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Authors	delBarco-Trillo, Javier
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1 **Shyer and larger bird species show more reduced fear of humans when living**  
2 **in urban environments**

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4 Javier delBarco-Trillo<sup>1,\*</sup>

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6 <sup>1</sup> *School of Biological, Earth and Environmental Sciences; University College Cork;*  
7 *Cork, Ireland*

8

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

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12

13 **ABSTRACT**

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

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

30

## 31 INTRODUCTION

32 The colonisation of urban environments by animals requires behavioural  
33 adjustments that maximise their fitness in these novel environments [1]. In  
34 particular, urban animals may benefit by decreasing their fear towards humans  
35 and other anthropogenic stimuli [2], as repeatedly fleeing from approaching  
36 humans and vehicles is energetically costly and prevents animals from optimal  
37 foraging and other relevant activities [3]. A well-supported measure of increased  
38 boldness in urban animals is shorter flight initiation distances (FID,  
39 methodologically defined as the distance at which an individual flees when  
40 approached by a human) [4-7]. There is inter-individual variability in FID within a  
41 species, although individuals within a population typically display consistent FIDs  
42 over time [8-10]. Importantly, in both intraspecific and interspecific studies, urban  
43 populations consistently have shorter FIDs than their rural counterparts [5-8, 11-  
44 13].

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

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

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

78

79 **METHODS**

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

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

103

## 104 **RESULTS**

105 As expected, across species rural FID was higher (mean  $\pm$  SD: 22.18  $\pm$  22.04 m;  
106 range: 4.93 – 180 m) than urban FID (mean  $\pm$  SD: 8.60  $\pm$  5.29 m; range: 2.31 –  
107 33.50 m; paired t-test:  $t_{129} = -15.49$ ,  $p < 0.0001$ ). Accordingly, rural FID was higher  
108 than urban FID in most species, although there were a few exceptions (absolute  
109  $\Delta$ FID mean  $\pm$  SD: 13.63  $\pm$  20.29 m; range: -11.78 – 167.58 m). Implementing a  
110 sequential sums of squares PGLS ( $\lambda = 0.17$ ), I found a positive association between  
111 body mass and relative  $\Delta$ FID between rural and urban populations ( $F_{1,127} = 8.18$ ,  $p$   
112 = 0.005). After removing the effect of body mass, a positive association was also  
113 apparent between natural shyness and relative  $\Delta$ FID between rural and urban  
114 populations ( $F_{1,127} = 7.37$ ,  $p = 0.008$ ; Fig. 1). The positive association between  
115 natural shyness and  $\Delta$ FID was also strong even without including body mass in the  
116 model ( $\lambda = 0.17$ ;  $F_{1,128} = 15.60$ ,  $p = 0.0001$ ). Natural shyness was also positively  
117 associated with an absolute change in FID ( $\lambda = 0.32$ ;  $F_{1,127} = 41.05$ ,  $p < 0.0001$ ;  
118 body mass was also included in this model:  $F_{1,127} = 32.24$ ,  $p < 0.0001$ ).  
119 Results were qualitatively similar when considering only those species for which  
120 sample sizes for both urban and rural FIDs were  $\geq 5$  ( $N = 103$ ;  $\lambda = 0.50$ ; positive  
121 association between natural shyness and relative  $\Delta$ FID between rural and urban  
122 populations:  $F_{1,100} = 6.56$ ,  $p = 0.01$ ; body mass also had a significant effect on  
123 relative  $\Delta$ FID:  $F_{1,100} = 5.47$ ,  $p = 0.02$ ).

124

## 125 **DISCUSSION**

126 I found that species that are naturally shyer are the ones that experience a higher  
127 change in FID when colonising urban environments. The mechanism underlying  
128 this association remains unclear. If changes in FID occur in response to the new  
129 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 shy  
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 shy (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



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

163

#### 164 **COMPETING INTERESTS**

165 I have no competing interests.

166

#### 167 **DATA ACCESSIBILITY**

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

169

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171 I have no funding sources to report.

172

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250

## 251 **FIGURE CAPTIONS**

252 Figure 1. The relative reduction of FID in urban populations is higher in those  
253 species that are naturally shyer after controlling for the effects of body mass and  
254 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.  $\Delta$ FID 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  $\Delta$ FID ( $(\text{rural FID} - \text{urban FID}) / \text{rural FID}$ ) 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  $\lambda$  for each PGLS). Such  
265 an approach was used only to create this plot and not for the formal analysis.