Herring gull aversion to gaze in urban and rural human settlements

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Abstract

With an increasing human population and expansion of urban settlements, wild animals are often exposed to humans. As humans may be a threat, a neutral presence, or a source of food, animals will benefit from continuously assessing the potential risk posed by humans in order to respond appropriately. Herring gulls (Larus argentatus) are increasingly breeding and foraging in urban areas, and thus have many opportunities to interact with humans. We recently found that herring gulls take longer to approach food when being watched by a human. However, it is not known whether aversion to human gaze arises from experience with humans, and whether individual differences in responsiveness are a result of differential exposure. Here, we test whether herring gulls’ responses to human gaze differ according to their age class and urbanisation of their habitat. We measured the gulls’ flight initiation distance when an experimenter approached with either a direct or averted gaze. Neither gull age class nor urbanisation significantly influenced the effect of human gaze on flight initiation distance. However, as recently fledged juveniles responded strongly to the experimenter’s gaze, aversion to human gaze may not require extensive exposure to humans to develop. Gulls in urban areas could be approached more closely than those in rural areas, consistent with
findings in other species. These results indicate that gaze aversion is present early in
development and that exposure to humans may influence gulls’ responses to perceived risk
from humans. Investigating the processes generating individual differences in responses to
humans will provide further insights into human-wildlife interactions and the effects of
urbanisation.

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

Gaze direction may be one such cue used to assess risk. A fearful response to gaze, termed “gaze aversion”, is widespread across vertebrate taxa and appears to function primarily as a means to avoid predation and competition (Davidson & Clayton, 2016). A predator that fixes its gaze on a subject is likely to pose more of a threat than a predator that is looking elsewhere (Davidson, Butler, Fernández-Juricic, Thornton, & Clayton, 2014). It would therefore benefit the subject to respond quickly to a predator gazing at it, whereas responding to all predators in the environment, regardless of whether they have spotted the subject, would incur an unnecessary energetic cost (Ydenberg & Dill, 1986).
Relatively little is known about the development of gaze aversion. There is uncertainty about the degree to which gaze aversion is innate (i.e. present at birth or hatching) or dependent on experience. Studies of young, predator-naïve fishes (jewel fish *Hemichromis bimaculatus* (Coss, 1978)) and paradise fish *Macropodus opercularis* (Altbäcker & Csányi, 1990; Miklósi, Berzsenyi, Pongrácz, & Csányi, 1995)) and chickens *Gallus gallus* (Jones, 1980; Scaife, 1976) indicate that aversive responses to two horizontally positioned eye-like stimuli are elicited early in development. However, experiments investigating possible effects of experience on the presence of gaze aversion have had conflicting results. Jewel fish that were deprived of seeing eyes or eye-like stimuli throughout early development showed a greater aversive response to two horizontal eye spots than did fish that were raised in the presence of conspecifics (Coss, 1979). This suggests that prior exposure to such stimuli is not required to elicit a fearful response, and that experience with conspecifics may reduce aversive behaviour. In contrast, bobwhite quails *Colinus virginianus* raised without exposure to human faces were less likely to exhibit aversive responses to human gaze than were those previously exposed to them (Jaime, Lopez, & Lickliter, 2009). These studies suggest that the development of gaze aversion may be species- and context-specific, and potentially dependent on experience.

Experiments testing responses to gaze have also been conducted on wild animals, and these have largely focused on how animals respond to human gaze. Unlike the simple, static eye-like stimuli often used in laboratory studies, humans can change eye gaze direction independently of head direction. This raises the question of whether wild animals attend to the direction of the eyes themselves rather than the direction of the head. Hampton (1994) found that captive, wild-caught house sparrows *Passer domesticus* took more escape flights in response to a human face oriented towards them versus away regardless of eye gaze direction, but the presence of eyes was also important: a model face with two “eyes” was more aversive than a model face with only one “eye”. Other studies of gaze aversion in free-living wild animals have
often tested responses to head direction rather than eye gaze direction (e.g. Watve et al. 2002; Bateman and Fleming 2011; Sreekar and Quader 2013; Davidson et al. 2015; Goumas et al. 2019). However, a few studies controlled for head direction and showed that passerines such as American robins *Turdus migratorius* (Eason, Sherman, Rankin, & Coleman, 2006), European starlings *Sturnus vulgaris* (Carter, Lyons, Cole, & Goldsmith, 2008), American crows *Corvus brachyrhynchos* (Clucas, Marzluff, Mackovjak, & Palmquist, 2013) and North Island robins *Petroica longipes* (Garland, Low, Armstrong, & Burns, 2014) exhibit aversive responses specifically to human eye gaze direction.

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

FID has also been used to test for differences in escape behaviour by animals living in urban and rural areas. Animals in rural areas flee sooner than conspecifics in urban areas in a variety of taxa (e.g. passerines, Cooke 1980; western fence lizards *Sceloporus occidentalis*, Grolle et al. 2014; Eurasian red squirrels *Sciurus vulgaris*, Uchida et al. 2016), suggesting that animals in urban areas may become habituated to the higher density of humans in these areas. Aversion to human gaze may similarly differ between urban and rural habitats if experience with humans is important in the development of gaze sensitivity. With an increased exposure to
humans, it is plausible that animals in urban areas may learn about the consequences of direct
gaze, whether through habituation if direct gaze is inconsequential, or associative learning if
direct gaze leads to negative outcomes such as being displaced, and modify their responses
accordingly.

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

In this experiment, we tested whether herring gulls respond to human eye gaze direction
independently of human head direction in the context of an experimenter directly approaching
the gull. As there is evidence that gaze aversion could be innate but may be affected by
experience in a range of taxa (Davidson & Clayton, 2016), we tested for an effect of age class
(i.e. recently fledged juvenile vs. adult) and location (urban vs. rural) on sensitivity to gaze. We
predicted that, if aversion to gaze is innate or mediated early in development, juveniles would
flee sooner when exposed to direct versus averted gaze. If learning from interactions with
humans shapes responses to human gaze, adults may exhibit either more or less pronounced differences in FID between the two gaze conditions depending on what is being learned. For example, a smaller difference in FID between gaze conditions in adults compared to juveniles may suggest that gulls develop gaze aversion early in life but learn not to fear human gaze through repeated exposure. Conversely, a bigger difference in FID between gaze conditions in adults compared to juveniles may suggest that gulls learn to avoid human gaze. Likewise, adult gulls in rural areas, where there are fewer humans, may exhibit similar patterns in FID as juvenile gulls, as their lower exposure to humans would result in fewer learning opportunities. To complement our measurements of FID, we also recorded the level of each gull’s response to the approaching experimenter. We predicted that gulls would be more likely to take flight than to walk or run when the experimenter’s gaze was directed at them, and in rural compared to urban settlements.
METHODS

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

Ethical note

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

Categorising herring gull test subjects by age class

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

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

Testing for an effect of gaze direction

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

Measuring flight initiation distance

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

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

*Measuring the level of the gulls’ responses*

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

*Additional variables*

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

**Statistical analyses**

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

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

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

Human gaze direction had a significant effect on herring gull FID (Figure 1), as did settlement type and experimenter starting distance (Table 1). Gulls could be approached more closely before fleeing (i.e. had shorter FID) when the experimenter was looking away from them versus at them (estimated difference in FID (ΔFID): -195.94 ± 83.70 cm, t = -2.34, N_at = 85, N_away = 70, P = 0.021; Table 1). Gulls in urban settlements could be approached more closely than gulls in rural settlements (ΔFID: -239.94 ± 88.52 cm, t = -2.71, N_rural = 60, N_urban = 95, P = 0.008).

Whether or not there were other humans present within a 20 m radius of the focal gull during the trial had a significant effect on FID, with the experimenter being able to approach gulls more closely in areas where other humans were present compared to areas where other humans were absent (ΔFID: -218.06 ± 89.62 cm, t = -2.43, N_absent = 71, N_present = 84, P = 0.016).

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

Gulls’ FID in response to gaze did not vary according to their age class or the settlement type in which they were tested: flight initiation distances were not significantly affected by the interaction between these variables (see Table 1). Although juvenile gulls appeared to tolerate a closer approach by the experimenter than did adults (ΔFID: -141.30 ± 85.74 cm; Figure 1), gull age did not have a significant effect on FID (t = -1.65, N_adult = 84, N_juvenile = 71, P = 0.101; Table 1). FID was not significantly affected by the presence of other gulls (Table 1).

Gulls were significantly more likely to fly rather than walk or run away from the experimenter when they were perched on elevated structures such as walls and posts rather than on the ground.
ground (binomial logistic regression, OR = 2.845, \( Z = 2.322 \), \( N_{\text{ground}} = 122 \), \( N_{\text{elevated}} = 33 \), \( P = 0.020 \); Table 2). Gulls in urban settlements were less likely to fly away rather than walk or run than gulls in rural settlements (OR = 0.320, \( Z = -2.697 \), \( N_{\text{rural}} = 60 \), \( N_{\text{urban}} = 95 \), \( P = 0.007 \)). Although gulls experiencing the “Looking Away” condition tended to be less likely to fly from the experimenter than were gulls experiencing the “Looking At” condition, this difference was not statistically significant (OR = 0.479, \( Z = -1.848 \), \( N_{\text{at}} = 85 \), \( N_{\text{away}} = 70 \), \( P = 0.065 \)). There was also no significant effect of the presence of other humans (OR = 1.731, \( Z = 1.305 \), \( N_{\text{absent}} = 71 \), \( N_{\text{present}} = 84 \), \( P = 0.192 \)) or experimenter starting distance (OR = 1.000, \( Z = 0.172 \), \( N = 155 \), \( P = 0.864 \)) on gulls’ response level.
Gaze aversion, whereby animals exhibit a fearful response to gaze, is taxonomically widespread in vertebrates, but the factors that underlie individual differences in responsiveness to human gaze are unclear. We recently showed that herring gulls respond to human gaze direction, but did not distinguish between experimenter head and eye direction (Goumas et al., 2019). Additionally, we reported large individual variation in gulls’ responses. In the present study, we first tested whether herring gulls respond to human eye gaze direction when head direction is kept constant. We found that flight initiation distances (FID) were significantly longer in gulls that were subjected to direct human gaze, indicating that herring gulls find human eye contact aversive. This effect was evident in gull populations tested in both urban and rural settlements.

We found that herring gulls in urban settlements could be approached more closely compared to gulls in rural settlements, implying that gulls in areas with a larger human population have a greater tolerance to humans than do gulls in less populated areas. Our findings are consistent with the results of previous research on birds (Cooke, 1980; Hall, Burns, Martin, & Hochuli, 2020; Møller, 2008) and other vertebrates (western fence lizards, Grolle et al. 2014; Eurasian red squirrels, Uchida et al. 2016; vervet monkeys Chlorocebus pygerythrus, Mikula et al. 2018).

Additionally, gulls could be approached more closely when there were other humans in the vicinity, which may also reflect tolerance of human presence. Previous research on American herring gulls *L. smithsonianus* and great black-backed gulls *L. marinus* found that both species tended to tolerate closer approach to their nests before fleeing in areas with high prior human disturbance (Burger & Gochfeld, 1983). Alternatively, the presence of other humans may have acted as a distraction from the approaching experimenter, thus affecting the gulls’ ability to assess risk.
We also compared the effect of human gaze on the FID of adult and juvenile herring gulls, as well as those living in urban and rural settlements, but there was no significant interaction between either of these factors: overall, gulls were averse to direct human gaze regardless of their age class and the human population size of the settlement in which they were tested. This implies that gaze aversion in herring gulls may not require extensive experience with humans to develop as a means of assessing the risk posed by an approaching human. Whether exposure to gaze from conspecifics, predators or humans is required to develop an aversive response to human gaze remains to be determined, but the existence of gaze aversion in recently fledged juveniles indicates that it is present at an early age.

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

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

Regardless of whether shorter FIDs in urban areas are indicative of predetermined boldness or a result of learning from repeated experiences with humans, it is clear that herring gulls in these areas respond as though humans present a lower risk. This is further supported by our finding that gulls in urban areas were more likely to walk rather than fly away when the experimenter approached. At present, it is unclear whether this lower-level response is beneficial to individuals. Studies comparing urban and rural populations have shown that urban-dwelling animals often do appear to benefit from their habitat choices. Silver gulls *Chroicocephalus novaehollandiae* in an urban location were heavier and in better body
condition than those in rural comparison sites (Auman, Meathrel, & Richardson, 2008). This was also the case in Eastern chipmunks *Tamias striatus*, which had lower fecal stress hormone concentrations in urban sites compared to rural sites (Lyons, Mastromonaco, Edwards, & Schulte-Hostedde, 2017). Animals in urban areas may be able to spend less time feeding because of the high availability and calorie content of anthropogenic food (Jaman & Huffman, 2013; Sears, 1989). Therefore, animals in urban areas may benefit by remaining rather than fleeing from humans in areas where there are greater feeding opportunities. They may also learn to associate the availability of food with the presence of humans, which will subsequently affect perception and assessment of risk (Ydenberg & Dill, 1986).

Our study indicates that herring gulls in urban and rural areas perceive a human making eye contact as posing a higher risk than a human looking elsewhere, and that gulls are sensitive to this differential risk early in life. The cues that wild animals use to assess the level of risk posed by humans remain relatively little studied. The consequences of an inappropriate response are not well understood, and whether high tolerance of humans through boldness or habituation tends to reduce or increase fitness remains an open question. Furthermore, it would be fruitful to quantify how positive reinforcement, for example through deliberate or inadvertent feeding by people, affects the way wild animals respond to human cues. Continued investigation into wild animals’ responses to human behaviour will provide a deeper understanding of the effects, both negative and positive, that humans have on wild animals and how detrimental aspects of human-wildlife interactions can be mitigated.
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0636-y


https://www.r-project.org


pредатор responses of a vulnerable marsupial prey to known and novel predators.  


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

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-174.20</td>
<td>395.10</td>
<td>-0.44</td>
<td>0.660</td>
</tr>
<tr>
<td>Gaze direction (away vs. at)</td>
<td>-195.94</td>
<td>83.70</td>
<td>-2.34</td>
<td>0.021</td>
</tr>
<tr>
<td>Age class (juvenile vs. adult)</td>
<td>-141.30</td>
<td>85.74</td>
<td>-1.65</td>
<td>0.101</td>
</tr>
<tr>
<td>Settlement type (urban vs. rural)</td>
<td>-239.94</td>
<td>88.52</td>
<td>-2.71</td>
<td>0.008</td>
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<tr>
<td>Humans within 20 m (present vs. absent)</td>
<td>-218.06</td>
<td>89.62</td>
<td>-2.43</td>
<td>0.016</td>
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<tr>
<td>Gulls within 20 m (present vs. absent)</td>
<td>-1.73</td>
<td>90.94</td>
<td>-0.02</td>
<td>0.985</td>
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<tr>
<td>Experimenter starting distance (cm)</td>
<td>0.70</td>
<td>0.17</td>
<td>4.02</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

*Dropped terms*

- Gaze direction*Age class
  -223.57 166.18 -1.35 0.181
- Gaze direction*Settlement type
  -44.88 166.70 -0.27 0.788

Adjusted $R^2 = 0.20$. 
Table 2. Results of a binomial logistic regression testing whether herring gulls’ level of response (0 = walk/run, 1 = fly away) to an approaching experimenter was affected by significant predictors of their flight initiation distance (Table 1).

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>Odds ratio</th>
<th>Z</th>
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<td>Intercept</td>
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<td>1.602</td>
<td>-</td>
<td>-0.539</td>
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<td>Humans (present vs. absent)</td>
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<td>0.420</td>
<td>1.731</td>
<td>1.305</td>
<td>0.192</td>
</tr>
<tr>
<td>Experimenter starting distance (cm)</td>
<td>0.000</td>
<td>0.001</td>
<td>1.000</td>
<td>0.172</td>
<td>0.864</td>
</tr>
<tr>
<td>Settlement type (urban vs. rural)</td>
<td>-1.138</td>
<td>0.422</td>
<td>0.320</td>
<td>-2.697</td>
<td>0.007</td>
</tr>
<tr>
<td>Gaze direction (away vs. at)</td>
<td>-0.735</td>
<td>0.398</td>
<td>0.479</td>
<td>-1.848</td>
<td>0.065</td>
</tr>
<tr>
<td>Height (not ground level vs. ground level)</td>
<td>1.045</td>
<td>0.450</td>
<td>2.845</td>
<td>2.322</td>
<td>0.020</td>
</tr>
</tbody>
</table>
Figure 1. The effect of human gaze direction (looking at or away) and settlement type (urban or rural) on the flight initiation distances of herring gulls (N = 155). There was no significant difference in flight initiation distance between age classes (adult and juvenile). Plot shows means and standard errors. Numbers indicate sample sizes for each category.