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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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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 (Δ 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 Δ 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 (λ) 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 ΔFID
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 Δ 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 Δ 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 Δ 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 Δ 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 ≥ 5 ($N = 103$; $\lambda = 0.50$; positive
121 association between natural shyness and relative Δ 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 Δ FID: $F_{1,100} = 5.47$, $p = 0.02$).

124

125 **DISCUSSION**

126 I found that species that are naturally shy 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.

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176

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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. 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 ($(\text{rural FID} - \text{urban FID}) / \text{rural FID}$) 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 λ for each PGLS). Such
265 an approach was used only to create this plot and not for the formal analysis.