CORA Cork Open Research Archive
Cartlann Taighde Oscailte Chorcaí

Title	Shyer and larger bird species show more reduced fear of humans when living in urban environments
Authors	delBarco-Trillo, Javier
Publication date	2018-04-01
Original Citation	delBarco-Trillo, J (2018) 'Shyer and larger bird species show more reduced fear of humans when living in urban environments'. Biology Letters, 14 (4). DOI: 10.1098/rsbl.2017.0730
Type of publication	Article (peer-reviewed)
Link to publisher's version	http://rsbl.royalsocietypublishing.org/content/14/4/20170730 - 10.1098/rsbl.2017.0730https://doi.org/10.6084/m9.figshare.c.4052384.v1
Rights	© 2018 The Author(s). Published by the Royal Society. All rights reserved.
Download date	2026-11-15 17:41:58
Item downloaded from	https://hdl.handle.net/10468/6375

UCC
University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

Shyer and larger bird species show more reduced fear of humans when living in urban environments

Javier delBarco-Trillo[1,*]

[1] *School of Biological, Earth and Environmental Sciences; University College Cork; Cork, Ireland*

* Corresponding author: Javier delBarco-Trillo; delbarcotrillo@gmail.com; ORCID ID 0000-0002-9948-6674

ABSTRACT

As the natural habitats of many species are degraded or disappear, there is scope for these species to be established in urban habitats. To ease the establishment and maintenance of urban populations of more species we need to better understand what degree of phenotypical change to expect as different species transition into urban environments. During the first stages of urban colonisation, behavioural changes such as an increase in boldness are particularly important. A consistent response in urban populations is to decrease the distance at which individuals flee from an approaching human (flight initiation distance, or FID). Performing a Phylogenetic Generalised Least Squares (PGLS) analysis on 130 avian species, I found that the largest changes in FID between rural and urban populations occur in species that are larger-bodied and naturally shy (higher rural FID), two phenotypic traits that are not normally associated with urban colonisers. More unlikely species may thus be able to colonise urban environments, especially if we design cities in ways that promote such urban colonisations.

Keywords: birds; body mass; FID; flight initiation distance; urban ecology; urbanisation

INTRODUCTION

The colonisation of urban environments by animals requires behavioural adjustments that maximise their fitness in these novel environments [1]. In particular, urban animals may benefit by decreasing their fear towards humans and other anthropogenic stimuli [2], as repeatedly fleeing from approaching humans and vehicles is energetically costly and prevents animals from optimal foraging and other relevant activities [3]. A well-supported measure of increased boldness in urban animals is shorter flight initiation distances (FID, methodologically defined as the distance at which an individual flees when approached by a human) [4-7]. There is inter-individual variability in FID within a species, although individuals within a population typically display consistent FIDs over time [8-10]. Importantly, in both intraspecific and interspecific studies, urban populations consistently have shorter FIDs than their rural counterparts [5-8, 11-13].

The differences in FID observed between urban and rural populations may arise from behavioural plasticity or adaptation after a species colonises an urban environment [14-16]. Species that are naturally bolder (i.e. with relatively small rural FID) may be more likely to initiate such urban colonisations [17; however, see 7]. Assuming similar selective pressures in the same urban environment across species, these naturally bolder species may not need to decrease their FIDs to the same degree as species that colonise the same urban environments but are naturally shyer (i.e. those with a relatively larger rural FID) [18]. That is, naturally shyer species may undergo greater behavioural changes when transitioning from rural to urban environments. Alternatively, urban colonisation may be restricted to only the boldest individuals, resulting in an immediate differentiation in FID

between urban and rural populations [7]. Under this scenario, the initial change in FID between rural and urban populations may be similar across species independently of whether these species are naturally bold or shy. However, after urban establishment, those species that are naturally shy may need to further decrease their FIDs via phenotypical plasticity or adaptation in order to succeed under urban conditions. This will also result in naturally shyer species being the ones changing the most when completing their transition from rural to urban environments.

I thus hypothesised that naturally shy species (high rural FID) will experience a higher degree of behavioural change in order to successfully colonise urban environments. Here, I addressed this hypothesis by quantifying the change in FID (ΔFID) between rural and urban populations in 130 avian species and determining how this change is associated with natural shyness. I also considered the effect of body mass, as FID is consistently higher in larger species [4, 5, 11, 19]. A positive association between ΔFID and rural FID would indicate that naturally shy species need to change the most when colonising urban environments, thus supporting the above hypothesis. No association would indicate that all species change similarly in response to urbanisation, regardless of their rural FID. Finally, a negative association would indicate that naturally shy species remain relatively shy under urban conditions, possibly by only invading urban areas with low levels of disturbance where they can maintain long FIDs that are still compatible with normal levels of activity.

METHODS

I made bibliographical searches in Web of Science up to 6 July 2017, using the term "urban*" combined with one of the following terms: "flight initiation distance", "flight distance", "escape distance", "flushing distance", "flush distance", or "disturbance distance". I compiled information from avian species on FID when this was available for both urban and rural populations. I only considered species in which both FID values were calculated using measurements from more than one individual. When values for the same species were available from more than one source, I used the study with larger sample sizes. I also obtained body mass for each species. The compiled dataset (see supplementary material) consisted of information from 130 species.

I conducted a phylogenetic generalised least-squares (PGLS) analysis in R (v.3.4.1) using the caper v0.5.2 package [20]. A PGLS includes the phylogenetic structure of the species under consideration as a covariance matrix within a linear model. An estimated phylogenetic scaling parameter lambda (λ) takes values from 0 to 1, with values close to 0 indicating that the relationship between the variables is largely independent of phylogeny, and values close to 1 indicating a strong association with phylogeny. For the phylogenetic reconstruction, I combined information from several sources, using Mesquite v.3.2 (see supplementary material for such sources and the resulting phylogeny). All variables were $\log_{10}$ transformed prior to analysis. A PGLS model included the relative change in FID as the response variable (ΔFID / rural FID), and body mass and rural FID (or natural level of shyness) as factors. An additional PGLS included the absolute ΔFID between rural and urban populations as the response variable.

RESULTS

As expected, across species rural FID was higher (mean ± SD: 22.18 ± 22.04 m; range: 4.93 – 180 m) than urban FID (mean ± SD: 8.60 ± 5.29 m; range: 2.31 – 33.50 m; paired t-test: $t_{129} = -15.49$, $p < 0.0001$). Accordingly, rural FID was higher than urban FID in most species, although there were a few exceptions (absolute ΔFID mean ± SD: 13.63 ± 20.29 m; range: -11.78 – 167.58 m). Implementing a sequential sums of squares PGLS ($\lambda = 0.17$), I found a positive association between body mass and relative ΔFID between rural and urban populations ($F_{1,127} = 8.18$, $p = 0.005$). After removing the effect of body mass, a positive association was also apparent between natural shyness and relative ΔFID between rural and urban populations ($F_{1,127} = 7.37$, $p = 0.008$; Fig. 1). The positive association between natural shyness and ΔFID was also strong even without including body mass in the model ($\lambda = 0.17$; $F_{1,128} = 15.60$, $p = 0.0001$). Natural shyness was also positively associated with an absolute change in FID ($\lambda = 0.32$; $F_{1,127} = 41.05$, $p < 0.0001$; body mass was also included in this model: $F_{1,127} = 32.24$, $p < 0.0001$).

Results were qualitatively similar when considering only those species for which sample sizes for both urban and rural FIDs were ≥ 5 (N = 103; $\lambda = 0.50$; positive association between natural shyness and relative ΔFID between rural and urban populations: $F_{1,100} = 6.56$, $p = 0.01$; body mass also had a significant effect on relative ΔFID: $F_{1,100} = 5.47$, $p = 0.02$).

DISCUSSION

I found that species that are naturally shyer are the ones that experience a higher change in FID when colonising urban environments. The mechanism underlying this association remains unclear. If changes in FID occur in response to the new conditions experienced by individuals in urban environments, such changes have

130 to be driven by local adaptation or phenotypic plasticity [15], and any of these
131 processes would be more intensely acting on individuals from naturally shyer
132 species. Alternatively, if bolder individuals in the rural populations are the ones
133 driving urban colonisations [7, 13], the results of this study suggest that those
134 species that are in average shyer (i.e. with higher average rural FID) are also the
135 ones with higher variation in FID [21]. If this is true, further investigation is
136 required to elucidate how this large variation is maintained in species with high
137 average rural FID, e.g. different behavioural strategies may exploit different social
138 and/or environmental conditions. All the above processes are obviously non-
139 exclusive, and there may be species in which the boldest individuals within a
140 species are the ones colonising urban environments, then FID within the resulting
141 urban population becomes shorter through behavioural plasticity, and it may be
142 even further decreased through adaptation depending on selective pressures.
143 I also found that larger species experience a higher change in FID when making the
144 transition from rural to urban environments, echoing results found in a recent
145 meta-analysis [21]. Large species in urban environments may suffer less predation
146 than small-sized species, and this reduced predation risk may lead to an increased
147 tolerance of humans [21, 22].
148 There are other factors here not considered that can also affect the difference in
149 FID between urban and rural populations within a species. For example, the
150 difference in FID between rural and urban populations may increase with the time
151 since urbanization [5], as the more generations are raised under urban conditions
152 the more opportunities for adaptations to urbanisation to occur, including
153 increased boldness and thus reduced FID; however, see [23].
154 The fact that the higher change in FID between rural and urban populations

occurred in species that are naturally shy and in larger species, two features that are not typical in successful urban colonisers, suggests that many more species than those currently described may have the potential to establish and maintain viable populations in urban environments, even those species that do not meet the characteristics normally associated with urban species. There is great scope to design urban environments that can promote the establishment of more species and their adaptation to these novel environments, for example by creating spaces where the close proximity to people and vehicle traffic is avoided [24, 25].

COMPETING INTERESTS

I have no competing interests.

DATA ACCESSIBILITY

All data used in the analyses are included as supplementary material.

FUNDING

I have no funding sources to report.

ACKNOWLEDGEMENTS

I thank James Savage, Kathryn Simmons, and two anonymous reviewers for their helpful comments on the manuscript.

REFERENCES

[1] Sol, D., Lapiedra, O. & González-Lagos, C. 2013 Behavioural adjustments for a life in the city. *Anim. Behav.* **85**, 1101-1112. (doi:10.1016/j.anbehav.2013.01.023).

180 [2] Tryjanowski, P., Møller, A.P., Morelli, F., Biaduń, W., Brauze, T., Ciach, M.,
181 Czechowski, P., Czyż, S., Dulisz, B., Goławski, A., et al. 2016 Urbanization affects
182 neophilia and risk-taking at bird-feeders. *Scientific Reports* **6**, 28575.
183 (doi:10.1038/srep28575).
184 [3] Tatner, P. & Bryant, D.M. 1986 Flight cost of a small passerine measured using
185 doubly labeled water: implications for energetics studies. *Auk* **103**, 169-180.
186 [4] Weston, M.A., McLeod, E.M., Blumstein, D.T. & Guay, P.-J. 2012 A review of
187 flight-initiation distances and their application to managing disturbance to
188 Australian birds. *Emu* **112**, 269-286. (doi:10.1071/MU12026).
189 [5] Møller, A.P. 2008 Flight distance of urban birds, predation, and selection for
190 urban life. *Behav. Ecol. Sociobiol.* **63**, 63-75. (doi:10.1007/s00265-008-0636-y).
191 [6] Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J. & Regis, Y. 2009
192 Antipredator behavior in blackbirds: habituation complements risk allocation.
193 *Behav. Ecol.* **20**, 371-377. (doi:10.1093/beheco/arn151).
194 [7] Carrete, M. & Tella, J.L. 2011 Inter-individual variability in fear of humans and
195 relative brain size of the species are related to contemporary urban invasion in
196 birds. *PLoS One* **6**, e18859. (doi:10.1371/journal.pone.0018859).
197 [8] Møller, A.P. 2010 Interspecific variation in fear responses predicts urbanization
198 in birds. *Behav. Ecol.* **21**, 365-371. (doi:10.1093/beheco/arp199).
199 [9] Evans, J., Boudreau, K. & Hyman, J. 2010 Behavioural syndromes in urban and
200 rural populations of song sparrows. *Ethology* **116**, 588-595. (doi:10.1111/j.1439-
201 0310.2010.01771.x).
202 [10] Carrete, M. & Tella, J.L. 2010 Individual consistency in flight initiation
203 distances in burrowing owls: a new hypothesis on disturbance-induced habitat
204 selection. *Biol. Lett.* **6**, 167-170. (doi:10.1098/rsbl.2009.0739).

205 [11] Cooke, A.S. 1980 Observations on how close certain passerine species will
206 tolerate an approaching human in rural and suburban areas. *Biological*
207 *Conservation* **18**, 85-88. (doi:10.1016/0006-3207(80)90072-5).
208 [12] Díaz, M., Møller, A.P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J.D., Jokimäki,
209 J., Markó, G. & Tryjanowski, P. 2013 The geography of fear: a latitudinal gradient in
210 anti-predator escape distances of birds across Europe. *PLoS One* **8**, e64634.
211 (doi:10.1371/journal.pone.0064634).
212 [13] Atwell, J.W., Cardoso, G.C., Whittaker, D.J., Campbell-Nelson, S., Robertson,
213 K.W. & Ketterson, E.D. 2012 Boldness behavior and stress physiology in a novel
214 urban environment suggest rapid correlated evolutionary adaptation. *Behav. Ecol.*
215 **23**, 960-969. (doi:10.1093/beheco/ars059).
216 [14] Carrete, M., Martínez-Padilla, J., Rodríguez-Martínez, S., Rebolo-Ifrán, N.,
217 Palma, A. & Tella, J.L. 2016 Heritability of fear of humans in urban and rural
218 populations of a bird species. *Scientific Reports* **6**. (doi:10.1038/srep31060).
219 [15] Vincze, E., Papp, S., Preiszner, B., Seress, G., Bókony, V. & Liker, A. 2016
220 Habituation to human disturbance is faster in urban than rural house sparrows.
221 *Behav. Ecol.* **27**, 1304-1313. (doi:10.1093/beheco/arw047).
222 [16] Lowry, H., Lill, A. & Wong, B.B.M. 2013 Behavioural responses of wildlife to
223 urban environments. *Biol. Rev.* **88**, 537-549. (doi:10.1111/brv.12012).
224 [17] Møller, A.P. 2009 Successful city dwellers: a comparative study of the
225 ecological characteristics of urban birds in the Western Palearctic. *Oecologia* **159**,
226 849-858. (doi:10.1007/s00442-008-1259-8).
227 [18] Ducatez, S., Audet, J.N., Rodriguez, J.R., Kayello, L. & Lefebvre, L. 2017
228 Innovativeness and the effects of urbanization on risk-taking behaviors in wild
229 Barbados birds. *Anim. Cogn.* **20**, 33-42. (doi:10.1007/s10071-016-1007-0).

[19] Blumstein, D.T. 2006 Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim. Behav.* **71**, 389-399. (doi:10.1016/j.anbehav.2005.05.010).

[20] Orme, D. 2013 *The caper package: comparative analysis of phylogenetics and evolution in R. R package version 0.5.2.* https://cran.r-project.org/web/packages/caper/vignettes/caper.pdf.

[21] Samia, D.S.M., Nakagawa, S., Nomura, F., Rangel, T.F. & Blumstein, D.T. 2015 Increased tolerance to humans among disturbed wildlife. *Nature Communications* **6**, 8877. (doi:10.1038/ncomms9877).

[22] Carrete, M. & Tella, J.L. 2017 Behavioral correlations associated with fear of humans differ between rural and urban burrowing owls. *Front. Ecol. Evol*. **5**, 54. (doi:10.3389/fevo.2017.00054).

[23] Gendall, J., Lill, A. & Beckman, J. 2015 Tolerance of disturbance by humans in long-time resident and recent colonist urban doves. *Avian Res.* **6**, 7. (doi:10.1186/s40657-015-0018-x).

[24] McDonnell, M.J. & Hahs, A.K. 2015 Adaptation and adaptedness of organisms to urban environments. *Annu. Rev. Ecol. Evol. Syst.* **46**, 261-280. (doi:10.1146/annurev-ecolsys-112414-054258).

[25] Johnson, M.T.J. & Munshi-South, J. 2017 Evolution of life in urban environments. *Science* **358**. (doi:10.1126/science.aam8327).

FIGURE CAPTIONS

Figure 1. The relative reduction of FID in urban populations is higher in those species that are naturally shyer after controlling for the effects of body mass and phylogenetic relationships. The log-transformed values for rural FID are shown in

255 the x axis, whereas the log-transformed relative change in FID (i.e. ΔFID divided by
256 rural FID) are shown in the y axis. Values of shyness in rural populations are the
257 residuals from a PGLS in which rural FID was the dependent variable and body
258 mass was the independent variable ($F_{1,128} = 111$, $p < 0.0001$). Values of relative
259 reduction of FID in urban environments are the residuals from a different PGLS in
260 which relative ΔFID ((rural FID – urban FID) / rural FID) was the dependent
261 variable and body mass was the independent variable ($F_{1,128} = 7.82$, $p = 0.006$).
262 That is, the shown association accounts for both body mass and the effect of
263 phylogeny. The same value of lambda ($\lambda = 0.17$) was used in both PGLS (a similar
264 figure was obtained using maximum likelihood to calculate λ for each PGLS). Such
265 an approach was used only to create this plot and not for the formal analysis.