

# 1 Herring gull aversion to gaze in urban and rural human settlements

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10

## 11 **Abstract**

12 With an increasing human population and expansion of urban settlements, wild animals are  
13 often exposed to humans. As humans may be a threat, a neutral presence, or a source of food,  
14 animals will benefit from continuously assessing the potential risk posed by humans in order to  
15 respond appropriately. Herring gulls (*Larus argentatus*) are increasingly breeding and foraging  
16 in urban areas, and thus have many opportunities to interact with humans. We recently found  
17 that herring gulls take longer to approach food when being watched by a human. However, it  
18 is not known whether aversion to human gaze arises from experience with humans, and  
19 whether individual differences in responsiveness are a result of differential exposure. Here, we  
20 test whether herring gulls' responses to human gaze differ according to their age class and  
21 urbanisation of their habitat. We measured the gulls' flight initiation distance when an  
22 experimenter approached with either a direct or averted gaze. Neither gull age class nor  
23 urbanisation significantly influenced the effect of human gaze on flight initiation distance.  
24 However, as recently fledged juveniles responded strongly to the experimenter's gaze,  
25 aversion to human gaze may not require extensive exposure to humans to develop. Gulls in  
26 urban areas could be approached more closely than those in rural areas, consistent with

27 findings in other species. These results indicate that gaze aversion is present early in  
28 development and that exposure to humans may influence gulls' responses to perceived risk  
29 from humans. Investigating the processes generating individual differences in responses to  
30 humans will provide further insights into human-wildlife interactions and the effects of  
31 urbanisation.

32

33 **Keywords:**

34 Herring gull; flight initiation distance; gaze aversion; risk perception; urbanisation; urban-rural  
35 gradient

36 Accurately perceiving, assessing and responding to risk are important for avoiding predation  
37 and agonistic interactions with competitors. Animals use a range of cues, such as predator  
38 approach speed (Stankowich & Blumstein, 2005) and odour (Saxon-Mills, Moseby, Blumstein,  
39 & Letnic, 2018; Wisenden, 2000), to inform their responses to potential threats. As the human  
40 population continues to expand, wild animals are increasingly coming into contact with  
41 humans, which subsequently affects their responses to the risk posed by these encounters  
42 (e.g. Geffroy et al. 2015; Williams et al. 2020). Humans can act both as predators and  
43 competitors for resources, killing both prey species and the predators of these prey (e.g.  
44 Gasaway et al. 1992); therefore it is beneficial for wild animals to be wary of humans.  
45 However, although humans as a species often present a significant threat to wild animals, in  
46 many cases, interactions with humans can be harmless or even beneficial. For example, wild  
47 animals can habituate to humans when human activity is frequent and inconsequential (e.g.  
48 Magellanic penguins *Spheniscus magellanicus* in a nature reserve (Walker, Dee Boersma, &  
49 Wingfield, 2006)), or learn that humans provide food (e.g. wild boar *Sus scrofa* in a nature park  
50 (Cahill, Llimona, Cabañeros, & Calomardo, 2012)). In areas where humans are regularly  
51 encountered, wild animals could be expected to benefit from using cues that enable them to  
52 accurately assess the potential risk posed by individual humans.

53 Gaze direction may be one such cue used to assess risk. A fearful response to gaze, termed  
54 “gaze aversion”, is widespread across vertebrate taxa and appears to function primarily as a  
55 means to avoid predation and competition (Davidson & Clayton, 2016). A predator that fixes  
56 its gaze on a subject is likely to pose more of a threat than a predator that is looking elsewhere  
57 (Davidson, Butler, Fernández-Juricic, Thornton, & Clayton, 2014). It would therefore benefit  
58 the subject to respond quickly to a predator gazing at it, whereas responding to all predators in  
59 the environment, regardless of whether they have spotted the subject, would incur an  
60 unnecessary energetic cost (Ydenberg & Dill, 1986).

61 Relatively little is known about the development of gaze aversion. There is uncertainty about  
62 the degree to which gaze aversion is innate (i.e. present at birth or hatching) or dependent on  
63 experience. Studies of young, predator-naïve fishes (jewel fish *Hemichromis bimaculatus* (Coss,  
64 1978)) and paradise fish *Macropodus opercularis* (Altbäcker & Csányi, 1990; Miklósi, Berzsenyi,  
65 Pongrácz, & Csányi, 1995)) and chickens *Gallus gallus* (Jones, 1980; Scaife, 1976) indicate that  
66 aversive responses to two horizontally positioned eye-like stimuli are elicited early in  
67 development. However, experiments investigating possible effects of experience on the  
68 presence of gaze aversion have had conflicting results. Jewel fish that were deprived of seeing  
69 eyes or eye-like stimuli throughout early development showed a greater aversive response to  
70 two horizontal eye spots than did fish that were raised in the presence of conspecifics (Coss,  
71 1979). This suggests that prior exposure to such stimuli is not required to elicit a fearful  
72 response, and that experience with conspecifics may reduce aversive behaviour. In contrast,  
73 bobwhite quails *Colinus virginianus* raised without exposure to human faces were less likely to  
74 exhibit aversive responses to human gaze than were those previously exposed to them (Jaime,  
75 Lopez, & Lickliter, 2009). These studies suggest that the development of gaze aversion may be  
76 species- and context-specific, and potentially dependent on experience.

77 Experiments testing responses to gaze have also been conducted on wild animals, and these  
78 have largely focused on how animals respond to human gaze. Unlike the simple, static eye-like  
79 stimuli often used in laboratory studies, humans can change eye gaze direction independently  
80 of head direction. This raises the question of whether wild animals attend to the direction of  
81 the eyes themselves rather than the direction of the head. Hampton (1994) found that captive,  
82 wild-caught house sparrows *Passer domesticus* took more escape flights in response to a  
83 human face oriented towards them versus away regardless of eye gaze direction, but the  
84 presence of eyes was also important: a model face with two “eyes” was more aversive than a  
85 model face with only one “eye”. Other studies of gaze aversion in free-living wild animals have

86 often tested responses to head direction rather than eye gaze direction (e.g. Watve et al. 2002;  
87 Bateman and Fleming 2011; Sreekar and Quader 2013; Davidson et al. 2015; Goumas et al.  
88 2019). However, a few studies controlled for head direction and showed that passerines such  
89 as American robins *Turdus migratorius* (Eason, Sherman, Rankin, & Coleman, 2006), European  
90 starlings *Sturnus vulgaris* (Carter, Lyons, Cole, & Goldsmith, 2008), American crows *Corvus*  
91 *brachyrhynchos* (Clucas, Marzluff, Mackovjak, & Palmquist, 2013) and North Island robins  
92 *Petroica longipes* (Garland, Low, Armstrong, & Burns, 2014) exhibit aversive responses  
93 specifically to human eye gaze direction.

94 Some studies have used a flight initiation distance (FID) experiment to test whether wild  
95 animals respond differently to direct versus averted gaze. In FID experiments, a human  
96 experimenter approaches a wild animal and measures how closely it can be approached  
97 before it flees (see e.g. Stankowich and Blumstein 2005). A short FID thus indicates that the  
98 animal perceives the human to present a lower risk than does an animal with a longer FID.  
99 Studies on American robins (Eason et al., 2006), hadeda ibis *Bostrychia hagedash* (Bateman &  
100 Fleming, 2011), American crows (Clucas et al., 2013) and Indian rock lizards *Psammophilus*  
101 *dorsalis* (Sreekar & Quader, 2013) found that animals could be approached more closely when  
102 the experimenter was looking away rather than directly at the animal.

103 FID has also been used to test for differences in escape behaviour by animals living in urban  
104 and rural areas. Animals in rural areas flee sooner than conspecifics in urban areas in a variety  
105 of taxa (e.g. passerines, Cooke 1980; western fence lizards *Sceloporus occidentalis*, Grolle et al.  
106 2014; Eurasian red squirrels *Sciurus vulgaris*, Uchida et al. 2016), suggesting that animals in  
107 urban areas may become habituated to the higher density of humans in these areas. Aversion  
108 to human gaze may similarly differ between urban and rural habitats if experience with  
109 humans is important in the development of gaze sensitivity. With an increased exposure to

110 humans, it is plausible that animals in urban areas may learn about the consequences of direct  
111 gaze, whether through habituation if direct gaze is inconsequential, or associative learning if  
112 direct gaze leads to negative outcomes such as being displaced, and modify their responses  
113 accordingly.

114 We recently found that herring gulls *Larus argentatus* exhibit aversion to human gaze in the  
115 context of approaching anthropogenic food (Goumas et al., 2019). However, the  
116 experimenter's head and eyes were always oriented in the same direction, so it was unclear  
117 whether gulls respond to human eye gaze direction alone. Furthermore, because most herring  
118 gulls were too wary to approach humans, we did not test for differences in gaze aversion  
119 according to the age or location of the gulls, two factors that may explain some of the large  
120 inter-individual variation in observed approach time. Herring gulls are common in built-up  
121 areas, where many breed and forage (Rock, 2005). Gulls in these areas therefore have  
122 numerous opportunities to interact with and learn about humans over the course of their lives.  
123 Herring gulls are semi-precocial, hatching with their eyes open, thus sensitivity to gaze upon  
124 hatching is possible and may be beneficial. Juveniles usually fledge from their rooftop nest  
125 sites in July and August (Huig, Buijs, & Kleyheeg, 2016), at which point they are likely to  
126 encounter humans for the first time.

127 In this experiment, we tested whether herring gulls respond to human eye gaze direction  
128 independently of human head direction in the context of an experimenter directly approaching  
129 the gull. As there is evidence that gaze aversion could be innate but may be affected by  
130 experience in a range of taxa (Davidson & Clayton, 2016), we tested for an effect of age class  
131 (i.e. recently fledged juvenile vs. adult) and location (urban vs. rural) on sensitivity to gaze. We  
132 predicted that, if aversion to gaze is innate or mediated early in development, juveniles would  
133 flee sooner when exposed to direct versus averted gaze. If learning from interactions with

134 humans shapes responses to human gaze, adults may exhibit either more or less pronounced  
135 differences in FID between the two gaze conditions depending on what is being learned. For  
136 example, a smaller difference in FID between gaze conditions in adults compared to juveniles  
137 may suggest that gulls develop gaze aversion early in life but learn not to fear human gaze  
138 through repeated exposure. Conversely, a bigger difference in FID between gaze conditions in  
139 adults compared to juveniles may suggest that gulls learn to avoid human gaze. Likewise, adult  
140 gulls in rural areas, where there are fewer humans, may exhibit similar patterns in FID as  
141 juvenile gulls, as their lower exposure to humans would result in fewer learning opportunities.  
142 To complement our measurements of FID, we also recorded the level of each gull's response  
143 to the approaching experimenter. We predicted that gulls would be more likely to take flight  
144 than to walk or run when the experimenter's gaze was directed at them, and in rural  
145 compared to urban settlements.

146 **METHODS**

147 We measured the flight initiation distances (FID) of herring gulls in West Cornwall, United  
148 Kingdom (approx. 50N, 5W) between 27<sup>th</sup> July and 30<sup>th</sup> August 2019, when juvenile gulls had  
149 recently fledged. As herring gulls have discrete territories, we minimised the chance of  
150 pseudoreplication by avoiding repeated experimental trials in the same locations, and by  
151 visually tracking the movements of gulls after testing. The same experimenter (“E”)   
152 approached the gulls in all trials, wearing the same or similar dark-coloured clothing. An  
153 observer (“O”) used a Panasonic HC-V770 camcorder to film the trials from a position  
154 approximately 5 m to the left or right of the experimenter and > 20 m from the gull.

155

156 *Ethical note*

157 This work was approved by the University of Exeter Ethics Committee (ref.: eCORN002171) and  
158 adhered to the Association for the Study of Animal Behaviour Guidelines for the Use of  
159 Animals in Research. No animals were captured as part of this study.

160

161 *Categorising herring gull test subjects by age class*

162 We targeted adults (individuals aged 4 years or older, evidenced by fully white and grey  
163 plumage) and juveniles (individuals that hatched in spring of the same year (2019), which have  
164 completely brown plumage) that were in stationary positions no more than ca. 200 cm above  
165 ground level.

166

167 *Categorising test locations by settlement type*

168 We categorised test locations into “urban” and “rural” by using the classification provided by  
169 the Office of National Statistics, whereby settlements with > 10,000 residents are categorised  
170 as “urban” and those with < 10,000 residents are “rural” (Bibby, 2013). We used data from the  
171 last census, conducted in 2011 (Nomis 2011), to gain precise localised population size data for  
172 each settlement where we conducted experimental trials. As the population of England is  
173 predicted to have increased by approximately 6% since the census (Office for National  
174 Statistics 2019), we increased these population estimates by this amount. This modification  
175 only affected St Ives, which had a population size of 9,966 in 2011. In two cases (Gwithian and  
176 Praa Sands), settlements were too small to have localised population data and were  
177 designated as “rural”.

178

#### 179 *Testing for an effect of gaze direction*

180 In “Looking At” trials, E oriented his head and eyes towards the gull. In the “Looking Away”  
181 trials, E oriented his head towards the gull but directed his line of gaze towards the ground in  
182 front of him. E randomly assigned the gaze direction of each trial. O was blind to the gaze  
183 direction of the trials.

184

#### 185 *Measuring flight initiation distance*

186 Upon locating a gull, E used an infrared Leica Rangemaster CRF 2400-R laser rangefinder to  
187 estimate a distance of approximately 20 m from the gull, which was the chosen starting point  
188 for the trials. E marked this position on the ground with chalk. O framed the gull within the  
189 viewfinder of the camcorder and cued the experimenter to start walking. E walked at a  
190 constant speed of 0.8 m/s (practised and measured before commencing the trials) directly  
191 towards the gull. O watched for movement of the gull away from its original position (i.e. the

192 “flight initiation”), at which point O called to E to stop walking. E then marked his current  
193 position on the ground.

194 Immediately following the trial, O marked the original position of the gull with chalk. E and O  
195 then used a measuring tape to measure the distance between the gull’s original position and  
196 the position of E when the gull moved away (i.e. the subject’s flight initiation distance). As the  
197 laser rangefinder only provided an approximation of the starting distance, we also measured  
198 the distance between the gull’s original position and E’s starting position to control for  
199 differences in FID being due to a longer experimenter approach (Blumstein, 2003). All  
200 distances were measured to the nearest centimetre.

201

#### 202 *Measuring the level of the gulls’ responses*

203 As FID does not capture the urgency of a subject’s movement away from the experimenter, O  
204 categorised the level of the gulls’ responses to being approached into two categories: “low”,  
205 where the gull walked or ran from the experimenter but did not take flight, and “high”, where  
206 the gull flew away from the experimenter.

207

#### 208 *Additional variables*

209 We measured additional variables that may have affected FID and the level of response. As a  
210 measure of human disturbance at the time of the trial, we counted the number of other  
211 humans present within an estimated 20 m radius of the focal gull at the end of the trial and  
212 added the number of passers-by in the video footage. We also recorded the number of other  
213 gulls within the 20 m radius. We measured the height of the gull from the ground at its starting  
214 position, as some gulls were at ground level and some on elevated structures such as walls and

215 posts, which may influence their method of escape.

216

### 217 *Statistical analyses*

218 We used a linear model in R version 3.5.3 (R Core Team, 2019) to test whether gull age class,  
219 human gaze direction and settlement type (urban/rural) had an effect on flight initiation  
220 distance (FID). We included an interaction term between gaze direction and age, and gaze  
221 direction and settlement type, to test whether urbanisation and age affected sensitivity to  
222 human gaze. We also included the number of humans, number of other gulls, and the  
223 experimenter's precise starting distance as additional fixed effects. As the number of humans  
224 and the number of other gulls were both highly heteroscedastic with many zero counts, we  
225 categorised these variables as 0 (absent) or 1 (present). We report the results of the full model  
226 after removing any non-significant interactions.

227 We then used a binomial logistic regression to test whether the gulls' level of response (low:  
228 running/walking, high: flying away) to the experimenter's approach was affected by gaze  
229 direction and settlement type, as well as any additional predictors found to significantly affect  
230 flight initiation distance in our linear model described above. We also included the height of  
231 the gull at its starting position, as gulls on elevated structures (categorised as "1") may have  
232 had less space than those on the ground (categorised as "0") to walk away from the  
233 experimenter, and might therefore have been more likely to take flight. We report the odds  
234 ratios (OR) of each variable on the outcome. An OR of 1 indicates that a variable has no effect  
235 on the outcome, while an OR > 1 indicates a higher odds of an outcome occurring and an OR <  
236 1 indicates a lower odds of an outcome occurring.

237

## 238 RESULTS

239 We recorded flight initiation distances for 155 herring gulls: 50 adults and 45 juveniles in urban  
240 settlements, and 34 adults and 26 juveniles in rural settlements.

241 Human gaze direction had a significant effect on herring gull FID (Figure 1), as did settlement  
242 type and experimenter starting distance (Table 1). Gulls could be approached more closely  
243 before fleeing (i.e. had shorter FID) when the experimenter was looking away from them  
244 versus at them (estimated difference in FID ( $\Delta$ FID):  $-195.94 \pm 83.70$  cm,  $t = -2.34$ ,  $N_{at} = 85$ ,  $N_{away}$   
245  $= 70$ ,  $P = 0.021$ ; Table 1). Gulls in urban settlements could be approached more closely than  
246 gulls in rural settlements ( $\Delta$ FID:  $-239.94 \pm 88.52$  cm,  $t = -2.71$ ,  $N_{rural} = 60$ ,  $N_{urban} = 95$ ,  $P = 0.008$ ).

247 Whether or not there were other humans present within a 20 m radius of the focal gull during  
248 the trial had a significant effect on FID, with the experimenter being able to approach gulls  
249 more closely in areas where other humans were present compared to areas where other  
250 humans were absent ( $\Delta$ FID:  $-218.06 \pm 89.62$  cm,  $t = -2.43$ ,  $N_{absent} = 71$ ,  $N_{present} = 84$ ,  $P = 0.016$ ).

251 The further away the experimenter started approaching, the less closely gulls could be  
252 approached: FID was estimated to increase by  $70 \pm 17$  cm for every 100 cm increase in  
253 experimenter starting distance ( $t = 4.02$ ,  $N = 155$ ,  $p < 0.001$ ).

254 Gulls' FID in response to gaze did not vary according to their age class or the settlement type in  
255 which they were tested: flight initiation distances were not significantly affected by the  
256 interaction between these variables (see Table 1). Although juvenile gulls appeared to tolerate  
257 a closer approach by the experimenter than did adults ( $\Delta$ FID:  $-141.30 \pm 85.74$  cm; Figure 1),  
258 gull age did not have a significant effect on FID ( $t = -1.65$ ,  $N_{adult} = 84$ ,  $N_{juvenile} = 71$ ,  $P = 0.101$ ;  
259 Table 1). FID was not significantly affected by the presence of other gulls (Table 1).

260 Gulls were significantly more likely to fly rather than walk or run away from the experimenter  
261 when they were perched on elevated structures such as walls and posts rather than on the

262 ground (binomial logistic regression, OR = 2.845,  $Z = 2.322$ ,  $N_{\text{ground}} = 122$ ,  $N_{\text{elevated}} = 33$ ,  $P =$   
263 0.020; Table 2). Gulls in urban settlements were less likely to fly away rather than walk or run  
264 than gulls in rural settlements (OR = 0.320,  $Z = -2.697$ ,  $N_{\text{rural}} = 60$ ,  $N_{\text{urban}} = 95$ ,  $P = 0.007$ ).  
265 Although gulls experiencing the “Looking Away” condition tended to be less likely to fly from  
266 the experimenter than were gulls experiencing the “Looking At” condition, this difference was  
267 not statistically significant (OR = 0.479,  $Z = -1.848$ ,  $N_{\text{at}} = 85$ ,  $N_{\text{away}} = 70$ ,  $P = 0.065$ ). There was  
268 also no significant effect of the presence of other humans (OR = 1.731,  $Z = 1.305$ ,  $N_{\text{absent}} = 71$ ,  
269  $N_{\text{present}} = 84$ ,  $P = 0.192$ ) or experimenter starting distance (OR = 1.000,  $Z = 0.172$ ,  $N = 155$ ,  $P =$   
270 0.864) on gulls’ response level.

271

272

273

## 274 DISCUSSION

275 Gaze aversion, whereby animals exhibit a fearful response to gaze, is taxonomically  
276 widespread in vertebrates, but the factors that underlie individual differences in  
277 responsiveness to human gaze are unclear. We recently showed that herring gulls respond to  
278 human gaze direction, but did not distinguish between experimenter head and eye direction  
279 (Goumas et al., 2019). Additionally, we reported large individual variation in gulls' responses.  
280 In the present study, we first tested whether herring gulls respond to human eye gaze  
281 direction when head direction is kept constant. We found that flight initiation distances (FID)  
282 were significantly longer in gulls that were subjected to direct human gaze, indicating that  
283 herring gulls find human eye contact aversive. This effect was evident in gull populations  
284 tested in both urban and rural settlements.

285 We found that herring gulls in urban settlements could be approached more closely compared  
286 to gulls in rural settlements, implying that gulls in areas with a larger human population have a  
287 greater tolerance to humans than do gulls in less populated areas. Our findings are consistent  
288 with the results of previous research on birds (Cooke, 1980; Hall, Burns, Martin, & Hochuli,  
289 2020; Møller, 2008) and other vertebrates (western fence lizards, Grolle et al. 2014; Eurasian  
290 red squirrels, Uchida et al. 2016; vervet monkeys *Chlorocebus pygerythrus*, Mikula et al. 2018).  
291 Additionally, gulls could be approached more closely when there were other humans in the  
292 vicinity, which may also reflect tolerance of human presence. Previous research on American  
293 herring gulls *L. smithsonianus* and great black-backed gulls *L. marinus* found that both species  
294 tended to tolerate closer approach to their nests before fleeing in areas with high prior human  
295 disturbance (Burger & Gochfeld, 1983). Alternatively, the presence of other humans may have  
296 acted as a distraction from the approaching experimenter, thus affecting the gulls' ability to  
297 assess risk.

298 We also compared the effect of human gaze on the FID of adult and juvenile herring gulls, as  
299 well as those living in urban and rural settlements, but there was no significant interaction  
300 between either of these factors: overall, gulls were averse to direct human gaze regardless of  
301 their age class and the human population size of the settlement in which they were tested.  
302 This implies that gaze aversion in herring gulls may not require extensive experience with  
303 humans to develop as a means of assessing the risk posed by an approaching human. Whether  
304 exposure to gaze from conspecifics, predators or humans is required to develop an aversive  
305 response to human gaze remains to be determined, but the existence of gaze aversion in  
306 recently fledged juveniles indicates that it is present at an early age.

307 Although the interaction between age and gaze direction was not significant, the difference in  
308 FID between “Looking At” and “Looking Away” conditions appeared to be more pronounced in  
309 juveniles, suggesting that gaze aversion may be reduced over the course of development. If  
310 this pattern is indicative of a true effect, reduced gaze aversion could occur through  
311 habituation to human gaze due to repeated exposure over time without negative  
312 consequences. Alternatively, it may be the case that adult herring gulls are more likely to  
313 respond sooner to an approaching human regardless of gaze direction, perhaps through  
314 experience of threatening encounters with humans. To address this question, repeated  
315 measurements of the same individuals would be required to establish whether FID changes  
316 throughout life as a result of habituation or sensitisation through recurrent experiences of the  
317 same stimuli or as a result of associative learning. The quantity and quality of interactions with  
318 humans may play an important role in shaping responses to the presence of humans as well as  
319 the direction of human gaze.

320 While responses to humans may be shaped by learning processes, the observed differences in  
321 FID between urban and rural herring gulls may not necessarily be explained by behavioural

322 adaptation to human activity. It is possible that herring gulls may colonise human settlements  
323 according to personality type through spatial assortment. For example, urban areas may be  
324 better suited to individuals that are already bold and exploratory, while shyer individuals may  
325 choose to reduce their encounters with humans by inhabiting areas populated by fewer  
326 humans. Evidence for such personality-matching habitat choice has been indicated by studies  
327 taking repeated measurements of FID for individuals living in territories with varying levels of  
328 human disturbance. Burrowing owls *Athene cunicularia* (Carrete & Tella, 2010) tested over one  
329 month on agricultural land, and dunnocks *Prunella modularis* (Holtmann, Santos, Lara, &  
330 Nakagawa, 2017) tested over three breeding seasons in an urban park, showed high  
331 repeatability in FID within individuals and little evidence of habituation. These studies suggest  
332 that individuals may select habitats based on pre-existing tolerance of human activity.  
333 However, a study of urban and rural house sparrows found that individuals from urban areas  
334 were not less fearful than those from rural areas on first exposure to a test situation involving  
335 human disturbance (Vincze et al., 2016). This suggests that the urban sparrows' subsequent  
336 faster habituation was a result of behavioural flexibility rather than differential colonisation.  
337 Without following individuals over their lifetimes, it is difficult to determine which factors best  
338 explain the differences in behaviour between individual gulls.

339 Regardless of whether shorter FIDs in urban areas are indicative of predetermined boldness or  
340 a result of learning from repeated experiences with humans, it is clear that herring gulls in  
341 these areas respond as though humans present a lower risk. This is further supported by our  
342 finding that gulls in urban areas were more likely to walk rather than fly away when the  
343 experimenter approached. At present, it is unclear whether this lower-level response is  
344 beneficial to individuals. Studies comparing urban and rural populations have shown that  
345 urban-dwelling animals often do appear to benefit from their habitat choices. Silver gulls  
346 *Chroicocephalus novaehollandiae* in an urban location were heavier and in better body

347 condition than those in rural comparison sites (Auman, Meathrel, & Richardson, 2008). This  
348 was also the case in Eastern chipmunks *Tamias striatus*, which had lower fecal stress hormone  
349 concentrations in urban sites compared to rural sites (Lyons, Mastromonaco, Edwards, &  
350 Schulte-Hostedde, 2017). Animals in urban areas may be able to spend less time feeding  
351 because of the high availability and calorie content of anthropogenic food (Jaman & Huffman,  
352 2013; Sears, 1989). Therefore, animals in urban areas may benefit by remaining rather than  
353 fleeing from humans in areas where there are greater feeding opportunities. They may also  
354 learn to associate the availability of food with the presence of humans, which will  
355 subsequently affect perception and assessment of risk (Ydenberg & Dill, 1986).

356 Our study indicates that herring gulls in urban and rural areas perceive a human making eye  
357 contact as posing a higher risk than a human looking elsewhere, and that gulls are sensitive to  
358 this differential risk early in life. The cues that wild animals use to assess the level of risk posed  
359 by humans remain relatively little studied. The consequences of an inappropriate response are  
360 not well understood, and whether high tolerance of humans through boldness or habituation  
361 tends to reduce or increase fitness remains an open question. Furthermore, it would be fruitful  
362 to quantify how positive reinforcement, for example through deliberate or inadvertent feeding  
363 by people, affects the way wild animals respond to human cues. Continued investigation into  
364 wild animals' responses to human behaviour will provide a deeper understanding of the  
365 effects, both negative and positive, that humans have on wild animals and how detrimental  
366 aspects of human-wildlife interactions can be mitigated.

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522 Table 1. The results of the linear mixed-effects model testing for an effect of human gaze  
 523 direction on herring gull flight initiation distance.

	Estimate	SE	<i>t</i>	P
Intercept	-174.20	395.10	-0.44	0.660
Gaze direction (away vs. at)	-195.94	83.70	-2.34	0.021
Age class (juvenile vs. adult)	-141.30	85.74	-1.65	0.101
Settlement type (urban vs. rural)	-239.94	88.52	-2.71	0.008
Humans within 20 m (present vs. absent)	-218.06	89.62	-2.43	0.016
Gulls within 20 m (present vs. absent)	-1.73	90.94	-0.02	0.985
Experimenter starting distance (cm)	0.70	0.17	4.02	< 0.001
<i>Dropped terms</i>				
Gaze direction*Age class	-223.57	166.18	-1.35	0.181
Gaze direction*Settlement type	-44.88	166.70	-0.27	0.788

524 Adjusted R<sup>2</sup> = 0.20.

525 Table 2. Results of a binomial logistic regression testing whether herring gulls' level of  
 526 response (0 = walk/run, 1 = fly away) to an approaching experimenter was affected by  
 527 significant predictors of their flight initiation distance (Table 1).

	Estimate	SE	Odds ratio	Z	P
Intercept	-0.864	1.602	-	-0.539	0.590
Humans (present vs. absent)	0.549	0.420	1.731	1.305	0.192
Experimenter starting distance (cm)	0.000	0.001	1.000	0.172	0.864
Settlement type (urban vs. rural)	-1.138	0.422	0.320	-2.697	0.007
Gaze direction (away vs. at)	-0.735	0.398	0.479	-1.848	0.065
Height (not ground level vs. ground level)	1.045	0.450	2.845	2.322	0.020

528

529 Figure 1. The effect of human gaze direction (looking at or away) and settlement type (urban  
530 or rural) on the flight initiation distances of herring gulls (N = 155). There was no significant  
531 difference in flight initiation distance between age classes (adult and juvenile). Plot shows  
532 means and standard errors. Numbers indicate sample sizes for each category.