Multiple indices of body condition reveal no negative effect of urbanization in adult house sparrows

Veronika Bókony [a,*], Gábor Seress [a], Szabolcs Nagy [a,b], Ádám Z. Lendvai [c], András Liker [a,d]

[a] Department of Limnology, University of Pannonia, Pf. 158, H-8201 Veszprém, Hungary
[b] Department of Animal Sciences and Animal Husbandry, Georgikon Faculty, University of Pannonia, Deák Ferenc u. 16, H-8361 Keszthely, Hungary
[c] Institute of Biology, College of Nyíregyháza, Sóstói út 31/b, H-4400 Nyíregyháza, Hungary
[d] Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

ARTICLE INFO

ABSTRACT

As urbanized areas expand and develop throughout the world, the importance of understanding their effects on wildlife increases. Living in cities may be stressful for animals but may also provide benefits at the same time, and the sum of these effects should manifest in the body condition of individuals. Studies addressing this phenomenon tend to evaluate one or few indices of body condition, each of which may be subject to various confounding effects and seasonal changes. In this study we used multiple approaches to assess the effects of urbanization on adult body condition in house sparrows (*Passer domesticus*), a passerine undergoing population declines in urban habitats. In line with earlier studies, we found that sparrows in more urbanized habitats have reduced body mass. However, birds had similar scaled mass index (body mass corrected for body size) along the urbanization gradient at all times of the year, contradicting the previous result on type-1 regression residuals. In the non-breeding season, urban and rural birds had similar levels of corticosterone, hematocrit, and heterophil:lymphocyte ratio. In the molting season, hematocrit indicated better condition in rural birds whereas H:L ratio showed the opposite; however, these trends were not consistent between age groups. Two condition-dependent plumage traits, male bib size and wing bar size, showed no systematic variation along the gradient of urbanization. These results suggest that the environmental conditions experienced by adult house sparrows are not more stressful in more urbanized habitats, and they also highlight the importance of considering multiple indices of body condition.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Natural habitats are being human-modified and converted into urbanized areas at an accelerating rate, and this process has powerful and complex effects on ecosystems (Marzluff, Bowman, & Donnelly, 2001; Marzluff et al., 2008). Urbanization exposes animals to potentially detrimental factors such as human disturbance, toxins, noise, and artificial lighting on the one hand, but can provide advantages like richer or more predictable sources of food and water, and milder climate on the other hand (Shochat, Warren, Faeth, McIntyre, & Hope, 2006). Responses to these effects are species-specific, depending on the life-history and ecological characteristics of each species (Croci, Butet, & Clergeau, 2008; Evans,

Chamberlain, Hatchwell, Gregory, & Gaston, 2011; Møller, 2009). As a result, urbanization alters the structure of native communities, which further changes the ecological conditions for species colonizing or inhabiting cities as they are facing a novel set of competitors, predators and parasites (Marzluff et al., 2001; Shochat et al., 2006; McKinney, 2008). Understanding and predicting these processes requires thorough mechanistic ecological studies at the level of individuals (Shochat et al., 2006).

One of the most fundamental questions in urban ecology studies is how urbanization affects the body condition of animals. Individual condition is a "composite of factors including nutritional state, level of health, experience, and amount of physiological wear and tear" (Schluter & Gustafsson, 1993) that can be a major determinant of fitness and may indicate environmental stress (Peig & Green, 2009, 2010). Despite its crucial importance in animal ecology, body condition remains difficult to measure and there is currently no consensus about the most appropriate method for quantifying it in a non-destructive way (Peig & Green, 2010). For example, vertebrates react to stressful challenges, including those attributable to urbanization, by a suite of neuroendocrine processes, central

* Corresponding author at: Department of Limnology, University of Pannonia, Pf. 158, H-8201 Veszprém, Hungary. Tel.: +36 88 624249; fax: +36 88 624747.
E-mail addresses: vbokony@almos.uni-pannon.hu (V. Bókony), seressg@almos.uni-pannon.hu (G. Seress), nagy.szabolcs@georgikon.hu (S. Nagy), lendvai@nyf.hu (Á.Z. Lendvai), aliker@almos.uni-pannon.hu (A. Liker).

to which is the acute release of glucocorticoid hormones that govern metabolic and behavioral responses, enabling the animals to overcome those challenges (Romero, 2004; Wikelski & Cooke, 2006). However, prolonged or repeated exposure to stressors can be harmful by inhibiting growth, immune functions, and reproduction (Wingfield & Sapolsky, 2003); such chronic stress may be diagnosed at several scales of body condition (Boonstra, Hik, Singleton, & Tinnikov, 1998; Clinchy, Zanette, Boonstra, Wingfield, & Smith, 2004). At the hormonal scale, it may lead to increased concentrations of glucocorticoids in the blood stream due to the enlargement of adrenals (although certain chronic stressors can lead to decreased glucocorticoid levels; Cyr & Romero, 2007; Rich & Romero, 2005). At the hematological scale, chronic stress may cause anemia (red blood cell loss, reflected by a lower hematocrit) and alter the distribution of white blood cells (due to changes in immune function), often resulting in a higher heterophil to lymphocyte (H:L) ratio (Davis, Maney, & Maerz, 2008). At the morphological scale, loss of body weight may result since glucocorticoids stimulate energy mobilization and inhibit energy storage. Each of these measures has the potential to reveal individual differences in body condition, although their utility may vary greatly depending on species and the extent by which confounding sources of variation are taken into account (Davis et al., 2008; Fair, Whitaker, & Pearson, 2007; Ots, Murumägi, & Hõrak, 1998; Peig & Green, 2009, 2010; Romero, 2004).

Up to now, several studies have investigated the above aspects of individual condition in relation to urbanization, ranging from lizards (French, Fokidis, & Moore, 2008) to bears (Beckmann & Berger, 2003), with most research focused on birds. Collectively, these studies do not outline a general effect of urbanization, as their results differ not only among but also within species (e.g. Evans, Gaston, Sharp, McGowan, & Hatchwell, 2009; Hõrak, Surai, Ots, & Møller, 2004; Ots et al., 1998; Partecke, Van't Hof, & Gwinner, 2005), and these differences cannot be fully accounted for by each species' adaptability to urbanization (Fokidis, Greiner, & Deviche, 2008; Fokidis, Orchinik, & Deviche, 2009). For example, when comparing urban to rural populations, baseline levels of corticosterone (the main avian glucocorticoid hormone) were higher in tree sparrows (*Passer montanus*; Zhang et al., 2011) and male (but not in female) white-crowned sparrows (*Zonotricha leucophrys*; Bonier et al., 2007) but lower in Florida scrub-jays (*Aphelocoma coerulescens*; Schoech, Bowman, Bridge, & Boughton, 2007), whereas corticosterone levels in response to a standard acute stressor (i.e. stress response) were higher in the scrub-jays (Schoech et al., 2007) but lower in captive-reared blackbirds (*Turdus merula*; Partecke, Schwabl, & Gwinner, 2006). One reason for such an inconsistency of findings may be that most studies were "snapshots" at different scales of body condition of different species in different life-history stages. Since each measure of body condition can be influenced by several extrinsic and intrinsic factors and may be sensitive to different aspects of environmental stress (Davis et al., 2008; Fair et al., 2007; Lendvai & Chastel, 2008; Lendvai, Giraudeau, & Chastel, 2007), using only one or few indicators of body condition might lead to incorrect or incomplete conclusions.

In this study, our aim is to draw a more detailed picture of the effects of urbanization on individual condition. Our study species is the house sparrow (*Passer domesticus*), one of the most intriguing cases of urbanization. Being a human commensalist, this species has accompanied man for centuries and became the most successfully urbanized bird until the mid-1980s; then its populations started to decline at many locations worldwide, especially in European cities (Shaw, Chamberlain, & Evans, 2008). Several hypotheses have been put forward to explain the decline of urban sparrows, including increased pollution by traffic and predation by domestic cats (*Felis catus*) and sparrowhawks (*Accipiter nisus*), and loss of nesting sites and food sources due to cities' socioeconomic changes (Shaw

et al., 2008; Summers-Smith, 2003). Recent studies showed that adults' body size and mass in the non-breeding season is smaller in more urbanized populations of house sparrows, suggesting inferior body condition for urban birds (Bókony, Kulcsár, & Liker, 2010; Fokidis et al., 2008; Liker, Papp, Bókony, & Lendvai, 2008). Altogether, we can thus hypothesize that more urbanized habitats are more stressful to house sparrows.

To test this idea, here we examine various indices of environmental stress along the urbanization gradient in adult sparrows. Specifically, first we evaluated hormonal and hematological measurements of body condition during molt and at the end of the non-breeding season to test whether birds in more urbanized habitats have higher baseline and stress-induced levels of corticosterone, lower hematocrit (i.e. less red blood cells), and higher H:L ratio. Then we examined two morphological aspects of body condition. Firstly, we re-assessed whether the actual amount of energy reserves, expressed as body mass corrected for body size (Peig & Green, 2009, 2010), decreases with increasing degree of habitat urbanization throughout the year, as found earlier by using a different analytical approach (Liker et al., 2008). Secondly, we investigated two condition-dependent traits of plumage coloration: the size of the black bib that is influenced by, among other factors, the body condition of males (Nakagawa, Ockendon, Gillespie, Hatchwell, & Burke, 2007) and the size of the white wing bar that is sensitive to nutritional conditions, i.e. protein intake (Poston, Hasselquist, Steward, & Westneat, 2005). Sparrows are expected to grow consistently smaller plumage ornaments in more urbanized habitats if the latter are more stressful, e.g. by providing inferior feeding conditions during molt than less urbanized habitats.

2. Methods

2.1. Urbanization intensity measurement

We studied house sparrows at several sites along the urbanization gradient in Hungary, ranging from small, isolated farms through villages and suburbs to the most heavily built-up city centres (Table 1). We sampled the gradient of urbanization not as a geographical gradient around a single city, but as a variety of differently urbanized sites at several geographic locations (McDonnell & Hahs, 2008). Urbanization intensity at these sites was quantified as in Liker et al. (2008) from digital aerial photographs. In short, vegetation cover, building density, and the presence of roads were scored for 100 cells of a $1\,km^2$ area around each capture site. For each site we calculated urbanization score by extracting the first principal component from a principal component analysis (PCA) of five urbanization measures (mean building density, number of cells with high building density, number of cells with road, mean vegetation density, number of cells with high vegetation density). The PCA extracted one component with >1 eigenvalue that accounted for 92.2% of the total variance and correlated strongly (component loadings ≥ 0.90) with reduced vegetation density and increased densities of buildings and roads (Table 1). We used this principal component as measure of urbanization in the analyses.

For each analysis, we chose study sites that represent independent local populations, i.e. are sufficiently far from each other to prevent significant exchange of birds between them (Table 1). 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, Braeckman, Matheve, & Lens, 2010). Distances between our capture sites ranged 1–263 km; note that even the closest study sites can differ considerably in the birds' body size and mass (Liker

Table 1

Degree of urbanization of the capture sites and the number of birds captured at each site (datasets: (a) physiological indices; (b) scaled mass index; (c) plumage coloration). Sites are listed in decreasing order of urbanization; "other sites" include 4 sites for which urbanization was not measured because they were too close to at least one of our study sites to be treated as independent sites for the analyses of urbanization. Sites marked with asterisk had been sampled by Liker et al. (2008).

Capture site	Mean vegetation density score	Mean building density score	Number of cells with road	Number of cells with high (>50%) vegetation density	Number of cells with high (>50%) building density	Urbanization score	Dataset (sample size)
Budapest, VI. 47°30′20″N, 19°04′01″E	0.54	1.97	99	1	97	1.841	ab (14)
Budapest, ÁOTK campus* 47°30′17″N, 19°04′28″E	0.80	1.85	99	3	85	1.588	bc (20)
Székesfehérvár 47°11′22″N, 18°24′29″E	0.78	1.65	87	6	65	1.290	ab (27)
Budapest, Lurdy Ház 47°28′08″N, 19°04′48″E	0.71	1.21	70	8	40	0.864	abc (14)
Veszprém, Hotel 47°05′29″N, 17°54′43′E	1.03	1.15	93	11	37	0.812	abc (21)
Budapest, Kőbánya-Kispest 47°27′43″N, 19°09′00″E	1.15	1.33	98	19	37	0.811	abc (22)
Budapest, Zoo* 47°31′11″N, 19°04′58″E	1.16	1.25	87	22	39	0.706	bc (55)
Várpalota 47°12′05″N, 18°08′22″E	1.13	1.16	95	15	19	0.634	ab (10)
Csepel 47°24′22″N, 19°04′49″E	1.18	1.17	80	18	23	0.533	abc (18)
Veszprém, PE campus* 47°05′12″N, 17°54′07″	1.34	1.20	84	35	29	0.448	abc (105)
Veszprém, Cholnoky ltp. 47°05′15″N, 17°55′36″E	1.41	0.77	56	49	13	-0.107	abc (13)
Veszprém, Zoo* 47°05′32″N, 17°53′43″E	1.80	0.75	58	80	17	-0.415	bc (1123)
Dunakeszi, Alag* 47°37′12″N, 19°08′55″E	1.96	0.69	56	86	8	-0.616	b (301)
Nemesvámos 47°03′16″N, 17°51′52″E	1.71	0.49	27	75	11	-0.682	bc (56)
Hajmáskér 47°08′14″N, 18°00′15″E	1.88	0.25	41	88	0	-0.904	abc (21)
Salföld 46°50′14″N, 17°32′57″E	1.84	0.17	27	84	1	-0.975	ab (31)
Üllő, Dóramajor* 47°20′43″N, 19°19′16″E	1.97	0.35	26	97	1	-1.045	abc (248)
Bánd 47°07′17″N, 17°47′34″E	1.95	0.16	29	95	0	-1.082	ab (12)
Szentgál 47°06′08″N, 17°42′20″E	2.00	0.03	20	100	0	-1.236	ab (26)
Hortobágy, Nyugati Fogadó* 47°35′24″N, 20°51′15″E	2.00	0.11	14	100	0	-1.245	bc (36)
Vilmapuszta 47°05′05″N, 17°52′03″E	2.00	0.06	0	100	0	-1.352	ab (9)
Other sites							b (163)

et al., 2008) with very little movement of birds between them (Liker et al., 2009).

2.2. Body condition measurements

We captured house sparrows in differently urbanized habitats in Hungary between 1997 and 2009 using mist-nets (Table 1). For all birds we measured tarsus length ($\pm$0.1 mm) and body mass ($\pm$0.1 g) upon capture, whereas other measurements were taken from various subsets of birds as described below. All capture procedures were in accordance with the relevant Hungarian laws and licensed by the local authorities (permission numbers: 847/3/2003, 9135/2004, 2255/2008).

2.2.1. Physiological indices

We captured 132 sparrows in 2009 in the end of the non-breeding season (January–March) at 12 sites and 157 birds in the molting season (September–October) at 10 sites (Table 1). In winter, birds were sampled for corticosterone assay by taking up to 150 μl blood within 3 min from capture. Because sparrows usually hit the net in flocks, we could sample corticosterone only for some of the captured birds. Within this short time frame (156 ± 4 s) corticosterone concentrations did not increase with handling time in our sample (slope $\pm$ SE = 0.006 ± 0.025, $r = 0.13$, $P = 0.886$, $N = 35$; P obtained by permutation test using the 'coin' package of R), so we refer to these as "baseline" (Romero & Reed, 2005; Wingfield, 1994). These birds were then kept in a cloth bag for 30 min, after which a second blood sample was taken from the other wing to measure the level of corticosterone induced by acute stress (capture-restraint protocol; Wingfield, 1994). In house sparrows, corticosterone concentrations are maximal 30 min after the initial stressor (Romero & Romero, 2002). As the amount of blood required for corticosterone assay is relatively large for sparrows, we did not take any more blood from birds sampled for corticosterone. From the rest of the captured birds we collected two blood samples from the brachial vein within 53 ± 1.75 min from the time of capture: up to 100 μl blood into a heparinized capillary tube for hematocrit measurement, and a smear from a 1 to 2 μl drop of blood on a microscope slide for blood cell counts. In the molting season we took blood samples for hematocrit and smears but not for corticosterone since the latter is at very low levels during molt (Romero, Strochlic, & Wingfield, 2005).

Smears were air-dried, fixed in absolute methanol, and stained with Hemacolor staining set (Merck KGaA, Darmstadt, Germany); then examined under oil immersion at 1000$\times$ magnification to count the proportion of different types of leukocytes in a total of 100 leukocytes per smear. Blood samples were stored on ice until transport to the laboratory within 8 h; they were then centrifuged for 5 min at 8000 rpm. Hematocrit was measured as the relative amount of red blood cells in total blood volume in the capillary tubes. For corticosterone measurement, blood plasma was extracted and kept at $-20\,°$C until radioimmunoassay at the Centre d'Études Biologiques de Chizé following the protocol that was validated for house sparrows (Lendvai, Bókony, & Chastel, 2011). Briefly, total plasma corticosterone was measured in samples (25 μl) after ethyl-ether extraction by radioimmunoassay using a commercial antiserum. Duplicate aliquots of the extracts were incubated overnight at 4$°$C with 3H-Corticosterone and antiserum. Bound and free corticosterone was separated by adding dextran-coated charcoal. After centrifugation, the bound fraction was counted in a liquid scintillation counter. Two assays were run, intra-assay and inter-assay coefficients of variation were 4.67% and 5.35%, respectively, for $N = 6$ duplicates of reference samples. Minimal detectable corticosterone levels were 0.52 ng/ml (lowest measurement: 1.47 ng/ml). Pooled plasma of different

house sparrows produced a dose–response curve that paralleled the corticosterone standard curve.

In the molting season, for each bird we recorded the stage of molt (the number of freshly molted primaries), and we assigned them into one of two age classes: "young" (first-year juveniles that fledged late in the season and had remnants of nestling plumage) and "older" (birds with completed molt, including both juveniles fledged early in the season and adults older than 1 year). In the wintering season, the age of the birds could not be determined; by that time all birds were considered as adults.

2.2.2. Scaled mass index

To quantify the birds' body mass relative to their body size, we calculated the scaled mass index following Peig and 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-length estimated by type-2 (standardized major axis; SMA) regression. For the calculation of this equation, we used the body mass and tarsus length data of 2345 adult sparrows from 30 sites, captured throughout the year between 1997 and 2009 (Table 1). Note that this dataset partially overlaps with the one used by Liker et al. (2008), however, in that study type-1 regression residuals were analyzed which is a less reliable index of body condition because it underestimates the true mass–length slope and thus the residuals are systematically biased towards larger individuals (Peig & Green, 2009, 2010). After excluding 13 outliers (i.e. |standardized residual| > 3), the regression slope was 1.71, whereas average tarsus length was 19 mm. Thus we calculated the scaled mass index as body mass $\times$ (19/tarsus length)$^{1.71}$ (Peig & Green, 2009, 2010). We chose tarsus length as the proxy for skeletal body size as this measure had been routinely taken during our captures. Wing length ($\pm$1 mm) and bill length ($\pm$0.1 mm) were measured for smaller subsets of birds; we used these data to verify our scaled mass index (see Section 3).

2.2.3. Plumage coloration

Bib size of 314 males was measured by a single person at seven sites between 1997 and 2008 (Table 1). The maximum length and width of the bib was measured by ruler to the nearest mm, and bib size was calculated following Veiga (1993). This estimate of bib size is highly repeatable (Liker & Barta, 2001). We used data only from November to April each year to exclude birds from the molting season (we had no comparable data for most study sites from the breeding season). We repeated the analysis of bib size using a smaller sample of males ($N = 89$) whose bib size was measured from digital photographs (see below), but since we obtained qualitatively identical results (i.e. no relationship with urbanization; see below), here we report results only for the larger sample (i.e. bib size measured by ruler).

Wing bar size was measured in 89 males and 80 females captured at 10 sites between 2007 and 2009 (Table 1) from digital photographs as described in Bókony, Lendvai, & Liker (2006) and Bókony, Liker, Lendvai, & Kulcsár (2008). The photos were taken between November and March (i.e. only non-molting birds were photographed) and measured by a single person with very high repeatability ($R = 0.95$, 95% confidence interval: 0.82–0.99, $F_{9,10} = 38.6$, $P < 0.001$) *sensu* Lessells and Boag (1987) using ScionImage software (see Bókony et al., 2006, 2008). As indicators of age, we measured wing length and tail length ($\pm$1 mm; Nakagawa & Burke, 2008; Selander & Johnston, 1967) and male mask size, i.e. the maximum length of the black mask on one side of the face ($\pm$0.1 mm; Nakagawa & Burke, 2008).

2.3. Data analysis

Measures of body condition were analyzed in linear mixed-effect (LME) models that contained capture site as random factor to control for the non-independence of individuals captured at the same site. Full models of corticosterone levels included urbanization (i.e. the principal component score), sex, date (number of days since 1 September, i.e. the peak of molting season each year), and time of day (number of minutes since 7:00 h each day) as predictors (i.e. fixed effects). Because preliminary analyses of baseline corticosterone revealed heterogeneity in the variances between the sexes, we used a constant variance structure ('varIdent' function in *R*) that allows for different variances in males and females. Full models of hematological indices (i.e. hematocrit and H:L ratio) included urbanization, sex, date, time of day, handling time (number of minutes from capture until blood sampling) and, for the molting season, age and molting stage (note that since the latter variables were only available for the molting season and not for winter, data from the two seasons were analyzed separately). The full model of the scaled mass index included urbanization, date, time of day, sex, and age (i.e. juvenile or adult); juveniles captured in May–September were omitted from this analysis because young birds might not finish growth until October (MacLeod, Barnett, Clark, & Cresswell, 2006). Full models of plumage coloration included urbanization, date and, for wing bar size, sex. Since the body size of sparrows is known to be related to urbanization (Liker et al., 2008), we controlled for body size in the analyses of bib size and wing bar size by including body mass into the full models and retaining this predictor throughout all steps of model reduction (see below). Each full model also included all 2-way interactions between urbanization and the other predictors. All models were checked for linearity by inspecting diagnostic graphs of residuals and fitted values; in no case did these indicate a non-linear relationship between urbanization and body condition indices.

As our research question was whether habitat urbanization has a considerable effect on the body condition indices, we preferred the frequentist (i.e. null-hypothesis testing) paradigm over the information-theoretic approach during our analyses for the following reasons. First, frequentist methods provide well-established, efficient statistical tests for bivariate comparisons (Richards, Whittingham, & Stephens, 2011). Second, in the case of multivariate analyses, our goal was to infer the effect of urbanization while controlling for potentially confounding variables, rather than to compare the relative importance of all initially considered predictors. The inference yielded by the information-theoretic method depends critically on the set of candidate models chosen (Hegyi & Garamszegi, 2011); how the potentially confounding variables interact to influence each index of body condition is beyond both our knowledge and the scope of this study. Therefore, we handled our multivariate models in the following way. We reduced each full model stepwise by excluding the confounding variable with the highest p-value in each step until only $P < 0.05$ predictors remained; we inspected the models in each step and never excluded our predictor of interest, i.e. urbanization. The aim of this process was to increase the accuracy of effect size estimates for urbanization since effect sizes in full models are usually inaccurate due to noise terms (Hegyi & Garamszegi, 2011). Note that our final models yielded qualitatively the same conclusions as the full models (i.e. when no stepwise selection was done). We present effect size estimates (Cohen's *d*) with 95% confidence intervals for the variables retained in the final models, mean ± SE for bivariate comparisons and two-tailed *P*-values throughout the paper. All statistical analyses were performed in the R computing environment (R 2.11.0; R Development Core Team, 2010), using the 'nlme' and 'smatr' packages. Sample size of each analysis is given in Table 2 (see Appendix 1 for further details).
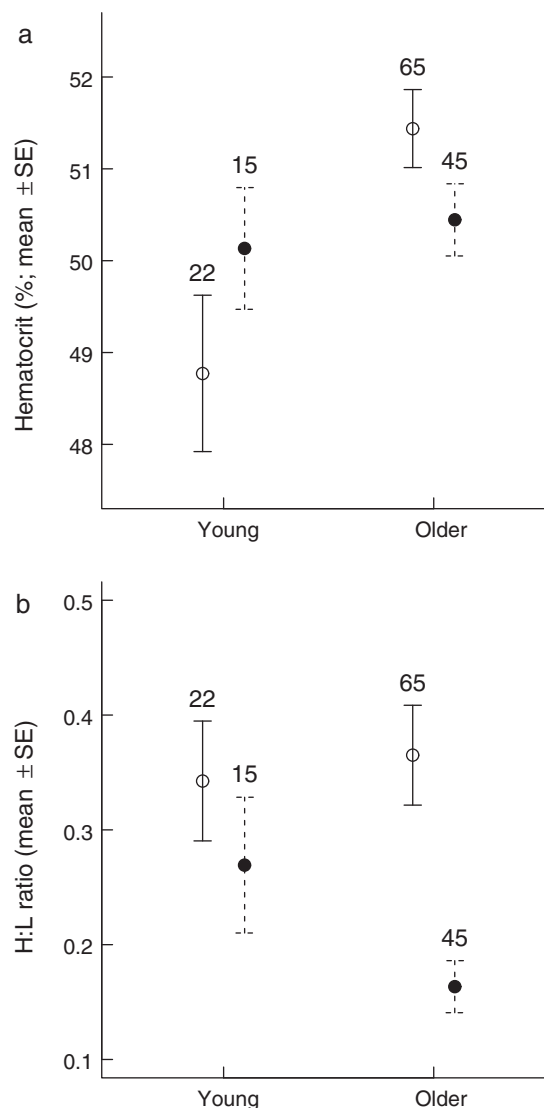

Fig. 1. Hematocrit and H:L ratio in relation to urbanization and age in the molting season. For illustrative purposes, habitat urbanization score is simplified as "rural" (negative scores; open circles) and "urban" (positive scores; filled circles). Young birds are first-year adults with remnants of juvenile plumage; older birds are adults with completed molt. Sample sizes (number of birds) are shown above each bar.

3. Results

3.1. Physiological indices

Corticosterone levels of wintering birds were not related to habitat urbanization either in baseline or stress-induced blood samples (Table 2). Hematocrit was significantly higher in winter ($57.2 \pm 0.4\%$) than in the molting season ($50.6 \pm 0.3\%$; $t_{230} = 14.55$, $P < 0.001$). Hematocrit was unrelated to urbanization in winter (Table 2), whereas in the molting season we found a significant interaction between urbanization and age (Table 2). In young birds, rural individuals tended to have lower hematocrit than urban individuals, whereas older adults showed the opposite trend (Fig. 1a); thus hematocrit increased with age in rural but not in urban birds (Fig. 1a).

H:L ratio was significantly higher in winter (0.40 ± 0.05) than in the molting season (0.29 ± 0.02; $t_{198} = 2.35$, $P = 0.020$), and increased slightly with handling time in both seasons (Table 2); the rate of this increase was similar in differently urbanized habitats (urbanization × handling time: $P > 0.109$). Urbanization showed no

Table 2
Final LME models of body condition indices. Urbanization was retained in each model during model reduction, and body mass was retained in the models of bib size and wing bar size; other predictors were excluded if they had *P* > 0.05.

	N (birds; sites)	Intercept ± SE	b ± SE	P	Cohen's d (95% CI)
Corticosterone levels (ng/ml)					
Baseline	37; 9	3.47 ± 0.34			
Sex (male vs. female)			3.19 ± 0.89	0.001	1.23 (0.49; 2.10)
Urbanization			0.05 ± 0.41	0.903	0.04 (−0.64; 0.73)
Stress-induced	35; 9	43.37 ± 1.60			
Urbanization			−1.80 ± 2.10	0.418	−0.30 (−1.03; 0.40)
Hematocrit (%)					
Winter	85; 12	57.40 ± 0.54			
Urbanization			0.08 ± 0.61	0.896	0.03 (−041; 0.47)
Molting season	147; 10	74.07 ± 10.88			
Molt stage			0.66 ± 0.19	<0.001	0.59 (0.26; 0.94)
Date			−0.11 ± 0.04	0.039	−0.43 (−0.77; −0.10)
Age (older vs. young)			0.004 ± 0.82	0.997	0.001 (−0.33; 0.33)
Urbanization			0.48 ± 0.47	0.346	0.17 (−0.16; 0.50)
Age × urbanization			−1.15 ± 0.54	0.035	−0.36 (−0.70; −0.03)
H:L ratio					
Winter[a]	41; 8	0.22 ± 0.12			
Handling time			0.005 ± 0.002	0.061	0.63 (−0.02; 1.34)
Urbanization			0.009 ± 0.083	0.922	0.03 (−0.61; 0.68)
Molting season	144; 10	0.16 ± 0.05			
Handling time			0.002 ± 0.001	0.011	0.43 (0.10; 0.78)
Urbanization			−0.06 ± 0.02	0.019	−0.50 (−0.84; −0.16)
Scaled mass index	1695; 21	28.49 ± 0.19			
Date			−0.002 ± 0.001	<0.001	−0.17 (−0.27; −0.08)
Time of day			0.003 ± 0.001	<0.001	0.38 (0.28; 0.48)
Sex (male vs. female)			−0.39 ± 0.10	<0.001	−0.19 (−0.29; −0.10)
Urbanization			−0.22 ± 0.16	0.205	−0.07 (−0.16; 0.03)
Body mass	1695; 21	28.50 ± 0.15			
Date			−0.003 ± 0.001	<0.001	−0.21 (−0.31; −0.11)
Time of day			0.003 ± 0.001	<0.001	0.42 (0.32; 0.52)
Sex (male vs. female)			−0.68 ± 0.09	<0.001	−0.37 (−0.47; −0.27)
Urbanization			−0.76 ± 0.12	<0.001	−0.30 (−0.40; −0.20)
Tarsus length	1809; 21	19.02 ± 0.04			
Sex (male vs. female)			−0.13 ± 0.04	<0.001	−0.17 (−0.26; −0.08)
Urbanization			−0.23 ± 0.04	<0.001	−0.25 (−0.34; −0.16)
Bib size (mm²)	314; 7	179.99 ± 43.74			
Date			0.27 ± 0.07	<0.001	0.42 (0.19; 0.65)
Body mass			4.03 ± 1.44	0.006	0.32 (0.09; 0.55)
Urbanization			1.95 ± 6.22	0.766	0.04 (−0.19; 0.26)
Wing bar size (mm²)	169; 10	46.14 ± 40.80			
Date			0.13 ± 0.07	0.048	0.31 (0.01; 0.62)
Sex (male vs. female)			68.27 ± 4.28	<0.001	2.49 (2.03; 3.01)
Body mass			−0.61 ± 1.37	0.655	−0.07 (−0.38; 0.23)
Urbanization			−0.70 ± 2.79	0.809	−0.04 (−0.35; 0.27)

[a] Excluding the marginally non-significant effect of handling time, the final model contains only urbanization: $b ± SE = 0.084 ± 0.096$ (intercept: $0.385 ± 0.071$), $P = 0.410$, Cohen's d (95% CI) = 0.27 (−0.34; 0.90), $N = 45$ birds from 9 sites.

significant relationship with H:L ratio in winter (Table 2), whereas in the molting season rural birds had higher H:L ratio than urban birds (Table 2). The latter difference was apparently due to older rather than young birds (Fig. 1b) although the interaction between age and urbanization was not statistically significant (*P* = 0.226).

3.2. Scaled mass index

The slope of the SMA regression of log-mass on log-tarsus was similar for males and females (*P* = 0.141) and for juveniles and adults (*P* = 0.960). The scaled mass index was not correlated with wing length (*r* = 0.03, *P* = 0.198, *N* = 1690) or bill length (*r* = −0.03, *P* = 0.228, *N* = 1401). These two lines of results imply that by calculating the scaled mass index we successfully controlled for body size differences among individuals. The scaled mass index showed no consistent relationship with urbanization (Table 2, Fig. 2). This was also the case when we restricted the analysis to those individuals that had been studied by Liker et al. (2008; slope ± SE for urbanization: −0.28 ± 0.32, *P* = 0.428). In contrast, both body mass

and tarsus length decreased significantly with increasing degree of urbanization (Table 2, Fig. 2).

3.3. Plumage coloration

Bib size and wing bar size were not significantly related to urbanization (Table 2). We found no relationship between urbanization and any age indicator after controlling for body mass by partial correlations (male mask size: *r* = −0.16, *P* = 0.886, *N* = 85; male wing length: *r* = −0.03, *P* = 0.632, *N* = 311; female wing length: *r* = 0.13, *P* = 0.379, *N* = 45; male tail length: *r* = 0.02, *P* = 0.907, *N* = 60; female tail length: *r* = −0.001, *P* = 0.993, *N* = 44).

4. Discussion

Several negative effects of ongoing urbanization can be expected to manifest in the body condition of house sparrows, such as increasing pollution or decreasing availability of human waste as food resource (Shaw et al., 2008; Summers-Smith, 2003). Despite these expectations, we found no evidence that habitat urbanization
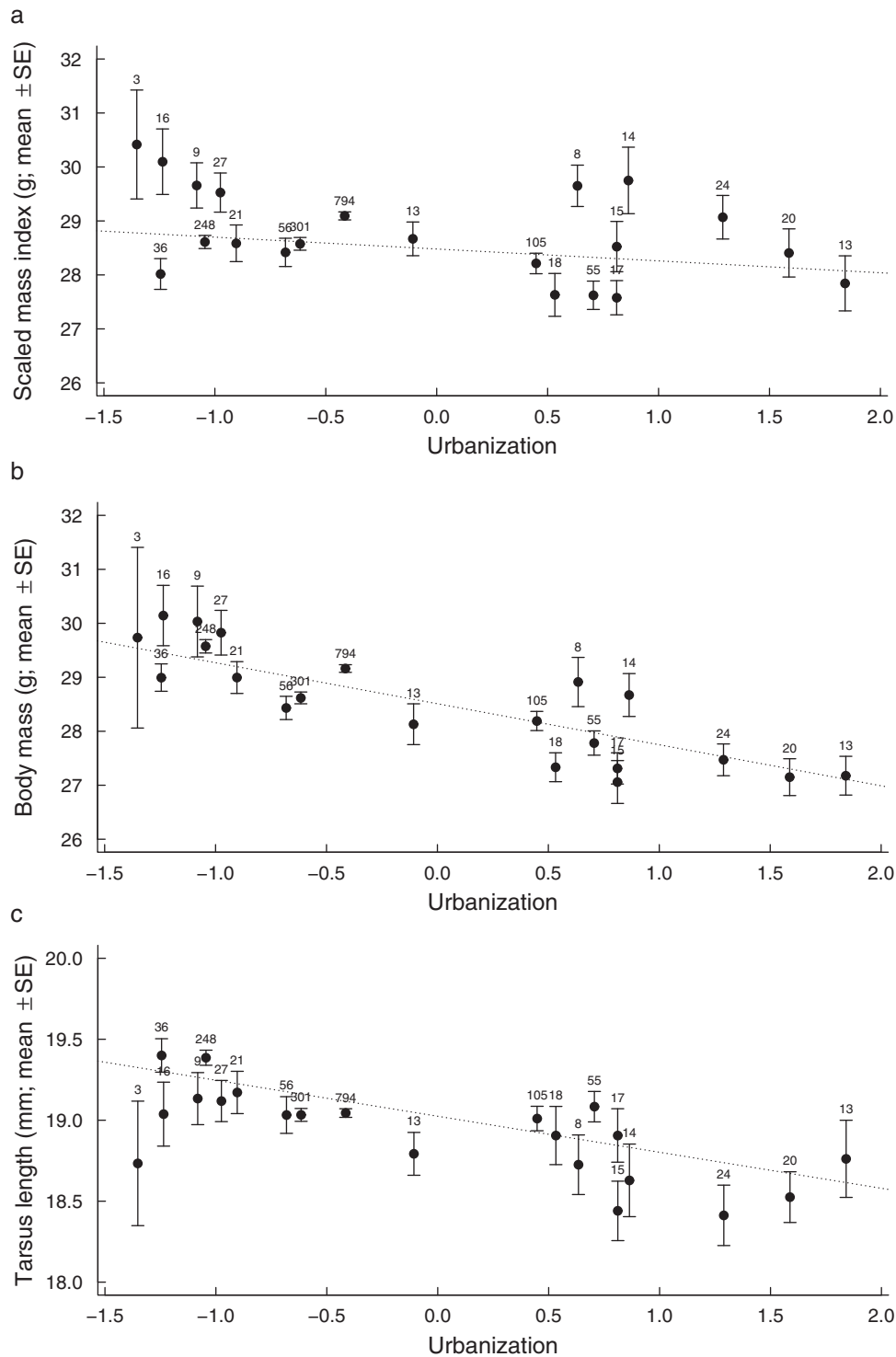
Fig. 2. Scaled mass index, body mass and tarsus length in relation to urbanization scores ranging from the least (negative values) to the most urbanized (positive values) sites. Each dot corresponds to a capture site (see Table 1 for description of the sites). Regression lines (dotted lines) are fitted using the parameter estimates of the final LME models in Table 2. Sample sizes (number of birds) are shown above each bar.

was affecting adult sparrows' physiological or morphological condition. Our study integrates a decade of investigations in various habitats along the urbanization gradient at several life-history phases, utilizing several potential indices of body condition. Out of these indices, only H:L ratio and only in the molting season showed a consistent relationship with the degree of habitat urbanization, unexpectedly indicating better condition in more urbanized habitats. This latter result, combined with the lack of habitat differences

in the rest of our analyses, suggests that urbanization is unlikely to have a general negative effect on the well-being of adult house sparrows.

4.1. Physiological indices

Individuals in poor body condition, such as those suffering from starvation or pollution, often circulate chronically elevated levels

of glucocorticoids (Romero, 2004; Wikelski & Cooke, 2006). Beside reflecting the current health state of the individual, baseline glucocorticoid concentrations can also predict (or even determine) later fitness; for example, house sparrows with lower baseline corticosterone in the pre-breeding season produce more fledglings during the breeding season (Ouyang, Sharp, Dawson, Quetting, & Hau, 2011). Thus, our finding that sparrows across the urbanization gradient had similar levels of baseline corticosterone at the end of the wintering season (on average at the same time as in Ouyang et al.'s study) suggests not only that they were in similar physiological condition but also that they might have had similar prospects for reproductive investment. Acute stress-induced levels of glucocorticoids are more difficult to compare among populations, as chronic stress may either enhance or attenuate the stress response (Romero, 2004); furthermore, a few studies imply that animals may have adapted to urbanization by reduced stress-responsiveness (Fokidis et al., 2009; Partecke et al., 2006). Our result that urban and rural sparrows mounted similar stress responses does not fit either scenario, suggesting that adult sparrows may perceive differently urbanized habitats equally stressful. In accordance with our findings, two recent studies found no difference in various corticosterone concentrations among differently urbanized sparrow populations in the non-breeding season (Chávez-Zichinelli et al., 2010; Fokidis et al., 2009). Although Fokidis et al. (2009) detected higher corticosterone levels in rural than in urban sparrows in the breeding season in a small sample of birds, such a comparison is potentially confounded by reproductive effort and brood value (Lendvai et al., 2007; Lendvai & Chastel, 2008) that may well be affected by urbanization (Peach, Vincent, Fowler, & Grice, 2008).

Similarly to corticosterone levels, hematocrit and H:L ratio showed no consistent relationship with urbanization in the winter, which is also in accordance with earlier results (Fokidis et al., 2008; Gavett & Wakeley, 1986). In the molting season, we obtained contradictory results, as hematocrit showed better condition in rural adults whereas H:L ratio showed the opposite; furthermore, these differences were weaker or even inverted in younger individuals. From our trans-sectional sample we can infer that hematocrit increased with age in rural but not in urban populations. Increasing hematocrit from hatching to fledging and later to adulthood seems to be the general pattern in birds (Fair et al., 2007), but our urban birds failed to fit this pattern. This could be a signal of impaired erythropoiesis in adults; however, the observation that young urban birds tended to have higher hematocrit than rural counterparts suggests an adaptive explanation by which individuals may preemptively circumvent the adverse conditions during early development. We believe that our hematological measurements were reasonable because they exhibited biologically meaningful relationships: the lower hematocrits of heavily molting birds (Table 2) and the increase of H:L ratio with handling time (Table 2) support that both measures are indicative of stress in general. Nevertheless, we might not have been able to control for all confounding effects; for example, both hematocrit and H:L ratio can be influenced by the individual's parasite load which may or may not be related to urbanization (Fair et al., 2007; Fokidis et al., 2008); e.g. the lower H:L ratio of urban birds might have been due to reduced rate of parasitic infections (Evans, Gaston, Sharp, McGowan, Simeoni, et al., 2009). Notably, H:L ratio had by far the largest coefficient of variation (CV; 95%) among our indices of body condition (7–63%). Although hematocrit seemed less noisy (9% CV), it differed mainly among older birds, a group in which individuals might have varied greatly in their exact age from first-year up to several years. Therefore, whether habitat urbanization affects the hematological condition of molting birds in interaction with their age, and whether this effect is attributable to pathogenic infections or other stressors, requires further investigations.

4.2. Scaled mass index

The most frequently applied index of body condition in animal ecology studies is body mass corrected for body size, which can express the amount of energy reserves such as fat and muscle and thereby reflect nutritional state (Peig & Green, 2009, 2010). When this index was calculated as residual body mass from type-1 (ordinary least-squares, OLS) regression with tarsus length, it showed a negative relationship with the degree of habitat urbanization (Liker et al., 2008). However, this method has several drawbacks (Peig & Green, 2009, 2010); therefore, here we re-evaluated this analysis by using a more reliable measure of body condition, the scaled mass index, and extending the earlier dataset by 14 additional capture sites, summing up to more than one and a half thousand individuals. While this revised and extended study corroborated the previous result that sparrows' body mass is reduced in more urbanized habitats (Liker et al., 2008), we found no consistent relationship between urbanization and the scaled mass index. Furthermore, the final model did not include the interaction term between urbanization and date, suggesting that the scaled mass index of adult sparrows did not differ among differently urbanized habitats at any time of the year, i.e. in any life-history phase after the first molt. Therefore, our results indicate that urban sparrows are smaller but not leaner than their rural counterparts. The previously found relationship between urbanization and OLS residuals (Liker et al., 2008) is probably an artifact simply reflecting the smaller size of urban birds, because the OLS method inflates residuals with increasing length (Peig & Green, 2009, 2010). As discussed earlier (Liker et al., 2008), the smaller body size of urban birds could be a consequence of inadequate growth during early development (Peach et al., 2008), adaptation to predation by cats and sparrowhawks (Beckerman, Boots, & Gaston, 2007; Bell, Sam, Parkes, Brooke, & Chamberlain, 2010; Seress, Bókony, Heszberger, & Liker, 2011), or the urban heat island effect (Evans, Gaston, Sharp, McGowan, & Hatchwell, 2009).

4.3. Plumage coloration

Finally, we found that neither bib size nor wing bar size varied consistently with urbanization, implying that differently urbanized populations experience similar nutritional conditions during the molting season. Although plumage coloration may be influenced by several intrinsic and extrinsic factors, these are unlikely to have confounded or biased our results concerning urbanization for the following reasons. First, age may be an important determinant of plumage coloration in sparrows (Nakagawa & Burke, 2008), however, plumage traits such as male mask size, wing length and tail length that all increase with age in sparrows (Nakagawa & Burke, 2008; Selander & Johnston, 1967) showed no indication that urbanization alters the age structure of populations. Second, both bib size and wing bar size may be subject to sexual selection, the strength of which may differ between differently urbanized habitats, e.g. due to competition for differently available nesting sites (Price, Yeh, & Harr, 2008; Yeh, 2004). However, the final model for wing bar size did not include the interaction term between urbanization and sex, suggesting that the degree of sexual dimorphism, a proxy for the strength of sexual selection, was not related to habitat urbanization across our study sites. Furthermore, a recent meta-analysis found very little evidence for sexual selection currently acting on bib size (Nakagawa et al., 2007). Although bib size signals dominance status in male sparrows (Nakagawa et al., 2007), previous results on competitive behaviors suggest that there is no considerable difference in the intensity of competition between urban and rural populations (Bókony et al., 2010). Thus, our result that neither bib size and nor wing bar size varies systematically along the urbanization gradient is in agreement with the repeated finding that urban and rural sparrows retain their

differences in body mass even when receiving the same diet under identical captive conditions (Bókony et al., 2010; Liker et al., 2008), implying that adult sparrows are unlikely to face different nutritional conditions at differently urbanized habitats. Interestingly, a recent study based on ptilochronology indicated that urban house sparrows experience nutritional stress where hedges and dense bushes are highly scattered and isolated (Vangestel et al., 2010), although this conclusion has to be treated with caution because growth bar widths were measured on normally grown feathers for which the method is less well validated than for feathers with experimentally induced growth (Kern & Cowie, 2002; Matysioková & Remes, 2010).

5. Conclusions

Taken together, our study demonstrates that adult house sparrows in urbanized areas are unlikely to be in inferior body condition compared to their conspecifics in rural habitats. Yet, urban sparrows are considerably smaller (Bókony et al., 2010; Liker et al., 2008; this study) and their populations are declining at several parts of the world (Shaw et al., 2008). Recent research shows that urban and rural sparrows have similar reproductive efforts in terms of clutch size and annual number of breeding attempts, but nestlings' growth and survival is reduced in urban nests (Peach et al., 2008; our unpubl. data). Combined with our present results that neither index of body condition supports an inferior health state of urban adults in any period of their yearly cycle, these findings imply that urbanized habitats are more likely to constitute a stressful environment for house sparrows in early developmental phases rather than in their adulthood.

Finally, the inconsistencies found between different body condition indices (Liker et al., 2008; this study) emphasize that drawing conclusions from a single measure of individual state can be misleading. Therefore, studies aimed at the monitoring of urban management effects on wildlife should rely on multiple approaches, taking alternative measurements in various life-history phases.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.landurbplan.2011.10.006.

References

Anderson, T. R. (2006). *Biology of the ubiquitous house sparrow: from genes to populations*. New York, USA: Oxford University Press.

Beckerman, A. P., Boots, M. & Gaston, K. J. (2007). Urban bird declines and the fear of cats. *Animal Conservation*, 10, 320–325.

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

Bell, C. P., Sam, W. B., Parkes, N. G., Brooke, M. D. L. & Chamberlain, D. (2010). The role of the Eurasian sparrowhawk (*Accipiter nisus*) in the decline of the house sparrow (*Passer domesticus*) in Britain. *Auk*, 127, 411–420.

Bókony, V., Lendvai, Á. Z. & Liker, A. (2006). Multiple cues in status signalling: The role of wingbars is agressive interactions of male house sparrows. *Ethology*, 112, 947–954.

Bókony, V., Liker, A., Lendvai, Á. Z. & Kulcsár, A. (2008). Risk-taking and survival in the house sparrow *Passer domesticus*: Are plumage ornaments costly? *Ibis*, 150, 139–151.

Bókony, V., Kulcsár, A. & Liker, A. (2010). Does urbanization select for weak competitors in house sparrows? *Oikos*, 119, 437–444.

Bonier, F., Martin, P. R., Sheldon, K. S., Jensen, J. P., Foltz, S. L. & Wingfield, J. C. (2007). Sex-specific consequences of life in the city. *Behavioral Ecology*, 18, 121–129.

Boonstra, R., Hik, D., Singleton, G. R. & Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, 68, 371–394.

Chávez-Zichinelli, C. A., MacGregor-Fors, I., Rohana, P. T., Valdéz, R., Romano, M. C. & Schondube, J. E. (2010). Stress responses of the house sparrow (*Passer domesticus*) to different urban land uses. *Landscape and Urban Planning*, 98, 183–189.

Clinchy, M., Zanette, L., Boonstra, R., Wingfield, J. C. & Smith, J. N. M. (2004). Balancing food and predator pressure induces chronic stress in songbirds. *Proceedings B*, 271, 2473–2479.

Croci, S., Butet, A. & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *Condor*, 110, 223–240.

Cyr, N. E. & Romero, L. M. (2007). Chronic stress in free-living European starlings reduces corticosterone concentrations and reproductive success. *General and Comparative Endocrinology*, 151, 82–89.

Davis, A. K., Maney, D. L. & Maerz, J. C. (2008). The use of leukocyte profiles to measure stress in vertebrates: A review for ecologists. *Functional Ecology*, 22, 760–772.

Evans, K. L., Gaston, K. J., Sharp, S. P., McGowan, A. & Hatchwell, B. J. (2009). The effect of urbanisation on avian morphology and latitudinal gradients in body size. *Oikos*, 118, 251–259.

Evans, K. L., Gaston, K. J., Sharp, S. P., McGowan, A., Simeoni, M. & Hatchwell, B. J. (2009). Effects of urbanisation on disease risk and age ratios in blackbird *Turdus merula* populations. *Oikos*, 118, 774–782.

Evans, K. L., Chamberlain, D. E., Hatchwell, B. J., Gregory, R. D. & Gaston, K. J. (2011). What makes an urban bird? *Global Change Biology*, 17, 32–44.

Fair, J., Whitaker, S. & Pearson, B. (2007). Sources of variation in haematocrit in birds. *Ibis*, 149, 535–552.

Fokidis, H. B., Greiner, E. C. & Deviche, P. (2008). Interspecific variation in avian blood parasites and haematology associated with urbanization in a desert habitat. *Journal of Avian Biology*, 39, 300–310.

Fokidis, H. B., Orchinik, M. & Deviche, P. (2009). Corticosterone and corticosteroid binding globulin in birds: Relation to urbanization in a desert city. *General and Comparative Endocrinology*, 160, 259–270.

French, S. S., Fokidis, H. B. & Moore, M. C. (2008). Variation in stress and innate immunity in the tree lizard (*Urosaurus ornatus*) across an urban–rural gradient. *Journal of Comparative and Physiology B*, 178, 997–1005.

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

Hegyi, G. & Garamszegi, L. Z. (2011). Using information theory as a substitute for stepwise regression in ecology and behavior. *Behavioral Ecology and Sociobiology*, 65, 69–76.

Hõrak, P., Surai, P. F., Ots, I. & Møller, A. P. (2004). Fat soluble antioxidants in brood-rearing great tits Parus major: Relations to health and appearance. *Journal of Avian Biology*, 35, 63–70.

Kern, M. D. & Cowie, R. J. (2002). Ptilochronology proves unreliable in studies of nestling Pied Flycatcher. *Ibis*, 144, 23–29.

Lendvai, Á. Z. & Chastel, O. (2008). Experimental mate-removal increases the stress response of female house sparrows: The effects of offspring value? *Hormones and Behavior*, 52, 395–401.

Lendvai, Á. Z., Bókony, V. & Chastel, O. (2011). Coping with novelty and stress in free-living house sparrows. *Journal of Experimental Biology*, 214, 821–828.

Lendvai, Á. Z., Giraudeau, M. & Chastel, O. (2007). Reproduction and modulation of the stress response: An experimental test in the house sparrow. *Proceedings B*, 274, 391–397.

Lessells, C. M. & Boag, P. T. (1987). Unrepeatable repeatabilities: A common mistake. *Auk*, 104, 116–121.

Liker, A. & Barta, Z. (2001). Male badge size predicts dominance against females in house sparrows. *Condor*, 103, 151–157.

Liker, A., Papp, Z., Bókony, V. & Lendvai, Á. Z. (2008). Lean birds in the city: Body size and condition of house sparrows along the urbanization gradient. *Journal of Animal Ecology*, 77, 789–795.

Liker, A., Bókony, V., Kulcsár, A., Tóth, Z., Szabó, K., Kaholek, B., et al. (2009). Genetic relatedness in wintering groups of house sparrows (*Passer domesticus*). *Molecular Ecology*, 18, 4696–4706.

MacLeod, R., Barnett, P., Clark, J. & Cresswell, W. (2006). Mass-dependent predation risk as a mechanism for house sparrow declines? *Biology Letters*, 2, 43–46.

Marzluff, J. M., Bowman, R. & Donnelly, R. (2001). *Avian ecology and conservation in an urbanizing world*. Norwell, MA, USA: Kluwer Academic Publishers.

Marzluff, J. M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., et al. (2008). *Urban ecology: An international perspective on the interaction between humans and nature*. New York, USA: Springer.

Matysioková, B. & Remes, V. (2010). Assessing the usefulness of ptilochronology in the study of melanin- and carotenoid-based ornaments in the Great Tit *Parus major*. *Ibis*, 152, 397–401.

McDonnell, M. J. & Hahs, A. K. (2008). The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: Current status and future directions. *Landscape Ecology*, 23, 1143–1155.

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11, 161–176.

Møller, A. P. (2009). Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, 159, 849–858.

Nakagawa, S. & Burke, T. (2008). The mask of seniority? A neglected age indicator in house sparrows *Passer domesticus. Journal of Avian Biology*, 39, 222–225.

Nakagawa, S., Ockendon, N., Gillespie, D. O. S., Hatchwell, B. J. & Burke, T. (2007). Assessing the function of house sparrows' bib size using a flexible meta-analysis method. *Behavioral Ecology*, 18, 831–840.

Ots, I., Murumägi, A. & Hõrak, P. (1998). Haematological health state indices of reproducing great tits: Methodology and sources of natural variation. *Functional Ecology*, 12, 700–707.

Ouyang, J. Q., Sharp, P. J., Dawson, A., Quetting, M. & Hau, M. (2011). Hormone levels predict individual differences in reproductive success in a passerine bird. *Proceedings B*, 278, 2537–2545.

Partecke, J., Van't Hof, T. J. & Gwinner, E. (2005). Underlying physiological control of reproduction in urban and forest-dwelling European blackbirds *Turdus merula. Journal of Avian Biology*, 36, 295–305.

Partecke, J., Schwabl, I. & Gwinner, E. (2006). Stress and the city: Urbanization and its effects on the stress physiology in European blackbirds. *Ecology*, 87, 1945–1952.

Peach, W. J., Vincent, K. E., Fowler, J. A. & Grice, P. V. (2008). Reproductive success of house sparrows along an urban gradient. *Animal Conservation*, 11, 493–503.

Peig, J. & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, 118, 1883–1891.

Peig, J. & Green, A. J. (2010). The paradigm of body condition: A critical reappraisal of current methods based on mass and length. *Functional Ecology*, 24, 1323–1332.

Poston, J. P., Hasselquist, D., Steward, I. R. K. & Westneat, D. F. (2005). Dietary amino acids influence plumage traits and immune responses in male house sparrows (*Passer domestcus*) but not as expected. *Animal Behaviour*, 70, 1171–1181.

Price, T. D., Yeh, P. J. & Harr, B. (2008). Phenotypic plasticity and the evolution of a socially selected trait following colonization of a novel environment. *American Naturalist*, 172, S49–S62.

R Development Core Team. (2010). *R: A language and environment for statistical computing, reference index version 2.11.0*. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0, URL: http://www.R-project.org

Rich, E. L. & Romero, L. M. (2005). Exposure to chronic stress downregulates corticosterone responses to acute stressors. *American Journal of Physiology*, 288, R1628–R1636.

Richards, S. A., Whittingham, M. J. & Stephens, P. A. (2011). Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, 65, 77–89.

Romero, L. M. (2004). Physiological stress in ecology: Lessons from biomedical research. *Trends in Ecology & Evolution*, 19, 249–255.

Romero, L. M. & Reed, J. M. (2005). Collecting baseline corticosterone samples in the field: Is under 3 min good enough? *Comparative Biochemistry and Physiology. A: Comparative Physiology*, 140, 73–79.

Romero, L. M. & Romero, R. C. (2002). Corticosterone responses in wild birds: The importance of rapid initial sampling. *Condor*, 104, 129–135.

Romero, L. M., Strochlic, D. & Wingfield, J. C. (2005). Corticosterone inhibits feather growth: Potential mechanism explaining seasonal down regulation of corticosterone during molt. *Comparative Biochemistry and Physiology A: Comparative Physiology*, 142, 65–73.

Schluter, D. & Gustafsson, L. (1993). Maternal inheritance of condition and clutch size in the collared flycatcher. *Evolution*, 47, 658–667.

Schoech, S. J., Bowman, R., Bridge, E. S. & Boughton, R. K. (2007). Baseline and acute levels of corticosterone in Florida Scrub-Jays (*Aphelocoma coerulescens*): Effects of food supplementation, suburban habitat, and year. *General and Comparative Endocrinology*, 154, 150–160.

Selander, R. K. & Johnston, R. F. (1967). Evolution in the house sparrow. I. Intrapopulation variation in North America. *Condor*, 69, 217–258.

Seress, G., Bókony, V., Heszberger, J. & Liker, A. (2011). Response to predation risk in urban and rural house sparrows. *Ethology*, 117, 896–907.

Shaw, L. M., Chamberlain, D. & Evans, M. (2008). The house sparrow *Passer domesticus* in urban areas: Reviewing a possible link between post-decline distribution and human socioeconomic status. *Journal fur Ornithologie*, 149, 293–299.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E. & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, 21, 186–191.

Summers-Smith, J. D. (2003). The decline of the house sparrow: A review. *British Birds*, 96, 439–446.

Vangestel, C., Braeckman, B. P., Matheve, H. & Lens, L. (2010). Constraints on home range behaviour affect nutritional condition in urban house sparrows (*Passer domesticus*). *Biological Journal of the Linnean Society*, 101, 41–50.

Veiga, J. P. (1993). Badge size, phenotypic quality, and reproductive success in the house sparrow: A study on honest advertisement. *Evolution*, 47, 1161–1170.

Wikelski, M. & Cooke, S. J. (2006). Conservation physiology. *Trends in Ecology & Evolution*, 21, 38–46.

Wingfield, J. C. (1994). Modulation of the adrenocortical response to stress in birds. In K. G. Davey, R. E. Peter, & S. S. Tobe (Eds.), *Perspectives in comparative endocrinology* (pp. 520–528). Ottawa, Canada: National Research Council of Canada.

Wingfield, J. C. & Sapolsky, R. M. (2003). Reproduction and resistance to stress: When and how. *Journal of Neuroendocrinology*, 15, 711–724.

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

Zhang, S., Lei, F., Liu, S., Li, D., Chen, C. & Wang, P. (2011). Variation in baseline corticosterone levels of Tree Sparrow (*Passer montanus*) populations along an urban gradient in Beijing, China. *Journal fur Ornithologie*, 152, 801–806.