Research

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Does urbanization select for weak competitors in house sparrows?

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How urbanization affects animal populations is in the focus of current ecological research. Existing theory of this topic suggests that the cities' more constant food supplies and lower predation pressure lead to a high proportion of weak competitors in urban populations. To evaluate this hypothesis, we tested whether competitive performance differs between differently urbanized populations of house sparrows *Passer domesticus*. We previously showed that wild urban sparrows are smaller and leaner than rural conspecifics, and this difference persists for months under identical captive conditions. Here we compared several aspects of their competitiveness (fighting, scrambling and searching for food) in captive mixed flocks of urban and rural birds. We found that sparrows exhibited consistent individual differences in competitiveness, but these differences were not related either to the degree of urbanization of their original habitats or to their body mass. Moreover, the variance in competitive abilities also did not differ between birds from more and less urbanized habitats. Thus our results did not support the hypothesis that urbanization shifts population structure towards an over-abundance of weak competitors in house sparrows. We discuss possible explanations why sparrow populations may not differ in competitiveness despite the smaller body mass of urban birds.

Urbanization and its effects on wildlife are topics of growing concern not only for conservation biologists but also for evolutionary ecologists (Marzluff 2001, Shochat et al. 2006). Besides re-structuring animal communities by decreasing diversity and increasing the density of a few, often non-native species (Marzluff 2001, Shochat et al. 2004), urbanization can induce substantial, rapid changes in the morphology (Beckmann and Berger 2003, Yeh 2004, Liker et al. 2008), physiology (Partecke et al. 2005, 2006, Bonier et al. 2007), behavior (Beckmann and Berger 2003, Slabbekoorn and Peet 2003, Yeh et al. 2007), and phenology (Fleischer et al. 2003, Partecke et al. 2004, Yeh and Price 2004) of wild animals. A recent theory (credit card hypothesis; Shochat 2004, Anderies et al. 2007) proposes that many of these changes are driven by two main factors: habitat productivity and predation pressure. Although direct evidence is scarce and controversial for both assumptions, urban habitats are thought to be characterized by predictable food and water supplies on the one hand and reduced mortality by predation on the other (Shochat et al. 2004). These two factors are predicted to lead to a "shift from small populations of mostly winners to large populations of mostly losers" (Anderies et al. 2007), because predictable food and low predation lead to high population densities and resource overmatching, so individuals eventually suffer reduced foraging success and maintain lower body reserves. Because these weak competitors can still 'live on the credit' of the predictable resource input in cities and are not selected out by predators, they are expected to constitute a high proportion of urban populations, while only a few individuals with superior competitive abilities are able to maintain high body condition (Shochat 2004, Anderies et al. 2007).

Up to now, several studies compared urban and non-urban populations of vertebrate species using various measures of body condition such as body mass (relative to skeletal size), plasma protein levels or white blood cell profiles. The results vary across species, seasons and the type of condition index used, some showing worse body condition in urban individuals (Ruiz et al. 2002, Partecke et al. 2005, Fokidis et al. 2008, Liker et al. 2008) while others showing the opposite or no difference (Gavett and Wakeley 1986a, Ots et al. 1998, Beckmann and Berger 2003, Schoech and Bowman 2003, Fokidis et al. 2008, French et al. 2008). However, the degree to which these studies support or conflict the credit card hypothesis is difficult to assess, because (1) they did not directly measure the competitive abilities of urban and non-urban individuals, and (2) they did not compare the distribution or variance of the measured variables between habitats.

To test one of the main predictions of the credit card hypothesis, in this study we aimed to investigate the competitive performance of individuals from differently urbanized habitats in house sparrows *Passer domesticus*. This species is one of the world's most common urban birds, occupying a variety of habitats from heavily built-up city centers to small, isolated farm sites in natural environments (Marzluff 2001, Kelcey and Rheinwald 2005, Anderson 2006). Along the urbanization gradient, the house sparrows' body size and body mass decrease with increasing urbanization (Liker et al. 2008), and urban birds are leaner than rural birds in the non-breeding season (Fokidis et al. 2008, Liker et al. 2008). The difference in body mass between urban and rural sparrows persists through several months of captivity under identical circumstances (Liker et al. 2008), suggesting that inferior body condition may be an inherent characteristic of urban birds. Since body size and condition often correlate with the general quality of individuals such as health and resource holding power (Navarro et al. 2003, Lindström et al. 2005), one may expect that the above habitat differences in sparrows indicate poor competitive abilities of urban birds.

We tested whether more urban sparrows are indeed weaker competitors than their less urban counterparts in a common garden experiment, in which birds from different habitats were kept together under identical conditions. The credit card hypothesis predicts that the distribution of competitiveness is skewed towards weaker individuals in urban populations, therefore (1) on average, less urban birds should perform better during food competition than more urban birds, and/or (2) the variance of competitive performance should be greater in more urban birds, since the weakest individuals are expected to survive only in the urban populations. Competition for food may arise through agonistic interactions (contest competition) or depletion of resources (exploitation or scramble competition), and both forms are relevant for sparrows that feed on both dense and scattered food patches such as human-provided seeds and garbage, respectively (Gavett and Wakeley 1986b, Sol et al. 1998). Since competitive abilities may vary with the characteristics of the resource patch and/or the type of competition (Humphries et al. 1999), we studied the performance of sparrows in multiple aspects of competition (contest and scramble for clumped food, and finding scattered food).

Methods

Study subjects

We captured 60 house sparrows with mist nets between 1–18 October 2007 in four differently urbanized habitats in Hungary (Table 1, Appendix 1). Two urban sites are within the built areas of two cities (the capitol of Budapest and the town of Veszprém), whereas two rural sites are extensively surrounded by non-built, agricultural areas (at the edge of a village Nemesvámos and at a small, isolated farm Dóramajor). We followed Liker et al. (2008) to quantify the degree of urbanization in each habitat by scoring the cover of vegetation, paved roads, and buildings in a 1 km^2 area around each capture site (for further details see Liker et al. 2008), and we also collected data on the density of multi-storey buildings and the residential human population for each settlement (Hungarian Central Statistical Office, Population Census 2001, <www.nepszamlalas.hu/eng/index.html>) as suggested by Marzluff (2001). Then we calculated an 'urbanization score' for each site as the PC1 score from a principal component analysis of the seven measures of urbanization (Table 1). The analysis extracted one principal component that accounted for 85.1% of the total variance and correlated negatively with vegetation cover and positively with the density of buildings, roads and humans (Table 1). According to this urbanization score, our capture sites represent fairly distinct habitats along the urbanization gradient occupied by sparrows in Hungary (Table 1).

Upon capture, we ringed each bird with a numbered aluminium ring and three color rings. Sparrows were transported to Veszprém, where they were housed in outdoor aviaries (3 × 4 m, 3 m high) in four mixed flocks (14–16 individuals per flock), each containing an equal number of urban and rural birds. We provided roosting trees and small boxes as shelter, ad libitum water and food (millet, wheat, and sunflower seeds), and we regularly added multivitamin

Table 1. Characteristics of the capture sites and the captured house sparrows.

	Budapest	Veszprém	Nemesvámos	Dóramajor
Capture site	urban train and bus station	urban quick-food restaurant	rural dairy farm	rural horse and cattle breeding farm
Geographical coordinates	47°28´N, 19°09´E	47°05´N, 17°55´E	47°03´N, 17°52´E	47°21´N, 19°19´E
Mean vegetation density score (−0.99)*	1.03	1.15	1.71	1.97
Number of cells with high vegetation density (−0.99)*	11	19	75	97
Number of cells with road (0.96)*	93	98	27	26
Mean building density score (0.94)*	1.15	1.33	0.49	0.35
Number of cells with high building density (0.98)*	37	37	11	1
Density of multi-storey buildings km^{-2} (0.79)*	75.6	9.3	0	1
Human population density km^{-2} (0.78)*	4524.5	471.5	63.8	49
Urbanization score*	1.08	0.60	–0.68	–1.00
Number of birds captured (males, females)	21 (11, 10)	9 (6, 3)	19 (8, 11)	11 (3, 8)

*Vegetation cover, building density, and the presence of roads were scored for 100 cells of a 1 km^2 area around each capture site; the mean of the 100 cell scores are given for each site. Density of multi-storey buildings and residential human population are given for each settlement. Urbanization scores are the PC1 values from a principal component analysis of the seven habitat variables; component loadings are given for each variable in brackets.

droplets to the water. During the five-months course of the study, four birds (two urban and two rural) died for unknown reasons; this rate of mortality (6.7%) is small compared to that observed in free-living house sparrows (Anderson 2006) and similar to that observed in other studies of captive sparrows (Lendvai et al. 2006). The rest of the birds remained apparently in good condition and many of them even bred successfully in the aviaries in summer 2008. 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).

Observing competition

We studied the competitive behaviors of sparrows in two different situations. First, we mimicked competition for a clumped, rich food source in two series of observations, one in the fall (seven days between 25 October – 2 November) and one in late winter (seven days between 19–29 February). In each period, birds got food in three regular observation sessions during each day, with at least one hour fasting before each session. The first observation began after overnight fast ca. one hour after sunrise, when each flock was observed for 30 min and birds on the feeder were also recorded by digital video cameras. Then each flock was observed in two additional, one-hour observations during the day (usually between 10–12 and 13–15 h, respectively). Food was provided in three plastic bowls (30 cm ø, 6 cm high) arranged next to each other in a triangle, placed on a 1 × 1 m wired-top platform on the ground. The platform collected spillage and prevented birds from accessing it, so they could obtain food only from the bowls. Birds were observed through one-way windows from hides placed next to the aviaries.

Second, we observed competition for more scattered and less predictable food in a food-finding task. In this test, a 60 × 60 cm plastic board feeder with 36 (6 × 6) equidistant wells (ø 3.5 cm) was placed on the wired-top platform (instead of the three bowls). In each trial, a small amount of seeds (2 ml millet) was hidden into six randomly chosen wells, and birds were given five minutes to find the seeds, after which all food was removed from the feeder. Trials were performed in the mornings after overnight fast, each flock receiving three subsequent trials each day for four subsequent days (12 trials per flock in total) between 6–11 February. Birds on the feeder were recorded by digital video cameras during the trials. Sparrows had been familiarized with the food-finding task before the actual test using the same protocol.

Competitive ability is often measured by two main components: absolute foraging rate, i.e. feeding rate in the absence of competitors; and susceptibility to interference, i.e. the decline in feeding rate with increasing competitor density (Cresswell 2001). Because sparrows typically forage in flocks, we performed an additional observation to quantify the absolute feeding rates of solitary birds. Between the two observation periods of the flocks (23 November – 25 January), each bird's feeding behavior was observed in an individual cage. Each week, half of a flock (six or eight randomly chosen birds, urban and rural ones equally) was captured from the aviary and placed indoors into individual cages (52 × 46 cm, 37 cm high), isolated from one another visually. Birds were left undisturbed for two days with ad libitum food (millet and wheat) and water. On day 3, after an overnight fast, we observed and video-recorded their first feeding for one hour in the morning (control test). We repeated the latter procedure on day 6, but for the purpose of another study we placed a taxidermally mounted collared dove *Streptopelia decaocto* ca 1 m from the front of the cages for the first 5 min of observation (dove test). Collared doves are frequent in both urban and rural habitats of house sparrows, and the two species often feed together in mixed flocks (Kelcey and Rheinwald 2005, Bókony et al. unpubl.). Pecking rates in the dove test (1.05 ± 0.08) were not different from those in the control test (1.00 ± 0.07; paired $t_{46} = 1.43$, $p = 0.159$), therefore we used the data from the dove test to check the repeatability of pecking rate in the solitary feeding situation. On day 7, birds were released back to the aviary.

We measured the birds' body mass (±0.1 g) five times during the study: (1) upon capture, (2) in the aviary before the beginning of observations in fall 2007, (3) prior to and (4) after the one week in individual cages in winter, respectively; and (5) after the end of observations in early March 2008.

Measures of competitiveness

From the clumped-food observations, we collected data on two aspects of competition: aggression (as proxy for contest competition; Sol et al. 1998) and feeding efficiency (as proxy for scramble competition; Sol et al. 1998). First, we observed 7324 dyadic agonistic interactions between the feeding birds, in which we identified the attacker and the winner (Liker and Barta 2001, Bókony et al. 2006). From these data, we calculated three measures of aggressive competitiveness: (1) fighting success, i.e. the proportion of fights won by the individual out of all fights participated; (2) fighting propensity, i.e. the proportion of fights initiated by the individual out of all fights participated; and (3) attack rate, i.e. the proportion of fights initiated by the individual out of all fights in the flock. Because we tried to record all fights in the flocks during the observations, the latter variable can be considered as a measure for the individual's overall aggressiveness.

Second, from the video-recordings of the morning feedings, we collected data on the birds' foraging behaviors, and calculated two measures of scramble competitiveness: (1) latency to first feeding, i.e. the time (in seconds) it took a bird to go to the feeder and peck at the seeds after the bowls were placed into the aviary; and (2) the relative size of joined groups, i.e. the number of birds on the bowl to which the individual went to feed, divided by the number of birds present on all three bowls at that time. This latter variable was measured for each bird in at least three (up to five) different feeding bouts each day whenever possible (26 ± 0.5 samples per bird), and the mean value was used in the analyses. The smaller the size of the joined group, the more the individual is thought to avoid competition (Sol et al. 1998). As a third measure of scramble competitiveness, we collected data on (3) pecking rate as a proxy for feeding rate (Sol et al. 1998, Johnson et al. 2001), i.e. the number of seed pecks per second during the first feeding that lasted at least 10 s, up to 20 s (the upper limit was chosen because data collection from the video-recordings is very time-consuming). We also noted the number of birds on the feeder (group size) when counting pecking rates, because feeding rate is known to be influenced by the number of competitors (Cresswell 2001, Johnson et al. 2001).

In the food-finding task, we defined food discoveries as events when a seed-filled well was found in the flock for the first time, i.e. when the first bird began to eat from it (note that discoveries do not include events when a bird began to feed from a well that had already been discovered by another flock-member). From the video-recordings we identified the individuals that made food discoveries, and for each bird we counted (1) the total number of discoveries (i.e. occasions being the first to find a seed-filled well), (2) the number of successful trials in which the bird was discoverer at least once, and (3) latency to find food, i.e. the average time (in sec) it took for the bird to discover a seed-filled well. If a bird had not discovered any well in a trial, it was assigned a latency of 300 s (i.e. the duration of the trial).

Absolute feeding rates were measured from the video-recordings of the individual-cages tests, as the number of seed pecks per second during the first 10–20 s of feeding. We also calculated the latency of each bird to first feeding from the start of observation (provision of food in the morning).

Statistical analysis

Prior to analyses, attack rate, latencies to first feeding, pecking rates, number of food discoveries and number of successful trials were log-transformed to improve their fit to normal distribution. We followed Lessells and Boag (1987) to check the repeatability of variables measured in fall and winter. For all repeatable variables, we used their means (fall and winter values averaged) for each bird in the analyses.

All statistical analyses were performed in the R computing environment (R Development Core Team 2006 <www.R-project.org>). We compared the variances of each measure of competitiveness between birds from the four sites using Levene tests. We tested the habitat differences in each measure of the birds' competitiveness in linear mixed-effects (LME) models that included flock as a random factor to control for the non-independence of flock-mates' behavior (Tóth et al. 2009, Zuur et al. 2009). In addition to habitat, flock, and their interaction, initial models included the effects of sex, body mass (averaged for the study period from five measurements), and their interactions with habitat. We then reduced the models stepwise by omitting the least significant effect in each step until only significant effects ($p < 0.05$) remained, but never excluding flock and habitat (Tóth et al. 2009). The flock × habitat interaction was non-significant and was therefore omitted from all models, except for the relative size of joined groups (Results); inclusion or exclusion of this interaction did not change any result on habitat qualitatively. Note that all results remained qualitatively identical when we used the type of habitat as urban vs. rural instead of capture site as a 4-level factor in the LME models (Bókony et al. unpubl.).

Absolute feeding rates (in the solitary control test) were analyzed similarly, with the initial LME model including habitat and sex as fixed factors, and body mass before the test, date of the test and latency to feed as covariates. Susceptibility to interference was analyzed following Cresswell (2001) in a LME model treating each datum on pecking rate (observed in flocks) as repeated measures, with individual identity and flock as nested random factors (individual nested in flock; Tóth et al. 2009, Zuur et al. 2009), group size as covariate, and sex and season (fall vs winter) as fixed factors.

Body mass was analyzed as repeated measures, i.e. with flock and individual identity entered as nested random factors, while the effects of habitat and sex were evaluated in a stepwise procedure as described above. We report means ± SE and two-tailed probabilities throughout.

Results

With a few exceptions, measures of competitive performance were correlated within a given aspect of competition (i.e. aggression, scramble, or food-finding) but not between different aspects (Table 2).

Aggression

Fights were less frequent in winter (n = 580, 700, 693, and 533 in the four flocks, respectively) than in fall (n = 1018, 837, 1183, and 1876). Yet, fighting success, fighting propensity and attack rate were all repeatable over seasons (Table 3). Birds from different habitats did not differ either in any measure of aggressive competitiveness or in the variance of these measures (Table 4).

Scramble

Latency to first feeding was repeatable over seasons (Table 3). Relative size of joined groups also tended to be repeatable (Table 3), and it was positively correlated between fall and winter (Pearson correlation, r = 0.346, p = 0.009, n = 56). Neither latency to first feeding nor the relative size of joined groups differed between birds from different habitats, and their variances were also similar (Table 4). Although the habitat × flock interaction was significant for the relative size of joined groups ($F_{9,44} = 2.75$, p = 0.038), this was due to a single urban female from Veszprém in flock 1 having a very low value, i.e. she joined 0 or 1 flock-mate in 91% of her observations.

As expected, pecking rate in the flocks declined with increasing group size on the feeders (r = –0.15; Table 5), and it was significantly higher in winter (1.13 ± 0.04) than in fall (0.72 ± 0.03; Table 5). In parallel with the latter, group size on the feeder was significantly smaller in winter (3.55 ± 0.16) than in fall (4.57 ± 0.24; paired $t_{55} = 3.396$, p = 0.001). Susceptibility to interference was not different between birds from different habitats, as shown by the non-significant interaction of group size and habitat (Table 5). Although the individuals' susceptibility to interference changed from fall to winter (significant group size × season

Table 2. Bivariate correlations (Pearson's r) among various measures of competitive performance. Framed values show correlations between different proxies for a certain aspect of competition (aggression, scramble, and food-finding, respectively); unframed values are correlations between different aspects of competition.

	Fighting propensity	Attack rate	Latency to first feeding	Relative size of joined groups	Absolute pecking rate	No. of food discoveries	No. of successful trials	Latency to find food
Fighting success	0.99**	0.90**	0.003	−0.08	0.25	−0.05	−0.08	0.06
Fighting propensity		0.93**	0.02	−0.09	0.26	−0.06	−0.09	0.03
Attack rate			−0.03	−0.06	0.24	−0.04	−0.05	−0.05
Latency to first feeding				−0.26*	−0.29*	−0.35**	−0.35**	0.38**
Relative size of joined groups					−0.005	0.05	0.08	−0.09
Absolute pecking rate						0.02	0.01	−0.03
No. of food discoveries							0.97**	−0.68**
No. of successful trials								−0.69**

*$p<0.05$.
**$p<0.01$.

interaction; Table 5), this change was similar in birds from different habitats (non-significant group size × habitat × season interaction; Table 5). Pecking rate had similar variance in birds from different habitats ($F_{736,737} = 1.70$, $p = 0.166$).

Absolute feeding rates

When sparrows were feeding solitarily in individual cages, their pecking rates were repeatable between the control test and the dove test (ICC = 0.73, $F_{46,47} = 6.33$, $p < 0.001$). Pecking rate in the control test decreased with body mass ($r = -0.34$, $F_{1,48} = 7.84$, $p = 0.008$). Birds from different habitats did not differ in absolute pecking rate ($F_{1,48} = 0.05$, $p = 0.984$) or in its variance ($F_{1,50} = 0.18$, $p = 0.911$).

Food finding

During the food-finding trials, sparrows discovered 72.6% of the seed-filled wells (209 out of 288 in total). Birds from different habitats did not differ in the number of food discoveries, number of successful trials, and latency to find food (Table 4), and their variances were also similar (Table 4).

Body mass

Body mass varied significantly over time ($F_{4,229} = 144.25$, $p < 0.001$) and differed significantly between habitats ($F_{1,58} = 4.33$, $p = 0.009$). Multiple comparisons of mean body mass (i.e. the five subsequent measures averaged for each individual) showed a significant difference between the two habitats with the largest sample sizes i.e. urban Budapest and rural Nemesvámos (Tukey's HSD test: $p = 0.006$; for all other pair-wise comparisons $p > 0.151$; Fig. 1). The variance of mean body mass did not differ between birds from different habitats ($F_{1,57} = 0.97$, $p = 0.413$).

Table 3. Repeatability (ICC, intraclass correlation coefficient) of the measures of competitive performance over seasons (fall vs winter).

	ICC	$F_{55,56}$	p
Fighting success	0.77	7.56	< 0.001
Fighting propensity	0.78	8.15	< 0.001
Attack rate	0.36	2.12	0.006
Latency to first feeding	0.27	1.75	0.038
Relative size of joined groups	0.26	1.69	0.054

Discussion

Our results consistently indicated that birds from differently urbanized habitats do not differ in their competitive abilities. We believe this result is robust since we found no effect of habitat on either the means or the variances of several measures capturing various aspects of competitiveness such as fighting, scrambling, and searching for food, in multiple situations and two seasons. Below we discuss alternative explanations for this consistent lack of habitat-differences.

First, our results may indicate that there is no difference in competitive abilities between urban and rural birds. If so, the credit card hypothesis that urban populations consist mostly of poor competitors (Shochat 2004) would be insufficient to explain the leanness of urban sparrows. Studies on other populations of house sparrows have also reported some findings inconsistent with the credit card hypothesis: urban and rural sparrows did not differ in an index of chronic stress, the heterophil/lymphocyte ratio (Fokidis et al. 2008), and higher levels of plasma cholesterol and blood urea nitrogen reflected higher protein and fat intake in urban sparrows compared to rural birds (Gavett and Wakeley 1986a). Combined with our result that individual differences in competitiveness were not explained either by body mass or by habitat of origin, these findings suggest that the leanness of urban sparrows is not a manifestation of poorer condition or weaker competitiveness. However, it must be born in mind that full evaluation of the credit card hypothesis would require the assessment of the two main driving factors i.e. resource predictability and predation risk along the urbanization gradient (Shochat 2004, Anderies et al. 2007). Our

Table 4. Comparison of means and variances of competitive behaviors between sparrows from different habitats. Final LME models include flock as random factor only; sex, body mass, and their interactions with habitat were dropped during model reduction. Results are qualitatively identical when habitat is treated as a two-level factor (urban vs rural).

						Final LME		Levene test	
	n	Dóramajor	Nemesvámos	Veszprém	Budapest	F	p	F	p
Fighting success	60	0.41±0.08	0.43±0.05	0.44±0.08	0.46±0.05	0.09	0.968	0.29	0.833
Fighting propensity	60	0.40±0.07	0.43±0.05	0.44±0.08	0.45±0.04	0.09	0.967	0.30	0.824
Attack rate	60	0.05±0.01	0.07±0.01	0.08±0.02	0.07±0.01	0.16	0.925	0.29	0.832
Latency to first feeding (s)	60	265.6±38.2	272.2±19.2	339.3±32.3	276.1±34.7	1.24	0.306	0.97	0.412
Relative size of joined groups	60	0.29±0.01	0.28±0.01	0.26±0.02	0.29±0.01	0.86	0.468	0.27	0.848
No. of food discoveries	58	2.36±0.68	3.39±0.89	4.22±0.97	4.20±1.01	0.89	0.455	0.51	0.677
No. of successful trials	58	2.00±0.56	2.50±0.53	3.22±0.64	2.90±0.59	0.78	0.511	0.34	0.798
Latency to find food (s)	58	147.7±32.1	141.5±22.8	95.9±16.4	131.4±22.1	0.73	0.538	1.65	0.189

negative results on competitive performance may have arisen because one or both of the main assumptions of the credit card hypothesis may not hold for house sparrows. For example, small body mass in the cities might be an adaptation to high predation pressure, as maintaining small body mass may be advantageous when the perceived risk of predation is high (Lilliendahl 1997, Gosler et al. 2002, Senar et al. 2002), and house sparrows are known to be leaner in areas with higher predation (MacLeod et al. 2006). Interestingly, the same birds we used in this study showed differential response to predation risk in an experimental situation, with urban sparrows being more risk-aversive (Bókony et al. unpubl.). Similarly, Florida scrub-jays *Aphelocoma coerulescens* allocated more time to sentinel behavior in the suburbs than in the wildland (Fleischer et al. 2003). These findings imply that for some species predation risk may be higher in more urbanized habitats, challenging the assumption that predation is generally low in cities (Shochat 2004, Anderies et al. 2007). Given the controversy of this topic, the perceived risk and actual rate of predation along the urbanization gradient deserve much more research attention.

Second, our results may have arisen by a combination of two antagonistic processes: while urban birds may have weaker physical abilities to compete due to their leanness and smaller size (Liker et al. 2008), they may be more practiced because they typically experience stronger competition than rural birds (Shochat 2004), and these two differences might have cancelled out each other. Learning is known to shape foraging behaviors in house sparrows (Turner 1965, Katsnelson et al. 2008), and in some species individuals get better competitors as they grow older (Sol et al. 1998, Cresswell 2001). To disentangle the effects of poorer abilities and better routine, captive-rearing experiments are needed in which nestlings of urban and rural parents are raised under identical conditions with equal chances to learn how to compete. Such experiments could also shed further light on the relationship between body mass, competitiveness and habitat of origin. Ultimately, clarifying whether and why urban sparrows are weaker than rural birds might benefit not only urban-ecology theory but also the conservation of this species, as the causes for the dramatic decline of house sparrow populations especially in urban areas are still very poorly understood (Robinson et al. 2005, Shaw et al. 2008).

Finally, a pessimistic interpretation could be that our study lacked the power to detect the effects of habitat because birds were not observed in their natural environments and any difference may have diminished during captivity. We consider this option unlikely because neither aggressive nor scramble behaviors varied with the time of

Table 5. Final LME model for pecking rates in the flocks. Susceptibility to interference is expressed by the effect of group size on pecking rate. Results are qualitatively identical when habitat is treated as a two-level factor (urban vs rural).

	DF	F	p
Intercept	1,666	23.10	<0.001
Group size	1,666	14.32	<0.001
Season	1,666	177.10	<0.001
Habitat	3,53	1.98	0.128
Group size × season	1,666	5.05	0.025
Group size × habitat	3,666	0.22	0.883
Habitat × season	3,666	1.37	0.250
Group size × habitat × season	3,666	1.15	0.330

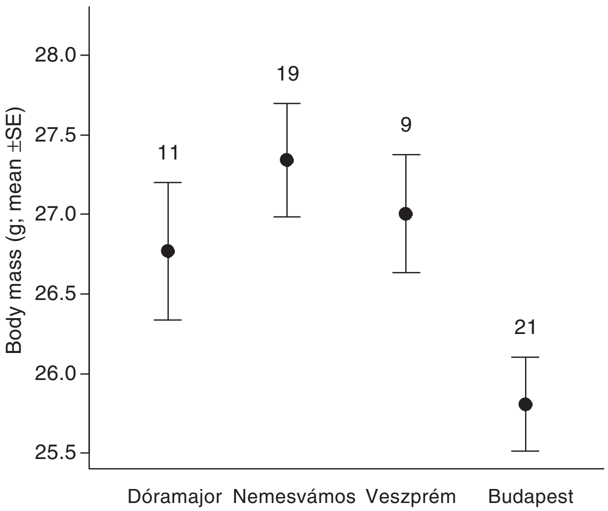

Figure 1. Average body mass during the study of house sparrows from differently (from least to most) urbanized habitats. Sample sizes are shown at the top of each error bar.

captivity within individuals; in fact, they were significantly repeatable between shortly after capture and five months later (which is a considerable time for a bird with an average life expectancy of 1–2 years). This is in line with findings on other species that competitive abilities remain relatively constant throughout an individual's life (Cresswell 2001). The only exception was pecking rate in the flocks (but not in the individual tests) that increased significantly from fall to winter. The latter may have been due to seasonal difference in the strength of competition, as suggested by both the reduced fighting frequency and the smaller size of feeding groups in winter. The reason for this is unknown, but it may be related to seasonal differences in ambient temperatures (Elgar 1986) or to increasing familiarity between flock-mates (Senar et al. 1990). In our view, the individual consistency we found in almost all variables despite the possibility that the strength of competition might have differed between seasons is strong support for the existence of inherent individual abilities for food competition in house sparrows.

Taken together, our study showed that house sparrows from differently urbanized habitats were equally likely to participate and succeed in various forms of competition for food, despite the most urbanized birds having the smallest body mass. We found no indication that urban populations are characterized by the distribution of competitiveness being skewed towards weak individuals, although the differences in inherent abilities might have been obscured by differences in practice and learning. Our results suggest that, at least for house sparrows, the effects of urbanization on population structure and individual competitiveness cannot be fully accounted for by the credit card hypothesis.

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References

Anderies, J. M. et al. 2007. Living in the city: resource availability, predation and bird population dynamics in urban areas. – J. Theor. Biol. 247: 36–49.

Anderson, T. R. 2006. Biology of the ubiquitous house sparrow: from genes to populations. – Oxford Univ. Press.

Beckmann, J. P. and Berger, J. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. – J. Zool. 261: 207–212.

Bókony V. et al. 2006. Multiple cues in status signalling: the role of wingbars in aggressive interactions of male house sparrows. – Ethology 112: 947–954.

Bonier, F. et al. 2007. Sex-specific consequences of life in the city. – Behav. Ecol. 18: 121–129.

Cresswell, W. 2001. Relative competitive ability does not change over time in blackbirds. – J. Anim. Ecol. 70: 218–227.

Elgar, M. A. 1986. The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. – Behav. Ecol. Sociobiol. 19: 433–438.

Fleischer, A. L. et al. 2003. Variation in foraging behavior, diet, and time of breeding of Florida scrub-jays in suburban and wildland habitats. – Condor 105: 515–527.

Fokidis, H. B. et al. 2008. Interspecific variation in avian blood parasites and haematology associated with urbanization in a desert habitat. – J. Avian Biol. 39: 300–310.

French S. S. et al. 2008. Variation in stress and innate immunity in the tree lizard (*Urosaurus ornatus*) across an urban–rural gradient. – J. Comp. Physiol. B 178: 997–1005.

Gavett, A. P. and Wakeley, J. S. 1986a. Blood constituents and their relation to diet in urban and rural house sparrows. – Condor 88: 279–284.

Gavett, A. P. and Wakeley, J. S. 1986b. Diets of house sparrows in urban and rural habitats. – Wilson Bull. 98: 137–144.

Gosler, A. G. et al. 2002. Predation risk and the cost of being fat. – Nature 377: 621–623.

Humphries S. et al. 1999. Patch choice and risk: relative competitive ability is context dependent. – Anim. Behav. 58: 1131–1138.

Johnson, C. A. et al. 2001. The effect of handling time on interference among house sparrows foraging at different seed densities. – Behaviour 138: 597–614.

Katsnelson, E. et al. 2008. Early experience affects producer-scrounger foraging tendencies in the house sparrow. – Anim. Behav. 75: 1465–1472.

Kelcey, J. G. and Rheinwald, G. 2005. Birds in European cities. – Ginster Verlag.

Lendvai, Á. Z. et al. 2006. The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. – Anim. Behav. 72: 747–752.

Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. – Auk 104: 116–121.

Liker, A. and Barta, Z. 2001. Male badge size predicts dominance against females in house sparrows. – Condor 103:151–157.

Liker, A. et al. 2008. Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. – J. Anim. Ecol. 77: 789–795.

Lilliendahl, K. 1997. The effect of predator presence on body mass in captive greenfinches. – Anim. Behav. 53: 75–81.

Lindström, K. M. et al. 2005. House sparrows (*Passer domesticus*) adjust their social status position to their physiological costs. – Horm. Behav. 48: 311–320.

MacLeod, R. et al. 2006. Mass-dependent predation risk as a mechanism for house sparrow declines? – Biol. Lett. 2: 43–46.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. – In: Marzluff, J. M. et al. (eds), Avian ecology and conservation in an urbanizing world. Kluwer, pp. 19–38.

Navarro, C. et al. 2003. Dynamics of an immune response in house sparrows *Passer domesticus* in relation to time of day, body condition and blood parasite infection. – Oikos 101: 291–298.

Ots, I. et al. 1998. Haematological health state indices of reproducing great tits: methodology and sources of natural variation. – Funct. Ecol. 12: 700–707.

Partecke, J. et al. 2004. Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? – Proc. R. Soc. Lond. B 271: 1995–2001.

Partecke, J. et al. 2005. Underlying physiological control of reproduction in urban and forest-dwelling European blackbirds *Turdus merula*. – J. Avian Biol. 36: 295–305.

Partecke, J. et al. 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. – Ecology 87: 1945–1952.

Robinson, R. A. et al. 2005. Size and trends of the house sparrow *Passer domesticus* population in Great Britain. – Ibis 147: 552–562.

Ruiz, G. et al. 2002. Hematological parameters and stress index in rufous-collared sparrows dwelling in urban environments. – Condor 104: 162–166.

Schoech, S. J. and Bowman, R. 2003. Does differential access to protein influence differences in timing of breeding of Florida scrub-jays (*Aphelocoma coerulescens*) in suburban and wildland habitats? – Auk 120: 1114–1127.

Senar, J. C. et al. 1990. Familiarity breeds tolerance: the development of social stability in flocking siskins (*Carduelis spinus*). – Ethology 85: 13–24.

Senar J. C. et al. 2002. Great tits (*Parus major*) reduce body mass in response to wing area reduction: a field experiment. – Behav. Ecol. 13: 725–727.

Shaw, L.M. et al. 2008. The house sparrow *Passer domesticus* in urban areas: reviewing a possible link between post-decline distribution and human socioeconomic status. – J. Ornithol. 149: 293–299.

Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city slicker birds. – Oikos 106: 622–626.

Shochat, E. et al. 2004. Urbanization and spider diversity: influences of human modification of habitat structure and productivity. – Ecol. Appl. 14: 268–280.

Shochat, E. et al. 2006. From patterns to emerging processes in mechanistic urban ecology. – Trends Ecol. Evol. 21: 186–191.

Slabbekoorn, H. and Peet, M. 2003. Birds sing at a higher pitch in urban noise – great tits hit the high notes to ensure that their mating calls are heard above the city's din. – Nature 424: 267–267.

Sol, D. et al. 1998. Competition for food in urban pigeons: the cost of being juvenile. – Condor 100: 298–304.

Tóth, Z. et al. 2009. Effects of relatedness on social-foraging tactic use in house sparrows. – Anim. Behav. 77: 337–342.

Turner, E. R. A. 1965. Social feeding in birds. – Behaviour 24: 1–46.

Yeh, P. J. 2004. Rapid evolution of a sexually-selected trait following population establishment in a novel habitat. – Evolution 58: 166–174.

Yeh, P. J. and Price, T. D. 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. – Am. Nat. 164: 531–542.

Yeh, P. J. et al. 2007. Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. – Oikos 116: 1473–1480.

Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.

Supplementary material (available online as Appendix 017848 at <www.oikos.ekol.lu.se/appendix>). Appendix 1