Animal Behaviour 117 (2016) 123–133

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Street smart: faster approach towards litter in urban areas by highly neophobic corvids and less fearful birds

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ARTICLE INFO

Article history:
Received 8 January 2016
Initial acceptance 11 February 2016
Final acceptance 8 March 2016
Available online 30 May 2016
MS number 16-00025R

Keywords:
categorization
Corvidae
litter
object neophobia
urban gradient

The extent to which animals respond fearfully to novel stimuli may critically influence their ability to survive alongside humans. However, it is unclear whether the fear of novel objects, object neophobia, consistently varies in response to human disturbance. Where variation has been documented, it is unclear whether this variation is due to a change in fear towards specific novel stimuli, or whether it is symptomatic of a general change in fear behaviour. We measured levels of object neophobia in free-flying birds across urban and rural habitats, comparing corvids, a family known for being behaviourally flexible and innovative, with other urban-adapting bird species. Neophobic responses were measured in the presence of different types of objects that varied in their novelty, and were compared to behaviour during a baited control. Corvids were more neophobic than noncorvid species towards all object types, but their hesitancy abated after conspecifics approached in experimental conditions in which objects resembled items they may have experienced previously. Both sets of species were faster to approach objects made from human litter in urban than rural areas, potentially reflecting a category-specific reduction in fear based on experience. These results highlight species similarities in behavioural responses to human-dominated environments despite large differences in baseline neophobia.

Animals' responses to novel stimuli may influence their survival as humans drastically alter habitats (Robertson, Rehage, & Sih, 2013). The extent to which animals respond fearfully to novelty (i.e. demonstrate neophobia) may help or hinder their success, depending on the dangers and benefits associated with novelty. For example, high levels of object neophobia may help animals avoid danger should the objects harbour predators or toxins, but reduced neophobia allows animals to approach and exploit potentially advantageous novel resources (Greenberg & Mettke-Hofmann, 2001). Since human-dominated habitats offer combinations of food, dangers and habitat types that differ substantially from less undisturbed environments, examining how animals respond behaviourally to novelty is important in understanding how they adjust to man-made changes in the environment (Greggor, Clayton, Phalan, & Thornton, 2014).

Urban areas exert strong selection pressures that often reduce species richness for vertebrate and invertebrate groups (McKinney, 2008). Although some bird species thrive in urban areas, no single defining trait predicts a species' urban presence (Croci, Butet, & Clergeau, 2008; Kark, Iwaniuk, Schalimtzek, & Banker, 2007; Møller, 2014; Shochat, Warren, Faeth, McIntyre, & Hope, 2006). Instead, success in urban environments may depend on species' ability to adjust to the demands of a new habitat by modifying behaviour, such as foraging strategies or the timing of breeding attempts (Kark et al., 2007; Shochat et al., 2006; Sol, Timmermans, & Lefebvre, 2002). Behavioural flexibility may be crucial in allowing animals to reduce costly and unnecessary fear responses or to increase them to deal with new dangers. For example, some urban birds are able to avoid investing in unnecessary antipredator responses by selectively responding to specific threatening humans (Davidson, Clayton, & Thornton, 2015; Lee, Lee, Choe, & Jablonski, 2011; Levey et al., 2009). However, it is unclear whether areas of human disturbance also favour selective reductions in fear towards other stimuli, such as potentially dangerous objects.

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http://dx.doi.org/10.1016/j.anbehav.2016.03.029

There is no consensus about the optimal level of object neophobia in urban environments because opposing hypotheses predict benefits for high or for low neophobia. Some studies suggest that less neophobic individuals are faster to interact with and solve novel foraging tasks (Benson-Amram & Holekamp, 2012; Biondi, Bó, & Vassallo, 2010; Boogert, Reader, Hoppitt, & Laland, 2008; Griffin & Guez, 2014). Since human litter provides opportunities for foraging that requires the manipulation of novel objects, such as food packaging, reduced neophobia may make animals more likely to innovate with novel food or objects when invading novel habitats (Greenberg, 2003; Greenberg & Mettke-Hofmann, 2001; Martin & Fitzgerald, 2005). Accordingly, urban common mynas, *Acridotheres tristis*, have been shown to be less neophobic than suburban conspecifics (Sol, Griffin, Bartomeus, & Boyce, 2011), and urban groups of house sparrows, *Passer domesticus*, solve tasks more quickly than rural ones (Liker & Bókony, 2009). Such reductions towards fear-related stimuli in urban environments has been documented in other behaviours such as flight initiation distance (Clucas & Marzluff, 2012; Mccleery, 2009; Moller, 2010; Møller, 2008), a dampened corticosterone stress response (Grunst, Rotenberry, & Grunst, 2014) or both (Atwell et al., 2012) (but note that these stress hormone patterns are not universal, see Bonier, 2012).

In contrast, increased neophobia may be favoured in potentially dangerous locations where exploration may expose animals to threats such as generalist predators or poisons (Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013; Greenberg, 2003). Urban areas typically contain more of these threats (Evans, Newson, & Gaston, 2009; Sims, Evans, Newson, Tratalos, & Gaston, 2008; Sorace, 2002; Sorace & Gustin, 2009). Laboratory manipulations of predation pressure in fish show that individuals' predator neophobia can plastically respond to the dangers of the environment (Brown et al., 2013), and that experience with these pressures can increase survival upon reintroduction into the wild (Ferrari, Mccormick, Meekan, & Chivers, 2015). Additionally, urban environments may select for increased neophobia over time. Human commensal species of wild rats, for example, show higher levels of object neophobia than laboratory and feral strains that do not have a history of surviving alongside a rat poison (Cowan, 1977). Similarly, elevated levels of object avoidance have been documented in house sparrows and shiny cowbirds, *Molothrus bonariensis*, in urban compared to rural habitats (Echeverría & Vassallo, 2008).

Studies may have found conflicting relationships between neophobia and urban areas for several reasons. First, different species may respond in divergent ways to urban selection pressures. Interspecies comparisons between and within environments are crucial to explaining human impact on temperament traits, such as neophobia, but they are rarely conducted in the wild (Archard & Braithwaite, 2010; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Second, studies often measure neophobia in subtly different ways. Tests must present objects that accurately represent either known or novel stimuli because avoidance should only be interpreted as neophobia if it reflects a response to novelty, rather than a generalized fear response (Greggor, Thornton, & Clayton, 2015). Third, neophobia tests are classically conducted on isolated individuals (e.g. Greenberg, 1990), yet the presence of foraging conspecifics is likely to influence novelty approach in groups in the wild. Therefore to assess wild birds' responses towards novelty and objects characteristic of urban and rural spaces, we compared behavioural responses of foraging groups towards several types of objects across a range of bird species.

We presented free-flying bird communities with an object made from either natural items that mirrored natural stimuli, litter items that mimicked anthropogenic foraging opportunities in urban areas, or entirely artificial objects designed not to resemble any familiar stimulus. We examined the responses of 12 species of urban-exploiting birds that ranged in size, foraging ecology and evolutionary history. Five of these species were corvids (Corvidae), a family often described as very neophobic (Greenberg & Mettke-Hofmann, 2001; Heinrich, Marzluff, & Adams, 1995; Marzluff & Heinrich, 1991) yet highly innovative and skilled at exploiting novel opportunities (Emery & Clayton, 2004; Nicolakakis & Lefebvre, 2000), a seemingly paradoxical combination considering that neophobia is commonly thought to inhibit innovation (Greenberg, 2003; Griffin & Guez, 2014). To our knowledge corvid object neophobia has not been tested across urban gradients before, nor has their reputed high level of neophobia been verified through comparison with other wild species. We compared their neophobic responses to those of the other seven participating species to determine how universal urban neophobia changes might be. Both sets of species could, in theory, benefit equally from reduced neophobia in urban areas if it allowed for increased feeding opportunities around human-created packaging and waste. Corvids in urban areas have been reported to consume more human refuse than rural conspecifics (Rowley & Vestjens, 1973), and other bird species have been known to rely on anthropogenic food sources, especially during the winter (Orell, 1989). However, both sets of species also face potential dangers associated with the novelty they encounter, such as urban predators, including cats (Evans et al., 2009; Sims et al., 2008; Sorace, 2002; Sorace & Gustin, 2009). Therefore selectively avoiding certain types of objects, without having to relax their overall defences, would allow urban birds to take advantage of beneficial types of novelty. Additionally, since both the corvid and noncorvid groups contained social foraging species, known to make foraging decisions based on the behaviour of conspecifics (e.g. Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Chiarati, Canestrari, Vera, & Baglione, 2012), the presence of conspecifics could help birds distinguish beneficial from dangerous novelty.

We predicted that: (1) corvids would show higher neophobia than noncorvids towards novel objects within habitats; (2) both sets of species would reduce their neophobic behaviour in urban areas towards objects that would be less novel there, such as litter in urban areas; and (3) foraging birds would be more likely to approach objects after a conspecific visited.

METHODS

Twelve feeding tables were set up across human population gradients in distinct geographical regions in the east and southwest of England (Cambridgeshire, eight tables; Cornwall, four). We estimated the extent of human presence in the vicinity of each table based on the amount of impervious surface cover, such as tarmac and rooftops, in the 1 km^2 surrounding the site. Surface cover area

Table 1
Percentage of impervious surface area within the 1 km^2 grid surrounding the feeding table

Feeding table ID	Region	Classification	Impervious surface area
PH-S, PH-D	Cornwall	Urban	55.25
J	Cambridgeshire	Urban	51.14
SC	Cornwall	Urban	20.87
M, H	Cambridgeshire	Rural	5.7
PF	Cornwall	Rural	3.56
I, K, N	Cambridgeshire	Rural	2.15
B, D	Cambridgeshire	Rural	4.1

Calculated with Google Earth Pro.