Response to Predation Risk in Urban and Rural House Sparrows

Gábor Seress*, Veronika Bókony*, János Heszberger† & András Liker*

* Department of Limnology, University of Pannonia, Veszprém, Hungary
† Endo Plus Service Kft, Budapest, Hungary

Correspondence
Gábor Seress, Department of Limnology,
University of Pannonia, Pf. 158, H-8201
Veszprém, Hungary.
E-mail: seressg@almos.uni-pannon.hu

Abstract

Habitat urbanization may change the density of predators, and it is often assumed that such changes lead to altered predation risk for urban populations of their prey. Although it is difficult to study predation hazard directly, behavior responses of prey species may be informative in inferring such habitat differences. In this study, we compared the risk-taking behavior of urban and rural house sparrows (*Passer domesticus*) after simulated attacks by two of their important predators (sparrowhawk *Accipiter nisus* and domestic cat *Felis catus*). The birds were startled by moving dummies of these predators and respective control objects, and their risk taking was estimated as their latency to feed after the startle. We found that sparrows responded more strongly (had longer post-startle feeding latencies) to sparrowhawk attacks than to the control object, and their responses differed between the habitats. First, risk taking of urban birds strongly decreased with age (older birds had longer latencies than young birds), while there was no such age difference in rural birds. Second, young urban birds responded less strongly, while older urban birds responded more strongly to the sparrowhawk than the same age groups of rural birds, respectively. We did not succeed in evoking antipredatory response by simulated cat attacks, because birds responded similarly to the dummy and the control object. Our results support that predation risk, posed at least by avian predators, is different in urban and rural habitats of house sparrows. The increased wariness of older, hence presumably more experienced, urban birds implies that sparrows may be more exposed to predation in cities.

Introduction

Habitat urbanization alters several ecological factors that shape the composition and structure of animal communities (Shochat et al. 2006). One of the most important ecological factors is predation pressure, which may have a strong effect on prey populations through lethal and non-lethal effects (Cresswell 2008). Despite its crucial role in population dynamics, it is controversial how predation risk for prey species changes along the urbanization gradient.

Predator densities often differ between differently urbanized sites. For example, domestic and feral predators (e.g. cats and dogs) may attain very high densities in urban areas (Sorace 2002). The abundance of native predators may be either reduced (Blair 2004) or increased, e.g. populations of some raptor species are currently increasing in cities (Chace & Walsh 2006; Rutz 2008). A recent large-scale study by Sorace & Gustin (2009) found that the abundance of predators changed in a complex manner with urbanization, e.g. differed between generalist vs. specialist species. In addition to these complexities, the density of predators in itself may not reflect the actual predation risk. For example, cats may act as predators of small birds and

mammals (Lepczyk et al. 2003; Woods et al. 2003; Baker et al. 2008), but it is unclear whether they cause significant mortality as they may also rely on refuse or food provided by humans. Urban prey may attract rural raptors into the cities to hunt (Newton 1986), which may lead to greater predation than that suggested by the breeding densities of urban raptors. Finally, the mere presence of predators may be detrimental for prey populations via indirect effects such as starvation or suppressed breeding, which may be greater than the mortality effect (Cresswell 2008).

Prey behavior and life history can reflect the risk of predation, thus providing a useful alternative approach to study habitat differences. To date, the results are similarly diverse as those inferred from predator densities. For example, field studies of birds' foraging behavior suggested lower predation risk in cities than desert areas (Shochat et al. 2004) and for more urbanized species (Tsurim et al. 2008). Chamberlain et al. (2009a) reported lower adult mortalities in urban populations of some passerines, although it is unclear whether this was the result of reduced predation. Similarly, the looseness of the rump feathers, which is thought to be an antipredatory adaptation, was found to be reduced in urban bird species compared to closely related rural species, implying that the former are less affected by density-dependent predation rates than the latter (Møller 2009). On the other hand, another study (Møller 2008) found that species with greater proportion of their population breeding in urban habitats are more susceptible to predation (i.e. occur more frequently in the diet of sparrowhawks than expected by chance), suggesting that increased abundance of urban birds (Møller 2009) makes them increasingly preferred as prey by the sparrowhawk (Møller 2008). House fiches (*Carpodacus mexicanus*) were also found to show increased levels of antipredatory behaviors in more urbanized habitats (Valcarcel & Fernández-Juricic 2009). In sum, the evidence of the relationship between habitat urbanization and predation risk is ambiguous. Although lower predation pressure on adult birds in cities is a central assumption of some models of urban population dynamics (Shochat 2004; Anderies et al. 2007), the effect of urbanization on predation may well be species-specific in terms of both predator and prey species (Sorace & Gustin 2009).

In this study, we focus on predation risk experienced by urban and rural house sparrows (*Passer domesticus*). This species is common in many differently urbanized habitats and is an important avian prey of several predators such as feral cats (*Felis catus*) and sparrowhawks (*Accipiter nisus*) (Sodhi & Oliphant 1993; Götmark & Post 1996; Gillies & Clout 2003; Baker et al. 2005). Whereas sparrow populations have been declining worldwide (Summers-Smith 2003; Shaw et al. 2008), several populations of their predators are increasing in urban habitats, including the sparrowhawk (Risch et al. 1996; Kelcey & Rheinwald 2005; Bérces 2007; Chamberlain et al. 2009b; Bell et al. 2010), other raptors (Sodhi & Oliphant 1992; Salvati et al. 1999; Morandini 2006; Rutz 2006), and the domestic cat (Woods et al. 2003; Beckerman et al. 2007).

To test whether sparrows in differently urbanized habitats experience different levels of predation risk, we exposed wild-caught birds from several urban and rural populations to simulated predator attacks and measured their subsequent risk-taking behavior. The assumption behind our study was that the birds' responses to predator exposure reflect the level of predation risk they have adapted to in their original habitats. In accordance with this assumption, a meta-analysis showed that experience with predators amplifies the perception of risk, i.e. animals are generally more wary when they are more frequently exposed to predators (Stankowich & Blumstein 2005). For example, Fernández-Juricic et al. (2004) found that birds preferentially attacked by magpies (*Pica pica*) increased their scanning time in the presence of magpies relative to less often attacked species. Studies on three-spined sticklebacks (*Gasterosteus aculeatus*) and water fleas (*Daphnia magna*) experimentally demonstrated higher risk aversion in high-predation than in low-predation populations (De Meester 1996; Brydges et al. 2008). Therefore, if urban and rural sparrows experience consistently different levels of predation risk, we expect that the birds from the riskier habitat take less risk.

Methods

Study subjects

In September 2009, we captured 58 house sparrows by mist-nets at five urban and five rural sites in Hungary (Table 1). Urban sites were heavily built-up areas in centers of four cities (two sites 5.3 km apart from each other were used in Budapest), while rural sites were located on small farms in vegetated areas remote from city borders and also from each other. We chose study sites that represent independent local populations by being sufficiently far from each other to prevent significant exchange of birds

Table 1: Characteristics of the capture sites and the number of birds used in the experiment

Capture site	Mean vegetation cover score	Mean building cover score	Number of cells with road	Number of cells with >50% vegetation cover	Number of cells with >50% building cover	Sample size in experiment
Rural sites						
Vilmapuszta 47°05′03″N, 17°52′07″E	2.00	0.06	0	100	0	5
Szentgál 47°06′09″N, 17°42′20″E	2.00	0.03	20	100	0	6
Üllő, Dóramajor 47º20′43″N, 19º19′16″E	1.97	0.35	26	97	1	5
Bánd 47°07′17″N, 17°47′34″E	1.95	0.16	29	95	0	2
Salföld 46°50′14″N, 17°32′57″E	1.84	0.17	27	84	1	6
Urban sites						
Várpalota 47°12′05″N, 18°08′22″E	1.13	1.16	95	15	19	4
Veszprém 47°05′29″N, 17°54′43″E	1.15	1.33	98	19	37	4
Budapest, Kőbánya-Kispest 47°27′43″N, 19°09′00″E	1.03	1.15	93	11	37	4
Székesfehérvár 47°11′22″N, 18°24′27″E	0.78	1.65	87	6	65	5
Budapest, Terézváros 47°30′20″N, 19°04′01″E	0.54	1.97	99	1	97	5

Vegetation cover, building density, and the presence of roads were scored for 100 cells of a 1-km^2 area around each capture site as 0 (absent), one (<50%) or two (>50%); the mean of the 100 cell scores are given for each site (see Liker et al. 2008 for further details).

between them (x ± SE distance between sites: 64.1 ± 6.4 km, range: 3.5–145.6 km). The house sparrow is a very sedentary bird: dispersal distances are typically 1–2 km (reviewed by Anderson 2006), and movements in the non-breeding season are usually <500 m (Liker et al. 2009; Vangestel et al. 2010).

Upon capture, we measured body mass (±0.1 g) and tarsus length (±0.1 mm) and ringed birds with a numbered aluminum ring and three color rings. By the development of the birds' plumage, we assigned them to two age categories: (1) young birds that did not have their complete adult plumage and (2) older birds with full adult plumage that were either adults older than 1 yr or juveniles fledged early in the breeding season of 2009. (We were not able to separate these two latter groups, but in any case they were older than the individuals categorized as young birds.)

Birds were transported to Veszprém and were housed in outdoor aviaries. These aviaries were ca. 3 m high and 3 × 4 m large, protected from rain and contained nest boxes and roosting trees. Birds had *ad libitum* access to food (millet, wheat, and sunflower seeds) and water amended by multivitamin droplets. During the first 3 mo, birds were left undisturbed and kept in four mixed flocks of similar size in the aviaries, all containing birds from all capture sites to control for any eventual aviary effect. Before the risk-taking tests, ten birds died for unknown reasons; however, the rest of the birds remained in good health and condition. This rate of mortality was small compared to that observed in free-living house sparrows (Anderson 2006) and similar to other studies where sparrows were kept in aviaries (Liker & Bókony 2009; Bókony et al. 2010). Captures and housing were in accordance with the relevant Hungarian laws and were licensed by the Balaton Upland National Park (permission number: 9135-2/2004).

Test procedure

We tested each bird individually by exposing them to moving sparrowhawk and domestic cat dummies. These risk-taking tests were conducted in Jan.–Apr. 2010 during 1-wk-long test periods. At the start of each test period, we captured two urban and two rural individuals from the aviary flocks; they were chosen randomly with the constraint that they were

from different capture sites. Each bird participated in the experiment only once (i.e. was included in one 1-wk test period). The identity of birds to be captured from the aviaries for each test period was determined before the beginning of the experiment; thus, the ease by which each individual could be captured had no effect on the order in which it participated in the experiment. During the whole study, a similar number of birds were tested from each capture site (Table 1). After weighing (pre-test body mass), the birds were put into individual indoor cages (75 cm high, 80 × 45 cm large) containing a feeder, a water cup, three horizontal perches, a shelter box, and a small artificial bush. The wire grid bottom of the cages prevented the birds from accessing the seed spilled from the feeder. Birds were left undisturbed for the next 3 d with *ad libitum* food and water.

On the following 4 d, we tested one bird per day. Each bird participated in four consecutive tests, all conducted on the same day. Birds were tested in a room separated from the other birds. We alternated the testing of rural and urban birds, and the choice of the first bird of the week was randomized. Every individual's test consisted of two types of aerial (a predator and a control) and two types of ground (a predator and a control) treatments, and the sequence of treatments was randomized.

At 3:00 p.m. before the test day, the actual test bird was placed in the test cage that was identical to the housing cages and contained the same food. The bird was left alone to feed until 4:00 p.m., and then the feeder lid was closed, so an overnight fasting preceded the next day's tests. At 8:00 a.m. on the test day, the lid of the feeder cup was opened remotely (from another room) by pulling a string. When the bird first pecked from the feeder, we startled it instantly by one of the treatment objects. If an individual did not peck from the feeder at all, the startle occurred 15 min after the feeder's opening. After the startle, the bird had up to 30 min to approach the feeder again and then had 10 min for feeding. After this period (or after 30 min if the bird did not resume feeding after the startle), the lid of the feeder was closed remotely, and a 60-min-long fasting period followed to ensure the birds' motivation for feeding in the next test. After the four consecutive tests, the bird was free to feed until 3:00 p.m.; then, we put it back to its former housing cage and moved the next bird to the test cage. After the 4th test of the 4th individual (i.e. at the end of the week), all four birds were weighed again (post-test body mass) and released back to the aviaries.

The aerial predator was a taxidermy-mounted sparrowhawk with body and wings in gliding posture and was moved on a wire ca. 1 m above the test cage. The dummy was remotely pulled out from a hide at one end of the test room and, after passing above the cage, disappeared behind another hide at the other end. It was visible for ca. 3 s for the test birds. A light brown paper box, operated in the same way, was used as control (it had approx. the same size as the sparrowhawk: 15 cm high and 30 × 20 cm large). The ground predator was a taxidermy-mounted cat attached onto a rolling board (a wooden plate equipped with four wheels). It was pulled out from a hide, moved ca. 1.5 m in front of the test cage, and after it was visible for ca. 4 s, it disappeared behind another hide at the other side of the room. We used a light brown paper box of similar size as control (25 cm high and 45 × 30 cm large) that was moved on the same lane as the cat dummy. We used one dummy per predator type throughout the experiment, assuming that the birds' responses to these dummies are representative of responses to live predators in the wild.

During the tests, the test bird was observed through a one-way window and the feeder's lid and the test objects were operated by a single experimenter from an adjoining room. The bird's presence on the feeder was detected by a small infrared detector placed at the top of the test cage: each time (±0.01 s) of arriving at and departing from the feeder was recorded on a computer. Additionally, the behavior of the test bird was recorded by a video camera. In the analyses, we used the infrared detector's recordings because these provided the most accurate measurements of the latencies, and the experimenter's observations and the video recordings were used to double-check these data.

Data analysis

To assess the birds' body condition prior to the tests, we quantified their body mass relative to their body size by calculating the scaled mass index as recommended by Peig & Green (2009, 2010). This index adjusts the mass of all individuals to that which they would have if they had the same body size, using the equation of the linear regression of log-mass on log-size estimated by type-2 [standardized major axis (SMA)] regression. For the calculation of this equation, we used our earlier data on the body mass and tarsus length of 2345 adult house sparrows (our unpublished data). The regression slope was 1.71, and average tarsus length was 19 mm; thus, we

calculated the scaled mass index as pre-test body mass × (19/tarsus length)$^{1.71}$ (Peig & Green 2009, 2010).

Of the 48 test birds, one died before its test day for unknown reasons and another one escaped, so we could finally use the data of 46 birds in total (30 young, 16 older). Using the infrared detector's data, we calculated two variables for each individual in every test situation: (1) latency to first feeding, measured from the opening of the feeder ('pre-startle latency'); and (2) latency to feed after the startle, measured from the appearance of the predator dummy or the control object ('startle latency'). Birds that did not feed before and/or after the startle stimulus were given maximum latencies (900 and/or 1800 s, respectively). Of the total of 92 aerial and 92 ground tests, pre-startle latencies were maximal in 18 aerial and 16 ground tests, whereas startle latencies were maximal in 17 aerial and 11 ground tests. Only one individual did not feed at all (i.e. had maximal latencies in each of its tests); additionally, two birds in the aerial tests and two birds in the ground tests did not feed in both the dummy and its control tests.

To compare the response (i.e. startle latencies) of urban and rural sparrows, we used linear mixed-effects models that contained the following random factors: bird ID (i.e. the latencies of each bird in the control and predator tests were treated as non-independent measures), capture site, test group (i.e. the four birds tested in the same weekly test period) and the position of the housing cage. Separate models were used for the analysis of the aerial and the ground treatments to avoid interactions between more than three variables, because antipredatory responses to different predators may show different interactions with variables such as habitat and age. Both models contained the following predictors: pre-startle latency, date, test day (order of the test birds within the week), and the scaled mass index as covariates; treatment type (control object or predator dummy), sex and age (young or older) as factors; and scaled mass index × habitat, sex × habitat, and habitat × age × treatment type interactions. Additionally, we tested the effects of treatment order by including the following three predictors. To test for habituation or sensitization during the day, we used a covariate giving the number of treatments the individual had received before the actual treatment (ranging 0–3; hereafter treatment order). Because experience in previous tests might affect the response to predatory attacks, we used two factors to encode whether the individual had received the respective control

treatment (hereafter control–predator order) and the other predator treatment (hereafter cat–sparrowhawk order) before or after the predator treatment being analyzed.

We report the full model as recommended by Forstmeier & Schielzeth (2011). Then, we reduced the full model by omitting the effect with the highest p-value step by step until only significant (p < 0.05) effects remained but never omitted habitat and the random factors. We also report the final model obtained by this approach, as recommended by Hegyi & Garamszegi (2011). We favored this model selection technique over the information-theoretic approach because it was suggested that the latter reduces the accuracy of effect size estimation for experiments designed to test the effect of one or two treatments (Richards et al. 2011), and our aim was to infer whether or not habitat has a considerable effect while controlling for confounding variables, rather than to compare the strength of evidence for each predictor. To check the robustness of our results, we reran all the analyses by omitting those cases in which the birds had maximal startle latency values (n = 17 tests in aerial and n = 11 tests in ground tests).

We also tested whether urban and rural birds differed in body mass change during the experiment because this may reflect their sensitivity to stress caused by the experimental conditions. For each bird, we calculated the difference between pre-test mass (i.e. when the bird was captured from the aviary) and post-test mass (i.e. when the bird was released back into the aviary). The full linear mixed-effects model for body mass change contained habitat, sex, age, and test day as fixed factors, date as covariate, the sex × habitat, age × habitat, and date × habitat interactions, and capture site, test group, and housing cage as random factors. Stepwise model selection was performed as described earlier, but we never omitted the age × habitat interaction.

Finally, to assess the potential effect of habitat or age differences in neophobia (i.e. fear of novelty) on the birds' responses in the test situations, we also analyzed (1) the birds' first pre-startle latencies, i.e. those after the first opening of the feeder (note that feeder lids were always open in the housing cages), and (2) the birds' startle latencies in the ground control treatment using linear mixed-effects models. Responses in these novel situations, i.e. the first encounter with the feeder lid opening up and the paper box moving on the ground, may reflect the birds' neophobia. The full models contained habitat, sex, age, pre-test body mass, date, test day, and habitat × age, habitat × mass

and habitat × sex interactions; and additionally, treatment order and pre-startle latency in the analysis of startle latency in the ground control treatment. Capture site, test group, and housing cage were included as random factors. We performed stepwise model selection as described earlier but never omitted the habitat × age interaction. Because the full model yielded qualitatively the same results as the final stepwise model in each case, for these additional analyses we only report the final models.

All statistical analyses were performed in the R computing environment (R 2.6.1; R Development Core Team 2010), using the nlme package. Statistical assumptions of linear models were checked and validated by diagnostic plots. Results are presented as x ± SE, and all tests are two-tailed with a 5% significance level.

Results

Birds' responses in test situations

Aerial treatments were successful in evoking behavioral response, as startle latencies were significantly higher than pre-startle latencies in both the sparrowhawk test (mean difference: 361.9 ± 79.3 s; paired t-test: $t_{45} = 4.66$, p < 0.001; Fig. 1) and the aerial control test (mean difference: 180.2 ± 59.3 s; paired t-test: $t_{45} = 4.13$, p < 0.001; Fig. 1). In the cat test, birds had slightly but non-significantly longer latencies after than before the startle (mean difference: 102.9 ± 49.9 s; paired t-test: $t_{45} = 1.75$, p = 0.086; Fig. 1), but not in the ground control test (mean dif-

ference: 98.7 ± 71.2 s; paired t-test: $t_{45} = 0.39$, p = 0.696; Fig. 1).

The birds' startle latency was significantly longer in the sparrowhawk test than in the aerial control test (mean difference: 221.5 ± 102.3 s; paired t-test: $t_{45} = 2.93$, p = 0.005; Fig. 1); however, there was no significant difference in the startle latencies between the cat test and the ground control test (mean difference 75.9 ± 97.6 s; paired t-test: $t_{45} = 0.71$, p = 0.479; Fig. 1).

Differences between urban and rural birds

In the aerial treatments, we found a strong habitat × age × treatment type interaction effect on the birds' startle latencies (Table 2). Relative to the control treatment, risk taking after the sparrowhawk attack strongly decreased with age in urban birds (i.e. older birds had longer latencies than young birds), while there was no such difference in rural birds (Fig. 2). Young urban birds responded less strongly, while older urban birds responded more strongly to the sparrowhawk attack than the same age groups of rural birds, respectively (Fig. 2). Startle latency in the aerial tests was not significantly related to the scaled mass index and its interaction with habitat (Table 2); using body mass instead of the scaled mass index yielded the same result (not shown). Startle latency did not vary consistently with test day and treatment order (Table 2), suggesting that birds showed no habituation or sensitization overall during the experiment. However, the effect of control–predator order was significant (Table 2): birds that had previous experience with the aerial control treatment showed weaker response to the sparrowhawk than those without such experience. Other predictors included in the initial model had no significant effect on the response to the sparrowhawk, except pre-startle latency (Table 2). Omitting birds with maximal startle latencies did not change our results qualitatively in any analysis (habitat × age × treatment type interaction in the aerial tests: p = 0.046 in the full model and p = 0.011 in the final model, n = 42 birds).

In the ground treatments, startle latencies were not related significantly to any predictor or interaction considered; urban and rural birds did not differ in their response to the cat dummy (urban birds: mean 215.2 ± 84.1 s; rural birds: mean 431.4 ± 136.3 s; paired t-test: $t_{37.5} = 0.52$, p = 0.604), and the effect of the habitat × age × treatment type interaction was non-significant (linear mixed-effect model: $t_{46} = -0.25$, p = 0.801).
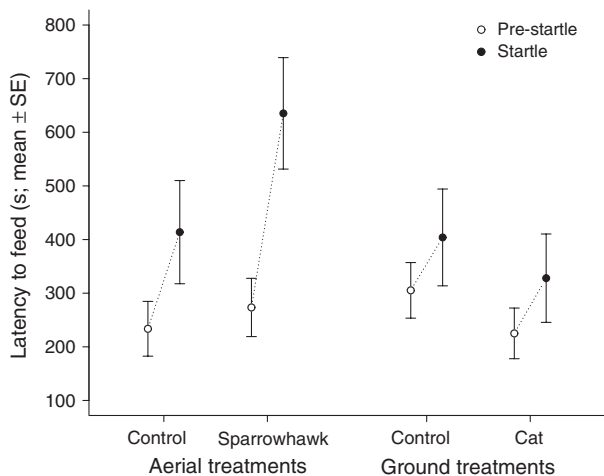

Fig. 1: Pre-startle and startle latencies of birds in the four test situations (n = 46).

	$\beta \pm SE$	t	p	Cohen's d (CI)
(a)				
Intercept	7.38 ± 3.50	2.11	0.038	0.80 (0.18; 1.49)
Pre-startle latency	0.56 ± 0.08	7.17	<0.001	2.71 (1.81; 3.85)
Date	0.00 ± 0.01	0.29	0.772	0.11 (−0.49; 0.72)
Test day	0.17 ± 0.14	1.25	0.216	0.47 (−0.13; 1.12)
Habitat[a]	-5.79 ± 4.38	−1.32	0.191	−0.49 (−1.15; 0.10)
Age[b]	0.29 ± 0.59	0.48	0.630	0.18 (−0.42; 0.79)
Treatment type[c]	-0.52 ± 0.32	−1.60	0.113	−0.60 (−1.26; 0.00)
Treatment order	0.01 ± 0.09	0.11	0.913	0.04 (−0.56; 0.65)
Scaled body mass	-0.16 ± 0.11	−1.42	0.159	−0.54 (−1.19; 0.07)
Control–predator order[d]	-0.80 ± 0.38	−2.14	0.036	−0.81 (−1.50; −0.19)
Cat–sparrowhawk order[e]	-0.05 ± 0.35	−0.14	0.889	−0.05 (−0.66; 0.55)
Sex[f]	0.41 ± 0.40	1.01	0.313	0.38 (−0.22; 1.02)
Habitat × sex	-0.89 ± 0.58	−1.54	0.128	−0.58 (−1.24; 0.02)
Habitat × scaled body mass	0.18 ± 0.15	1.18	0.240	0.45 (−0.16; 1.09)
Habitat × age	1.79 ± 0.77	2.32	0.023	0.88 (0.25; 1.58)
Habitat × treatment type	0.95 ± 0.49	1.91	0.060	0.72 (1.09; 1.39)
Age × treatment type	-0.19 ± 0.61	−0.32	0.750	−0.12 (−0.73; 0.49)
Habitat × age × treatment type	-2.29 ± 0.83	−2.77	0.007	−1.05 (−1.78; −0.41)
(b)				
Intercept	3.43 ± 0.44	7.86	<0.001	2.62 (1.73; 3.74)
Pre-startle latency	0.56 ± 0.07	8.23	<0.001	2.74 (1.84; 3.90)
Habitat	-1.14 ± 0.44	−2.61	0.011	−0.87 (−1.57; −0.25)
Age	0.49 ± 0.53	0.93	0.355	0.31 (−0.29; 0.94)
Treatment type	-0.53 ± 0.32	−1.65	0.103	−0.55 (−1.20; 0.05)
Control–predator order	-0.69 ± 0.28	−2.48	0.015	−0.83 (−1.52; −0.21)
habitat × age	1.66 ± 0.73	2.29	0.025	0.76 (0.15; 1.45)
Habitat × treatment type	0.95 ± 0.49	1.95	0.055	0.66 (−0.04; 1.34)
Age × treatment type	-0.19 ± 0.59	−0.33	0.743	−0.11 (0.73; 0.50)
Habitat × age × treatment type	-2.28 ± 0.82	−2.80	0.006	−0.31 (−0.95; −0.30)

Table 2: (a) Full and (b) final linear mixed-effects model of birds' startle latencies in the aerial treatments (n = 46)

The models included bird ID, capture site, test group, and housing cage as random factors. Effect size estimates (Cohen's d) are given with 95% confidence intervals (CI). Non-significant terms included in the habitat × age × treatment type interaction were retained in the final model. Parameter estimates (β) express the effects of factors as differences between factor levels as follows.
[a]Rural–urban.
[b]Young–old.
[c]Predator dummy–control object.
[d]Control first–predator first.
[e]Cat first–sparrowhawk first.
[f]Female–male.

Urban birds had smaller pre-test body mass than rural birds, and this difference was similar in both age groups (linear model, habitat: $t_{42} = -2.41$, p = 0.020, age: $t_{42} = -0.89$, p = 0.379, habitat × age interaction: $t_{42} = -0.29$, p = 0.777; n = 46 birds). The tarsus length of urban birds was also smaller (linear model, habitat: $t_{42} = -2.49$, p = 0.017, age: $t_{42} = 1.48$, p = 0.147, habitat × age interaction: $t_{42} = -0.95$, p = 0.348; n = 46 birds); therefore, the scaled mass index did not differ between urban and rural birds (linear model, habitat: $t_{42} = -0.13$, p = 0.899, age: $t_{42} = -1.98$, p = 0.054, habitat × age interaction: $t_{42} = 0.44$, p = 0.664). Furthermore, we found no significant habitat × age interaction in body mass loss during the experiment (Table 3a). Our analyses on the potential effect of neophobia on birds' responses showed that the habitat × age interaction was not significant for either the first pre-startle latency of the test day (Table 3b) or the startle latency in the ground control treatment (Table 3c).

Discussion

In this study, we investigated whether there are habitat-related differences in house sparrows' responses to the predation risk by two of their
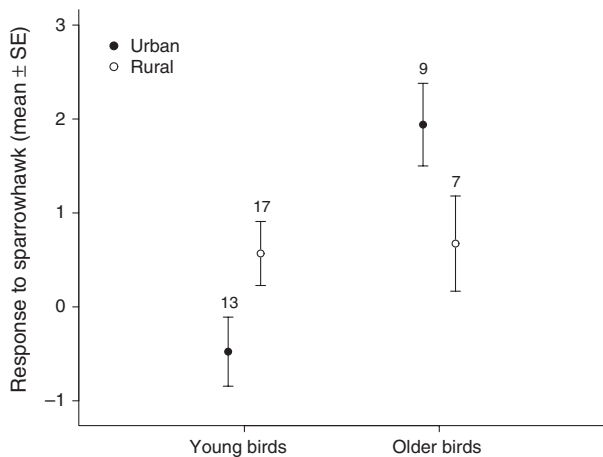
Fig. 2: Response to the sparrowhawk dummy, expressed as the difference in residual startle latency between the raptor treatment and the aerial control treatment, in relation to habitat and birds' age. Residual startle latencies were calculated from a linear model containing pre-startle latency as predictor.

typical predators, the sparrowhawk and the domestic cat. We successfully simulated predation risk by sparrowhawk, because birds' startle latencies were higher than their pre-startle latencies, and startle latencies were higher following the sparrowhawk attack than following its control treatment. Our results showed that the risk taking of birds after the sparrowhawk attacks was related to both their age and original habitat in an interacting way. These

findings support that sparrows are likely to experience different levels of predation risk in cities and rural sites, although the behavioral consequences are different in young and older birds. Because we included birds from several rural and urban localities, these results are likely to represent a general trend in our region and not the particular situation at a specific locality.

Two lines of evidence from this sparrowhawk test suggest that sparrows in cities may be exposed to greater predation risk than in rural habitats. First, response to the sparrowhawk attack increased strongly with age in the urban group, while no such increase was detected in rural birds. Such a difference is expected when predator attacks are more frequent in urban habitats, and gaining more experience with predators during an individual's life causes a larger increase in the birds' risk aversion (Stankowich & Blumstein 2005). Second, among older, hence presumably more experienced, birds, urban individuals responded more strongly than rural individuals, which is also consistent with a higher predation risk in urban habitats. Only the comparison of young, relatively inexperienced sparrows did not conform to this scenario, i.e. habitat difference was the opposite as in older birds, for which we do not have an unequivocal explanation. One possibility is that young birds might be safer from avian predators in the cities than at rural sites, although we are not aware of any mechanism that

Table 3: Final linear mixed-effects models of the birds' (a) body mass loss during the experiment, (b) first pre-startle latencies during the test day, and (c) startle latencies in the ground control treatment (n = 46)

	$\beta \pm$ SE	t	p	Cohen's d (CI)
(a)				
Intercept	2.91 ± 0.49	5.91	<0.001	1.85 (1.09; 2.77)
Habitat	−0.46 ± 0.53	−0.85	0.398	−0.26 (−0.89; 0.34)
Age	−1.08 ± 0.67	−1.62	0.112	−0.50 (−1.16; 0.10)
Habitat × age	0.34 ± 0.78	0.43	0.665	0.13 (−0.48 0.76)
(b)				
Intercept	6.19 ± 0.79	7.79	<0.001	2.46 (1.61; 3.54)
Habitat	0.43 ± 0.66	0.64	0.522	0.20 (−0.39; 0.82)
Age	0.79 ± 0.89	0.89	0.380	0.28 (−0.32; 0.90)
Sex	−1.28 ± 0.55	−2.34	0.024	−0.74 (−1.42; −0.13)
Date	−0.03 ± 0.01	−2.16	0.036	−0.68 (−1.35; −0.07)
Habitat × age	−1.11 ± 1.12	−0.99	0.325	−0.31 (−0.94; 0.29)
(c)				
Intercept	1.63 ± 0.67	2.44	0.019	0.76 (0.14; 1.45)
Pre-startle latency	0.67 ± 0.12	5.74	<0.001	1.79 (1.06; 2.69)
Habitat	0.26 ± 0.47	0.54	0.590	0.17 (−0.43; 0.79)
Age	−0.36 ± 0.58	−0.63	0.534	−0.20 (−0.82; 0.40)
Habitat × age	0.04 ± 0.80	0.05	0.958	0.02 (−0.60; 0.62)

The models included capture site, test group, and housing cage as random factors. Effect size estimates (Cohen's d) are given with 95% confidence intervals (CI). See Table 2 for explanation of the parameter estimates.

could account for such an age-dependent habitat difference. Alternatively, in the lack of strongly developed antipredator responses, young birds' feeding latencies might have been influenced primarily by other factors than the actual predation risk. For example, their readiness to resume feeding after startle may reflect differences mostly in energy reserves, in which case the higher body mass of young rural sparrows would permit them to wait longer than the relatively smaller urban birds. However, because the scaled mass index did not differ between urban and rural birds, it is unlikely that they differed considerably in their energy reserves. Both the latter finding and the fact that the birds' response to predators was not significantly related to their scaled mass index may be due to our experimental design, i.e. we deliberately tried to minimize the differences in individuals' body condition (thus, their motivation) by allowing them to feed *ad libitum* prior their test day. Nevertheless, the smaller body mass and size of urban birds might have affected their responses to predators independently of their energy reserves. For example, it is possible that increased body weight and thereby increased wing loading of rural birds hinder their maneuvering ability, which could reduce their willingness to take predation risk (e.g. Witter et al. 1994; Lind et al. 1999).

The reduced risk taking of urban sparrows after the attack by aerial predators such as the sparrowhawk is consistent with several observations indicating increased raptor densities in cities. The sparrowhawk is a main predator of the house sparrow, and its numbers are increasing in several urbanized habitats (Chamberlain et al. 2009b; Bell et al. 2010), reaching high densities in large European cities like Hamburg (Risch et al. 1996) or Prague (Kelcey & Rheinwald 2005). In Budapest (where two of our urban capture sites were located), breeding sparrowhawks are present from the early 1980s (Bagyura 1985); since then, their population has been increasing, and in 2007, the number of breeding pairs was estimated to 200 (Bérces 2007), which exceeds the breeding density of sparrowhawks in many natural habitats (Newton 1986). Furthermore, the number of sparrowhawks hunting in Budapest during winters is estimated to reach 500–600 individuals (Z. Bajor, pers. comm.). Other raptors such as the kestrel (*Falco tinnunculus*), the merlin (*Falco columbarius*), and the northern goshawk (*Accipiter gentilis*) also readily occupy metropolitan areas in both Europe and North America (Sodhi & Oliphant 1992; Salvati et al. 1999; Morandini 2006; Rutz 2006). Additionally, raptors such as the kestrel and the

tawny owl (*Strix aluco*) readily adapt their diet to the altered prey species composition of cities by taking more birds, including house sparrows, than in their natural habitats (Goszczyński et al. 1993; Kelcey & Rheinwald 2005; Kübler et al. 2005). Although an interspecific comparison of birds' foraging behavior indicated reduced sensitivity to predation risk in the house sparrow compared to the more rural Spanish sparrow (*Passer hispaniolensis*), that study used only one foraging patch per species in a single suburban habitat where the two species co-occurred (Tsurim et al. 2008).

The higher sensitivity of urban sparrows to predation risk is also consistent with our previous results that sparrows have smaller body mass in more urbanized habitats than at rural sites, a difference that persists in captivity for several months (Liker et al. 2008; Bókony et al. 2010). This may be the result, at least in part, of strategic body mass regulation and/or selection for smaller weight on an evolutionary scale, because reduced body mass may be adaptive when the risk of predation is high (Gosler et al. 1995; Pérez-Tris et al. 2004; although other factors such as poor-quality diet in cities might also be important; see Mennechez & Clergeau 2006; Peach et al. 2008). In line with this idea, house sparrows have smaller body mass in areas with higher predation risk posed by sparrowhawks (MacLeod et al. 2006). Similar to these earlier findings, in our present study, rural birds were heavier than urban birds. Heavier birds may store more fat and therefore be less motivated to take the risk of predation, which might have biased the outcome of our experiment. However, differences in energy reserves are unlikely to explain the habitat differences in risk taking in our experiment, as detailed earlier.

Birds of different age and habitat might differ in their sensitivity to stress, which might have an impact on their behavioral responses. However, we did not find any significant difference in birds' body mass change related to habitat, age, or their interaction; thus, it is unlikely that differences in coping with the stress of captivity influenced our results. Differences in the level of neophobia between urban and rural birds might also influence their behavioral responses, as more complex urbanized habitats may contribute to reduced neophobia (Greenberg 2003; Echeverría & Vassallo 2008). However, we found no significant habitat × age interaction either in the first pre-startle latency (i.e. the bird's response to the first opening of the feeder's lid on the test day) or in the startle latency in the ground control test (i.e. the bird's response to a paper box moving on the

ground). In line with these results, previous studies have found that the object neophobia of urban house sparrows is not different from, or even somewhat higher than, the neophobia of rural conspecifics (Echeverría & Vassallo 2008; Liker & Bókony 2009).

In the cat test, we did not manage to evoke antipredator response as there was no difference in the birds' responses given to the dummy cat and its control object. One reason for this may be that cats might pose little threat for adult birds, e.g. because they may mostly catch recently fledged young. Another possible explanation could be that sparrows did not perceive the dummy as dangerous because the cat was passing by the test cage instead of moving toward the bird, and its eye-gaze direction was not focused on the cage. This is likely because both the direction of the predator's movement (Stankowich & Blumstein 2005) and their face orientation and eye-gaze focus (Hampton 1994; Watve et al. 2002; Carter et al. 2008) are known to be used as cues for risk assessment by birds. Because pet cats are regularly fed by humans and do not necessarily have to rely on hunting, it could be adaptive for sparrows to assess the actual risk by the behavior of the cat and adjust their response to it.

In conclusion, our findings do not support a reduced predation risk for urban house sparrows. The increased wariness of older, hence presumably more experienced, urban birds suggests that sparrows are more exposed to predation in cities. As our cat test was not effective, further studies are needed to investigate whether the stronger antipredatory response of urban sparrows is specific to the sparrowhawk (or raptors) or represents a more general response to predation risk.

Acknowledgements

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