

Lean birds in the city: body size and condition of house sparrows along the urbanization gradient

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Summary

1. Urbanized habitats differ from natural ones in several ecological features, including climate, food availability, strength of predation and competition. Although the effects of urbanization on avian community composition are well known, there is much less information about how individual birds are affected by these human-generated habitat differences.

2. In this study we investigated the relationships between the morphological characteristics and the degree of habitat urbanization in house sparrows, *Passer domesticus* (Linne 1758). We collected data for more than 1000 non-breeding adult birds in Hungary between 1997 and 2006, from seven sites including farmlands, suburban areas and city centres.

3. We found that the body mass, tarsus length and body condition of free-living sparrows differed among the sites: birds in more urbanized habitats were consistently smaller and in worse condition than birds in more rural habitats. A composite measure of habitat urbanization (based on building density, road density and vegetation cover) explained over 75% of variance between sites in the studied traits, after we controlled for the effects of sex, year, season and time of capture.

4. The difference in body mass between rural and urban sparrows was significant when birds were kept in aviaries under identical conditions, with constant *ad libitum* food availability. It is therefore unlikely that the reduced body size and condition of urban sparrows are a consequence of reduced access to food for adults (e.g. due to strong competition), or their short-term responses to high food predictability (e.g. by strategic mass regulation).

5. We suggest that habitat differences in nestling development or adaptive divergence of sparrow populations due to distinct environmental conditions (such as differing predation pressure) may account for the differences along the urbanization gradient.

Key-words: food availability, individual quality, pollution, predation, urban birds

Introduction

Urbanization of natural landscapes occurs at an accelerating rate worldwide, changing the physical structure and ecological processes of the original habitats (Marzluff 2001). For avian communities, it is often found that urban habitats have a less diverse species composition than rural ones, and are dominated by a few generalist, often non-native bird species (Marzluff 2001; Chace & Walsh 2006; Shochat *et al.* 2006). These community-level changes are attributed to the differential responses of bird species to human-related habitat alteration: some of them are adversely affected and decline, whereas others take advantage of the altered habitat characteristics (new food sources, different predation or competition, milder

climatic conditions) and reach high abundance (reviewed by Marzluff 2001). However, populations of both 'winner' and 'loser' species may be influenced by the changed conditions in urbanized habitats.

The ecological mechanisms underlying community changes and their individual-level effects are poorly understood (Shochat *et al.* 2006). In a recent paper, Shochat (2004) proposed the idea that, for many urban exploiter species, urban habitats are characterized by high food predictability and low mortality (e.g. due to low predation risk and mild climate). Bird populations may respond to such conditions with dramatic increases in their abundances, leading to overexploitation of resources. The characteristics of individuals building up these populations may also change. First, the average body mass and/or condition of adult birds is expected to decrease, because overexploitation of food may reduce the foraging success of

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less competitive individuals, whereas predictable food may allow superior competitors to maintain lower body reserves than they would need in a harsher environment ('living on the credit' of tomorrow's feeding trips; Shochat 2004). Second, urban birds are expected to produce lower-quality offspring than rural birds. One reason for this is that selection may favour parents producing large broods at the expense of fledglings' body condition, because even low-quality offspring may have high chances of survival in urban habitats (Shochat 2004). On the other hand, adverse ecological effects may constrain the body size or condition of offspring. For example, several studies found that nestlings in urban habitats are fed by a reduced amount of, or lower quality, food and reach lower body mass than nestlings in natural habitats (Richner 1989; Pierotti & Annett 2001; Mennechez & Clergeau 2006). The contamination of food, water or soil by toxic materials (e.g. heavy metals) may have similar detrimental effects on nestling development (Eeva & Lehikoinen 1996; Janssens *et al.* 2003). However, as young birds with low body condition can survive for long periods due to low mortality, they may constitute a high proportion of the adult population (Shochat 2004).

In summary, the credit card hypothesis proposes that populations of urban exploiters, although they can reach high abundances, contain a significant proportion of low-quality individuals. It predicts that the average quality of individuals (as measured by adult body size or condition) should be worse in urban populations than in natural habitats. Although a large number of avian studies have compared urban and rural populations (Marzluff 2001), the impacts of urbanization on individual quality have rarely been tested. Two studies reported that urban populations may contain more individuals with inferior body size and condition. First, Partecke, Van't Hof & Gwinner (2005) showed that fat reserves of prebreeding blackbirds, *Turdus merula*, were lower in a city than in a rural forest. Second, Ruiz *et al.* (2002) found that urban-dwelling rufous-collared sparrows, *Zonotrichia capensis*, had lower body mass than their conspecifics in rural sites. Although the latter study suggested that the difference may only be temporary, their experiment with captive birds, on which their conclusion was based, lacked an adequate control. Here we use the largest data set to date, from a long-term study of house sparrows, *Passer domesticus* (Linne 1758), to test whether body size and condition are related to the degree of urbanization across a wide spectrum of differently urbanized habitats.

The house sparrow is one of the most common birds in the urban environment worldwide (Marzluff 2001; Kelcey & Rheinwald 2005), and is ecologically tightly linked to this special habitat (Anderson 2006). It occupies a variety of environments along the urban gradient, making it a suitable model species to study the effects of urbanization on individual characteristics. In this study, we first investigated whether the body size and condition of free-living adult house sparrows differed among populations of differently urbanized habitats. We studied the full range of habitat types the species currently occupies in Hungary, from rural farms with negligible urban influence to the inner centre of a metropolitan area, where urban effects may be maximal. Furthermore, we studied

sparrows' body mass in captivity to test whether differences in wild birds are caused by ecological factors to which birds respond flexibly (e.g. by regulating their mass according to the actual feeding conditions), or instead are a more permanent consequence of habitat differences.

Materials and methods

MEASURING FREE-LIVING SPARROWS IN URBAN AND RURAL HABITATS

Data on free-living house sparrows were collected between 1997 and 2006, at seven sites in Hungary. These sparrow populations were investigated in separate studies, thus the sites differed in the length of the study period and in the frequency and intensity of capturing birds (Appendix S1 in Supplementary material). Otherwise the methods used for collecting morphological data were identical at all sites: sparrows were captured with mist-nets and their body mass (± 0.1 g) and length of left tarsus (± 0.1 mm) were measured with a Pesola spring balance and calliper, respectively, immediately after capture. Body condition index was calculated as residuals from a least-squares linear regression analysis between body mass (dependent variable) and tarsus length (Schulte-Hostedde *et al.* 2005). We also noted the sex of the birds, and the capture date and time. The birds were measured by one of three ringers (A.L., Á.Z.L. and C. Tóth), who standardized the measuring methods before fieldwork. The identity of the ringer was noted.

We captured birds at three urban sites (campus of the Faculty of Veterinary Sciences, Szent István University, Budapest; zoo, Budapest; campus of the University of Pannonia, Veszprém); two suburban sites (zoo, Veszprém; Horse Training Farm, Dunakeszi); and two rural sites (Animal Breeding Station of Szent István University, Üllő; Nyugati Fogadó Farm, Hortobágy, Tiszafüred). The urban sites are situated within the built (mainly office and residential) areas of the cities of Budapest and Veszprém, whereas the suburban sites are at the edges of these cities and are directly connected to non-built (agricultural or forested) areas. The rural sites are several kilometres apart from the nearest city or village, and are surrounded by extensive agricultural areas (for details see Appendix S1).

Distance from city centre is not always a good predictor of habitat urbanization, because sites within the commonly used broad urbanization categories (urban, suburban, rural) may differ in important landscape characteristics (Alberti, Botsford & Cohen 2001). Thus we quantified the degree of urbanization of the study sites and their surroundings by scoring the occurrence of three major land-cover types: buildings, paved roads and vegetated areas (mainly parks, forests and agricultural lands). These land-cover types capture important habitat features for birds as they are strongly correlated with bird abundances and species richness along the urban-rural gradient (Germaine *et al.* 1998). From high-resolution digital aerial photographs, we selected a 1×1 -km area around each capture site, which probably included the core home-range areas of resident sparrows (Anderson 2006; our personal observations) and was large enough to provide meaningful data on habitat urbanization at landscape scale (Alberti *et al.* 2001; Marzluff, Bowman & Donnelly 2001). Each 1-km² area was divided into 100 cells (using a 10×10 grid), and for each cell we scored building cover (0, absent; 1, <50%; 2, >50%); the presence of roads (0, absent; 1, present); and vegetation cover (0, absent; 1, <50%; 2, >50%). From these cell scores we calculated the following summary land-cover statistics for all seven capture sites: mean building density score (potential range 0–2), number

Table 1. Habitat characteristics of the capture sites

Capture site	Mean building density score	Number of cells with high (>50%) building density	Number of cells with road	Mean vegetation density score	Number of cells with high (>50%) vegetation density	Urbanization score (PC1)
Tiszafüred (T)	0.11	0	14	2	100	-1.19
Üllő (Ü)	0.35	1	26	1.97	97	-0.99
Dunakeszi (D)	0.69	8	56	1.96	86	-0.44
Veszprém, zoo (VZ)	0.75	17	58	1.8	80	-0.28
Veszprém, campus (VU)	1.20	29	84	1.34	35	0.57
Budapest, zoo (BZ)	1.25	39	87	1.16	22	0.78
Budapest, campus (BU)	1.85	85	99	0.8	3	1.55

Building density, the presence of roads and vegetation cover were scored for 100 cells of a 1-km² area around each capture site. Density scores are given as the mean of the 100 cell scores. Urbanization scores are the PC1 values from a principal components analysis conducted on scores of the five habitat variables (larger values suggest higher building and road densities and less vegetation cover).

of cells with high building density (>50% cover; range 0–100), number of cells with road (range 0–100), mean vegetation density score (range 0–2), and number of cells with high vegetation density (>50% cover; range 0–100). Then an ‘urbanization score’ for each site was calculated as the PC1 score of a principal components analysis that included the above five summary scores (Table 1). The principal components analysis extracted only one component that accounted for 95.1% of the total variance. By the loading of the original variables, higher urbanization scores can be interpreted as reduced vegetation density and increased building and road densities.

Sparrows were captured year-round at most sites. To ensure that our data set included only fully developed birds, we restricted analyses to the period between October and April. There were no fledged young sparrows before May in the populations studied (our personal observations). By the beginning of October, most first-year sparrows reach their adult body mass (MacLeod *et al.* 2006) and their sex can also be determined reliably. For this period, we have data for 1092 birds (654 males, 438 females).

We compared morphological traits among sparrow populations using general linear models (GLM). One model was built for each dependent variable (body mass, tarsus length, body condition index) that included the following predictor variables as factors: capture site, sex, year, season (date of capture), time of day, and ringer of the bird. Season was included as a three-level factor (autumn, October–November; winter, December–February; spring, March–April) instead of as a linear covariate, because body mass and condition changed nonlinearly during the periods studied. Time of day was included as a five-level factor (by dividing the time between sunrise and sunset into five equal-length periods for each capture day), to express capture time relative to day length, which varied over the study (MacLeod *et al.* 2006). The initial models included all two-way interactions between capture site and the other factors. Non-significant factors and interactions were removed from the models in a backward manner, removing the one with the largest *P* value in each step. Tarsus length was log₁₀-transformed before the analyses. We used Tukey’s honestly significant difference (HSD) *post hoc* tests for pairwise comparisons between capture sites. To control for confounding effects of other significant predictor variables in the pairwise comparisons, tests were conducted on residuals calculated from the final GLMs that included all significant factors except capture site.

To analyse whether the variation in body size and condition between capture sites is directly related to the degree of habitat urbanization, we also investigated the strength of relationship between habitat

urbanization and the studied traits using Pearson correlations. To remove the effects of other variables, first we calculated residuals for body mass, tarsus length and condition index as described above. Then we calculated the averages of these residuals for each capture site, and correlated average residual body mass, tarsus length and condition index with the urbanization scores of the capture sites (as measured by PC1).

BODY MASS IN CAPTIVITY

Body mass changes of urban and rural sparrows during captivity were studied in two experiments. For both experiments, urban birds were captured in the Budapest Zoo, and rural birds were captured at the Animal Breeding Station, Üllő. All birds were transported to the campus of the Szent István University on the day of capture, where they were kept under identical conditions in indoor aviaries (2 × 3 m, 2 m high). Aviaries contained artificial roosting trees, several small (10 × 10 × 10-cm) boxes for sleeping and resting, dishes with water, sand and fine gravel, and a plywood feeding table (80 × 80 cm). Water and food were provided constantly *ad libitum*. Food consisted of millet, oat, wheat, hemp and sunflower seeds. In addition, multivitamin droplets were added to the water. The aviaries were lit by artificial light.

In experiment 1, 15 urban and 18 rural male sparrows were kept in separate flocks (one urban and one rural) between October 2000 and January 2001. Birds were kept in the aviaries for various periods (urban, 11–71 days, mean ± SE 37.7 ± 5.3; rural, 15–81 days, mean ± SE 47.3 ± 5.0), and each male was involved in a behavioural test (unrelated to the present study) at the end of its aviary period. Although the mean length of the captive period did not differ between urban and rural birds (independent samples *t*-test: $t_{31} = 1.32$, $P = 0.198$), the mean flock size throughout the experiment differed (urban, 8.0 ± 0.5 birds; rural, 10.4 ± 0.5 ; $t_{148} = 3.39$, $P = 0.001$). Thus we controlled for variation in both in the analyses (see below). The birds’ body mass was measured twice: at capture and before release. In experiment 2, 14 urban and 14 rural males were held in four flocks (two urban and two rural) for 12 weeks between January and April 2001 (neither had participated in experiment 1). As part of another study (unrelated to the present one), males received one of three treatments 1 week after capture: implanted with testosterone, implanted with flutamide, or empty implants (controls). Each treatment involved equal numbers of urban and rural birds (except that one more rural bird was treated with testosterone). In the middle of the captive period birds were involved in a behaviour test (identical

for all birds), otherwise they were held undisturbed. Implants were removed before the release of birds. Their body mass was measured three times: at capture, in the middle of the captive period (37 days after capture), and before release (81 days after capture).

We analysed body mass changes separately for the two experiments by GLM. For experiment 1, the two body mass data per bird were included as repeated measures (within-subject factor), with capture site (urban, rural) as a between-subject factor, the length of the birds' captive periods and the mean flock size during that period as covariates. For experiment 2, the three body mass data of the individuals were included as repeated measures, with capture site and hormone treatment as between-subject factors. We tested for main effects and all possible interactions in both models, and removed non-significant effects as described above.

All statistical analyses were conducted using SPSS ver. 11. We report mean \pm SE and two-tailed 5% significance values throughout the paper. The sample sizes differed between the analyses because our data set was incomplete for some birds.

Results

BODY MASS, SIZE AND CONDITION OF FREE-LIVING BIRDS

Body mass, tarsus length and body condition index differed between sexes and years, and body mass and condition were also related to the season and time of capture (Table 2). There were no significant differences between the measurements of different ringers, as reflected by the consistent rejection of this factor from the final models. After controlling for the above effects, body mass of adult sparrows differed significantly among capture sites (Table 2; Fig. 1a). Specifically, birds captured in more urbanized habitats generally weighed less than those captured at less urbanized sites (in all cases of the nine significant pairwise differences). The largest mean

Table 2. Results of the final general linear models analysing variation in body mass, tarsus length and body condition index

Dependent variable	Predictor variable	d.f.	F	P
Body mass*	Capture site	5	10.9	<0.0001
	Sex	1	29.0	<0.0001
	Year	8	3.6	<0.0001
	Season	2	7.4	0.001
	Time of day	4	13.2	<0.0001
Tarsus length†	Capture site	5	9.1	<0.0001
	Sex	1	10.5	0.001
	Year	7	2.8	0.008
Body condition‡	Capture site	5	7.9	<0.0001
	Sex	1	16.3	<0.0001
	Year	7	4.3	<0.0001
	Season	2	11.1	<0.0001
	Time of day	4	16.2	<0.0001

Initial models included capture site, sex, year, season, time of day, and ringer as explanatory variables. Excluded variables are not shown. Sample sizes vary among models due to missing data.

Final models: *, adjusted $R^2 = 0.182$, $df = 917$; †, adjusted $R^2 = 0.069$, $df = 932$; ‡, adjusted $R^2 = 0.166$, $df = 856$.

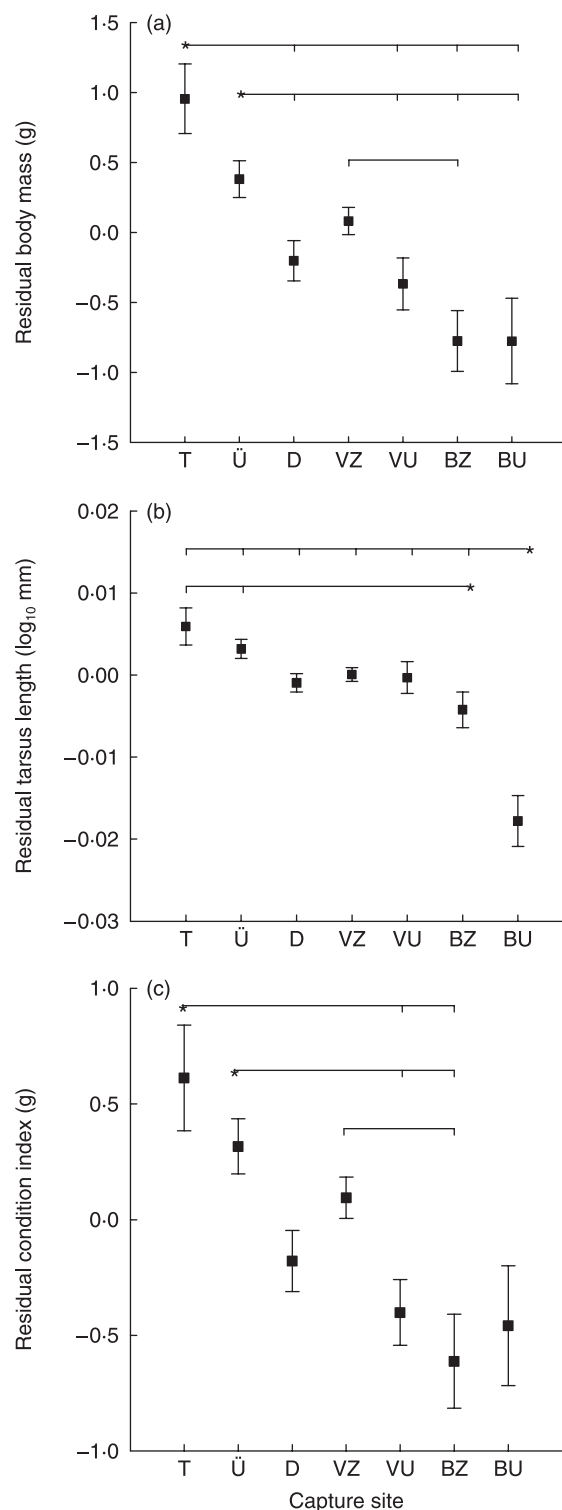


Fig. 1. Differences in (a) body mass; (b) tarsus length (\log_{10} -transformed); (c) body condition index of adult house sparrows between differently urbanized habitats. Figures show mean \pm 1 SE of residuals from the final general linear models containing significant predictor variables except capture site (Table 2). Horizontal lines indicate significant pairwise differences between capture sites (where lines connect more than two sites, an asterisk indicates the site from which the others differ). Capture sites are arranged from least to most urbanized (abbreviated site names as in Table 1).

difference in residual mass of the birds was 1.7 ± 0.4 g (Tukey's HSD test, $P < 0.0001$), which occurred between the most urbanized (University Campus, Budapest) and the least urbanized (Tiszafüred) study sites. Tarsus length and body condition index also differed significantly among capture sites (Table 2), and the pairwise comparisons suggested that birds in less urbanized habitats have larger skeletal size (in all cases of the eight significant pairwise differences) and better body condition (in all cases of the five significant pairwise differences) than birds captured in more urbanized habitats (Fig. 1b,c). None of the other explanatory variables (sex, year, season, time of day, ringer) had significant interactions with capture site for either body mass, tarsus length or body condition ($P = 0.08-0.99$), which indicates that the differences were not the consequence of an uneven distribution of captures from different years, seasons, etc. among the study sites.

The effect of urbanization appears to be independent of the type of human utilization of the sites. We found significant mass differences (less urbanized > more urbanized) between the two zoo sites (Veszprém vs. Budapest, Tukey's HSD test, $P = 0.015$) and between the two animal breeding sites (Üllő vs. Dunakeszi, $P = 0.048$). There were also significant differences in tarsus length between the two university campus sites (Veszprém vs. Budapest, $P < 0.0001$), and in body condition between the zoo sites (Veszprém vs. Budapest, $P = 0.032$). (Note that all the other, non-significant differences between pairs of similarly utilized capture sites were in the predicted direction: less urbanized > more urbanized; Fig. 1a-c.)

The linear relationship between the urbanization scores of capture sites and the average body sizes of birds corroborated the above results. Urbanization scores were strongly and negatively correlated with average residual body mass ($r = -0.918$, $P = 0.004$, $n = 7$), average residual tarsus length ($r = -0.887$, $P = 0.008$, $n = 7$) and average residual body condition of birds ($r = -0.895$, $P = 0.006$, $n = 7$), explaining 77–84% of the variation in each of these variables.

BODY MASS IN CAPTIVITY

The body mass of urban and rural sparrows differed throughout the captive periods: birds from urban habitat weighed consistently less than rural birds in both experiment 1 (repeated-measures GLM, capture site effect: $F_{1,31} = 8.0$, $P = 0.008$; Fig. 2a) and experiment 2 ($F_{1,26} = 11.4$, $P = 0.002$; Fig. 2b). In experiment 1, body mass decreased during captivity (effect of the time of body mass measurement, $F_{1,31} = 34.1$, $P < 0.0001$), and urban birds lost more weight than rural birds by the end of their captive periods (interaction between capture site and time of measurement: $F_{1,31} = 8.5$, $P = 0.007$; Fig. 2a). The length of the aviary period ($F_{1,29} = 1.1$, $P = 0.30$) and flock size ($F_{1,29} = 0.5$, $P = 0.475$) had no effect on birds' body mass and had no interaction with either site or time effects ($P > 0.3$ for all interactions). In experiment 2, body mass decreased during captivity ($F_{1,26} = 68.9$, $P < 0.0001$), weight loss being similar in urban and rural birds (interaction between capture site and time of measurement: $F_{1,26} = 0.3$, $P = 0.725$). Hormone treatments had no effect on body mass

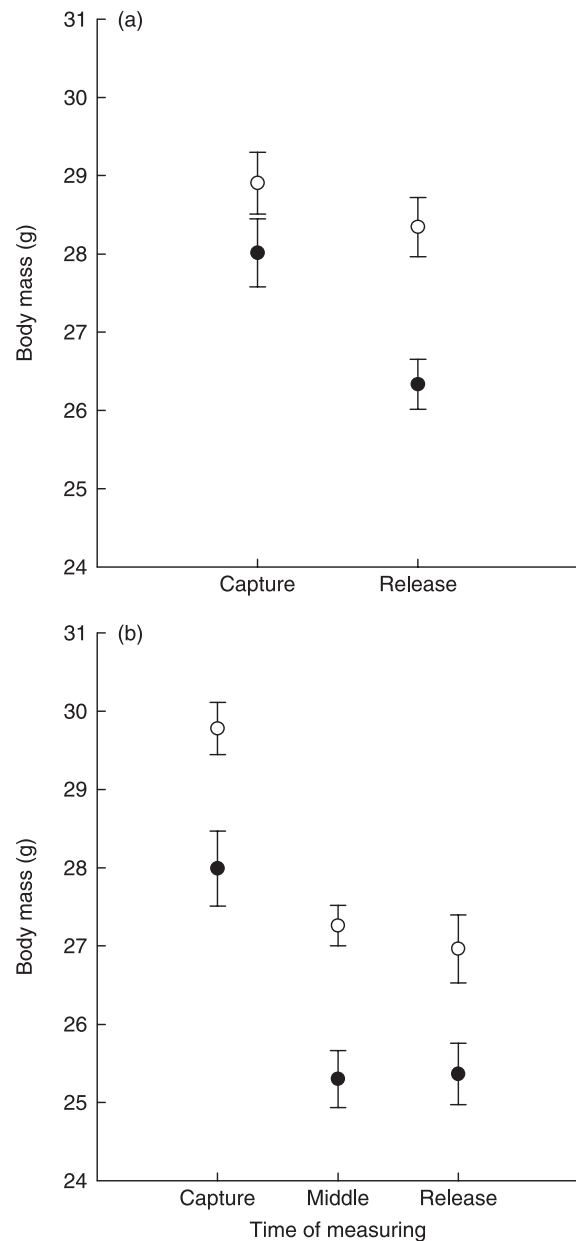


Fig. 2. Body mass changes of rural (open circles) and urban (filled circles) house sparrows in captivity, (a) in experiment 1; (b) in experiment 2. Figures show mean ± 1 SE values at capture and release of the birds, and also in the middle of experiment 2.

($F_{2,22} = 0.2$, $P = 0.818$) and had no significant interactions with site ($F_{2,22} = 2.8$, $P = 0.084$) or time effects ($F_{2,22} = 1.4$, $P = 0.267$).

Discussion

In this study, we tested whether the degree of habitat urbanization affects individual characteristics, namely body mass, size and condition, in a bird successfully exploiting a variety of human-altered habitats. We found for all traits studied that populations differed significantly, house sparrows being consistently larger and in better condition in rural than in

urbanized habitats. Birds at the most urbanized study site (Budapest city centre) were more than 5% lighter than sparrows at the least urbanized places, and the leanness of urban birds was detectable even when we compared differently urbanized habitats with similar utilization (campuses, zoos or animal husbandry farms). The relationships between habitat urbanization and body size and condition were strong, explaining over 75% of morphological variance after we controlled for the effects of some well known factors affecting body mass or condition (sex, year, season, time of day). Although there is geographical variation in body size in house sparrows (Anderson 2006), this cannot account for our results because many of our study sites were close to each other, and changes in size or condition were not associated with a specific geographical gradient. Therefore our results suggest that there may be a substantial link between the degree of urbanization and the size and condition of individual sparrows in different habitats.

Our results support some of the predictions of Shochat's (2004) credit card hypothesis, which suggests that birds may differ along the urbanization gradient due to changes in foraging behaviour, reproductive decisions and survival. First, the hypothesis predicts the observed decrease in size and condition along the urban gradient. Second, the smaller tarsus length at urban than at rural sites may indicate the production of lower-quality offspring in cities: nestling sparrows reach their near-final tarsus length by fledging (Anderson 2006), thus the difference in this trait between habitats is likely to originate from the pre- or early postfledgling period. Finally, birds from both habitats lost weight in captivity, which could be a response to increased food predictability (Cuthill *et al.* 2000), which is considered a hallmark of urban habitats. However, the credit card hypothesis would predict larger mass loss by rural birds when fed *ad libitum*, because their original habitat was less predictable and thus they maintained larger mass before capture than urban birds. Yet we found the opposite in experiment 1, and no habitat difference in the magnitude of weight loss in experiment 2. Thus it is likely that other factors, such as the higher indoor temperature or stress due to the novel environment, may play an important role in body mass loss (Piersma & Ramenofsky 1998; Kelly *et al.* 2002). The difference in adult body mass between urban and rural birds persisted for several months in captivity. This result, together with that for tarsus length, makes it unlikely that reduced mass and condition of urban sparrows is an easily reversible consequence of either reduced access to food by adults (e.g. due to strong competition) or adaptive responses to increased food predictability (e.g. by strategic mass regulation). Instead, it suggests that a substantial part of these differences may originate during nestling development.

The credit card hypothesis predicts lower-quality offspring in urban habitats because parents here may prefer to increase offspring number at the expense of their quality. Contrary to this, a recent study in house sparrows found an opposite trend in clutch size and no consistent habitat difference in fledgling number (Vincent 2005). As an alternative, we suggest that adverse environmental effects are likely to constrain nestling size in

urbanized breeding sites. First, a major component of the diet of nestling sparrows is arthropod prey (Anderson 2006), which may be less available in heavily urbanized habitats where vegetation is scarce (but see McIntyre *et al.* 2001). According to this idea, Vincent (2005) found that sparrow broods' biomass increased with the extent of vegetated area around nest sites. Second, nestling body weight and condition in house sparrows decreased with higher levels of lead (Pinowski *et al.* 1993) and nitrogen dioxide pollution (Vincent 2005), and the concentrations of both these pollutants were higher at more urbanized breeding sites (Vincent 2005; Swaileh & Sansur 2006).

In addition to environmental constraints on nestling growth, populations may also differ between habitats for adaptive reasons due to habitat-specific costs and benefits of large or small body size. For example, selection by strong predation may favour small adult body size due to the enhanced escape of lighter birds (Gosler, Greenwood & Perrins 1995). Accordingly, the body mass of house sparrows is greater on British islands where sparrowhawks, *Accipiter nisus*, are absent, than on other islands and mainland sites where this principal predator of sparrows is present (MacLeod *et al.* 2006). However, it is currently unknown whether predation hazard for house sparrows is reduced or increased in their urban habitats relative to rural sites. Although the density of potential predators may be higher in urban than in rural locations (Sorace 2002), this need not necessarily mean that the actual predation rate on adults is likewise high. Some current reviews favour the view that predation in urbanized habitats may be reduced, at least in the case of high-density urban exploiter birds (Marzluff 2001; Shochat 2004; Shochat *et al.* 2006), and the generally low mortality reported from such habitats seems to support this assumption (Marzluff 2001).

In conclusion, our study showed that body size and condition of adult house sparrows decrease consistently along the urbanization gradient from rural habitats to urban centres. We suggest that environmental constraints on nestling development may be important in generating these habitat differences. Although adaptive differences between the populations may also contribute to the observed divergence in body size, the effects of relevant selection forces such as the strength of predation are difficult to evaluate, because it is unclear how these pressures change along the urbanization gradient. This highlights the need for studies to clarify how basic ecological processes are affected by habitat urbanization (Shochat 2004; Shochat *et al.* 2006). Experimental studies, e.g. by manipulation of the rearing condition of nestlings, would also be useful in disentangling the various ecological and evolutionary processes that may be involved in generating individual-level differences along the urbanization gradient.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Description of the study sites.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2008.1402.x>

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