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Carrion crows are sensitive to human head, but not eye, orientation

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Abstract

Escape is a vital survival mechanism, shaped by numerous factors relating to risk assessment. Birds rely on flight as a primary escape mechanism with flight initiation distance (FID) commonly used to quantify responses. In this study we tested whether carrion crows (*Corvus corone*) were sensitive to human gaze when approached with direct gaze and head orientation, direct head but averted eyes, or averted head and eyes. We also explored how contextual variables such as the birds' initial posture, starting distance, temperature, and weather affect FID. We conducted an independent groups field experiment with 172 naturally foraging crows randomly assigned to one of three gaze conditions. Each was approached by the experimenter, while recording their position throughout. Once the subject left their initial location, the distance between experimenter's initial position and subject's location (starting distance), where the experimenter stopped and the subject's location (FID), and environmental and situational factors were recorded. Results demonstrated a significant difference in FID based on gaze condition: FID was about 3.5m shorter when head and eyes were averted than when both were direct or head was direct and eyes were averted. Initial posture and starting distance also significantly affected FID but weather and temperature had no significant effects. These findings suggest that carrion crows are sensitive to human head orientation but not eye direction specifically. They also contribute to our understanding of human-wildlife interactions.

Significance statement

The main way birds escape from potential threats is to fly away. The decision of when to fly depends on their perception of the threat. We measured whether the gaze direction of an approaching human altered carrion crows' flight responses while they foraged naturally. When both head and eyes were looking away, crows allowed a human to get several metres closer than when head and eyes or just head were towards the bird. These results suggest that carrion crows are sensitive to head orientation when making escape judgements, but not eye gaze specifically. Sensitivity to gaze is widely studied in social perception in both humans and other animals, so understanding which species are sensitive to particular cues in particular contexts is important to understanding the evolution of this ability and human-wildlife interactions in general.

Keywords: Gaze sensitivity; flight initiation distance; crow.

Introduction

Being able to escape from dangerous or threatening situations is essential for the survival of many animals, with failure leading to reduced fitness or death (Evans et al., 2019). Two predominant models have emerged to explain when prey animals should flee (Stankowich & Blumstein, 2005). Ydenberg and Dill (1986) proposed an economic model where escape is not optimal immediately but should begin when the cost of fleeing and remaining are equal, to avoid the loss of fitness-enhancing activities. In contrast, Broom and Ruxton (2005) argued that prey should either flee immediately after detecting a predator, or only escape once the predator has initiated a chase, stating "if the prey is going to flee of its own volition, it should do so as soon as possible".

Some species benefit from conspecifics being present to alert them of predators or other natural environmental threats, but some species that scavenge or hunt alone lack this benefit (Lima, 1995). These solitary animals must independently detect these cues to keep them alive, which due to the complex nature of perceiving, assessing, and responding to threats or risks, is an energetically taxing task (Godin, 1992). Despite the cost, this vigilance is crucial for effective resource collection while maintaining a secure level of predator avoidance (Kent et al., 2019).

In bird species, escape behaviours include alarm vocalisations and flight, which have been investigated across a variety of species and environments. Morelli et al. (2022) defined flight initiation distance (FID) as "the distance at which individuals take flight when approached by a potential predator (typically a human)", a measure widely used when investigating factors and quantitatively investigate avian anti-predator behaviours (Cooper & Blumstein, 2015).

Understanding FID provides a key insight into the anti-predator behaviours adopted and the risk assessment undertaken by birds (Tätte et al., 2019). Understanding the factors affecting FID is important for assessing human impact while developing strategies to minimise ecological disturbance in birds' natural habitats.

Gaze sensitivity

While human-wildlife interactions can be innocuous and sometimes beneficial, humans can pose a threat to life and potential resource pools in urban areas (Król & Hernik, 2020; Marzluff & Neatherlin, 2006). Crows, like many animals, use various behavioural cues to assess such risks, with one of the most salient being gaze. For instance, the head and gaze orientation of a predator may reveal information regarding its intentions (Bateman & Fleming, 2011). Many species can alter gaze without a corresponding head movement, adding complexity to this cue and requiring animals to interpret signals from a variety of orientations (Guitton & Volle, 1987).

Sensitivity to the gaze of others and discerning information about their visual focus is a central aspect of social cognitive research across species (Davidson & Clayton, 2015). In humans, this involves characterising eye contact, acknowledging that others have divergent visual perceptions to our own, and discerning inferred meaning based on gaze (Bettle & Rosati, 2016). However, humans are not alone in sensitivity to the gaze of another individual. The ability to co-orient gaze with a conspecific or human experimenter (gaze following) has been shown in apes (Bräuer et al., 2005), dogs (Bräuer et al., 2004), reptiles (e.g. red-footed tortoise,*Geochelone carbonaria*, Wilkinson et al., 2010) and birds such as ravens *(Corvus corax*, Bugnyar et al. 2004). These studies aim to identify the capacity for gaze sensitivity

and understand the cognitive abilities that subject animals may possess that enable risk assessment, perceptions of others and the attribution of attention (Davidson et al., 2014). Gaze sensitivity investigations with bird species have been particularly fruitful, adopting a wide range of contexts and experimental set-ups.

Several studies have examined how gaze direction affects a bird's FID and risk assessment behaviours. Herring gulls (*Larus argentatus*) permitted a closer approach when the people adopt a diverted gaze away from the bird (Goumas et al., 2020). This finding was mirrored in related work in which gulls approached the experimenter while they adopted a still, crouching position near a visible food source. Findings revealed that a direct gaze resulted in a longer time for approach as well as some incomplete trials (Goumas et al., 2019). 22% of the direct gaze birds never reached the food source whereas all the averted gaze birds reached the food at least once within the research window. Jackdaws showed a similar result with approach influenced by even subtle changes in gaze direction, with a direct gaze again resulting in increased latency to approach (von Bayern & Emery, 2009). A direct-gaze approach has been found to result in the longest FID and increased urgency of escape, with crows becoming aware of the approach earlier, discriminating the type of gaze and adjusting urgency accordingly with the gaze condition adopted (Clucas et al. 2013).

Despite these insights, there is a need for further and more extensive research to be conducted including consideration for head orientation and the repercussions this may have on the importance of gaze. Along with this, Goumas et al. (2019) used a repeated measures design which may have introduced learning effects, altering the responses of the gulls due to prior experiences with experimenters.

Integration of head and eye cues is used by a number of species when interpreting gaze direction. Studies have found that while a direct gaze facilitated the fastest processing, with a special mechanism for direct head and gaze orientations (Palanica & Itier, 2014), head orientation can bias judgements with increasing levels for stimulus in the periphery. One such bias is called the 'overshoot effect', which causes observers to misperceive the direction of a gaze if the head and body orientations are misaligned. For example, when the head is turned while the eyes maintain a fixed position, the perceived gaze direction can shift opposite to the head turn, even when the head orientation is vertically altered (Moors et al., 2015). This is not only seen in humans but also in primate species such as macaques, whose face-responsive neurons in the amygdala discriminated between variations in gaze direction and head orientation (Tazumi et al., 2010). These findings demonstrate the complexity of gaze perception, highlighting that while eye direction is informative, head orientation can modulate how gaze is interpreted (Whitham et al., 2022).

Corvid intelligence

Crows are widely regarded as one of the most intelligent bird species. Many anecdotal and scientific accounts of crows show an advanced understanding in various domains. In physical cognition crows show remarkable skills in tool use and manufacture (e,g, Hunt & Gray, 2003; Kenward et al., 2006; Cnotka et al., 2008). There are many anecdotal stories surrounding crows and their foraging behaviours, many of which contain descriptions of corvids as mischievous (Marzluff & Angell, 2007, 2012), entertaining (Hunter, 2018) and curious (Swift, 2015).

Crows also demonstrate advanced social cognition (Holzhaider et al., 2011). Crows can recognise familiar and unfamiliar human faces (Miller et al., 2015). American crows (*Corvus*

144 *brachyrhynchos)* learned to recognise novel 'dangerous' faces/masks worn by humans during
145 trapping and tagging. They responded with alarm vocalisations, scolding and mobbing
146 behaviour that persisted years after exposure (Marzluff et al., 2010). This demonstrates rapid
147 learning ability, fine-feature discrimination, and long-term memory for inter-species
148 interactions, making crows ideal subjects for examining how human attentional cues
149 influence behaviour. Nieder et al., (2020) even showed neural correlates of sensory
150 consciousness in carrion crows (*Corvus corone*), whereby neural activity regarding a
151 subjective experience was maintained throughout each trial, similar to findings with primates.
152 Crows' myriad cognitive abilities have drawn parallels with primate cognition (Emery &
153 Clayton, 2004).
154
155 In terms of gaze sensitivity, Yu et al. (2023) explored how Azure-winged magpies
156 (*Cyanopica cyanus)* responded to human gaze as a predatory cue using FID. Two
157 experiments were conducted to see if age or breeding status and approach direction affected
158 sensitivity to human gaze. In the first, birds were approached directly under one of three gaze
159 conditions (directly with eyes and head, eyes down with head towards, eyes and head down).
160 In the second experiment, only adults in breeding season were tested using approaches from
161 three directions: directly (like experiment 1) or tangentially with bypass distances of 2.5m
162 and 5m, with the same three gaze conditions. Adult magpies were more sensitive to direct
163 human gaze, while the juvenile birds showed no significant sensitivity, suggesting that
164 aversion to gaze develops with age and experience. Additionally, breeding adults permitted
165 closer approaches before fleeing, likely due to the increased cost of abandoning potential
166 food or mating resources at this time. The magpies were more sensitive to a moderately
167 tangential approach (2.5m) than to direct or more distant approaches. The presence of other
168 magpies and an away-facing initial posture resulted in later fleeing and shorter FID.

This study

Therefore, the aim of this study was to investigate the sensitivity of carrion crows to human eye gaze and head direction. We conducted a field experiment similar in concept to Yu et al., (2023) with a human approaching under different gaze conditions in which eye direction and head orientation were manipulated to test their effects on FID. Furthermore, we explored the role of the bird's initial posture on escape behaviour.

We made the following hypotheses:

1. FID will be longest with direct head and eye direction.
2. FID will be shorter when either the eyes or head are averted.
3. FID will be longest when the birds' initial posture is towards the human.
4. FID will be shorter when the birds' initial posture is in profile or facing away from the human.

Method

To investigate the effect of gaze sensitivity on the flight initiation of crows, a field experimental design was implemented. This method minimized stress on the animals while obtaining real-world behavioural data.

Compliance with Ethical Standards

The study was approved by the Animal Behaviour Ethics Subcommittee of the University of Portsmouth (ABES 2024 – 008). The study involved no physical with animals and minimal disruption to their natural behaviour.

Pilot testing

Originally, an interaction area circle of 0.5m radius was established containing a sealed but visible food source of sunflower seeds inside a weighted down transparent plastic container to attract crows into the experimental area. However, this approach did not work as there was no interest and interaction from the crows Therefore, based on this pilot test, an updated design was adopted, whereby the experimenter would approach crows that were already naturally foraging on the ground. We had intended to use a standardised approach distance of 25m following Goumas et al. (2020); however, we had to change this given that the crows were naturally foraging rather than entering a designated interaction area, there was no way to ensure the approach distance was the same for each trial.

Participants and study area

The subjects were 172 crows (*Corvus corone*) that were sampled based on their availability on experimental trial days which were between November 2024 – January 2025. The flight initiation distance of each crow was measured as the primary response variable for this

research with the gaze condition being randomised in each trial. The trials were conducted in open green areas around Portsmouth where crows are naturally found. The primary locations were Southsea common, Southsea coastline, and the Alverstoke shoreline (see Figures 1 & 2). All three locations contain a significant natural crow population that made them appropriate for conducting this experiment.

Figure 1: *Alverstoke coastline used for data collection*



Note:Ordnance Survey. (2025). Alverstoke | OS Maps. Lat: 50.78689, long: -1.15015. Grid reference: SZ 60004 98935.

Figure 2: *Southsea common and coastline used for data collection*



Note: Ordnance Survey. (2025b). Southsea | OS Maps. Osmaps.com. Lat: 50.78640, long: -1.08137 Grid reference: SZ 64852 99050.

Materials/ apparatus

This study made use of droppable place markers to indicate the locations of approach start and stop and the focal bird during each trial. A digital display trundle wheel was then used after the trial had finished to measure the distance between markers in meters. Weather conditions were measured using daily online reports from BBC weather (*Southsea - BBC Weather*, 2025).

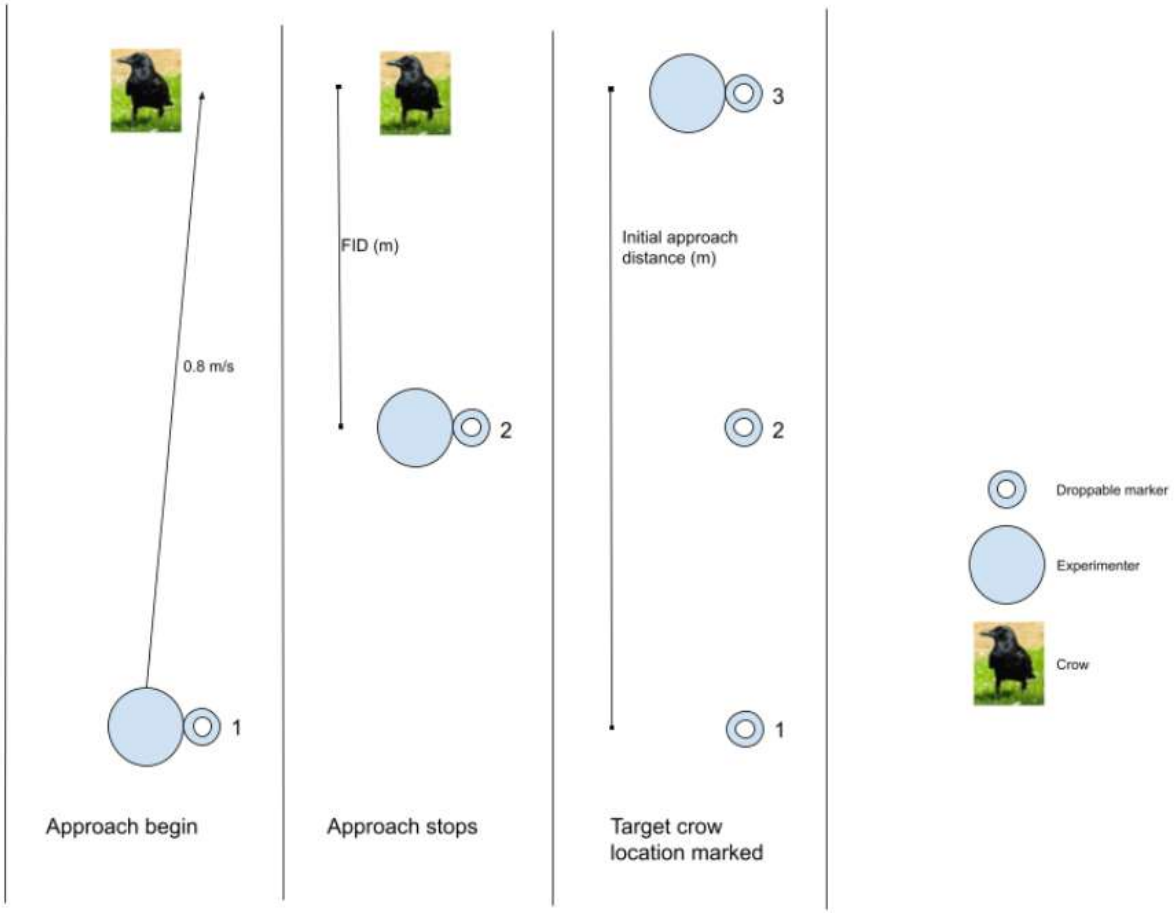
Procedure

To examine the effects of gaze sensitivity on the flight response variable, three gaze conditions were implemented during direct approach. Each trial was randomly assigned one of the conditions: (1) *eyes and head towards*; the experimenter approached with eye gaze and

head posture facing the bird; (2) *eyes down and head towards*: the experimenter approached with upright head posture but eye gaze aimed at the ground; or (3) *eye and head down*: the experimenter approached with head and eye gaze directed at the ground. The assignment of gaze conditions to each trial was randomly predetermined using an online random number generator to assign condition 1, 2 or 3 to each trial number. These were pre-recorded on the excel spreadsheet where the experimental data was added following each trial. Due to the crow's initial location not being marked prior to each trial commencing, the experimenter had to maintain a visual of the crow's location using direct eye contact in condition 1 or peripheral vision when the condition was assigned as ‘eyes down’ in either condition 2 or 3.

The experimenter waited, and once a crow was seen naturally foraging in one of the experiment locations, the experimenter would mark their initial location on the ground with a droppable marker to measure the approach distance (marker 1). The experimenter recorded the initial posture of the target bird and began a direct approach at approximately 0.8 m/s, adopting one of the three gaze conditions that were randomly assigned to each trial. The walking speed of the researcher was standardised to 0.8 m/s through recording and repetition under lab conditions prior to engaging in fieldwork. Each target crows' initial posture was recorded as forward (facing experimenter), profile (one side facing experimenter) or away (facing away from experimenter) following Yu et al. (2023). Once the crow demonstrated flight from their initial location the experimenter would stop approach and drop another marker at her location to measure flight initiation distance (marker 2). A third marker was dropped at the crow's initial location prior to taking flight (marker 3) and then flight initiation distance and initial approach distance were recorded using the previously dropped markers. A diagram showing the experimental set up can be seen in figure 3.

Figure 3: *Experimental set-up*



Design/Measures

This study was conducted using an independent groups experimental design where no participant was knowingly included more than once. The dependent variable was flight initiation distance (FID) measured in meters (m). The experimental manipulated independent variable was gaze condition. The initial posture, weather conditions, starting distance and outside temperature were all measured as possible observed independent variables.

After each trial was concluded, the initial posture, starting approach distance, FID, weather conditions and temperature were recorded. The weather conditions were recorded as one of the following: cloudy, partly cloudy, heavy rain, light rain/drizzle, clear/sunny, foggy, snow or windy. The weather conditions and temperature were collected to investigate the effect of extraneous variables on flight initiation distance.

Despite the random allocation of gaze conditions, due to the nature of this experiment, there was a chance for the same crow to be measured more than once. As the crows were naturally occurring and the population was not being experimentally controlled or manipulated, there was no way of identifying each crow individually. Therefore, there may have been a degree of unavoidable pseudoreplication in this experiment and consequently the results of this experiment should be treated with appropriate caution (Farrar, 2021).

Coding

The data was coded to represent the details of the crow's initial posture, environmental conditions as well as their flight behaviour. Measurements for initial posture, weather conditions and gaze conditions were qualitative descriptors which were numerically coded for analysis and testing. Other measurements of FID, temperature and starting approach distance are already numerical values (*m* and °C) and therefore do not require further processing for quantitative analysis.

Reliability

The reliability of observations was checked using Cohen's κ to determine if there was agreement between two observers' judgement of distances and category of initial posture

across 19 trials. There was near perfect agreement of initial posture judgement, $\kappa = .921$ (95% CI), $p < .001$.

Two-way mixed model ICC (intraclass correlation coefficient) reliability analysis estimations were conducted on measures of FID and starting distance between two observers. ICC rating values for starting distance (.998) and FID (.999) were both excellent with a confidence interval of 95% (see Appendix 1).

Statistical analysis

Data was exported from Microsoft Excel to SPSS Statistics (version 29), with the initial posture, gaze condition and weather conditions being numerically coded. To evaluate whether gaze condition had a significant effect on the flight initiation distance of crows, a one-way 3x3 ANCOVA was conducted to test for main effects while accounting for variation due to the initial posture of the birds as well as weather and temperature. A linear regression was also conducted to determine if there was a significant impact of the starting distance on the FID measure and quantify it.

Results

Descriptive statistics are given in Table 1.

Table 1

Descriptive statistics

	Mean	*SD*	*N*
FID (m)			
Overall	11.02	3.59	172
Condition 1	12.07	3.39	59
Condition 2	12.28	3.02	56
Condition 3	8.69	3.20	57
Forward	12.12	3.53	59
Profile	10.82	3.43	61
Away	9.99	3.56	52
Temperature (°C)	9.91	2.71	172
Starting distance (m)	21.06	3.70	172

A 3 (gaze condition) x 3 (initial posture) independent groups ANCOVA was conducted to explore the effects of three different gaze conditions (1: eyes and head towards; 2: eyes down and head towards; 3: eyes and head down) on FID. A significant main effect was observed with condition 3 having the shortest distance, while condition 1 and condition 2 had longer distances. Pairwise comparisons (with Bonferroni corrections) revealed that the difference

between conditions 1 and 2 were not significant but that FID in condition 3 was significantly shorter compared to condition 1 ($p < .001$) and condition 2 ($p < .001$). The raw effect size of the difference between condition 1 and 2 was negligible (. 21m), whereas the differences between conditions 1 and 2 with condition 3 were substantial (in both cases >3.3m). Thus hypotheses 1 and 2 were partially supported, but it was only when both head and eyes were averted that FID was shorter. The covariates of starting distance and initial posture had significant effects on FID. Forward posture had the longest FID, while profile posture was significantly shorter, and away posture was significantly shorter than both. Table 2 highlights that 26% of the variance in FID was explained by gaze condition, followed by 16% by the starting distance and 14% by the initial posture of the focal bird which, according to Cohen's guidelines, are all large effects. The outside temperature ($p = .70$) and the weather conditions ($p = .20$) had no significant effect on FID. The mean FID for each gaze condition combined with initial posture can be seen in figure 4.

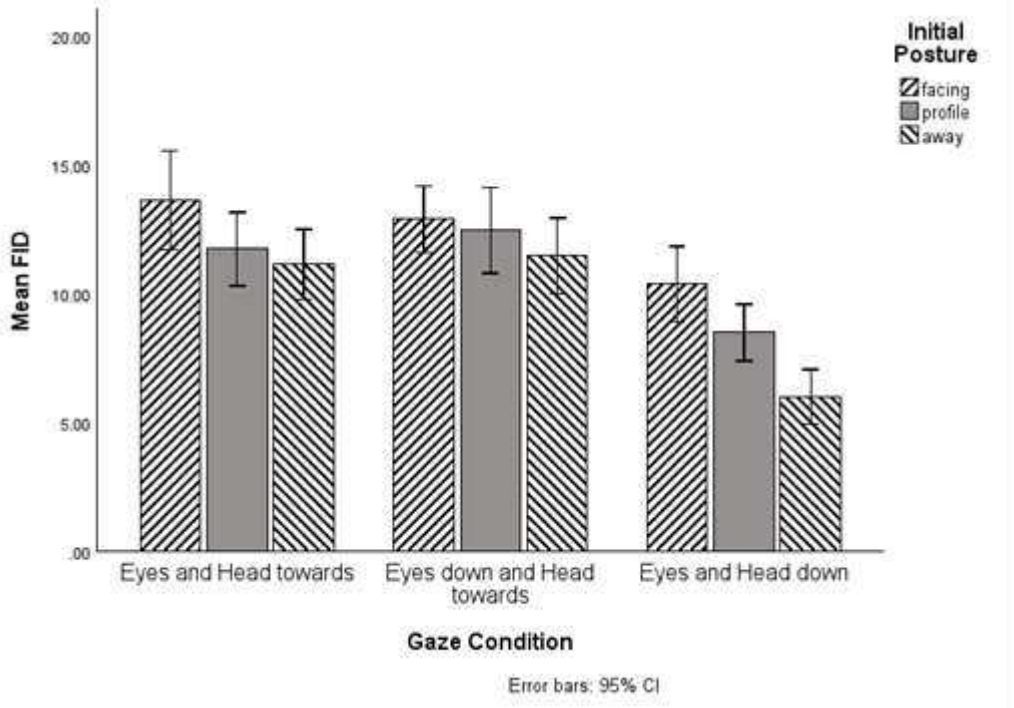
Table 2

Effects of variables on FID

	F (df)	*p*	η^2_p
Gaze condition	28.96 (2, 165)	< .001	.26
Starting distance	30.95 (1, 165)	< .001	.16
Initial posture	25.82 (1, 165)	< .001	.14
Temperature	.15 (1, 165)	.70	.001
Weather condition	1.70	.20	.01

Figure 4

Effect of initial posture and gaze condition on FID

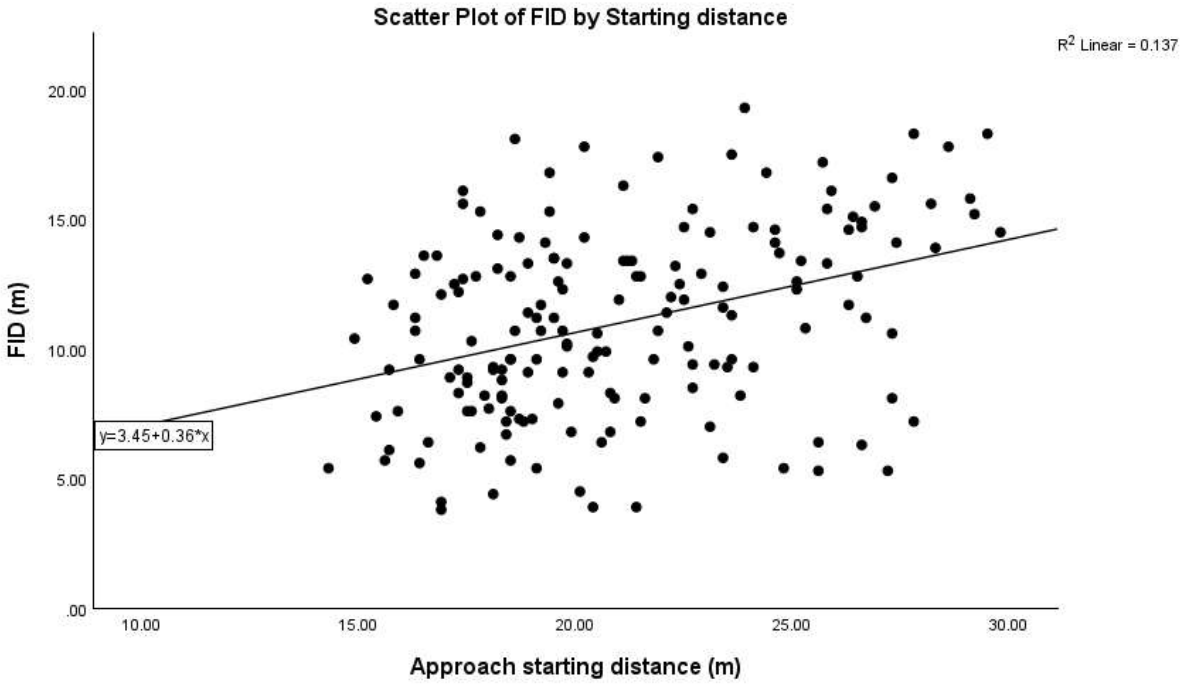


Confirming hypothesis 2, figure 4 shows that adopting a gaze condition with eyes and head down allowed for the closest approach and resulted in the shorted FID. The graph also shows that for each gaze condition FID varied depending on initial posture, which had a significant impact, with away posture (M = 9.99 SD = 3.56) having the shortest FID, followed by profile (M = 10.82 SD = 3.43) and facing (M = 12.12 SD = 3.53).

Given the significant effect of starting distance identified above, a Pearson's correlation was run between the starting distance and FID. This correlation was significant and positive, $r(170) = .37$, $p < .001$ (figure 5).

Figure 5

Relationship between starting distance and FID



A simple linear regression was carried out on the effect of starting distance on FID following the correlation above and the scatter plot in Figure 5. A significant regression was found (F (1,170) = 26.92, p = <.001). The R^2 was .137, indicating that starting distance explained approximately 13.7% of the variance in FID. The regression equation was:

FID = 3.45 + .36 (starting distance)

That is, for each one additional meter increase in starting distance, the predicted FID increased by approximately .36 meters (95% CI .22–.50).

Discussion

Our study shows that carrion crows are sensitive to human gaze, but this sensitivity is based on head rather than eye orientation. Crows initiated flight at a significantly greater distance when being approached with eye and head oriented directly towards them (about 12 metres). When both head and eye orientation were averted, crows initiated flight about 3.5 metres closer. Importantly, when eyes were averted but head oriented directly towards them, crows still initiated flight around 12 metres. Sensitivity to human gaze has been demonstrated in several bird species such as jackdaws (von Bayern & Emery, 2009), herring gulls (Goumas et al., 2019, 2020), Azure-winged magpies (Yu et al., 2023), and American crows (*Corvus brachyrhynchos*). However, these species are also sensitive to eye gaze independent of head orientation, whereas house sparrows (*Passer domesticus*) respond to head orientation but not eye gaze itself (Hampton , 1994).

A tempting hypothesis is that the lack of variation in carrion crow response to eye gaze direction alone may be partially explained by anatomical differences in the eye. Humans, herring gulls, and jackdaws have a prominent contrast between the pupil and iris/sclera, making eye direction more distinct and easily visible potentially enhancing non-verbal conspecific communication using eye orientation (Kobayashi & Kohshima, 1997; Lamond & Fisher, 2023). In contrast, carrion crows have uniform, dark-coloured eyes which act as a form of gaze-camouflage where any intent revealed by gaze is hidden (Kobayashi & Kohshima, 2001). The lack of contrast between carrion crows' pupil and sclera and the subsequent difficulty in determining the gaze orientation may explain the degree of insensitivity to gaze, and also the case in house sparrows. However, American crows and Azure-winged magpies also have non-contrasting eyes, and they do show sensitivity to eye

gaze specifically, although in the latter case this ability was not consistent and depended on age and breeding season (Yu et al., 2023).

Head orientation in general may be a more noticeable cue than gaze alone. This is supported by research on human gaze perception such as, Palanica and Itier (2014) and Moors et al., (2015) who found that head orientation significantly influenced perception, and an integration of both cues facilitated more accurate judgment of attentional direction. This may reflect natural predator recognition mechanisms as many predators possess forward-facing eyes that are simultaneously oriented with the head orientation, making it a reliable indicator of behavioural intent (Davidson & Clayton, 2015).

Initial posture also had an influence on FID. If the subject was initially facing the experimenter, the subsequent recorded FID was larger than if the subject was facing away. This was found consistently across all three gaze conditions and mirrors the findings of Yu et al. (2023). This is a logical assumption as the subject may not have noticed the approaching threat when facing away until the distance between them is small enough for detection (Butler & Fernández-Juricic, 2018). Body posture of foraging animals has been shown to influence the transmission of environmental information, such as the presence of a predator, in socially foraging birds (Fernández-Juricic et al., 2003).

Starting distance also had a significant effect on FID, consistent with Blumstein (2003). A longer starting distance corresponded to an increased FID, with every extra meter of distance between the start of approach and the subject, increasing FID by approximately 36cm. Blumstein (2003) found that starting distance accounted for 67% of the variance in responses across all species included in their testing. This result is rational as a larger starting distance

would allow for a longer period in which the bird can observe and become alert to the approaching threat (Dumont et al., 2012). Our result suggests that crows maintain a safe buffer-zone that facilitates dynamic, gradual assessment of risk rather than employing purely reactive escape behaviours. This supports the idea that crow anti-predator responses are shaped by constant analysis, consistent with the optimal escape theory.

Temperature and weather conditions had no significant impact on behavioural measures in our study. Weather conditions and temperature have previously been examined in relation to some roosting behaviours, but conclusions have either found minimal or negligible effects (Janicke & Chakarov, 2006; Obrecht & Dinsmore, 2008). It is notable that our data were collected within roughly the same season (autumn and winter). Within such narrow seasonal ranges, these environmental factors may not substantially and anti-predator behaviours, but perhaps during a much warmer summer season differences might be apparent.

Several methodological limitations must be acknowledged. Firstly, although the use of natural foraging conditions adds ecological validity to the study, it also results in the inclusion of uncontrollable variables that could have altered the subject's awareness and perception of the approaching threat. Variables such as level of urbanisation (Goumas et al., 2020), approach distance and direction (Møller & Tryjanowski, 2014), presence of other birds and humans (De Resende et al., 2024), age and breeding state (Yu et al., 2023) have all been previously shown to influence avian anti-predator behaviour. It is possible that some of these unmeasured variables may affect escape behaviour in carrion crows too.

Another limitation of this research was the lack of control over the starting approach distance. As noted, this variable affected FID, meaning that control over this variable is important. In

482 the initial pilot study, we attempted to control for this using a standardised approach distance
483 and a food container to lure subjects into the experimental area, but it was not practically
484 feasible since the crows were not interested in the bait. Findings by Blumstein (2003)
485 confirmed that starting distance had a significant effect but, due to the nature of pilot testing
486 this variable had to be reassessed for trials to continue. Nevertheless, the redesigned study
487 confirms that starting distance is important in escape behaviour.
488
489 A common issue in animal research with free-ranging animals is pseudoreplication, which is
490 defined as testing for treatment effects where replicates may not be statistically independent
491 (Hurlbert, 1984). This may have occurred as none of the subjects were marked or tagged
492 during the trials meaning there is no realistic way of knowing if a subject has participated in a
493 previous trial, meaning data from one subject may have been included multiple times. This is
494 unfortunately unavoidable without marking the birds. We tried to reduce potential
495 pseudoreplication by visually selecting a different birds after each trial. However, over hours
496 and between days, it is impossible to rule out using the same individual twice. The fact that
497 our results broadly align with other studies of bird gaze sensitivity suggest that effects are
498 real and not simply due to pseudoreplication. Future research using identifiable crows would
499 be useful to completely eliminate pseudoreplication. Furthermore, another experimental
500 condition could be included (eyes towards and head down) to fully explore whether birds
501 respond to head orientation or eye gaze specifically.
502
503 This research expands our knowledge of urban bird behaviours focussing on how human-
504 animal interactions alter perception of threat and risk. Understanding the impact that human
505 presence has on increasingly urbanised species is crucial as it allows us to take relevant steps
506 to ensure minimisation of harm and ecological disturbance incurred when altering, interacting

with or expanding into animal habitats. Understanding how urban crows perceive and react to human attentional cues has practical implications for conservation strategies, urban management, and minimising human-wildlife conflict. This study contributes to the growing body of knowledge surrounding human-wildlife interactions, while emphasising that further research is still key to a comprehensive and evolving understanding of corvid behaviour.

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Statements and Declarations

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Data availability statement

The raw data for this study are available at Morrison, E. (2025, September 10). Ablett&Morrison: Crow Gaze Sensitivity. Retrieved from osf.io/r2nm7.

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