1 **An Ethogram Identifies Behavioural Markers of Attention to Humans in European**

2 **Herring Gulls (*Larus argentatus*)**

4 Franziska Feist[1] (franziska.feist6@gmail.com), Paul Graham[1] (p.r.graham@sussex.ac.uk)

6 [1]School of Life Sciences, University of Sussex, Brighton, East Sussex, BN1 9QG, United

7 Kingdom

Abstract

Herring gulls are one of the few species that thrive in anthropogenic landscapes. Their longstanding history of urbanisation and familiarity with people makes them an excellent target for studies of the effects of urban living and cognition. Previous studies highlight a connection between food-stealing behaviour, success in anthropogenic areas and an increase in attention towards humans, opening up questions about the exact extent of a gull's knowledge of human food cues and how this manifests itself in behavioural changes. To investigate these questions further, behavioural responses to human cues in a food-related context are investigated and presented in a systematic ethogram, which identifies three distinct markers of attention. Those behaviours – head turns, approaches, and the angular body position relative to the experimenter – differ significantly between control and food conditions, showing that attention towards humans in a food-related context is upregulated and this is reflected in the gull's behaviour. In food condition trials, head turns occur more often and gulls face towards the experimenter (≤90°) with occasional approaches that are never seen in control conditions. Acoustic and behavioural human food-like cues alone were insufficient to elicit a response similar to that seen in presence of a real food item, indicating that gulls specifically pay attention to humans in foraging contexts. The results show situation-dependent attentional modulation in gulls, highlight knowledge gaps about how Herring gulls might identify food objects and provide an ethogram description of attentive behaviours that can be used in further study of attentional modulation in gulls.

Keywords: Herring gull; attentional modulation; ethogram; behaviour

Introduction

The human population is increasing, and with it comes the expansion of cities and urban landscapes (Lowry, Lill and Wong, 2013). Often, this negatively affects local wildlife and causes species to retreat and avoid urbanised areas (Bateman and Fleming, 2012). Few manage to survive in anthropogenic landscapes, but, interestingly, those that do can be very successful and in some species, urban numbers exceed the population densities found in natural environments (Bateman and Fleming, 2012). This is true for the European Herring gull (*Larus argentatus*). First instances of urban nesting occurred in the 1940s, but by the 1960s urban breeding colonies had spread throughout the United Kingdom's coastal areas, becoming a nationwide phenomenon (Rock, 2005). Today, while the species' overall population numbers are declining (BirdLife International, 2018), urban populations continue to increase (Rock, 2005). As a result, urban gulls are familiar with the presence of people and anthropogenic food, which makes them an excellent target for studying this species' ecology, cognition and factors that contribute to the success of urban populations as well as resulting human wildlife conflicts.

Their kleptoparasitic nature suggests that they have a high degree of behavioural flexibility (Spencer et al., 2017) and an ability to store, integrate and use information about their environment and others in decision-making (Morand-Ferron, Sol and Lefebvre, 2007; Lee and Thornton, 2021), which may be useful for adaptation to anthropogenic landscapes (Bateman and Fleming, 2012; Plumer, Davison and Saarma, 2014). Recently, urban gulls have been shown to pay attention to humans and human food cues (Goumas et al., 2019; Kelley, Boogert and Goumas, 2020). When approaching a person in possession of food, gulls are aware of human gaze direction (Goumas et al., 2019), and they preferentially peck at a food item that has been handled by a person when given the choice between two identical food objects (Kelley, Boogert and Goumas, 2020).

Based on these recent findings, we sought to continue the investigation of human-gull interactions in a food-related context. To aid future investigations, observational studies were conducted with the aim to create a systematic ethogram that describes distinct attentive behaviours and confirms whether urban gulls pay attention to humans in general or specifically in a food-related context.

Methods

Experiments were conducted at the Brighton beachfront from March to April 2021

between 7:00am and 11:00am on weekdays only, which minimised the chances of pedestrian

disturbances. No research was conducted on rainy days. Pilot surveys had shown that gulls

preferred to remain in the air on days with high wind speeds, and that the gulls would not

engage with the experimenter during low tide since they would be preoccupied with natural

foraging in tidal areas. Hence, no experiments were conducted on days on which low tide

occurred between 7:00am and 11:00am. During all field research, government guidelines

around Covid-19 were followed.

Recordings were made with a GoPro Hero 8 or an Honor 20 phone mounted on a

LINKCOOL tripod. Video recording was paused or terminated when pedestrians walked into

the camera's field of view. It was always ensured that the animals were not disturbed or forced

to engage with the experimenter. All gulls had the freedom to remove themselves from the

situation by either flying or walking away at any time during a trial. The experimenter adhered

to the guidelines for the treatment of animals in behavioural research and testing by the

Association for the Study of Animal Behaviour (ASAB) (Buchanan et al., 2012) and all

necessary ethical approval was obtained from the University of Sussex.

Subjects

Single Herring gulls and groups were approached for observations and the camera was

set up about 10m from the closest individual. Each group was observed five to 20 minutes,

depending on disturbances. Each five-minute block consisted of one of three conditions: a no-

food condition (NFC) during which the birds were observed by the experimenter from behind

the camera, a food condition (FC) during which the experimenter remained in the same position

but retrieved a bag of red Walkers crisps from their backpack, pretending to eat from the bag,

and a paper condition (PC) during which the experimenter took a receipt from their bag and

simulated the rustling noises of a crisps bag along with eating and chewing motions. This would

allow for a three-way comparison between a normal control (NFC), a food condition (FC) and

a secondary control simulating acoustic and behavioural human food-like cues without

presence of a real food item (PC). If groups remained undisturbed and could undergo a

complete recording session of 20 minutes, the following conditions were tested in random

sequence: two NFCs, one FC and one PC.

Video Analysis

Recorded video files were analysed using the Behavioural Observation Research

Interactive Software (BORIS) program (Friard and Gamba, 2016). General variables such as

weather condition (sun, cloudy, rain), average temperature in C° and wind speed in mph during

the time of recording were noted, along with low and high tide time and height on survey days.

Later analysis showed that weather conditions on recording days only affected gull presence,

but not their behaviour. All gulls were given a unique subject ID and their age was recorded as

either juvenile, adult or NA if unsure based on recorded footage. Recordings were then re-

watched until the three selected behaviours of interest, head turns, body orientation relative to

the experimenter and approaches towards them, had been logged for all subjects. These three

distinct behavioural responses were hypothesised to be indicative of attention towards a

person or situation.

Statistics and Modelling

To investigate whether the three selected behaviours were indeed markers of vigilance,

statistical analysis focussed on comparing them across conditions. If they were indicative of

an increase in attention in a food-related context, it was expected to see more head turns and

approaches during FC trials and gulls were hypothesised to orient themselves towards the

experimenter. Head turns and approaches were counted, and the weighted average angular

body position (0-180°) of test subjects relative to the experimenter was calculated for each

individual to obtain one measurement per bird per trial. Furthermore, head turns were divided

by the time a gull was in camera view to give "head turns per gull minute", which was used for

analysis.

All statistical analysis was done in RStudio. First, it was investigated whether the

sequence of trials had an effect on head turn counts. Where Mann Whitney U tests indicated

no significant difference between earlier and later trials of the same condition, head turn counts

were pooled. If the test showed a significant order effect, only first trials were used in the

analysis. To model the effect of condition type on head turns, a quasi-Poisson generalised

linear model was applied to correct for overdispersion (dispersion parameter of 8.19 with a

residual deviance of 874.63 on 126 degrees of freedom). While diagnostic plots did not differ

to those of a negative binomial model of the data, the quasi-Poisson represented a better fit to

the data's variance to mean relationship. For investigation of the effects of condition type on

the weighted average of body position a linear regression model was used. Lastly, a Pearson's Chi-square test was conducted to confirm that there was a relationship between condition type and approach occurrence. Here, the complete dataset (N=211) was used as no order effects were found.

Results

The aim of this observational study was the creation of the systematic ethogram to identify markers of attention. This could then be used to investigate whether gulls specifically pay more attention to humans in a food-related context, and whether acoustic and behavioural human food-like cues without the presence of a real food object are enough to elicit a behavioural response similar to that evoked by a food item. It was found that, compared to NFC trials, attentive behaviours are upregulated during FC trials but not during PC trials which mimicked acoustic and behavioural food stimuli.

The presence of a food stimulus increases head turn counts. After pooling data from trials that were not influenced by order effects, statistical analysis of the effect of condition type on head turns found that during FC trials, counts were significantly increased from NFC trials (NFC=53, FC=22, p=<0.0001) but counts from PC trials did not differ significantly from NFC trials (NFC=53, PC=26, p=0.3), as shown in figure 1A. The model estimates are shown in figure 1B alongside a scatter plot of collected data (dispersion parameter: 8.19, residual deviance: 874.63 on 126 DF, Fisher Scoring iteration: 5). This confirms that head turns are an indicator of increased vigilance in a food-related context.

More gulls faced towards the experimenter when they were in possession of food. The weighted average of angular body position relative to the experimenter differed significantly between NFC and FC trials (NFC=53, FC=22, p=0.0052), but not between NFC and PC trials (NFC=53, PC=26, p=0.81), with more subjects facing 90° or less towards the experimenter during FC trials, as visualised in figure 1C. Figure 1D highlights the model fit alongside the collected data points (Multiple R-squared: 0.081, Adjusted R-squared: 0.062, F-statistic: 4.33 on 2 and 98 DF, p-value=0.019).

Approaches only occurred when the experimenter signalled food. Order effects did not influence approach occurrence and, therefore, the entire data set could be used (NFC=111, FC=58, PC=42). Figure 1E highlights that while no birds started approaching during NFC or PC trials, 14 out of 58 gulls (24.14%) did approach the experimenter during FC

trials, with between one and five approach instances per trial. A Pearson's Chi square test confirmed that there was an association between trial type and approach occurrence (Pearson's Chi-squared test, X-squared=39.56, df=2, p-value=<0.0001, N=211).

Together, these results highlight that gulls pay increased attention to humans in possession of food (FC), but not when they only mimic acoustic and behavioural food-like cues (PC). In turn, this lead to particular behavioural changes in food trials. Head turn counts increased significantly, more gulls oriented themselves towards or perpendicular to the experimenter, and some started approaching, which is not seen in other conditions. In contrast, the acoustic and behavioural human food-like cues given during PC trials were not sufficient to elicit responses similar to those recorded in the presence of a real food item.

Discussion

We have identified three behaviours: head turns, orientation towards an experimenter and approaches, that are upregulated during FC trials only, which shows that they are reflective of increased attention towards people in possession of food, and, with that, confirms that the presented stimulus is interesting to the birds. It is suggested that all three behaviours allow gulls to combine attention towards a potential food source with generally higher vigilance and the possibility to escape when necessary. The fact that PC trials, during which human food-like cues were mimicked, seemed insufficient to elicit behavioural responses similar to those seen in FC trials confirms that the recorded response is specific to a foraging context.

What purpose do these behaviours serve?

Having identified specific markers of attention towards humans in possession of food, we must ask what purpose these behaviours serve, and how this might benefit the birds.

First, approaches can be interpreted as interest in the experimenter, the food item and, potentially, a sign for preparations for a food-stealing attempt. We report that approaches only ever occur in trials where a food item was present, which supports this idea and confirms that the stimulus presented in this condition was attractive to the gulls. The approach rate of the studied population (24.14%) is in line with what was expected based on previous reports and the experimental set-up used in this study. A previous experiment that recorded approaches of urban Herring gulls towards a person in possession of food found the approach rate to be at around 26% (Goumas et al., 2019). In turn, approaches towards a food source that was

presented to Herring gulls at 8m away from the experimenter were recorded to be around 68%

(Kelley, Boogert and Goumas, 2020). Keeping in mind the fact that in our study the food item

had not been removed from the experimenter but remained in their hands the entire time, the

relatively low percentage of potential food-stealers (as indicated by approach attempts) is in

line with our expectations.

Head movements have previously been suggested to be proxies for scanning

behaviours (Fernández-Juricic, 2012), which are often used to identify vigilance rates in birds

(Hart and Lendrem, 1984). While foraging birds have been shown to be able to detect predation

risks, raising their head for scanning increases their detection abilities (Lima and Bednekoff,

1999). Therefore, by interrupting foraging or sleep and turning their head in various directions,

gulls may improve their ability to scan their environment for potential predation risks or foraging

opportunities. As such, the increase in head turns we present in FC trials of this study can be

seen as an indicator of increased vigilance in subjects towards an attractive food item. More

frequent head movements in such a situation may allow gulls to identify a food source and plan

their approach accordingly, while simultaneously keeping watch for competition from other

members of the flock and predation risks.

Lastly, while body orientation itself may not be an example of scanning behaviours,

subjects were shown to face 90° or less towards the experimenter if a food object was present,

which could be reflective of a gull's attempt to prepare for an approach to steal food while

ensuring that escape is possible in case the experimenter were to pose a threat. Predators

that are preparing for an attack orient their head and body towards their target, which is used

by prey to assess immediate predation risks (Book and Freeberg, 2015). At the same time,

since humans can pose a threat to gulls (Goumas et al., 2020), subjects should orient

themselves in a way that allows rapid escape, if necessary, such as facing predators side on,

which has been shown to increase predator detection (Kaby and Lind, 2003). Losing an

encounter as prey (unsuccessful escape and capture) will have more serious consequences

than an unsuccessful foraging attempt (van den Hout et al., 2010), which may help explain

why the birds tend to favour perpendicular positions towards the experimenter, a potential

threat and food source, essentially trading off a good escape opportunity with ideal approach

conditions. The fact that during NFC trials the majority of birds faced away from the

experimenter may support this hypothesis, indicating that individuals may prioritise escape

efficiency in situations where no foraging opportunity is available, or they may simply be

disinterested.

How do gulls identify food objects?

While we did show that the specific food stimulus we presented during FC trials seemed

to be attractive to the gulls, this interpretation does open up questions about the mechanisms

of food choice in gulls, which may influence success rates of future experiments working with

food items. Our PC control trials, which consisted of human behavioural and acoustic food-like

cues without presence of an actual food item, were seemingly insufficient to signal food

availability and, in turn, cause upregulation of attentive behaviours. Instead, occurrence rates

of our focal behaviours remained similar to true NFC control trials. As a result, it seems that

both this and previous studies highlight the fact that gulls specifically pay attention to humans

in possession of food, and that these combined cues can influence approach towards a food

source as well as food choice (Goumas et al., 2019; Kelley, Boogert and Goumas, 2020).

Our observations may indicate that human behavioural cues are only used in situations

where gulls already know the object in question to be a food item. When the experimenter was

in possession of a piece of paper instead of a crisp bag, the acoustic stimuli of the paper

combined with eating (handling the crisps bag, looking inside, reaching inside and drawing the

hand to the mouth) and chewing motions were insufficient to illicit a response similar to that

seen in food trials, where a crisp bag was visible. This suggestion is supported by the fact that

when given the choice about two non-food items, gulls do not peck at the handled non-food

item above chance levels (Kelley, Boogert and Goumas, 2020), indicating that gulls may make

a decision about the nature of an object based on the object's characteristics before attending

to human cues associated with it. As such, the object itself is used to determine whether it is

indeed a food item, while human cues are used to make choices about multiple foraging

opportunities and, therefore, only paid attention to in foraging contexts.

Little is known about what types of sensory cues gulls use or need to identify food

items, but the topic of food choice has been studied in a variety of other species. In primates,

visual cues are used most often to identify familiar food items, while the identification of novel

items relies on olfactory, gustatory, visual and tactile cues (Laska, Freist and Krause, 2007).

Interestingly, the importance of each type of sensory cue varies between species (Laska, Freist

and Krause, 2007) and is associated with their foraging ecology (Rushmore, Leonhardt and

Drea, 2012). To reliably identify preferred food items, folivores have been shown to require

both visual and olfactory cues, while generalists could identify their preferred foods using either

cue alone, and frugivores could identify their favourites using olfactory cues alone while visual

cues by themselves did not suffice (Rushmore, Leonhardt and Drea, 2012). The importance

of olfactory cues in food choice is further highlighted by studies of a variety of taxa. In fruit bats,

foraging activity is altered based on the presence of light, but olfactory cues are used to locate

food items. In addition, they can quickly learn to associate the presence of accessible fruits

with non-fruit scents, such as that of cedar wood oil (Kshitish Acharya, Roy and Krishna, 1998).

Sea turtles have been shown to be able to detect airborne odours and start to display foraging

behaviours when such odours signal the presence of food (Pfaller et al., 2020), suggesting

that, for them, olfactory stimuli alone are sufficient to identify foraging opportunities. Lastly,

models of foraging strategies in sea birds have shown that olfactory senses confer significant

advantages in ocean environments (Bastos et al., 2020), and experimental studies confirm that

some species make use of olfactory cues to locate food (Schreiber and Burger, 2001).

It seems, therefore, that both visual and olfactory cues specifically play an important

role in food choice in a variety of taxa, which may indicate that gulls apply a similar strategy to

identify food objects as such, providing a possible explanation for why human acoustic and

behavioural food-like cues were insufficient to elicit a response similar to that seen when a real

food item is present. Further investigations similar to those conducted with other species will

provide insight into which type of sensory cue is necessary and sufficient for gulls to identify a

food item as such, expanding our knowledge of how gulls use their senses within their

environment and in foraging situations.

Application of the presented ethogram

The above presented results show that urban Herring gulls are capable of modifying

their behaviour in response to humans according to whether food is present or not. Three

distinct behaviours – head turns, approaches and body orientation relative to the experimenter

– are upregulated only when gulls pay attention to an experimenter in possession of food,

highlighting increased attention towards them. As such, these behaviours can be used as

markers of attention towards human cues, which will, in turn, be useful in future studies of

Herring gull behaviour and attention. It has previously been suggested that their success in

urban environments may be due to their cognitive capabilities and high behavioural flexibility

(Bateman and Fleming, 2012; Plumer, Davison and Saarma, 2014), which is what makes them

an interesting subject for future studies of cognition, urbanisation and human-wildlife conflicts.

Aided by the description of attentive behaviours we present here, to expand our

knowledge in this area one could first investigate how such a response, food-dependent

modulation of attention, develops in urban Herring gulls. While our more complex model did

not find an effect of age on behavioural responses, a more detailed investigation would be

useful. Here, we split gulls in "adult" or "juvenile" based on the colouration of their plumage,

but since Herring gulls have a juvenile period of multiple years (Mullarney, Zetterström and

Grant, 2010), differences between first winter juveniles and older individuals may be present.

Investigations of potential age differences would highlight whether this specific attentional

modulation is a learned skill and, if so, when it develops.

Similarly, we may want to ask whether a gull's response would be the same when they

pay attention to other animals they have identified as a potential target for kleptoparasitism, or

whether these behaviours are human-specific. We know that gulls specifically pick more

successful individuals as food-stealing targets (Busniuk, Storey and Wilson, 2020), which may

imply that gulls have a certain degree of knowledge about their targets that allows them to

modulate their approach strategy accordingly. As a result, their behavioural response to a non-

human individual in possession of food may differ from the responses we present here.

Comparisons of how urban gulls attend to food cues from other species and of how non-urban

gulls react to human food cues will provide more detailed insight into whether urbanisation and

frequent contact with people may have caused specific human-centred behaviours to arise in

urban populations.

Lastly, with the ethogram presented here it will be possible to investigate social

contagion in Herring gull groups. Attentional cues may be transferred across a group, even

when direct visual cues of the item are lacking. Previous investigations of vigilance in Herring

gull groups have reported mixed results. Some highlight that vigilance spreads throughout a

group, with individuals interrupting their sleep more often to scan their environment if their

neighbours are more vigilant (Beauchamp, 2009). Others suggest that groups should follow

the "many eyes" hypothesis, according to which individuals decrease their own vigilance when

surrounded by highly vigilant neighbours (Roberts, 1996). Using the above identified

attentional markers we can investigate how vigilance travels through a group of urban gulls,

and how the presence of human food cues could affect this.

Conclusion

We present a systematic ethogram that identifies three specific markers of attention in
urban Herring gulls. Head turns and approaches are upregulated during trials in which a real
food item was present, and gulls face towards or perpendicular to the experimenter more often,
highlighting context-dependent attentional modulation in gulls. Individuals seem to be more
attentive to people in possession of food as well as their surroundings, which could be
indicative of preparations for a kleptoparasitic attack. Subjects may face a trade-off between
ideal approach conditions for a food-stealing attempt and retaining an escape route should the
person pose a threat to them. In contrast, such behavioural responses are not seen in
response to acoustic and behavioural human food-like cues without the presence of a real food
item, which suggests that gulls may identify objects as potential food without relying on human
cues, using those only when making foraging decisions about two food items.

Figures

Figure 1. Upregulation of attentive behaviours during food trials. (A) The box plot graph

shows the number of head turns of each subject per minute during each tested condition, 1st

and 3rd quartiles and the median. During FC trials, head turns per minute were significantly

higher than in NFC trials (p=<0.0001). (B) A scatter plot of the recorded head turns in red with

the model estimates visualised by the grey lines, showing the mean and the 95% confidence interval (CI). (C) Violin plots of the weighted average of angular body position relative to the experimenter during the three conditions, highlighting 1st and 3rd quartiles and the median. During FC trials, orientations differed significantly from NFC trials (p=0.0052), with more gulls facing ≤90° towards and none facing >115° away from the experimenter. (D) Recorded body positions in all three conditions in red, with the grey lines indicating model estimates of the mean and the 95% CI. (E) A histogram of approach instances during all conditions. No gulls tested in either NFC or PC trials approached, while 14/58 or 24.14% of gulls tested in FC trials did. Within one trial, gulls that did approach did so within one to five individual approach instances. A Pearson's Chi-square test confirmed an association between trial type and approach occurrence (Pearson's Chi-squared test, X-squared=39.556, df=2, p-value=<0.0001, N=211). Since trial sequence was not found to have an effect on approach occurrence, the entire data set was used (NFC=111, FC=58, PC=42).

Data availability. The data are available upon request.

Competing interests. We declare we have no competing interests.

Acknowledgements. We thank Professor Pierre Nouvellet (University of Sussex) for his support with the statistical modelling of the data.

References

Bastos, R., Martins, B., Cabral, J.A., Ceia, F.R., Ramos, J.A., Paiva, V.H., Luís, A. and Santos, M. (2020) 'Oceans of stimuli: an individual-based model to assess the role of olfactory cues and local enhancement in seabirds' foraging behaviour', Animal Cognition, 23(4), pp. 629–642. doi:10.1007/s10071-020-01368-1.

Bateman, P.W. and Fleming, P.A. (2012) 'Big city life: carnivores in urban environments', *Journal of Zoology*, 287(1), pp. 1–23. doi:https://doi.org/10.1111/j.1469-7998.2011.00887.x.

Beauchamp, G. (2009) 'Sleeping gulls monitor the vigilance behaviour of their neighbours', *Biology Letters*, 5(1), pp. 9–11. doi:10.1098/rsbl.2008.0490.

BirdLife International (2018) *Larus argentatus. The IUCN Red List of Threatened Species, IUCN Red List of Threatened Species.* Available at: https://www.iucnredlist.org/en (Accessed: 22 August 2021).

Book, D.L. and Freeberg, T.M. (2015) 'Titmouse calling and foraging are affected by head and body orientation of cat predator models and possible experience with real cats', *Animal Cognition*, 18(5), pp. 1155–1164. doi:10.1007/s10071-015-0888-7.

Buchanan, K., Burt de Perera, T., Carere, C., Carter, T., Hailey, A., Hubrecht, R., Jennings, D., Metcalfe, N., Pitcher, T., Peron, F., Sneddon, L., Sherwin, C., Talling, J., Thomas, R. and Thompson, M. (2012) 'Guidelines for the treatment of animals in behavioural research and teaching', 83(1), pp. 301–309. doi:10.1016/j.anbehav.2011.10.031.

Busniuk, K., Storey, A.E. and Wilson, D.R. (2020) 'Herring gulls target profitable Atlantic puffins during kleptoparasitic attack', *Animal Behaviour*, 166, pp. 273–279. doi:10.1016/j.anbehav.2020.05.012.

Fernández-Juricic, E. (2012) 'Sensory basis of vigilance behavior in birds: Synthesis and future prospects', *Behavioural Processes*, 89(2), pp. 143–152. doi:10.1016/j.beproc.2011.10.006.

Friard, O. and Gamba, M. (2016), BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol Evol*, 7: 1325–1330.

Goumas, M., Burns, I., Kelley, L.A. and Boogert, N.J. (2019) 'Herring gulls respond to human gaze direction', *Biology Letters*, 15(8), p. 20190405. doi:10.1098/rsbl.2019.0405.

Goumas, M., Collins, T.R., Fordham, L., Kelley, L.A. and Boogert, N.J. (2020) 'Herring gull aversion to gaze in urban and rural human settlements', *Animal Behaviour*, 168, pp. 83–88. doi:10.1016/j.anbehav.2020.08.008.

Hart, A. and Lendrem, D.W. (1984) 'Vigilance and scanning patterns in birds', *Animal Behaviour*, 32(4), pp. 1216–1224. doi:10.1016/S0003-3472(84)80239-0.

van den Hout, P.J., Mathot, K.J., Maas, L.R.M. and Piersma, T. (2010) 'Predator escape tactics in birds: linking ecology and aerodynamics', *Behavioral Ecology*, 21(1), pp. 16–25. doi:10.1093/beheco/arp146.

Kaby, U. and Lind, J. (2003) 'What limits predator detection in blue tits (Parus caeruleus): posture, task or orientation?', *Behavioral Ecology and Sociobiology*, 54(6), pp. 534–538. doi:10.1007/s00265-003-0665-5.

Kelley, L., Boogert, N. and Goumas, M. (2020) 'Urban herring gulls use human
behavioural cues to locate food', *Royal Society Open Science*, 7(2), p. 191959.
doi:10.1098/rsos.191959.

Kshitish Acharya, K., Roy, A. and Krishna, A. (1998) 'Relative role of olfactory cues and
certain non-olfactory factors in foraging of fruit-eating bats', *Behavioural Processes*,
44(1), pp. 59–64. doi:10.1016/S0376-6357(98)00028-X.

Laska, M., Freist, P. and Krause, S. (2007) 'Which senses play a role in nonhuman
primate food selection? A comparison between squirrel monkeys and spider monkeys',
American Journal of Primatology, 69(3), pp. 282–294. doi:10.1002/ajp.20345.

Lee, V.E. and Thornton, A. (2021) 'Animal Cognition in an Urbanised World', *Frontiers
in Ecology and Evolution*, 9, p. 120. doi:10.3389/fevo.2021.633947.

Lima, S.L. and Bednekoff, P.A. (1999) 'Back to the basics of antipredatory vigilance:
can nonvigilant animals detect attack?', *Animal Behaviour*, 58(3), pp. 537–543.
doi:10.1006/anbe.1999.1182.

Lowry, H., Lill, A. and Wong, B.B.M. (2013) 'Behavioural responses of wildlife to urban
environments', *Biological Reviews*, 88(3), pp. 537–549.
doi:https://doi.org/10.1111/brv.12012.

Morand-Ferron, J., Sol, D. and Lefebvre, L. (2007) 'Food stealing in birds: brain or
brawn?', *Animal Behaviour*, 74(6), pp. 1725–1734.
doi:10.1016/j.anbehav.2007.04.031.

Mullarney, K., Zetterström, D. and Grant, P.J. (2010) *Collins Bird Guide: The Most
Complete Guide to the Birds of Britain and Europe*. William Collins.

Pfaller, J.B., Goforth, K.M., Gil, M.A., Savoca, M.S. and Lohmann, K.J. (2020) 'Odors
from marine plastic debris elicit foraging behavior in sea turtles', *Current Biology*, 30(5),
pp. R213–R214. doi:10.1016/j.cub.2020.01.071.

Plumer, L., Davison, J. and Saarma, U. (2014) 'Rapid Urbanization of Red Foxes in
Estonia: Distribution, Behaviour, Attacks on Domestic Animals, and Health-Risks
Related to Zoonotic Diseases', *PLOS ONE*, 9(12), p. e115124.
doi:10.1371/journal.pone.0115124.

Roberts, G. (1996) 'Why individual vigilance declines as group size increases', *Animal
Behaviour*, 51(5), pp. 1077–1086. doi:10.1006/anbe.1996.0109.

Rock, P. (2005) 'Urban Gulls: Problems and Solutions', *British Birds*, 98, pp. 338–355.

Rushmore, J., Leonhardt, S.D. and Drea, C.M. (2012) 'Sight or Scent: Lemur Sensory

Reliance in Detecting Food Quality Varies with Feeding Ecology', *PLOS ONE*, 7(8), p.

e41558. doi:10.1371/journal.pone.0041558.

Schreiber, E.A. and Burger, J. (2001) *Biology of Marine Birds*. CRC Press.

Spencer, R., Russell, Y.I., Dickins, B.J.A. and Dickins, T.E. (2017) 'Kleptoparasitism in

gulls Laridae at an urban and a coastal foraging environment: an assessment of

ecological predictors', *Bird Study*, 64(1), pp. 12–19.

doi:10.1080/00063657.2016.1249821.