The use of human behavioural cues by urban herring gulls

Submitted by Madeleine Claire Goumas to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, November 2021.

I certify that all material in this thesis that is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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Abstract

Populations of herring gulls (*Larus argentatus*) have declined rapidly in Britain and Ireland, but this species is increasingly breeding and foraging in urban areas and has become a source of human-wildlife conflict. Although there is a large body of literature on the behaviour of herring gulls in traditional rural colonies, urban-dwelling gulls and the behavioural drivers of their apparent success in urban areas have been less studied. Gaining a better understanding of the factors that lead to negative interactions between humans and gulls would provide an insight into how human-gull conflict can be mitigated. As gulls in urban areas often forage on anthropogenic food, they are likely to interact with humans regularly and may therefore make foraging decisions based on human cues. In this thesis, I investigate whether herring gulls use behavioural cues from humans when foraging in urban areas. I first tested whether herring gulls use the direction of human gaze when approaching an anthropogenic food source. I found that herring gulls do respond to this cue: gulls took longer to approach and peck at food when they were subjected to direct gaze. I then tested whether gulls respond specifically to human eyes rather than head direction, and whether this response is influenced by gull age or location. I found that both adult and juvenile gulls responded aversively to direct gaze, and that gulls in urban areas could be approached more closely than their counterparts in rural areas. Next, I considered whether herring gulls are attracted to objects with which humans have associated. To do this, I tested whether herring gulls peck at objects more frequently after observing a human handling the object. I found that the type of object was important: gulls pecked at handled objects comprised of packaged food, but were less likely to approach and peck at handled objects when they were not food-related. Taken together, these results strongly suggest that herring gulls foraging in urban areas use human cues. Finally, I developed an individual-based model to investigate how free-living, wild animals respond to humans in a landscape where some humans provide food or behave neutrally, while others present a threat. I showed that (a) a fast learning rate is adaptive when it would be better to avoid humans but not when it would be less energetically costly to remain close to humans, (b) an ability to recognise individual humans can help animals overcome this problem, but may only be useful if animals repeatedly encounter humans who differ inter-individually in their behaviour, and (c) socially learning about humans is likely to help animals approximate an optimal avoidance strategy. These findings provide an insight into how herring gulls, and potentially other animals, are able to forage successfully in human-dominated environments. Furthermore, by understanding the cues that gulls use, people have the opportunity to modify their behaviour to reduce the frequency of negative interactions with gulls.

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Contents

Figures and Tables

Author's declaration

Several people other than the doctoral candidate contributed to this thesis. Their contributions are as follows:

Introduction

Two sections from a review article entitled "The role of animal cognition in human-wildlife interactions" (Goumas, Lee, Boogert, Kelley, & Thornton, 2020) have been included. These were written by Madeleine Goumas (MG) with feedback from and edits by Neeltje Boogert (NJB), Laura Kelley (LAK), Alex Thornton and Victoria Lee.

Chapter 1

MG devised the study and developed the experimental procedure with NJB and LAK. MG conducted the experiments. Isabella Burns filmed the trials and assisted with locating gulls for the experiments. MG wrote the first draft of the manuscript and revised the manuscript with significant input from NJB and LAK.

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Chapter 2

MG and NJB conceived the idea, and MG, Thomas Collins (TC) and Leo Fordham (LF) developed the method. TC and LF conducted the experiments with oversight from MG. MG wrote the manuscript with significant input from NJB and LAK.

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Chapter 3

MG conceived the idea and developed the protocol with NJB and LAK. MG conducted each trial with assistance from one of the following volunteers who filmed the trials: Tom Holding (TH), Emma Inzani, TC, LF, Angharad Jeremiah and Drew Baigent. MG wrote the first draft of the manuscript and LAK and NJB contributed significantly to the content of the final version. LAK conducted the visual analyses and wrote the corresponding section of the manuscript's supplementary material.

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Chapter 4

MG conceived the idea and developed it with TH, NJB and LAK. MG and TH wrote the code. MG wrote the first draft of the manuscript and TH, NJB and LAK contributed to the final version.

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General Introduction

Conflict between humans and other animals

The human population is expected to reach 8 billion in 2023 (United Nations, Department of Economic and Social Affairs, 2019) and humans now inhabit every continent on Earth (Palinkas, 2003). Humans and domesticated animals currently represent 95% of tetrapod biomass, leaving little space for wild mammals, reptiles and birds (Bar-On, Phillips, & Milo, 2018). Indeed, competition for land and resources is a leading cause of habitat loss (WWF, 2018). The hugely damaging impacts of humans on biodiversity are well-known but show little sign of abating (Barnosky, 2014).

Conflict can occur when interactions between humans and wild animals result in losses to either humans or wildlife, or both (Nyhus, 2016). Human-wildlife conflict is widespread and particularly acute where wild animals have the ability to cause loss of human life or negatively impact livelihoods (Woodroffe, Thirgood, & Rabinowitz, 2005). For example, in Africa and Asia, large felids are killed in retaliation for hunting farmed mammals (Kruuk, 2002). Retaliatory killing is a major factor contributing to the decline of lion (*Panthera leo*) populations in some parts of Africa, and lions are currently classed as “Vulnerable” by the International Union for the Conservation of Nature (Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, 2016).

In Britain, historic conflict between humans and wildlife is evident from the extinction of large carnivores (C. J. Wilson, 2004). However, conflict still occurs between humans and extant carnivores: foxes (*Vulpes vulpes*) can be shot without licence as a preventative measure for protecting domesticated animals (Natural England, 2016), badgers (*Meles meles*) face culling in an effort to decrease the spread of bovine tuberculosis in cattle (Natural England, 2019c), and there have been calls by anglers for a cull of otters (*Lutra lutra*) (Copping & Mole, 2009). Carnivores are not the only animals that face ongoing control. General licences have also been issued by the government-funded body Natural England to kill certain species of bird “to preserve public health or public safety” and “to prevent serious damage to livestock, foodstuffs for livestock, crops, vegetables, fruit, growing timber, fisheries or inland waters” (Natural

England, 2019b). These licences stipulate that lethal control should be a last resort, and encourage stakeholders to use methods that instead deter wild birds or reduce negative impacts by other means. However, there may be little desire for humans to coexist with other animals if there is no incentive for doing so (Dickman & Hazzah, 2015).

Without understanding the behaviour of animals, including how, when and why they act as they do, it is difficult to develop effective solutions to reduce or prevent human-wildlife conflict. For instance, research on the cognitive abilities and social structure of species, the behavioural characteristics that predict conflict with humans, and how problematic behaviours spread in animal populations may inform strategies to mitigate human-wildlife conflict more effectively (Greggor, Berger-Tal, et al., 2016). Applying principles from the study of animal behaviour to conflict management is likely to be fruitful: as an example, the knowledge that behaviour can be modified through conditioning leads to the application of aversive stimuli to prevent wild animals consuming commercial products. For example, acoustic devices, which produce alarming or painful sounds are sometimes used to deter marine mammals from fisheries (Schakner & Blumstein, 2013).

Additionally, it is important to engage with people who are involved in human-wildlife conflict. Solutions cannot be found without considering the needs, values and perspectives of affected parties (Madden, 2004), as well as cultural factors that affect people’s propensity to resort to killing wild animals (Hazzah, Bath, Dolrenry, Dickman, & Frank, 2017). However, it is widely acknowledged among conservation biologists that changing human behaviour would probably prevent many cases of conflict; for example, securing household waste is likely to avert negative encounters with opportunistic animal species, such as black bears (*Ursus americanus*; Baruch-Mordo et al. 2009). As humans continue to expand their range and urbanisation increases, thereby altering entire ecosystems and depleting natural resources, wild animals will often be unable to avoid interacting with humans (McKinney, 2006). Solutions therefore need to be found that benefit both humans and wild animals.

Coping with “mixed messages” from humans

Humans are an unusual species in that they can take a wide range of roles in their interactions with heterospecifics. Humans present a unique challenge to wild animals, as different humans can pose different levels of threat: while many people ignore wild animals, some people kill them, and others actively feed them. Wild animals that live alongside humans would benefit from being able to discriminate between humans taking these vastly different roles.

Humans pose a threat to wild animals for a range of reasons and these individuals or groups can thus be considered “dangerous”. Humans may act as predators, killing animals for food (Ripple et al., 2015), sport (Loveridge, Searle, Murindagomo, & Macdonald, 2007) or even for conservation purposes (Russell et al., 2016). They may also act as competitors and kill animals to prevent or reduce consumption or damage of resources, as mentioned above (Ango, Börjeson, & Senbeta, 2017; Gebhardt, Anderson, Kirkpatrick, & Shwiff, 2011). Animals targeted by lethal practices may benefit from showing heightened fear of humans. For example, an experimental study found that black-billed magpies (*Pica hudsonia*) flew away sooner from an approaching human in rural agricultural areas, where they are persecuted, than in rural parks, where they face no such persecution (Kenney & Knight, 1992). A long-term study found that coyotes (*Canis latrans*) became more active during the daytime after intense persecution from humans had ended (Kitchen, Gese, & Schauster, 2000), and a recent meta-analysis indicated that mammals in areas of high human disturbance have become more nocturnal compared with conspecifics in areas where human disturbance is lower (Gaynor, Hojnowski, Carter, & Brashares, 2018). The type of persecution animals face also appears to be important: crows (*Corvus macrorhynchos* and *C. corone*) are more wary of humans in areas where they are shot rather than cage-trapped, perhaps because associations between humans and dead conspecifics are formed more easily in the former case (Fujioka, 2020). A particularly striking example of how wild animals might learn to evade human predation comes from Diana monkeys (*Cercopithecus diana*), which usually respond to predators by alarm calling and approaching. Human hunters have taken advantage of this by imitating calls of predators and distressed prey. Monkeys in areas where poaching occurs have an increased ability to distinguish between imitations by humans and real alarm calls, and subsequently call less, compared to monkeys in areas where there is no poaching (Bshary, 2001). These studies indicate that individuals of targeted species are able to respond flexibly to direct threats posed by humans. Moreover, these examples show how human perceptions and differences in cultural practices can ultimately shape wild animal behaviour.

Many humans present no direct threat to wild animals. A “neutral” human will either ignore wild animals or observe them from afar, and will not interfere with their behaviour. An example of a neutral human could be someone who allows wild animals to live close by without either deterring or encouraging them. If an animal only ever encounters neutral humans, they are likely to exhibit behaviour that differs from that of animals with experience of dangerous humans. Responding aversively to humans that do not present a threat is suboptimal as it is likely to entail unnecessary energetic costs and reduced feeding time (Ydenberg & Dill, 1986). Animal populations that experience high human disturbance, such as those in urban areas, are often more tolerant of humans than are those in areas of lower human disturbance (Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015). This could be a result of habituation to repeated non-threatening encounters, or reflect population-level differences in tolerance that enable certain individuals to settle in areas where they will be frequently disturbed (Blumstein, 2016).

Of course, humans can intend to be neutral but their behaviour could have unintentional consequences that create positive or negative outcomes for wild animals, e.g. through accidentally dropping food or littering. Additionally, whether or not wild animals make aversive or appetitive associations with humans in general can be out of an individual human’s control. As animals are able to associate events with neutral environmental stimuli (Cassens, Roffman, Kuruc, Orsulak, & Schildkraut, 1980), wild animals may perceive humans as “dangerous” or “rewarding” irrespective of whether that human caused a particular outcome. How animals view neutral humans may also be affected by their previous experiences with other people, and the extent to which they generalise or discriminate between individual humans.

Although many interactions with humans appear to be neutral or negative from the perspective of wild animals, interacting with humans can also be advantageous. Many humans purposefully provide care to wild animals, including through direct feeding interactions (Marion, Dvorak, & Manning, 2008). While such close contact can carry a risk of harm to both humans and wild animals (e.g. from disease and aggression; Orams, 2002), such interactions provide at least short-term benefits and often result in attraction to humans (Donaldson, Finn, & Calver, 2010; Sabbatini, Stammati, Tavares, Giuliani, & Visalberghi, 2006). Humans also provide food indirectly, for example by accidentally dropping food during picnics, and may thus be associated with reward (Marion et al., 2008). Relatively little research has focused on the effects of "rewarding" humans on wild animal behaviour. However, risk-sensitive foraging theory predicts that the cost of failing to respond appropriately to humans in dangerous roles (i.e. by fleeing or hiding) would outweigh the benefits of being attracted to humans in a rewarding role: even if the risk of being killed is low, the risk of starving from a lack of extra food is likely to be far lower (McNamara & Houston, 1992).

Animals may respond differently to different groups of humans and exhibit a specific response only to humans displaying a particular cue, such as a distinctive item of clothing (e.g. Bates et al., 2007). If only a certain behaviour or type of human represents a threat, animals will benefit from attending to these cues rather than those of neutral humans. Animals may respond to cues that are threatening regardless of the species displaying them if they are intrinsically associated with negative outcomes; these cues may or may not require learning. Examples of such general threat cues that affect wild animals' behaviour include direct gaze (discussed below and in Chapters 1 and 2), direct approach (Burger & Gochfeld, 1981) and a fast approach speed (Cooper et al., 2003). Wild animals may also learn to attend to cues that are specific to humans.

Sensitivity to human gaze direction

Animals may use the direction of human gaze to identify and avoid dangerous humans. Gaze direction is an indication of where attention is directed, and human gaze direction is likely to be particularly discernible as humans have forward-facing eyes. Additionally, humans have visible white sclerae which, contrasted against the darker irises, potentially make the direction of their gaze more conspicuous (Kobayashi & Kohshima, 1997). Gaze aversion, whereby animals exhibit a fearful response to another's eye direction, appears to be taxonomically widespread among vertebrates and likely functions as a means of avoiding predation and altercations with competitors (see Davidson et al., 2014 and Davidson and Clayton, 2016 for reviews of gaze sensitivity). Using gaze direction as a cue should enable animals to attend to dangerous or aggressive individuals in the environment while ignoring those that do not pose a threat. Indeed, wild animals of a wide range of species respond differently when a human is looking at them compared to looking away; they typically flee sooner (e.g. Burger et al., 1992; Eason et al., 2006; Bateman and Fleming, 2011; Clucas et al., 2013; Cooper and Sherbrooke, 2015), or take longer to approach food (Carter, Lyons, Cole, & Goldsmith, 2008; Garland, Low, Armstrong, & Burns, 2014; Goumas, Burns, Kelley, & Boogert, 2019) or their nests (Watve et al., 2002) when exposed to direct human gaze.

Animals may not necessarily respond aversively to human gaze in all contexts. Being approached by a human could be perceived as a predation attempt, whereas a human sitting passively while directing their gaze at an animal may have no such connotations. It may even be possible for wild animals to come to associate direct human gaze with reward. In cases of wildlife feeding, for example around duck ponds, human gaze may be appetitive rather than aversive, as a human is likely to direct food towards an individual it is looking at. However, to our knowledge, there has been no research on whether wild animals respond appetitively to human gaze. Interestingly, in a study of hand-raised, captive jackdaws, von Bayern and Emery (2009) found that test subjects only responded aversively to human gaze, measured by latency to retrieve food, when the human was unfamiliar to them. Whether free-living animals adjust their behaviour in this manner has not been tested.

Gaze aversion experiments have not always distinguished between head direction and eye direction, but a response to head direction is not necessarily indicative of a reaction to eyes. In humans and other predators, head direction may be a good proxy for eye direction, and is potentially more salient, and therefore may be a useful cue for wild animals to use. However, using a cue that is only sometimes informative is not optimal. Hampton (1994) showed that captive house sparrows (*Passer domesticus*) attempted to escape most often when his head was facing them rather than turned away, regardless of eye direction. Some studies have found that several other passerine species do appear to pay attention to eyes specifically (American robins *Turdus migratorius*, Eason et al., 2006; European starlings *Sturnus vulgaris*, Carter et al., 2008; American crows *Corvus brachyrhynchos*, Clucas et al., 2013; North Island robins *Petroica longipes*, Garland et al., 2014).

The widespread nature, early-life presence and clear utility of gaze aversion have led to the assumption that such responses to gaze are “innate” (Coss, 1979; Shepherd, 2010). We interpret “innate” in this context to mean that animals do not require prior experience of gaze stimuli in order for gaze aversion to manifest. Although this may be a parsimonious explanation for its documented presence in several vertebrate classes, few studies have actually attempted to address this question. While several species show aversive responses to two horizontally-positioned eye-like stimuli early in development (ray-finned fishes: Coss, 1978; Altbäcker and Csányi, 1990; Miklósi et al., 1995; chickens *Gallus gallus*: Scaife, 1976; Jones, 1980), whether or not experience is required to mediate these responses is unclear and may be species-specific. For example, jewel fish (*Hemichromis bimaculatus*) that were deprived of seeing eyes or eye-like stimuli during early life showed an aversive response to two horizontal eye spots, whereas fish that were raised in the presence of conspecifics did not (Coss, 1979). Conversely, bobwhite quails (*Colinus virginianus*) raised without exposure to human faces tended to ignore the direction of human gaze, whereas those previously exposed to them avoided areas where a human was looking (Jaime, Lopez, & Lickliter, 2009). Without further studies that begin at birth or hatching, and control for exposure to all eyes or eye-like stimuli, it is impossible to conclude that gaze aversion is innate. There is some evidence that attention to eyes or eye-like stimuli may be innate by our definition (see e.g. Batki et al., 2000; Sewards and Sewards, 2002 for evidence from human neonates and other amniotes), and this may facilitate early development of gaze aversion. An evolved mechanism for attending to eye-like stimuli, and an ability to learn quickly, would provide animals with the capacity to use gaze cues.

Individual recognition of humans

Humans that may appear very similar can act very differently. In places where wild animals repeatedly encounter humans that exhibit consistent inter-individual differences in the level of threat they present, being able to accurately identify individual humans would facilitate avoiding risky encounters with dangerous individuals. Conversely, responding fearfully to humans that do not present a threat may lead to reduced feeding opportunities and increased movement, both of which would incur an energetic cost (Ydenberg & Dill, 1986); therefore, responding appropriately to those people who are known to be threatening or rewarding could be advantageous.

In order to recognise an individual, an animal must first be able to discriminate between members of a species, subsequently remember the individual’s features and then match the cues stored in its memory with the observed cues of the individual at a later time (Tibbetts & Dale, 2007). Many animals appear to be able to distinguish between members of their own species, which should be beneficial in social interactions such as pair-bonding (Jouventin, Mouret, & Bonadonna, 2007), attending to offspring (Beecher, Beecher, & Hahn, 1981) and defending territories from unfamiliar intruders (Molles & Vehrencamp, 2001). If animals are able to discriminate between conspecifics, the same cognitive processes may also enable them to discriminate between heterospecifics, such as humans.

Several studies have tested whether wild animals can recognise individual humans. One of the first was conducted on northern mockingbirds (*Mimus polyglottos*): in the experiment, a human repeatedly approached and touched a mockingbird’s nest, thus presenting a salient threat (Levey et al., 2009). Mockingbirds responded to successive approaches by flushing earlier, increasing alarm calling and attacking the intruder. In contrast, their responses to a novel intruder did not differ from those they made in response to the original intruder on their first encounter.

Which features do wild animals use to differentiate between individual humans? Subsequent studies on other bird species have used masks to standardise the appearances of faces and test for discrimination of facial features (Davidson, Clayton, & Thornton, 2015; Marzluff, Walls, Cornell, Withey, & Craig, 2010).

This may be particularly important in recognising individual humans, as humans may change their clothing and hairstyles on a frequent basis. Indeed, humans heavily rely on facial features to recognise each other (Maurer et al., 2007). Experiments that used masks to test individual human recognition in free-living American crows have indicated that facial features are important cues in identifying dangerous humans (Marzluff et al., 2010). Interestingly, although crows scolded masks that had been worn during their capture more than they did previously unseen masks, crows also mobbed a person wearing a hat previously paired with a ‘dangerous’ mask in the absence of that mask, suggesting that crows may sometimes use more conspicuous, but changeable, cues rather than identify individual faces.

In another study, American crows were brought into captivity to assess the neural circuitry underlying their responses to familiar human faces (Marzluff, Miyaoka, Minoshima, & Cross, 2012). The crows were exposed to one of three stimuli: a human wearing a “threatening” mask that had been worn during the test subjects’ capture, a human wearing a “caring” mask that had been worn while feeding the crows while they were in captivity, and an empty room as a control. Positron emission tomography revealed that the sight of both of the masks activated the rostral forebrain, an area associated with memory and learning (Marzluff et al., 2012). Parts of the amygdala and thalamus, areas associated with fear, were activated more strongly at the sight of the threatening mask than the caring mask. A follow-up experiment that used a human wearing a novel mask as a stimulus, either empty-handed or holding a dead crow, found that certain brain areas, such as the hippocampus and optic tectum, were more strongly activated at the sight of the person with the dead crow, which may facilitate learning of danger (Cross et al., 2013). However, additional control conditions are necessary to determine to what extent the sight of a dead crow itself triggers specific neural activity independent of human presence.

Most of the studies testing individual recognition of humans by wild animals have focused on birds, particularly members of the Corvidae (e.g. Marzluff et al., 2010; Lee et al., 2011; Davidson et al., 2015), a family often described as “feathered apes” because of their comparatively large brains (Emery, 2004; Lambert, Jacobs, Osvath, & Von Bayern, 2019). However, a study of feral pigeons (*Columbia livia*) in an urban park indicated that this species may also have the ability to recognise individual humans (Belguermi et al., 2011). The experimenters counted the number of pigeons feeding next to a “hostile” and “friendly” human, where the hostile human had interrupted and chased away pigeons in the training sessions, while the friendly human had kept still and allowed the pigeons to feed. Pigeons discriminated between the “hostile” and “friendly” human, even when the experimenters switched locations and coats, suggesting that pigeons may have been using facial cues. If so, this would show that corvids are not unique among birds in recognising human facial features. This may not be surprising considering the results of a study on honeybees (*Apis mellifera*), which found that these insects were able to discriminate between images of different humans’ faces, and later recognised the target face with a high degree of accuracy (Dyer, Neumeyer, & Chittka, 2005). This indicates that a capacity to learn human facial features is not limited to the comparatively large and complex brains of vertebrates.

It may be expected that only species or populations that have historically been in regular contact with humans would have an ability to recognise individual humans. A study of Antarctic skuas (*Stercorarius antarcticus*) suggests that this may not be the case (W. Y. Lee et al., 2016). Skuas on King George Island, which has been colonised by humans only relatively recently, were repeatedly approached at their nests by one of two “intruders”. On the fourth visit, the intruder was joined by a neutral human, whom the skuas had not seen before, and both wore identical clothes. The experimenters walked in opposite directions away from the nest and recorded which person the skuas followed. All seven skua pairs tested chased after and attacked the intruder rather than the neutral human. This study shows that an evolutionary history of living alongside humans does not appear to be necessary for discrimination of individuals, and suggests that the ability to recognise individual humans could be a general ability originating from a need to recognise individual conspecifics. However, it remains to be shown whether wild animals that are completely naïve to humans would be able to discriminate between individuals.

A study of house sparrows provides evidence that the ability to recognise individual people may not arise from extensive experience with humans (Vincze et al., 2015). Subjects were brought into captivity from the wild, from locations designated “urban” and “rural” according to human population density. They were then exposed to an experimenter wearing different masks. The “hostile” mask was paired with a simulated attack from behind the bars of their cages, while the “non-hostile” mask was worn for encounters where the experimenter stayed still in front of the cage. An unfamiliar mask was also used in the test trials, where the sparrows’ risk-taking behaviour in response to each mask was quantified. Contrary to the authors’ expectations, sparrows from rural but not urban locations showed a difference in response to the hostile and non-hostile masks, with rural sparrows taking more risks in the presence of the non-hostile mask. While this finding might suggest that urban sparrows do not have the ability to recognise individual humans, it may more likely be a result of other factors such as a difference in boldness, particularly as rural sparrows were more risk-averse than urban sparrows when exposed to the unfamiliar mask. It is therefore important to consider variation among subjects when studying their responses to human cues.

In many species, information about danger can spread through a population by social learning, often through observational conditioning, whereby an animal learns from another’s interaction with a stimulus (Griffin, 2004). This can be facilitated by exposure to conspecific alarm calling and mobbing the threatening stimulus, usually a predator. Alarm calls function to alert other individuals in the vicinity to danger, and alarm calling can cause an otherwise innocuous stimulus to be perceived as a threat (Curio, Ernst, & Vieth, 1978). Following up on the finding by Marzluff et al. (2010) that American crows remember people that have previously captured them, Cornell et al. (2011) tested whether this information subsequently spreads to conspecifics. They found that, even five years after the capture event, crows continued to scold the dangerous mask to a greater extent than the neutral mask. The increasing number of crows scolding over time, combined with scolding by lone crows that had never been captured, indicated that the stimulus had been learned socially via observational conditioning, with the sight and sound of conspecifics scolding allowing naïve crows to learn the association. A study of another corvid, the Eurasian jackdaw (*Corvus monedula*), found that just the sound of conspecifics scolding was sufficient to cause a change in behaviour towards a human wearing a particular mask (V. E. Lee, Régli, McIvor, & Thornton, 2019): jackdaws returned to their nest-boxes more quickly when confronted with the “scolding” mask compared to a previously-seen neutral mask. These experiments highlight the potential benefit of learning the cues of individual humans through social means: a subject need not experience a dangerous encounter with a human in order to learn to avoid the same human in later encounters, which could have considerable implications for survival.

The choice of wild animals to interact with humans

While some species actively avoid human-dominated environments, others are able to adapt to them or even exploit them, choosing to settle in urban areas (Blair, 1996). Wild animals can live commensally with humans, making use of anthropogenic food and buildings for nesting, sometimes even relying on human settlements to survive (as in the case of house sparrows; Ravinet et al. 2018). Animals that live alongside humans have the potential to make use of human signals and cues (i.e. information that is deliberately or inadvertently shared, respectively). Most research on human cue use by non-human animals has been on domesticated animals, which are expected to use such cues due to selective breeding and reliance on humans (Hare, Brown, Williamson, & Tomasello, 2002). Research on human cue use by wild animals is often limited to captive animals, but this may provide a poor representation of the behaviour of the free-living members of these species, which are able to choose whether or not to interact with humans and do not rely on them for nourishment. It would therefore be useful to consider whether animals that live in close proximity to humans in the wild are using human behaviour to inform their foraging decisions.

The case of gulls

One group of animals that frequently interacts with humans and consumes anthropogenic food is the gulls (Laridae). The gull family is globally widespread and is comprised of around 100 species (Coulson, 2019). Across their range, there are many places where gulls encounter humans. Roof-nesting has been documented in several species around the world (Dwyer, Belant, & Dolbeer, 1996; Pierotti & Annett, 2001; Rock, 2005; Temby, 2004; Vermeer, Power, &

Smith, 1988). Gulls also engage in direct interactions with humans, and these are often unwelcome. One behaviour that is frequently reported to local authorities is defence of nest sites. During the breeding season, gulls may perceive humans as potential predators and attempt to drive humans away from their nest sites or offspring (Kilpi, 1987), which often fall from roofs into gardens and streets (pers. obs.). Gulls defending their offspring swoop towards the threat, often while alarm-calling, and, if the threat gets particularly close, they may make contact with their feet and sometimes injure people in the process (Rock, 2005). Another gull behaviour that appears to be relatively widespread is human-directed kleptoparasitism (food theft). Whereas chick defence may be seen as an aggressive response to a potential threat, this is a feeding behaviour and may involve gulls swooping to take food from humans, often from their hands (Deering, 2017), which can cause a similar level of alarm in unsuspecting passers-by.

In Britain, two species of gull commonly breed and forage in urban areas and are frequently associated with conflict with humans. These are the herring gull (*Larus argentatus*) and the closely related lesser black-backed gull (*L. fuscus*) (Rock, 2005). Herring gulls are found year-round in coastal areas throughout Britain and Ireland, with a range extending across northern and western Europe, whereas many lesser black-backed gulls migrate and spend the winter in Africa (Coulson, 2019). However, both species have recently been breeding in increasing numbers inland, often selecting the roofs of buildings as nest sites (Rock, 2005). Local authorities receive many complaints each year related to noise, mess and other undesirable behaviour (Trotter, 2019). Gulls are widely disliked: a YouGov poll in 2015 found that only 19% of 1,746 respondents considered them not to be in some way “bad”, and 44% supported a cull compared to 36% opposing such action (Dahlgreen, 2015). Considering the numerous negative media stories about gulls “stealing” food from people (Deering, 2017), much of this negative attitude is likely to be explained by their kleptoparasitic behaviour.

A brief overview of herring gulls

Compared to most members of the Laridae, herring gulls are large gulls, with an estimated mean wingspan of 144 cm and weighing approximately a kilogram (Robinson, 2005). Although both sexes are similar, there is some degree of sexual dimorphism: males are on average larger than females, with longer heads and bills (Coulson et al., 1983), and, while there is a population-level overlap in size, males in a mated pair are larger than their mates (Tinbergen, 1953). Males also form and defend territories (Drury & Smith, 1968). Like all gull species, herring gulls are usually colonial breeders and often forage in flocks (Malling Olsen, 2018).

Herring gulls form monogamous pair bonds that often last throughout successive years (Tinbergen, 1953 and pers. obs.). They produce one brood per year, and the eggs are usually laid in May (Parsons, 1972). The typical clutch size is three eggs (Robinson, 2005). Both male and female share incubation and the feeding of the chicks, which normally fledge 35-40 days after hatching (Robinson, 2005). Juveniles may remain with and be fed by their parents for an extended period of time, occasionally until the start of the next breeding season (pers. obs.). Maturity is not reached until four years of age, evident by a complete transition from brown immature plumage to the white and grey plumage of adults, although some immature gulls attempt to breed at three years of age (Tinbergen, 1953).

Herring gulls are currently on the Red List of Birds of Conservation Concern (Eaton et al., 2015), but the history and geography of their population dynamics are somewhat complex. This species, along with many others, was persecuted in the 1800s, which led to a severe decrease in numbers (Coulson, 2015). In the early part of the twentieth century, the British population of herring gulls began to increase. This was likely due to protection and aided by the availability of anthropogenic food (Coulson, 2015). Fishing discards and waste food at landfill sites provided novel scavenging opportunities. Since around 1970, the population has again decreased, and intensive culling and botulism contracted from feeding at landfill sites are thought to have been responsible (Coulson, 2015). While populations at traditional colonies (i.e. nesting on natural rather than manmade structures) have declined greatly because of these threats, the number of herring gulls breeding on roofs has increased (Rock, 2005). However, relatively little is known about the ecology of gulls that breed in urban environments, and whether such habitats may pose different threats.

The apparent success of herring gulls in urban environments may be partially explained by their diet (Fuirst, Veit, Hahn, Dheilly, & Thorne, 2018). Herring gulls are generalists, and eat a wide range of food. Herring gulls can be seen in coastal locations, foraging on disturbed shoals of fish, scavenging on the carcases of marine mammals and extracting meat from mussels and other aquatic invertebrates. They also forage inland, feeding on earthworms in lawns, flying ants on pavements, and vertebrates such as young rabbits and other birds (Tinbergen, 1953). The widespread availability of anthropogenic food sources in urban and surrounding areas can attract gulls that nest in traditional colonies (Huig, Buijs, & Kleyheeg, 2016) as well as roof-nesting gulls. With an expansive diet breadth that enables foraging in diverse habitats, and with anthropogenic food discards readily available, gulls thus may need not travel far to find suitable food. As herring gulls are one of the most abundant gull species in Britain and Ireland (Coulson, 2019), and are known for nesting on residential roofs (Rock, 2005) and for kleptoparasitism of humans (Deering, 2017), it is likely that they are most commonly implicated in human-gull conflict.

Kleptoparasitism

Interspecific and intraspecific kleptoparasitism, whereby individuals steal food from heterospecifics or conspecifics respectively, is taxonomically widespread among birds and is a common feeding behaviour in gull species (Brockmann & Barnard, 1979; Morand-Ferron, Sol, & Lefebvre, 2007; Steele & Hockey, 1995). Kleptoparasites tend to target foods with long handling times as it is easier to procure these from their hosts (Steele & Hockey, 1995). Food presented by humans is often large in size compared to traditional prey and easy to digest, thus being both a conspicuous and attractive source of nutrition. To the best of my knowledge, no formal research has been conducted on the factors affecting kleptoparasitic behaviour by gulls towards humans and the relative frequency and success rate of such encounters. However, as kleptoparasitism towards other birds and towards humans appears similar, it is likely that such behaviour towards humans represents a diversification of target species.

The frequency of kleptoparasitism among species in an avian family is related to residual brain size rather than body size (Morand-Ferron et al., 2007), implying that kleptoparasites do not rely on mere force to overcome their hosts, but rather that it requires some degree of cognitive skill. It is as yet unclear exactly how kleptoparasites might outwit their targets, but some studies may provide a clue. Research into kleptoparasitism and displacement from feeding areas (a similar behaviour in terms of outcome) has shown that vigilance may be important for avoiding attacks by kleptoparasites and competitors. Taylor (2008) surmised that Arctic skuas (*Stercorarius parasiticus*), a prolific kleptoparasite of other seabirds, approached their targets from outside their field of view to evade detection, although this was not explicitly tested. Beauchamp (2016) found that semipalmated sandpipers (*Calidris pusilla*) were more likely to instigate attacks from behind foraging conspecifics and such attacks were detected less often. Therefore, it may be possible that kleptoparasites, such as gulls, use gaze direction as a cue when foraging, and that human-directed kleptoparasitism may be reduced through increased vigilance and eye contact with gulls.

Research aims

This thesis aims firstly to test whether herring gulls use behavioural cues from humans when foraging on anthropogenic items in urban environments. Chapter 1 investigates whether herring gulls respond to the direction of human gaze in the context of approaching anthropogenic food, and Chapter 2 builds on this work by asking whether gulls' aversion to gaze is in response to eye contact specifically. Chapter 3 assesses whether gulls use the human behavioural cue of handling to decide whether to preferentially approach an object, and whether they respond differently to anthropogenic food vs. non-food items. Given that humans vary in their behaviour towards gulls and other wild animals, Chapter 4 uses an individual-based model to explore the question of when animals would be expected to benefit from foraging alongside humans, with a focus on the ability of some animals to recognise individual humans based on their unique features. Understanding whether gulls in urban areas use direct human cues such as these will provide an insight into how gulls are making foraging decisions in the presence of humans and will have the potential to inform ways of mitigating conflict caused by foraging behaviour.

Chapter 1: Herring gulls respond to human gaze direction

Abstract

Human-wildlife conflict is one of the greatest threats to species populations worldwide. One species facing national declines in the UK is the herring gull (*Larus argentatus*), despite an increase in numbers in urban areas. Gulls in urban areas are often considered a nuisance due to behaviours such as food-snatching. Whether urban gull feeding behaviour is influenced by human behavioural cues, such as gaze direction, remains unknown. We therefore measured the approach times of herring gulls to a food source placed in close proximity to an experimenter who either looked directly at the gull or looked away. We found that only 26% of targeted gulls would touch the food, suggesting that food-snatching is likely to be conducted by a minority of individuals. When gulls did touch the food, they took significantly longer to approach when the experimenter's gaze was directed towards them compared to directed away. However, inter-individual behaviour varied greatly, with some gulls approaching similarly quickly in both treatments while others approached much more slowly when the experimenter was looking at them. These results indicate that reducing human-herring gull conflict may be possible through small changes in human behaviour, but will require consideration of behavioural differences between individual gulls.

Introduction

Interactions between humans and wildlife often have detrimental impacts on a wide variety of taxa, and human-wildlife conflict is a major cause of species declines and limited success of conservation efforts (Woodroffe et al., 2005). Intervention tends to focus on reducing negative effects on humans through managing wildlife populations. However, wildlife management is often ineffective (Walsh, Wilson, Benshemesh, & Possingham, 2012), targets non-problem individuals, or jeopardises the conservation status of the targeted species (Woodroffe et al., 2005). It is increasingly being recognised that, rather than solely imposing controls on wildlife, changes in human behaviour could alleviate these conflicts while also benefiting conservation efforts (Baruch-Mordo et al., 2009).

Conflict between herring gulls (*Larus argentatus*) and humans is an ongoing source of debate and control measures. This species is on the UK's Red list of Birds of Conservation Concern as the British population decreased by 60% between 1969 and 2015 (Eaton et al., 2015) due to rapid anthropogenic change (Rock, 2005). Despite their decreasing overall population size, increasing numbers of herring gulls are breeding in urban areas (Rock, 2005); the traditional nesting sites of cliffs and islets have been exchanged for roofs, and marine prey is sometimes largely substituted with anthropogenic food (Rock, 2005).

As well as being scavengers and predators, herring gulls are kleptoparasites (Brockmann & Barnard, 1979) and take food from both conspecifics and heterospecifics. Herring gulls in urban environments appear to have generalised their kleptoparasitic activities to target humans, resulting in numerous complaints to local authorities and increasing human-herring gull conflict (Rock, 2005). Attempts to decrease this conflict have focused largely on lethal control or deterrents (e.g. birds of prey), which often prove costly and ineffective and ignore species- and individual-specific behaviour (Rock, 2005). Understanding the behaviour of wildlife at both the population and individual level is important in delivering both effective conservation measures and managing negative impacts of wildlife on human wellbeing (Greggor, Berger-Tal, et al., 2016). Therefore, identifying how herring gulls in urban areas respond to human behaviour is likely to be key in developing effective means of mitigating conflict, but has largely been overlooked.

One possible method of lessening problematic behaviour by wildlife is through exploiting natural reactions to perceived threats, such as a sensitivity to gaze. Gaze aversion is the tendency to show a fearful response towards being watched (Davidson & Clayton, 2016), which may be characterised by avoidance or a slower approach towards a desired object or location. It is thought to be an adaptive anti-predator response across a range of vertebrate taxa (Davidson & Clayton, 2016). Several bird species show aversion towards human gaze (Bateman & Fleming, 2011; Carter et al., 2008; Clucas et al., 2013; Eason et al., 2006; Garland et al., 2014; Hampton, 1994; Watve et al., 2002). Nesting American herring gulls (*L. smithsonianus*) left their nests sooner when experimenters approached their nests directly rather than walking past them (Burger & Gochfeld, 1981), indicating that they modify their fleeing response according to subtle differences in human behaviour. However, the authors did not explicitly test for gaze aversion. Here, we exploited a common scenario in coastal towns where herring gulls approach humans for food, and tested whether herring gull approach behaviour towards food was affected by human gaze direction. We predicted that herring gulls would take longer to approach the food source when an experimenter was looking directly at them rather than looking away.

Methods

Test subjects

We studied herring gulls (hereafter “gulls”) in coastal towns in Cornwall, UK, as these individuals are likely to have experienced anthropogenic food and to be habituated to human presence. We targeted gulls that were not in flight nor engaged in antagonistic interactions. Individual gulls or mated pairs inhabit spatially distinct feeding areas (Drury & Smith, 1968), from which they chase away intruders. This, as well as the presence of identifiable gulls (either because they were colour-ringed by the West Cornwall Ringing Group, or because they had individual differences in morphological traits), allowed us to avoid mistakenly testing the same individual multiple times.

Experimental protocol

Experiments were conducted between 16th November and 11th December 2018. We placed 250 g of fried potato chips ca. 1.5 m in front of the experimenter. The food was presented inside a sealed, transparent freezer bag weighed down with a 550 g weight to prevent gulls from eating the food, as rewarding the gull in the first trial might have generated order effects. The experimenter took a crouched position with her body oriented towards the gull to enable a direct line of sight with it once it walked towards the food. The experimenter initially looked intermittently at the gull to locate it, but once in position she used her peripheral vision to watch for it to approach. When the gull started approaching (either placing a foot forward towards the food, or landing with both feet on the ground if starting from an elevated position), the experimenter started a stopwatch and adopted the gaze direction associated with the experimental treatment assigned to the trial.

In the “Looking At” treatment, the experimenter directed her gaze towards the eye(s) of the gull and turned her head, if necessary, to follow its approach path until the gull completed the trial by pecking at the food bag. We counted the number of head movements to control for the possibility that gulls may be responding to head movement alone. In the “Looking Away” treatment, the experimenter turned her head and eyes approximately 60° (randomly left or right) away from the gull and maintained this position until she heard the gull peck at the food bag. If a gull did not touch the food within 300 s of starting its approach but remained in the vicinity, the trial was deemed complete and a time of 300 s was recorded. Only completed trials, where the gull remained in the area, were included in analyses. We recorded approach times to the nearest second. A second experimenter used a Panasonic HC-V770 video camera mounted on a tripod and placed ca. 8 m from the main experimenter to capture trials and verify distances and timings. The same or similar dark clothes were worn by the experimenter for each trial.

We adopted a repeated measures design to assess the effect of gaze direction within individuals. We randomly assigned individuals to receive “Looking At” or

“Looking Away” first, and trial order was counterbalanced across individuals. Second trials commenced 180 s after the completion of the first trial to allow normal behaviour to resume. During this inter-trial interval, we tracked the gull using peripheral vision and concealed the food. Trials in which gulls went out of sight were excluded from the analysis.

To measure the distances between the food and the starting location of the gull, we held an Excelvan laser range finder parallel to the ground and pointed it towards a flat surface where the gull had been positioned at the start of its approach. Approaches were only timed when the gull was level with the food: where gulls began their approach on elevated surfaces, we measured the distance from the position at which the gull landed on the ground. In the cases where gulls began their approach before the experimenter took position, we started the timer, and determined the distance, when the experimenter was in the correct position.

We also determined whether gulls that did not approach on the ground during the trials were motivated to consume the food but had been deterred by the experimenter’s proximity. To quantify this, we recorded if they i) had approached from an elevated position but did not land on the ground (thus not meeting the experimental starting conditions) or ii) approached the packaged food after the 300 s trial within a further 60 s of the experimenter retreating to the camera positioned ca. 8 m away.

Statistical analysis

We analysed the data in R version 3.5.2 (R Core Team, 2021) using a linear mixed-effects model (LMM) from the package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). We log-transformed the approach times (response variable) to satisfy the normality assumptions of the model, and diagnostic plots of the residuals were used to assess the suitability of the model. Fixed effects were treatment (Looking At/Looking Away), the distance between the gull and food at the start of the trial, the distance between the experimenter and food, the presence (i.e. within ca. 8 m radius of the focal gull) of people (yes/no) and other gulls (yes/no), and trial order (to test for habituation). Gull identity was included as a random effect. We compared this full model with one excluding gaze treatment using a Likelihood Ratio Test (LRT) to test whether gaze better explained approach times. As “Looking At” was associated with an increased number of head movements, we also compared the gaze model with one that, instead of gaze, contained the number of head movements as a fixed effect, using another LRT. An independent observer scored all videos and inter-observer agreement was very high (intraclass correlation coefficient (ICC) for gull approach times (n = 38 trials): ICC = 0.99, $p < 0.001$; head movements (n = 38 trials): ICC = 0.93, $p < 0.001$)).

To explore inter-individual differences in approach behaviour, we conducted a Spearman’s rank correlation to test (a) whether individuals’ approach times in “Looking At” were correlated with approach times in “Looking Away”, and (b) whether gulls that took longer to approach in “Looking At” showed the greatest decrease in approach time during “Looking Away”.

Results

We attempted to test 74 herring gulls. Only 27 of these (36%) initiated the start of at least one trial. The remaining gulls either flew away soon after presentation of the food or did not approach on the ground within 300 s. Twenty-three (49%) of the 47 gulls that did not approach during a trial approached the food outside the trial conditions (supplementary material, Table S1.1). Nineteen gulls (26% of all those targeted) completed the paired trials and the analysis is based on these data.

Gulls took significantly longer to approach the food source when the experimenter looked at them vs. away (LMM, effect of gaze in full model: t_{18} = 2.27, $p = 0.037$, Table 1; LRT, effect of gaze when dropped: $\chi^2_8 = 5.41$, $p = 0.020$; supplementary material, Table S1.2). The median difference in approach time between treatments was 21 s. The effect of experimenter gaze direction was apparent while the model also controlled for the gull’s starting distance from the food (LMM, effect of distance: t_{30} = 3.33, $p = 0.002$). Gulls also took longer to approach the food when other people and other gulls were present (effect of people: t_{30} = 2.78, $p = 0.009$; gulls: t_{16} = 4.01, $p < 0.001$). There was no significant effect of experimenter distance to the food (LMM, $t_{18.6}$ = -0.69, p =

0.500) nor of trial order ($t_{17.5}$ = 0.86, p = 0.404) on approach time. Gaze direction was a significantly better predictor of the gulls' latency to approach the food than was the number of experimenter head movements (LRT, χ^2_7 = 2.14, p < 0.0001; supplementary material, Table S1.3). In 10 (53%) of the 19 "Looking At" trials, the experimenter did not move her head.

There was large inter-individual variation in time taken to approach the food ("Looking At" range: 4-300 s; "Looking Away" range: 3-167 s; Figure 1). Six individuals did not touch the food within the 300 s time limit in "Looking At", but all touched the food in "Looking Away". Individual approach times in "Looking At" were positively correlated with approach times in "Looking Away" (Spearman's correlation, S = 562.29, ρ = 0.54, n = 19, p = 0.027), but this relationship appears to be principally driven by two individuals with exceptionally long approach times (> 150 seconds in "Looking Away"; supplementary material, Figure S1.1). Gulls that took the longest time to approach in "Looking At" showed the largest reduction in approach time in "Looking Away" (S = 188.35, ρ = 0.83, n = 19, p < 0.0001; Figure S1.2), suggesting that these individuals were particularly sensitive to human gaze direction.

Discussion

Interactions between herring gulls and humans are increasingly leading to conflict and may have the potential to exacerbate population declines of this species. Characterising the nature of these interactions is therefore an important first step in mitigating negative effects on both humans and gulls. We found that the majority of gulls in urban areas would not approach a food source placed in close proximity to a human, despite many displaying interest in the food, suggesting that most gulls may be too fearful to engage in food-snatching and that this behaviour is likely to be conducted by a select few individuals. Those that did approach were also more hesitant in the presence of other people and gulls. These findings may have implications for management policies: control measures that are aimed at the species or populations as a whole may target non-problem individuals and this could have the potential to be detrimental to this species' conservation status.

We found that human gaze direction significantly affected gulls' latency to approach the food: gulls took less time to approach when the experimenter was facing away vs. looking directly at them. This demonstrates that gulls use behavioural cues from humans when making foraging decisions in urban environments, and that they find human gaze aversive.

Gulls' approach times varied widely, with some touching the food within 10 seconds in both treatments, whereas others did not complete their approach when human gaze was directed towards them. The difference in approach time between treatments was largest for those gulls that took the longest time to approach when being watched, indicating variation in the degree to which gulls find human gaze aversive. This may be because of differences in attention towards the experimenter's eyes or head, variation in boldness or cognitive abilities, or through associative learning during previous interactions with humans (Davidson & Clayton, 2016). If aversion to human gaze is a learned response, those individuals that have been chased away from food by humans may learn to associate human eye contact with potential danger, and therefore this behaviour would only become apparent with increasing maturity and exposure. However, gaze aversion is thought to be an "innate" anti-predatory response (Shepherd, 2010), and thus present in birds from hatching age. There were very few immature gulls in our sample, which may be because adults dominate the prime foraging areas. These birds showed a range of behaviour, but the small number precludes analyses testing for differences in gaze aversion between juvenile and adult birds. At the time when the experiments were conducted, even the youngest generation of gulls would have been several months old, which could be long enough to make associations between eye contact and subsequent human behaviour, or to become habituated to human eye contact. Testing juveniles close to fledging age and comparing their responses to those of adults would help to answer the question of whether gaze aversion requires learning in order to develop.

Gulls may have taken more time to approach food while being looked at because they can take another's perspective and thus have an awareness not only that a human's head and eyes are directed towards them but also that they are actively being watched. However, such perspective-taking remains difficult to disentangle from simpler cognitive processes, such as associative learning, which would generate the same behavioural responses as those produced in response to knowing what another sees, unless a method is used that could unambiguously differentiate between the two hypotheses (Heyes, 2015). Gaze aversion, and gaze sensitivity more broadly, occurs in all three amniote classes and, as such, may have deep evolutionary origins (Wilkinson, Mandl, Bugnyar, & Huber, 2010). Further work that focuses on differences in gaze sensitivity at the individual, population and species level will improve our understanding of the development and evolution of gaze-mediated behaviour. Our experiment tested whether gulls respond to the direction of both the head and eyes. Whether gulls can attend to the more subtle cue of eye gaze direction, independent from head orientation, is still unknown and warrants further study, and would provide a greater insight into how gulls use human gaze cues. During the Looking At trials, the experimenter was able to view the eyes of the gulls and whether they returned her gaze. Whether those gulls that made eye contact with the experimenter took longer to approach was not empirically tested, and attention to human gaze and other human behaviour may be an important predictor of whether gulls approach humans and engage in problematic behaviour. Additionally, other cognitive traits allowing the ability to adapt to anthropogenic environments, such as boldness, neophilia and innovation, may be important in understanding and mitigating conflict between humans and gulls (Barrett, Stanton, & Benson-Amram, 2019).

In summary, our results indicate that the majority of urban herring gulls are unlikely to approach food when humans are nearby. Overall, those gulls that did approach responded to the gaze direction of the experimenter, suggesting that gulls may be more likely to approach food from out of human sight and therefore increased vigilance by humans could reduce instances of food-snatching. Understanding individual variation in behaviour, and responses towards human behavioural cues more generally, may help inform conservation and control strategies for managing conflict between humans and wildlife in a wide range of taxa.

Table 1. *Results of the full linear mixed-effects model of herring gull latency to approach food when the experimenter's gaze was directed at the gull ("Gaze (Looking At)" vs. "Looking Away"), with log approach time (seconds) as the response variable.*

Fixed effects	**Estimate**	**SE**	**DF**	***T***	**p-value**	
Intercept	3.03	2.10	19.1	1.44	0.166	
Gaze (Looking At)	0.650	0.287	17.2	2.27	0.037	
Distance	0.411	0.123	30.0	3.33	0.002	
Other gulls (Yes)	1.50	0.375	16.0	4.01	0.001	
People (Yes)	1.16	0.415	30.0	2.78	0.009	
Exp. distance	-0.972	1.41	18.6	-0.688	0.500	
Trial order (2)	-0.247	0.288	17.5	-0.856	0.404	
Random effect	**Variance**					
Gull identity	0.224					
Correlation of fixed effects						
	Intercept	Gaze	Dist	Oth.gulls	People	Exp.dist
Gaze	-0.081					
Distance	0.07	0.157				
Other gulls	-0.209	0.16	-0.011			
People	0.016	-0.048	-0.304	0.003		
Exp. distance	-0.962	0.003	-0.203	0.191	-0.061	
Trial order	-0.281	-0.097	-0.165	-0.136	0.036	0.117

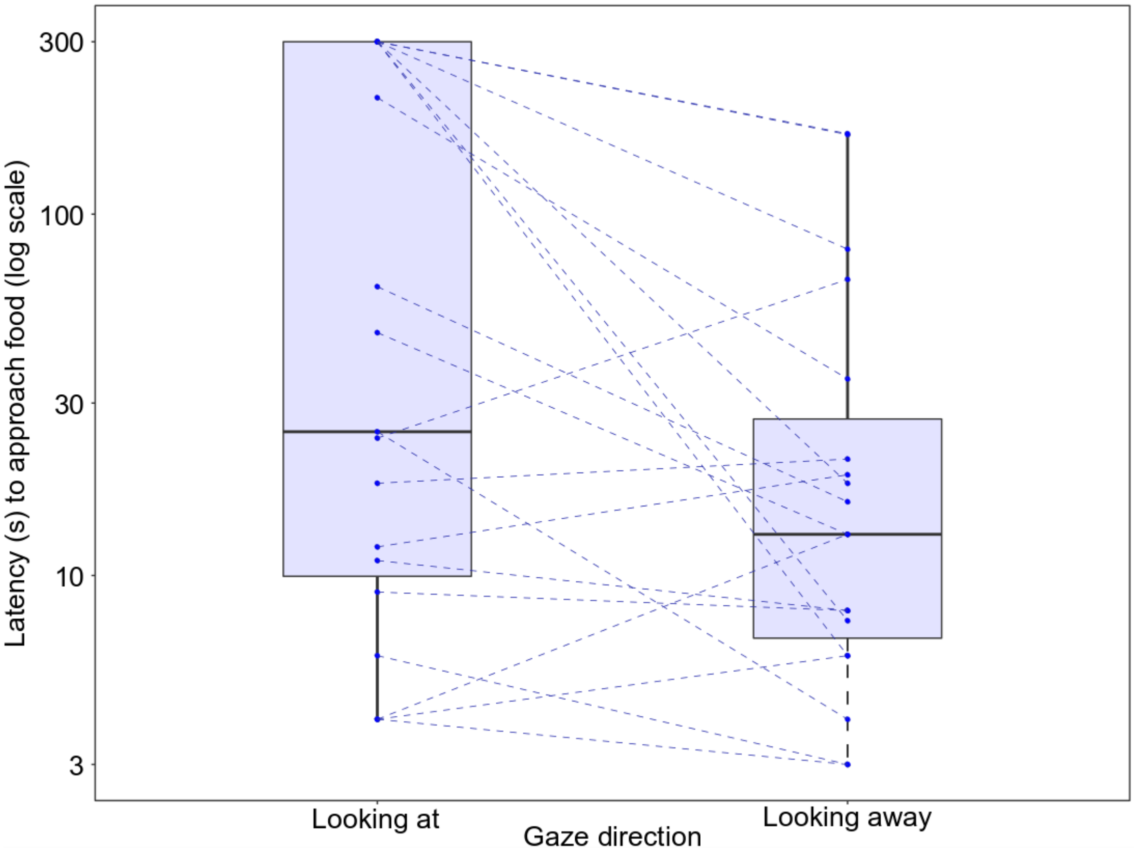

Figure 1. *Paired plot of the time taken for individual herring gulls (n = 19) to approach a food source when an experimenter was gazing at them vs. away. Dashed lines indicate within-individual differences in approach time. The majority of individuals took less time to approach when the experimenter's gaze was directed away.*

Chapter 1: Supplementary Material

Supplementary Methods

Our study sites were in Falmouth (50.2N, 5.07W), Hayle (50.2N, 5.42W), Helston (50.1N, 5.28W), Newquay (50.4N, 5.08W), Penryn (50.2N, 5.12W), Penzance (50.1N, 5.53W), Perranporth (50.3N, 5.16W), Porthleven (50.1N, 5.32W), Portreath (50.3N, 5.29W), St Ives (50.2N, 5.48W) and Truro (50.3N, 5.05W). Exact coordinates for the locations of each of the gulls tested and included in the paired analysis are included in the dataset. We used potato chips (fries) inside a clear bag as bait because this food source is likely to be widely recognised by gulls in coastal towns, and pilot tests showed that they would consistently approach food presented in this manner. We used chalk to mark the placements of the food and experimenter, and measured the distance, to the nearest cm, after each trial to avoid deterring the gull from approaching (i.e. a distance of 1.5 m between the food and experimenter was estimated at the start of the first trial and the exact distance was included in the model in case the experimenter's proximity affected approach time). In some cases, these marks could be used for positioning in second trials on the same test subject. The same or similar dark-coloured clothes (brown/green coat, black jeans and brown boots) were worn by the experimenter for each trial. Trials were not carried out in rainy weather or when winds were high (forecast gusts of 30 mph or more); thus weather variables were not recorded.

To measure the distances between the food and the starting location of the gull, we held an Excelvan laser range finder parallel to the ground and pointed it towards a flat surface where the gull had been positioned at the start of its approach. Approaches were only timed when the gull was level with the food: where gulls began their approach on elevated surfaces, we measured the distance from the position at which the gull landed on the ground. In the cases where gulls began their approach before the experimenter took position, we started the timer, and determined the distance, when the experimenter was in the correct position.

We also determined whether the gulls that did not approach the food and thus did not start an experimental trial had noticed the food and were motivated to try to consume it. Some gulls started an approach towards the food from an elevated surface, such as a wall, but did not come down to the level of the food. Some gulls flew down towards the food and then flew away. These gulls were recorded as not approaching, as they did not meet the criterion of approaching on the ground, but they were recorded as being motivated (i.e. it was assumed that the gull would have continued to approach the food if the experimenter had not been present). For all gulls that did not approach on the ground but remained in the area, the experimenter left the food in place and retreated to establish whether the gulls would approach within 60 s if she was not in close proximity. These data are reported in Table S1.1 below. It was not possible to determine whether or not those gulls that flew away upon the experimenter taking position, or that did not approach while in close proximity to conspecifics, would otherwise have been motivated to approach the food.

Trials were aborted if gulls left the area, either through disturbance by people or dogs, or of their own volition. The number of people present was not recorded: as people were not expected to be present in a large number of trials (i.e. there would be many zero counts), this variable was treated as a binary.

The sex and age of the gulls were recorded where it was possible to do so. Sex was determined by dominance and pair bond behaviour and size differences when present with the mate. Lone gulls and juveniles were recorded as being of unknown sex, with the exception of two particularly large adult individuals with large heads and bills, which were presumed to be male (Coulson et al., 1983). Age was determined by the plumage and was categorised as first calendar year (1CY), second calendar year (2CY), fourth calendar year (sub-adult) and adult (fifth calendar year or older; no third calendar year birds participated in the trials).

Supplementary Results

We were unable to determine the sex of the majority of gulls that participated in our study with certainty. We identified six gulls as being male and one female. Most of the individuals participating in the experiments were adults, with two 1CY, three 2CY and one sub-adult participating. The small sample of juveniles precludes statistical analyses of age effects. Five gulls used in the analysis were present with their mates. Gulls took longer to approach when another gull was present, whether it was their mate or another individual (main text, Table 1). With further study, it may become apparent that sex may explain some of the variation in approach behaviour, but we were unable to test for its effect here.

Table S1.1. *The locations and total numbers of the herring gulls that a) were targeted for the experiment, b) did not approach during the trials but approached the food outside the trial conditions, c) approached but did not complete the first (n = 6) or the second (n = 2) trial, and d) completed both trials (paired treatments).*

Town	**a) Targeted**	**b) No approach, motivated**	**c) Approached during one trial**	**d) Completed paired trial**
Falmouth	24	8	0	5
Hayle	6	5	1	0
Helston	4	0	1	1
Marazion	3	2	0	0
Mousehole	2	2	0	0
Newquay	4	1	0	3
Penryn	6	1	3	1
Penzance	4	0	0	2
Perranporth	1	0	0	1
Porthleven	7	1	1	0
Portreath	1	0	1	0
St Ives	11	3	1	5
Truro	1	0	0	1
TOTAL	**74**	**23**	**8**	**19**

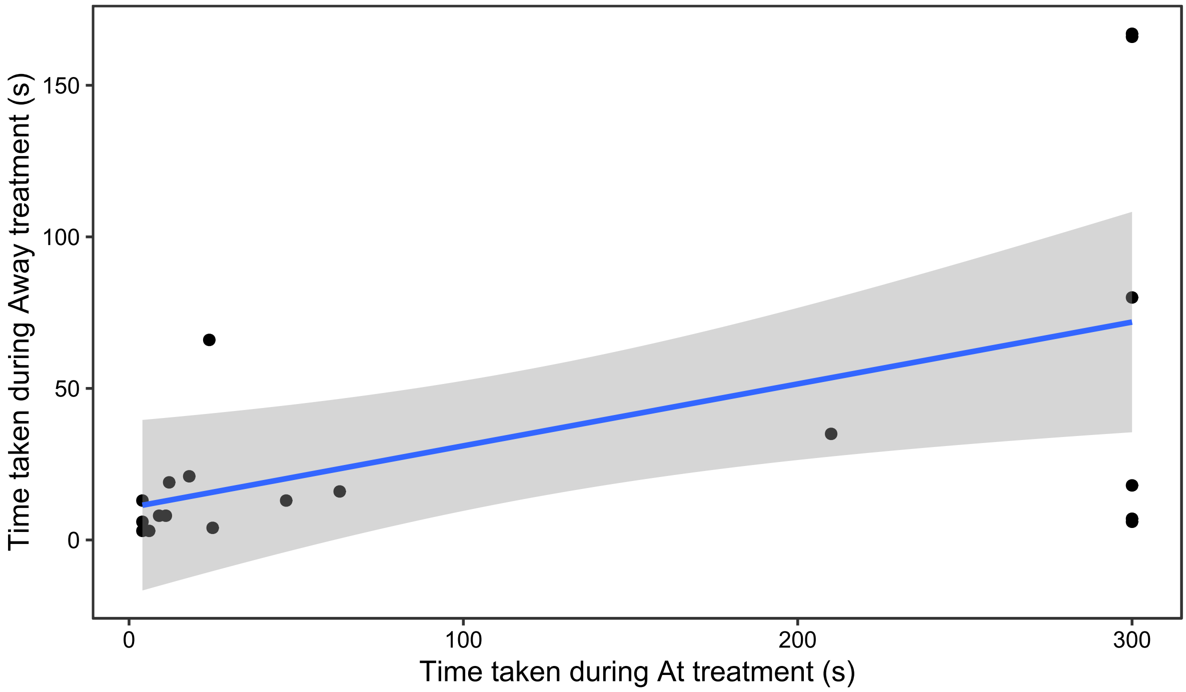

Figure S1.2. *Herring gulls appeared to show some repeatability in their latency to approach a food source: individuals that approached slowly when an experimenter directed gaze towards them also tended to approach slowly when gaze was directed away, perhaps suggesting that herring gulls show consistent inter-individual differences in risk-taking behaviour across contexts. The shaded area represents the 95% confidence interval.*

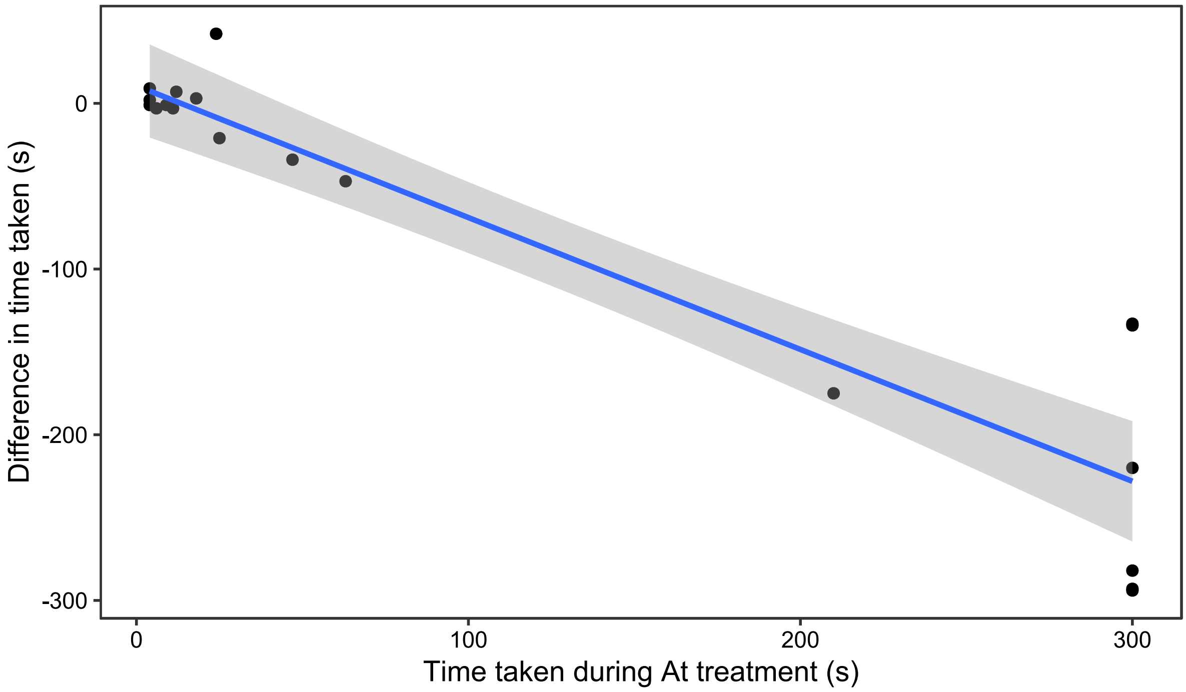

Figure S1.3. *Herring gulls that took longest to approach when an experimenter was gazing at them exhibited the largest decreases in approach times when the experimenter was gazing away. The shaded area represents the 95% confidence interval.*

Table S1.2. *Results of the likelihood ratio test comparing the effect of the addition of gaze treatment to the model. Both models contained the gull's starting distance from the food, the presence of other gulls, the presence of people, trial order and the experimenter's distance from the food. Model 1a included gaze treatment (Looking At vs. Looking Away) whereas Model 2a did not.*

	DF	**AIC**	**BIC**	**logLik**	**Deviance**	**ChiSq**	**P-value**
Model 1a	9	115.63	130.37	-48.81	97.63		
Model 2a	8	119.03	132.13	-51.52	103.03	5.41	0.020

Table S1.3. *Results of the likelihood ratio test comparing the effect of gaze treatment with the effect of head movements. Both models contained gull starting distance from the food, the presence of other gulls and the presence of people. Model 1b featured the number of head movements made by the experimenter as the fixed effect, and Model 2b featured the gaze treatment type. As these two variables were correlated, they were compared in separate models.*

	DF	**AIC**	**BIC**	**logLik**	**Deviance**	**ChiSq**	**P-value**
Model 1b	7	115.09	126.55	-50.54	101.09		
Model 2b	7	112.95	124.41	-49.48	98.95	2.14	<0.0001

Chapter 2: Herring gull aversion to gaze in urban and rural human settlements

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.

Introduction

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 et al., 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; Ádám Miklósi et al., 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 et al., 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 et al., 2006), European starlings *Sturnus vulgaris* (Carter et al., 2008), American crows *Corvus brachyrhynchos* (Clucas et al., 2013) and

North Island robins *Petroica longipes* (Garland et al., 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 et al., 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.

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, 2021) to test whether gull age class, human gaze direction and settlement type (urban/rural) had an effect on flight initiation distance (FID). The appropriate fitting of data to the model was checked using diagnostic plots of the residuals. 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, determined by a likelihood ratio test (LRT).

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 2), as did settlement type and experimenter starting distance (Table 2.1). 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, $t = -2.34$, $N_{\text{at}} = 85$, $N_{\text{away}} = 70$, $P = 0.021$; Table 2.1). Gulls in urban settlements could be approached more closely than gulls in rural settlements (ΔFID: -239.94 ± 88.52 cm, $t = -2.71$, $N_{\text{rural}} = 60$, $N_{\text{urban}} = 95$, $P = 0.008$). 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, $t = -2.43$, $N_{\text{absent}} = 71$, $N_{\text{present}} = 84$, $P = 0.016$). 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 2.1; LRT, effect of dropping interaction terms: $F_2 = 0.96$, $P = 0.386$). Although juvenile gulls appeared to tolerate a closer approach by the experimenter than did adults (ΔFID: -141.30 ± 85.74 cm; Figure 2), gull age did not have a significant effect on FID ($t = -1.65$, $N_{\text{adult}} = 84$, $N_{\text{juvenile}} = 71$, $P = 0.101$; Table 2.1). FID was not significantly affected by the presence of other gulls (Table 2.1).

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 (binomial logistic regression, OR = 2.845, Z = 2.322, N_{ground} = 122, N_{elevated} = 33, P = 0.020; Table 2.2). 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_{rural} = 60, N_{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_{at} = 85, N_{away} = 70, P = 0.065). There was also no significant effect of the presence of other humans (OR = 1.731, Z = 1.305, N_{absent} = 71, N_{present} = 84, P = 0.192) or experimenter starting distance (OR = 1.000, Z = 0.172, N = 155, P = 0.864) on gulls’ response level.

Discussion

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.

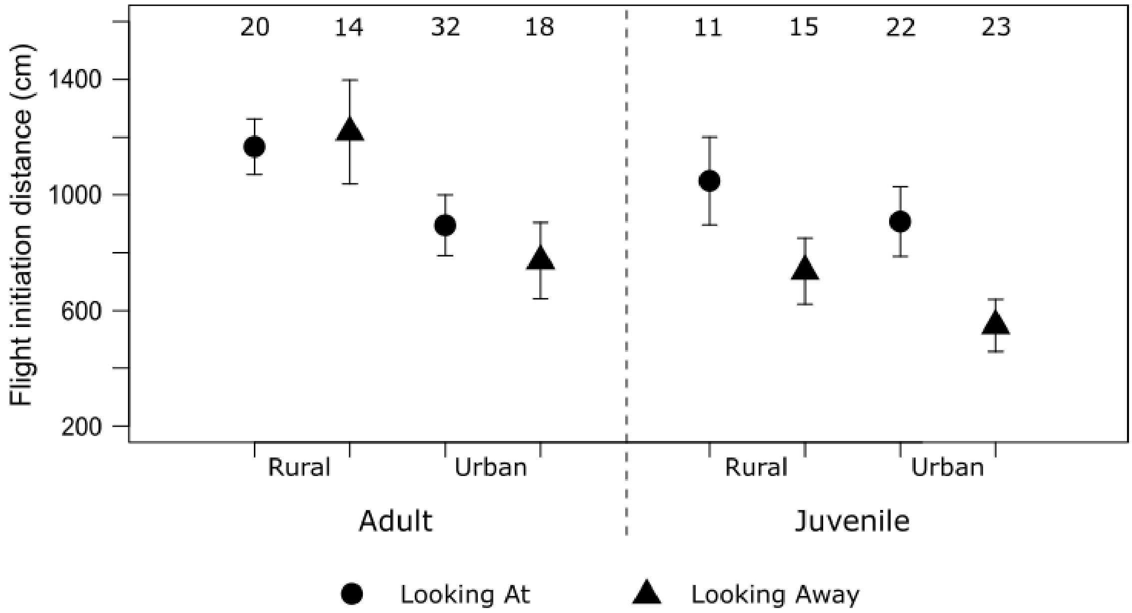

Figure 2. *The effect of human gaze direction (looking at or away) and settlement type (urban or rural) on the flight initiation distances of herring gulls (N = 155). Plot shows means and SEs. Numbers indicate sample sizes for each category.*

Table 2.1. *The results of the linear mixed-effects model testing for an effect of human gaze direction on herring gull flight initiation distance.*

	Estimate	SE	*t*	P
Intercept	-174.20	395.10	-0.44	0.660
Gaze direction (away vs. at)	-195.94	83.70	-2.34	0.021
Age class (juvenile vs. adult)	-141.30	85.74	-1.65	0.101
Settlement type (urban vs. rural)	-239.94	88.52	-2.71	0.008
Humans within 20 m (present vs. absent)	-218.06	89.62	-2.43	0.016
Gulls within 20 m (present vs. absent)	-1.73	90.94	-0.02	0.985
Experimenter starting distance (cm)	0.70	0.17	4.02	< 0.001
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 2.2. *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 2.1).*

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

Chapter 3: Urban herring gulls use human behavioural cues to locate food

Abstract

While many animals are negatively affected by urbanisation, some species appear to thrive in urban environments. Herring gulls (*Larus argentatus*) are commonly found in urban areas and often scavenge food discarded by humans. Despite increasing interactions between humans and gulls, little is known about the cognitive underpinnings of urban gull behaviour and to what extent they use human behavioural cues when making foraging decisions. We investigated whether gulls are more attracted to anthropogenic items when they have been handled by a human. We first presented free-living gulls with two identical food objects, one of which was handled, and found that gulls preferentially pecked at the handled food object. We then tested whether gulls' attraction to human-handled objects generalises to non-food items by presenting a new sample of gulls with two non-food objects, where, again, only one was handled. While similar numbers of gulls approached food and non-food objects in both experiments, they did not peck at handled non-food objects above chance levels. These results suggest that urban gulls generally show low levels of neophobia, but that they use human handling as a cue specifically in the context of food. These behaviours may contribute to gulls' successful exploitation of urban environments.

Introduction

Finding food is essential to survival but is potentially more challenging in changing environments. Humans have altered most environments extensively, and the ability of animals to adapt to human-mediated change may depend on behavioural traits that facilitate the use of anthropogenic resources (Lowry, Lill, & Wong, 2013), such as neophilia, boldness and the ability to learn quickly (Barrett et al., 2019). Whereas some species respond flexibly to endure increasing urbanisation, others are less able to modify their behaviour to cope with the challenges that large-scale urbanisation brings (Sol, Lapiedra, & González-Lagos, 2013). Urbanisation can have a direct effect on mortality rates; for instance, turtle hatchlings orient towards street lighting rather than the sea and are subsequently killed on roads (McFarlane, 1963), and various bird species are vulnerable to collisions with buildings (Loss, Will, Loss, & Marra, 2014).

Although living alongside humans affects many species negatively, it creates new opportunities for others. For example, house sparrows (*Passer domesticus*) and house martins (*Delichon urbica*) commonly nest in or on buildings (Bouldin, 1968; Summers-Smith, 1958), mammalian carnivores (Carnivora) across the world scavenge on human refuse (Bateman & Fleming, 2012) and geckos (Gekkota spp.) increase their feeding opportunities by exploiting the attraction of insects to artificial light (Perry & Fisher, 2006).

Exploitation of anthropogenic resources in urban environments may be acquired through social learning, as in the case of blue tits (*Cyanistes caeruleus*) learning from each other how to peck through the foil caps on milk bottles to obtain cream (Aplin, Sheldon, & Morand-Ferron, 2013; Lefebvre, 1995). Animals are expected to use social learning more than individual learning to locate food and other resources when their habitat is changing at a moderate pace (Boyd & Richerson, 2013), which might, for example, be caused by human activity and urbanisation (McKinney, 2008). Additionally, an existing propensity to learn socially may enable animals to deal with challenges that are directly linked with human activity. For example, American crows can learn the facial features of dangerous humans and spread this information to naïve conspecifics (Cornell et al., 2012).

While social learning between conspecifics may help animals to thrive in urban environments, frequent interactions with humans could result in interspecific social learning from humans themselves. Such interspecific social learning could occur as a result of associations between human presence and strong reinforcers such as food (Whittaker & Knight, 1998). It is possible that wild animals may learn to associate human behavioural cues, such as touching or gesturing, with the location of food. To date, research on the use of human behavioural cues by non-human animals has often focused on domesticated animals, and it has been suggested that domestication has selected for increased attentiveness towards humans (Hare et al., 2002). Dogs, for example, can use a human's gaze direction to locate food (Agnetta, Hare, & Tomasello, 2000), although their performance on this task has been mixed (see e.g. Osborne and Mulcahy 2019). Goats (Kaminski, Riedel, Call, & Tomasello, 2005; Nawroth, von Borell, & Langbein, 2015) and horses (Maros, Gácsi, & Miklósi, 2008; Proops & McComb, 2010) can use human pointing cues to locate hidden food in object choice tasks. Similar research has also been conducted on non-domesticated animals, with some primates (Call & Call, 2009; Essler, Schwartz, Rossettie, & Judge, 2017), elephants (Ketchaisri, Siripunkaw, & Plotnik, 2019; Smet & Byrne, 2013), seals (Scheumann & Call, 2004), dolphins (Pack & Herman, 2004), parrots (Giret, Miklósi, Kreutzer, & Bovet, 2009) and corvids (Schloegl, Kotrschal, & Bugnyar, 2008; Tornick, Gibson, Kispert, & Wilkinson, 2011; von Bayern & Emery, 2009) using human cues to locate food. However, such research on human cue use has been limited to captive animals that often have extensive experience with human caretakers and trainers.

Wild animals that live alongside humans and make substantial use of anthropogenic resources are likely to have many opportunities to make use of human behavioural cues, but this has rarely been studied. Herring gulls are one such example of an animal species that has increased in numbers in urban areas and is often observed feeding on food discarded by humans (Pierotti & Annett, 1991). We recently found that herring gulls are aware of human gaze direction when approaching a food source placed in close proximity to a human, and that they take longer to approach the food when human gaze is directed at them versus away (Goumas et al., 2019). However, it is not known whether gulls might actually learn from humans about novel foraging opportunities. In our previous study, gulls were attracted to the placement of a bag of chips on the ground (Goumas et al., 2019). It is possible that the gulls were attracted simply to the sight of food, but it is also possible that, through repeated exposure to humans, observing the act of the experimenter handling the food may have attracted their attention. Gulls may therefore use a form of social learning called “local enhancement” (Hoppitt & Laland, 2013) when foraging in areas populated by humans, whereby they are drawn to an object at a particular location after observing a human interacting with the object at that location.

We aimed to test whether human behavioural cues increase the probability of a gull interacting with an object, measured as the number of gulls making contact with the object by pecking at it. We first tested whether gulls would be more likely to peck at a food object that they had previously observed being handled by a human compared to an identical, non-handled food object. We then tested whether gulls would be attracted to any object previously handled by a human by repeating the experiment with similarly sized non-food objects. The aim of this second experiment was to determine whether human behavioural cues alone can attract gulls to peck at a particular item, or if herring gulls are only attracted by human behavioural cues when they are directed towards food objects.

Methods

Test subjects

We tested adult herring gulls in urban locations in South West England (approx. 50°N, 5°W; see Supplementary Table S3.1 for location details). We selected individuals that were in resting positions on the ground or on elevated structures (e.g. fences or lamp posts), and where the ground in front of the gull was flat and consisted of concrete, sand or short grass. Experiment 1 was conducted between 19th March and 28th May 2019, and Experiment 2 was conducted between 14th June and 25th July 2019. All trials were conducted by the same experimenter (MG) during daylight between 0630 and 2115 hours, and were recorded by a second experimenter who used a Panasonic HC-V770 video camera mounted on a tripod and was positioned ca. 10 m away from the objects presented in the experiments.

Experiment 1: Are gulls more attracted to the handled than non-handled food object?

The experimenter (MG) used two identical black plastic buckets (rim diameter 250 mm, 180 mm deep) to conceal two identical food items that were taped on top of, and weighed down by, dark grey slate tiles (100 x 100 mm, weight ca. 250 g) to reduce the chance of the gulls flying off with them. The food items were ‘Ma Baker’ blueberry flapjacks (130 x 50 x 20 mm, 90 g) in their original plastic wrappers (Supplementary Figure S3.3, left object in each picture). We chose these food items because they were identical in size, shape and appearance, with conspicuously coloured (blue) labels, and they were in transparent packaging that allowed the food to be partially seen.

MG held a black bucket concealing the food/tile item (hereafter referred to collectively as a ‘food object’) in each hand and approached the gull so that it was approximately 8 m directly in front of her, at which point she placed the buckets on the ground with the food objects concealed underneath. To do this, she crouched down and outstretched her arms 90° to the left and right so that the food objects were equally spaced either side of her body and equidistant from the gull (Figure 3). The food objects were positioned in the same orientation with the long axis of the flapjack pointing towards the gull and were not visible to the gulls before the removal of the buckets. MG wore dark glasses to avoid giving eye gaze cues.

After removing the two buckets to reveal both food objects simultaneously, MG placed the buckets behind her, picked up one of the two food objects and stood up. MG alternated handling the left vs. right object between completed trials. MG used a stopwatch to record a time of 20 s, during which she handled the object by picking it up and raising it up towards her face. She then repositioned the object in the same location, taking care to ensure that it remained in the same orientation as the other object, picked up the buckets and retreated to a position ca. 10 m away. If gulls moved while MG was handling the object, she oriented her body so that she continued facing the gull and the two objects remained equidistant at right angles to her body upon replacement of the handled object. MG mentally noted the position of the gull at the time when she replaced the handled object, and this was verified with the video footage. She monitored the gull for an approach within 120 s of the object being repositioned and recorded which object the gull pecked at. The time taken for approaching gulls to peck at an object was recorded. A trial was considered “complete” when a gull pecked at one of the presented objects. The experimenter terminated the trial if the gull walked or flew away.

Immediately after each trial, MG measured the distance between the presented food objects and the gull, and the gull’s elevation from the ground at the point in time when she replaced the handled object, in case these variables affected the gulls’ choices through differences in viewing distance. Because there was also some variation in how far apart the objects were placed, MG also measured the distance between the objects after complete trials. We avoided conducting trials when there were humans or conspecifics other than mates (see Supplementary Materials) in close proximity (within ca. 10 m from the objects or focal gull) and ended trials if the gulls were disturbed by humans or other animals. These trials were therefore not used in analyses. After each trial, the food objects were checked and replaced if damaged.

For incomplete trials in which gulls did not peck at either of the objects, we measured the distance between the objects and the gull at the time of the object being replaced and the elevation of the gull from the ground. These incomplete trials included gulls that remained in their original location for 120 s after the food object presentation and those that approached the objects by walking towards them but did not peck at either object. For all trials, we recorded the time of day to account for daily variation in motivation to feed and/or approach objects, and whether the gull’s mate was present in case this affected the focal gull’s behaviour. We also recorded the number of gulls that flew or ran away upon MG initiating the trials.

Experiment 2: Are gulls more attracted to the handled than non-handled non-food object?

Having found an effect of human handling on herring gulls' choice of food objects (see Results), we tested whether this effect would generalise to non-food objects. We used blue sponges cut to the same size and shape as the food objects (weight 10 g) and repeated the above experiment with a new sample of gulls so that subjects would not be familiar with the experimental setup. By choosing different test locations, we could reliably ascertain that none of these gulls had been tested in the first experiment, owing to the territoriality of herring gulls (Drury & Smith, 1968).

Statistical analyses

Statistical analyses were conducted in R version 3.5.3 (R Core Team, 2021). For each experiment, we used a generalised linear model with a binomial error distribution to test whether gulls' choice of object (left/right) was influenced by which object the experimenter had handled (left/right). The model included the following potential confounds: the distance between the two objects, the distance between the objects and the gull and the elevation of the gull from the ground. Diagnostic plots of the residuals were used to ensure appropriate fitting of data to the model.

To test which factors affected whether or not gulls approached the objects (regardless of whether the gulls pecked at them), we used a generalised linear model with binomial error distribution on the data for both experiments combined and included the following variables as predictors of approaching an object (yes/no): object type (food vs. non-food), the distance between the objects and the gull, the elevation of the gull from the ground at the time of the object being replaced, the time of day and whether the gull's mate was present. As some gulls approached the objects without pecking at either of them, we used another generalised linear model with binomial error distribution to test whether the same variables affected whether or not approaching gulls pecked at either of the presented objects. We report here the results of the full models and the odds ratios (OR) of each predictor (the exponential of the regression coefficient). An OR of 1 indicates that exposure to an experimental treatment (e.g. handling) has no effect on the odds of an outcome of interest occurring. An OR > 1 indicates that the treatment is associated with a higher odds of the outcome occurring and an OR < 1 (bounded by 0) indicates that the treatment is associated with a lower odds of the outcome occurring.

To determine whether gulls' behaviour might be affected by their perception of the two different objects used in experiments 1 and 2, we quantified their appearance in terms of visual contrast and visual acuity using avian visual models (see Supplementary Methods).

Results

Experiment 1: Are gulls more attracted to the handled than non-handled food object?

We presented 38 herring gulls with the two food objects. Twenty-six gulls approached the objects and 24 pecked at one of the objects (see Supplementary Table S3.1). Human handling of a food object had a significant effect on the gull's choice of which object to peck at (binomial GLM, OR = 20.199, Z = 2.196, p = 0.028; Table 3): 19 (79%) of the 24 participating gulls pecked at the food object that the experimenter had handled. There was no significant effect on food object choice of the gull's distance from the objects, the gull's elevation from the ground or the distance between the objects (Table 3).

Experiment 2: Are gulls more attracted to the handled than non-handled non-food object?

After completing the food object trials, we presented 41 experimentally naïve herring gulls with the two non-food objects (blue sponges cut into the same size and shape as the flapjacks presented in Experiment 1). Thirty-two gulls approached the objects and 23 pecked at one of these objects (see Supplementary Table S3.1). Fifteen (65%) of these gulls pecked at the handled non-food item, which was not significantly different from chance levels (binomial GLM, OR = 7.484, Z = 1.183, p = 0.237; Table 3). There was no significant effect of the gull's distance from the objects, the gull's elevation from the ground or the distance between the objects (Table 3).

Do gulls behave differently towards food vs. non-food objects?

All gulls that pecked at one of the two presented objects did so within 42 seconds of the experimenter replacing the handled object. There was no significant difference in the time taken for a gull to peck at an object in each experiment (mean ± SD, food objects: 18.5 ± 2.07 s, non-food objects: 17.9 ± 2.15 s; see Supplementary Table S3.3).

There was no significant difference in the number of gulls that approached the non-food objects compared to the food objects (binomial GLM, OR = 0.830, Z = -0.255, p = 0.799; food object trials: 26 of 38 gulls, non-food object trials: 32 of 41 gulls). Whether gulls approached the objects was not significantly affected by the time of day (OR = 0.999, Z = -0.937, p = 0.349), the elevation of the gull from the ground at the start of the trial (OR = 0.998, Z = -1.409, p = 0.159) or whether the mates of gulls were present during the trials (OR = 1.061, Z = 0.067, p = 0.946). However, the distance between the objects and the gull at the time the experimenter replaced the handled object was a significant predictor of whether gulls approached the objects (OR = 0.996, Z = -3.043, p = 0.002), with gulls significantly less likely to approach when objects were placed further away from them.

Of those gulls that did approach the objects, significantly fewer pecked at an object in the non-food trials than the food trials (binomial GLM, OR = 0.163, Z = -0.255, p = 0.046; food object trials: 24 of 26 gulls, non-food object trials: 23 of 32 gulls). There was no significant effect of the time of day (OR = 1.002, Z = 1.263, p = 0.207), the distance between the objects and the gull (OR = 0.997, Z = -1.343, p = 0.179), the elevation of the gull from the ground (OR = 1.004, Z = 1.075, p = 0.283) or whether the gull’s mate was present (OR = 1.747, Z = 0.472, p = 0.637).

Perception of food and non-food objects

Both food and non-food items were easily discriminable from the grey tile background, and each other, in both colour and luminance (see Supplementary

Table S3.4). The non-food object was particularly salient against the grey background tile. Gulls could also visually resolve details of the food and non-food objects throughout the trials (i.e. at distances ranging from 30 cm to 8 m) based on our acuity analysis (Supplementary Figure S3.3).

Discussion

Despite interactions between humans and wildlife becoming increasingly common, little research has been conducted on how wild animals may use direct human cues to exploit anthropogenic resources in urban environments. Here, we tested whether herring gulls use human behaviour to locate food. Gulls were significantly more likely to peck at a food object that a human had handled than an equally accessible, identical object that had not been handled. This shows that human handling of food attracts the attention of gulls and that handled food is more attractive than food that gulls have not observed being handled.

To determine whether this attractive effect of human handling was a result of the experimenter drawing attention to the presence of food or if handling alone was sufficient to motivate gulls to peck at the objects, we repeated the experiment using an identical protocol but instead presented non-food objects. Gulls did not peck at the handled non-food object above chance levels, suggesting that the appearance of food is likely to be particularly important in drawing gulls' attention to a specific object or location.

Although more gulls pecked at the handled food object compared to the handled non-food object, the total number of gulls pecking at either of the objects was similar in the food and non-food object trials. This indicates that, while visual cues of food appear to be important in making foraging decisions, gulls are also attracted to objects without these food cues. Food cues may include the appearance of the food itself as well as the plastic packaging that is used to wrap many different types of food items and thus may be associated with food. We also cannot rule out other effects on gulls' motivation to explore objects, especially as the food trials were completed before the non-food trials were started. During the non-food trials, many gulls would likely have had dependent chicks to feed and may have approached objects more readily in search for food than at other times of the year. However, within each experiment there was no significant effect of date on the number of approaches or pecks at food items (ten-week test duration) or non-food items (six-week test duration; Table S3.2).

Despite similar numbers of gulls approaching food and non-food objects, more gulls approached the objects without pecking at them in the non-food trials than in the food trials. This suggests that gulls may approach objects before distinguishing what they are, and discriminate between types of object at a closer distance. It is improbable that the gulls had previously encountered the exact food and non-food objects we presented, and it is likely that they were initially attracted to both types of object to determine whether they contained or were composed of food. Our results imply that, while gulls are attracted to non-food objects, and many peck at them, they may be more selective or cautious once they can observe such objects more closely.

It is perhaps not surprising that more gulls pecked at the objects associated with a food reward, but it is difficult to determine why so many gulls also pecked at the non-food objects. It may be worthwhile for urban herring gulls to peck at novel objects of any type if there is a chance that they could contain food. It is possible that the gulls that pecked at the non-food objects did so because these objects did not appear sufficiently different from food, but this seems unlikely because food is rarely the colour of the objects we chose (completely blue sponges), nor were the objects shiny as in the case of most food packaging. Furthermore, our visual models demonstrate that gulls could visually discriminate between the food and non-food items, but also that the non-food item was more salient against the visual background and so may have been more conspicuous or attractive

There may be several reasons why some of the gulls pecked at objects that were not handled by the experimenter. Firstly, it is conceivable that the presence of the experimenter alone was sufficient to create an effect of local enhancement (Hoppitt & Laland, 2013), with gulls’ attention being drawn to the general location of the object presentation including the non-handled object as it remained in view while the experimenter handled the other object close by. In a study of horses, test subjects were more likely to choose feed buckets that were in close proximity to the experimenter (Krueger, Flauger, Farmer, & Maros, 2011), indicating that direct contact with the object is not necessary to generate an effect. There may also have been an effect of stimulus enhancement, whereby a demonstrator's interaction with an object results in an observer being more likely to interact with an object of the same type (Hoppitt & Laland, 2013): if gulls saw that the handled object was identical to the non-handled object, they may have been drawn to either object equally as there would be no apparent difference in consequence. Gulls may have pecked at handled food objects more often than handled non-food objects owing to having learned from previous experiences in their urban habitat that food packages are usually opened by humans and thus handled food objects tend to be more profitable. However, it is far less likely that the gulls would have had previous experiences of human handling making food accessible from the type of novel, non-food objects we presented.

As many gulls approached and pecked at novel objects, this implies that they have a low level of neophobia (fear of novelty), and could even be neophilic (attracted to novelty), which may facilitate their successful exploitation of urban environments (Barrett et al., 2019). A high exposure to anthropogenic items could have influenced this behaviour, with gulls having perhaps learned that objects of a wide variety of shapes, sizes and colours may have food concealed inside, and tests specifically aimed at measuring neophobia or neophilia would be required to fully understand gulls' perception of novel objects (Greggor, Thornton, & Clayton, 2015). It is possible that urban-living gulls may categorise anthropogenic items by similarities in physical features (e.g. size, shape, material) in the same way that jackdaws (*Corvus monedula*) in urban areas appear to be able to categorise food litter (Greggor, Clayton, Fulford, & Thornton, 2016). In addition, gulls may be attracted to handled food objects not because of the appearance of food but because food packaging is associated with food.

Although the majority of gulls that remained in the area after presentation of both object types approached, we found that they were less likely to do so when the objects were placed further away from them. This could have been because gulls were less able to see the objects clearly, but our visual analyses indicate that this may be unlikely. An alternative explanation is that some of the gulls that pecked at the objects began approaching before the experimenter repositioned the object, thus the distances would be shorter for these individuals, as the distance was measured from the position of the gull at the time of the handled object being replaced. Additionally, the experimenter was aware of behavioural cues from the gulls and was wary of placing the objects too close in order not to cause them to flee, and fearful gulls are unlikely to approach.

Individual differences may also explain the differing choices of gulls in the trials. While the choices in the non-food object trials may have been random, they could also be representative of different strategies being used by different individuals. There may be variation in gulls’ attentiveness towards humans, which would influence their ability to use human cues and could partly explain both whether gulls approached and whether or not they pecked at the handled object. Research methods that seek to quantify the direction of attention of gulls will provide a further insight into how gulls utilise cues from humans.

Our experimental setup potentially selected the least fearful individuals in the population, as only those that did not flee when the experimenter approached or placed the buckets were tested. Consequently, the patterns in behaviour may not be representative of all urban-living herring gulls, and may not be representative of gulls living in areas that are less populated by humans. Nevertheless, the individuals we tested are the ones that are most inclined to interact with humans and potentially be involved in “nuisance” behaviour (Barrett et al., 2019). Increasing our understanding of these individuals and how they make foraging decisions will be beneficial in generating methods to reduce negative interactions between humans and herring gulls without compromising this species’ conservation status.

Other research on human cue use by wild animals has been restricted to animals that have been to some degree, and sometimes extensively, socialised with humans (Ádam Miklósi & Soproni, 2006). It is unlikely that herring gulls would use human cues had they not had previous experience of humans and associated human activity with food litter. Although studies on social learning have largely focused on intraspecific information use, it is widely recognised that social learning between heterospecifics is widespread and confers many of the same benefits as intraspecific social learning, as well as other benefits such as reduced competition (Avarguès-Weber, Dawson, & Chittka, 2013). Gulls rely extensively on conspecifics to locate food and often procure food after watching other gulls flocking to food sources (Frings, Frings, Cox, & Peissner, 1955). Using humans as an additional source of information is likely to be advantageous if there is a reliable association between humans and the availability of food.

The previous research on human cue use by other animals has usually involved object-choice tasks in which food is hidden and not directly touched by humans (e.g. Giret et al. 2009; Nawroth et al. 2015). The animals in these studies are usually tested on their understanding and use of gestures rather than direct experimenter handling of an object, and as such our results cannot be directly compared. However, our study is similar in design and results to that conducted by Schloegl et al. (2008), where captive, hand-raised ravens preferentially touched objects that had been handled by the experimenter, and indicates that free-living animals are able to learn from humans in a similar manner as captive animals. Research that assesses the relative importance of human behavioural cue use to animals in urban environments and the ontogeny of such behaviour will aid in understanding the ecological drivers and cognitive mechanisms of learning from humans.

It is highly unlikely that herring gulls are the only wild animals to use human behavioural cues in urban areas. As urbanisation increases, more wild animals will come into contact with humans and anthropogenic items. There may be an increased number of incidences of individuals of certain species displaying problematic behaviour, which can create conflicts between human activity and conservation (Greggor, Clayton, Phalan, & Thornton, 2014). Additionally, although purposeful provisioning of wildlife may in certain cases appear to be beneficial (such as the feeding of garden birds; Plummer et al. 2019), being attracted to anthropogenic items and feeding on anthropogenic food can be harmful for wildlife (De León et al., 2018; Wilcox, Van Sebille, Hardesty, & Estes, 2015). A more comprehensive understanding of the cues that cause wild animals to engage in interactions with humans is likely to be key in developing preventative measures that not only reduce negative encounters for humans but also potentially lessen the impact of anthropogenic items on wild animal populations.

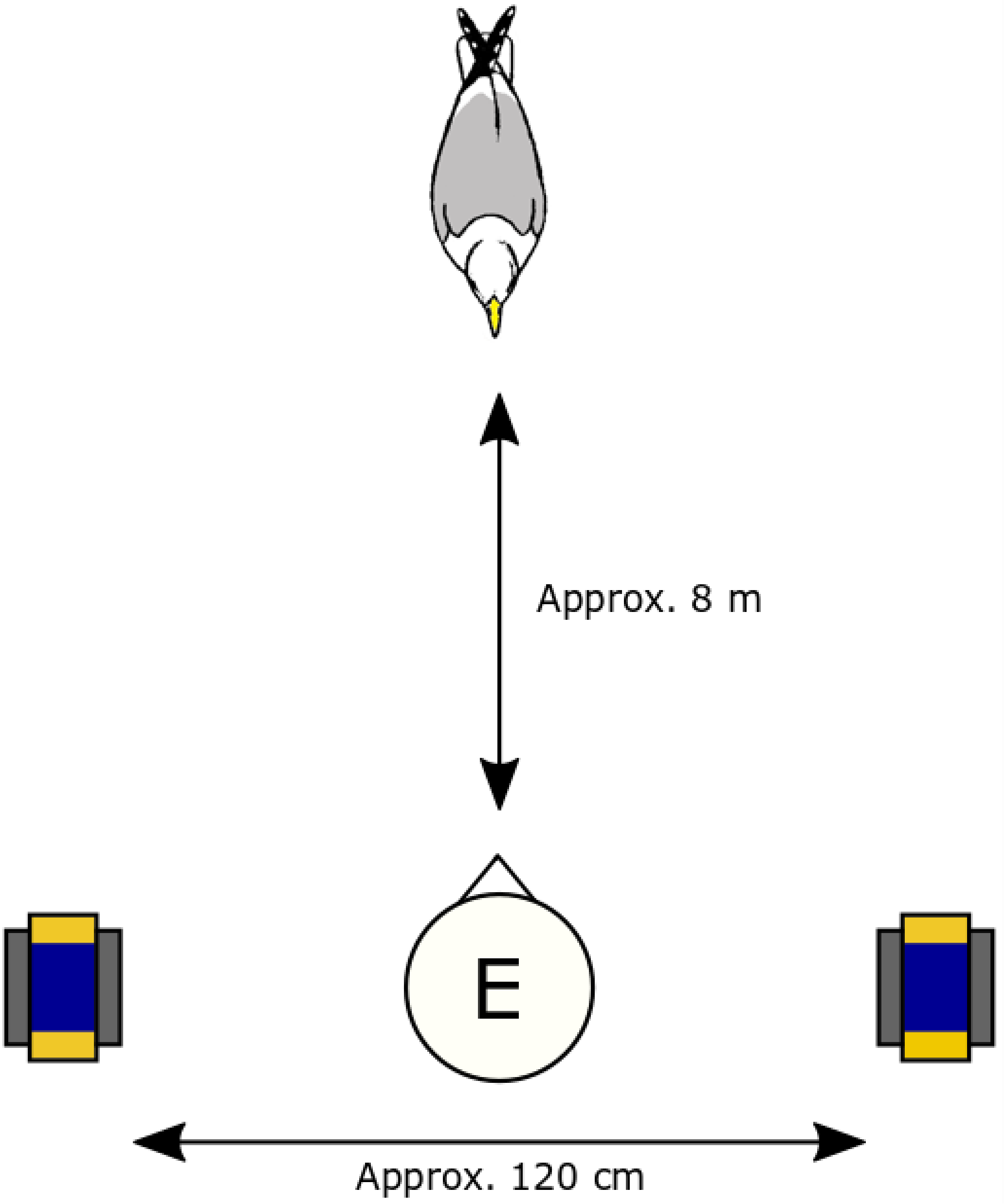

Figure 3. The experimental set-up. The experimenter (E) faced the gull and placed an upturned bucket, under which she held an object, either side of her body. She then removed the buckets to reveal the objects and picked up and handled one of the objects for 20 s before replacing it. Food objects (flapjacks in partially transparent, blue-coloured plastic wrappers, attached to grey slate tiles) depicted. Not to scale.

Table 3. *The results of Experiments 1 and 2 testing herring gulls' use of human handling as a cue when choosing between two identical objects. Section (a) shows the results of the food object trials, and (b) shows the results of the non-food object trials. The effect of potential confounds are also shown. Significant predictors are printed in italics.*

(a) Food objects (n=24)	**Estimate**	**SE**	**Z**	**Odds ratio**	**P**
Intercept	-1.263	6.978	-0.181	-	0.856
Handling	*3.006*	*1.369*	*2.196*	*20.199*	*0.028*
Distance between objects	-0.011	0.055	-0.197	0.989	0.844
Distance to gull	0.000	0.003	0.091	1.000	0.928
Starting height of gull	0.001	0.004	0.275	1.001	0.783
(b) Non-food objects (n=23)	**Estimate**	**SE**	**Z**	**Odds ratio**	**P**
Intercept	-4.303	7.607	-0.566	-	0.572
Handling	2.013	1.701	1.183	7.484	0.237
Distance between objects	0.038	0.065	0.585	1.039	0.559
Distance to gull	0.000	0.004	0.086	1.000	0.932
Starting height of gull	-0.004	0.005	-0.764	0.996	0.445

Chapter 3: Supplementary Material

Supplementary Methods

Choice of food items

Pre-packaged flapjacks were chosen because of the homogeneity of their appearance: each is manufactured to be identical and they were therefore a suitable option for a choice test. We felt that it was important that the food in a “food object” experiment was visible to the gulls, but also that they were not able to access it. Many local authorities discourage the feeding of gulls and we did not want to encourage potentially problematic behaviour by rewarding the gulls for approaching the food objects. The shiny plastic packaging of these items is also likely to be associated with food by gulls that regularly forage in urban areas.

Choice of non-food items

As our aim was to compare the number of gulls approaching in food and non-food trials, we chose items that were the same size and shape as the food items because perceived differences in quantity may affect approach rate. Sponges could be easily cut to the same dimensions. We also chose items that were of the same colour (blue) as the food items, in case gulls reacted differently to different colours. While we aimed to keep features similar for comparisons, we were also wary of making non-food items look too much like food items, and therefore we did not make any further modifications to the sponges. We wanted to use items that gulls were unlikely to have any prior associations with, and thus be novel to the gulls.

Locations

We tested gulls in discrete urban areas in West Cornwall and Plymouth. We focused on major towns as these are densely populated by humans, and gulls in such locations should have experience of humans and (food) litter. The locations used in the analysis and numbers of gulls in each location are summarised in Table S3.1 below.

We avoided testing individual gulls more than once by sampling in different locations and using individual markers of identity (such as colour rings used by the West Cornwall Ringing Group).

The presence of mates

We noted whether the mates of focal gulls were present during the trials, in case it affected their approach behaviour (as we previously found that gulls take longer to approach food while in the presence of other gulls, including their mates; Goumas et al. 2019). Adult gulls are often paired and thus it can be difficult to find a lone adult gull to test. We were able to identify these individuals as mates because of their behaviour: gulls do not tolerate other conspecifics in their territories and will chase them away or otherwise display agonistic behaviour (Tinbergen 1953; pers. obs.). We avoided selecting gulls that were engaged in agonistic interactions and targeted those in resting positions (lying down or standing still).

Calendar date

We also recorded the date that each trial took place. However, as the non-food experiment took place after the food experiment had been completed, the date of testing was confounded with the type of object, which was the main variable of interest when comparing the approach rate of gulls in the two experiments. For each experiment, we ran binomial generalised linear models that included calendar date as a sole continuous variable and approached (yes/no) and pecked (yes/no) as the response variables, and the results are reported below.

Approach time

We recorded the time taken for approaching gulls to peck at one of the presented objects. To determine whether there was a significant difference in approach time when gulls were presented with a food or non-food object, we used a linear model with approach time (in seconds) as the response variable and object type as a predictor variable. We also included the distance between the objects and the gull, the elevation of the gull from the ground at the time of the object being replaced, the time of day and whether the gull's mate was present as covariates.

Visual analyses

To conduct the visual analyses, we placed the food and non-food items next to each other on the dark grey slate tiles used in the experiments (Supplementary Figure S3.3) and took two photographs using a Nikon A7 converted to full spectrum sensitivity (Advanced Camera Services Limited, Norfolk, UK) fitted with a Nikkor EL 80mm lens, in RAW format with a fixed aperture. We held the camera in position with a tripod and used a custom-made lens slider to change between filters without moving the camera. We took a human visible spectrum (400 to 680nm) photograph through a Baader UV-IR blocking filter (Baader Planetarium, Mammendorf, Germany) and a UV (320 to 380nm) photograph with a Baader UV pass filter. Each photo also contained two grey standards of 7% and 93% reflectance (Spectralon, Congleton, UK) and a scale bar.

We checked photographs for suitable exposure levels and then analysed the images using the quantitative colour pattern analysis (QCPA) framework within the multispectral image calibration and analysis (MICA) toolbox in Image J (Troscianko & Stevens, 2015; Van Den Berg, Troscianko, Endler, Marshall, & Cheney, 2020). We created a multispectral image in the MICA toolbox, which aligns the visible and UV photographs and then uses the grey standards to linearise and standardise to control for light conditions. We then selected the food and non-food items and an equivalent area of the grey background tile as regions of interest to measure.

We modelled gull colour vision (which includes sensitivity to UV) using the visual sensitivity of the tetrachromatic blue tit (*Cyanistes caeruleus*) by converting the standardised multispectral image into cone catch data, using a Weber fraction of 0.05. To determine colour and luminance match of the food and non-food objects to the visual background, we calculated just noticeable differences (JNDs), where a JND of > 3 indicates that the objects are discriminable under most lighting conditions (Vorobyev & Osorio, 1998). We then modelled gull spatial acuity to determine the appearance of the objects at various distances (Caves & Johnsen, 2018). Spatial acuity has not been determined in any gull species or close relative, so eye size was used to calculate approximate acuity. We calculated the regression equation of eye size against acuity of diurnal birds with known visual acuity (Martin 2017; E Caves pers. comm.), and estimated an acuity of 13.2 cycles per degree (CPD) based on a herring gull axial eye diameter of 18.2 mm (Iwaniuk, Heesy, & Hall, 2010). We modelled the appearance of the food and non-food items from distances of 8 m (approximate initial viewing distance), 6.5 m (the approximate mean distance of gulls from the experimenter at the time of replacing the handled object), 1 m (close approach), and 30 cm (standing directly in front of the item). The acuity model blurs images to eliminate details that cannot be resolved by the viewer, which includes the removal of edge information that is integrated at a later processing stage. Resolution of edges was restored using a receptor noise level mediated filter that takes into account the viewer's discrimination ability.

Supplementary Results

We attempted to conduct a total of 168 trials across both experiments. Aside from the 79 trials included in our analyses (Table S3.1), 26 were interrupted by humans or other birds before the target gull could make a choice and thus were discarded. Sixty-one gulls flew or ran away from the area at the start of the trials, when the experimenter approached, placed the buckets or stood up. Two gulls attempted to peck at the non-handled food object while the experimenter was in the process of handling the other object, so these gulls could not be tested, and these trials were terminated.

Table S3.1. *Locations and responses of the herring gulls tested in object choice experiments. The reported numbers exclude gulls that flew or ran away when the experimenter presented the objects.*

	Food objects			**Non-food objects**		
Town	Pecked at an object	Did not approach (remained in position)	Approached without pecking	Pecked at an object	Did not approach (remained in position)	Approached without pecking
Hayle	1	7	0	0	0	0
Helston	0	0	0	1	0	0
Falmouth	12	0	1	6	4	1
Marazion	1	0	0	0	0	0
Mousehole	2	0	0	0	0	0
Newquay	0	0	0	3	2	2
Penzance	3	0	0	1	0	1
Penryn	2	0	0	2	0	0
Plymouth	0	0	0	4	1	5
St Ives	3	5	1	1	1	0
Truro	0	0	0	5	1	0
TOTAL	**24**	**12**	**2**	**23**	**9**	**9**

In our food object experiment, we presented 38 herring gulls with the two food objects, and 24 pecked at one of the objects. Twelve of these participating test subjects were in Falmouth, three were in Penzance, three in St Ives, two in Mousehole, two in Penryn and one each in Hayle and Marazion (Table S3.1).

In the non-food object experiment, we presented 41 herring gulls with the two non-food objects, and 23 pecked at one of the objects. Six of these test subjects were in Falmouth, five were in Truro, four in Plymouth, three in Newquay, two in Penryn, and one each in Helston, Penzance and St Ives (Table S3.1).

Models including calendar date

For each experiment, we looked at the potential effect of date on the number of gulls approaching, and found no significant effect within either the food trials or non-food trials (Table S3.2). The number of gulls approaching and pecking at an object are shown respectively in Figures S3.1 and S3.2 below.

Table S3.2. *Results of binomial generalised linear models assessing the effect of calendar date on the number of gulls approaching and the number of approaching gulls that pecked at an object, separately within food and non-food trials.*

	Estimate (SE)	**Z**	**P**
Approached (Y/N)			
Model 1: Date - Food trials	0.038 (0.021)	1.803	0.071
Model 2: Date - Non-food trials	0.024 (0.027)	0.873	0.383
Pecked (Y/N)			
Model 3: Date - Food trials	0.035 (0.035)	1.017	0.309
Model 4: Date - Non-food trials	0.057 (0.033)	-1.747	0.081

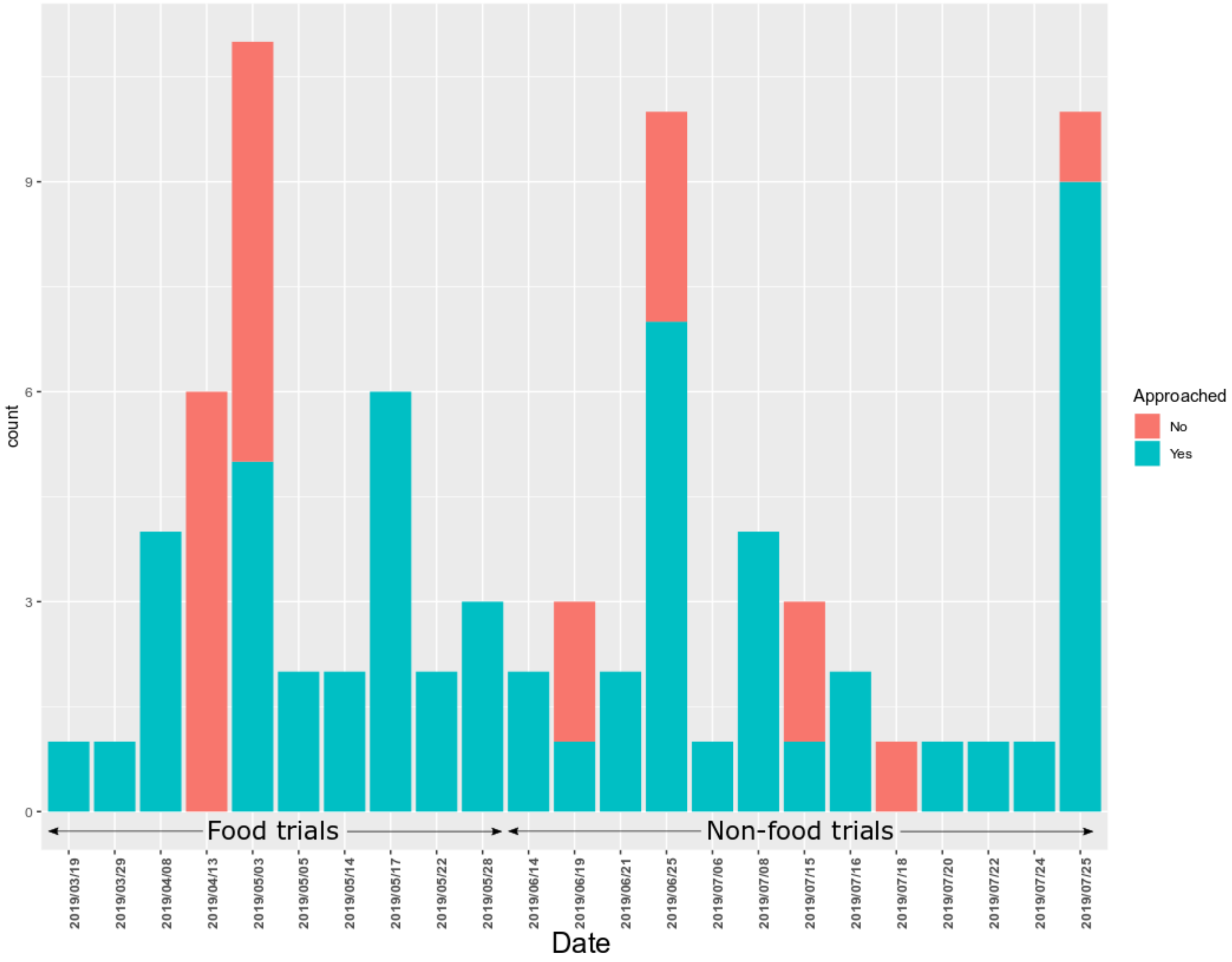

Figure S3.1. *The number of gulls approaching objects in food and non-food trials. The food object experiment was conducted before the non-food object experiment and hence object type is confounded with date. Dates where no trials were conducted are not shown.*

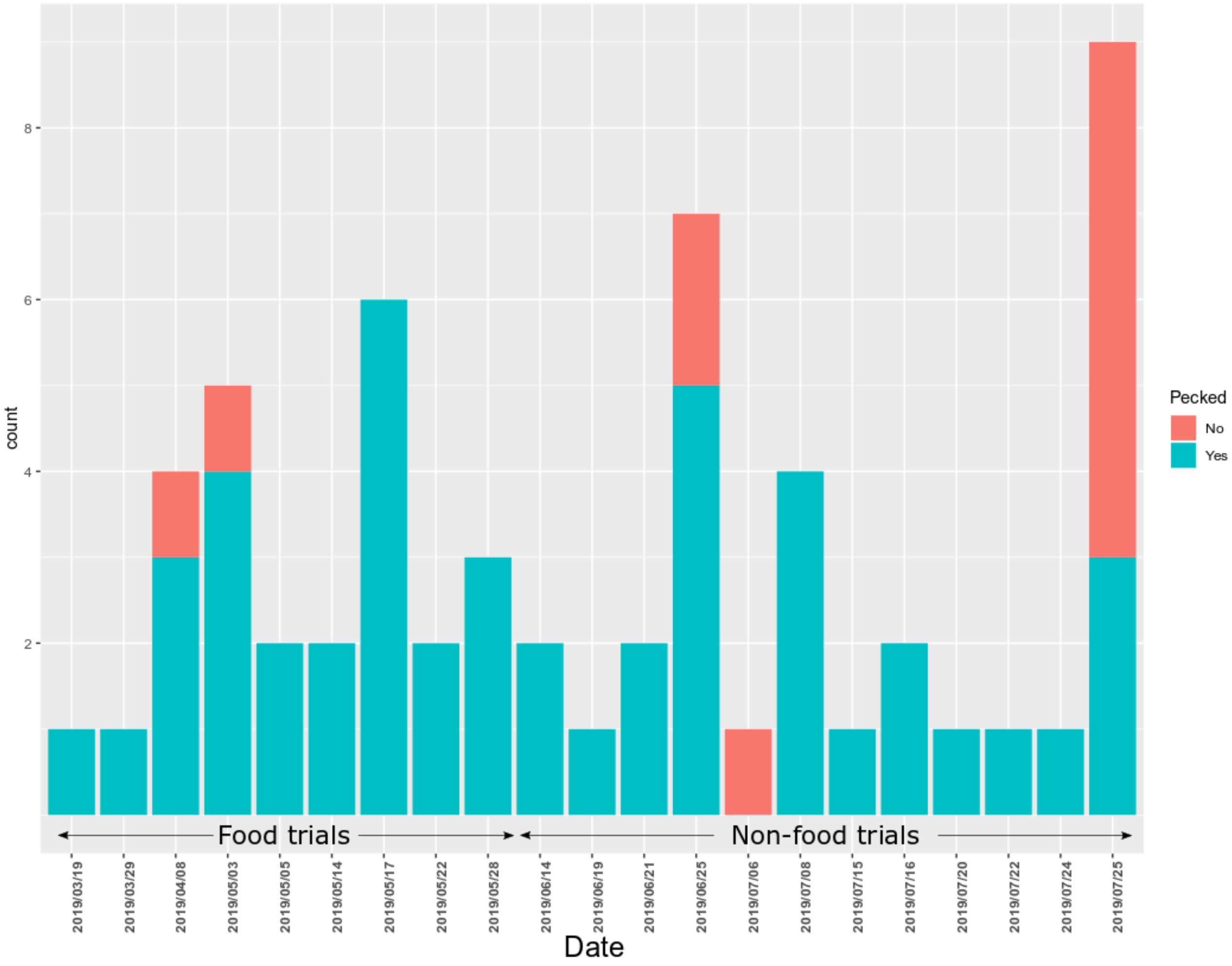

Figure S3.2. *The number of gulls pecking at objects (either handled or non-handled) in food and non-food trials. The food object experiment was conducted before the non-food object experiment and hence object type is confounded with date. Dates where no trials were conducted are not shown. All gulls (both approaching and non-approaching) are shown.*

Time taken for gulls to peck at an object

There was no significant difference in the time taken for gulls to peck at food objects compared to non-food objects (Table S3.3).

Table S3.3. *Results of a linear model comparing the approach time (in seconds) of gulls pecking at food objects vs. non-food objects, along with covariates.*

	Estimate	**SE**	***t***	**P**
Intercept	6.710	6.569	1.021	0.313
Item (Non-food)	-0.326	2.907	-0.112	0.911
Distance to gull	0.018	0.007	2.489	0.017
Starting height of gull	0.015	0.010	1.406	0.167
Time of day	-0.001	0.006	-0.232	0.818
Mate (Present)	2.895	3.317	0.873	0.388

Visual analyses

Our visual models indicated that gulls would have been able to distinguish both food and non-food objects from the background and from each other (Table S3.4).

Table S3.4. *Just noticeable difference (JND) scores for food and non-food objects used in object choice trials. JNDs of > 3 indicate that the objects are discriminable under most lighting conditions.*

Comparison	**JND luminance**	**JND colour**
Food vs background	23.38	8.77
Non-food vs background	38.36	30.10
Food vs non-food	18.43	33.53

Figure S3.3. Appearance of food and non-food objects to a herring gull at distances of (from left to right) 30 cm, 1 m, 6.5 m and 8 m.

Chapter 4: Predator or provider? How wild animals respond to mixed messages from humans

Abstract

Wild animals encounter humans on a regular basis, but humans vary widely in their behaviour: whereas many people ignore wild animals, some people present a threat, while others encourage animals' presence through feeding. Humans thus send mixed messages to which animals must respond appropriately to be successful. Some species appear to circumvent this problem by discriminating among and/or socially learning about humans, but it is not clear whether such learning strategies are actually beneficial in most cases. Using an individual-based model, we consider how learning rate, individual recognition of humans, and social learning affect wild animals' ability to reach an optimal avoidance strategy when foraging in areas frequented by humans. We show that "true" individual recognition of humans could be costly. We also find that a fast learning rate, while useful when human populations are homogeneous or highly dangerous, can cause unwarranted avoidance in other scenarios if animals generalise. Social learning reduces this problem by allowing conspecifics to observe benign interactions with humans. Social learning and a fast learning rate also improve the viability of individual recognition. These results provide an insight into how wild animals may be affected by, and how they may cope with, contrasting human behaviour.

1. Introduction

Humans present a threat to a wide range of animal species, and many populations of wild animals have decreased as a result of human activity (Díaz et al., 2019). The magnitude of human impacts on biodiversity loss is predicted to worsen as the human population continues to grow (Andermann, Faurby, Turvey, Antonelli, & Silvestro, 2020). While indirect effects such as anthropogenic climate change and pollution present key challenges, competition for space and overexploitation of species also have large impacts (WWF, 2018), revealing the importance of direct encounters between humans and wildlife. Consumptive activities, where wild animals are removed from populations through, for example, hunting or culling, are major causes of mortality. It is common for targeted animals, such as deer, to be wary of humans as a result (Stankowich, 2008). Avoidance of humans is likely to be adaptive and protective; in areas where species are naïve to humans, animals tend to be tamer and more vulnerable to human predation (Cooper, Pyron, & Garland, 2014).

Although humans are a major predator of many wild animal species, numerous people coexist alongside other species without attempting to harm them. In stark contrast to other predators, humans vary widely in their behaviour towards other animals. In situations where humans do not present a threat, it is not optimal for animals to avoid humans, as doing so may result in lost foraging opportunities. When humans are not harmful, animals frequently show signs of habituation to human encounters, foraging in areas of human activity without fleeing (Blumstein, 2016). Habituation to humans appears to be more common in urban areas where human traffic is high and predation by humans tends to be low; increased tolerance to humans has been shown in urban populations of birds, mammals and lizards (Samia et al., 2015).

Besides simply ignoring wild animals, many humans provide them with food, both purposefully through targeted feeding and unintentionally by disposing of waste inadequately. Intentional feeding of wild animals is often discouraged as it changes natural behaviour patterns, but is popular in many parts of the world (Orams, 2002). In the United Kingdom, garden bird feeding is so prevalent that it has selected for longer bills in great tits (*Parus major*) (Bosse et al., 2017).

Humans also feed animals in direct encounters (Orams, 2002). As food is a necessary resource and will often be time-consuming for animals to procure, there is little doubt that direct feeding provides an incentive for animals to approach humans more closely. This potentially creates a new challenge for animals: will the next human they encounter reward them with food, ignore them, or try to harm them? Some species, such as garden birds, may not be a target of consumptive activities and will be at little risk of harm. However, others, such as bears (*Ursus* spp.) and red foxes (*Vulpes vulpes*) (Bateman & Fleming, 2012), are often targets of lethal control as well as recipients of food provisioning, and therefore receive what can be considered to be “mixed messages” from human populations.

Responding appropriately to humans is a challenge that has the potential to greatly affect the survival prospects of wild animals, yet relatively little research has been conducted on how wild animals may be able to succeed in environments where humans differ in their behaviour (Goumas, Lee, et al., 2020). The relative number of humans in the population who feed vs. seek to harm animals is likely to be an important determinant of how wild animals fare in human-dominated environments. Furthermore, wild animals’ capacity to learn affects their subsequent behaviour and may therefore improve their ability to respond optimally to human presence (Barrett et al., 2019). As individual humans are likely to be consistent in their behaviour, discriminating among individuals rather than responding to all humans in the same way may be beneficial. There is evidence that some species can recognise individual humans. For example, northern mockingbirds (*Mimus polyglottos*) become more inclined to mob people who have disturbed their nests (Levey et al., 2009), while feral pigeons (*Columba livia*) preferentially approach people who provide food rewards (Belguermi et al., 2011). Information about dangerous individual humans has also been shown to spread through wild animal populations via social learning, such that animals need not experience a direct encounter with a human to respond appropriately in the future (Cornell et al., 2012). Whether such abilities to learn about humans actually benefit animals across a range of scenarios, is, however, unclear.

Here, we present an individual-based model of human-animal interactions where animals can either avoid encountering a human, or stay on their foraging ground and be subject to the human’s actions, whether dangerous, rewarding or neutral. We first consider the factors determining the theoretical optimal avoidance strategy when animals receive mixed messages from the human population. We then ask how animals’ learning rate can affect their ability to make optimal foraging decisions when encountering humans from populations that differ in their level of threat. Next, we consider how a varying ability to recognise individual humans could affect energetic outcomes. Finally, we extend the model to explore how the capacity to socially learn from conspecifics modifies avoidance behaviour.

2. The model

The agents in our individual-based model are referred to here as “critters”; these are intended to represent a generic vertebrate species that may come into contact with humans. At each discrete time step in the model, each critter encounters a randomly selected “human”, an agent representing a member of a human population. Each individual critter is associated with an energy value, which changes as a result of their encounters with humans; as the model concerns only the effect of encountering humans, it does not consider energy that critters would gain from foraging elsewhere. Critters begin with an energy value of 0 and can gain or lose energy as the simulation progresses. During an encounter with a human, the critter must decide either to remain on their foraging ground, i.e. “stay”, or to flee and “avoid” the human. Each human is assigned one of the following characteristics: neutral, dangerous or rewarding. These characteristics remain constant through time and can be considered to represent a “type” of human. Encounters with humans can cause a change in critter energy, simulating the effects humans have on animals in the wild. Neutral humans cause no change in energy as they have no direct effect on an animal’s food intake, dangerous humans cause a decrease in energy and rewarding humans cause an increase in energy. Avoiding humans causes a decrease in energy, simulating lost foraging opportunities caused by fleeing. Each of the parameters governing change in energy for different types of encounter can be adjusted independently. There is no death in the model; therefore critters remain throughout simulation runs. Unless otherwise stated, models are run with a population of 100 humans and 500 critters and were run to equilibrium. See Table 4 for a description of parameters and baseline values used in the model. All models were run in R version 4.0.5 (R Core Team, 2021).

2.1 Stay or avoid? Finding the theoretical optimal strategy

For wild animals, the optimal response to encountering a human depends on the trade-off between risk and reward associated with each possible response. Our simplified model considers a choice between staying and avoiding an encounter with a human. The relative payoff for staying vs. avoiding is determined by the proportions of different types of human in the population and the loss or gain in energy associated with each human type. The theoretical optimal strategy can therefore be calculated by comparing the expected payoff from staying ($\bar{E}_S$) and avoiding ($\bar{E}_A$) using Equations 1 and 2, respectively.

$$\bar{E}_S = P_D \cdot E_D + P_R \cdot E_R \qquad (1)$$

$$\bar{E}_A = E_A \qquad (2)$$

P_D is the proportion of dangerous humans in the population, E_D is the energy lost at each encounter with a dangerous human, P_R is the proportion of rewarding humans in the population, E_R represents the energy gained from encountering each rewarding human, and E_A is the energy lost from avoiding an encounter.

Figure 4.1 shows the optimal strategy (stay or avoid) over the complete parameter space for any given human population composition, with neutral, dangerous and rewarding humans each represented by an axis on the ternary plot. The theoretical optimal strategy is calculated by subtracting the mean energy change when avoiding from the mean energy change from staying, i.e. $\bar{E}_S - \bar{E}_A$. Therefore, values above zero (blue) indicate regions of parameter space where it is better to stay, values below zero (red) indicate it is better to avoid and values of zero (white) indicate that neither strategy is better than the other. Note that, since critters initially have no ability to distinguish between types of human, the theoretical optimal strategy is constrained to either “always avoid” or “always stay”.

The optimal strategy is determined by whether staying or avoiding results in the least amount of energy loss. The higher the proportion of dangerous humans in the population, the more critters benefit from avoiding, particularly when there are few rewarding humans to offset the costs of staying. Increasing the cost of encountering dangerous humans (i.e. Fig. 1, panel b vs. panel a) necessitates that fewer dangerous humans are needed for the cost of staying to exceed the cost of avoiding, and therefore increases the range of parameter space where it is optimal to avoid humans. Similarly, increasing both the energy gained from encountering rewarding humans (Fig. 1, panel c vs. panel a) and the cost of avoiding (Fig. 1, panel d vs. panel a) increases the amount of parameter space where energy is maximised by staying. The optimal strategies derived from Equations 1 and 2 provide a baseline from which we can assess how critters in the model perform in response to mixed messages from humans. In the following sections, we explore how different types of learning about humans affect critters' ability to reach an optimal avoidance strategy when encountering different people. For guidance on how to read our ternary plots (Hamilton & Ferry, 2018), please see Supplementary Figure S4.1.

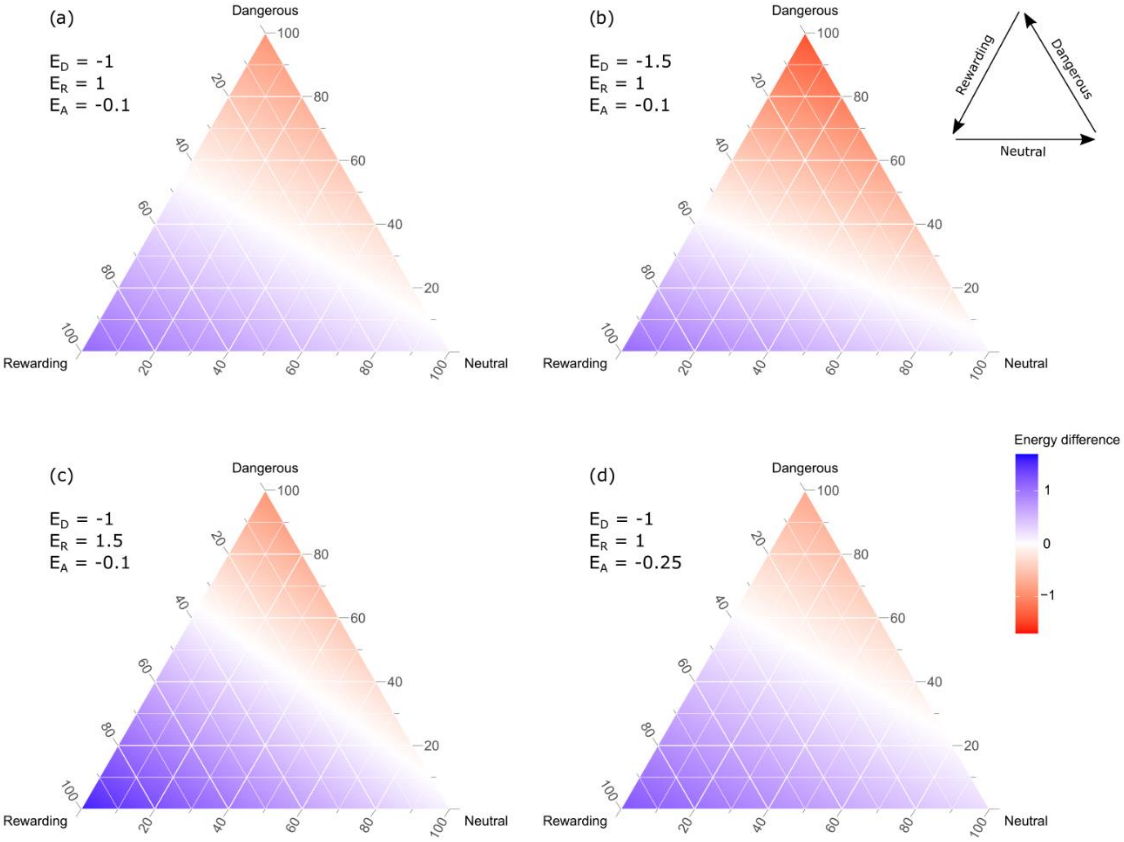

Figure 4.1. *Optimal strategies to avoid or stay in scenarios of varying danger and reward. Each ternary plot shows the complete parameter space of all possible human population compositions, with proportions (as percentages) of neutral, dangerous and rewarding humans on each axis. For each set of proportions, the energy lost from avoiding an encounter with a human has been subtracted from the mean energy gained or lost by staying. Parameter space shaded red indicates scenarios where the optimal strategy is to avoid interacting with humans, parameter space shaded blue indicates scenarios where the optimal strategy is to stay, and white indicates neither strategy is better than the other. Panel (a) depicts a scenario where the cost of encountering a dangerous human is equal in magnitude to the benefit of encountering a rewarding human (here, a change in energy of -1 vs. +1, respectively). Panel (b) shows the effect of increasing the cost of encountering a dangerous human by 50% (a change in energy of -1.5). Panel (c) shows the effect of increasing the benefit of encountering a rewarding human by 50% (to 1.5). Panel (d) shows the effect of increasing the cost of avoiding an encounter from 0.1 (shown in panels a – c) to 0.25. Inset in top right shows direction of axes.*

3. Learning

As animals are able to learn to avoid aversive stimuli, approach appetitive stimuli, and become habituated to harmless stimuli, we incorporated these types of learning into our model. In this section, we describe the effect of learning on the ability of critters to reach the theoretical optimal strategy. Each critter's behaviour is modelled by their probability of avoiding, which is set to 0.5 (i.e. an equal probability of staying or avoiding when encountering a human) at the beginning of the simulation. We used the following equation to update each critter's probability of avoiding a human at each encounter:

$$P_{A_{t+1}} = P_{A_t} \cdot (1 - W) + LW \qquad (3)$$

where P_{At} is the probability of avoiding an encountered human at time t, W is the learning weight, and L is the direction of learning. With each encounter, critter P_A is updated according to W, and is generalised to all humans in the population. W controls the proportion of the updated P_A at $t + 1$ that is determined by new information from the most recent encounter and, correspondingly, how much information from prior encounters is retained. W therefore controls the rate of learning: a high W results in rapid changes in P_A, whereas a low W results in smaller changes owing to more weight being placed on the accumulated information from previous encounters. Accordingly, a W of 0 results in no learning. L takes the value of 0 or 1, depending on whether the encounter encourages critters to stay or avoid, respectively. It remains constant throughout simulation runs. Encountering neutral and rewarding humans results in a tendency to stay whereas encountering dangerous humans results in a tendency to avoid. When critters avoid a human, they are unable to learn from the encounter and their P_A at the next encounter remains the same as for the previous encounter. Note that, as long as the starting value of P_A is < 1, it does not affect the P_A at equilibrium (see Supplementary Figure S4.2).

3.1 Learning in an environment of mixed messages

When the human population is homogeneous, with all humans acting in the same manner, reaching the optimal avoidance strategy is straightforward and learning is always expected to be beneficial. In such a scenario, increasing the learning weight enables critters to reach the optimal strategy more quickly (see

Supplementary Figure S4.3 for an example). However, human populations are likely to be heterogeneous and therefore learning may not necessarily result in the most optimal outcome. For example, when the human population is composed of both dangerous and rewarding humans, it will be difficult to converge on the optimal strategy because critters will continually receive mixed messages. We therefore considered how different human population compositions affect critter learning, energy change and, ultimately, how closely critters can approximate the optimal strategy.

We first ran simulations with a relatively low learning weight of 0.1 (Figure 4.2a). In this scenario, the energetic benefit of encountering a rewarding human is set to be equal in magnitude to the cost of encountering a dangerous human (i.e. the absolute value of E_D is equal to E_R), and the cost of avoiding is set at 25% of the cost of encountering dangerous humans. Where the proportion of dangerous humans is intermediate between 0 and 1, critters tend to avoid at rates matching the frequency of encountering them (Figure 4.2a, column i, reddish region). Only where there are relatively high numbers of rewarding humans can critters gain energy (Figure 4.2a, ii, magenta region). Where there are few dangerous humans or where all humans are dangerous (i.e. there is low heterogeneity in the human population), critters converge on the optimal strategy. In contrast, when the human population is even moderately heterogeneous, critters tend to avoid when they should stay and stay when they should avoid, resulting in greater losses in energy than could otherwise be achieved (Figure 4.2a, iii, yellowish regions). There is also a narrow band of blue parameter space where critters behave optimally simply because neither strategy is better than the other (cf. Figure 4.1d).

3.2 Fast learning has divergent effects

It may be expected that faster learning should be beneficial. However, learning is contingent on critters staying to experience an encounter, and there is an inherent asymmetry in learning: once animals learn to avoid a stimulus, they are no longer able to gain new information about it (Fazio, Eiser, & Shook, 2004). To investigate the effect of faster learning, we repeated the simulations of Figure 4.2a but with a high learning weight of 0.9 (Figure 4.2b). Now, critters quickly reach a high P_A after encountering dangerous humans (Figure 4.2b, column i), making it less likely that they will encounter rewarding humans in the future. Only where there are few dangerous humans do critters continue to stay for encounters, while others forfeit further learning opportunities. Consequently, a lower proportion of critters gain energy from their encounters, despite the energy parameters remaining constant (Figure 4.2b, ii vs. 2a, ii). Because of this learning asymmetry, it is easy for critters to reach the optimal strategy when the optimal strategy is to avoid, namely where there is a high proportion of dangerous humans (the large blue region in Figure 4.2b, iii). However, fast learning also leads to a greater amount of avoidance, and greater loss of energy, when it would be beneficial to stay (the red/orange shading where rewarding humans outnumber dangerous humans; Figure 4.2b, iii).

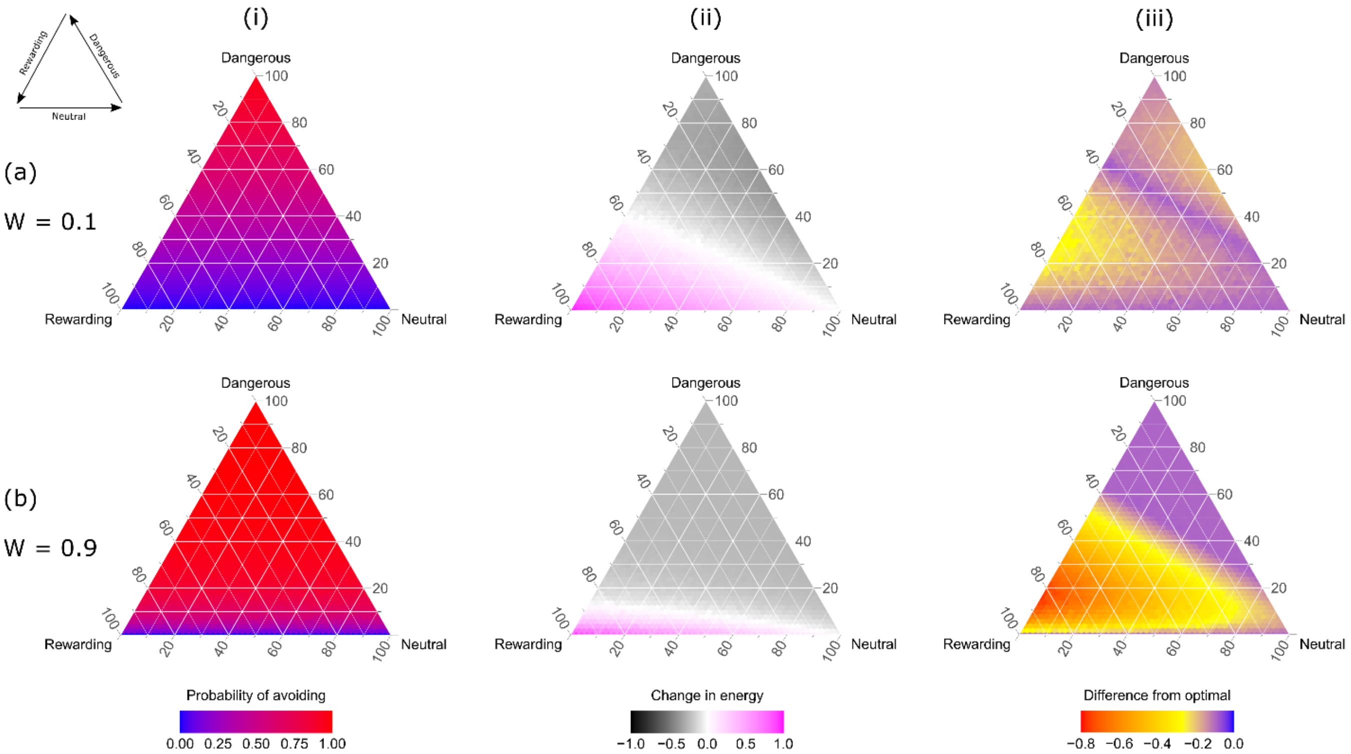

Figure 4.2. *Results of model simulations where critters are able to learn to avoid dangerous humans and to stay when they encounter neutral and/or rewarding humans. Models have been run to equilibrium (200 time steps). Each ternary plot shows the complete parameter space of all possible human population compositions, with percentages of neutral, dangerous and rewarding humans on each axis. The cost of encountering a dangerous human is set to be equal in magnitude to the benefit of encountering a rewarding human (i.e. change in energy of -1 vs. +1). The cost of avoiding is 0.25. Each row displays a different learning weight. Row (a) shows a low learning weight of 0.1 whereas row (b) shows a high learning weight of 0.9. Columns show different metrics for each scenario. Column (i) shows the population mean probability of avoiding an encounter with a human: blue indicates that critters tend to stay whereas red indicates that critters tend to avoid. Column (ii) shows the mean energy gained at each encounter. Parameter space shaded magenta indicates a net gain in energy and parameter space shaded grey indicates a net loss in energy, with saturation indicating the degree of loss/gain. Column (iii) shows closeness to the optimal avoidance strategy: the mean energy change at each encounter subtracted from the maximum theoretical energy possible. Blue indicates convergence on the optimal strategy and shades moving towards red show increasing distance from the optimal strategy. Inset in top left shows direction of each axis.*

4. Individual recognition

Our simulations show that it is likely to be difficult for animals to respond optimally to the presence of humans if they are only able to generalise from their encounters. However, some wild animal species can discriminate among individual humans and respond differently to different people in subsequent encounters, indicating that they are capable of individual recognition (IR) of humans (W. Y. Lee et al., 2016; Levey et al., 2009; Marzluff et al., 2010). We thus extended the model to explore the effect that IR has on critters' ability to reach an optimal avoidance strategy. We added a new parameter, *D*, which controls the degree to which critters discriminate among individual humans. When *D* > 0, critters can have a different P_A for each human. The following equations were used to update each critter's P_A for each human:

$$\Delta P_A = P_{A_{h,t+1}} - P_{A_{h,t}} \tag{4}$$

If h is the individual human encountered:

$$P_{A_{h,t+1}} = P_{A_{h,t}} + \Delta P_A \tag{5}$$

If h is not the individual human encountered (all other humans in the population):

$$P_{A_{h,t+1}} = P_{A_{h,t}} + (1 - D)\Delta P_A \tag{6}$$

ΔP_A is the change in P_A between the current and previous encounter (see Equation 3 for the calculation for updating P_A), and *D* is the degree to which critters discriminate among humans rather than generalise their experiences. *D* is set on a continuous scale and can be adjusted. When *D* = 0, critters completely generalise from each encounter, and P_A is updated in an identical manner for all humans, as in Equation 3. When *D* = 1, critters fully discriminate among humans and therefore retain different, and independent, P_A values for each human. As an example of the function of the parameter, if *D* = 0.5, the P_A for an encountered human is updated identically to when *D* = 1, but half of the value of ΔP_A is also added to the P_A of all the other humans in the population, simulating some degree of generalisation. This is intended to represent an animal's ability to attend to a human's unique features while also responding less strongly to features shared by all humans. For simplicity, we assume that critters retain their memory of encounters with humans throughout simulation runs.

4.1 The effect of individual recognition

The optimal strategy for animals with IR is to avoid only dangerous humans. Animals with perfect IR can respond appropriately to previously encountered humans as they have the ability to learn about each individual rather than the human population as a whole. However, novel humans will present a challenge to such animals as they have no prior information upon which to base their response. As a result, the benefits of IR may only become apparent over time, or when the number of humans in the population is small (Supplementary Figure S4.4a). IR is expected to only be advantageous when the human population is heterogeneous (i.e. there are both dangerous and non-dangerous humans; see Supplementary Figure S4.4b for an example of IR in a homogeneous human population). Given that IR gives critters the flexibility to learn human traits individually, a high learning weight should always be beneficial as it serves to accelerate convergence on the optimal strategy in human populations of any composition (Supplementary Figure S4.4b). This contrasts with generalised learning, where human traits can only be learned at the population level and high learning weights can generate maladaptive effects because of learning asymmetry (see Section 3.2).

4.2 In-between all or nothing: varying the degree of discrimination

As animals are unlikely to completely generalise or completely discriminate among individual humans, it is important to understand the effects of incomplete discriminative abilities; that is, when D is greater than 0 but less than 1. Certain cues are possessed by almost all humans (for example, two forward-facing eyes, upright posture, bipedalism), and these are likely to be particularly salient. In contrast, those human traits facilitating IR (such as face shape, hair colour and walking gait) may be less so. Our IR parameter thus approximates this trade-off between responding to shared vs. individual cues.

Generalised learning ($D = 0$) outperforms full IR ($D = 1$) in human populations with low heterogeneity (Figure 4.3, shown by dark blue shading). As the heterogeneity of the human population increases, full IR, which facilitates only the avoidance of known dangerous humans, becomes the better strategy.

Additionally, as the number of encounters increases (Figure 4.3, column ii vs. i), there is more time for the benefits of IR to accumulate, and IR becomes a more viable strategy over a greater range of human population compositions. Even a modest ability to discriminate among humans can result in relatively high energy gains and outperform both full IR and generalised learning in some scenarios. However, when the learning weight is high (Figure 4.3b), learning asymmetry causes critters with any degree of generalisation to avoid both familiar and unfamiliar humans, which causes those in mostly dangerous but heterogeneous populations to fare worse than conspecifics with full IR (*D* = 1). These simulations provide an indication of when animals may be able to benefit from using a combination of discrimination and generalisation, and the precise scenarios where full IR or complete generalisation are favoured. Note that substituting rewarding for neutral humans generates qualitatively similar results (Supplementary Figure S4.5).

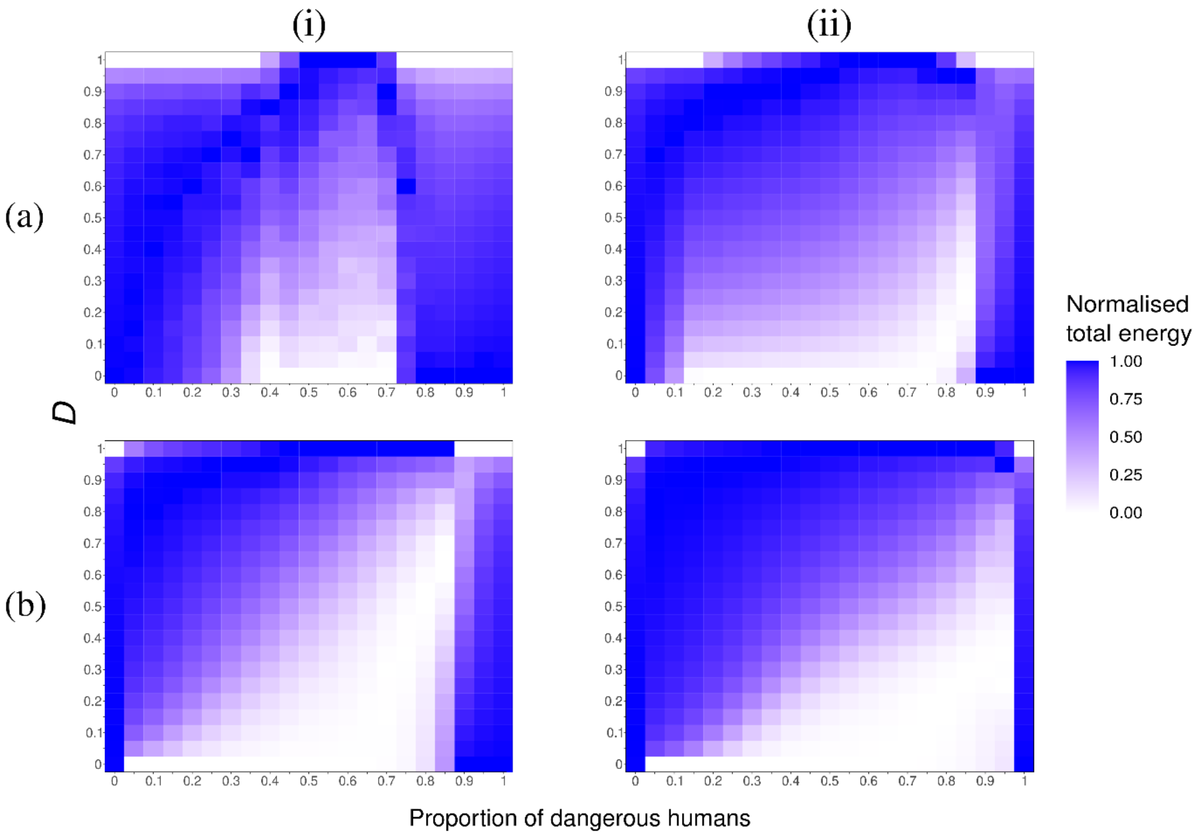

Figure 4.3. *Heat maps demonstrating how changing the proportion of dangerous humans in the population affects the utility of varying degrees of discrimination (D) in terms of total energy gained or lost over time. In these scenarios, only populations with dangerous and rewarding humans are considered; neutral humans are ignored as they cause no change in energy. Thus, a value of 0 dangerous humans indicates a scenario where all humans are rewarding. Dangerous humans cause a decrease in energy equal to the gain in energy caused by rewarding humans (i.e. -1 vs. +1). Because the proportion of dangerous humans in the population determines the absolute possible final energy value, the energy values have been normalised to be between 0 and 1 within each level of human population composition. Values are therefore relative within columns along the x-axis: white squares indicate the worst performing D value for a given proportion of dangerous humans and shaded squares indicate how much better alternative levels of D fare in a given scenario. Row (a) shows a low learning weight of 0.1 and row (b) shows a high learning weight of 0.9. Column (i) shows energy after 500 encounters and column (ii) shows energy after 3000 encounters.* $N_{humans} = 100$; $N_{critters} = 500$.

5. Social learning

Many animals learn via social learning (SL), which is defined as "learning that is facilitated by observation of, or interaction with, another individual or its products" (Hoppitt & Laland, 2013). Social learning may occur as a result of observational conditioning, whereby an observer forms a relationship between a stimulus (such as a human) and a demonstrator's response (Curio et al., 1978; Hoppitt & Laland, 2013); the observation of conspecifics is likely to be important in learning about humans. Some species (American crows, *Corvus brachyrhynchos* (Cornell et al., 2012); Eurasian jackdaws, *C. monedula* (V. E. Lee et al., 2019)) appear to learn the characteristics of individual humans in this manner and scold or mob dangerous humans more frequently than non-dangerous humans. Social learning can also take the form of social facilitation, whereby the mere presence of other individuals can alter an animal's behaviour (Hoppitt & Laland, 2013). Social facilitation can result in wild animals becoming habituated to humans after being attracted to foraging grounds by conspecifics (Samuni, Mundry, Terkel, Zuberbühler, & Hobaiter, 2014). We therefore also included SL in the model. With SL, critters can observe one conspecific from the critter population at each time step as well as encountering a human themselves. Thus, the learning equation for SL is identical to the equation for asocial learning (Equation 3), though the degree to which critters learn by SL is scaled by the social learning coefficient, S, which takes a value between 0 and 1. When $S = 1$, critters learn as much from conspecifics as they would if they encountered the human themselves, but do not experience a change in energy as a result. For a fuller exploration of the effect of changing S, see Supplementary Figure S4.6. Here, we first consider a situation where critters do not learn from conspecifics that avoid encounters with humans, and its effect at the critter population level when there is a change in the human population composition. We then consider a situation where critters with IR use alarm signals to spread information obtained from conspecific avoidance to others in the critter population.

5.1 Social learning can reverse maladaptive avoidance in a changing environment

Critters with SL are able to observe conspecifics, which means they can observe others' encounters with humans even if they have learned to avoid humans themselves. This has the potential to allow critters to overcome the problem of learning asymmetry generated by asocial learning (Section 3), which may have implications for when human populations change in composition over time. Examples of such change include hunting seasons and tourist seasons, when numbers of dangerous and rewarding humans in the population may temporarily increase, respectively. Animals that have learned to avoid humans in the hunting season could be disadvantaged when the human population becomes less dangerous. It would thus be beneficial for animals to be able to alter their behaviour to match the optimal strategy in changing environments. There is evidence that wild animals do adjust their responses to human activity; for instance, mouflon (*Ovis gmelini musimon*) show greater avoidance of humans in the hunting season than in the tourist season (Marchand et al., 2014). We therefore further extended the model to allow a temporal shift in the human population composition, to assess the effect of SL on maladaptive avoidance behaviour in critters that generalise ($D = 0$).

Specifically, we looked at the ability of critters with ($S = 1$) and without SL ($S = 0$) to modify their avoidance behaviour when the human population becomes less dangerous. First, we ran a simulation with a population of 80% dangerous humans for 200 time steps, such that there was a high level of avoidance behaviour in the critter population. We then ran a simulation that included a change in the human population composition, reducing the number of dangerous humans to 20% after 100 time steps. At this point, the previously optimal strategy of avoiding is now maladaptive. Figure 4.4 shows the change in P_A over time for critters with (orange) and without (blue) SL in this scenario. When the learning weight is low ($W = 0.1$, Figure 4.4a), critters can converge on the same P_A as they would if they had not previously experienced a different human population composition. SL speeds up convergence on this strategy but does not alter it greatly. In contrast, when the learning weight is high ($W = 0.9$, Figure 4.4b), the P_A of critters without SL barely changes from 1 (always avoid) because of learning asymmetry (see Section 3.2), while those with SL quickly converge on the same strategy as critters with the lower learning weight. SL thus provides critters that have already learned to avoid humans with an opportunity to discover a more optimal strategy.

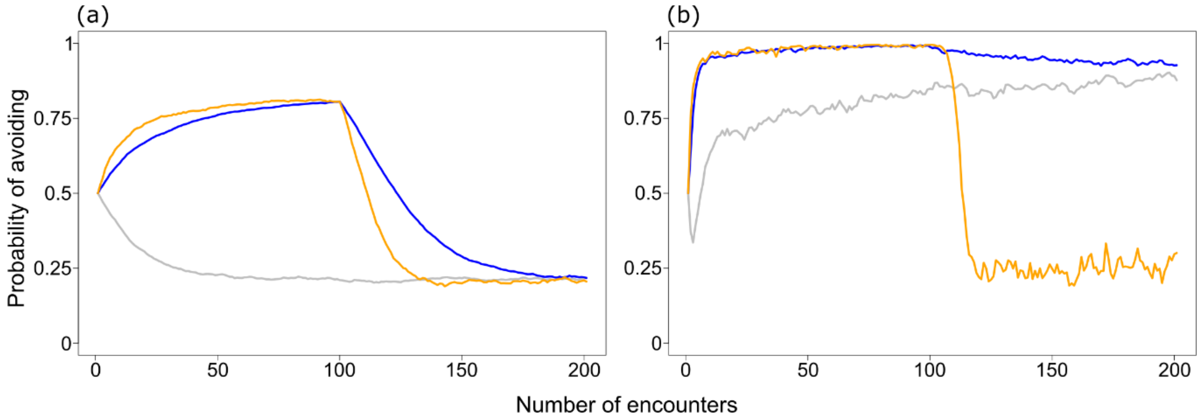

Figure 4.4. *The effect of social learning on critters' ability to adjust their avoidance behaviour following a change in human population composition. After 100 encounters, the human population is reduced from 80% dangerous to 20% dangerous. Blue lines depict critters without social learning (S = 0), orange lines depict critters with social learning (S = 1), and grey lines indicate the probability of avoiding without social learning when the human population is comprised of 20% dangerous humans at the beginning of and throughout the time series. Results are shown for critters with a low learning weight of 0.1 (a) and a high learning weight of 0.9, showing the associated effect of learning asymmetry (b).*

5.2 Alarm signals upon avoidance improve the effectiveness of individual recognition

We have considered scenarios where critters do not learn from another's avoidance. However, many species produce alarm signals upon fleeing a perceived threat (Taylor, Balph, & Balph, 1990), which function to alert others to danger (Curio et al., 1978). Furthermore, alarm signals such as calling and mobbing have been shown to facilitate individual recognition of dangerous humans (Cornell et al., 2012). Some animals can even learn to recognise individual humans based on their pairing with negatively-valenced vocalisations alone: for example, jackdaws (*Corvus monedula*) are more likely to scold humans that previously have been paired with playbacks of scolding calls (V. E.

Lee et al., 2019). As a final exploration of how SL affects animals' responses to humans, we modelled these alarm signals by allowing critters with IR to also learn from conspecifics that avoid humans. It may be expected that an animal that is capable of recognising individual humans would only produce alarm signals when a human is known to be dangerous. We therefore set the initial P_A to 0, as this enables alarm signalling only for dangerous humans rather than any newly-encountered human (starting with a P_A of 0.5 would introduce misinformation into the critter population). Critters can then learn from conspecifics' later avoidance of these individuals, allowing the information spread through the critter population. Indeed, we find that the inclusion of alarm signals enables critters to reach their optimal strategy far sooner than when critters do not use such signals (Figure 4.5). This highlights the potential role of SL in making IR a more viable strategy, and the importance of good discriminative abilities for spreading correct information about the level of threat each human poses. See Supplementary Figure S4.7 for an exploration of the effect of alarm signalling on the avoidance behaviour of critters that generalise ($D = 0$).

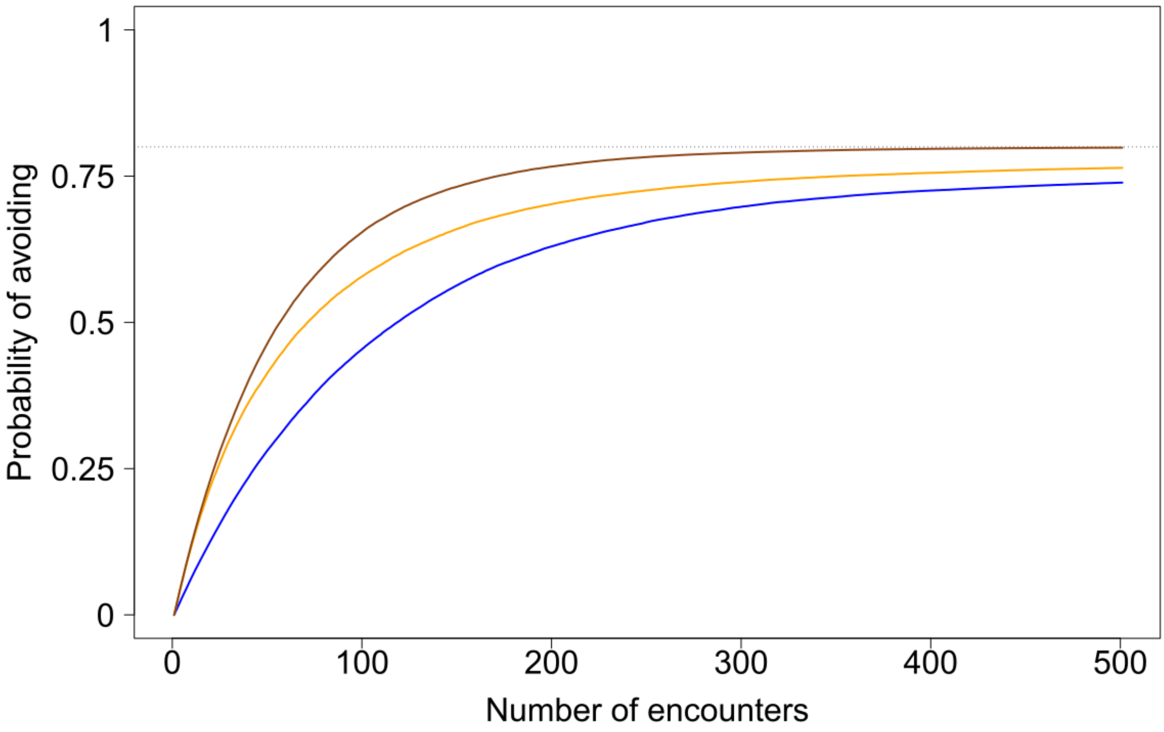

Figure 4.5. *Time series showing the effect of social learning on the ability of critters with individual recognition (D = 1) and a high learning weight (W = 0.9) to reach the optimal avoidance strategy in a population of 80% dangerous humans. Here, three scenarios are shown: one where critters do not socially learn (S = 0; blue line), one where critters socially learn from observing the nature of conspecific interactions alone (S = 1, no alarm signalling; orange line) and one where critters also learn from conspecifics' avoidance of a dangerous human (S = 1, alarm signalling; dark brown line). The optimal avoidance strategy is indicated by a dotted line.*

6. Discussion

In many parts of the world, wild animals live alongside humans. The challenges that arise from their encounters have a profound effect on behaviour and, ultimately, survival. In particular, humans differ greatly in how they behave towards animals, and animals potentially differ in the strategies they use to cope with human disturbance, both of which will influence whether encountering humans is beneficial, inconsequential or detrimental. Using our simulated population of "critters", we examined how animals can converge on an optimal avoidance strategy in environments where human behaviour may vary. Specifically, we considered how cognitive processes such as a fast learning rate, individual recognition and social learning affect critters' avoidance strategies when encountering humans, and ultimately their energetic outcomes.

6.1 How to learn about humans if they all appear to be the same?

When critters generalise from their encounters with humans, they are unable to discriminate among individuals and all humans are treated as the same type of stimulus. This may be an accurate representation of humans for many animal species: consider how it is often impossible for humans to differentiate among members of another species unless they are purposefully marked or tagged. Furthermore, cues that appear salient to humans might not necessarily appear salient to other animals (Caves, Brandley, & Johnsen, 2018). If there is any uncertainty regarding the discriminability of the cue, it may be far more beneficial to flee than to remain and risk being injured or killed (Bouskila & Blumstein, 1992). We showed that generalisation is a good strategy when human populations are homogenous in their behaviour. However, the constraint imposed by generalising experiences to the whole human population makes it very difficult to reach an optimal strategy when there is a moderate amount of heterogeneity in human population composition and humans thus give "mixed messages".

6.2 Learning rate and the potential for a perceptual trap

Learning rate is determined by how much weight animals place on their most recent experiences compared to their previous experiences (Groß et al., 2008). A higher learning weight results in a faster rate of learning at the cost of potentially discarding information from older experiences. As such, a fast rate of learning may only be useful when the stimulus, in this case, humans as a class, is consistent; otherwise, animals would be sensitive to random fluctuations in their environment that might not be truly informative. With our model, we showed that, when the learning weight is increased, critters become more likely to avoid humans if there are any dangerous humans in the population. This is because a high weighting of new encounters reveals an asymmetrical effect: a high learning weight means animals are more likely to avoid humans in the future after experiencing a threatening encounter, and, once animals have learned to completely avoid a stimulus, they cannot learn to stay. A fast learning rate can therefore be adaptive or maladaptive depending on how dangerous the human environment is. A high learning weight generates high avoidance, but, if the population is not sufficiently dangerous to warrant such behaviour, it essentially creates a perceptual trap (Patten & Kelly, 2010). However, there may be times when even a small number of humans (for example, hunters) present a high level of threat and it would be costly to risk staying, so high avoidance after even a single encounter could be beneficial. At a low learning weight, learning tends to be more symmetrical, with critters staying frequently enough to learn from rewarding and neutral encounters as well as dangerous encounters. Therefore, when there is an equal number of dangerous and non-dangerous humans in the population, critters' probability of avoiding remains close to chance, with critters tending to avoid for the average proportion of encounters they have with dangerous humans. As there is no ability to discriminate among humans, their avoidance behaviour is independent of the occasions when they actually encounter dangerous humans, and they are unable to reach an optimal avoidance strategy.

6.3 Recognising individual humans

Individual recognition (IR) of humans enables animals to escape the problems generated by the mixed messages of heterogeneous human populations. When animals have full IR, they are able to exhibit a discrete response to each human, fleeing only from dangerous individuals. This means that a high learning weight is always better, providing that individual humans are consistent in their behaviour and animals have identified individuals correctly. The benefits of IR are greater and manifest earlier when the human population is heterogeneous, in particular, when the number of dangerous humans in the population is intermediate. Animals that fully discriminate among individual humans and live amid homogeneous human populations will fare poorly early on compared to animals that learn predominantly through generalisation. Because of this, lifespan could be important: the benefits of human IR often only become apparent over time and, as such, only longer-living species may be able to make use of it. Animals that recognise individual humans must have the capacity to remember them over a period of time; indeed, our model was not designed to consider memory constraints. How many individuals an animal can remember, and for how long, is a critical question and likely important for understanding which species are capable of IR and how human IR can develop. Most of the species that have exhibited human IR have been corvids (Blum, Fitch, & Bugnyar, 2020; Davidson et al., 2015; V. E. Lee et al., 2019; W. Y. Lee et al., 2011; Marzluff et al., 2010), a family of birds known for their relatively large brain size, complex cognition and long lifespans (Uomini, Fairlie, Gray, & Griesser, 2020), although it is not clear whether there has been a bias towards testing corvids for this ability. Nevertheless, storing and accurately remembering the cues associated with multiple humans over extended periods of time is likely to be cognitively demanding, and may only be expected in species that have already evolved the ability to recognise individual conspecifics (Miller, Sheehan, & Reeve, 2020).

6.4 Beyond “true” individual recognition

Relatively few studies show the ability of free-living, wild animals to recognise individual humans or other conspecifics, and, to our knowledge, none demonstrates what would be considered “true” IR; that is, when cues are associated specifically with one individual and no other (Tibbetts & Dale, 2007). This, however, may simply be because experiments investigating IR in wild animals have not been designed to explicitly test this hypothesis, instead measuring behavioural responses to a relatively small number of human stimuli (either individuals or masks). It is therefore unknown whether the bird species (e.g. mockingbirds (Levey et al., 2009), brown skuas (W. Y. Lee et al., 2016)) that have demonstrated IR have truly recognised an individual rather than responded to a particular cue that could either be shared by another individual (for example, the same hairstyle) or isolated (i.e. animals would react in the same way if the relevant cue were somehow abscised and presented alone). While assessing the specificity of individual human cues was outside the scope of our study, we did approximate a situation where there is neither complete discrimination nor complete generalisation of human individuals. We showed that an intermediate level of discrimination, whereby critters learn strongly about a particular individual as well as generalising about all humans in the population to a lesser extent, can result in similar outcomes to pure discrimination or generalisation, often achieving close to optimal avoidance behaviour across a wide range of scenarios. As animals will not be able to predict the human environment they find themselves in, nor whether the next encounter will be dangerous or benign, it appears to be useful to balance generalisation and discrimination. This finding may explain why, in the studies of IR of dangerous humans in birds, subjects often display at least some defensive behaviour to behaviourally neutral human stimuli (Levey et al., 2009; Marzluff et al., 2010). Thus, it appears unlikely that these species display true IR, although it of course cannot be ruled out that perception and responses are not necessarily always coupled. For example, animals may regard an unfamiliar or less familiar human with wariness until they have gained sufficient experience of them. Furthermore, it may be rare for animals to encounter the same individual repeatedly. It is therefore possible that some wild animals may be able to recognise individual humans but do not behave as such because doing so might be costly.

6.5 Social learning about humans

Many animals are capable of social learning and a small number of studies demonstrate the ability of animals to socially learn the characteristics of dangerous humans (Cornell et al., 2012; V. E. Lee et al., 2019). To our knowledge, no studies have shown social learning of rewarding humans, although there is good reason to assume that it could occur: observational conditioning of rewarding stimuli has been documented in several species, such as feral pigeons (Biederman, Robertson, & Vanayan, 1986) and bumblebees (*Bombus terrestris*) (Avarguès-Weber & Chittka, 2014). We found that social learning can reduce the number of encounters with humans required to reach the equilibrium avoidance strategy. Perhaps more importantly, our model suggests that social learning could help animals overcome the problem of learning asymmetry, as, through observing conspecifics foraging alongside humans without harm, they will become less likely to flee. This will encourage wary animals to learn to tolerate humans, and may enable conspecifics that have learned to avoid humans through asocial learning to become less wary in the future, should the level of threat decrease.

Animals that socially learn the characteristics of dangerous individual humans may use alarm signals, which facilitate the spread of information through a population (Cornell et al., 2012). Exclusively producing negatively-valenced signals when an individual is a known threat is a useful way of learning about the human population more quickly and without having to face the risk of a direct encounter, thus reducing costs. At least two species that have been tested for human IR have been later assessed for social learning of individual humans (Cornell et al., 2012; V. E. Lee et al., 2019), suggesting that social learning may be an important ability to function alongside IR. Our model supports this: we found that social learning increases the utility of IR by enabling the optimal avoidance strategy to be reached sooner. Additionally, it is plausible that animals may learn more from social learning than from asocial learning: while animals cannot learn if they are killed, the death of conspecifics provides useful information (Swift & Marzluff, 2015).

6.6 Humans as a discrete stimulus

Our critters were simulated in an environment free from other predators. In reality, animals face predation and competition from other species besides humans, and therefore their behaviour in response to humans may be affected by these other encounters (Frid & Dill, 2002). Animals may either be more or less likely to flee depending on the presence of other species in the landscape. This is most evident from studies of island tameness (Cooper et al., 2014), which provide evidence that animals that have evolved alongside terrestrial predators show greater fear responses to humans, while those that evolved in the absence of predation pressure can be approached at close range and are thus most vulnerable to human activity. We expect that, if animals are not able to reasonably distinguish between humans and other large predators, and these other predators are present, avoidance of humans will be greater (Goumas, Lee, et al., 2020). This may explain why some species that frequently encounter humans, but which are not at risk of predation by them, maintain wariness of humans.

6.7 How do animals respond to humans in real life?

Our model is simple: we forced our agents to make a dichotomous choice between staying and avoiding. In reality, although animals flee from humans (demonstrated by flight initiation distance experiments such as (Carrete & Tella, 2010; Goumas, Collins, Fordham, Kelley, & Boogert, 2020; Runyan & Blumstein, 2004)), they may also use intermediate strategies such as maintaining a certain distance, and be unable to escape injury because of humans' use of projectile weapons. In any case, our model approximates this decision-making behaviour.

We assume that dangerous encounters cause a loss in energy and create the ability for animals to learn concordantly from them. As animals cannot learn from their encounters if they are killed by them, we did not include death in our agent population and thus we cannot model how lethal encounters affect conspecifics' responses to humans. It is possible that dangerous encounters that are not injurious may not be particularly costly. For example, if the human's objective is to deter animals from a location, they may only be harmed if they do not flee. Even if the risk of death at any one time is very low, animals may need to maintain a high level of wariness to ensure that they are able to avoid being killed or injured over a longer time period. Although animals tend to learn faster about dangerous stimuli than rewarding stimuli (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001), it may be possible that animals are able to evade harm in many cases and thus learn more strongly from rewarding encounters with humans. Indeed, animals will habituate to an aversive stimulus if it benefits them to ignore it (Schakner & Blumstein, 2013). Maintaining an appropriate level of wariness may be difficult if animals learn to approach humans as a result of being fed, and could leave them vulnerable to negative encounters (Orams, 2002).

6.8 The implications of feeding wild animals

While there has been ample research on the negative effects of humans on wild animals and many accounts of humans feeding wildlife (Orams, 2002), relatively little research has been conducted on the effect of direct feeding interactions on wild animal behaviour. However, there is evidence that food provisioning can alter large-scale behaviour patterns, such as the migratory behaviour of birds (Plummer, Siriwardena, Conway, Risely, & Toms, 2015). Additionally, anthropogenic food may improve the body condition of animals that consume it (Auman et al., 2008), but food provisioning may have detrimental effects in the longer term, for example by encouraging the abandonment of other beneficial behaviours or by increasing disease transmission risk (M. W. Wilson et al., 2020). The implications of widespread food provisioning by humans are potentially important for avoiding or mitigating conflict, particularly when interactions with wild animals are unwanted or pose a threat to species of conservation concern.

7. Conclusions

Knowing how to behave in the presence of humans may be one of the most difficult challenges wild animals face. As individual humans may act very differently from one another towards wild animals, they thus send “mixed messages”, to which animals must respond effectively in order to succeed in human-dominated environments. There are a few ways by which animals can do this, but their effectiveness depends on the relative number of dangerous humans present, the frequency of encounters, and how quickly animals can learn. An inability to learn quickly may be an issue for species that have little experience of humans but which are subject to consumptive activities such as hunting, trafficking and persecution.

Conversely, animals that learn quickly are vulnerable to falling into a trap of avoidance despite there being a low likelihood of danger. The ability to learn socially can help animals overcome this perceptual trap, as they can gain information from observing others foraging alongside humans without harm; this could be especially effective when the human population composition fluctuates over time, for example because of hunting or tourist seasons. Social learning can also accelerate convergence on a more optimal avoidance strategy, and may be particularly valuable when animals are capable of recognising individual humans. The ability and utility of individual recognition is likely to require fast learning, although animals need not fully discriminate among humans to reap considerable benefits over counterparts without this ability.

Animals are unlikely to use or require full individual recognition, but some ability to discriminate among humans will always be beneficial when different, but repeatedly-encountered, humans engage in contrasting behaviours. Further research is required to reveal the specificity of the cues used to identify individuals, how sensitive animals are to them, how many individuals can be remembered, and the length of time for which individuals can be recognised, as well as whether wild animals are capable of what can be described as “true individual recognition”. Furthermore, whether animals view humans as a category separate from other species, and thus are able to respond to them independently, is still unknown. Fully deciphering the mechanisms underlying recognition of humans will be valuable in predicting how animals respond and adapt to human activity, and in understanding which species may be most vulnerable to human exploitation.

Table 4. *Baseline parameters used in the individual-based model of "critter" encounters with neutral, dangerous and rewarding humans.*

Parameter	**Representation**	**Baseline values**
$N_{critters}$	Number of critters	500
N_{humans}	Number of humans	100
P_D	Proportion of the human population that is dangerous	Variable
P_R	Proportion of the human population that is rewarding	Variable
E_D	Energy change associated with encountering a dangerous human	-1
E_R	Energy change associated with encountering a rewarding human	1
P_A	Probability of avoiding an encounter with a human	Usually initialised at 0.5; varies over time
W	Learning weight	0.1 (low) or 0.9 (high)
D	Discrimination (individual recognition)	0 (no discrimination; full generalisation) 1 (full discrimination; no generalisation)
S	Social learning	0 (no social learning) 1 (full social learning)

Chapter 4: Supplementary Material

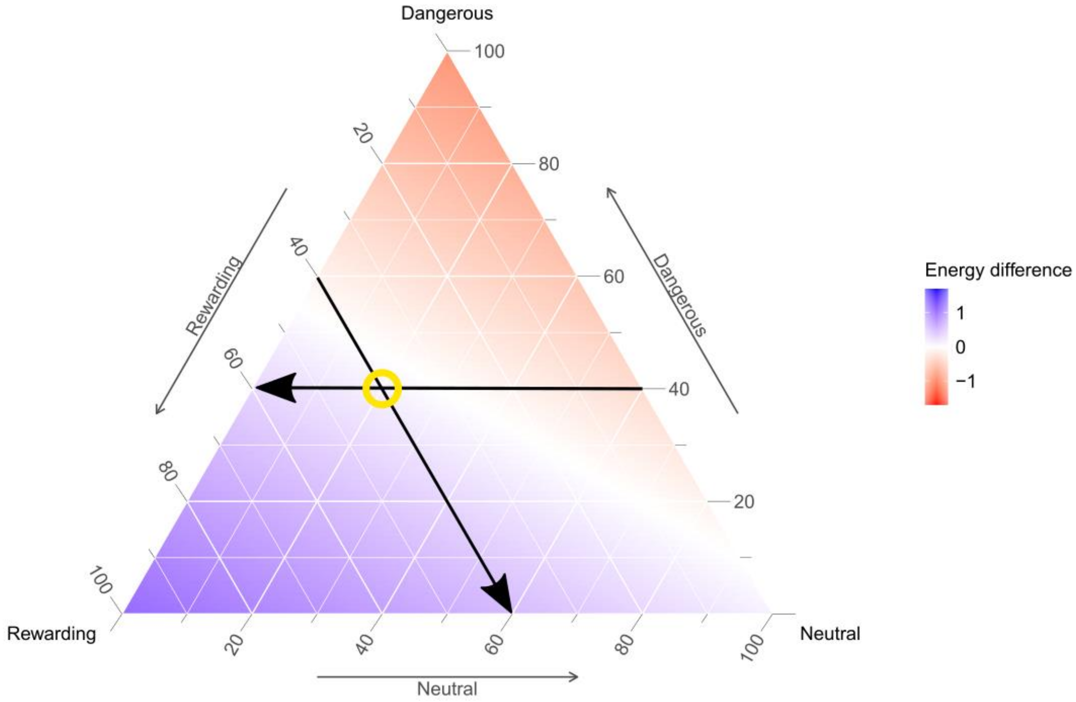

Figure S4.1. *An example of a ternary plot showing how to find an approximate value for a human population composition of 40% dangerous humans and 40% rewarding humans, and therefore also 20% neutral humans. These plots are heat maps designed for three dimensions where the value of each dimension depends on the others (as proportions or percentages can only add up to 1 or 100% respectively). The percentage of neutral humans in the population increases from 0 in the bottom left hand corner of the triangle to 100% in the bottom right. The percentage of dangerous humans in the population increases from 0 in the bottom right hand corner to 100% at the top of the triangle. The percentage of rewarding humans in the population increases from 0 at the top of the triangle to 100% in the bottom left. The direction of the tick marks shows which lines to follow to get the values for each type of human. For dangerous proportions, use the horizontal lines from right to left. For rewarding proportions, use the diagonal lines travelling from the top left of the triangle to the bottom right. For neutral proportions, use the diagonal lines travelling from the bottom to the top right side of the triangle. Where the lines intersect is the value for a given set of proportions/percentages, marked by a yellow circle. In this example, the value falls in the blue shaded area, indicating that the optimal strategy is to stay.*

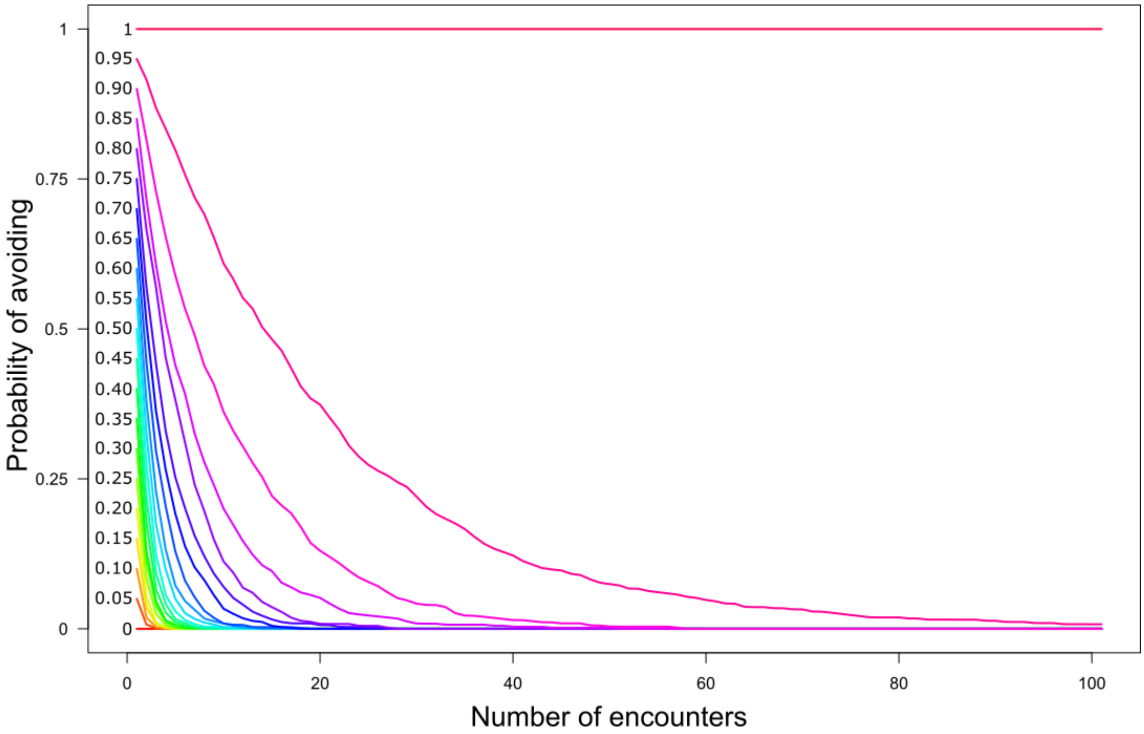

Figure S4.2. *Sensitivity analysis of the initial probability of avoiding (PA). As long as the initial PA is set below 1, critters will converge on the same equilibrium strategy. In this case, all humans are neutral (there are no dangerous humans), so the optimal strategy is to stay (a PA of 0). Each line shows a different initial PA at the beginning of the simulation (values labelled beside the y-axis).*

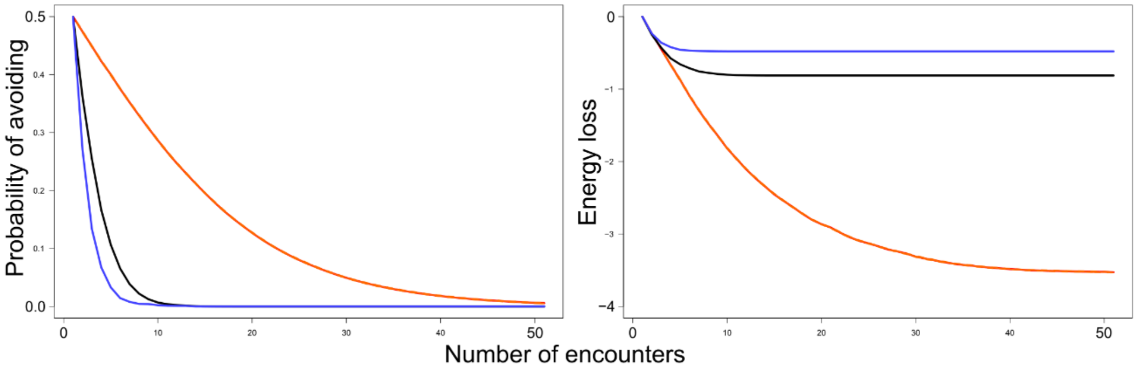

Figure S4.3. *Example time series showing the effect of learning weight (W) when the human population is homogeneous, i.e. all humans in the population act in the same way. In this scenario, all humans are neutral and thus cause no change in energy, so the optimal strategy is to stay. The effect on (a) critters' probability of avoiding humans, and (b) the total energy lost as a result, are shown. The energetic cost of avoiding is 0.25. Learning weights of 0.1 (low learning rate; orange lines), 0.5 (medium learning rate; black lines) and 0.9 (high learning rate; blue lines) are shown. Here, critters with a high learning weight quickly learn to stay, minimising their energy loss to 0.*

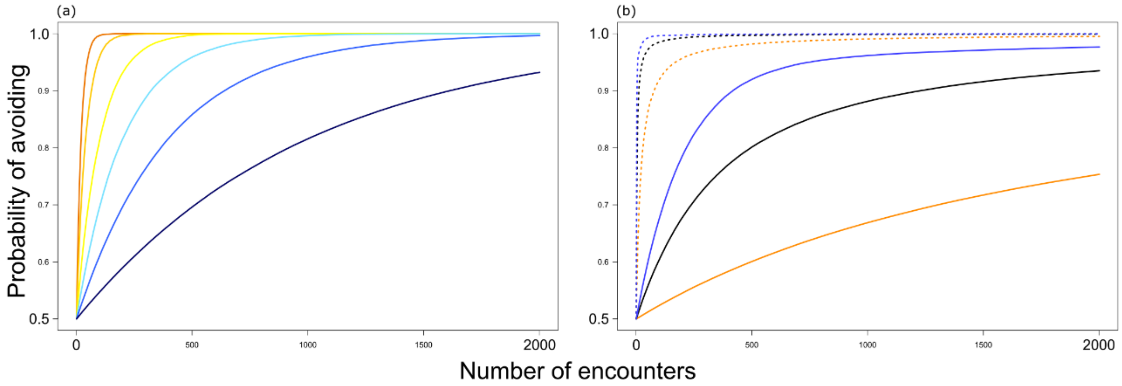

Figure S4.4. *The effect of (a) the number of humans and (b) learning weight on critters' ability to reach the optimal avoidance strategy. In this scenario, the human population is entirely composed of dangerous individuals and thus the optimal strategy is to avoid every human (i.e. a probability of avoiding of 1). In panel (a), critters have a learning weight of 1, so they learn perfectly to avoid each human after a single encounter. This demonstrates the amount of time taken to learn to avoid all humans when all in the population are dangerous and there are many humans to learn to recognise individually. Lines for a human population of 10 (dark orange), 20 (orange), 50 (yellow), 100 (light blue), 200 (blue) and 500 (navy) individuals are shown (progressing from left to right). In panel (b), there are 100 humans in the population, amounting to a mean of 20 encounters per critter of each individual. Lines indicate the change over time in the probability of avoiding for each learning weight: 0.1 (orange), 0.5 (black) and 0.9 (blue). Solid lines show full individual recognition; dotted lines show generalised learning as a comparison.* $N_{critters}$ *= 500.*

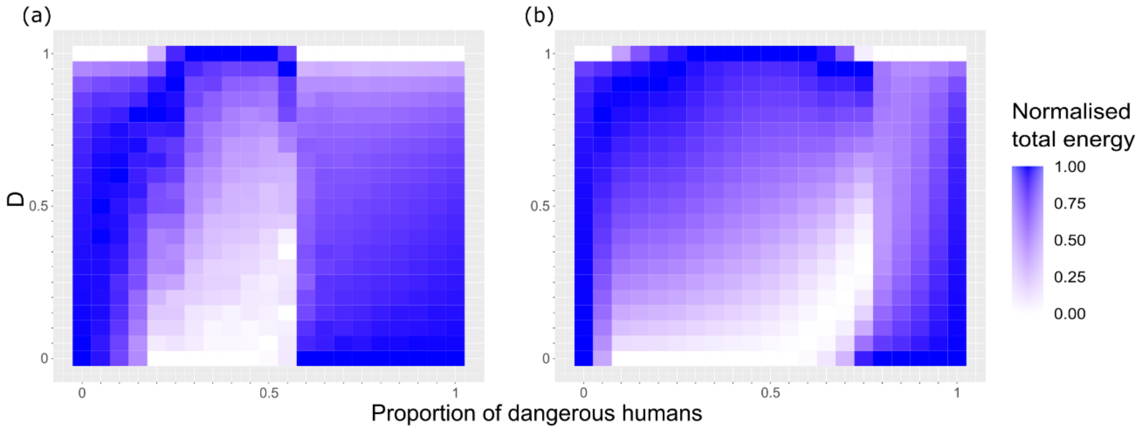

Figure S4.5. *Heat maps demonstrating how changing the proportion of dangerous humans in the population affects the utility of varying degrees of discrimination (D) in terms of total energy lost over time. In this example, only populations with dangerous and neutral humans are considered. A value of 0 dangerous humans therefore indicates a scenario where all humans are neutral. Dangerous humans cause a decrease in energy of -1 at each time step. Because the proportion of dangerous humans in the population determines the absolute possible final energy value, the energy values have been normalised to be between 0 and 1 within each level of human population composition. Values are therefore relative within columns along the x-axis: white squares indicate the worst performing D value for a given proportion of dangerous humans and shaded squares indicate how much better alternative levels of IR fare in a given scenario. Panel (a) shows energy after 500 encounters and panel (b) shows energy after 3000 encounters for critters with a learning weight of 0.1.* $N_{humans} = 100$; $N_{critters} = 500$.

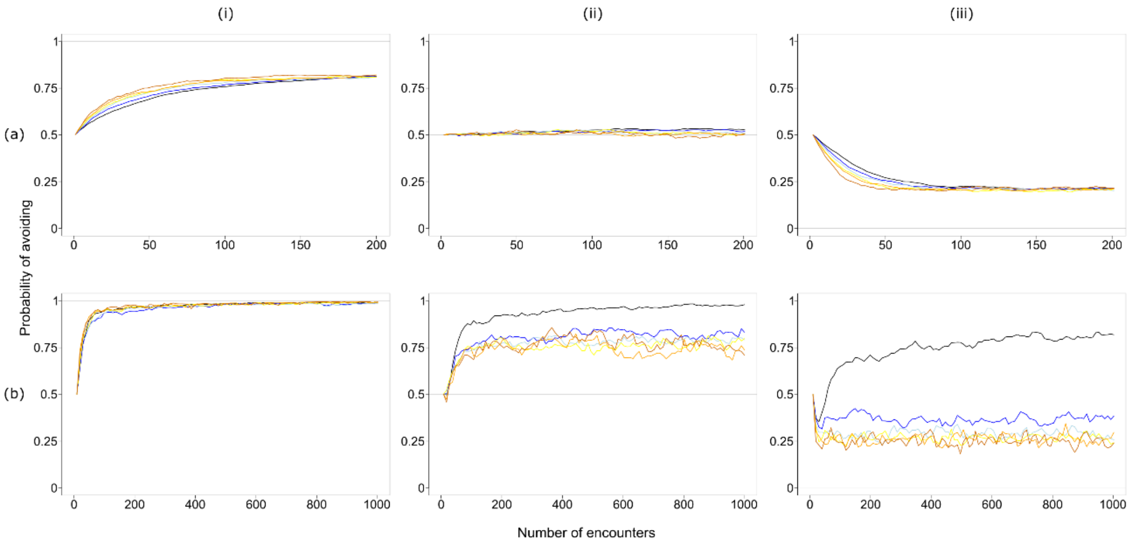

Figure S4.6. *Time series showing the effect of social learning on the change in probability of avoiding a human when the human population differs in its level of threat. Here, critters with full generalisation (D = 0) learn from observing conspecifics' encounters with humans but not from their avoidance. Column (i) shows a scenario where 80% of humans are dangerous, (ii) 50% and (iii) 20%. Row (a) shows a base learning weight of 0.1 and row (b) 0.9. The degree to which critters are able to learn by social learning, S, is depicted by the coloured lines; black: S = 0, blue: S = 0.2, light blue: S = 0.4, yellow: S = 0.6, orange: S = 0.8, dark orange: S = 1. Grey lines are plotted to indicate the optimal strategy for each scenario.* $N_{humans} = 100$; $N_{critters} = 500$.

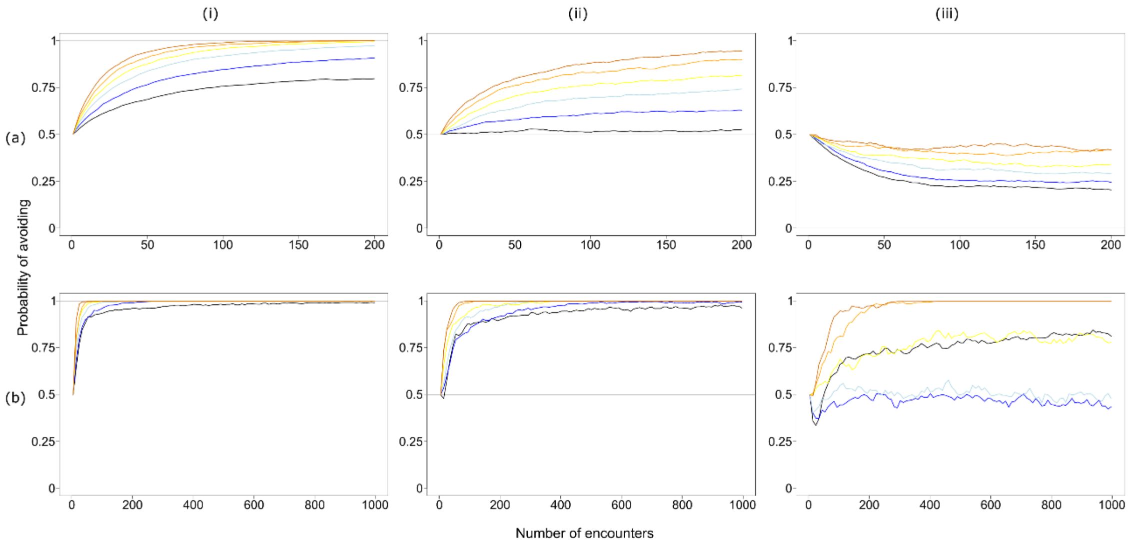

Figure S4.7. *Time series showing the effect of social learning with alarm signalling on the change in probability of avoiding a human when the human population differs in its level of threat. Here, critters with full generalisation (D = 0) learn from observing conspecifics' encounters with humans as well as from their avoidance. Column (i) shows a scenario where 80% of humans are dangerous, (ii) 50% and (iii) 20%. Row (a) shows a base learning weight of 0.1 and row (b) 0.9. The degree to which critters are able to learn by social learning, S, is depicted by the coloured lines; black: S = 0, blue: S = 0.2, light blue: S = 0.4, yellow: S = 0.6, orange: S = 0.8, dark orange: S = 1. Grey lines are plotted to indicate the optimal strategy for each scenario. Note the competing effects of social and asocial learning in column (iii), row (b).* $N_{humans} = 100$; $N_{critters} = 500$.

General Discussion

Summary of research chapters

Despite a growing history of conflict between humans and herring gulls, the behaviour of herring gulls in urban areas has received relatively little research attention. This thesis aimed to address this lack of research and to begin to understand the behaviours that are likely to be at the root of some of the conflict. Specifically, the research chapters addressed whether and how herring gulls in urban environments use human behavioural cues when making decisions about where and on what to forage. I conducted three field experiments, which examined the use of human cues: in Chapter 1, I investigated the effect of human gaze direction on the time taken for herring gulls to approach an anthropogenic food source; in Chapter 2, I considered the factors underlying the variation in responses to gaze direction indicated in the experiment of Chapter 1; and in Chapter 3, I tested whether gulls were more likely to approach an anthropogenic food item that had been handled by a human, compared to an equally accessible, identical, but unhandled, food item. Finally, in Chapter 4, I used a theoretical model to explore the effects of humans presenting differing levels of danger and reward on the avoidance behaviour of a population of a generic wild animal species.

The results of the three field experiments demonstrate that herring gulls do indeed use behavioural cues from humans. These findings may potentially be beneficial when attempting to mitigate conflict between humans and gulls. For example, now that it is known that herring gulls respond aversively to the direction of human gaze, humans can modify their own behaviour to reduce the likelihood of food theft by not allowing opportunities for gulls to approach from outside their field of view. Equally, if there is an awareness that herring gulls are more likely to approach anthropogenic food items that have been handled, care can be taken to prevent such cues being given, or for interactions with food items to be less conspicuous. Herring gulls were more likely to approach handled food items than handled non-food objects, indicating that the gulls attend to the appearance of food when using human cues. The visual cues of the objects themselves are therefore likely to be important in determining whether herring gulls approach and interact with them. Understanding the types and features of objects that herring gulls prefer to interact with could potentially be a useful consideration in the choice and production of objects such as food and food packaging.

How herring gulls acquire the ability to use human cues has not been studied, but it is likely to be, at least in part, a result of repeated interactions with humans. However, herring gulls may have certain genetic predispositions to responding to human cues, as many of these cues are not uniquely “human”. Gaze aversion is likely to be a heritable trait with deep evolutionary origins (Shepherd, 2010; Wilkinson et al., 2010) but it is also possible that exposure to humans in the context of food could cause a fear of gaze to develop, or exacerbate or reduce existing tendencies to avoid direct gaze. Differing experiences of gulls may also explain the large variation in behaviour that was observed during the experiments of Chapters 1 and 2. The majority of gulls tested in Chapter 1 would not approach the experimenter, either staying in position or flying away. Those that did approach the food did not uniformly exhibit the same behaviour. Several gulls would not peck at the food at all in the direct gaze treatment, but all of those that engaged with the experiment did so when the experimenter’s gaze was averted. While, overall, gulls took longer to approach the food when they were subject to the direct gaze treatment, some gulls approached within a short amount of time in both the direct gaze and averted gaze treatments. It is possible that the latter gulls may have had either positive or inconsequential experiences approaching food in the proximity of humans, and therefore their approaches may have been rewarded or the gulls could have become habituated to close human proximity or even human gaze itself. As some people actively feed gulls, and many leave food litter upon which gulls feed (pers. obs.), this seems plausible. Other gulls may have had negative experiences through being chased away from food, which could result in learning to avoid humans, or, if this only happened in the context of direct gaze, may have associated direct gaze with a negative outcome, whereas human presence alone may be perceived as neutral. It seems probable that the chasing away of gulls could be associated with direct gaze; firstly, a human must notice a gull approaching, which is normally achieved by eyesight, and, secondly, humans that chase gulls away from a food source are likely to be looking at them. However, responding to human gaze necessitates that gulls pay attention to humans and where their gaze is directed. There may not only be differences in how gulls respond to direct gaze, but also in where gulls direct their attention.

Chapter 2 built on the findings of Chapter 1 by asking whether (1) aversion to human gaze is present in recently-fledged juvenile gulls, (2) gulls respond aversively to human eye direction rather than the more salient head direction, and (3) gulls in urban settlements respond differently from gulls in rural settlements. For this experiment, I decided to use the flight initiation distance method of approaching gulls, as I predicted that it would enable the testing of a far larger sample of gulls than was possible with the method used in Chapter 1, which required gulls to voluntarily approach a human and thus could not test all targeted gulls. The study presented in Chapter 2 explored some of the factors that were hypothesised to cause variation in gull behaviour in response to human gaze. As found in previous studies of other species (Grolle et al., 2014; Uchida et al., 2016; Vincze et al., 2016), urban-dwelling herring gulls could be approached more closely than their rural counterparts. The cause of this difference is undetermined, and may be through urban gulls becoming habituated to human presence as a result of the amount of time spent in disturbed areas, or through differential settlement of gulls into these differing habitat types, with comparatively bolder gulls more willing to tolerate high human disturbance (Goumas, Lee, et al., 2020). Gaze direction had an effect on flight initiation distance, with gulls fleeing at greater distances when the experimenter was looking at them rather than looking down. This shows that gulls are able to pay attention specifically to human eyes. There was no interaction between settlement type (urban or rural) and gaze direction, nor between age class (adult or juvenile) and gaze direction, suggesting that gulls of all ages and in both urban and rural locations respond aversively to human gaze. The presence of gaze aversion in juveniles is congruent with the hypothesis that gulls, along with other vertebrates, have a heritable predisposition to at least recognise eyes as informative stimuli (Batki et al., 2000). However, as gulls were not tested under controlled conditions from hatching, it is not possible to draw firm conclusions on the development of gaze aversion in herring gulls.

Given that interactions between humans and herring gulls are a relatively recent occurrence (Rock, 2005), it may be assumed that the attraction of herring gulls towards anthropogenic objects is a result of learning. In the first instance, because of the widespread prevalence of anthropogenic food in urban areas, herring gulls would have associated humans with the presence of food, and then potentially also the handling of items, and their subsequent availability, with obtaining food. The results of the research in Chapter 3 indicate that herring gulls are drawn to food items that have been handled by humans. This is likely to indicate an effect of local or stimulus enhancement (Hoppitt & Laland, 2013), although the experiment did not test whether gulls learn from humans to modify their behaviour towards the same or similar objects subsequently. The type of object was important, and gulls only approached handled objects at a higher rate than would be expected by chance when the objects were food items. These objects had different features from the non-food objects, namely the visibility of food and shiny plastic wrapping, and gulls may have previously learned that these features (possibly including the sound of the plastic) are a cue for food. Perhaps, had the sponges used been wrapped in such plastic, gulls may have displayed similar attraction towards them. The fact that gulls approached both food and non-food objects in similar numbers suggests that their attention towards the objects may have been gained by the experimenter initially, but that the gulls may have identified the objects as being food or non-food on closer inspection. Food objects may have been more attractive, as evidenced by the larger number of approaching gulls pecking at food objects compared to non-food objects. As in the gaze aversion experiments, the focus of the gulls’ attention is likely to be important in determining whether they respond to human cues. Both experiments indicate that quantifying attention may be particularly useful in understanding the behaviour of gulls in the presence of humans.

In the final chapter of the thesis, I simulated the effect of contrasting human behaviour on the avoidance strategies of wild animal species that live in close proximity to humans, and how these animals can best overcome this unique challenge. To do this, I used an individual-based model, which allowed research questions to be considered in an environment free of the noise generated by real-life factors. I found that, when animals generalise from their encounters with humans, they are likely to be vulnerable to harm from humans if they are exposed to sizeable numbers of both rewarding humans (i.e. people who provide food) and dangerous humans (i.e. people who seek to kill or harm members of the animal species concerned). I showed that a fast learning rate is likely to be beneficial when the optimal strategy is to avoid humans, but detrimental, in comparison to a slow learning rate, when the optimal strategy is to remain on foraging grounds despite human presence. The ability to discriminate among and recognise individual humans, which has been demonstrated by some studies of wild birds (e.g. Levey et al. 2009; Lee et al. 2011), appears to be beneficial when human behaviour varies greatly among individuals. However, given the large numbers of humans each animal may encounter, individual recognition takes time to be effective and may sometimes be detrimental if animals are not also able to generalise to some extent. Social learning, whereby animals observe and learn from others' encounters, can aid animals in achieving the optimal strategy of either avoiding humans or staying. If animals simply observe the nature of others' encounters with humans, social learning can reduce avoidance when the level of threat does not warrant such behaviour. This may enable animals to exploit resources when the level of threat from humans becomes lower over time. However, if animals also facilitate social learning by emitting alarm calls upon avoidance, this is likely to be beneficial when the optimal strategy is to avoid humans. Alarm calling also appears to improve the effectiveness of individual recognition. Future research is required to assess the true costs and benefits of using individual recognition as a means of learning about humans in the wild. Exploring the degree to which wild animals discriminate among individual humans will be valuable for understanding the full range of impacts that humans have on wild animal populations. In addition, research that focuses on the effect of food provisioning on animal behaviour and survival will reveal whether or not this uniquely human behaviour benefits wild animals or puts them at risk of harm.

Areas for future research

The research conducted for this thesis has shown that urban-living herring gulls use behavioural cues from humans, but it also highlights various areas for further study. There are several reasons why a greater understanding of the individual and population-level behaviour of herring gulls would be beneficial. Using principles from the study of animal behaviour is likely to play a key role in mitigating human-wildlife conflict (Blackwell et al., 2016; Caro, 2007), which will not only reduce the number and severity of unwelcome encounters with wildlife for people but also promote healthy, minimally-impacted populations of wild animals. In addition, knowledge of the behavioural repertoire of species is useful in the study of comparative cognition: by gaining an insight into the origins of certain behaviours and the environmental variables that are associated with their presence or absence, we can begin to understand the conditions under which particular cognitive abilities evolve.

Individual recognition of humans

Individual recognition of humans entails an animal discriminating between two or more people and remembering the difference between them at a later date. Whether the animal is capable of recognising individual humans can be tested by giving them a reason to respond differently to different people. Several bird species have been found to recognise individual humans (Belguermi et al., 2011; Blum et al., 2020; Davidson et al., 2015; W. Y. Lee et al., 2016, 2011; Levey et al., 2009; Marzluff et al., 2010). In each of these experiments, a “dangerous” human, who displays threatening behaviour, has been used as a stimulus. As the species in these experiments are taxonomically diverse, including a member of the Lari (brown skua; Lee et al. 2016), it seems likely that herring gulls too may be able to recognise dangerous individuals. However, in some human-wildlife encounters, humans provide food, and thus are “rewarding” rather than dangerous. To my knowledge, no research has sought to establish whether free-living, wild animals can discriminate between rewarding and neutral human stimuli and remember this association subsequently. Whether or not gulls and other animals do respond differently towards people who have fed them has implications for predicting how they will respond to encounters with new people and for dealing with nuisance behaviour. Local authorities focus on persuading people not to feed gulls through messaging and fines (Trotter, 2019). However, if feeding does not make a significant difference to gull behaviour, this advice is redundant and other measures should be prioritised. Furthermore, it is still unknown whether wild animals can truly recognise individual humans and the implications this may have on their behaviour and ability to forage optimally.

Quantifying attention

The results of the field experiments indicate that a means of quantifying the attention of herring gulls would potentially be a useful avenue of research. Attention is important for avoiding predation (Dukas & Kamil, 2000) and learning from conspecifics (Day, Coe, Kendal, & Laland, 2003). Herring gulls can only respond to human cues if they are paying attention to them, and whether gulls display undesirable behaviour may be a result of either their propensity or failure to notice human cues. There is likely to be individual variation in this trait, as appeared to be apparent during the experiments.

During the trials of the human gaze experiment described in Chapter 1, I was able to clearly observe the responses of herring gulls to my presence and gaze direction, which was aimed at the eye(s) of the gulls in one of the two treatments. I noticed that there was a difference in the gulls' responses. Some of the gulls would unmistakably look back at my own eyes, and these gulls were invariably the ones that were more cautious in approaching, presumably because they had noticed the potential threat. Some of the other gulls completely failed to look at me, focusing entirely on the food, and these individuals were quick to peck at the food in both trial treatments.

Likewise, during experimental trials for the object choice experiment described in Chapter 3, I again found that there was variation in how attentive the gulls were during the handling of an object. In this experiment, gulls remained at a distance until I placed the food item down and left the area. In some cases, the gulls were clearly focused on me and/or the handled object, as was evident from the direction of their gaze. Gulls focusing on me and/or the handled object appeared to peck at the handled object more often than did gulls that appeared to pay little attention, who instead sometimes appeared to focus more on the non-handled object that was lying unattended on the ground or on their surroundings.

These tentative indications could provide a basis for further work that seeks to understand which herring gulls make eye contact with humans, and which gulls pay attention to human handling, and the consequences of such attentiveness. It is plausible that gulls who pay attention to human cues are less likely to approach humans closely but more able to exploit resources left behind by humans. Unfortunately, it is difficult to accurately quantify the direction of gaze of free-living, wild birds with laterally-positioned eyes, but a good estimation may be possible if multiple cameras are used. In experiments with captive animals, attention is often measured by their use of an observation hole which is provided by the experimenter (Range, Horn, Bugnyar, Gajdon, & Huber, 2009; Scheid, Range, & Bugnyar, 2007), but this is likely to be impractical for use with wild animals.

Neophobia and neophilia

In Chapter 3, herring gulls were presented with objects that they were unlikely to have seen before. Both the food objects (flapjacks in blue plastic packaging) and non-food objects (blue sponges) would, with a reasonable degree of certainty, have been novel stimuli, although it may be expected that the non-food objects would present a greater novelty if gulls categorise food objects by shared features such as the appearance of food and shiny plastic wrapping. As a large proportion of targeted gulls (59% across both experiments) pecked at one of these novel objects, these results indicate that gulls in urban areas may have low levels of neophobia (fear of novel objects), and may potentially be neophilic (attracted specifically to novel, non-food objects; Greenberg and Mettke-Hofmann 2001).

To be an appropriate test of neophobia or neophilia, a comparison with approach behaviour towards a familiar stimulus would be required to quantify the baseline response in terms of latency to approach (Greggor et al., 2015). The novel stimuli presented should also not share features with familiar objects to avoid them being categorised with previously seen stimuli and therefore not be considered truly novel by the gulls (Greggor et al., 2015). The novel objects should not involve food so that apparently neophilic behaviour could not be confused with a motivation for satiety. Additionally, it would be important to distinguish between low neophobia, which involves approaching a novel and therefore supposedly neutral stimulus, and high risk-taking behaviour (boldness), which should be measured in the presence of a known threat (Greggor et al., 2015).

Neophilia and/or low levels of neophobia may facilitate success in urban environments (Barrett et al., 2019), and could explain why herring gulls appear to thrive in areas where human-made items of a vast array of types are common. Understanding whether urban-living gulls are generally neophilic or neophobic would also determine whether or not it is effective to attempt to deter gulls with simple measures such as placing novel objects in or near nest sites or eating areas.

Personality

Personality, or temperament, is defined as “individual behavioural differences (that) are repeatable over time and across situations” (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). The results of the research in Chapter 1 suggest that herring gulls may have distinct personality types. There was a positive correlation in the time taken for each gull to approach in both treatments. Gulls that approached within a short amount of time (i.e. less than 25 seconds) when the experimenter was looking away from them were more likely to approach within a short amount of time when the experimenter was looking at them, and *vice versa*, although those that took the longest time to approach during the “Looking At” treatment showed the greatest reduction in approach time in the “Looking Away” treatment. Although personality traits were not explicitly measured in the experiment, it may show that herring gulls in urban areas differ in their boldness, which is considered to be a greater propensity to take risks (compared to shyness; Sloan Wilson et al. 1994). An understanding of boldness in urban-living herring gulls is likely to be beneficial, as it may be expected that the boldest individuals would be the ones most likely to approach humans for food and become implicated in “nuisance” behaviour (Barrett et al., 2019). If lethal or aversive methods are to be used, an approach that is targeted towards these individuals in particular will be necessary both to be effective in reducing incidences of problematic behaviour and to reduce the impact on the wider population, although it is possible that these foraging niches will be replaced by other individuals (Swan, Redpath, Bearhop, & McDonald, 2017).

Social learning

The mechanisms by which herring gulls acquire new behaviours is likely to be a fruitful area of research. Currently, relatively little is known about social learning in herring gulls. It is known that herring gulls use visual and vocal cues or signals from conspecifics to locate food: herring gulls follow flocks of conspecifics and use a “food-finding call” to attract conspecifics when they discover a large quantity of food (Frings et al., 1955). Many species learn from conspecifics, and many of those can also learn from heterospecifics (Avarguès-Weber et al., 2013). Little research has examined whether free-living wild animals can learn from humans. I tested whether gulls used a direct human cue (handling) to locate food, but a key objective for future research would be to test whether this attractive effect towards a particular object is long-lasting, thus providing evidence of social learning from heterospecifics. This may be in the form of local enhancement (Hoppitt & Laland, 2013), if gulls are drawn to the same area that they have previously observed a human interacting with an object (most likely food), or stimulus enhancement (Hoppitt & Laland, 2013), if gulls seek out or select food objects of a similar type to the ones that they have seen associated with a human.

It might also be useful to find out whether stimulus enhancement is important in herring gulls learning from each other. If gulls learn from each other which food types to consume, this will affect behaviour at the population level and may result in certain types of anthropogenic food being targeted more than others, with implications for potential management strategies. Discrete populations of herring gulls appear to have local feeding specialisations (Evans, Pearce, & Foote, 2017; Holman, Rius, & Blackburn, 2019), suggesting that social transmission may occur, although other explanations, such as heritable foraging behaviour or differential access to resources, would need to be ruled out and the precise social learning mechanism identified. Learning socially which items to exploit may also have an effect on the health of gull populations, particularly if the items contain plastic, a material that has often been shown to have a detrimental impact on seabirds (Wilcox et al., 2015).

Furthermore, whether gulls learn socially how to respond to humans is an open question. Gulls could potentially learn to tolerate humans through social facilitation (Hoppitt & Laland, 2013), whereby the presence of conspecifics attracts others to a location that they may otherwise avoid due to the proximity of an anxiogenic stimulus; in this case, humans. The attracted conspecifics are then able to habituate to human presence. This phenomenon has occurred with wild chimpanzees (Samuni et al., 2014) and could potentially alter the behaviour of many other species. It is also possible that gulls could learn to approach or avoid humans through observational conditioning (Hoppitt & Laland, 2013), when humans feed or attack other gulls, respectively. As human behaviour varies widely, gulls are likely to receive “mixed messages” from humans, and how they weight rewarding and threatening encounters will provide an insight into the relative success of urban foraging strategies. Gulls may also potentially have the ability to recognise individual humans, and, if they can do this, there is the further potential that they may be able to transmit this information to others.

The causes of human-directed kleptoparasitism

It is often assumed that herring gulls learn to steal food from humans as a result of purposeful feeding by other people. While this may be true, it ignores the fact that interspecific kleptoparasitism is a natural feeding behaviour in gulls and other avian taxa. It is therefore unlikely that purposeful feeding alone is an explanation for human-directed kleptoparasitism, as other species do not intentionally provide food to kleptoparasites. There is currently no evidence that provisioning gulls with food causes these individuals to steal food from humans. Kleptoparasitism does not appear to be a behaviour that is common to all urban herring gulls (pers. obs.) and there is tentative evidence that a small number of individuals conduct this behaviour repeatedly and thus may specialise in taking food from people (shown on "Nature's Boldest Thieves" (BBC Television); University of Exeter 2015). However, while there is an absence of research on this topic regarding humans, it is possible that learning may play a role in the development of kleptoparasitism. Hesp and Barnard (1989) found that immature black-headed gull (*Chroicocephalus ridibundus*) kleptoparasites become more efficient at procuring food from lapwings (*Vanellus vanellus*) with increasing age and presumably increasing experience, suggesting that kleptoparasites must learn how to kleptoparasitise others successfully. It would be interesting to investigate whether differential success in kleptoparasitising food at a young age could contribute to the persistence or extinction of this behaviour in an individual. Furthermore, it is also unknown whether the tendency to kleptoparasitise can be acquired socially. It may be that gulls genetically inherit their propensity to steal food, but learning through observation from parents or other conspecifics could potentially be involved. There is some evidence that gulls can learn how to exploit novel feeding opportunities through observation (glaucous-winged gulls, *L. glaucescens*, were able to quickly extract hidden bait from a box after observing trained conspecifics do so; Obozova et al. 2011) and therefore observational learning may be involved in the ontogeny of kleptoparasitic behaviour.

Although it remains unclear whether provisioning gulls with food causes human-directed kleptoparasitism (excepting cases where food is passed directly to gulls' mouths, and thus the behaviour is directly encouraged and rewarded), there is little doubt that feeding wild animals of any species encourages them to approach humans (Orams, 2002). Feeding wild animals, and thus rewarding them for approaching humans, which are often otherwise perceived as a threat, changes behaviour through positive reinforcement (Whittaker & Knight, 1998), potentially making wild animals appear bolder. In addition, gulls may not take food directly from human hands but from a nearby location such as a table or picnic blanket, and gulls are often considered a nuisance for other foraging-related behaviours such as rummaging through bins. Therefore, there is little reason not to strongly discourage feeding.

Long-term consequences of urban life

The research described in this thesis has focused largely on gulls' behaviour towards humans and anthropogenic food sources and may have implied that gulls benefit from consuming such food. However, little is known about whether consumption of anthropogenic foods provides greater nutritional benefits than natural (non-anthropogenic) foods. Because anthropogenic foods tend to be higher in calories (Pierotti & Annett, 1990) and have high digestibility (Ottoni, de

Oliveira, & Young, 2009), there is potential for both positive and negative effects on wildlife. The fitness of urban-living gulls compared to their counterparts in traditional habitats is a budding area of research, and is likely to provide insights into the effects, if any, that a diet high in anthropogenic food have on chick growth and survival, as well as adult lifespan. However, it should be noted that it is unlikely that any population of herring gull remains unaffected by human activity and does not consume any kind of anthropogenic food, whether it is discarded food in towns, grain from agricultural areas, food waste from landfill sites, or fishing discards.

In addition to potential hazards from a poor-quality diet, there may be a suite of threats in urban areas that are specific to human activity and are thus new and different from threats in rural areas. For example, road traffic accidents are probably extremely rare in traditional colonies, but seem to be relatively frequent in urban areas (pers. obs.; Rosemullion Veterinary Practice, pers. comm.). Additionally, people who are concerned about problem behaviour in gulls may take matters into their own hands. There have been some high-profile attacks on gulls in recent years (e.g. Embury-Dennis 2019) but it is unlikely that these attacks would have a significant impact at the population level. However, there is potential that they could remove the boldest or most aggressive gulls from the population, and, if these characteristics have a heritable component or can be socially learned, may reduce the spread of such behaviour through the population and have a longer-term effect on the behaviour of gulls in a given area.

Although illegal killing of adult gulls may not affect the population size in urban areas, it would be worthwhile to compare the average lifespan of gulls breeding and foraging in urban areas with those that breed and forage in rural areas, on mostly natural (non-anthropogenic) foods. With few natural predators, adult herring gulls are relatively long-lived (Monaghan, 1980), which may mean that road traffic accidents and purposeful killing (licensed culling as well as illegal persecution) have an effect on average lifespan.

Up until recently, the removal of herring gull nests and eggs was permitted without individual licence by the government body Natural England for the purpose of preserving public health and safety (Natural England, 2019a). Landowners, including members of the public, were able to use the provisions of a general licence to remove any number of eggs from their property. The removal of chicks, however, was not permitted without an individual licence. In June 2019, Natural England announced that the herring gull, owing to its conservation status, would no longer be listed on any of its general licences (Natural England, 2019d). Instead, any person wanting to take the eggs of this species would need to apply for a class licence, which, unlike the general licence, requires registration and is granted to individuals. It would be pertinent to note whether this change in policy has an effect on herring gull numbers and the incidence of problematic behaviour in areas that are affected by the change. As herring gulls modify their behaviour when they are incubating and are generally responsible for fewer “nuisance” behaviours during this time, egg removal without replacement with dummy eggs may not alleviate the perceived problem (Rock, 2005).

A further question is whether bolder individuals and kleptoparasites are more successful in producing offspring that survive to breed. It may be expected that such individuals would procure more food than shyer individuals and therefore raise more chicks, but perhaps these behaviours are riskier and more energy-consuming, and those individuals that refrain from such encounters are better at assessing risk and minimising energy expenditure. Shyer individuals may operate a “sit and wait” strategy, avoiding direct encounters with humans but gaining food rewards by delaying their approach until danger passes and thus benefit most from living in urban areas.

An understanding of herring gull population trends and the precise causes of the observed changes is required. Due to difficulties in surveying nests on buildings, there is as yet no accurate estimate of the number of herring gulls breeding in urban areas (Joint Nature Conservation Committee, 2021). As herring gull populations in traditional coastal habitats continue to decrease (Defra, 2019), it is important to quantify the extent of urban gulls’ use of anthropogenic foods. If it is found that gulls in urban areas are sustained because of a reliance on anthropogenic food, it will be difficult to implement a conservation strategy that benefits both humans and gulls through cessation of anthropogenic food provisioning alone. The body condition and average clutch size of yellow-legged gulls (*L. michahellis*) breeding in a nature reserve in Spain decreased after the closure of a local landfill (Steigerwald, Igual, Payo-Payo, &

Tavecchia, 2015), suggesting a reliance on anthropogenic food. The effect of withdrawing anthropogenic food on wider gull populations will need to be monitored where approaches that seek to reduce urban gull numbers in this way are undertaken.

Concluding remarks

Herring gulls are a common sight in coastal towns, and an increasingly common sight in urban locations further inland. However, such abundance masks a steep and apparently unrelenting population decline. As gulls are responsible for several “nuisance” behaviours and, unlike many animals at the centre of conservation campaigns, arguably have few redeeming characteristics, it will probably be difficult to gain public support for conserving gulls. Nevertheless, solutions to the conflict between humans and gulls are desirable, and will only be possible with a more thorough understanding of urban gull ecology and behaviour.

This thesis examined a particular aspect of gull behaviour in relation to urban gulls’ foraging interactions with humans. The results of the data chapters showed that human behaviour can affect gull behaviour, and therefore humans may be able to lessen problematic interactions with gulls by modifying their own actions. As with all human-wildlife conflict, part of the problem is the perception by humans of wildlife and the extent of damage caused (Dickman & Hazzah, 2015). It may therefore be beneficial to address how humans perceive particular species and to focus on disseminating knowledge and encouraging uptake of established preventative measures (Madden, 2004). Additionally, increasing public understanding of how and why non-human animals behave as they do, and the importance of a diverse community of species for a functioning ecosystem, may be possible through targeted education and has the potential to create a society that is better equipped to deal with wildlife encounters.

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