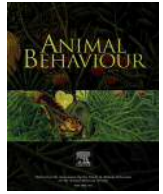




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The cognition of 'nuisance' species

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Recent work in animal cognition has focused on how animals respond to new or changing environments. Although many species are currently in decline, other species are thriving in human-altered habitats by taking advantage of new resources and opportunities associated with anthropogenic disturbance. Yet, as a result, these same species are often in conflict with humans and treated as a nuisance. Therefore, cognitive abilities such as innovation and behavioural flexibility may, paradoxically, lead to the demise of especially adaptive individuals. Here we review what is known about the cognition of 'nuisance' species and 'problem' individuals to shed light on the struggles of coexistence with humans along disturbed landscapes. We take an in-depth look at several cognitive abilities that are hypothesized to be of critical importance for species that are successfully utilizing human-altered environments, including neophilia, boldness, categorization, innovation, memory, learning, social learning and behavioural flexibility, and examine evidence that these cognitive abilities may also bring animals into conflict with humans. We also highlight some examples of species that may be using cognitive mechanisms to change their behaviour to avoid conflict with humans. We then discuss the role of animal cognition in current mitigation strategies that have been developed to address human–wildlife conflict. Additionally, we consider the role that human behaviour and perception of animals might play in either worsening or lessening conflict with wildlife. Finally, we propose some directions for future research and suggest that empirical investigation of 'nuisance' animal cognition could reveal the cognitive mechanisms underlying adaptation to anthropogenic change as well as help mitigate human–wildlife conflict.

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Recent work in behavioural ecology and animal cognition has focused on how animals respond to new or changing environments, with particular emphasis on urban habitats (Greggor, Clayton, Fulford, & Thornton, 2016; Griffin, Netto, & Peneaux, 2017; Griffin, Tebbich, & Bugnyar, 2017). Many species are currently in decline (Pimm et al., 2014), while others are thriving in human-altered habitats by taking advantage of new opportunities associated with anthropogenic disturbance (Lowry, Lill, & Wong, 2013; Sol, Lapiedra, & González-Lagos, 2013; Wong & Candolin, 2015). Living in a city, or exploiting other human-disturbed habitats, such as agricultural fields, requires animals to respond to a number of novel challenges. For example, to survive in urban environments, animals must locate and exploit new food resources (Sol et al., 2013), deal with new predators and competitors (Bílá, Berankova, Vesely, Bugnyar, & Schwab, 2017; Seress, Bókony, Heszberger, &

Liker, 2011), develop different navigation strategies, including coping with challenging barriers such as roads and fences (Coulon et al., 2008; Proppe, McMillan, Congdon, & Sturdy, 2017; Seidler, Long, Berger, Bergen, & Beckmann, 2015) and overcome elevated levels of noise (Kight & Swaddle, 2015) and light pollution (Dominoni, Carmona-Wagner, Hofmann, Kranstauber, & Partecke, 2014). An individual's ability to solve novel challenges in human-altered habitats can greatly affect its fitness (Cole, Morand-Ferron, Hinks, & Quinn, 2012; Ricklefs, 2004).

The cognitive buffer hypothesis proposes that large brains evolved primarily to facilitate the production of behavioural responses when animals are faced with novel or changing environments (Sayol et al., 2016; Sol, 2009a). Animals with larger relative brain sizes are thought to exhibit enhanced domain-general cognitive abilities, such as innovation, behavioural flexibility and learning, compared to animals with smaller relative brain sizes (Sol, 2009b; but see Roth & Dicke, 2005). Animals that exhibit these cognitive abilities are hypothesized to be better at solving problems they encounter when living in human-dominated landscapes (Griffin, Netto, et al., 2017; Lowry et al., 2013). Innovation, the invention of new behaviours or the modification of existing behaviours to solve

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novel problems (Lefebvre et al., 1997; Reader & Laland, 2003; Reader, 2003), can be assessed through problem-solving tests (Griffin & Guez, 2014; Roth & Dicke, 2005). Recent work consistent with the cognitive buffer hypothesis suggests that urban individuals have higher rates of innovation (Møller, 2009; but see Kark, Iwaniuk, Schalimtzek, & Banker, 2007) and may be better at problem solving (Audet, Ducatez, & Lefebvre, 2016; Liker & Bókony, 2009; Sol, Griffin, Bartomeus, & Boyce, 2011; but see Papp, Vincze, Preiszner, Liker, & Bókony, 2015) than rural conspecifics.

Behavioural flexibility can facilitate the expression of innovations (Logan, 2016a) and is defined as an individual's ability to alter its behaviour in response to changing environments and to inhibit behaviours that were previously successful (Coppens, de Boer, & Koolhaas, 2010; Logan, 2016a; Sol, Timmermans, & Lefebvre, 2002; Wright, Eberhard, Hobson, Avery, & Russello, 2010). Behavioural flexibility predicts animals' success at invading new areas, with successful invaders exhibiting a higher frequency of innovations (Lowry et al., 2013; Sol & Lefebvre, 2000; Sol et al., 2002; Wright et al., 2010). Learning and neophilia are predicted to be especially adaptive in urban environments due to the extreme spatial complexity of cities, as well as the increased predictability of anthropogenic resources resulting from routine human activities, such as trash collection (Griffin, Tebbich, et al., 2017). Additionally, learning via habituation to humans likely helps animals cope with urbanization (Blumstein, 2016; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015). Moreover, neophilia and boldness could facilitate range expansion into new environments (Liebl & Martin, 2014), and tolerance of novel objects is predictive of utilization of novel foods in urban environments (Kark et al., 2007; Lowry et al., 2013).

Although some cognitive traits may aid in the adaptation of animals to urban environments, animals that exhibit these same cognitive abilities could be more likely to come into conflict with humans. For example, trapping efforts highlight potential sampling biases towards bolder individuals (Carter, Heinsohn, Goldizen, & Biro, 2012; Stuber et al., 2013), and individuals from invasive populations may be less neophobic of novel food than conspecifics from resident populations (Martin & Fitzgerald, 2005). When animals approach and engage with novel objects and food in human-disturbed habitats, they are probably at greater risk of coming into conflict with humans. Additionally, urban individuals habituate to anthropogenic disturbance through learning, and as a result may become bolder with time (Lowry et al., 2013). Therefore, it appears likely that human–wildlife conflict in cities will become more frequent and problematic. Unfortunately, when animals learn to associate humans with food, or come into conflict with humans over habitat or other resources, they are usually viewed as pests or nuisance animals, and the outcomes of these interactions are typically fatal for the animals (Conover, 2002). Thus, animals that are the most adept at acquiring anthropogenic resources, and those that exhibit high levels of cognitive abilities such as boldness, learning, innovation and behavioural flexibility, may also be the most at risk for lethal encounters with humans.

Here, we examine what is known about the cognitive abilities of species that often come into conflict with humans. We consider whether cognition plays a significant role in the conflict that we see between 'nuisance' species and humans. Examples of conflict include wildlife depredating livestock, crop raiding, damaging residential property, stealing food and personal items, colliding with vehicles, transmitting zoonotic diseases, and even potentially killing humans (Conover, 2002). We consider the possibility that some animals may be using cognition to avoid human activity and conflict. We then examine the role of cognition in some common human–wildlife conflict mitigation strategies. Finally, we propose future research that would advance our understanding of

adaptation to human-altered environments, and consider how human behaviour and culture influence nuisance animal cognition, and can help reduce conflict.

COGNITION INVOLVED IN HUMAN–WILDLIFE CONFLICT

Neophilia

Neophilia, an attraction to novelty, is likely a critical component of the success of animals in human-altered landscapes (e.g. birds: Evans, Hatchwell, Parnell, & Gaston, 2010; Lowry, Lill, & Wong, 2011; Myers & Hyman, 2016; mammals: Bowers & Breland, 1996; Found & St Clair, 2016; Lyons, Mastrotonaco, Edwards, & Schulte-Hostedde, 2017; but see Griffin, Netto et al., 2017). Attraction to novelty, such as anthropogenic foods or human-made structures, helps animals to take advantage of new resources. Neophilia in response to novel food items may facilitate range expansion into new environments (Chapple, Simmonds, & Wong, 2012; Liebl & Martin, 2014) and persistence in urban areas (Sol et al., 2011). For example, object neophilia allows great tits, *Parus major*, to readily exploit novel and sometimes unpredictable resources in urban environments (Tryjanowski et al., 2016). Over time, success in these situations could lead to increased selection of neophilic behaviour in species living alongside humans (Carrete & Tella, 2010; MacDonald & Ritvo, 2016).

Despite its advantages, increased neophilia in animals could instigate conflict with humans. For example, kea, *Nestor notabilis*, are characterized by extreme object attraction and object play behaviour (Diamond & Bond, 1999; Federspiel, Clayton, & Emery, 2009; O'Hara, Schwing, Federspiel, Gajdon, & Huber, 2016) and will readily approach and manipulate objects associated with humans. This lack of inhibition fosters their ability to open cars, trash bins and other objects; however, these innovations often damage human property and have led to humans killing kea (BirdLifeInternational, 2017; Diamond & Bond, 1999; Orr-Walker, Kemp, Adams, & Roberts, 2015). Similarly, the attraction of long-tailed macaques, *Macaca fascicularis*, to human items facilitates the stealing of these objects in exchange for food, which leads to humans losing property, being bitten or shooting macaques (Brotcorne, 2014; Fuentes & Gamerl, 2005; Fuentes, 2010).

Boldness

When confronted with potentially risky situations in an anthropogenic environment, having a bolder temperament, or a willingness to take risks in novel situations (Coleman & Wilson, 1998), enables animals to capitalize on new resources (Chapple et al., 2012; Ducatez, Audet, Rodriguez, Kayello, & Lefebvre, 2017; Dugatkin & Alfieri, 2003; Fogarty, Cote, & Sih, 2011; Griffin, Netto et al., 2017). However, a willingness to take risks likely means that an animal will more frequently come into conflict with humans. Some monkey species are notorious for their bold or threatening behaviour towards humans, including scavenging for and stealing food (Chuah & Pira, 2010; Hsu, Kao, & Agoramorthy, 2009). In Bali, Indonesia, free-ranging longtailed macaques engage in stealing and begging behaviour from humans at temple sites and tourist areas (Brotcorne et al., 2017; Fuentes, 2010). Chacma baboons, *Papio ursinus*, in South Africa engage in risky behaviour by food raiding to exploit anthropogenic resources (Fehlmann et al., 2017). Bolder individuals may also habituate to human presence more rapidly than shyer individuals, which could make these animals more susceptible to being hunted or more likely to engage in risky behaviours (Biro & Post, 2008; Ciuti et al., 2012; Madden & Whiteside, 2014; McDougall, Réale, Sol, & Reader, 2006).

Categorization

The ability to perceive, discriminate and classify cues underlies an animal's response to novel stimuli. Rats, *Rattus* spp., a common urban pest, are able to categorize objects and sounds based on their characteristics (Astikainen, Ruusuvirta, & Naataanen, 2014; Brooks et al., 2013; Vermaercke, Cop, Willems, D'Hooge, & Op de Beeck, 2014; Wasserman, Castro, & Freeman, 2012). Some insects, including honey bees (*Apis* spp.), are capable of categorizing odours and colours via simple forms of rule learning (Chittka & Niven, 2009; Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001; Menzel & Giurfa, 2001). Categorization allows animals to adjust their response to novel items in their environment. For example, members of the family Corvidae are more likely to approach litter-based objects than they are other novel objects (Greggor, Clayton et al., 2016). In this way they demonstrate a less neophobic response to items that are more familiar to them (Greggor, Clayton et al., 2016). Categorization may help species thrive in urban areas by enabling them to identify nest locations and learn the difference between poison baits and safe food resources.

Innovation

Innovation may increase the ability of an individual to modify or expand its ecological niche (Overington, Griffin, Sol, & Lefebvre, 2011), leading to the successful invasion of novel environments and adaptation to urbanization (Lowry et al., 2013; Sol & Lefebvre, 2000; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). This is because innovation allows animals to solve novel problems (Reader & Laland, 2003), thereby opening new avenues of survival in otherwise challenging environments. Solving problems in an anthropogenic environment typically involves the exploitation of anthropogenic entities, and inherently creates conflict with humans. For example, innovation allows animals to capitalize on anthropogenic sources of food, such as trash receptacles and bird feeders (Liker & Bókony, 2009). Milk bottle opening by great tits is a classic example of innovative foraging that occurred in an urban environment (Fisher & Hinde, 1949), and similar examples of innovation, such as sugar packet opening (noisy miners, *Manorina melanocephala*: Delgado-V & Correa-H, 2015; bullfinches, *Loxigilla* spp.: Ducatez, Audet, & Lefebvre, 2013; Reader, Nover, & Lefebvre, 2002) or picking dead insects off car license plates (great-tailed grackles, *Quiscalus mexicanus*: Grabrucker & Grabrucker, 2010), have been documented in other urban-dwelling species. Grey squirrels, *Sciurus carolinensis*, have one of the largest brain-to-body ratios in Rodentia (Mace, Harvey, & Clutton-Brock, 1981) and are notoriously skilled at getting into bird feeders. This problem-solving ability may partially explain their invasion success (Chow, Lea, & Leaver, 2016; Chow, Lurz, & Lea, 2018). Many generalist mammalian carnivores are also skilled at novel, extractive foraging. Spotted hyaenas, *Crocuta crocuta* (Benson-Amram & Holekamp, 2012), bears, *Ursus* spp. (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016), and raccoons, *Procyon lotor* (Daniels, 2016; MacDonald & Ritvo, 2016) have succeeded in empirical investigations of problem solving and often raid human subsidies in urban environments. Invasion of property and exploitation of resources may be perceived as a nuisance, or even a danger, by humans.

Innovation by nuisance species can motivate people to create exclusion structures to prevent unwanted residency and foraging. Yet, such mitigation efforts essentially create further novel challenges for these innovative individuals, who may subsequently engage in further problem solving. For example, electric fences are commonly used to prevent African bush elephants, *Loxodonta africana*, from entering villages or exiting protected areas, and some

individuals have been known to pick up trees or use their tusks to move electric fences so that they can pass through without receiving an electric shock (Mutinda et al., 2014; Sukumar, 2003). Although barriers may effectively exclude some nuisance species, the same barriers may exacerbate conflict with other sympatric nuisance species. In one study of depredation by African carnivores, livestock enclosures made of 'pole' timber reduced attacks by hyaena, but doubled the likelihood of attacks by leopards, *Panthera pardus*, that found ways to scale the fencing materials. Likewise, fences made of bush material reduced leopard attacks but were ineffective against hyaena, which were capable of simply pushing through the dense vegetation (Kolowski & Holekamp, 2006). Furthermore, innovative animals often eventually open or destroy 'animal-proof' products, even when additional reinforcement is added (e.g. kea: Gajdon, Fijn, & Huber, 2006). Thus, innovation by nuisance animals and mitigation by humans may create an 'arms race' between humans and nuisance animals, which is maintained via cognitive abilities like innovation and learning.

Learning

Nuisance species undoubtedly learn to capitalize on anthropogenic resources via positive experiences with humans or human entities. Successful encounters may range from the more inconspicuous, such as learning to raid crops or garbage at night, to the more risk-prone, such as taking shelter in anthropogenic structures or stealing from humans. Similarly, increased exposure to negative or dangerous stimuli introduced by humans, such as toxins or traps, may strengthen the ability of nuisance animals to evade persecution in the future via learning. The more salient the cue or experience, the faster it will be learned (Shettleworth, 2010), thus the payoffs and costs experienced via association with humans often result in effective nuisance behaviours.

Repeated exposure to the sights, smells and sounds of anthropogenic disturbance may lead to either habituation or sensitization to humans (Blumstein, 2016). Sensitization generally causes animals to avoid humans and human subsidies, whereas habituation enables animals to reside in close proximity to humans, increasing the potential for conflict. Many studies have found that individuals living in urban environments exhibit faster rates of habituation and an increased tolerance of humans compared to their rural counterparts (Carrete & Tella, 2011; McGiffin, Lill, Beckman, & Johnstone, 2013; Møller, 2008; Vincze et al., 2016). Yet the factors that predispose a species to habituation are not well understood. Certain traits, including body mass, diet and clutch size, may contribute to increased human tolerance in birds (Samia et al., 2015), and there is a trend for birds with a larger body size to exhibit shorter flight-initiation distances when approached by humans (Blumstein, 2006).

Although further study is needed to understand habituation and tolerance of humans (Blumstein, 2016), contact with humans clearly affects risk perception by wildlife, and alters animal behaviour (Caro & Sherman, 2011). For example, there are consistent reports of avian species exhibiting greater flight-initiation distances to humans during hunting seasons than during other times of year (Stankowich & Blumstein, 2005). Male red deer, *Cervus elephas* (Lone, Loe, Meisingset, Stamnes, & Mysterud, 2015), and elk, *C. elephas canadensis* (Paton, Ciuti, Quinn, & Boyce, 2017), which experience higher hunting pressure than females, shift habitat use during hunting seasons. Human behaviour, such as food provisioning of wildlife, can promote conflict-prone behaviours via conditioning (Dubois & Fraser, 2013). Direct and indirect feeding of wildlife increases begging behaviour (Donaldson, Finn, Bejder, Lusseau, & Calver, 2012) and aggression (Southwick, Siddiqi, Farooqui, & Pal, 1976) directed towards humans. Furthermore,

there is growing evidence of animals stealing food or other objects directly from humans (i.e. kleptoparasitism) in birds (herring gulls, *Larus argentatus*: Deering, 2017), primates (macaques: Brotcorne et al., 2017) and cetaceans (dolphins, *Tursiops truncatus*: Pennino, Mendoza, Pira, Floris, & Rotta, 2013). Because kleptoparasitism can enhance fitness (Shealer, Spendlow, Hatfield, & Nisbet, 2005), and there may be a relationship between kleptoparasitism and relative brain size, this behaviour is likely perpetuated via cognitive abilities such as learning (Morand-Ferron, Sol, & Lefebvre, 2007).

Memory

Various forms of memory likely affect the success of nuisance species. Spatial memory is important in navigating complex anthropogenic environments (Maguire et al., 2000), however, little is known about spatial memory and cues used by nuisance species when navigating cities. Urban mesocarnivores, such as raccoons (Dalgish & Anderson, 1979) and badgers, *Meles meles* (Mellgren & Roper, 1986), can quickly locate a new food source in their home range in a single night and remember its location thereafter. Spatiotemporal memory could allow individuals to predict foraging opportunities based on the routine behaviours of humans, such as garbage collection or maintenance of bird feeders (Griffin, Tebbich et al., 2017). Members of the family Corvidae demonstrate use of episodic-like (i.e. what-where-when) memory (Clayton & Dickinson, 1998; Emery, 2006), which could afford corvids more accurate predictions of the best sources of food (e.g. trash collection schedules) and detect human cues that lead to food (e.g. crowds leaving sports stadiums). Episodic-like memory may also be exhibited by other mammalian nuisance species, including rats (Roberts, 2006), pigs, *Sus scrofa* (Kouwenberg, Walsh, Morgan, & Martin, 2009), and chimpanzees, *Pan troglodytes* (Martin-Ordas, Haun, Colmenares, & Call, 2010). Although there have been many empirical investigations of memory in species that are coincidentally often involved in conflict (Shettleworth, 2010), memory in nuisance species has not yet been investigated as a factor that facilitates human–wildlife conflict.

Social Learning

Animals should copy the behaviour of others when the cost of individual learning is high, or when there is moderate predictability in the environment (Boyd & Richerson, 1985). Many species learn both adaptive (Page & Ryan, 2006) and maladaptive (Sigaud, Merkle, & Berdahl, 2017) behaviours from others, and thus social learning and cultural transmission of behaviour has become an important consideration in contemporary conservation and management of wildlife (Greggor, Clayton, Phalan, & Thornton, 2014; Keith & Bull, 2017). Similarly, nuisance species can learn conflict-prone behaviours from conspecifics (Donaldson et al., 2012). For example, foraging on anthropogenic sources of food may be a socially learned phenomenon in species such as black bears, *Ursus americanus* (Hopkins, 2013; Mazur & Seher, 2008; but see Breck et al., 2008) and jackdaws, *Corvus monedula* (Greggor, McIvor, Clayton, & Thornton, 2016). Bottlenose dolphins may learn to forage for fish in trammel nets from other dolphins, which results in a loss of resources to fishermen and risk of entanglement in nets for dolphins (Pennino et al., 2013). Male African elephants that crop-raid tend to be associated with other crop-raiding males (Chiyo, Moss, & Alberts, 2012), and crop-raiding behaviour is probably, at least partially, socially learned (Sukumar, 2003). Additional evidence in other species spanning geese, *Anser brachyrhynchus* (Gill, Watkinson, & Sutherland, 1997) to chimpanzees (McLennan & Hockings, 2014) suggests that crop-raiding behaviour could be transmitted socially. Social transmission of information

among some mesocarnivores, such as raccoons, is hypothesized to contribute to their heightened efficiency in urban environments, especially compared to more solitary mesocarnivores, such as striped skunks, *Mephitis mephitis* (Gehrt, 2004; Gehrt, Riley, & Cypher, 2010; O'Donnell & DeNicola, 2006; Prange & Gehrt, 2004).

Other types of social cognition also likely enhance success in disturbed environments while influencing conflict with humans. Animals engaging in group foraging and raiding of urban areas can benefit from sentinel behaviour, where one vigilant individual alerts the rest of the group about a threat, such as a nearby human or domestic dog, *Canis lupus familiaris* (Chapman et al., 2016). Similarly, animals may rely on cues from conspecifics and hetero-specifics to learn about threats in human-altered areas. Crows demonstrate horizontal social learning of information about dangerous humans (Cornell, Marzluff, & Pecoraro, 2012), and learn to avoid specific places and humans associated with dead conspecifics (Swift & Marzluff, 2015).

Possessing an understanding of another's intention may also contribute to success for animals living alongside humans. Scrub-jays cache food behind barriers to block a conspecific's view, and they use personal knowledge gained from stealing another bird's caches (Dally, Emery, & Clayton, 2010). Ravens, *Corvus corax*, assume that conspecifics can see them if they are aware of conspecifics nearby, even if they cannot actually see the conspecifics (Bugnyar, Reber, & Buckner, 2016). Thus, animals living alongside humans may similarly be able to deceive humans, such as by hiding 'stolen' anthropogenic items, by being aware of what humans can see, or by foraging when humans are not looking. Eavesdropping on antipredator cues may also be an effective strategy of avoiding persecution by humans. For example, mule deer, *Odocoileus hemionus*, who share a common coyote, *Canis latrans*, predator with yellow-bellied marmots, *Marmota flaviventris*, are able to respond to marmot alarm calls (Carrasco & Blumstein, 2012), and it is likely that nuisance animals living in urban environments could similarly benefit from interspecific communication. However, we can only speculate on the potential role of much of social cognition on human–wildlife conflict, as there are few empirical investigations on this topic.

Behavioural Flexibility

Plastic behavioural responses enable animals to cope with change or devise novel solutions to problems in their environment (Ricklefs, 2004). Individuals with increased behavioural flexibility may possess larger brains (Sol, 2009b) and are equipped to readily recognize and utilize unfamiliar resources (Martin & Fitzgerald, 2005). For instance, behavioural flexibility is important for invasion success in several bird species (Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011; Logan, 2016b; Sol et al., 2002; Wright et al., 2010). Urban-adapted species are also known for their flexible use of anthropogenic resources and response to disturbance, which has contributed to their reputation among humans as nuisance animals.

Flexibility in home range size allows some species in developed areas to reduce their range and take advantage of new resources (raccoons: Bozek, Prange, & Gehrt, 2007; Prange, Gehrt, & Wiggers, 2004; white-tailed deer, *Odocoileus virginianus*: Cornicelli, Woolf, & Roseberry, 1996; Storm, Nielsen, Schaubert, & Woolf, 2007). However, such flexibility comes at the cost of increased interaction with humans and their belongings, because these ranges often include residential areas. Plasticity in social systems could likewise contribute to human conflicts with animals. For example, in urban areas, ants, *Tapinoma sessile*, switch mating systems and form supercolonies, often making them a dominant pest compared to their rural single-colony counterparts (Buczowski, 2010).

Flexible foraging strategies enable nuisance animals to cope with environmental change by switching between resources or discovering new ways of accessing resources. Raccoons (Daniels, 2016), kea (Auersperg et al., 2011) and crows (Auersperg et al., 2011) have all demonstrated behavioural flexibility in captivity by switching among different solutions on multi-access puzzle boxes. Captive raccoons have also demonstrated creative problem solving and flexibility in an Aesop's Fable task, in which subjects must drop objects into a water-filled tube to raise the water level and obtain an out-of-reach food reward (Stanton, Davis, Johnson, Gilbert, & Benson-Amram, 2017), and crows have demonstrated behavioural flexibility in tool use (Knaebe, Taylor, Elliffe, & Gray, 2017; Taylor et al., 2011). Raccoons, kea and crows are also all notorious for their abilities to forage on anthropogenic items in urban areas, even when trash bins have been altered by humans to keep out animals, such as by adding a heavy item or bungee cord on top of the lid (Auersperg et al., 2011; Diamond & Bond, 1999; Gajdon et al., 2006; MacDonald & Ritvo, 2016). Likewise, invasive great-tailed grackles demonstrate flexibility on Aesop's Fable and colour association tasks and are infamous for feeding on human refuse, roosting in large groups in urban areas, and even attacking humans in flocks (Logan, 2016a, 2016b). Chacma baboons are also known as agricultural pests and may switch between high-risk, high-reward crop-raiding behaviour and low-risk foraging (Fehlmann et al., 2017).

A variety of taxa, including birds (jackdaws: Röell, 1978), rodents (rats and mice, *Mus* spp.: Conover, 2002) and carnivores (skunks and raccoons: Gehrt, Riley, & Cypher, 2010), use chimneys or other structural vulnerabilities for shelter. Brushtail possums, *Trichosurus vulpecula*, also reside in artificial structures, from nestboxes to wall cavities to ceilings (Statham & Statham, 1997), and consume a variety of resources, including human-provided food (McDonald-Madden et al., 2000). It is possible that some species are pre-adapted to environmental conditions that are commonly found in urban habitats, such as window ledges that mimic the nesting locations of cliff-nesting birds, including rock pigeons, *Columba livia*. These preadapted species are not necessarily using cognition to thrive in urban areas. However, it appears likely that behavioural flexibility is highly advantageous for some species living in areas of anthropogenic disturbance, particularly those species that are able to take advantage of many different types of human resources. However, behavioural flexibility is also a trait that can lead animals to persecution from humans (McLennan, Spagnoletti, & Hockings, 2017).

USING COGNITION TO AVOID HUMAN–WILDLIFE CONFLICT

In contrast to tolerating or soliciting resources from humans, some animals minimize contact with humans or avoid humans altogether. By increasing nocturnal activity, many species demonstrate an association between human activity and daylight (Dowding, Harris, Poulton, & Baker, 2010; Ihwagi et al., 2018). Some carnivores, like bobcats, *Felis rufus* (Tigas, Van Vuren, & Sauvajot, 2002), coyotes (Murray & St Clair, 2015; Tigas et al., 2002), red foxes, *Vulpes vulpes* (Baker, Dowding, Molony, White, & Harris, 2007), and black bears (Beckmann & Berger, 2003), change the timing of their activity in response to human presence. Urban marmosets, *Callithrix penicillata*, even avoid areas with heavy sound pollution on certain days of the week (Duarte, Goulart, & Young, 2012). There is high individual variation in the propensity of coyotes to use human subsidies (Newsome, Garbe, Wilson, & Gehrt, 2015), and some individuals have learned to use bridges, avoid major freeways, avoid developed areas within their home range (Gehrt, Anchor, & White, 2009), and even possibly avoid human refuse for food (Gehrt & Riley, 2010; but see Murray & St Clair,

2015). Chimpanzees in Uganda have learned to look left and right before and while crossing busy roads to avoid vehicle collisions (Cibot, Bortolamiol, Seguya, & Krief, 2015). Additionally, migration may even be a strategy that some animals use to avoid anthropogenic disturbance (Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016). In this case, migration can be viewed as a form of behavioural flexibility (Eggeman et al., 2016), although further research is needed to determine whether migrants exhibit enhanced cognitive abilities compared to residents (Griffin, Tebbich et al., 2017; Mettke-Hofmann, 2017).

Discrimination learning allows animals to identify individual humans who pose a threat based on previous interactions with that human (magpies, *Pica pica*: Lee, Lee, Choe, & Jablonski, 2011; northern mockingbirds, *Mimus polyglottos*: Levey et al., 2009; crows: Marzluff, Walls, Cornell, Withey, & Craig, 2010; but see Vincze et al., 2015). Some animals identify humans based on facial features (pigeons: Belguermi et al., 2011; Stephan, Wilkinson, & Huber, 2013; sheep, *Ovis aries*: Knolle, Goncalves, & Morton, 2017), and may even perceive human gestures as threatening or safe (crows: Clucas, Marzluff, Mackovjak, & Palmquist, 2013). African elephants can learn to identify poachers based on their odour, garments, acoustic cues, age, sex and ethnicity (Bates et al., 2007; McComb, Shannon, Sayialel, & Moss, 2014) and use that information to avoid different threats depending on experience (Plotnik & de Waal, 2014). Remarkably, this cognitive ability may be inherent or quickly acquired in species that have had little evolutionary experience with humans. For example, brown skuas, *Stercorarius antarcticus*, an Antarctic species with minimal exposure to humans, quickly learn to direct attacks towards nest intruders, but not towards nonthreatening humans (Lee et al., 2016).

Nuisance species have experienced numerous control measures, many of which are designed to deliver pain, fear and death (Vantassel & Groepper, 2016). These animals may, therefore, learn to avoid dangerous situations associated with humans via sensitization. Taste is an especially salient cue because it can be indicative of a toxin (Greggor et al., 2014). Nuisance species have heightened exposure to toxins in areas of disturbance and, as a result, many species learn to avoid toxic baits or become 'bait shy' (e.g. possums: Morgan, Milne, O'Connor, & Ruscoe, 2001). Rats (Modlinska & Stryjek, 2016) and rabbits, *Oryctolagus cuniculus* (Devine & Cook, 1998; Oliver, Wheeler, & Gooding, 1982), are thought to be food neophobic as a direct result of poisoning by humans over time, making these species difficult to control with oral baits. Similarly, nuisance species may have heightened exposure to traps, which could lead to individuals becoming 'trap shy' and avoiding traps (Roche, Brown, Brown, & Lear, 2013). Therefore, although learning to avoid humans and human entities could reduce conflict, it also results in animals' circumvention of conflict mitigation strategies.

COGNITION INVOLVED IN MITIGATING HUMAN–WILDLIFE CONFLICT

A wide variety of human–wildlife conflict mitigation strategies exist, ranging from lethal control or removal of problematic individuals, to nonlethal deterrents and structural exclusions (Treves, Wallace, & White, 2009). Lethal methods may be ineffective or cause negative consequences on ecosystems (Bergstrom et al., 2014; McManus, Dickman, Gaynor, Smuts, & Macdonald, 2015) and are increasingly less tolerated by the public (Vantassel & Groepper, 2016). Several challenges exist with current nonlethal strategies, which often can be attributed to animal cognition, namely learning. For example, it is common for animals across diverse species to habituate to stationary effigies, such as plastic owls or scarecrows (Vantassel & Groepper, 2016). This is unsurprising, given that basic learning mechanisms such as habituation

and sensitization are ubiquitous across species (Mackintosh, 1974). Deterrents tailored towards specific sensory modalities, including taste, smell and sound, have experienced mixed success across species and contexts (Conover, 2002). For example, conditioned taste aversion (CTA) has been used to reduce nest depredation and agricultural damage. Although some success has been reported in several taxa including herbivores (deer: Kimball, Taylor, Perry, & Capelli, 2009), carnivores (raccoons: Semel & Nicolaus, 1992; foxes: Maguire, Stojanovic, & Weston, 2009; badgers: Baker, Ellwood, Slater, Watkins, & Macdonald, 2008) and corvids (Avery et al., 1995; Nicolaus, Carlson, & Gustavson, 1983), the results are widely mixed. CTAs also may be extinguished by social learning of dietary preferences in some species (e.g. rats; Galef, 1985). Thus, the effectiveness of CTA in many taxa is controversial (e.g. large carnivores: Shivik, 2006). Similarly, some animals respond fearfully to audio playbacks of predator vocalizations and do not habituate to these calls (Suraci, Clinchy, Dill, Roberts, & Zanette, 2016), whereas others habituate to some playbacks but not others (Thuppil & Coss, 2016). An animal's response to nonlethal deterrents can also vary based on individual variation in physiological state (e.g. male elephants in musth: Schulte, Freeman, Goodwin, Hollister-Smith, & Rasmussen, 2007; female raccoons with offspring: Vantassel, Hygnstrom, & Hiller, 2013) or personality (boldness in eastern chipmunks, *Tamias striatus*: Couchoux, Clermont, Garant, & Réale, 2017). Given that the success of nonlethal deterrents remains equivocal even after decades of use, further research on the behaviour and cognition of nuisance species is needed to better design and execute humane mitigation strategies (Blackwell et al., 2016).

Devices incorporating multiple sensory modalities to frighten animals may be some of the more effective nonlethal intervention methods available (Blumstein, 2016), especially for cognitively advanced species. Such methods might include the simultaneous use of lights, audio playbacks, pyrotechnics, adverse taste or scent conditioning, high-pressure water sprayers, and more. Effigies of different colours, sizes, shapes and sounds that facilitate movement and are changed at irregular intervals may also be effective for more neophobic species, such as corvids (Greggor, Clayton et al., 2016). Novel forms of conflict mitigation derived from knowledge of animal cognition may be possible with further investigation. For example, setting evolutionary traps for pest species by creating appealing, yet misleading, cues has been suggested as a contemporary method to eliminate or control pest species (Robertson, Ostfeld, & Keesing, 2017). Similarly, animal training and general cooperation between free-ranging animals and humans (e.g. birds acting as 'honeyguides': Isack & Reyer, 1989; coordinated fishing with dolphins: Peterson, Hanazaki, & Simões-Lopes, 2008) could be repurposed to mitigate conflict by capitalizing on our close relationship with nuisance species. For example, training captive elephants to drive out or dissuade wild, crop-raiding elephants is a current conflict mitigation strategy (Sukumar, 2003), and similar training techniques could be used to introduce desired behaviours to wild populations of nuisance species that learn socially (Keith & Bull, 2017). Other innovative methods could include the use and strategic placement of garbage receptacles with built-in automated feeders that reward animals for the disposal of litter (Klein, 2007). Candidates for training or cooperative mitigation strategies could begin with species that are known to be neophilic or exploratory (e.g. corvids, keas, macaques, raccoons). Such innovative methods may not only redirect the attention of nuisance individuals away from conflict-prone activities, but also illustrate the cognitive capabilities of nonhuman animals, which in turn may promote a more harmonious relationship between humans and nuisance species. Empathy towards animals is often elicited by animals' anthropogenic qualities, including cognition, and can influence our

relationships with wildlife (Carr, 2016; Conover, 2002; Kansky, Kidd, & Knight, 2016; Root-Bernstein, Douglas, Smith, & Verissimo, 2013). For example, humans who consider wolves, *C. lupus*, and coyotes to be intelligent also value conservation of the animals (Kellert, 1985; Marzluff & Swift, 2017).

CONCLUSIONS

The same cognitive abilities that aid animals in coping with human-altered environments may paradoxically predispose animals to conflict with humans. Neophilia, innovation and behavioural flexibility are likely sources of conflict with humans, and various learning mechanisms undermine current conflict mitigation strategies. It is interesting that despite efforts to use biologically or ecologically relevant cues as deterrents, many species are able to eventually overcome such nonlethal control measures. Therefore, we encourage more research on the cognition of nuisance species so that we may better understand their risk perception, cue interpretation and how general cognitive mechanisms may be changing over time as animals are exposed to environmental disturbance and change. This can be achieved via further comparisons of the cognition of species along urban–rural gradients, as well as comparisons among populations that have had different types of experiences with humans historically. Such comparisons could be made between populations that live in areas with heavy hunting or trapping versus those that live in areas where hunting and trapping are illegal, or between animals that hold cultural or religious significance in some parts of the world but are treated as pests in other locations.

Despite recent advances in understanding the cognitive mechanisms that facilitate success in urban environments, many questions remain unanswered. Our review identified several critical gaps in knowledge, both in the cognition of nuisance animals specifically, and in the effect of different cognitive abilities on the adaptation of species to human-altered environments more generally. Although social learning and cultural transmission of behaviours, including maladaptive ones, have been widely studied, we found few studies that have identified the transmission of conflict-prone behaviours in urban environments. Similarly, spatial cognition is likely to be essential for navigating a fragmented urban matrix, and although some studies have investigated home range characteristics and animal movement in cities (e.g. Gehrt et al., 2009), there is little work investigating nonhuman spatial cognition with regard to the cues animals use when navigating cities. We also lack an understanding about which life history traits may predispose animals to conflict via cognitive abilities such as habituation, and could benefit from further study on memory, learning and behavioural flexibility. Furthermore, many reports of nuisance behaviour are based on anecdotal accounts, such as stories about gulls that frequent baseball stadiums at the ninth inning to access leftover trash. Such anecdotes, especially those that suggest animals may be learning to avoid conflict in urban areas, would benefit from further empirical investigation. Moreover, future research should avoid the bias of investigating heightened cognitive abilities in species that humans encounter frequently by studying a wide range of urban-dwelling species, including those with which humans may not regularly interact. Thus, further study on the relationship between animal cognition and urbanization will inform our knowledge of the contemporary evolution of cognition as well as humane conflict mitigation.

Finally, it is critical to note that whether or not an animal is viewed as a nuisance is a matter of human perspective (Jerolmack, 2008; Marchini, 2014; Saraswat, Sinha, & Radhakrishna, 2015), and this perspective has significant consequences for wildlife. Human disturbance could unknowingly select for bolder, or more

cognitively advanced, individuals that habituate to humans. Given that human behaviour has the potential to shape animal behaviour and the evolutionary trajectory of cognition, public education and human behaviour modification continue to be strong tools for conflict mitigation. For example, soliciting public assistance in citizen science projects that involve hazing nuisance species in public spaces could resensitize animals to humans while simultaneously helping people to understand and appreciate animal behaviour in urbanized areas (Bonnell & Breck, 2017). By increasing our comprehension of the cognitive mechanisms underlying adaptation to anthropogenic change, we can better communicate our lessons to the public, fostering empathy for these clever species that may otherwise continue to be considered mere pests.

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