were observed to lose interest and stop foraging in them. It is thus safe to assume that the birds did not stop foraging in the trays due to satiation, but rather because it was not beneficial to keep exploiting that patch any more, and that the amount of seeds left in the trays actually reflected the GUD.

Experiments were conducted in two sites on the outskirts of the city of Beer-Sheva (34°44′E, 31°15′N) in the northern Negev, Israel. While Spanish Sparrows occur mainly in wildlands outside the city and House Sparrows mainly in the urban area, the two species co-occur on the outskirts of the city and in large city parks. The two species are sister taxa and are morphologically similar, but they represent two separate lines of evolutionary background. The Spanish Sparrow kept "natural" habitats as its core habitat, whereas the House Sparrow became a human commensal and has a relatively long evolutionary history in urban environments (Ericson et al. 1997). For these reasons, and their relative abundance, the two species are good model species to study differences in the importance of predation risk to urban and nonurban birds.

Because of their morphological similarity, we were unable to construct seed trays that would allow only one species access to the trays and thus ensure that we were measuring the GUDs of each species separately in sites where the two species co-occurred. We thus chose study sites where both species were known to occur, but which were occupied by only one of the species at the time the experimental sessions were conducted.

We did not specifically quantify predator abundance in our study sites during the experiments. However, based on long-term

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field experience in both sites, we are not aware of any marked differences in predator abundance and composition between them. The diurnal predators in both sites during winter, when we performed our experiments, were feral cats (*Felis catus*), feral dogs (*Canis familiarus*), Eurasian Kestrels (*Falco tinnunculus*), Eurasian Sparrowhawks (*Accipiter nisus*), and Black Kites (*Milvus migrans*). The level of human activity appeared to be similar in the two sites.

SPANISH SPARROWS

We measured GUDs for Spanish Sparrows at various distances from shelter in three sessions during December 1999. The experiment was conducted in a patch of large shrubs located at the edge of Hazerim, a small settlement <5 km west of Beer-Sheva's main urban area. Foraging flocks in the immediate vicinity totaled ~150 individuals that mostly foraged on the ground and frequently flew to cover in the nearby shrubs. Experimental sessions were conducted just after sunrise, during which time foraging activity was the most intense. We simultaneously placed seed trays at three different distances from each of three shrubs (shelters). Overall, there were nine replicate seed trays on each of three experimental days. Distances ranged from 0 to 5 m from shelter, with all distances represented on each day. Overall, there were five replicate seed trays at distances of 0, 2, and 4 m, and four replicate seed trays at distances of 1, 3, and 5 m.

We used round seed trays, 40 cm in diameter and 5 cm deep. We filled the trays with 2 liters of sifted soil, mixed with 20 g of millet seeds. We placed the seed trays just before sunrise, ~30 min before the first individuals arrived from their roosts, and ended each session ~30 min after the last forager was seen feeding from any of the trays. Total time of each session was ~4 hr. After each session we sifted the trays to retrieve the remaining seeds (GUD). To reduce the variance in the data that may have originated from differences in initial conditions among shrubs and dates (shrub size, wind direction, temperature, etc.), and to allow direct comparison with the House Sparrow data, we standardized the GUD data for each tray by subtracting from it the average measured GUD for the trays at the same shrub for a given day. We used least squares regression to analyze the data, with distance as the predictor variable and the standardized GUDs as the response variable.

HOUSE SPARROWS

We measured GUDs of House Sparrows at varying distances from shelter along a row of large shrubs located in the Zoological Gardens, on the western outskirts of Beer-Sheva, ~4 km from the location at which we measured the GUDs of foraging Spanish Sparrows. There were approximately 150–200 House Sparrows present during the experiment. We conducted four experimental sessions (days) during January–February 2005. In each session, we placed five seed trays along the row of shrubs at distances of 0, 1, 2, 3, and 4 m from the shrubs. We changed the locations of the seed trays along the row of shrubs between each session, with all distances equally represented in each session.

Sessions were conducted between sunrise and noon. House Sparrows responded poorly to the seed trays used for the Spanish Sparrows. We thus used a different kind of tray, consisting of 40 × 55 cm sheets of dense artificial grass, 2.5 cm thick, upon which we scattered 10 g of millet seeds. While some seeds remained on the surface, most of the seeds settled between the blades of grass so that foraging birds had to spend time and effort to extract them. As for the Spanish Sparrow data, GUD values were standardized, and least squares regression was used to analyze the data, with distance as the predictor variable and the standardized GUDs as the response variable.

RESULTS

Standardized GUDs of Spanish Sparrows increased significantly with increased distance between the seed tray and the nearest large shrub (Fig. 1a). In contrast, House Sparrows showed no relationship between standardized GUDs and the distance between the seed tray and the nearest large shrub (Fig. 1b). ANCOVA with distance to shelter as the predictor variable, standardized GUDs as the response variable, and species as the categorical variable, resulted in a significant interaction term between species and the distance to shelter (Table 1).

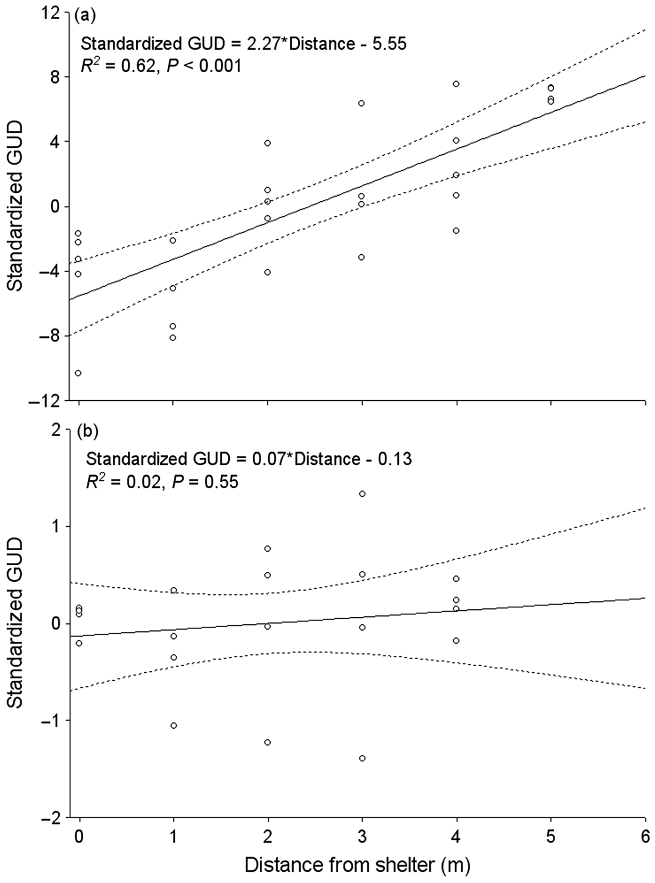


FIGURE 1. The effect of the distance from shelter on depletion of resource patches by (a) Spanish Sparrows, measured in a patch of large shrubs located at the edge of Hazerim, a small settlement <5 km west of Beer-Sheva's main urban area, and (b) House Sparrows, measured along a row of large shrubs located in the Zoological Gardens, on the western outskirts of Beer-Sheva, Israel. Linear least squares regressions with 95% confidence intervals of the relationship between standardized giving-up densities (GUDs) and distance from shelter show that the foraging efficiency of Spanish Sparrows decreased significantly with increasing distance to shelter, whereas that of House Sparrows was unaffected by distance to shelter. Each data point represents one seed tray on a single day. Note the different *y*-axis scales.

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TABLE 1. ANCOVA of the standardized giving-up densities (GUDs) of Spanish and House Sparrows, foraging in seed trays, with distance from shelter as the covariate. GUDs of Spanish Sparrows were measured in a patch of large shrubs located at the edge of Hazerim, a small settlement <5 km west of Beer-Sheva's main urban area, and those of House Sparrows were measured along a row of large shrubs located in the Zoological Gardens, on the western outskirts of Beer-Sheva, Israel.

	SS	df	MS	*F*	*P*
Intercept	122.7	1	122.7	20.8	< 0.001
Species	111.8	1	111.8	18.9	< 0.001
Distance	144.6	1	144.6	24.5	< 0.001
Species*Distance	129.1	1	129.1	21.9	< 0.001
Error	253.9	43	5.9		

DISCUSSION

Both Spanish and House Sparrows readily used large bushes as shelter when alarmed or faced with potential predators. However, as we predicted, their foraging behavior with respect to the proximity to these shelters was markedly different. The GUDs of Spanish Sparrows increased with increasing distance from shelter, while the GUDs of House Sparrows were unrelated to distance from shelter. Thus, foraging efficiency, and possibly also time allocation, of Spanish Sparrows decreased significantly with increasing distance to sheltering vegetation. Conversely, the foraging efficiency of House Sparrows, a common and widespread human commensal and a sister species of the Spanish Sparrow, seemed unaffected by distance to shelter.

One may wonder whether our results demonstrate genuine interspecific differences in patch use behavior, or merely reflect potential confounding effects originating from between-site variability and differences in the experimental designs between study sites and species. We do not think that any fundamental changes occurred in the study species' behavior in the six years between conducting the two experiments. In addition, both experiments were conducted during the same period in the circannual cycle (winter). Quantitative differences that may have occurred due to different environmental conditions (such as temperature) were mostly accounted for by analyzing standardized rather than absolute GUDs, as was most additional unmeasured variability originating from differences in specific experimental design and between-day variability. Furthermore, recent experiments, in which we studied seed-tray utilization by House and Spanish Sparrows at varying distances from shelter under identical experimental designs, in large outdoor aviaries, support the results of the present study (IT et al., unpubl. data). In the aviary experiments, both species displayed increasing giving-up densities with increasing distance from shelter. However, the two species differed significantly in their response to distance from shelter, with House Sparrows showing only a very slight increase in GUDs with increasing distance, while GUDs of Spanish Sparrows increased sharply with increasing distance from shelter.

Under the experimental design we applied, differences in foraging efficiency between microhabitats reflect differences in the predation cost experienced by the foragers in these microhabitats (Brown 1988, Kotler et al. 1994). Our results indicate that while the Spanish Sparrow, a nonurban species, probably perceives a gradient of increasing predation risk with increasing distance to shelter, the House Sparrow, a human commensal, is indifferent to the same variable. This suggests that House Sparrows perceive all microhabitats as equally risky (or equally safe), and indicates a fundamental difference in the way that human commensals, such as House Sparrows, and species that occur in natural habitats, such as Spanish Sparrows, perceive the distribution of predation risk across their foraging habitats.

Alternatively, the behavioral differences between the two species in this study might have resulted from differences in their degree of neophobia (Greenberg 1989, 1995), with House Sparrows being less neophobic and less reluctant to forage in unfamiliar patches, away from shelter. However, we suspect that neophobia plays only a negligible role in our system, because the sparrows are local and the foraging environment is likely not novel to them. Also, we provided a habituation period to the seed trays, and began taking the GUD measurements only after we ensured that the birds readily fed from the trays as soon as they were presented with food.

One may also argue that the House Sparrow, if it is less neophobic, is better able to assess the risk of predation in the environment than the Spanish Sparrow. If predation risk is actually lower in the urban area, this may result in similar response curves to ours, but for a different reason. This is a plausible alternative hypothesis to ours, but we presently do not have the data to test it.

Predation risk has been shown to be a major determinant of foraging behavior in many species and particularly birds (Brown 1988, Kotler and Brown 1988, Lima and Dill 1990, Kotler et al. 1994, Lima 1998), and it has been argued that this is also the case in urban environments (Sorace 2002, Woods et al. 2003). Contradictorily, Shochat (2004) and Shochat et al. (2004) advocate the idea that urban bird populations and communities are strongly controlled by bottom-up mechanisms. They suggest that ecological conditions in the urban environments lead to overmatching between bird population densities and actual food availability, resulting in intense competition for food at the individual level (Sol et al. 1998, Marzluff 2001) and substantially increased marginal value of energy (food). Brown (1988) and Brown (1992) suggest that the cost of predation (P) is directly related to the risk of predation (μ) and inversely related to the marginal value of energy ($\partial F/\partial e$). Hence, increased $\partial F/\partial e$ may reduce P even if μ has not changed or has even increased. Thus, the hypothesized intense competition for food in urban ecosystems may reduce the impact of predation on bird behavior. Our findings support this hypothesis, indicating reduced behavioral sensitivity to predation risk in an urban bird species in comparison to its "wild" sister taxon. We suggest that House Sparrows differ from Spanish Sparrows in their response to the proximity of shelter not because they are safer, but because their behavior has evolved in an environment in which they have historically been safer and in which energy gain has been more important than safety. Thus, House Sparrows are less sensitive to predation risk and may be more likely to trade food for safety.

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