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Wild boar in the city: Phenotypic responses to urbanisation

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HIGHLIGHTS

- Human-modified environments are an increassing selective pressure for wildlife.
- We address how a large mammal urban adapter responds to the urban environment.
- The urban environment changes the wild boar diet, biometric and physiological traits.
- Urban wild boars show larger body size, mass and condition than non-urban ones.
- Wild boars are thriving in urban areas.

GRAPHICAL ABSTRACT

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ABSTRACT

Urbanisation is a global human-induced environmental change and one of the most important threats to biodiversity. To survive in human-modified environments, wildlife must adjust to the challenging selection pressures of urban areas through behaviour, morphology, physiology and/or genetic changes. Here we explore the effect of urbanisation in a large, highly adaptable and generalist urban adapter species, the wild boar (*Sus scrofa*, Linnaeus 1758). From 2005 to 2018, we gathered wild boar data and samples from three areas in NE Spain: one urban (Barcelona municipality, $n = 445$), and two non-urban (*Serra de Collserola* Natural Park, $n = 183$, and *Sant Llorenç del Munt i Serra de l'Obac* Natural Park, $n = 54$). We investigated whether urbanisation influenced wild boar body size, body mass, body condition, and the concentration of serum metabolites, considering also the effect of age, sex and use of anthropogenic food resources. Wild boars from the urban area had larger body size, higher body mass, better body condition, and a higher triglyceride and lower creatinine serum concentrations than non-urban wild boars. In addition, urban wild boars consumed food from anthropogenic origin more frequently, which suggests that differences in their diet probably induced the biometric and the metabolic changes observed. These responses are probably adaptive and suggest that wild boars are thriving in the urban environment. Our results show that urbanisation can change the morphological and physiological traits of a large mammal urban adapter, which may have consequences in the ecology and response to urban selection pressures by the species.

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The phenotypic plasticity shown by wild boars provides both further and new evidence on the mechanisms that allow urban adapter species of greater size to respond to urbanisation, which is expected to continue growing globally over the coming decades.

1. Introduction

Urbanisation is a global, human-induced rapid environmental change (Sih et al., 2011). It transforms rural into urban settlements and shifts the spatial distribution of the population from rural to urban areas (United Nations, 2018). The expansion of urban areas is one of the most important threats to biodiversity, as it reduces species richness, alters species composition and increases biotic homogenisation (Leong et al., 2016; McKinney, 2006; Piano et al., 2020; Shochat et al., 2010). Moreover, urban habitats entail novel challenges to wild individuals and populations, including anthropogenic disturbances such as human presence and traffic noise (Fernández-Juricic and Tellería, 2000; Reijnen et al., 1997), exposure to toxic substances (Murray et al., 2016; Murray et al., 2019) and increased disease transmission (Bradley and Altizer, 2007; Murray et al., 2019).

While many species cannot cope with the challenges of urbanisation, others are able to survive and even thrive in urban environments by exploiting the anthropogenic resources available and even depending on them (urban adapters and exploiters, respectively; Blair, 1996; McKinney, 2006). The key to survive in human-altered habitats is adjusting to the new selection pressures, which can induce adaptive changes in behaviour, morphology, physiology and the genetic structure of animal populations (McDonnell and Hahs, 2015; Shochat et al., 2006). Phenotypically plastic individuals achieve this by producing different phenotypes under different environmental conditions (DeWitt and Scheiner, 2004) and the rates of phenotypic change are greater in human-dominated environments than in less disturbed and natural environments (Alberti et al., 2017; Hendry et al., 2008).

Vertebrate responses to urbanisation have been mostly studied in birds (Chace and Walsh, 2006; Marzluff, 2001) and, to a lesser extent, in small and medium sized mammals. For instance, urban red foxes (*Vulpes vulpes*) successfully exploit anthropogenic food sources in urban areas (Contesse et al., 2004), urban great tits (*Parus major*) change their song frequency at noisy urban locations (Slabbekoorn and Peet, 2003), urban stone martens (*Martes foina*) select buildings as den sites over natural den sites (Herr et al., 2010), suburban Australian magpies (*Gymnorhina tibicen*) start breeding earlier than rural ones (O'Leary and Jones, 2006), and urban lizards (*Anolis sagrei*) show bolder and more exploratory behaviour than rural ones (Lapiedra et al., 2017).

However, the response of larger mammals to urbanisation have been less studied, yet an increasing number of cities throughout the world are registering conflicts due to the presence of large carnivores and ungulates such as American black bear (*Ursus arctos*) (Beckmann and Lackey, 2008), red deer (*Cervus elaphus*), fallow deer (*Dama dama*) (Duarte et al., 2015) or wild boar (*Sus scrofa* Linnaeus 1758) (Cahill et al., 2012). These conflicts commonly include traffic accidents, property damage and risk of attacks and of disease transmission (Soulsbury and White, 2015; Zuberogoitia et al., 2014).

The wild boar fits both the description of urban adapter (Stillfried et al., 2017a; Stillfried et al., 2017b) and phenotypically plastic species (Gamelon et al., 2013; Podgórski et al., 2013), and thus can be a suitable model to improve our knowledge about the adjustment of large mammals to urban areas (Stillfried et al., 2017c). On one hand, the population numbers and geographical range of wild boars have been growing all over Europe for nearly five decades (Massei et al., 2015; Sáez-Royuela and Tellería, 1986), and reports on wild boars in urbanised areas, along with human-wild boar conflicts, are increasing accordingly (Cahill et al., 2012; Licoppe et al., 2013; Stillfried et al., 2017c). In our study area in north-eastern Spain, wild boars have been reported in urban and peri-urban areas around the city of Barcelona since at least 1998 (Minuartia, 2005). On the other hand, examples of wild boar phenotypic plasticity in urban areas are few but increasingly present in literature, mainly reporting behavioural changes (Davidson et al., 2018; Podgórski et al., 2013; Stillfried et al., 2017c). However, and to the best of our knowledge, there is little knowledge on wild boar morphological and physiological responses to urban environments. Understanding the mechanisms that allow individuals and populations to deal with urban environmental change is essential to estimate the impact of urbanisation on wildlife (McDonnell and Hahs, 2015). Moreover, this knowledge will be useful to design better management practices aimed at reducing the human-wildlife conflicts in urbanised environments.

In this study, we aim to measure the phenotypic changes that urbanisation can cause on the body size, mass, condition, diet and serum metabolites of the wild boar, as a large mammal model of an urban adapter species. More precisely, we expect increasing wild boar body size, body condition and serum concentration of triglycerides, urea and creatinine in the urbanised area. We also expect these changes to be a result of a change in their diet towards using anthropogenic food sources in the urban environment.

2. Material and methods

2.1. Study area

The study areas are located in north-eastern Spain (Fig. 1) and comprise the Barcelona municipality and two forested, non-urbanised areas, *Serra de Collserola* Natural Park (Collserola, hereafter) and *Sant Llorenç del Munt i Serra de l'Obac* Natural Park (SLMO). The municipality of Barcelona has 1,600,000 inhabitants in 10,353.301 ha of surface (Statistical Institute of Catalonia, 2019). It is a predominantly urbanised city, with 1328.6 ha of urban green areas (13.1% of the city surface) (Ajuntament de Barcelona, 2018). Barcelona is located south-east to Collserola, a Mediterranean forested area that belongs to the Catalan coastal mountain range and where a growing wild boar population thrives (González-Crespo et al., 2018). Collserola has a surface of 10,100 ha, is 17 km long and 6 km wide and has the highest summit at 512 m above sea level (Parc de Collserola, 2020a). Collserola landscape is composed by a mixture of habitats, predominated by Mediterranean forests (mainly Aleppo pine *Pinus halepensis* and holm oak *Quercus ilex*) and scrubland, but also grasslands, croplands, riparian woodlands and built-up areas (roads, residential areas and recreational spaces) (Parc de Collserola, 2020b). It receives approximately three million visitors a year (Parc de Collserola, 2020c). Last, SLMO is located approximately 20 km north to Collserola, has an area of 15,000 ha, an altitude ranging from 400 to 1103 m above sea level, and a vegetation predominated by Mediterranean forest (mainly holm oak *Quercus ilex*) and scrubland (Diputació de Barcelona, 2020a, 2020b).

2.2. Data collection and sampling

Sampling and data collection took place from 2013 to 2018 in Barcelona, from 2015 to 2018 in Collserola, and from 2005 to 2013 in SLMO. For simplicity, the wild boars captured within the Barcelona municipality limits will be referred to as “urban”, in contrast to the “non-urban” wild boars, which are those hunted in Collserola or captured in SLMO.

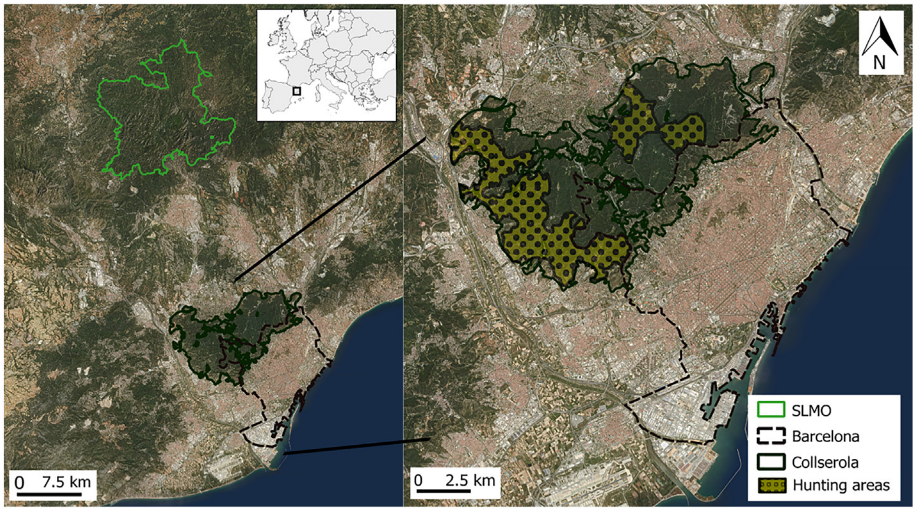

Fig. 1. Study areas. Left, from South to North: Barcelona, Collserola Natural Park and *Sant Llorenç del Munt i Serra de l'Obac* (SLMO) Natural Park. Right: detail of Barcelona and Collserola. Orthophoto source: Institut Cartogràfic i Geològic de Catalunya (ICGC).

We recorded location, date, sex, age, body mass (kg, ± 0.5 kg), body length (cm, ± 0.5 cm), wither height (cm, ± 0.5 cm), chest girth (cm, ± 0.5 cm), tarsus (cm, ± 0.5 cm), and stomach contents of 445 wild boars captured and subsequently euthanized in the urban area of Barcelona, and 183 wild boars hunted in Collserola (Supplementary file 1). We also estimated a body condition index as the body mass to tarsus ratio, and collected blood samples. Moreover, since serum biochemical analyses could not be reliably performed in the wild boars hunted in Collserola due to post-mortem blood changes, we used data from 54 wild boars from a previous study developed in SLMO (Casas-Díaz et al., 2015), including wild boar location, date, sex, age class and serum biochemistry data. These wild boars from SLMO were only used for the physiology analysis.

The urban wild boars were captured either when causing potentially dangerous situations for citizens and/or traffic or by capture events to prevent conflicts in sensitive areas. These captures were performed within the framework of the service contracts 13/051, 15/0174, 16/0243 and 16/0243–00-PR/01 with the Barcelona city council. Wild boars were dart-anesthetised (using a blowpipe) with xylazine, tiletamine and zolazepam (3 mg/kg each) by a veterinarian, following the tele-anaesthesia protocol described in Torres-Blas et al. (2020). Non-urban wild boars from Collserola were shot during the regular hunting season (from October to February) in drive hunts conducted by local hunters in the Collserola designated hunting areas (Fig. 1). Non-urban wild boars from SLMO were captured by cage-trap and tele-anaesthesia (Barasona et al., 2013; Torres-Blas et al., 2020). Further details on the capture method of SLMO wild boars are described in Casas-Díaz et al. (2015).

After immobilisation and sampling, the urban wild boars were euthanized (T-61®; 1.2 mL/10 kg) according to national laws regarding animal euthanasia (Protección de los animales utilizados en experimentación y otros fines científicos, BOE 2013, c. 2, s. 7 (annex III)), and transported to a necropsy room at the Veterinary Faculty of the *Universitat Autònoma de Barcelona* (UAB) to complete data and sample collection. Once hunted, the non-urban wild boars from Collserola were eviscerated and their offal (digestive and respiratory tract) were transported the to the necropsy room of the Veterinary Faculty of the UAB to finish data collection and sample processing.

For both Barcelona and Collserola wild boars, we kept blood samples at 4 °C in a cold box until arrival at the laboratory, and serum was extracted by centrifugation at 1800 x g for 10 min within 12 hour post capture or hunt. Sera were stored at −20 °C until analysis. Further details on the sample collection and processing of SLMO wild boars are described by Casas-Díaz et al. (2015).

We estimated the age of wild boars through tooth eruption and replacement up to three years (Boitani and Mattei, 1992; Matschke, 1967) and wear patterns beyond three years (Potel, 1979). We also assigned an age class to each wild boar: piglets (under 6 months old), juveniles (between 6 and 12 months old), yearlings (between 12 and 24 months) or adults (over 24 months). For the study of physiological variables, the adult and yearling categories were grouped together to make possible the comparison with the previous data from SLMO (Casas-Díaz et al., 2015), where all the wild boars older than 12 months were considered adults and pooled together.

We performed a macroscopic analysis of the wild boar stomach contents. We spread the stomach contents in a 60 × 40 cm tray and searched for identifiable food fragments and other items from anthropogenic origin (human food waste, plastic pieces, pet food, etc.). We registered the presence or absence of these anthropogenic contents and classified the stomachs as "anthropogenic" or "natural", respectively. We further classified the anthropogenic findings into four categories: human food waste, plastic bags and pieces, pet food and others.

2.3. Data analyses

We performed all analyses using R software (Version 3.5.0; R Development Core Team, 2018), including exploratory analyses for data distribution and outliers following Zuur et al. (2010).

For wild boar age comparison, we calculated the age range of 127 urban and 183 non-urban wild boars sampled during the period comparable between areas (determined by the hunting season, October to February).

Regarding the analyses involving statistical modelling, we used "area" (urban vs. non-urban) to address our question of whether urbanisation influenced the phenotypic traits of wild boars. The analyses performed and the variables used are detailed in the following sections. We visually explored the model residuals for normality, homoscedasticity and independence through histograms, a normal probability plot and plots of the residuals against fitted values and predictor variables.

2.3.1. Effects of urbanisation on wild boar body measurements

We analysed the effect of urbanisation on wild boar body mass, body length, wither height, chest girth, tarsus, and a body condition index (body mass-tarsus ratio) in 280 wild boars (106 from Barcelona and 174 from Collserola) older than four months, and sampled from October to February (Supplementary file 2). These analyses were age and period restricted due to the lack of data from non-urban wild boars outside this period (determined by the hunting season in Collserola) and the lack of non-urban piglets younger than four months.

Since body measurements were correlated, first we performed a principal component analysis (PCA) on all of them using the built-in R function princomp. For result visualization, we used the factoextra library (Kassambara and Mundt, 2020).

To address the differences between areas, we drew 95% confidence ellipses around the categories of area in the PCA (fviz function, factoextra library), and used the scores on the first two components of the PCA as the response variables in a multivariate multiple regression. In this latter analysis, we included area (urban vs. non-urban), age class (piglet, juvenile, yearling or adult) and sex (female vs. male) as explanatory variables, as well as interactions among them. We used the built-in R function cbind to combine two response variables in the same model and the lm function within the stats library to fit the models (Fox and Weisberg, 2019). We selected the best model by backward elimination, i.e. we fitted the full model and dropped the terms which did not worsen the model when removed. For model comparison, we used the anova function (stats package). For two-way post-hoc comparisons, we used the lsmeans function (lsmeans package), with the Tukey adjustment method (Mangiafico, 2016).

In addition, to address the differences between areas in the wild boar body condition index, we fitted a linear model with this index as the response variable, and area, age class and sex (and interactions among them) as predictors. We used the lm function (stats library) to fit the models, and selected the best model according to the Akaike Information Criterion (AIC; Akaike, 1973; Burnham and Anderson, 2002). We used the lsmeans function (package lsmeans) from R to perform two-way post-hoc comparisons with the Tukey adjustment method (Mangiafico, 2016).

2.3.2. Effects of urbanisation on wild boar diet

We investigated the wild boar diet by looking at the stomach contents of 236 urban wild boars (74 from October to February, simultaneous to the hunting season, and 162 from March to September) and 180 non-urban wild boars (October through February, Supplementary file 2). We used a Pearson's Chi-squared test to determine whether the stomach contents (anthropogenic vs. natural) were related to the area (urban vs. non-urban) and period (spring-summer vs. autumn-winter), the latter only in urban wild boars.

2.3.3. Effects of urbanisation on wild boar physiology

We determined the concentration of three serum metabolites (triglycerides, urea and creatinine) in the sera from 100 urban wild boars sampled from 2013 to 2015, in order to maximise the overlap with the sampling period of the study by Casas-Díaz et al. (2015) in SLMO. The samples were analysed by using an Olympus AU400 (Olympus, Mainz, Germany) at the Veterinary Clinical Biochemistry Service of the Veterinary Faculty of UAB. We compared the urban wild boar results to those from 54 wild boar sera from the non-urban SLMO study area (Casas-Díaz et al., 2015), in which the serum samples were analysed following the same methodology.

To assess whether the concentrations of triglycerides, urea and creatinine in serum were affected by urbanisation, we performed another PCA and draw 95% confidence ellipses around the categories of area (urban vs. non-urban), age class (those defined for the physiological studies: adult-yearling, juvenile or piglet), and sex (female vs. male).

Table 1
Coordinates and loadings of variables related to wild boar body size and body condition on the two first principal component axes (PCs).

	PC1	PC2	PC1	PC2
	Coordinates		Loadings	
Body mass	0.977	0.167	0.417	0.311
Body length	0.966	−0.109	0.413	−0.203
Wither height	0.968	−0.095	0.414	−0.178
Chest girth	0.954	0.140	0.408	0.262
Tarsus	0.909	−0.386	0.389	−0.722
Body condition	0.958	0.263	0.409	0.491

3. Results

The age of the wild boars sampled October through February ranged from one day to 5–6 years in the urban area, and from 4 to 5 months to 8–10 years in the non-urban area.

3.1. Effects of urbanisation on the wild boar biometric data

The PCA of the six variables related to wild boar body size and condition (Fig. 2) yielded six principal components (PCs), the first one accounting for most of the variance (91.3%). All the variables were positively and highly correlated with PC1 (coordinates >0.91 in all cases) and their loadings to this axis ranged from 0.39 to 0.42 (Table 1). The variables with higher loadings on PC2 (4.8% of variance explained) were tarsus (−0.72) and the body condition index (0.49, Table 1). The distribution of variables and individuals in the surface determined by PC1 and PC2 (Fig. 2) suggested that wild boars with the largest body size (indicated by tarsus, body length and wither height) were located to the right of the plot, with those having the highest

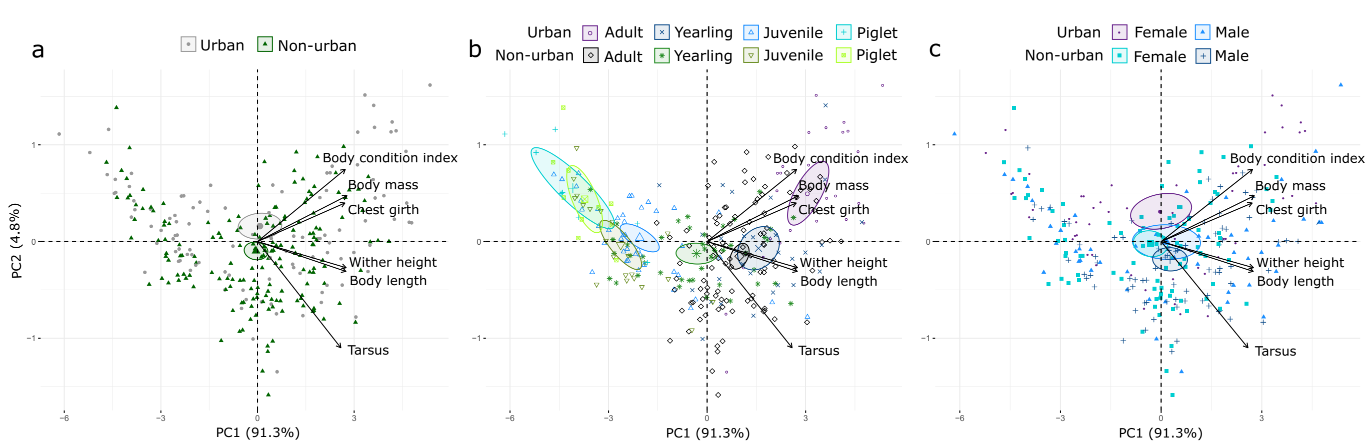

Fig. 2. Projections of 280 wild boars from Barcelona (urban area) and Collserola Natural Park (non-urban area) on the two-dimensional space defined by principal component axes (PC) 1 and 2. Arrows indicate the direction and contribution to the axes of each of the six variables included in the PCA, related to body size and body condition. Confidence (95%) ellipses of the categories of area, age class and sex indicate whether there are differences (ellipses not overlapping) between a) urban and non-urban wild boars, b) urban and non-urban wild boars among age classes, and c) urban and non-urban wild boars between sexes.

Table 2
Comparison of candidate multivariate multiple regression models fitted to explain the first (PC1) and second (PC2) principal component scores. Statistics refer to the comparison between each model and the selected one (in bold).

Predictors	Degrees of freedom	Pillai statistic	*P*
Area + age class + sex + area x age class x sex	−7	0.020	0.982
Area + age class + sex + area x age class + area x sex	−1	0.001	0.929
Area + age class + sex + area x age class	–	–	–
Area + age class + sex	3	0.122	<0.001
Area + age class + area x age class	1	0.059	<0.001

body condition (indicated by body mass, chest girth and the body condition index) located above the first axis.

The confidence ellipses (95%) drawn on the surface determined by PC1 and PC2, corresponding to the urban and non-urban wild boars, did not overlap (Fig. 2a), indicating that urban and non-urban wild boars differed in terms of body size and condition. The highest values of variables related to size (body length, whither height, tarsus) and especially with body condition (body mass, chest girth, body condition index) corresponded to urban wild boars, in the upper right part of the plot (Fig. 2a). The interaction of age class and area showed that urban and non-urban wild boars overlapped considerably as piglets, started to diverge as juveniles, almost did not overlap as yearlings and where more apart when adults, with urban yearlings showing higher body condition not only than non-urban yearlings, but also than non-urban adults (Fig. 2b). The combination of sex and area showed that urban and non-urban females differed more than urban and non-urban males (Fig. 2c).

The selected multivariate multiple regression model with PC1 and PC2 scores as the response variables (see Table 2 for details on model selection) found joint effects of area (Pillai = 0.22, df = 2, $P < 0.001$), age class (Pillai = 0.72, df = 6, $P < 0.001$), sex (Pillai = 0.06, df = 2, $P < 0.001$) and the interaction between area and age class (Pillai = 0.12, df = 6, $P < 0.001$). Urban wild boars had higher values of both PCs, i.e. larger body size and higher body condition, than non-urban ones (PC1: estimate = 2.18, $T = 7.28$, $P < 0.001$, PC2: estimate = 0.62, $T = 5.79$, $P < 0.001$), but only for adults (estimate = 1.40, $T = 8.54$, $P < 0.001$) and yearlings (estimate = 0.96, $T = 5.42$, $P < 0.001$), as indicated post-hoc comparisons. This model explained 66.5% and 17.3% of PC1 and PC2 variance, respectively, and met the assumptions of residual normality and homoscedasticity.

The selected linear model with the body condition index as the response included the variables area, age class and sex, and the interaction between area and age class (see Table 3 for information on the other models). A higher body condition index was found in urban wild boars (estimate = 0.69, $T = 8.32$, $P < 0.001$), although only for the age classes of adults (estimate = 0.69, $T = 8.31$, $P < 0.001$) and yearlings (estimate = 0.44, $T = 4.90$, $P < 0.001$), as indicated by post-hoc comparisons. This model explained 59.7% of the variance and met the assumptions of residual normality, homoscedasticity and independence. The means, medians and ranges for all the wild boar biometric data per age class and area can be found in Supplementary file 3.

3.2. Effects of urbanisation on the wild boar diet

During the hunting season, we found a higher percentage of stomachs with anthropogenic contents in urban wild boars than in non-urban wild boars (39.2% vs. 4.4%; $\chi^2 = 48.12$, df = 1, $P < 0.001$). This difference was also detected when comparing the urban wild boars sampled during the whole year with the non-urban wild boars sampled only during the hunting season (48.7% vs. 4.4%; $\chi^2 = 94.05$, df = 1, $P < 0.001$). In addition, the urban wild boar stomachs contained anthropogenic food more often in spring-summer than in autumn-winter (60.2% vs. 40.6%, $\chi^2 = 9.371$, df = 1, $P < 0.05$).

Most stomachs classified as anthropogenic included human food waste (in almost 68% of the year-round stomachs), food wrappers, plastic bags or other plastic pieces (nearly 50%), and pet food (19%; Supplementary file 4).

3.3. Effects of urbanisation on the wild boar physiology

The PCA of the three variables related to wild boar physiology (triglycerides, urea and creatinine) yielded three PCs, the two first ones accounting for 68.8% of the variance (see Table 4). All three variables were negatively correlated with PC1 and their loadings to this axis ranged from 0.52 to 0.62 (Table 4). Creatinine (positively correlated) and triglycerides (negatively correlated) were the two variables most correlated and with higher loadings on PC2 (loadings of 0.55 and −0.81, respectively). The distribution of variables and individuals in the surface defined by PC1 and PC2 (Fig. 3) suggested that wild boars with the highest values of the three variables were located to the left of the plot; with those having the highest creatinine values located in the upper part, and those with the highest triglyceride values in the lower part.

Regarding the distribution of individuals and the confidence ellipses in the surface defined by PC1 and PC2, the ellipses corresponding to the urban and non-urban areas partially overlapped (Fig. 3a), but the non-urban wild boars tended to have higher values of creatinine and lower of triglycerides than the urban wild boars (Fig. 3a). When assessing the differences between areas for each age category, the urban adults-yearlings had lower creatinine and higher triglyceride concentrations than their non-urban counterparts, while the urban piglets showed less creatinine concentration than the non-urban ones (Fig. 3b). Regarding the differences between areas for each sex, the non-urban males had higher creatinine values than the urban males (Fig. 3c).

See Supplementary file 5 for a comprehensive list of means and 95% confidence intervals of triglycerides, urea and creatinine serum concentration per wild boar age class, sex and area.

4. Discussion

The urban wild boars in this study had larger body size and mass, and had better body condition than non-urban wild boars; all of these probably being changes in phenotypic traits influenced by urbanisation.

Table 3
Candidate linear models (LMs) fitted to explain the wild boar body condition index (body mass-tarsus ratio). The selected model appears in bold.

Predictors	Degrees of freedom	AICΔ	Weight
Area + age class + sex + area x age class	**10**	**0.00**	**0.506**
Area + age class + area x age class	9	1.34	0.259
Area + age class + sex + area x age class + area x sex	11	2.15	0.173
Area + age class + sex + area x age class + age class x sex	13	4.83	0.045
Area + age class + sex + area x age class + age class + sex + area + sex	14	6.95	0.016
Area + age class + sex + area x age class + age class + sex + area + sex + area x age class x sex	17	11.76	0.001

Table 4
Coordinates and loadings of variables related to wild boar physiology on the three principal component axes (PCs).

	PC1	PC2	PC1	PC2
	Coordinates		Loadings	
Urea	−0.653	0.169	−0.624	0.172
Triglycerides	−0.546	−0.805	−0.521	−0.818
Creatinine	−0.610	0.5389	−0.583	0.548

In addition, urban wild boars changed their diet by using anthropogenic food sources, having higher energetic input as shown by their higher serum triglyceride concentrations at all ages (Fig. 3b). The higher use of anthropogenic food resources probably induced the described biometric and metabolic changes in urban wild boars and could potentially enhance their reproduction performance (see Table 5).

These results are in accordance with previous studies showing phenotypic changes in response to urbanisation in several avian and mammalian urban adapters (increased body mass, size and condition, adjusted diet and altered metabolism; Auman et al., 2008; Bateman and Fleming, 2012; Beckmann and Berger, 2003; Townsend et al., 2019). Our findings not only agree with previously reported phenotypic responses in urban wildlife, but provide new evidence on the morphological and physiological responses shown by large mammal urban adapters in urban areas.

The higher body measurements in urban wild boars also align with higher body mass previously reported specifically in wild boars (Cahill et al., 2012). The greater biometric and body condition values in the urban wild boars (mainly in the older age classes) suggest that the responses shown by wild boars might be adaptive (Donihue and Lambert, 2015) and that wild boars are thriving in the urban environment, especially from the period of maternal independence to adulthood (Kaminski et al., 2005).

Changes in the foraging behaviour and diet are common behavioural responses of wildlife to urban environments (Lowry et al., 2012). Our results further confirm that urban individuals exploit anthropogenic food sources, which was previously suggested in wild boars from our study area (Cahill et al., 2012; Castillo-Contreras et al., 2018) and was reported in other cities (Hafeez et al., 2011; Lee and Lee, 2019). A higher use of anthropogenic food could be the main factor favouring the larger wild boar body measurements and condition, as suggested for other urban populations (Beckmann and Berger, 2003; O'Leary and Jones, 2006). Moreover, urban wild boars consumed anthropogenic food more often in spring and summer, which coincides with the higher energetic needs of the wild boar population due to the birth of piglets (mainly in spring; Fonseca et al., 2011), their growth (mainly in summer), and the natural food shortage in Mediterranean areas (from late spring to early autumn). The combination of these biological and environmental aspects probably pushes wild boars to enter the urban area and feed on anthropogenic food resources (Cahill and Llimona, 2004; Castillo-Contreras et al., 2018; Massei et al., 1997).

The predictability in space and time of food resources in urban areas may also lead to a reduction in the foraging time and to a higher body mass (Oro et al., 2013). Anthropogenic food resources may enhance wild boar survival through harsh periods, i.e. hot and dry summers in Mediterranean areas (Cahill and Llimona, 2004; Massei et al., 1997). Furthermore, the higher concentration of triglycerides shown by urban wild boars is probably explained by a diet richer in fatty acids, which may be higher in human organic waste than in natural forage (Braun and Lefebvre, 2008; Bruss, 2008; Hansen et al., 2007; Van Dam and Hunter, 2012). Conversely, the lower serum creatinine concentration in the urban wild boars as compared to the non-urban ones, in spite of their bigger body size, suggests that a high-energy diet makes urban wild boars bigger and fatter but does not increase their muscle mass, since creatinine is directly correlated to muscular mass (Finco, 1997). Similarly, a recent experimental study demonstrated that American crows (*Corvus brachyrhynchos*) fed with high-cholesterol fast food showed higher plasma cholesterol concentrations and better body condition with respect to unsupplemented crows (Townsend et al., 2019).

Human food subsidies favour higher body mass and higher fertility in several avian and mammalian species (Oro et al., 2013). Reproductive performance, e.g. breeding condition, offspring number or reproduction onset, is also positively influenced by body mass in the wild boar (Drimaj et al., 2019; Fernández-Llario and Mateos-Quesada, 1998; Massei et al., 1996). Therefore, the richer-fed and heavier urban wild boars could probably show higher reproductive performance, which might also contribute to increase the number of urban wild boars, probably along with an increase of human-wild boar interactions (Fernández-Aguilar et al., 2018; Soulsbury and White, 2015).

However, studies on the effect of supplementary feeding in wildlife have also shown that long-term feeding practices can lead to reliance on supplemented food, habituation to humans, disruption of normal activities and nutritional problems such as metabolic diseases including obesity (Murray et al., 2016; Newsome and Rodger, 2008). The consumption of anthropogenic food could expose the urban individuals to pollutants, poisons or toxins from human waste (Birnie-Gauvin et al., 2016; Murray et al., 2016), as already

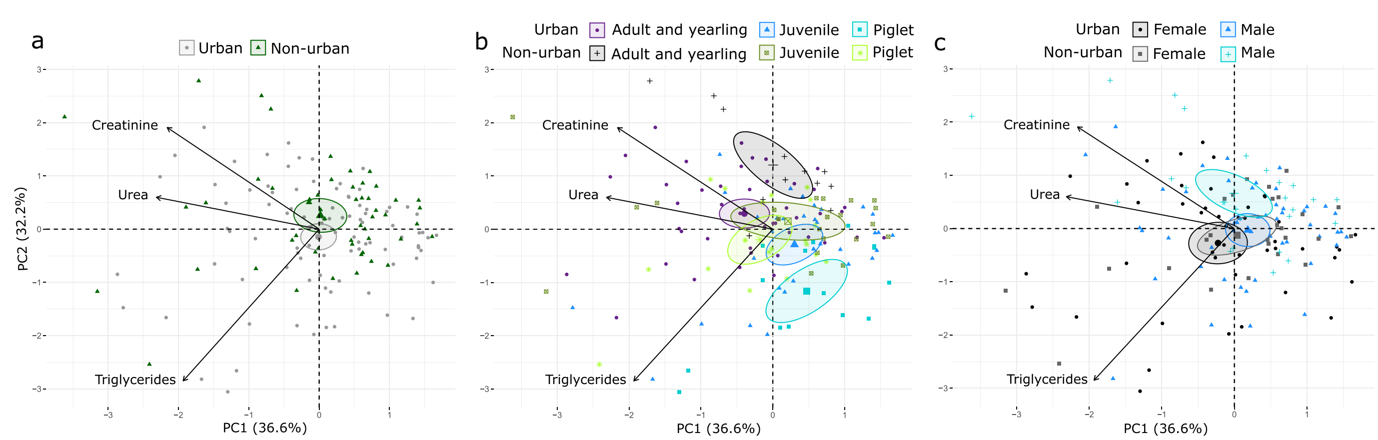

Fig. 3. Projections of 148 wild boars from Barcelona (urban aera) and *Sant Llorenç del Munt i Serra de l'Obac* Natural Park (SLMO; non-urban area) on the two-dimensional space defined by principal component axes (PC) 1 and 2. Arrows indicate the direction and contribution to the axes of each of the variables included in the PCA, related to wild boar physiology. Confidence (95%) ellipses of the categories of area, age class and sex indicate whether there are differences (ellipses not overlapping) between a) urban and non-urban wild boars, b) urban and non-urban wild boars among age classes, and c) urban and non-urban wild boars between sexes.

Table 5
Morphological and physiological responses of wild boars (WBs) in the urban area with respect to the non-urban area.

Finding	Evidence	Potential consequences
Larger body size and higher body condition	- Larger body size and higher body condition in urban yearling and adult WBs	- Increased survival - Increased recruitment - Higher reproductive performance (e.g. higher mean litter size, earlier reproductive onset)
Higher use of anthropogenic food resources	- Higher frequency of stomachs with anthropogenic contents in urban WBs - Higher concentration of triglycerides in sera from urban WBs	- Increased body mass, size and growth - Increased survival - Increased recruitment - Higher reproductive performance (e.g. higher mean litter size, earlier reproductive onset) - Increased body measurements and growth - Nutritional problems (e.g. metabolic diseases) - Exposure to pathogens, pollutants, poisons and toxins

reported in wild boars from Barcelona (Alabau et al., 2020). Furthermore, aggregating around feeding locations may also increase pathogen transmission (Becker et al., 2015; Bradley and Altizer, 2007; Murray et al., 2016; Wang et al., 2019).

In addition, urbanised areas entail other adverse impacts that can directly affect the wild boar survival or persistence in such environment, for instance vehicle collisions (Zuberogoitia et al., 2014) and the removal of problem individuals for human safety or management purposes (Torres-Blas et al., 2020; Ikeda et al., 2019), as occurs in Barcelona (Ajuntament de Barcelona, 2018b). This, together with the abovementioned behavioural and health-related potential detrimental effects, might compromise the wild boar survival in the urban area and could counter, to some extent, the positive responses shown by the wild boars in this study (Beckmann and Lackey, 2008; Gundersen et al., 2001).

Collserola wild boars enter Barcelona mainly through streams and are attracted to green areas and cat colonies probably because of the food available in those areas (Castillo-Contreras et al., 2018). In the present study, no urban wild boar from Barcelona reached the older ages detected in Collserola, which would agree with the previous study and with wild boars dispersing from the non-urban area to the urban one, according to a population dynamics source-sink system (Pulliam, 1988). Moreover, the increased food availability in the urban area could be perceived as an environmental proxy for good habitat quality, misleading the wild boars into an area where human-related risks may cause higher mortality than in the natural area. Since attractive sinks or deceptive sources occur when suboptimal habitats are perceived as good ones and are selected instead of avoided (Battin, 2018; Delibes et al., 2001), our results would agree with Barcelona acting as an attractive sink for the wild boar population, which seems to be the case in other urbanised areas (Beckmann and Lackey, 2008; Stillfried et al., 2017a). More research is needed since evidence to prove that certain habitats are sinks is extensive and difficult to acquire (Mannan et al., 2008).

When comparing the urban wild boars captured and euthanized in Barcelona to the non-urban ones hunted in Collserola, we must acknowledge a possible bias introduced by the different capture method used in both areas (dart-anaesthesia with blowpipe in Barcelona, drive hunts in Collserola). Non-urban, hunted wild boars may be biased towards bigger males and older individuals in general (Cahill and Llimona, 2004; Náhlik et al., 2017), whereas physical and chemical capture methods are more prone to capture a higher proportion of piglets and juveniles (Torres-Blas et al., 2020). The size-related bias does not seem to be an issue in the present study, as urban wild boars were bigger than non-urban ones, overcoming any possible bias introduced by the capture method. Regarding the wild boar age, the possible bias towards older individuals in Collserola prevented us from directly comparing the wild boar age between areas. However, the age range of urban wild boars in this study is probably representative of the age range of wild boars present in Barcelona, as the capture is triggered by their presence in the city.

5. Conclusions

Our results show that urbanisation shapes the morphology and physiology traits of a large mammal urban adapter. This phenotypic plasticity shown by wild boars provides both further and new evidence on the mechanisms that allow urban adapter species of greater size to thrive in urban environments, contributing to the knowledge of urban wildlife ecology. Species without such plasticity will not be able to take advantage, persist or colonise urbanised areas, which are expected to continue growing globally over the coming decades. In turn, the results from this study may inform for better management practices for the human-wildlife conflicts in urban environments, where the need to minimise habitat and biodiversity loss by urban environmental change faces the challenges of management of overabundant and problem species, and wildlife-human conflict mitigation.

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CRediT authorship contribution statement

Raquel Castillo-Contreras: Methodology, Formal analysis, Investigation, Data curation, Writing-original draft, Visualization. **Gregorio Mentaberre:** Conceptualization, Methodology, Investigation, Resources, Writing-review & editing, Supervision. **Xavier Fernández-Aguilar:** Investigation, Resources, Data curation, Writing-review & editing. **Carles Conejero:** Methodology, Investigation, Resources, Data curation, Writing-review & editing. **Andreu Colom-Cadena:** Investigation, Resources, Data curation. **Arián Ráez-Bravo:** Investigation, Resources. **Carlos González-Crespo:** Methodology, Writing-review & editing, Visualization. **Johan Espunyes:** Investigation, Resources, Writing-review & editing. **Santiago Lavín:** Writing-review & editing, Supervision, Funding acquisition. **Jorge R. López-Olvera:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing-original draft, Writing-review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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