

Research



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Evolutionary biology

Sex in the city: sexual selection and urban colonization in passerines

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Urbanization leads to a rapid and drastic transformation of habitats, forcing native fauna to manage novel ecological challenges or to move. Sexual selection is a powerful evolutionary force, which is sometimes predicted to enhance the ability of species to adapt to novel environments because it allows females to choose high-quality males, but other times is predicted to reduce the viability of populations because it pushes males beyond naturally selected optima. However, we do not know whether or how sexual selection contributes to the likelihood that animals will establish in urban areas. We use a comparative analysis of passerine birds to test whether traits associated with pre- and post-mating sexual selection predict successful colonization of urban areas. We found that plumage dichromatism was negatively associated with urban tolerance, but found no relationship with sexual size dimorphism or testes mass relative to body mass. While we cannot determine the exact reason why species with high plumage dichromatism occur less in cities, it is likely that urban areas increase the costs of expressing bright coloration due, for instance, to dietary constraints, limited male parental care or increased predation.

1. Introduction

Urbanization causes rapid and profound changes to natural environments, which can have dramatic effects on diversity (i.e. diversity homogenization [1,2]). Despite the often-documented negative effects of urban habitats on individuals and populations, many species successfully colonize and persist in these novel environments. In order to predict how urbanization impacts biodiversity, many studies aim to identify traits that are important in determining whether a species is successful at colonizing and persisting in urban environments. In birds, behavioural flexibility, nest type, brain size, migration and environmental tolerance have all been suggested to be important in allowing successful colonization of urban areas ([3–5], but see [6]). Strikingly, however, the role that sexual selection plays in determining colonization success and population persistence in urban areas has received little attention. This is surprising because sexual selection is often predicted to impact how animals respond to novel and/or stressful environments [7].

Sexual selection is a powerful evolutionary force that has been shown to both increase and reduce population viability and hence affect the potential of species to establish in novel environments [7]. If sexually selected traits reflect male quality, then female mate choice or male–male competition may favour underlying alleles that maintain high population fitness, enhancing population persistence in novel environments [7]. However, sexual selection is also related to several costs that might hamper the ability of species to colonize novel habitats. These costs arise

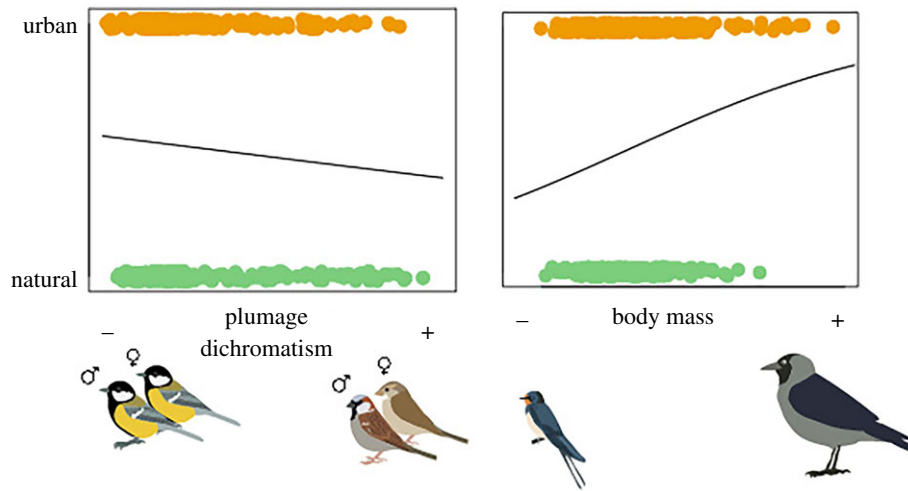


Figure 1. Plot and model estimate of the effect of plumage dichromatism and body mass on urban tolerance.

from either ecological factors (e.g. predation or infections) or genetic factors (e.g. reduced effective population sizes due to reproductive skew or sexual conflict [8–10]). Altered ecological conditions in novel environments (e.g. changes in predation and infection dynamics, variation in food resources, etc.) may increase the costs of sexual selection, and consequently affect the chances of colonization and adaptation.

To test whether sexual selection predicts the ability of species to successfully colonize urban areas, we analysed two components of pre-mating sexual selection (plumage dichromatism and sexual size dimorphism) and a component of post-mating sexual selection (relative testes mass) in passerine birds. We used phylogenetic regression to test whether the measures of sexual selection influence species colonization/persistence success in urban areas. Based on a previous study which showed that species undergoing strong sexual selection are unlikely to establish populations in novel island environments [11], we predicted that taxa with traits suggesting strong sexual selection would be less likely to occur in urban areas if these increase the costs of expressing such traits or the costs of mating multiply.

2. Material and methods

We compiled published data on plumage dichromatism (a continuous numerical score), sexual size dimorphism and relative testes mass as measures of sexual selection, as well as information on body mass and presence/absence in urban areas (see electronic supplementary material). A species was considered to be ‘absent’ when it was not found in urban areas but appeared in the nearby non-urban environment. ‘Present’ species were those found in urban areas, but which might be either present or absent from the nearby non-urban environment. Plumage dichromatism, sexual size dimorphism and testes mass are often used as measures of sexual selection in birds (for example [12]). Although the use of plumage dichromatism as a proxy of sexual selection has recently been questioned [13,14], previous studies have shown that it is associated with a variety of measures that are likely to indicate stronger sexual selection, such as avian mating systems, testes size, the degree of polygyny and the frequency of extra-pair paternity [15,16]. This indicates that even though this trait may not always provide an ideal proxy for sexual selection *per se*, it still provides information about the likely strength of pre-mating sexual selection that is relevant in the context of the current study. Likewise sexual size dimorphism has been associated with pre-mating male–male

competition and male display [17], while testis size has been associated with sperm competition [15]. Presence/absence in urban areas was assessed from 26 previously published studies (see electronic supplementary material and [1] for details on data collection) that included complete bird communities of both urban areas and the surrounding non-urban areas from 17 countries and 4 continents. This allows the comparison of the potential pool of species that have colonized urban areas with those in surrounding areas and excludes species that are unlikely to encounter urban environments.

We retained data on urban tolerance for all the passerine birds present in the original dataset ([1], $N = 506$) and discarded other avian groups. We focused our analysis on passerines because they represent around 61% of the avian diversity and they exhibit high variation in the strength of sexual selection across species. We matched urban presence/absence records with each measure of sexual selection compiled from the literature. The number of species with data available for all three components of sexual selection, and urban tolerance simultaneously was very low, so we analysed each proxy of sexual selection separately to maximize our sample size for each (see dataset in [18]). We also collected data on body mass because it is a key trait of organisms that is strongly correlated with colonization and establishment in novel environments [19,20], and with several evolutionarily conserved life-history traits (e.g. clutch size). Since small-bodied species also tend to be more dichromatic than large species [16], including body mass as covariate in our analysis allows us to control for potential variation arising from this trait.

To test whether the three components of sexual selection are associated with species presence in urban areas, we used phylogenetic generalized least-squares regression, using the `phylolm` function in the R package `phylolm` [21]. This function allows the use of binomial response variables while controlling for phylogeny (extracted from [22]). Urban tolerance was treated as a binomial response variable (0, absent; 1, present). We ran independent models where we included either plumage dichromatism ($N = 506$, see electronic supplementary material, figure S1 for phylogenetic distribution of the species), sexual size dimorphism ($N = 327$), or relative testes size (measured as testes mass relative to body mass, $N = 195$) and the interaction of each with body mass (ln transformed) as explanatory variables. When interactions were not significant, we ran a reduced model to allow interpretation of the main effects.

3. Results

Sexually dichromatic species were less likely to inhabit urban areas ($p = 0.038$, figure 1 and table 1). By contrast, neither

Table 1. Parameter estimates for main effect models testing the effect of (a) plumage dichromatism, (b) sexual size dimorphism and (c) relative testes mass in the ability to colonize urban habitats in passerine birds. Significant values are in italics.

		estimate	s.e.	t	p-value
(a) plumage dichromatism (AIC = 686.8)	(intercept)	−3.039	0.929	−3.271	0.001
	sexual dichromatism	−0.025	0.012	−2.078	0.038
	body mass	0.407	0.119	3.42	<0.001
(b) sexual size dimorphism (AIC = 443.3)	(intercept)	−3.028	1.106	−2.739	0.006
	size dimorphism	−0.273	0.986	−0.277	0.782
	body mass	0.406	0.141	2.878	0.004
(c) relative testes mass (AIC = 245.6)	(intercept)	−4.018	1.509	−2.664	0.008
	testes mass	0.098	0.499	0.196	0.844
	body mass	0.601	0.197	3.051	0.002

sexual size dimorphism ($p = 0.782$) nor testes size ($p = 0.844$) were associated with species-specific urban tolerance. Body mass was a strong predictor of presence in urban areas (all $p < 0.004$), with larger species more likely to be found in urban areas. None of the sexual selection variables interacted with body mass to predict urban establishment success (all $p > 0.603$; electronic supplementary material, table S1).

4. Discussion

We found that passerine birds with greater colour dichromatism are less likely to be present in urban environments than species with low colour dichromatism, and this effect was detectable after controlling for the strong effect of body mass. Further, we found no relationship between either size dimorphism or testes mass and presence of birds in urban areas. Our result is consistent with the idea that urban areas cause a moderate ‘island effect’, comparable to previous observations of a negative association between sexual dimorphism and introduction success on islands [11]. This finding is also consistent with several models predicting that sexual selection reduces the viability of populations in novel environments [7]. The strong significant effect of body mass predicting colonization success of urban areas is unsurprising, since this trait is positively correlated with dispersal ability, competitive ability and environmental tolerance, and it is a good predictor of colonization and establishment success [19].

Several factors may explain why birds with greater plumage dichromatism are less likely to occur in urban areas. First, urban habitats could disrupt intraspecific communication of species that use coloration as a signal when competing for mates. Previous studies often show that signal transmission and reception is less efficient when animals are taken out of the environment in which they evolved [23,24]. If urban habitats disrupt visual signalling, we might expect links between the signal and male quality to be weakened leading females to mate with poor quality mates which could impact on the viability of future generations.

Alternatively, in our dataset, there was a strong positive relationship between plumage dichromatism and male brightness ($p < 0.001$). As such, it could be that the patterns that we see result from costs associated with expressing bright coloration rather than dichromatism *per se*. Several studies have suggested that urban areas have lower abundance of

high-quality food resources than non-urban areas (e.g. [25], but see [26]). If this is the case then poor nutrition or reduced availability of necessary components (e.g. carotenoids) in urban areas may limit the expression of costly male coloration. This could reduce male investment in mate attraction or competition [27] and/or disrupt the honesty of signalling and subsequently lead to reduced population viability in novel habitats [7]. Likewise, brighter males could be more conspicuous in urban environments and thus suffer from increased predation risk. Although this explanation would also require that predators occur in urban areas.

Finally, plumage dichromatism could correlate with other characteristics of a species, and it might be these correlated characters that drive the patterns seen. For instance, previous studies show that species with high plumage dichromatism tend to have low levels of male paternal care (e.g. nest building [28]). If urban environments increase the costs of rearing offspring, females may not be able to rear offspring alone. If this was the case then only species that are able to modify their parental investment [29], or monogamous species that tend to invest more in the care of offspring would be able to colonize urban areas.

In contrast with the pattern found for plumage dichromatism, we found no relationship between the presence/absence of passerines in urban environments and our other proxies for sexual selection—sexual size dimorphism and relative testes mass. This is somewhat surprising since novel evolutionary pressures in urban areas might be expected to exacerbate the costs associated with post-mating sexual selection and multiple mating including the high rates of socially or sexually transmitted infections, high sensitivity to inbreeding depression (due to the reproductive skew) and the energetic costs associated with sperm production and cryptic female choice [12]. The fact that we found evidence for an effect of sexual dichromatism and not sexual size dimorphism or testis size reinforces the idea that colonization of urban areas is constrained by the increased costs associated with coloration, rather than costs related to multiple mating.

Our study sets up the basis for future potentially interesting avenues for research in this area. For example, when sufficient high-quality data are available, future research would benefit from exploring changes in the relative abundance (not only presence/absence) of dichromatic versus monochromatic species to determine the effects of urbanization at a community level. It would also be interesting to

explore whether specific biological traits of species buffer the detrimental effects of urbanization on dichromatic species (e.g. if variation in resource quantity and quality is less important for generalists than specialist species). Additionally, it would be fruitful to explore how the potential for dispersal (e.g. birds versus reptiles) and continuous new colonizations affect the establishment or extinction of sexually selected species in urban areas [30].

5. Conclusion

We provide evidence that birds with high plumage dichromatism are less likely to occur in urban areas than monochromatic species. This finding is consistent with the idea that plumage dichromatism is important in mediating the extent of diversity homogenization in urban areas and that this may be driven through changes in costs of expressing bright coloration or costs associated with reduced male parental care. However,

colour dichromatism is likely to interact with other biological factors to predict the potential colonization success of species. Exploring whether pre- and post-mating sexual selection differ between urban and non-urban populations of different species and geographical regions is likely to bring important insights into species sensitivity to future urbanization and anthropic habitat change more generally.

Data accessibility. Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5bp74q1> [18].

Authors' contributions. M.I.-C. conceived the idea, M.I.-C., D.A.D., A.P.M. and K.C. collected the data, M.I.-C., D.A.D. and M.L.H. analysed the data, all authors helped drafting the manuscript and all authors agree to be held accountable for the content therein and approve the final version of the manuscript

Competing interests. We declare we have no competing interests.

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