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Urbanization and blood parasite infections affect the body condition of wild birds

Jéssica Jiménez-Peñuela [a,*], Martina Ferraguti [a], Josué Martínez-de la Puente [a,c], Ramón Soriguer [b,c], Jordi Figuerola [a,c]

[a] Departamento de Ecología de Humedales, Estación Biológica de Doñana (EBD-CSIC), C/Américo Vespucio, 26, 41092 Seville, Spain
[b] Departamento de Etología y Conservación de la Biodiversidad, Estación Biológica de Doñana (EBD-CSIC), C/Américo Vespucio, 26, 41092 Seville, Spain
[c] Centro de Investigación Biomédica en Red de Epidemiología y Salud Pública (CIBERESP), Spain

HIGHLIGHTS

- The joint effect of urbanization and parasite infection on birds was investigated.
- 45 populations of house sparrow from Spain in an urbanization gradient were studied.
- Bird body mass decreased along the urbanization level, especially in urban areas.
- *Plasmodium* and *Haemoproteus* infections were positively associated with body mass.
- Selective mortality may explain the higher body mass of urban infected birds.

GRAPHICAL ABSTRACT

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ABSTRACT

Human landscape transformation, especially urbanization, strongly affects ecosystems worldwide. Both urban stressors and parasites have negative effects on organism health, however the potential synergy between those factors has been poorly investigated. We analysed the body condition (i.e. body mass after controlling for wing chord) of 2043 house sparrows (adults and yearlings) captured in 45 localities along an urbanization gradient in relation to *Plasmodium*, *Haemoproteus* and *Leucocytozoon* infection status. Body condition was negatively related to urbanization level and to urbanized land coverage but only in yearling birds from urban habitats. In addition, bird body condition tended to increase in rural habitats, significantly in the case of yearlings. Infected individuals by *Plasmodium* or *Haemoproteus* had higher body condition than un-infected birds, but this pattern could be due to a selective disappearance of infected individuals with lower body condition as suggested by the reduced variance in body condition in infected birds in urban habitats. These results provide support for a negative impact of urbanization on bird body condition, while *Plasmodium* and *Haemoproteus* may exert selection against individuals with lower body condition living in urban habitats, especially during earlier life stages, underlining the synergistic effects that urbanization and parasites may have on wild birds.

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* Corresponding author.
E-mail addresses: jjimenez@ebd.csic.es (J. Jiménez-Peñuela), mferraguti@ebd.csic.es (M. Ferraguti), jmp@ebd.csic.es (J. Martínez-de la Puente), soriguer@ebd.csic.es (R. Soriguer), jordi@ebd.csic.es (J. Figuerola).

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1. Introduction

The urbanization process implies important landscape transformation and environmental impacts that widely exceed the geographic limits of cities (Bradley and Altizer, 2007; Grimm et al., 2000). Urbanization is usually associated with a general loss of biodiversity (Seress and Liker, 2015) creating altered environments where only a reduced number of species are capable to survive (Mckinney, 2002; Sol et al., 2014). Most avian species have a low tolerance to urbanization suffering important costs in body size and condition (Liker et al., 2008). Survival, infection levels, oxidative status, stress levels and colouration are common animal life-history traits affected by urbanization (Sepp et al., 2018).

Different factors may explain the impact of urbanization on wildlife populations. For instance, food resources provided by humans in urban habitats are rich in carbohydrates and fats, and poor in protein content compared to natural food (Heiss et al., 2009; Meyrier et al., 2017) which may compromise avian reproductive success (Chamberlain et al., 2009; Pollock et al., 2017; Sumasgutner et al., 2014). This can affect population demography (Salleh Hudin et al., 2016) even for omnivorous species able to feed on human waste (Meyrier et al., 2017). Furthermore, urban habitats are polluted with toxic chemicals such as heavy metal particles, gases and other substances (Herrera-Dueñas et al., 2014). These urban pollutants cause oxidative damage as well as long and short-term stress imposing deleterious effects on wild bird populations (Bauerová et al., 2017; Herrera-Dueñas et al., 2014; Isaksson, 2015; Salmón et al., 2016; Watson et al., 2017). Birds from urban populations have a higher telomere shortening rate and higher expression of genes related to immune, inflammatory and oxidative stress responses than individuals living in rural populations (Salmón et al., 2016; Watson et al., 2017). Additionally, Bailly et al. (2016) experimentally demonstrated that the activation of constitutive immunity was more costly in urban great tits (*Parus major*), as confirmed by a decrease in haptoglobin production and a loss of body mass.

However, other species are capable of thriving in such urban environments reaching high abundances in these areas (Meyrier et al., 2017; Seress and Liker, 2015). The potential benefits provided by urban habitats include milder climate (Saaroni et al., 2000), higher predictability of food and water (Fokidis et al., 2008) and higher availability of nesting sites through nest boxes or buildings (Sumasgutner et al., 2014). Overall, these factors can improve the health status and survival of birds (Chamberlain et al., 2009; Dulisz et al., 2016), or at least buffer the negative impact of urbanization (Sumasgutner et al., 2014). Thus, urban habitats could represent ecological traps for wildlife due to mismatches between animal perception of attractive urban features and the cost imposed on fitness (Meyrier et al., 2017; Pollock et al., 2017; Sumasgutner et al., 2014). Therefore, it is essential to identify the factors affecting urban wildlife and determine their consequences for individuals living in these habitats (Seress and Liker, 2015).

Urbanization may influence pathogen epidemiology and host susceptibility to infectious diseases (Bradley and Altizer, 2007). Although the effects of urban areas may differ when the host-parasite assemblage is considered (Delgado-V and French, 2012), landscape disturbance is expected to affect the dynamics of vector-borne parasites (Calegaro-Marques and Amato, 2014; Ferraguti et al., 2018). However, analyses of the urbanization effect on the prevalence and impact of pathogen infections have provided contradictory results. While the severity of infections by *Plasmodium*, poxvirus and coccidians in birds increased with urbanization (Bichet et al., 2013; Giraudeau et al., 2014), a decrease was found for the case of infection by different blood parasites (Fokidis et al., 2008; Geue and Partecke, 2008).

The avian malaria parasites of the genus *Plasmodium* and the related genera *Haemoproteus* and *Leucocytozoon*, are common vector-borne parasites infecting birds (Atkinson and Van Riper III, 1991; Valkiūnas, 2004). Experimental and correlative studies have provided support for the impact of blood parasite infections on bird health (Valkiūnas et al., 2006), reproductive success (Marzal et al., 2005; Merino et al., 2000), susceptibility to predation (Garcia-Longoria et al., 2015; Møller and Nielsen, 2007) and life expectance (Martínez-de la Puente et al., 2010; Marzal et al., 2008). Immune responses to fight off infections by blood parasites are costly, with only those individuals in better body condition being able to develop more effective responses (Navarro et al., 2003). A diet of bad quality or quantity, as may be the case in birds living in urban habitats, may increase host susceptibility to infectious diseases (Cornet et al., 2014).

Here, we assess the impact of both urbanization and blood parasite infection on the body condition (i.e. body mass after controlling for wing chord) of wild house sparrows (*Passer domesticus*) through an urbanization gradient in southern Spain. We sampled birds in habitats with different landscape use, from urban habitats to rural and natural environments. We selected house sparrows as the model species because this bird is ubiquitous, sedentary and abundant throughout most of their distribution range, especially when linked to human settlements (Sætre et al., 2012; Seress and Liker, 2015). House sparrows are also found in natural habitats although this species usually occurs within or nearby human constructions, being uncommon in forest habitats, scrublands and wetlands (Bichet et al., 2014; BirdLife International, 2017). This species is considered the best example of an urban exploiter (Meillère et al., 2015), even though it is currently undergoing consistent population decline across Europe (De Laet and Summers-Smith, 2007). House sparrows are commonly infected by haemosporidian parasites (Bichet et al., 2013), and at least 49 different genetic lineages of *Plasmodium*, *Haemoproteus* and *Leucocytozoon* have been recorded in this species (according to MalAvi, accessed 24 September 2018, Bensch et al., 2009). Thus, this species represents a suitable study model to assess the impact of urbanization and parasite infection on individual traits (Liker et al., 2008). Based on previous studies on passerines (Isaksson, 2015; Sepp et al., 2018), we predict a negative impact of urban environments on house sparrow body condition, particularly in those individuals infected by avian haemosporidians.

2. Material and methods

2.1. Study area and bird sampling

Field work was conducted at 45 localities in the provinces of Cadiz ($n = 15$), Huelva ($n = 15$) and Seville ($n = 15$), southern Spain (Fig. 1). These localities were geographically grouped into triplets formed by one urban (with a high human population density), one rural (with a high density of livestock) and one natural habitat (a better conserved region where wildlife predominated in comparison to livestock and human populations). Human density (people/250m^2) differed between habitats ($\chi^2 = 26.72$; d.f. $= 2$; $p < 0.001$) with urban areas being more densely populated (mean population = 187.41) than both rural (mean population = 11.70; Tukey post hoc test; $p < 0.001$) and natural (mean population = 5.47; $p < 0.001$) ones. The average distance within localities of the same triplet was 5739.87 m (±SD 4465.12 m), which minimize the possibility of individuals moving from one habitat to another. House sparrows have a home range radius of 1000 to 2000 m with <10% of individuals dispersing over 2000 m (Snow and Perrins, 1998; Summers-Smith, 1956, 1963).

Wild house sparrows were sampled in these localities from July to October 2013 by three teams of specialized ringers. Birds were captured using mist-nets and a bird call playback recorded, which was used every single time to minimize potential bias in bird sampling (Figuerola and Gustamante, 1995). Each bird was ringed with a numbered metal ring, and its age and sex was determined when possible according to their plumage characteristics and skull ossification (Svensson, 2009). Birds were identified as yearlings (birds younger than one year, Euring code 3) or adults (birds older than one year, Euring code 4). Those birds identified as unknown age (Euring code 2) were excluded from the analyses ($N = 271$ in this study). Body mass of each bird was measured with an

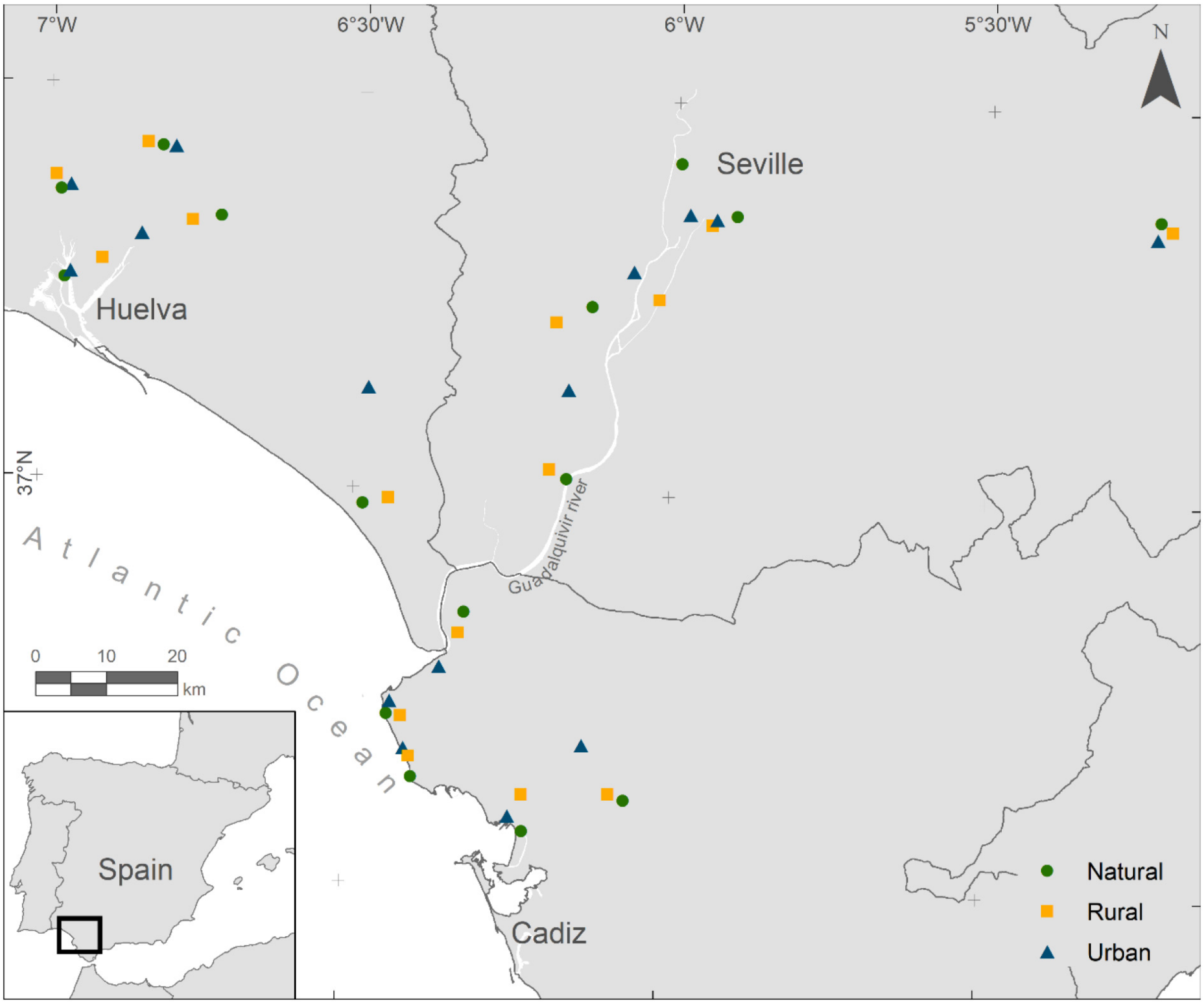

Fig. 1. Distribution of the 45 sampling sites (localities) grouped in 15 triplets of urban (blue triangle), rural (yellow square) and natural (green point) habitats from southern Spain. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

electric balance (to the nearest 0.1 g) and wing chord was measured with a metal ruler (to the nearest 1 mm) by the same ringer in each tripled of the same province. Both, wing chord ($r = 99.93$) and body mass ($r = 99.99$) were highly repeatable measurements between observers as estimated from 12 individuals measured. Finally, a blood sample was obtained from the jugular vein using a sterile syringe, never exceeding 1% of the body mass. Blood samples were transferred to Eppendorf tubes and preserved in cold-boxes during the field work. In the laboratory, the samples were kept at 4 °C up to 24 h and subsequently centrifuged for 10 min at 1700*g* (4,000 rpm) to separate serum and cellular fractions, which were frozen at −80 or −20 °C, respectively.

2.2. Molecular analyses

Genomic DNA was extracted from the blood cellular fraction using Maxwell®16 LEV System Research (Promega, Madison, WI) (Gutiérrez-López et al., 2015). For those birds which were not sexed based on morphology (mainly juveniles), bird DNA was used to molecularly sex birds following Griffiths et al. (1996, 1998). In addition, the infection status by *Plasmodium*, *Haemoproteus* and *Leucocytozoon* was assessed following the protocol detailed by Hellgren et al. (2004). PCR of samples providing negative results (absence of parasite DNA) were repeated to avoid the occurrence of false negatives (McClintock et al., 2010). Both negative controls for PCR reactions (at least one per plate) and DNA extraction (one per 15 samples) were included in the analysis. PCR amplifications were resolved in 1.2% agarose gels and positive samples were sequenced uni-directionally from the 5′ end using the Macrogen sequencing service (Macrogen Inc., Amsterdam, The Netherlands). Amplicons were sequenced uni-directionally to reduce the cost of sequencing a large number of amplicons (Dubiec et al., 2016). Sequences were edited using the software Sequencher™ v 4.9 (Gene Codes Corp. © 1991–2009, Ann Arbor, MI 48108, USA) and parasite genera were identified by BLAST comparison to previously identified sequences deposited in the GenBank database (National Center for Biotechnology Information).

2.3. Landscape characterization

Urbanization scores of the 45 sampling localities were obtained following Czúni et al. (2012), Seress et al. (2014) and Lipovits et al. (2015) (http://keplab.mik.uni-pannon.hu/en/urbanization-index). Satellite images taken in 2013 (the year of bird sampling) were obtained for the 45 localities from Google Maps in '.jpeg' format. Satellite images covered an area of 1 square km around each bird sampling locality. For each square, the software estimates the proportion of buildings, vegetation and paved surface coverture, which are then combined in a Principal Components Analysis (PCA) to obtain an 'urbanization score'. The urbanization score ranges from negative values for the case of less urbanized areas to higher values for more intensely urbanized areas.

Moreover, to obtain a more complete estimation of the environmental characteristics of the sampling localities, the percentage of the total area occupied by agricultural, natural and urban lands was characterized (see details in Ferraguti et al., 2016). To do that, we used the cartography from the study area (http://www.juntadeandalucia.es/institutodeestadisticaycartografia/DERA/) considering a 2000 m radius buffer around the bird sampling sites, covering approximately the range of dispersal of adult house sparrows (Snow and Perrins, 1998). Spatial analyses and zonal statistical tools for raster files and the geoprocessing intersect tool for vector variables were used with the software ArcGis v10.2.1 (ESRI, Redlnad). The land surface covered by forests was not considered in our analyses as house sparrows are commonly absent or very uncommon in most of these habitats (Anderson, 2006). Finally, human population density was estimated as the number of people living in a grid of 250 × 250 m according to the data registered on 1st January 2013 by the Institute of Statistics and Cartography of Andalusia.

2.4. Statistical analyses

Statistical analyses were conducted using Linear Mixed-Effects Models (LMM) in R (v, 3.5.1.; R Foundation for Statistical Computing 2018) using the packages: MASS, car, lattice, Matrix, Rcpp, lme4, MuMIn, arm, stats, multcomp, ggplot2, nlme and scales (Crawley, 2007). Dependent and independent variables and the residuals of the models were checked for normality with *qq plots*. Also, we checked for collinearity in independent variables by calculating their Variance Inflation Factor (VIF) in all models, not including the variables with VIF values higher than 5 (Zuur et al., 2010). Human population density was log transformed, the land use variables were log ratio transformed to normalize their distributions (Aitchison, 1986). In addition, the urbanization index was re-scaled to avoid any negative values. Tukey's test was used for Post-hoc comparisons. The best final model selection was based on Akaike's Information Criterion (AIC), and parameters were estimated by model averaging of all models with ΔAIC ≤ 2, which were considered to be similarly supported by the data (Symonds and Moussalli, 2011).

Two sets of analyses were performed. First, we fitted a general model including body mass as the dependent variable. Date and hour of capture, wing chord and urbanization indexes (both linear and quadratic terms) were used as independent continuous variables and bird age, bird sex, bird infection status by *Haemoproteus, Plasmodium* and *Leucocytozoon* and habitat (urban/rural/natural) as categorical factors. Locality nested by triplet and triplet nested by province were included as random factors in the analyses (Appendix A, Table A.1.).

Second, due to the differences found in the bird body condition with respect to the urbanization index (see Section 3.2), further analyses were conducted separately for birds from each habitat category (urban/rural/natural). Thus, three models were fitted including body mass as the dependent variable. Date and hour of capture, wing chord, percentage of area covered by urban, crop and natural lands as well as human density were incorporated as independent continuous variables; and bird age, bird sex, bird infection status by *Haemoproteus, Plasmodium* and *Leucocytozoon* were included as independent categorical factors. Locality nested by province was considered as a random factor (Appendix A, Table A.2.).

Due to the significance of bird age (see Section 3.2), each analysis was carried out separately including: 1) both adults and yearlings, 2) only adults or 3) only yearlings. The variance explained by these models was calculated using both the marginal R^2 (proportion of variance explained only by the fixed factors) and the conditional R^2 (proportion of variance considering both fixed and random factors) following Nakagawa and Schielzeth (2013). Finally, variances in body mass from urban birds of all ages were compared between infected and not infected individuals using Bartlett test (Crawley, 2007).

3. Results

3.1. Prevalence of blood parasites

Overall, 59% of the 2043 individuals analysed for this study were infected by at least one parasite genus. The prevalence of *Plasmodium* (29%) and *Leucocytozoon* (30%) parasites were similar and higher than the prevalence of *Haemoproteus* (16%). We found a mean prevalence of infection of 52%, 60% and 67% in urban, rural and natural habitats, respectively. The highest prevalence of infection by *Plasmodium* parasites was found in rural habitats (33%), followed by natural (30%) and urban (25%) habitats. For the case of *Leucocytozoon* parasites, the highest prevalence was found in natural habitats (36%) followed by urban (31%) and rural habitats (25%). Finally, *Haemoproteus* parasites were more prevalent in natural habitats (22%), followed by rural (16%) and urban habitats (12%). However, the prevalence of the three blood parasite genera did not differ statistically between habitat categories (data not shown). See further information in Appendix B, Table B.1 and Appendix C, Table C.1.

3.2. Bird body condition and habitat categories

Older birds showed a higher body condition (Table 1). Considering all age categories, bird body condition was negatively associated with the urbanization index and tended but not significantly to be higher in rural habitats compared with urban ones (Table 1). However, both the urbanization index variable and the habitat categories reflect very similar information, the first one as a continuous variable and the second one as categories. Consequently, when urbanization index (and its quadratic) are removed from the model, the statistical significance of habitat increases ($X^2 = 7.45$, $df = 2$, $p = 0.02$) and post-hoc test confirms that birds from rural habitats had a higher body condition than those from urban habitats (Rural – Urban: $est = 0.58$, $z = 2.84$, $p = 0.01$), while body condition did not differ between birds from rural and natural habitats (Rural – Natural: $est = 0.16$, $z = 0.77$, $p = 0.72$) and between birds from natural and urban habitats (Natural – Urban: $est = 0.42$, $z = 1.95$, $p = 0.13$). Bird body condition was positively related with the prevalence of infection by *Plasmodium* or *Haemoproteus* parasites after controlling for the significant effect of wing chord, bird age, date and time of capture (Table 1).

The body condition of yearlings was negatively related to urbanization and was significantly higher in rural habitats compared with urban ones. Also tended, but not significantly, to be higher in natural compared with urban habitats. Yearling birds body condition was likewise higher for individuals infected by *Plasmodium* or *Haemoproteus* after controlling for the significant effect of wing chord, date and time of

Table 1
Results of the LMMs on the effect of urbanization on the bird body condition including the three habitat categories and all ages (N = 2043). Body mass was included in the analysis as a dependent variable. Estimate (*est*), *z* and *p* values from the models are shown. Significant associations ($p < 0.05$) are shown in bold. Conditional and marginal (in brackets) R^2 values are shown.

Independent variables	*est*	*z*	*p*
(Intercept)	**25.51**	**143.19**	<**0.001**
Wing chord	**1.85**	**20.05**	<**0.001**
Age (adults)	**0.90**	**8.66**	<**0.001**
Sex (female)	−0.09	1.01	0.32
Date of capture	**0.90**	**8.20**	<**0.001**
Time of capture	**1.31**	**12.02**	<**0.001**
Urbanization index	**−10.84**	**2.67**	**0.008**
Quadratic urbanization index	−1.52	0.45	0.66
Natural habitat	0.28	0.93	0.35
Rural habitat	0.47	1.79	0.07
Haemoproteus infection status (infected)	**0.40**	**3.09**	**0.002**
Plasmodium infection status (infected)	**0.24**	**2.50**	**0.012**
Leucocytozoon infection status (infected)	−0.05	0.54	0.59
R^2	0.41 (0.37)		

capture (Table 2). Body condition of adult birds was negatively associated to the urbanization index, while no relationship was found in relation to Haemosporidians infection after controlling for the significant effect of wing chord, date and time of capture (Table 2).

Independent models considering the local landscape characteristics were fitted for each of the three habitats. In urban habitats bird body condition decreased with the area covered by urbanized lands and in rural habitats it appears as a tendency (Table 3). Significant associations between bird body condition and parasite infection status were only found in birds from urban habitats where *Plasmodium* and *Haemoproteus* infected birds showed a higher body condition than uninfected ones (Table 3). Body condition of birds from rural and natural areas was not related significantly to any of the land cover or infection status variables (Table 3).

Bird body condition decreased with the area covered by urbanized lands and increase with the infection of *Haemoproteus* or *Plasmodium* in yearling birds from urban habitats (Table 4). Similarly, in urban adult birds, a negative association was found between the area covered by urbanized land and bird body condition, but body condition was unrelated to the infection by any Haemosporidian (Table 4). Body condition of adults and yearlings from rural and natural habitats was not related to land cover variables nor Haemosporidian infection status (Appendix D, table D.1. and table D.2.)

Finally, although *Plasmodium* and *Haemoproteus* infected birds from urban habitats showed a higher body condition, birds infected by *Plasmodium* had a lower variance in body mass than uninfected individuals (Fig. 2; Bartlett test, *Plasmodium*: all ages, $K^2 = 7.51$, $p = 0.006$; Haemoproteus: all ages, $K^2 = 2.93$, $p = 0.09$). This lower variance was confirmed when analysed yearling birds (*Plasmodium*, $K^2 = 4.92$, $p = 0.026$; *Haemoproteus*, $K^2 = 1.02$, $p = 0.31$) but not for adult birds (*Plasmodium*, $K^2 = 0.05$, $p = 0.82$; *Haemoproteus*: $K^2 = 0.14$, $p = 0.71$).

4. Discussion

Results from this study provide strong evidence supporting the impact of human land-use transformation on the body condition of wild birds. Although the use of bird body mass as a measure of bird body condition has been debated, this variable is easy to measure, repeatable and allows to describe energy and nutrient reserves (Labocha and Hayes, 2012). Different methods have been proposed to control for or remove the effects of individual size on body mass (i.e. Bókony et al., 2012; Peig and Green, 2009), and in this study we have done so by including individual size (wing chord) as a covariate on the analyses with body mass as dependent variable as recommended by Garcia-Berthou (2001). After controlling for the effect of wing chord and other variables potentially affecting body mass (i.e. age, sex, date and hour of capture) we obtained a simplistic body condition index as previously used in studies on the effect of urbanization on bird populations (Liker et al., 2008). Using this approach, we found that birds from urban habitats had lower body condition than rural birds. Additionally, extend of urbanization was negatively related to bird body condition in urban habitats. However, it was surprising that yearlings infected by *Plasmodium* or *Haemoproteus* parasites in urban areas had a higher body condition than uninfected individuals.

Table 2

Results of the LMMs on the effect of urbanization on the bird body condition including the three habitat categories in adults (N = 542) and yearlings (N = 1501). Body mass was included in the analysis as a dependent variable. Only estimate (*est*), *z* and *p* values from the independent variables included in the final models are shown. Significant associations ($p < 0.05$) are shown in bold. Conditional and marginal (in brackets) R^2 values are shown.

Independent variables	Adults			Yearlings		
	est	*z*	*p*	*est*	*z*	*p*
(Intercept)	**26.47**	**244.51**	**<0.001**	**25.24**	**134.28**	**<0.001**
Wing chord	**1.32**	**7.26**	**<0.001**	**2.03**	**18.77**	**<0.001**
Sex (female)	−0.22	1.20	0.23	−0.08	0.83	0.41
Date of capture	**0.84**	**4.65**	**<0.001**	**0.88**	**7.00**	**<0.001**
Time of capture	**1.33**	**7.69**	**<0.001**	**1.31**	**9.81**	**<0.001**
Urbanization index	**−7.33**	**2.99**	**0.003**	**−9.56**	**2.77**	**0.006**
Quadratic urbanization index	−1.15	0.50	0.62	−1.94	0.60	0.55
Natural habitat				0.41	1.80	0.07
Rural habitat				**0.57**	**2.68**	**0.007**
Haemoproteus infection status (infected)	−0.09	0.46	0.65	**0.69**	**4.31**	**<0.001**
Plasmodium infection status (infected)	−0.10	0.56	0.57	**0.36**	**3.35**	**<0.001**
Leucocytozoon infection status (infected)	−0.17	1.04	0.30	0.07	0.60	0.55
R^2	0.30 (0.26)			0.43 (0.39)		

4.1. Effect of landscape on bird body condition

When comparing birds from habitats with different characteristics, urbanization score was negatively related to the body condition of house sparrows. In the urban habitats, the surface covered by urbanized areas was negatively linked with bird body condition. Similar conclusions were also found by Bókony et al. (2012) and Liker et al. (2008) who reported a negative association between urbanization and the body mass of house sparrows (but see Meillère et al., 2016). Different reasons may explain these results. Urban stressors like chemical pollutants affect bird health (Isaksson, 2015) potentially decreasing the body condition of both adult (Dulisz et al., 2016; but see Salmón et al., 2018) and nestling birds (Salmón et al., 2016), as shown in this study. Also, birds exposed to air pollution in cities may upregulate the antioxidant machinery (Herrera-Dueñas et al., 2014; Salmón et al., 2018) and trace element contamination may increase the stress response in birds (Meillère et al., 2016). Urban stressors including chemical, noise, artificial light pollution, diseases and diet may increase the oxidative stress of organisms and their responses against these stressors to maintain homeostasis (e.g. synthesis of HSPs) are energetically costly (Chávez-Zichinelli et al., 2010; Isaksson, 2015), finally reducing the body condition of individuals from urban habitats.

The low concentrations of essential nutrients found in urban food resources (Heiss et al., 2009; Meyrier et al., 2017), may negatively affect the health status of wild birds (Dulisz et al., 2016). Thus, both urban pollution and dietary differences could explain our results (see Salmón et al., 2016). However, urban habitats offer more abundant and seasonally stable food sources (Shochat et al., 2006). Under this scenario, birds do not need to accumulate energy reserves in their bodies (Salleh Hudin et al., 2016). Thus, we cannot rule out the alternative that birds from urban habitats had a lower body condition because of a higher food predictability in these habitats. Nevertheless, food is as well predictable in rural habitats where birds may feed on food resources provided to farm animals and we found that birds from rural habitats had higher body condition than those from urban habitats, especially during the earliest stages of life. Liker et al. (2008) found similar differences between urban and rural bird body mass that remained during an experiment with ad libitum access to food, supporting our results. These authors suggested that these differences in body condition could originate during nestling development.

The availability of high quality food for house sparrows (e.g. food storage or feeders used by livestock) in rural habitats can explain the higher body condition of birds from this habitat (Salleh Hudin et al., 2016). Historically, the expansion of house sparrows was favoured by an increased amount of food available at human agricultural settlements (Sætre et al., 2012). Cropland species, such as house sparrows, reach higher richness in borders surrounding natural areas and are more dependent on the abundance of crops and on landscape diversity (Pino et al., 2000).

4.2. Effects of parasitism on bird body condition

Host-parasite interactions may vary with habitat urbanization (Delgado-V and French, 2012). Environmental factors that affect bird

Table 3

Results of the LMMs on the effect of habitat uses and infection status on the bird body condition in the three habitat categories: urban (N = 735), rural (N = 717) and natural (N = 591). Body mass was included in the analyses as the dependent variable. Only estimate (*est*), *z* and *p* values from the independent variables included in the final models are shown. Significant associations ($p < 0.05$) are shown in bold. Conditional and marginal (in brackets) R^2 values of the models are shown.

Independent variables	Urban			Rural			Natural		
	est	*z*	*p*	*est*	*z*	*p*	*est*	*z*	*p*
(Intercept)	**25.08**	**202.37**	**<0.001**	**26.05**	**237.88**	**<0.001**	**25.62**	**179.63**	**<0.001**
Wing chord	**2.26**	**14.32**	**<0.001**	**1.50**	**9.23**	**<0.001**	**1.69**	**11.03**	**<0.001**
Age (adults)	**0.90**	**5.19**	**<0.001**	**1.02**	**6.02**	**<0.001**	**0.55**	**2.75**	**0.006**
Sex (female)				−0.25	1.65	0.10			
Date of capture	**0.83**	**4.56**	**<0.001**	**0.96**	**5.42**	**<0.001**	**0.98**	**4.98**	**<0.001**
Time of capture	**1.26**	**7.30**	**<0.001**	**1.09**	**6.10**	**<0.001**	**1.40**	**8.36**	**<0.001**
Crops land coverage	0.29	1.15	0.25	−0.10	0.36	0.72	−0.13	0.47	0.64
Urbanized land coverage	**−0.68**	**2.58**	**0.010**	−0.41	1.85	0.06	−0.11	0.42	0.68
Natural land coverage	−0.24	0.95	0.34				−0.09	0.30	0.76
Population density				−0.11	0.51	0.61	−0.13	0.67	0.50
Haemoproteus infection status (infected)	**0.82**	**3.40**	**<0.001**				0.27	1.46	0.14
Plasmodium infection status (infected)	**0.52**	**3.02**	**<0.001**	0.11	0.76	0.45			
Leucocytozoon infection status (infected)				−0.25	1.46	0.14	0.30	1.85	0.06
R^2	0.46 (0.44)			0.35 (0.33)			0.40 (0.35)		

community abundance and composition, may also affect vector development and abundance (Ferraguti et al., 2016), which in last term may determine the differences found between habitats in the prevalence and risk of infection of parasites (Lachish et al., 2013). The effects of parasite infections on vertebrate hosts may be modulated by the environmental conditions where they occur. The degree of virulence of avian Haemosporidians have been largely discussed with studies reporting positive (Bichet et al., 2013), negative (Martínez-de la Puente et al., 2010; Marzal et al., 2005, 2008; Merino et al., 2000) or even non-significant (Carrete et al., 2009) associations between parasite infection status and the body condition of wild birds.

We found a positive relationship between *Plasmodium* and *Haemoproteus* infections and bird body condition, which was only significant in yearling birds from urban habitats. These unexpected results could be explained by a differential mortality rate of infected birds with respect to uninfected ones. If only infected birds showing a better body condition were able to face and survive parasite infections (Houston et al., 2007; Moreno-Rueda, 2011; Navarro et al., 2003), it is possible that infected individuals showed a higher body condition than uninfected birds (Sorci, 2013). Moreover, the mortality cost of malaria infections occurs during a short stage of high parasitaemia, and after such period surviving individuals harbour chronic infections with lower fitness costs (Bensch et al., 2007; Valkiūnas, 2004, but see Asghar et al., 2015; Martínez-de la Puente et al., 2010). Thus, yearling birds who probably get infected right after or during nestling time when they are immunologically naive (Merino, 2010), may suffer a higher impact of parasite infections than adults. Which may explain that in this study, we found differences in body mass in relation to infection status only in yearlings.

Table 4

Results of the LMMs on the effect of habitat uses and infection status on the bird body condition in urban areas. Body mass was included in the analyses as the dependent variable. Overall, data from adults (N = 225) and yearlings (N = 510) was analysed. Only estimate (*est*), *z* and *p* values from the independent variables included in the final models are shown. Significant associations ($p < 0.05$) are shown in bold. Conditional and marginal (in brackets) R^2 values of the models are shown.

Independent variables	Adults			Yearlings		
	est	*z*	*p*	*est*	*z*	*p*
(Intercept)	**26.06**	**225.59**	**<0.001**	**24.68**	**152.28**	**<0.001**
Wing chord	**1.06**	**3.67**	**<0.001**	**2.68**	**13.74**	**<0.001**
Sex (female)	**−0.54**	**1.98**	**0.048**	0.10	0.57	0.57
Date of capture	0.33	1.35	0.18	**0.92**	**4.26**	**<0.001**
Time of capture	**1.14**	**4.73**	**<0.001**	**1.17**	**5.32**	**<0.001**
Crops land coverage	0.26	1.08	0.28	0.19	0.56	0.57
Urbanized land coverage	**−0.76**	**3.13**	**0.002**	**−0.77**	**2.14**	**0.032**
Natural land coverage				−0.15	0.47	0.64
Population density				0.16	0.53	0.60
Haemoproteus infection status (infected)	−0.18	0.57	0.57	**1.29**	**3.97**	**<0.001**
Plasmodium infection status (infected)	0.21	0.82	0.41	**0. 68**	**3.21**	**0.001**
Leucocytozoon infection status (infected)	−0.14	0.57	0.57	0.07	0.36	0.72
R^2	0.25 (0.25)			0.52 (0.49)		

Moreover, Fokidis et al. (2008) found that a higher energetic cost was associated to immunological responses against infections in urban birds, rather than in birds from rural environments. This costly immunity activation caused a decrease in haptoglobin production and a loss of body condition (Bailly et al., 2016). The higher expression of immunoregulatory genes found in urban habitats with respect to those from natural environments may also explain the higher body condition of infected vs uninfected birds in urban habitats (Watson et al., 2017).

5. Conclusions

Our results support the adverse effects of urbanization on bird body condition, although local scale habitat characteristics and the infection status by Haemosporidian parasites, may modulate these relationships. Therefore, birds in urban habitats may suffer, among other potential factors, the synergistic effects of pollution, bad quality diet, and parasite infections, especially during the earliest stages of life. Also, our results suggest that in urban habitats, only those individuals showing a higher body condition were able to survive to parasite infection while dealing with these other adverse factors.

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Ethical approval

This study was done with all the necessary permits issued by the regional Department of Environment (Consejería de Medio Ambiente, Junta de Andalucía) and all the animal experimentation licences

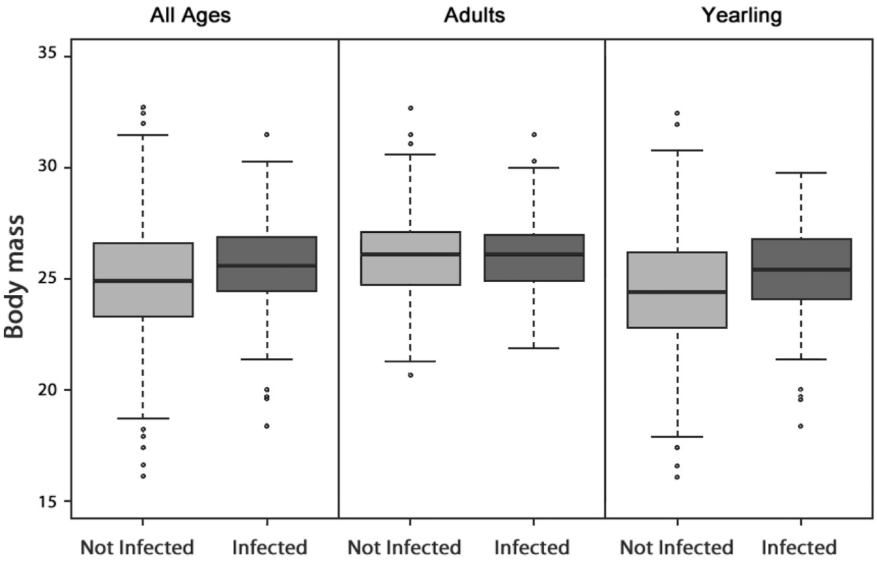

Fig. 2. Boxplots of bird body mass in urban areas with respect to the infection status by *Plasmodium*: infected (black) and not infected (grey) birds according to the age categories (yearlings, adults or both). Boxplots show median values, the lower (Q1) and upper (Q3) quartile and the range (9–91%).

required according to Spanish law. The CSIC Ethics Committee approved the experimental procedures on 9th March 2012. Surveys on private lands were conducted with the verbal consent of the owners. Birds were released in the area immediately after sampling without any apparent damage.

Conflict of interest

The authors declare they have no actual or potential competing financial interest.

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Supplementary data

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