

Research paper

Growing in a city: Consequences on body size and plumage quality in an urban dweller, the house sparrow (*Passer domesticus*)



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HIGHLIGHTS

- Juvenile and adult sparrows were captured at 30 sites that differ in urbanization rates.
- Body size and plumage quality were negatively correlated with urbanization.
- The impact of urbanization on feather quality was only observed in juveniles.
- Urban environments energetically constrain sparrows during their development only.

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ABSTRACT

In urban environments, wild vertebrates have to adjust to new environmental challenges (e.g., modified resource availability, increased chemical, noise and light pollutions). However, while the pace of urbanization is constantly increasing, little is known about the ultimate consequences of urban life on the condition of free-living organisms during different life-history stages. In this study, we investigated the influence of urbanization on the condition and non-ornamental feather quality in a common wild bird species, the House sparrow (*Passer domesticus*). Using a national network of trained ringers, almost 600 juvenile (early post-fledging) and adult sparrows were captured at 30 sites that differ in urbanization rates. To specifically test whether urbanization differentially affect individuals during different parts of the life cycle, we used several proxies for the energetic and nutritional conditions experienced during (1) the developmental period (body size, juvenile feather quality), (2) at the time of capture (body condition), or (3) during the molting period (adult feather quality). Using this methodology, we showed for the first time that urbanization is associated with both reduced body size and feather quality in this urban-dweller species across a large geographical scale. Importantly, only tarsus length and juvenile plumage quality, both determined during development in the nest, were affected by the degree of urbanization. Conversely, body condition and plumage quality did not differ along the urbanization gradient in adults. Our results thus suggest that urban house sparrows could suffer from nutritional deficit during their development while such constraints disappear once the chicks have completed their growth.

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1. Introduction

Increasing urbanization is currently among the most important human-induced environmental changes, and poses an important

threat to biodiversity (Grimm et al., 2008; Seto, Güneralp, & Hutyra, 2012). Indeed, compared to natural environments, urban areas are often characterized by highly altered environmental conditions that can have detrimental effects on wildlife (e.g., habitat fragmentation and degradation; increased chemical, noise and light pollutions; modified resource availability and micro-climate; Chace & Walsh, 2006; Grimm et al., 2008; McKinney, 2008; Pickett et al., 2011). As a result, species richness and diversity are often reduced in urban environments (Clergeau, Croci, Jokimäki, Kuisma, & Dinetti, 2006; McIntyre, 2000; McKinney,

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2008). Yet, for species that persist in cities, the consequences of urban life are poorly understood (Bonier, 2012; Partecke, 2014; Shochat, Warren, Faeth, McIntyre, & Hope, 2006; Sol, Lapiedra, & González-Lagos, 2013). Although several studies have shown that survival and reproductive performances are often impaired in cities (Chamberlain et al., 2009; Ryder, Reitsma, Evans, & Marra, 2010), a few species seem to be able to benefit from the urban environment. These successful city dwellers are regularly found in higher densities in urban compared to rural environments (Chace & Walsh, 2006; Møller et al., 2012; Shochat et al., 2006). However, to date, the proximate and ultimate causes of these inter-specific differences remain subject to debate, and better assessing them is considered as a research priority in urban ecology (Evans, Chamberlain, Hatchwell, Gregory, & Gaston, 2011; Lowry, Lill, & Wong, 2013; Shochat et al., 2006).

Although several traits are certainly involved in the ability of species to adapt to urbanized habitats (Evans et al., 2011; Gil & Brumm, 2014; Lowry et al., 2013; Møller, 2009; Sol et al., 2013), the capacity to switch from natural to anthropogenic food, in particular, may be a pre-requisite of an urban way of life (Lowry et al., 2013; Møller, 2009; Sol et al., 2013). Indeed, urban environments greatly differ from natural habitats in terms of food types and abundance (Chamberlain et al., 2009; Shochat et al., 2006). For instance, while natural food availability is often reduced as a result of reduced vegetation cover in cities, urban vertebrates can have access to large amounts of new types of food (i.e., anthropogenic food, birdseed, refuse; Chace & Walsh, 2006; Chamberlain et al., 2005, 2009; Davies et al., 2009). The consequences of the ability of species to adjust to this new trophic situation is however complex because urban food may benefit to individuals during specific phases of their life cycle only, while imposing important constraints during others (Heiss, Clark, & McGowan, 2009; Peach, Mallord, Ockendon, Orsman, & Haines, 2015; Plummer, Bearhop, Leech, Chamberlain, & Blount, 2013; Seress et al., 2012). Thus, anthropogenic food may be sufficient to sustain nutritional needs during most of the life cycle, but not during specific life-history stages (e.g., reproduction, development, molt). Moreover, in addition to this new trophic situation, urban vertebrates are exposed to other environmental constraints, such as increased noise, light and chemical pollutions or modified biotic interactions (e.g., competition, predation regimes), that are also likely to differentially affect individuals during different parts of the life cycle (Bonier, 2012; Chace & Walsh, 2006; Gil & Brumm, 2014). Because of these potential stage-dependent impacts of urbanization and associated environmental constraints, it is often difficult to evaluate the overall impact of urban life on individual constitution and life history traits.

Indeed, the impacts of urbanization on condition or physiology seem inconsistent. For instance, urban individuals are in poorer condition than their rural conspecifics in some studies (e.g., Chávez-Zichinelli et al., 2013; Fokidis, Greiner, & Deviche, 2008; French, Fokidis, & Moore, 2008; Partecke, Van't Hof, & Gwinner, 2005) but not in others (e.g., Foltz et al., 2015; Giraudeau, Mousel, Earl, & McGraw, 2014; Grunst, Rotenberry, & Grunst, 2014). Importantly, such discrepancies can also be found within the same species (e.g., Bókonyi, Kulcsár, & Liker, 2010; Bókonyi, Seress, Nagy, Lendvai, & Liker, 2012; Fokidis et al., 2008; Liker, Papp, Bókonyi, & Lendvai, 2008; Meillère, Brischoux, Parenteau, & Angelier, 2015), with differences depending on the sex, age, or life-history stage of individuals or the geographic area of the study sites (e.g., due to region- or city-specific environmental characteristics). This supports the idea that the influence of urbanization on condition is not only species-specific but also that urbanization may be primarily detrimental during specific life-history stages. To our knowledge, most studies have focused on adults during the pre-breeding or the breeding season while neglecting other phases of the life cycle (but see Fokidis et al., 2008). For example, only a few studies have investigated

the impact of urbanization on the developmental (growth) or the molting period (e.g., Grunst et al., 2014; Hope, Stabile, & Butler, 2016; Seress et al., 2012) despite these two phases of the life cycle being the most energy and nutrient demanding (beside reproduction; Dawson, Hinsley, Ferns, Bonser, & Eccleston, 2000; Monaghan, 2008). The developmental phase is crucial for vertebrates because poor developmental conditions can alter the growth of the organism with potential long-lasting detrimental effects on morphology, behavior, physiology, and consequently, individual performances during adulthood (reviewed in Monaghan, 2008). Similarly, the molting period is crucial because this is an energetic demanding period and plumage quality is known to further affect individual performances during the following seasons (Dawson et al., 2000). Finally, the influence of urbanization on condition has mainly been investigated by comparing very few urban and rural sites only (but see Bókonyi et al., 2012; Evans, Gaston, Sharp, McGowan, & Hatchwell, 2009), and as a consequence, it remains difficult to make general inferences of the influence of urbanization on wild vertebrates.

Citizen science and the use of networks of volunteers could help urban ecologists to circumvent these problems because this methodology allows scientists to gather relevant data over large geographic and time scales. Accordingly, citizen science has been used to study ecological processes at national scale and/or during long-term periods (Dickinson, Zuckerberg, & Bonter, 2010; Morrison, Robinson, Leech, Dadam, & Toms, 2014; Silvertown, 2009). Obviously, one of the drawbacks of this method is the inability of volunteers to collect complex data (e.g., blood samples), but several basic measurements can be accurately and easily assessed by trained people (Couvett, Jiguet, Julliard, Levrel, & Teysseire, 2008; Dickinson et al., 2010; Schmeller et al., 2009). For instance, morphological data are relevant to assess the impact of environmental conditions on individuals in birds (Tellería, Herra, & Perez-Tris, 2013). Thus, body size is often a reliable proxy for developmental conditions, with small individuals having been energetically constrained during their growth (although adaptive reduction of body size is also possible, see Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011). Body condition (i.e., energetic or nutritional state of an individual – e.g., estimated using size-adjusted body mass) is also relevant because it can provide cues on the ability of individuals to sustain their energetic needs (Peig & Green, 2009, 2010). Similarly, feather collection (easily performed by volunteers) can provide ecologists with crucial data on the molting period as feathers integrate the conditions encountered by the individual during molt (Harms et al., 2015; Saino et al., 2013). Thus, feather length, mass and density are often used as proxies for feather quality and a nutritional deficit during the molt is often associated with shorter and lighter feathers (Murphy, King, & Lu, 1988; Pap, Vágási, Cziráj, & Barta, 2008). In addition, fault bars (i.e., narrow, translucent bands found in the plumage of many bird species) are linked with malnutrition and the occurrence of stressors during the molt (Bortolotti, Dawson, & Murza, 2002; Machmer, Esselink, Steeger, & Ydenberg, 1992; Vágási et al., 2012). Finally, the fluctuating asymmetry of feathers has been suggested as a proxy for nutritional and energetic stress during the molting period (Møller, 1992; Swaddle & Witter, 1994). Therefore, the number of fault bars and the fluctuating asymmetry of feathers can be relevant complementary indices to assess the nutritional constraints that occur during the molt.

In this study, we investigated the influence of urban life on the condition and non-ornamental plumage quality in a common wild bird species, commensal of human settlements, the House sparrow (*Passer domesticus*). To do so, we used a national network of trained bird ringers to obtain reliable measurements of body size and condition and to collect tail feathers from both juvenile and adult sparrows over a large geographical scale across France. Our objective was to test whether urbanization had detrimental

tal effects only during specific parts of the life cycle. The house sparrow is especially relevant to test our hypothesis for several reasons. First, this species is quite common in France and, contrary to most species, can be found along the whole urbanization gradient (from rural to highly urbanized areas; Anderson, 2006; Bichet et al., 2013). Second, although the house sparrow is certainly one of the most successful birds in the urban environment, it has undergone important population declines in urbanized areas during the past decades (De Coster, De Laet, Vangestel, Adriaensen, & Lens, 2015; Robinson, Siriwardena, & Crick, 2005; Shaw, Chamberlain, & Evans, 2008), suggesting that this species has recently suffered from urban environmental conditions. Finally, previous studies have suggested that the urban nutritional environment could be sufficient to sustain adults' nutritional needs, but may be inadequate to satisfy the nutritional requirements of developing chicks (Bókony et al., 2012; Meillère, Brischoux, Parenteau et al., 2015; Peach et al., 2015; Seress et al., 2012). Here, to specifically test whether urbanization differentially affect sparrows during different parts of the life cycle, we used several proxies for the energetic and nutritional conditions experienced during the developmental period (body size, juvenile feather quality), at the time of capture (body condition), or during the molting period (adult feather quality). Based on the previous findings described above, we predicted that urbanization is associated with altered phenotypes in sparrows (reduced body size and condition, poor plumage quality). Moreover, we also predicted that the detrimental influence of urbanization may be exacerbated during energetically demanding life-history stages when rich-protein diet is required to fulfil nutritional needs (i.e., development and molt).

2. Methods

2.1. Study species and sites

Between February and August 2014, a total of 599 house sparrows (353 adults and 246 juveniles) were captured with mist-nets at 30 sites in France (Fig. 1; geographic coordinates of the capture sites and samples sizes for each population are summarized in Table 1). The 30 populations were sampled in locations that differ in urbanization rates, ranging from sparsely populated areas (e.g., isolated farms, small villages) to highly urbanized city centers. Importantly, the house sparrow is an extremely sedentary species with a very restricted home range, limited postnatal dispersal and negligible breeding dispersal (Anderson, 2006; Summers-Smith, 1988). To accurately quantify the degree of urbanization at each capture site, we followed the method developed by Liker et al. (2008) for house sparrows. In brief, using digital aerial photographs (GoogleMaps) of 1 km² areas, centered on the capture site and divided into 100 cells, we first extracted five habitat characteristics for each capture site (see Liker et al. (2008) for more details): mean building density score, number of cells with high building density, mean vegetation density score, number of cells with high vegetation density, and number of cells with road (Table 1). Second, we used the PC1 value from a principal component analysis on these five habitat variables to compute an "urbanization score" for each site (Table 1). The PC1 accounted for 92.7% of the total variance and correlated strongly (1) positively with artificial surfaces (building density and roads; all $r > 0.934$) and (2) negatively with vegetation cover (all $r < -0.972$).

2.2. Morphological measurements

All birds were weighed (scale: ± 0.1 g), and their wing (steel rule: ± 1 mm) and tarsus lengths (vernier caliper: ± 0.1 mm) were measured. In addition, birds were aged as adult or juvenile (i.e.,

first year individual) based on plumage characteristics (Anderson, 2006), banded with a metal ring, and prior to release, their two innermost tail feathers (rectrices) were collected. The capture and morphological measurements of birds were made by volunteer bird ringers that had all received the same training with the French Bird Ringing Office (CRBPO, National Museum of Natural History). This study was carried out in accordance with all applicable institutional and/or national guidelines for the care and use of animals. All capture procedures and feather sampling were approved by the "Comité d'Éthique en Expérimentation Animale" and authorized by the CRBPO.

To assess body condition, we used the "scaled mass index" as recommended by Peig and Green (2009, 2010), which adjusts the mass of all individuals to that expected if they had the same body size (Peig and Green, 2009). We calculated the scaled mass index separately for adults and juveniles because the relationship between body mass and tarsus length was different between the two age classes (Likelihood ratio = 23.49, $p < 0.001$). The scaled mass index was computed using the equation $SMI_i = M_i \times \left(\frac{L_0}{L_i}\right)^b$ (Peig & Green, 2009), where M_i and L_i are the body mass and the tarsus length of the individual i , respectively; L_0 , the arithmetic mean value of tarsus length for the whole study population (adults: $L_0 = 19.20$ mm, $n = 353$; juveniles: $L_0 = 19.00$ mm, $n = 246$) and b the slope estimate of a standardized major axis (SMA) regression of log-transformed body mass on log-transformed tarsus length (adults: $b_{SMA} = 1.29$; juveniles: $b_{SMA} = 1.87$).

Body size, mass and condition were used as proxies for the energetic and nutritional conditions experienced during the developmental period and at the time of capture. First, body size is determined during the developmental period. In particular, the tarsus is almost fully grown at fledging in house sparrows (Anderson, 2006) and was thus used to understand whether developmental conditions differed along the urbanization gradient (Gardner et al., 2011). Second, body mass and body condition (i.e., size-adjusted body mass) reflect the nutritional status at the time of capture (Peig & Green, 2009, 2010), and were thus used to evaluate the influence of urbanization on the condition of juvenile and adult sparrows.

2.3. Feather quality and fluctuating asymmetry measurements

For each captured individual, the two innermost rectrices collected were stored in dry paper envelopes until laboratory analyzes (except for 24 individuals for whom only one feather had been sampled). Importantly, because house sparrows replace their feathers a few weeks after fledging (post-fledging molt of juvenile birds), and then, every year after the breeding season (post-nuptial molt of adult birds; Anderson, 2006), only birds that did not start their annual molt were sampled.

All feathers were weighed (high-resolution balance: ± 0.01 mg), and their total length were measured (digital caliper: ± 0.01 mm). We calculated the mass/length ratio ($\mu\text{g}/\text{mm}$) to estimate feather density, as proxy for feather quality (De La Hera, Pérez-Tris, & Tellería, 2010; Murphy et al., 1988). Reduced feather density can reflect a nutritional deficit during feather growth as nutritional stress is associated with a reduced density of structural elements (Murphy et al., 1988). In addition, we recorded the number of fault bars (i.e., translucent bands in feathers caused by adverse and stressful conditions during feather growth; Bortolotti et al., 2002; Machmer et al., 1992) on each feather. All feathers measurements were made by the same person (B.M.). For these feather traits (density and number of faults bars), we used the average values of both feathers in our analyzes. Furthermore, for the 575 individuals for which we had the two rectrices, we also calculated the fluctuating asymmetry (FA) in length of feathers (Palmer & Strobeck, 1986). FA reflects small random (non-directional) deviations from perfect

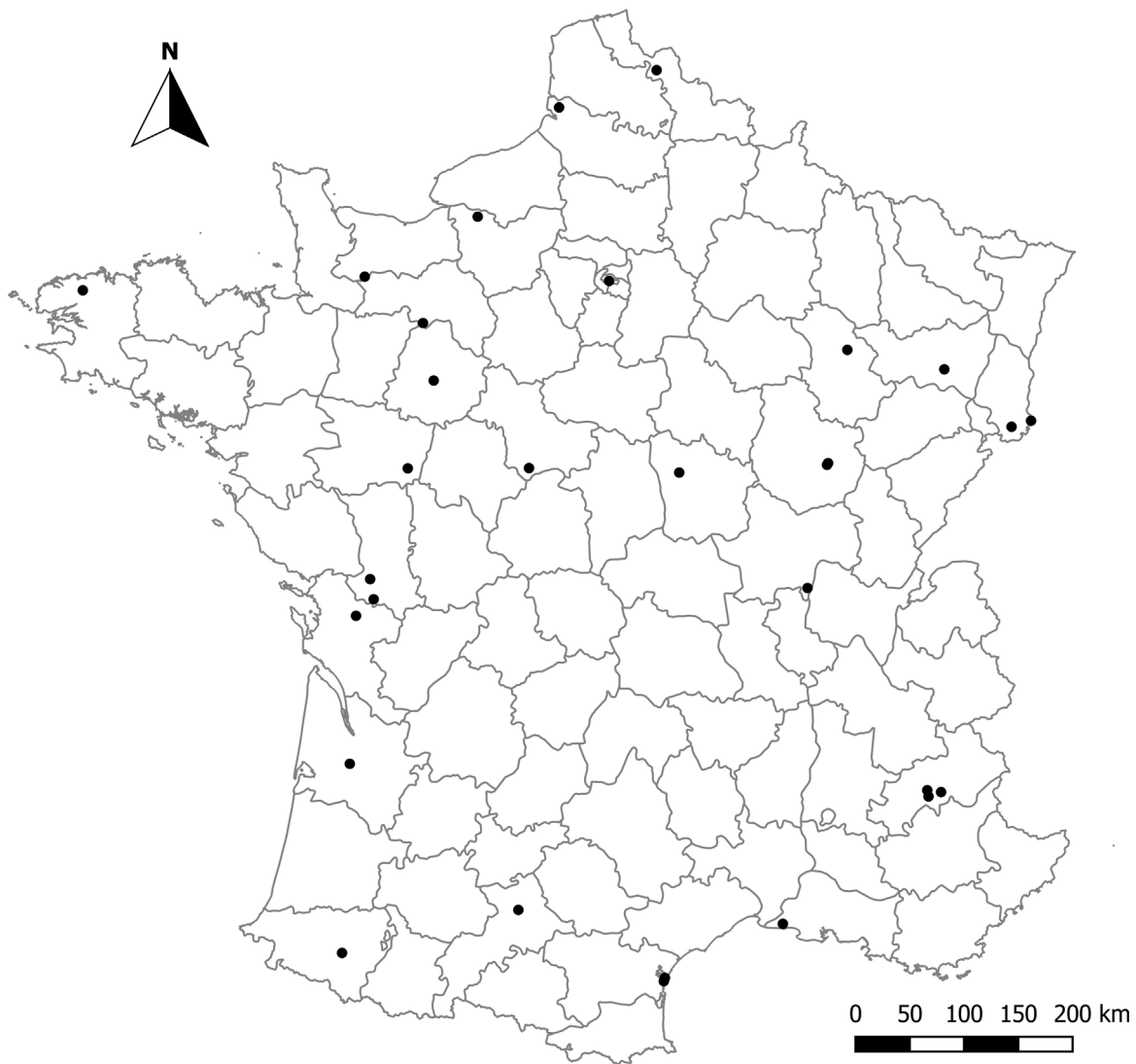


Fig. 1. Geographical localization of the 30 capture sites sampled in this study.

bilateral symmetry and is often used as a proxy for developmental instability (Palmer & Strobeck, 1986). For instance, nutritional stress during feather formation has been shown to increase levels of FA in feathers (Swaddle & Witter, 1994). Here, we used the absolute value of the difference between the two lengths (because we did not know whether a feather was the right or the left innermost rectrice) divided by their mean value in order to avoid the effect of size variation in feather length (relative asymmetry): $FA = \frac{(|R1 - R2|)}{\frac{R1 + R2}{2}}$

(Anciaes & Marini, 2000; Palmer & Strobeck, 1986), where R_1 and R_2 are the length of each rectrice. It is important to acknowledge that we did not exactly measure “fluctuating” asymmetry since we could not differentiate left from right rectrices in our study and thus could not rule out directional asymmetry. However, because directional asymmetry of the measured trait (non-ornamental feather length) is very unlikely, we therefore practically refer to this measured asymmetry as FA.

Feather density, number of fault bars and FA in length of feathers were used as proxies for plumage quality and allowed us to evaluate the influence of urbanization on the energetic and nutritional condition of sparrows during the developmental period and the molting period. These feather traits indeed integrate the environmental conditions experienced by the individual during feather formation (Harms et al., 2015; Saino et al., 2013). Therefore, adult

feather quality was used to assess the constraints that potentially occurred during the previous molt (as house sparrows replace their feathers every year), whereas juvenile feather quality was used to assess the constraints of the developmental period (as juveniles were captured before their first molt, their plumage had grown while they were developing in the nest).

2.4. Statistical analyzes

All statistical analyzes were performed in R 3.1.0 (R Core Team, 2014). Because the influence of urbanization on sparrows' body size, condition and plumage quality could be sex-dependent (e.g., see Bonier et al., 2007), it was important to consider the sex of individuals in our analysis. Since juveniles were of unknown sex, adults and juveniles were considered separately. First, to test the influence of urbanization on body size (tarsus and wing length), body mass, and body condition (scaled mass index) of sparrows, we fitted linear mixed models (LMMs, normal error distribution, identity link function) with capture site as a random factor to control for the non-independence of individuals captured at the same site. For adults, we used “urbanization” (PC1 score), “sex” (two-level factor: female and male), the “urbanization × sex” interaction, and capture “date” as fixed effects in our models. For juveniles, LMMs only

Table 1

Habitat characteristics of the capture sites and sample sizes. Sites are ordered from most to least urbanized (in bold: PC1 values from a principal component analysis conducted on the five habitat variables).

Capture site (Geographic coordinates)	Habitat characteristics						Sample sizes	
	Mean building density score	Number of cells with high building density	Mean vegetation density	Number of cells with high vegetation density	Number of cells with road	Urbanization score (PC1)	Adults	Juveniles
Paris (48.845; 2.359)	1.60	74	0.65	17	87	4.30	14	10
Dijon (47.312; 5.053)	1.53	54	0.72	6	91	3.94	15	0
Niort (46.313; -0.479)	1.18	24	0.82	11	97	2.88	11	12
Le Mans (47.985; 0.198)	1.36	48	1.12	24	77	2.74	10	17
Port-la-Nouvelle (43.022; 3.042)	1.07	33	0.75	14	81	2.72	15	10
Gradignan (44.771; -0.621)	1.23	34	1.25	36	87	2.20	9	9
Gap (44.566; 6.107)	1.17	36	1.14	31	70	2.05	12	13
Saint-Louis (47.595; 7.559)	1.18	39	1.29	41	70	1.84	14	0
Oloron-Ste-Marie (43.196; -0.611)	1.11	31	1.17	32	68	1.81	3	11
Dijon – Periurban (47.299; 5.040)	0.97	26	1.09	30	61	1.54	7	0
Saumur (47.247; -0.080)	0.88	30	1.20	37	66	1.44	14	4
Santes (50.596; 2.955)	1.00	24	1.36	41	54	0.98	31	11
Toulouse – Periurban (43.603; 1.380)	0.78	21	1.65	65	46	0.32	6	6
Noyers-sur-Cher (47.279; 1.399)	0.66	19	1.44	55	56	-0.06	8	1
Waldighofen (47.554; 7.316)	0.76	10	1.79	80	66	-0.30	15	10
Chorges (44.546; 6.266)	0.30	8	1.71	81	42	-1.14	10	10
Loché (46.279; 4.768)	0.32	3	1.87	87	51	-1.32	15	0
Rimaucourt (48.250; 5.329)	0.40	6	1.88	89	34	-1.53	12	13
Arbourse (47.252; 3.233)	0.20	0	1.97	97	55	-1.66	13	15
Raon-aux-Bois (48.059; 6.523)	0.43	3	1.94	94	35	-1.68	10	11
Saint-Loup (46.003; -0.628)	0.23	2	1.95	96	45	-1.74	12	15
Lonrai (48.459; 0.039)	0.28	2	1.90	90	33	-1.78	12	5
Cantine (43.050; 3.055)	0.01	0	1.60	69	14	-1.83	12	0
Rully (48.824; -0.715)	0.15	2	1.97	97	27	-2.17	13	10
Eturqueraye (49.358; 0.683)	0.19	2	1.98	98	26	-2.18	9	0
Plouneventer (48.549; -4.230)	0.13	1	1.96	97	26	-2.22	13	14
Rue (50.280; 1.693)	0.12	1	1.96	96	24	-2.25	7	3
Stes-Maries-de-la-Mer (43.490; 4.401)	0.12	0	2.00	100	30	-2.26	16	11
Jarjayes (44.514; 6.118)	0.09	0	1.99	99	27	-2.32	5	11
Villiers-en-Bois (46.147; -0.426)	0.11	1	1.98	98	23	-2.33	9	15

included “urbanization” and capture “date” as fixed effects. Second, to test the influence of urbanization on plumage quality of sparrows (feather density, number of fault bars and FA in length of feathers), we fitted LMMs (normal error distribution, identity link function, for the “feather density” variable) or generalized linear mixed models (GLMMs, Poisson error distribution, log link function, for the “number of fault bars” and the “FA in length” variables) with capture site as a random factor. Each full model included urbanization, sex and the “urbanization $\times$ sex” interaction (except for juveniles), and capture date as fixed effects.

We used an information-theoretic approach to select the best models (Burnham & Anderson, 2002). Criteria used in model selection included the Akaike Information Criterion (AIC), the difference in AIC between each candidate model and the model with the lowest AIC (Δ AIC) and Akaike weights (wi). Akaike weights represent the relative likelihood of a model and indicate the probability that a model is selected as the best model among the whole set of models considered. The best model was generally taken to be the one with the lowest AIC value. However, when models had AIC values differing by less than two (Δ AIC < 2), they were considered to have similar support in the data (Burnham & Anderson, 2002; Burnham, Anderson, & Huyvaert, 2011), and the model including the least number of parameter was selected as the best model. To test the strength of the variables, we also calculated each variable’s relative importance (VI) by summing the Akaike weights of all models which included that variable (Burnham & Anderson, 2002). Models fit was checked by residual analysis, and parameters’ estimates ($\pm$ SE) and 95% confidence intervals (CIs) of fixed effects are given for best models.

3. Results

3.1. Body size, mass and condition

Model selection procedure to determine the best models explaining variation in adult and juvenile sparrows’ body size (tarsus and wing length), body mass and body condition (scaled mass index) is presented in Table 2. As shown by the sum of Akaike weights across all models (i.e., variable relative importance), urbanization had a very high explanatory power for tarsus length and body mass in both juveniles and adults (VI > 0.88 and > 0.94 for juveniles and adults respectively; Table 3). In juveniles, tarsus length and body mass were best explained by a model including only the urbanization variable and parameter estimates showed that tarsus length and body mass decreased with increasing urbanization (Table 2, Fig. 2A for tarsus length). In adults, the best model explaining variation in tarsus length also included sex and the “urbanization $\times$ sex” interaction (Table 2 and 3), suggesting that the relationship between the degree of urbanization and tarsus length may differ between males and females. Specifically, males had overall longer tarsi than females (Table 2, parameter estimates of the sex variable). Moreover, tarsus length was negatively correlated with the degree of urbanization in both males and females but the relationship was more pronounced in males than females (females: slope estimates ($\beta \pm$ SE): -0.15 ± 0.06 (95% CI: -0.27 ; -0.04); males: -0.24 ± 0.06 (95% CI: -0.35 ; 0.13)). Variation in adults’ body mass was best explained by a model including only the urbanization variable (Table 2; overall low variable importance of sex and the “urbanization $\times$ sex” interaction: VI < 0.41, Table 3),

Table 2
Model selection table using the AIC to determine the best models when investigating the influence of urbanization on tarsus length, wing length, body mass and scaled mass index in adult and juvenile sparrows.

Models	K	Log (L)	AIC	Δ AIC	wi	Parameter	Estimate $\pm$ SE	t	p	95% CI
Adults – Tarsus length										
1. Urbanization, Sex, Urbanization $\times$ Sex, Date	5	−426.83	867.7	0	0.399	Intercept	19.15 $\pm$ 0.12	156.06	<0.001	18.91; 19.39
2. Urbanization, Sex, Urbanization $\times$ Sex	4	−427.92	867.8	0.17	0.366	Urbanization	−0.15 $\pm$ 0.06	−2.61	0.015	−0.27; −0.03
3. Urbanization, Sex, Date	4	−429.28	870.5	2.88	0.094	Sex ^a	0.18 $\pm$ 0.08	2.10	0.036	0.01; 0.34
4. Urbanization, Sex	3	−430.46	870.9	3.26	0.078	Urbanization $\times$ Sex ^a	−0.09 $\pm$ 0.04	−2.25	0.025	−0.17; −0.01
5. Urbanization	2	−432.37	872.7	5.07	0.032					
Adults – Wing length										
1. Sex, Date	3	−691.98	1394.0	0	0.525	Intercept	77.19 $\pm$ 0.44	176.22	<0.001	76.33; 78.06
2. Urbanization, Sex, Date	4	−691.98	1395.9	1.99	0.194	Sex ^a	2.56 $\pm$ 0.18	14.43	<0.001	2.21; 2.91
3. Sex	2	−694.36	1396.7	2.76	0.132	Date	−0.006 $\pm$ 0.003	−2.19	0.029	−0.012; −0.001
4. Urbanization, Sex, Urbanization $\times$ Sex, Date	5	−691.88	1397.8	3.80	0.078					
5. Urbanization, Sex	3	−694.33	1398.7	4.69	0.050					
Adults – Body mass										
1. Urbanization	2	−683.67	1375.3	0	0.334	Intercept	27.63 $\pm$ 0.19	142.31	<0.001	27.25; 28.01
2. Urbanization, Date	3	−683.12	1376.2	0.91	0.212	Urbanization	−0.25 $\pm$ 0.09	−2.70	0.012	−0.43; −0.06
3. Urbanization, Sex	3	−683.34	1376.7	1.35	0.170					
4. Urbanization, Sex, Date	4	−682.72	1377.4	2.11	0.116					
5. Urbanization, Sex, Urbanization $\times$ Sex	4	−683.34	1378.7	3.35	0.063					
Adults – Scaled mass index										
1. Null model	1	−719.29	1444.6	0	0.211					
2. Urbanization, Sex, Urbanization $\times$ Sex	4	−716.39	1444.8	0.20	0.191					
3. Urbanization	2	−718.79	1445.6	0.99	0.128					
4. Sex	2	−718.88	1445.8	1.18	0.117					
5. Date	2	−719.26	1446.5	1.93	0.080					
Juveniles – Tarsus length										
1. Urbanization	2	−297.02	602.0	0	0.692	Intercept	19.01 $\pm$ 0.12	164.89	<0.001	18.79; 19.24
2. Urbanization, Date	3	−296.99	604.0	1.93	0.264	Urbanization	−0.16 $\pm$ 0.06	−2.99	0.007	−0.28; −0.05
3. Null model	1	−301.12	608.2	6.20	0.031					
4. Date	2	−301.07	610.1	8.09	0.012					
Juveniles – Wing length										
1. Null model	1	−581.05	1168.1	0	0.412					
2. Urbanization	2	−580.32	1168.6	0.54	0.314					
3. Date	2	−581.03	1170.1	1.96	0.155					
4. Urbanization, Date	3	−580.29	1170.6	2.47	0.120					
Juveniles – Body mass										
1. Urbanization	2	−512.90	1033.8	0	0.546	Intercept	25.19 $\pm$ 0.26	97.16	<0.001	24.67; 25.70
2. Urbanization, Date	3	−512.38	1034.8	0.97	0.336	Urbanization	−0.30 $\pm$ 0.12	−2.48	0.021	−0.56; −0.05
3. Null model	1	−515.90	1037.8	4.01	0.074					
4. Date	2	−515.43	1038.9	5.06	0.044					
Juveniles – Scaled mass index										
1. Null model	1	−556.64	1119.3	0	0.394					
2. Date	2	−555.95	1119.9	0.61	0.291					
3. Urbanization	2	−556.41	1120.8	1.53	0.184					
4. Urbanization, Date	3	−555.74	1121.5	2.19	0.132					

All models (linear mixed models) include capture site as a random factor. Models are ranked according to their AIC values (only the 5 most competitive models are presented for adults) and the selected models are shown in bold. *K* indicates the number of model parameters. The right part of the table includes the parameter estimates and 95% CIs for the selected models.

^a Estimates are for males in comparison to females.

Table 3
Variable importance (VI) of different parameters explaining variations in tarsus length, wing length, body mass and scaled mass index in adult and juvenile sparrows. Variables with a high VI (i.e., >0.75) are shown in bold.

	Variable	Tarsus length	Wing length	Body mass	Scaled mass index
Adults	Urbanization	1.00	0.34	0.94	0.55
	Sex	0.94	1.00	0.41	0.53
	Urbanization $\times$ Sex	0.76	0.10	0.11	0.27
	Date	0.52	0.80	0.39	0.28
Juveniles	Urbanization	0.96	0.43	0.88	0.32
	Date	0.28	0.27	0.38	0.42

with individuals being lighter in more urbanized habitats (Table 2, parameter estimates of the urbanization variable).

In contrast to tarsus length and body mass, urbanization showed overall low variable importance in explaining variation in wing

length in both juveniles and adults (Table 3). In juveniles, the best model was found to be the null model (Table 2), indicating that urbanization and capture date had no significant influence on wing length. In adults, sex was clearly the most influential vari-

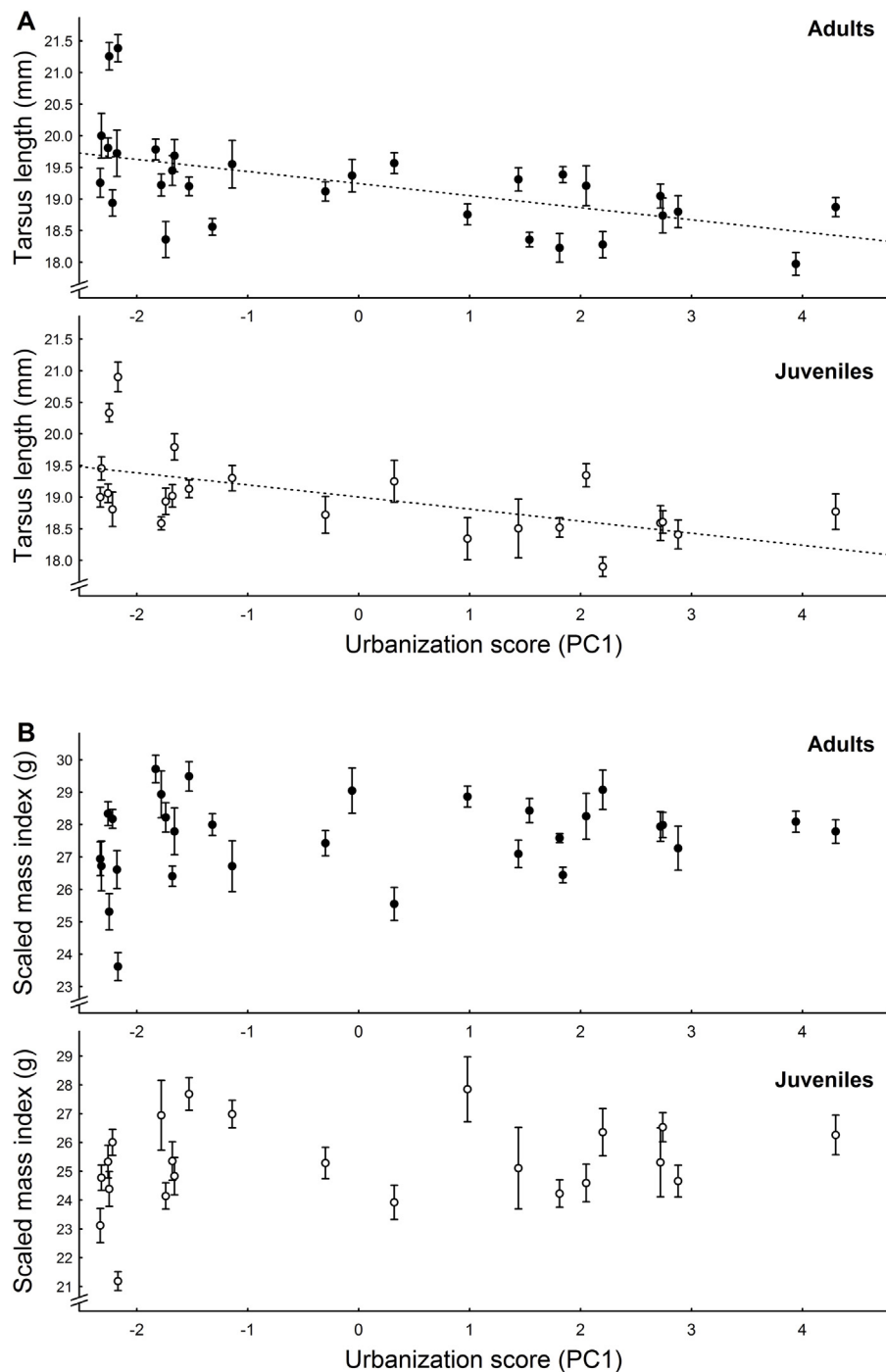


Fig. 2. Relationship between the degree of urbanization and (A) tarsus length and (B) body condition (scaled mass index) in adult (filled circles) and juvenile (open circles) house sparrows.

able, with capture date having also a relatively high explanatory power (Table 3). Specifically, wing length was longer in males than females (Table 2, parameter estimates of the sex variable) and was negatively related to capture date, as expected since feathers wear through time (Table 2, parameter estimates of the date variable).

Finally, the best model explaining variation in scaled mass index was found to be the null model in both juveniles and adults (Table 2), indicating that body condition was unrelated to the degree of urbanization (Fig. 2B) or the capture date and did not differ between adult males and females (all variables $VI < 0.42$ and < 0.55 for juveniles and adults respectively; Table 3).

3.2. Feather quality and fluctuating asymmetry

Urbanization had a high explanatory power in explaining variation in feather density of juvenile sparrows ($VI = 0.85$; Table 4) and parameter estimates showed that juveniles' feather density decreased with increasing urbanization (slope estimates ($\beta \pm SE$): -1.47 ± 0.63 (95% CI: -2.78 ; -0.17), $t = -2.34$, $p = 0.029$, Fig. 3). In contrast, urbanization had no important influence on the feather density of adult sparrows ($VI = 0.50$, Fig. 3) and the best model only included the sex variable ($VI = 1.00$; Table 4). Specifically, females had less dense rectrices than males (females: $141.5 \pm 1.3 \mu\text{g/mm}$

Table 4
Model selection table using the AIC to determine the best models when investigating the influence of urbanization on feather density, number of fault bars, and FA in length of feathers in adult and juvenile sparrows.

Models	K	Log (L)	AIC	ΔAIC	wi
Adults – Feather density					
1. Sex	2	−1382.03	2772.1	0	0.293
2. Urbanization, Sex	3	−1381.35	2772.7	0.62	0.214
3. Sex, Date	3	−1381.45	2772.9	0.83	0.193
4. Urbanization, Sex, Date	4	−1380.66	2773.3	1.25	0.156
5. Urbanization, Sex, Urbanization × Sex	4	−1381.29	2774.6	2.52	0.083
Adults – Number of fault bars					
1. Null model	1	−366.59	737.2	0	0.725
2. Date	2	−367.26	740.5	3.34	0.137
3. Sex	2	−367.53	741.1	3.88	0.104
4. Sex, Date	3	−368.46	744.9	7.73	0.015
5. Urbanization	2	−369.80	745.6	8.41	0.011
Adults – FA in length of feathers					
1. Null model	1	−1011.83	2025.7	0	0.766
2. Sex	2	−1012.16	2028.3	2.66	0.203
3. Urbanization	2	−1014.26	2032.5	6.86	0.025
4. Urbanization, Sex	3	−1014.80	2035.6	9.94	0.005
5. Urbanization, Sex, Urbanization × Sex	4	−1015.47	2038.9	13.29	0.001
Juveniles – Feather density					
1. Urbanization	2	−965.17	1938.3	0	0.598
2. Urbanization, Date	3	−965.06	1940.1	1.76	0.248
3. Null model	1	−967.87	1941.7	3.39	0.110
4. Date	2	−967.79	1943.6	5.23	0.044
Juveniles – Number of fault bars					
1. Null model	1	−237.68	479.4	0	0.960
2. Urbanization	2	−239.91	485.8	6.45	0.038
3. Date	2	−242.875	491.8	12.39	0.002
4. Urbanization, Date	3	−245.11	498.2	18.85	0.000
Juveniles – FA in length of feathers					
1. Null model	1	−690.53	1383.1	0	0.889
2. Urbanization	2	−691.80	1387.6	4.53	0.092
3. Date	2	−693.50	1391.0	7.93	0.017
4. Urbanization, Date	3	−694.74	1395.5	12.42	0.002

All models (linear mixed models or generalized linear mixed models) include capture site as a random factor. Models are ranked according to their AIC values (only the 5 most competitive models are presented for adults) and the selected models are shown in bold. *K* indicates the number of model parameters.

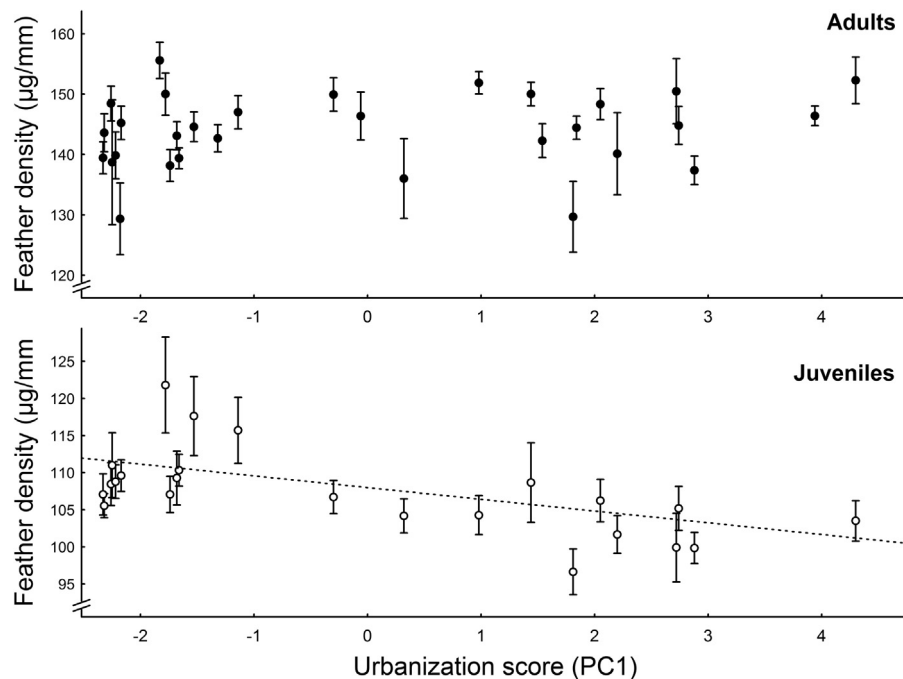


Fig. 3. Relationship between degree of urbanization and feather density in adult (filled circles) and juvenile (open circles) house sparrows.

(95% CI: 139.0; 144.0); males: $147.0 \pm 1.2 \mu\text{g}/\text{mm}$ (95% CI: 144.6; 149.4).

Finally, the best models explaining variation in the number of fault bars and FA in length of feathers were found to be the null model in both juveniles and adults (Table 4), indicating that the number of fault bars and FA in length of feathers were unrelated to the degree of urbanization ($VI < 0.09$ and $VI < 0.03$ for juveniles and adults respectively) or the capture date and did not differ between adult males and females.

4. Discussion

By capturing several hundred house sparrows over a large geographical scale (30 sites across France), we were able to show for the first time that urbanization is clearly associated with modifications of both body size and non-ornamental feather quality in an urban dweller species. Importantly, only tarsus length (juveniles and adults) and juvenile plumage quality were affected by the degree of urbanization, highlighting therefore that the influence of urbanization on these variables is especially exacerbated during the developmental period (when body size and juvenile plumage are determined) as hypothesized by recent studies (Meillère, Brischoux, Parenteau et al., 2015; Peach et al., 2015; Seress et al., 2012). In contrast, we did not report any significant influence of urbanization on body condition (juveniles and adults) and adult plumage quality, emphasizing that the urban environment allows individuals to sustain their nutritional needs during their adult life. Overall, our study suggests that urban house sparrows probably suffer from nutritional deficit during their development while such constraints disappear once the chicks have left their nest. However, because the observed traits variations along the urbanization gradient could also result from an adaptive divergence between urban and rural populations (see below for details), further investigations are now needed to better evaluate whether the smaller size and lower juvenile plumage quality of urban sparrows are associated with important fitness costs.

4.1. Consequences of living in an urbanized area during early life

Although we were not able to access the chicks while they were at the nest, we captured juveniles and adults and measured several parameters that are reliable proxies for the developmental conditions. We found that body size was negatively correlated with the degree of urbanization, urban sparrows having smaller tarsi than rural ones (Fig. 2A). Interestingly, this pattern was also found in Eastern Europe (i.e., Hungary; Bókonyi et al., 2012), demonstrating that this phenomenon is probably general and not limited to a specific geographical region or climate. In birds, structural size, and specifically tarsus length, is mainly determined during the developmental period (Anderson, 2006; Lindström, 1999). Previous studies have demonstrated that poor developmental conditions are associated with shorter structural size in house sparrows (Peach, Vincent, Fowler, & Grice, 2008; Seress et al., 2012), supporting therefore the idea that sparrows' development is constrained in urban environments. Indeed, urbanization is thought to deeply modify the trophic resources vertebrates rely on (Chamberlain et al., 2009; Fuller et al., 2008). Accordingly, a few studies recently demonstrated that fledging success of urban sparrows is limited by poor nutritional conditions (Peach et al., 2008, 2015; Seress et al., 2012). In the house sparrow, the chicks rely on protein-rich invertebrates during their development (Anderson, 2006). Yet, urbanization and associated reduction in green spaces are likely to reduce the amount of invertebrates available to sparrows (McIntyre, 2000). Moreover, the foraging range of chick-rearing house sparrows is limited, precluding them from traveling long distance to find invertebrates

(Vangestel, Braeckman, Matheve, & Lens, 2010). Such a lack of protein-rich diet probably limits chicks' growth, resulting therefore in small body sizes (Peach et al., 2008, 2015; Seress et al., 2012).

By studying the plumage of juveniles, we were able to further confirm this interpretation. Juvenile sparrows had grown their feathers while developing at the nest (Anderson, 2006), and thus, their plumage characteristics can provide us with reliable information on their developmental conditions. In that respect, our study is, to our knowledge, the first to demonstrate that feather quality is tightly correlated with urbanization in juveniles: juveniles from urban sites had less dense rectrices than those from rural sites (Fig. 3). In contrast, we did not find any evidence of an effect of urbanization on the number of fault bars or the fluctuating asymmetry of feathers in juvenile sparrows. However and interestingly, there is recent evidence that fault bars are usually not caused by nutritional stressors but rather by psychological stressors (Jovani & Diaz-Real, 2012). Moreover, feather fluctuating asymmetry seems to be a highly variable trait that is weakly correlated with nutritional stress in birds (Leung, Forbes, & Houle, 2000), and specifically in house sparrows (Vangestel & Lens, 2011). This could explain why these two variables did not differ between urban and rural juvenile sparrows in our study.

Because our study is correlative, it is obviously challenging to assess the exact causes of the observed reduced body size and juvenile plumage quality with increasing urbanization. In particular, as we did not specifically measure diet variation along the urbanization gradient, further investigations using additional parameters, such as diet examination (e.g., stomach content, dietary isotopic signatures) and/or physiological indices (e.g., fat and protein content, plasma triglycerides levels) are now needed to fully assess whether urban diet is driving urban-rural variations in morphology and feather quality. Moreover, although our results suggest that urban environments are likely to energetically constrain sparrows during their development, other factors than urban diet could also be involved. For instance, urbanization is associated with increased chemical pollution (Meillère et al., 2016), which could affect growth and development in passerine birds, either directly (direct toxic effects) or indirectly (e.g., pollution-related changes in invertebrate availability; Eeva, Ryömä, & Riihimäki, 2005). Previous studies have indeed reported that nestlings exposed to toxic contaminants, such as trace elements, have reduced body mass and condition (Janssens et al., 2003; Roux & Marra, 2007). Similarly, anthropogenic noise could also affect nestling growth through direct (e.g., noise-induced stress; Crino, Johnson, Blickley, Patricelli, & Breuner, 2013) or indirect impact (e.g., through altered parental behavior; Meillère, Brischoux, Angelier et al., 2015; Schroeder, Nakagawa, Cleasby, & Burke, 2012). Therefore, because birds inhabiting urban areas are exposed to numerous environmental challenges (e.g., increased light, noise and chemical pollutions, competition, predation, human disturbance) that could affect their development, future experimental studies would be useful to disentangle the relative importance of these confounding factors.

The smaller body size and lower plumage quality of urban juvenile sparrows could potentially have important consequences for fitness and could potentially lead to a lower recruitment into the population (Ringsby, Saether, & Solberg, 1998) that could explain the recent declines of urban sparrow populations (De Coster et al., 2015; Robinson et al., 2005; Shaw et al., 2008). Feather quality plays indeed a crucial role in flight and thermoregulation abilities in birds (Dawson et al., 2000; Swaddle, Witter, Cuthill, Budden, & McCowen, 1996) and a reduced body size is often associated with poorer conditions during development and poorer performances later in life (Gebhardt-Henrich & Richner, 1998; Lindström, 1999). However, the observed traits variations along the urbanization gradient could

also be adaptive if a smaller body size and lower juvenile plumage quality are associated with fitness benefits in urban environments. For instance, reduced body mass could increase escape abilities and may therefore be beneficial to individuals when the risk of predation is high (MacLeod, Barnett, Clark, & Cresswell, 2006). Similarly, a plumage of poor quality could be adaptive if a reduced investment in feather growth is made at the benefit of other traits that are essential to fitness in an urbanized environment (e.g., trade-off between immunity and plumage quality; Martin, 2005; Moreno-Rueda, 2010). Because we did not measure any fitness parameters (e.g., reproductive success, survival), we could not assess the fitness consequences associated with variation in body size and juvenile plumage quality along the urbanization gradient, making difficult to disentangle the two hypothesis (“constraints” versus “adaptive”). Future studies should therefore explore these questions to assess whether the reduced body size and lower plumage quality observed in urban populations might result from an adaptive divergence between urban and rural populations or might lead to important fitness costs.

4.2. Consequences of living in an urbanized area during adulthood

We did not find any evidence that urbanization had an effect on juvenile or adult body condition (Fig. 2B). This supports the idea that sparrows may not be nutritionally constrained by the urban environment once they fledge (Bókonyi et al., 2012; Meillère, Brischoux, Parenteau et al., 2015). Actually, urban sparrows can rely on anthropogenic food (i.e., human-provided food, such as bird seeds, pet foods and human food waste), which differ from natural food in terms of fat and protein content and provide birds with easily available energy-rich food resources (Gavett & Wakeley, 1986; Harrison et al., 2010). Importantly, this anthropogenic food is thought to be highly reliable (Davies et al., 2009; Shochat et al., 2006) and has been directly linked to the presence and density of avian species in urbanized areas (Chamberlain et al., 2005; Fuller et al., 2008). The absence of an effect of urbanization on body condition in adult birds is confirmed by two other large geographical scale studies (Bókonyi et al., 2012; Evans et al., 2009). However, numerous other studies have reported conflicting patterns regarding the influence of urbanization on body condition in birds (negative, positive or null relationships; e.g., see Chávez-Zichinelli et al., 2013; Fokidis et al., 2008; Foltz et al., 2015; Giraudeau et al., 2014; Grunst et al., 2014; Partecke et al., 2005; Schoech & Bowman, 2003), and specifically in house sparrows (Bókonyi et al., 2010, 2012; Fokidis et al., 2008; Liker et al., 2008; Meillère, Brischoux, Parenteau et al., 2015). But, most of these studies have focused on a few sites only and these discrepancies may consequently be explained by site-specific environmental conditions. Here, we studied multiple sites (30) spanning from highly urbanized cities (e.g., Paris) to highly rural places (e.g., isolated farms, small village of a dozens of inhabitants) and this powerful multi-sites approach allowed us to report a large inter-site variability in body condition (see Fig. 2B). Such variability suggests that sparrows' body condition may be affected by multiple parameters that are not solely linked to urbanization. For example, a poorer body condition could be associated with a high predation risk (MacLeod et al., 2006). Body condition could also be linked to the predictability of food resources (Cuthill, Maddocks, Weall, & Jones, 2000), as high food predictability is usually associated with reduced body reserves. Finally, body condition could be related to parasite and disease prevalence (Giraudeau et al., 2014; Pap et al., 2011), as a poor health status is usually associated with a reduced body condition. Together with other studies (Bókonyi et al., 2012; Evans et al., 2009), our study emphasizes that using a large geographical scale and a multi-site approach is required to pro-

vide robust patterns regarding the influence of urbanization on the phenotype of individuals.

Supporting further the idea that urban sparrows are not energetically constrained during their adulthood, we did not find any relationship between feather quality and urbanization in adult sparrows. Assessing feather quality is very useful to understand the influence of environmental constraints (Harms et al., 2015; Saino et al., 2013). Feather quality has ultimate consequences for individuals because it plays a crucial role in flight abilities, thermoregulation, and sexual signaling (Dawson et al., 2000; Swaddle et al., 1996). Moreover, feather quality is a proxy for the energetic and nutritional constraints experienced during the molting period, but also during the breeding period through carry-over effects (Dawson et al., 2000; Nilsson & Svensson, 1996). For example, poor nutritional conditions and high parasitic loads have been shown to have strong detrimental effects on feather length and plumage ornaments in adult house sparrows (Pap et al., 2008; Vágási et al., 2012). Here, we specifically showed that feather density, number of fault bars and fluctuating asymmetry in length of the feathers were not correlated with the degree of urbanization in adults, highlighting that adult urban sparrows did not suffer from nutritional constraints during the molting period. Confirming this result, we also found that wing size was not correlated with the degree of urbanization in adults. Adult wing size strongly and mainly depends on primary feather lengths, which are determined during molt.

4.3. Conclusions

Overall, our study clearly shows that urban life has an influence on structural growth (body size) and juvenile feather quality, suggesting therefore that urban sparrows probably suffer from nutritional constraints during development. Alternatively, such reduced body size and low-quality plumage could result from micro-evolution and genetic factors (Partecke, 2014; Plummer et al., 2015) and be adaptive if they are associated with fitness benefits in urban sparrows. However, this adaptive interpretation of reduced body size and low-quality plumage in urban environments is counter-intuitive and seems unlikely for house sparrows. Indeed, urban sparrow populations are currently declining in several European countries (De Coster et al., 2015; Robinson et al., 2005; Shaw et al., 2008), highlighting that these urban populations must suffer from specific urban-related constraints. Moreover, a few experimental studies have shown that food-supplemented urban chicks have a better fledging probability and a larger body size than controls (Peach et al., 2015; Peach, Sheehan, & Kirby, 2014; Seress et al., 2012). Future studies investigating the fitness consequences of reduced body size and low-quality plumage in urban populations would therefore be very useful to definitely disentangle the two hypothesis (“constraints” versus “adaptive”). Overall, the urban environment is complex and involves multiple and extreme environmental modifications (Grimm et al., 2008; McKinney, 2008) that may differentially affect wild vertebrates depending on their life-history strategies (Evans et al., 2011; Gil & Brumm, 2014; Lowry et al., 2013; Sol et al., 2013). Recently, urban diet has been suggested as one of the major constraints for urban sparrows (Bókonyi et al., 2012; Meillère, Brischoux, Parenteau et al., 2015; Peach et al., 2015; Seress et al., 2012), but not for other species that rely on other types of food (Evans et al., 2009; Ibáñez-Álamo & Soler, 2010). Moreover, additional constraints certainly occur (e.g., chemical, electromagnetic, noise and light pollutions, competition, predation; Gil & Brumm, 2014). Future studies need to tease apart the relative importance of these environmental constraints on wild vertebrates with various life-history strategies in order to better evaluate the impact of urbanization on biodiversity.

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