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Human–wildlife interactions in urban areas: a review of conflicts, benefits and opportunities

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Abstract. Wildlife has existed in urban areas since records began. However, the discipline of urban ecology is relatively new and one that is undergoing rapid growth. All wildlife in urban areas will interact with humans to some degree. With rates of urbanisation increasing globally, there is a pressing need to understand the type and nature of human–wildlife interactions within urban environments, to help manage, mitigate or even promote these interactions. Much research attention has focussed on the core topic of human–wildlife conflict. This inherent bias in the literature is probably driven by the ease with which it can be quantified and assessed. Human–wildlife conflicts in terms of disease transmission, physical attack and property damage are important topics to understand. Equally, the benefits of human–wildlife interactions are becoming increasingly recognised, despite being harder to quantify and generalise. Wildlife may contribute to the provision of ecosystem services in urban areas, and some recent work has shown how interactions with wildlife can provide a range of benefits to health and wellbeing. More research is needed to improve understanding in this area, requiring wildlife biologists to work with other disciplines including economics, public health, sociology, ethics, psychology and planning. There will always be a need to control wildlife populations in certain urban situations to reduce human–wildlife conflict. However, in an increasingly urbanised and resource-constrained world, we need to learn how to manage the risks from wildlife in new ways, and to understand how to maximise the diverse benefits that living with wildlife can bring.

Additional keywords: biodiversity, health and wellbeing, human–wildlife conflict, human–wildlife benefit, infectious disease, interdisciplinary, urbanisation, wildlife–vehicle collisions.

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Introduction: the urban environment and urban wildlife

Urban areas are made up of a complex habitat mosaic containing a mix of buildings, streets, and green space (Forman and Godron 1986; Mazerolle and Villard 1999). The urban matrix is not homogenous; it may contain a mix of high- and low-density building clusters, small to large green spaces containing intensively managed parkland through to natural habitat remnants, or linear structures such as rivers, roads and railway tracks. This mingling of habitats, along with their size and extent, give each urban area its own unique habitat mosaic (Werner 2011).

At the same time, urban habitats across the world exhibit some common ecological characteristics, even in very different biogeographic locations (Savard *et al.* 2000; Groffman *et al.* 2014). The impact of urbanisation on the environment is substantial and can result in substantial changes to ecosystem structure and processes (Grimm *et al.* 2008). Existing natural habitat is either lost or fragmented and new habitats are created, and physico-chemical properties such as hydrology, soil geochemistry (De Kimpe and Morel 2000), nutrient

cycling and temperature (Taha 1997) can be altered. In addition, there are novel pressures on the ecosystem such as light pollution (Longcore and Rich 2004), noise pollution (Francis *et al.* 2009) and invasive species (e.g. Blair 1996), which include new or a lack of predators (Crooks and Soulé 1999) and disease (Lafferty and Kuris 2005). Combined, these effects make urban areas challenging environments for wildlife to survive in and have profound impacts at all levels for the plant and animal communities that live there (Marzluff 2001; Miller and Hobbs 2002; McKinney 2002, 2008).

Wildlife has existed in urban areas for as long as humans have lived in settlements. For example, there are records of scavenging birds and mammals entering urban areas to forage during ancient Egyptian times (Dixon 1989). The first formal studies on urban ecology did not occur until the late 1600s, with basic descriptions of plant diversity (Sukopp 1998). As a discipline, urban wildlife research did not really begin till the late 1960s and early 1970s (Magle *et al.* 2012). Since that time, it has undergone rapid growth (Adams 2005; Gehrt 2010; Magle *et al.* 2012), although, in general, this still represents a small proportion of

published research output on wildlife (Magle *et al.* 2012). With urbanisation increasing globally, both in terms of the total urban area covered and the rate of the process (Ramalho and Hobbs 2012), there is a real research need to look at the ecology of urban wildlife and, in particular, the relationship between wildlife and humans.

Wildlife of urban areas

There is a general trend for biotic diversity in urban areas to decline (McKinney 2006; Groffman *et al.* 2014) and, across the urban–rural gradient, this decline tends to increase as habitats become more and more urbanised (McKinney 2002). Although the biotic diversity decreases, urban areas still typically retain the biogeographic fauna and flora of the local area (Aronson *et al.* 2014; La Sorte *et al.* 2014). Patterns of biotic diversity can vary with urban intensity, with some studies reporting higher species richness at intermediate urban intensity (McKinney 2008). Some of this increased diversity is caused by an increasing number of invasive species (Blair 1996; Shochat *et al.* 2010; Dolan *et al.* 2011; Wang *et al.* 2011). Evidence from a range of taxa shows that urbanisation leads to the loss of species that have specialist diets (e.g. birds: White *et al.* 2005; Devictor *et al.* 2007; Evans *et al.* 2011), breeding locations (Devictor *et al.* 2007; Fattorini 2011) or habitat requirements (Ordeñana *et al.* 2010). Species that do well in urban areas also tend to have narrower ranges of body sizes, i.e. few very small or very large species (Niemelä *et al.* 2002; Van Der Ree and McCarthy 2005; Bateman and Fleming 2012). At the same time, there is considerable diversity in how wildlife uses the urban environment. Landscape usage by wildlife follows a continuum of ‘contact’, ranging from use that is concentrated outside the urban area but occasionally includes the urban fringe, to use that spans the entirety of the urban space (Riley *et al.* 2010a). How wildlife species use urban areas, and the ways in which they utilise the resources available, has profound impacts on human–wildlife interactions.

Several studies have tried to categorise urban wildlife in different ways, often trying to capture some ecological criteria usually based on the status and sustainability of the population. The commonest categorisation uses the terms of urban ‘exploiters’, ‘adapters’ or ‘avoiders’ (McKinney 2006). In birds, determinants of species as ‘urban exploiters’ or ‘urban adapters’ include diet, degree of sociality, sedentariness, preferred nesting sites and personality (Kark *et al.* 2007; Croci *et al.* 2008; Evans *et al.* 2011; Meffert and Dziok 2013; Vines and Lill 2015). Other studies have used the term ‘residency’ or ‘transiency’ as another defining characteristic. ‘Resident’ urban carnivorous mammals tend to be smaller than and have more generalist diets than do ‘transient’ species (Iossa *et al.* 2010). Whether this is important is open to conjecture, but terms such as ‘exploiter’ and ‘adapter’ have the ability to shape perceptions about the wildlife they label (e.g. Hoon Song 2000) and, at the same time, may obscure the ecological mechanisms that may be affecting urban biodiversity (Fischer *et al.* 2015). Recent attempts to clarify the terminology have suggested the terms ‘avoiders’, ‘utilisers’ and ‘dwellers’, with the emphasis on the terms fitting into a gradient of responses to urbanisation (Fischer *et al.* 2015). Although an undoubted improvement, it is important to consider that categorisation may

have its limitations; there can be strong temporal and spatial variation in the responsiveness of wildlife to urban areas, including accompanying shifts in human behaviours or perceptions. Hence, categorisation as a tool, may in fact be counterproductive because it could obscure important inter-species variability in ecology.

Human–wildlife interactions

At some point in their lives, animals living in urban areas will interact with humans, because of the high density of human population in these areas. These interactions vary on a continuum from positive and neutral through to negative, vary in intensity from minor to severe, and vary in frequency from rare to common. Negative interactions, more correctly termed *human–wildlife conflict*, emphasise the conscious antagonism between wildlife and humans (Graham *et al.* 2005). Interestingly, there is no alternative term to describe positive human–wildlife interactions, probably reflecting the significant bias towards negative interactions in the literature (Peterson *et al.* 2010).

Human–wildlife interactions are not random. Human–wildlife interactions typically occur in a non-linear fashion along a gradient of development, with higher concentrations of interactions occurring in the intermediate levels of development, namely the ex-urban and suburban landscape, often in the vicinity of natural patches of habitat or green spaces (Kretser *et al.* 2008; Lukasik and Alexander 2011; Merkle *et al.* 2011; Poessel *et al.* 2013; Teixeira *et al.* 2015). At the same time, the species involved in conflict tend to be non-random. They tend to have broad dietary requirements, which contribute to them being able to live at high population densities (Iossa *et al.* 2010; Charles and Linklater 2013). Interactions can have a strong seasonal component, occurring during critical parts of the animal’s lifecycle, e.g. nesting or denning (Jones and Thomas 1999; Lukasik and Alexander 2011).

The human participants in interactions are important, because outcomes are dependent on the socio-economic and political context (Mascia *et al.* 2003) and a ‘conflict’ in one context may not be considered as such in another. Indeed, many conflicts are more about social and cultural values than they are about actual impacts (McIntyre *et al.* 2008). Understanding how individuals and communities respond to wildlife and the impacts it has is therefore a key part of understanding and dealing with potential human–wildlife conflict situations in urban areas. Factors including gender, ethnicity, wealth, education and experience may all affect values and attitudes (Dietz *et al.* 2002; Dickman 2010) and, therefore, determine the likelihood that a species or its impact are viewed positively or negatively in a particular situation (Bjerke and Østdahl 2004). At the same time, humans may be motivated to directly engage in interactions, and so human participants can vary from being active, through to indirect, passive or reluctant participants. This further increases the complexity of human–wildlife interactions.

Recent years have seen an increase in human–wildlife conflict in urban areas (Delahay *et al.* 2009; Davison *et al.* 2011; Kistler *et al.* 2013). Some of this is due to increasing urban human populations and the encroachment of urban areas into the surrounding countryside, particularly in Africa and Asia (Ditchkoff *et al.* 2006), as well as increases in urban green spaces and spread of residential areas in western countries (Kabisch and

Haase 2013). Human–wildlife conflicts are caused where the movement and activities of wildlife, such as those associated with foraging or reproduction, have an adverse impact on human interests, whether in a primary way, such as through aggression or nuisance behaviour, or in a secondary way, such as through the spread of parasites or infectious disease. In the following sections, we will explore some of these major areas of conflict in the context of urban wildlife.

Human–wildlife conflict: aggression, injury and death

The most direct impact of wildlife on humans is that of direct attacks. Attacks by wildlife on humans can be broadly categorised as predatory, territorial or defensive (Conover 2001). In urban areas, predatory attacks are rare because of the general absence of large predators. Nevertheless, they do occur, and in some less developed countries, large predators use some urban areas, e.g. spotted hyenas (*Crocuta crocuta*; Abay *et al.* 2011), occasionally causing injuries and even fatalities. Despite this, fatalities or serious injury from urban wildlife are very rare (Mayer 2013). It is more common for human–wildlife conflict to arise from some sort of territorial or defensive aggression by wildlife, with no or only minor injuries to humans taking place. Attacks can occur when individuals are protecting young (e.g. raptors: Parker 1999; Australian magpies, *Cracticus tibicen*: Jones and Thomas 1999; masked lapwings, *Vanellus miles*: Lees *et al.* 2013) or over food (e.g. long-tailed macques, *Macaca fascicularis*: Sha *et al.* 2009; marmosets *Callithrix penicillata*: Goulart *et al.* 2010). For some species, attacks on humans are a very small but growing problem (e.g. wild pigs, *Sus* spp.: Mayer 2013; coyote, *Canis latrans*: Timm *et al.* 2004), usually associated with increasing populations of these species. Even though attacks by wildlife on humans are rare, the consequences of attacks on the attitudes and perception of urban wildlife can be dramatically negative (Cassidy and Mills 2012), and a significant proportion of people still fear attack by urban wildlife (18.5% respondents feared bobcats, *Lynx rufus*; Harrison 1998; 15% respondents feared red foxes, *Vulpes vulpes*, could injure people: König 2008).

There is often a significant perceived threat of urban wildlife attack on domestic pets (Harrison 1998; König 2008; Spacapan 2013). Depending on the species, some threats can be serious, e.g. coyote predation of cats (Grubbs and Krausman 2009; Alexander and Quinn 2011); dietary analysis has indicated that the frequency of cats in coyote scats varies depending on location (1–13%), indicating a strong spatial component to risk (MacCracken 1982; Quinn 1997; Morey *et al.* 2007). For other species, risks of attack on pets seem to be more minor or absent (Cooke *et al.* 2006; Riley *et al.* 2010b). Urban foxes, which are commonly perceived to kill pets, only do so at a very low rate. Diet analysis shows that pets (including hens, cats, dogs, rabbits and cattle) made up 4.5% of the gut volume of foxes in Zürich (Contesse *et al.* 2004) and 2.4% of the content of fox scats in Bristol, UK (Ansell 2004); scat analysis does not differentiate between killed or scavenged prey. Surveys have also shown that relatively few pets are actually killed, with 8% of householders losing chickens, rabbits or guinea pigs and 0.7% losing a cat (Harris 1981). Even so, pet–urban wildlife interactions are not random. They often occur at night (Grubbs and Krausman 2009) and during certain seasons (e.g. denning season: Lukasik and Alexander 2011).

Hence, appropriate management of pets would certainly reduce the risk of conflict in several situations.

At the same time, urban areas are important sources of mortality for wildlife. It is beyond the scope of this review to detail all possible human–wildlife interactions in this context, but it is important to acknowledge that sources of mortality in and deriving from urban areas, such as disease (see *Human–wildlife conflict: disease*), roads (Forman and Alexander 1998) and bird strike of windows (Loss *et al.* 2014) may have significant impact on urban wildlife populations. It is not only direct anthropogenic sources of mortality that are important. The global impact of domestic cat predation on wildlife in urban areas is also widely recognised (Loss *et al.* 2013). It is clear that managing and conserving urban wildlife requires greater consideration for such negative effects of mortality on the future viability of populations.

Human–wildlife conflict: nuisance and property damage

Surveys in urban areas in the Europe and the USA have revealed that from 20% to over 60% of respondents report having had a wildlife-related problem at some time (Conover 1997; Messmer *et al.* 1999; Bjerke and Østdahl 2004). Most of these problems are minor and, by comparison, respondents usually report more problems with neighbours' cats and dogs, than with wildlife (Bjerke and Østdahl 2004). However, the relatively high frequency of reported problems is reflected in a general perception that urban wildlife is a nuisance (Table 1). This can be linked to individual's past experience of damage or conflict (Bjerke *et al.* 2003) or a more general 'perception' that the species is a problem, e.g. snakes (Butler *et al.* 2005). Quite often there is a discord between the perceived problem and the actual problem (Dickman 2010).

Damage caused by wildlife can sometimes be substantial. In the UK, subsidence damage to property or infrastructure caused by badgers digging setts is an increasing problem (Harris and Skinner 2002; Davison *et al.* 2011). Although badgers are protected by law in England under the *Protection of Badgers Act* 1992, there is provision to allow actions under licence that would normally be prohibited by the *Act*. Thus, where badgers are causing damage to property, licences can be granted to allow their removal. Licence applications related to badger damage problems in England increased from 1581 in 1994–95 to 2614 in 2002–04, with the proportion of these in urban areas in the three worst-affected regions increasing from an average of 19% in 1994–96 to 36% in 2002–04 (Delahay *et al.* 2009).

Wildlife may also inflict damage and potentially serious injury through their involvement in road vehicle collisions (Rowden *et al.* 2008; Found and Boyce 2011; Rea 2012). In urban and peri-urban areas, larger typically herbivorous species such as deer (several species), moose (*Alces alces*), macropods (*Macropus* spp., *Wallabia* spp.) and camels (*Camelus dromedaries*) can pose a significant hazard for road vehicle collisions (Rowden *et al.* 2008). Deer–vehicle collisions are increasing in many countries (Seiler 2005; Langbein 2007; Ng *et al.* 2008; Found and Boyce 2011). For example, in Iowa, deer–vehicle collisions account for 13% of all crashes reported (Gkritza *et al.* 2014). This is a trend that is likely to continue as urban areas spread, deer become more common within them and traffic levels increase. Increases in

Table 1. Positive and negative attitudes for different species in urban areas and for seeing urban wildlife in general

Species	Positive attitudes and enjoyment in seeing wildlife (%)	Considered a nuisance (%)	References
Moose, <i>Alces alces</i>	92		McDonald <i>et al.</i> 2012
Coyote, <i>Canis latrans</i>	33–52	28–29	Lawrence and Krausman 2011; Spacapan 2013
Long-nosed bandicoots, <i>Perameles nasuta</i>	55	28	Dowle and Deane 2009
Brown bandicoots, <i>Isodon macrourus</i>	85		FitzGibbon and Jones 2006
Black-tailed prairie dogs, <i>Cynomys ludovicianus</i>	40		Morse <i>et al.</i> 2012
Possums, <i>Pseudocheirus peregrinus</i> and <i>Trichosurus vulpecula</i>	66.7–77	34.3–35	Hill <i>et al.</i> 2007; Russell <i>et al.</i> 2011
Kaka, <i>Nestor meridionalis</i>	61.8		Charles 2013
Red fox, <i>Vulpes vulpes</i>	60–36		Harris 1985; König 2008
Eurasian badger, <i>Meles meles</i>	66		Harris and Skinner 2002
White-tailed deer, <i>Odocoileus virginianus</i>	46		Comicelli <i>et al.</i> 1993
Wild boar, <i>Sus scrofa</i>	77	59	Kotulski and König 2008
Kit fox, <i>Vulpes macrotis</i>	~20–50		Bjurlin and Cypher 2005
Bobcat, <i>Lynx rufus</i>	86.2		Harrison 1998
Urban birds	61–72	0	Clergeau <i>et al.</i> 2001
Arthropods	6–69.2	88–85.9	Byrne <i>et al.</i> 1984; Hahn and Ascerno 1991
		(indoor arthropods)	

wildlife–vehicle collisions in urban areas may sometimes be an unintended consequence of other policy initiatives such as enhancing green infrastructure (Benedict and McMahon 2006; Tzoulas *et al.* 2007; Baycan-Levent and Nijkamp 2009).

Nevertheless, most damage or problems caused by urban wildlife are minor. Depending on the species, it can include damage to landscaping such as lawns or fences (Harris 1985; FitzGibbon and Jones 2006; Urbanek *et al.* 2011), loss of crops (Harris 1985) or low-level damage to cars or property (Herr *et al.* 2009). In some areas, bin-raiding (Harris 1985; Clark 1994; Belant 1997; McKinney 2011), fouling and noise (Gorenzel and Salmon 1992; Belant 1997; Clergeau *et al.* 2001; FitzGibbon and Jones 2006; Phillips *et al.* 2007) are commonly reported problems with urban wildlife, especially from species living in colonies or that have semi-permanent den sites. Some of these are associated with a defacing of buildings and sites and loss of aesthetic value, not necessarily damage (Coluccy *et al.* 2001). Although, clearly, most forms of damage caused by urban wildlife are minor, at the local or individual level, they can be very distressing. However, with appropriate education and/or mitigation, many of these conflicts can be reduced or negated.

Human–wildlife conflict: disease

Approximately 60% of diseases causing pathogenic illness in humans originate in animals (Bengis *et al.* 2004). The emergence or re-emergence of zoonotic and vector-borne diseases pose considerable risks to public health, the environment and the economy across the globe (Daszak *et al.* 2000; Bengis *et al.* 2004). Vector-borne diseases in particular may flourish with rapid urbanisation (Vora 2008). Expanding cities can encroach on neighbouring environments, thereby increasing exposure to some vectors and non-human hosts of vector-borne diseases, especially in countries with a wide range of background diseases, such as developing countries in tropical regions. Urbanisation also tends to lead to a greater density of people as well as domestic and peridomestic animals, creating conditions that can propagate, rather than reduce, disease transmission (Enserink 2008;

Alirol *et al.* 2011). In particular, urban areas in developing countries may often have multiple conditions that allow certain vector-borne disease to persist in urban environments (De Silva and Marshall 2012). Although typically thought of as a developing-country health issue, vector-borne diseases are an important problem even within developed countries (Nash *et al.* 2001; WHO 2002). The control of vector-borne diseases in urban areas is a critical issue; ongoing and new strategies need to be developed to effectively tackle this current and emerging health problem.

In a similar way to vector-borne disease, zoonotic diseases are also of considerable importance in urban settings (Mackenstedt *et al.* 2015). Although urban areas frequently reduce the number of species of wildlife (McKinney 2006), those species that do live in urban areas often do so at higher densities than they do in rural areas. Combined with high densities of humans and domestic and companion animals, there is considerable opportunity for diseases to transmit from wildlife to humans or from wildlife to pets (Bradley and Altizer 2007; Mackenstedt *et al.* 2015). Urban wildlife provides an important conduit for diseases to enter the human population, and sometimes may act as a reservoir to enable diseases to persist in urban areas, e.g. rabies (Favoretto *et al.* 2013). Direct transmission of a disease from wildlife to humans may be relatively rare, but pets are often important parts of the disease cycle, and can act as a transmission link between wildlife and humans (Deplazes *et al.* 2011). The risk posed by zoonotic disease is often reflected in people's attitudes towards wildlife (König 2008).

The increasing policy emphasis of the benefits of green infrastructure for health and wellbeing (Tzoulas *et al.* 2007; Lee and Maheswaran 2011) may have consequences for the spread and prevalence of wildlife disease in urban areas in the future. Some diseases have lower prevalence currently in urban areas. For example, *Echinococcus* prevalence in foxes in a Swiss study was 52% in rural areas, compared with 31% in urban areas (Fischer *et al.* 2005). It has been hypothesised that this difference may be linked with flexibility in fox feeding behaviour via changes in levels of predation on intermediate rodent hosts

(Hegglin *et al.* 2007). However, with an increase in urban greening, and particularly the establishment of rural–urban corridors, more urban–rural fringe habitats will be created, which pose a high disease hazard (Deplazes *et al.* 2004). Whilst policy initiatives on urban greening have clear benefits to human health and wellbeing in terms of alleviating chronic disease and stress (Tzoulas *et al.* 2007), the presence of more green infrastructure in urban areas may also have adverse consequences in relation to enhancing transmission opportunities for a range of zoonotic and vector-borne disease (Hamer *et al.* 2012; Santiago-Alarcon *et al.* 2013).

In some situations, rather than being a sink for diseases found predominantly in rural areas, urban areas themselves serve as sources of disease to wildlife populations in the surrounding areas. For example, sea otter (*Enhydra lutris*) populations in California have been infected with *Toxoplasma gondii* and *Sarcocystis neurona* from land-based run-off from urban areas (Miller *et al.* 2010; Shapiro *et al.* 2012). Similarly, feral or free-ranging dogs (*Canis familiaris*) and cats (*Felis catus*; Acosta-Jamett *et al.* 2011; Hughes and Macdonald 2013) and even humans can directly or indirectly transmit diseases to wildlife (Carver *et al.* 2012). Disease, both wildlife to human and human to wildlife, remains one of the most pressing types of human–wildlife conflict. Given the significant financial cost disease can entail and the threat to human, companion animal and wildlife populations, there is a continued need to study zoonotic diseases in an urban setting (Bradley and Altizer 2007).

Human wildlife conflict: economic costs

Estimates of costs of urban wildlife conflict are rarely properly calculated, often because most human–wildlife conflict is minor. It is also difficult to properly assess the ‘hidden’ costs of human–wildlife conflict such as diminished psychosocial wellbeing, disruption of livelihoods and food insecurity (see Barua *et al.* 2013). However, a proper estimation of costs of damage and urban wildlife control is needed to understand the costs and benefits of alternative management strategies (White *et al.* 2003). There are only a few estimates of urban wildlife damage; for example, urban stone marten (*Martes foina*) damage to cars is estimated to cost ~€1.6 million per annum across all of Switzerland (Kistler *et al.* 2013). It was estimated that trapping nuisance animals (skunk, coyote and raccoon) in Chicago in 1999 cost ~US\$1 million (Gehrt 2004). Where badgers in some parts of the UK are causing damage to property, the cost of repairing damage and removing badgers may run into thousands of pounds. For example, the cost of excluding badgers from a modest-sized sett (four to six holes) costs £5000–£10 000 for proofing and remedial work to buildings (Davison *et al.* 2011). However, if there is more extensive damage to infrastructure, such as canals, the costs of remediation may exceptionally run into hundreds of thousands of pounds. Such reactive and targeted control is much more common than systematic control because of the prohibitive costs. The systematic, proactive control of wildlife in urban areas is generally not carried out because of the cost. For example, urban foxes used to be controlled in London; however, this was abandoned because it was uneconomical (Harris 1985).

The greatest economic costs associated with urban wildlife are probably related to wildlife diseases. The economic cost of

vector-borne diseases is substantial, and globally amounts to billions of US dollars per annum (WHO 2009). Costs can include direct treatment; *Echinococcus multilocularis* has been estimated to cost €182 594 (€144 818–€231 448) to treat each case (Torgerson *et al.* 2008) or costs can include loss of opportunity through sickness (Walsh 1984). Wildlife diseases are also costly to control and to prevent. For example, prevention of vector-borne diseases relies heavily on vector control, which can be expensive (Mills 1993). Similarly, the costs of trap-translocation (Beringer *et al.* 2002) or trap-vaccination of wildlife can be very high (Rosatte *et al.* 1992). Large-scale baiting strategies can be costly, especially if conducted over several years (Rosatte *et al.* 2007; Hegglin and Deplazes 2013). White *et al.* (2003) calculated the costs of trapping urban red foxes in Britain and estimated that the benefits outweighed the costs only at unfeasibly high fox densities. However, should a zoonotic disease enter the fox population, this would drastically alter the outcome of the cost–benefit analysis (White *et al.* 2003).

Overall, it is very hard to understand the true costs of human–wildlife conflict in urban areas. Most people coexists with wildlife and conflict, where it occurs is minor and relatively difficult to cost. So far, an extrapolation study suggests that urban wildlife costs in excess of US\$8.6 billion in damage and cost of control across the USA (Conover 2001). By comparison, expenditure in relation to wildlife benefits is an order of magnitude higher. For example, expenditure on wildlife watching approaches US\$55 billion and US\$90 billion is spent on hunting and fishing (US Fisheries and Wildlife Service 2012). More specifically, US\$7 billion is spent on wildlife food (mainly birds) and bird boxes (US Fisheries and Wildlife Service 2012). Clearly, the economic costs of human–wildlife conflict can be large, especially in certain situations, but in comparison to expenditure on benefits associated with wildlife, the costs are relatively small.

Human–wildlife benefits

Urban wildlife can provide a range of positive values to humans, including opportunities for physical utility, and health, recreational, scientific, ecological and historical values (Conover 2001). Depending on the philosophical viewpoint, urban wildlife may also have intrinsic, or existence, value. Many of these benefits are difficult to quantify (but see Dallimer *et al.* 2014), because many of the outcomes are often intangible, but their impact may be considerable.

In an increasingly urban society, there is recognition that humans are becoming more remote from the natural environment. Increasing mental health problems are associated with increased urban living. Mental ill-health is a considerable drain on society and the economy, accounting for ~14% of the global burden of disease (Prince *et al.* 2007) and its economic impact globally has been estimated as equivalent to 3–4% of total GDP (WHO 2004) and there is increasing evidence that nature can provide benefits in terms of mental health and wellbeing (Maller *et al.* 2006; Tzoulas *et al.* 2007). However, public health policy tends to concentrate on lifestyle change at an individual level, and the potential transformative capacity of natural environments in enhancing population health remains a neglected and relatively untapped area (Maller *et al.* 2006).

In urban area, there has traditionally been a greater focus on the less tangible benefits of wildlife, such as recreation or wellbeing value, than that of monetary value. The benefits of urban wildlife are generally much harder to quantify than are human–wildlife conflicts, and, consequently, research in this area has been limited. The potential role of urban wildlife in promoting mental wellbeing may be one area in which the value of urban wildlife is very significant, and where more research is needed to understand beneficial outcomes as a function of wildlife properties and ecological processes.

Human–wildlife benefits: keystone species and ecosystem

In faunally impoverished urban areas, the loss of keystone species or ecosystem engineers can have a disproportionately large effect on ecosystem processes, because there is unlikely to be any compensation by other species. As in more natural ecosystems, species in urban areas can play a keystone role through different mechanisms. These can include top-down control through predation or regulation of other species through competition. For example, the loss of coyotes from urban ecosystem caused avifaunal declines by removing suppression of smaller mesopredator populations (Crooks and Soulé 1999). Similarly, the decline in vulture populations in India has led to dramatic increases in feral dog populations in urban and rural areas (Markandya *et al.* 2008). This has increased the prevalence and risk of rabies transmission to humans, and higher dog densities also increase competition and predation on wildlife (Markandya *et al.* 2008; Vanak and Gompper 2009). Less commonly, ecosystem engineers can also provide important habitat modifications that increase biodiversity. For example, species such as black-tailed prairie dogs and great spotted woodpeckers (*Dendrocopos major*) can change biological diversity and communities through cavity nest building and grazing (Kotaka and Matsuoka 2002; Beals *et al.* 2014).

It may be argued that keystone species do not directly benefit humans themselves, but this is a somewhat short-sighted view. Urban biodiversity has considerable aesthetic value to humans. Therefore, species that act to increase or maintain biodiversity in urban areas may be of considerable indirect value to humans.

Human–wildlife benefits: provisioning regulating and supporting ecosystem services

Ecosystem services are the benefits provided by ecosystems that contribute to making human life both possible and worth living. Ecosystem services comprise provisioning services (e.g. food, fresh water), regulating services (e.g. flood protection), cultural services (e.g. tourism, cultural heritage) and supporting services (e.g. nutrient cycles; UK NEA 2011; Ford-Thompson *et al.* 2014). In urban areas, most of these services tend to relate to urban green spaces and the benefits that these provide, such as flood regulation, carbon sequestration and recreation, rather than the value of urban wildlife (Bolund and Hunhammar 1999; Tratalos *et al.* 2007). However, many parts of the world do rely on urban wildlife for some form of ecosystem service. Historically, many animals have used urban waste as food sources (Dixon 1989; O'Connor 2000). Such was their importance in this role, some species such as red kites (*Milvus milvus*) and ravens (*Corvus corax*) were afforded protection (Gurney 1921). Many animals

have a similar role today. Rubbish dumps or other waste facilities are still important feeding sites for many species, although often the animals feeding from them are regarded as pests (Baxter and Allan 2006). However, some animals have crucial roles in waste disposal, e.g. spotted hyenas (Abay *et al.* 2011) and predatory/scavenging birds (Pomeroy 1975; Markandya *et al.* 2008), especially in developing countries.

Many urban animals act as important predators of pest species. This was first recognised in newspapers as far back as 1884, where songbirds were encouraged into gardens to consume insect pests (Vuorisalo *et al.* 2001). Recent evidence suggests that this role is still important (Orros and Fellowes 2012). Many of the commoner urban wildlife species have omnivorous diets that include pest insects. For example, skunks (*Mephitis* spp.) in urban areas eat a range of important garden insect pests (Rosatte *et al.* 2010) and some cities within Italy have begun to use artificial bat roosts to encourage predation of invasive tiger mosquitos (*Aedes albopictus*; The Independent 2010). Predatory birds and snakes too contribute effectively to rodent control (Meyer 2008), although human tolerance of snakes in urban areas tends to be low.

Overall, the role of urban wildlife as providers of, or contributors to, ecosystem services has received relatively little recognition. Some animal groups, such as pollinators, probably contribute substantially to ecosystem services in urban areas (Matteson and Langelotto 2009; Bates *et al.* 2011), but the topic as a whole is in need of more thorough research.

Human–wildlife benefits: cultural ecosystem service

Urban areas, and particularly urban green spaces have long been recognised as providing important cultural and recreational ecosystem services (Bolund and Hunhammar 1999). In contrast, there has been much less study on the cultural and recreational value of wildlife in urban areas. The purely aesthetic value of wildlife in urban areas has long been recognised, (Vuorisalo *et al.* 2001), and we now know that urban residents can gain considerable enjoyment from encounters with urban wildlife (Dandy *et al.* 2011) or from sharing the local environment with a species (Dandy *et al.* 2009; Morse *et al.* 2012; Hedblom *et al.* 2014). This is reflected in attitude surveys, which consistently report a high proportion of respondents having positive attitudes to certain types of wildlife (Table 1). Within this, there are often both species-specific and locational differences in attitudes (Clucas and Marzluff 2012). These often link back to cultural perceptions (Clucas and Marzluff 2012), socioeconomic or demographic factors (Bjerke and Østdahl 2004) or the presence/absence of perceived risk (e.g. disease risk: Peterson *et al.* 2006). The real exception tends to arthropods, which tend to be more unpopular (Bjerke and Østdahl 2004; Table 1), although this varies widely with the type of arthropod and the location (indoors/outdoors; Hahn and Ascerno 1991; Bjerke and Østdahl 2004). In general, there is real enjoyment in seeing urban wildlife (Bjerke and Østdahl 2004; Goddard *et al.* 2013), even for those species that can potentially cause damage or pose a threat (Table 1).

Of all positive human–wildlife interactions, globally, the commonest is feeding of garden birds (Jones and Reynolds 2008; Goddard *et al.* 2013). The reasons that people feed wildlife are often extremely complex (Jones and Reynolds

2008; Jones 2011). Many people simply derive pleasure from doing so (Clergeau *et al.* 2001; Howard and Jones 2004; Miller 2005), whereas others also couch the practice within conservation-based themes (Howard and Jones 2004; Jones and Reynolds 2008). Evidence certainly shows the considerable value placed on these interactions (Clucas *et al.* 2014).

More generally, there is a growing body of evidence that both the presence and viewing of urban wildlife are beneficial for mental health and bring psychological benefits (Maller *et al.* 2006; Fuller *et al.* 2007; Luck *et al.* 2011; Dallimer *et al.* 2012). There is often a link, albeit not a straightforward one, among preferences, wellbeing and species richness (Dallimer *et al.* 2012; Shwartz *et al.* 2014). Such evidence suggests that conserving and enhancing biodiversity in urban areas has knock-on health benefits. Linked to this, there has been a real growth in the concept of ‘wildlife gardening’ in recent years. As well as potentially being beneficial to wildlife (Gaston *et al.* 2005), wildlife gardening also provides health and psychological benefits to people (Catanzaro and Ekanem 2004; Van den Berg and Custers 2011; Curtin and Fox 2014). It often again links back to ‘seeing’ wildlife and the motivation to be involved in conservation (Goddard *et al.* 2013). Evidence suggests that these interactions can increase the value and appreciation of the urban landscape (Hedblom *et al.* 2014). Although often hard to define and quantify, the presence of wildlife in urban areas gives people an opportunity to connect locally and directly with nature. In an increasingly urbanised society, this may be the sole direct contact with nature that people have. It is clear that there are considerable benefits from these interactions, yet we are only now starting to recognise their full value. In the longer term, it is important to better understand the mechanisms involved and, hence, the actions that can be taken to enhance this important relationship. In particular, one of the areas in which there is considerable scope to improve our understanding is the role of urban wildlife and urban biodiversity in general, in the promotion of mental health and its greater role as a recreational and cultural ecosystem service.

A complex web of interactions: the future research priorities

It is clear that urban wildlife has both positive and negative interactions with people. Historically, much research emphasis has been placed on the conflicts between urban residents and wildlife, whereas there is now growing recognition of the benefits wildlife can bring. There is an important role for wildlife agencies and non-governmental organisations in promoting education about urban wildlife and its risks. It is important that differing and sometimes contradictory messages are avoided and the real risks and how to avoid or mitigate them are presented to the public (Gompper 2002; König 2008). Better education has an important role in preventing hysteria and ill-informed management decisions when an attack occurs. At the same time, education has an important role in increasing the ‘value’ placed on urban wildlife (Caula *et al.* 2009). However, behavioural change requires more than education alone, and it is also important that the benefits of living with wildlife are apparent to people at the individual level, so that there is a cultural shift from considering urban wildlife as a problem to a situation in which wildlife is viewed as an integral part of the urban ecosystem.

In conclusion, research priorities need to focus much less on human–wildlife conflict in urban areas and accept that urban wildlife is part of the urban ecosystem. Eradication of wildlife species from urban areas is extremely expensive and not feasible in most of cases. Some management of problem species will always be necessary, but research also needs to consider the human–wildlife relationship in a more holistic way. We need to improve education around the risks, including damage and infectious disease, but we also need to identify ways of maximising the significant benefits, both physical and mental, that human–wildlife interactions can bring. In particular, increasing the accessibility of natural greenspaces and promotion of interactions as a form of nature-based therapy may bring considerable future benefits (Maller *et al.* 2006; Tzoulas *et al.* 2007; Keniger *et al.* 2013; Lovell *et al.* 2014). At the same time, there is critical need to develop improved conceptual frameworks to understand human–wildlife interactions (e.g. Morzillo *et al.* 2014), and this will require researchers in wildlife ecology working more closely and actively with researchers from other disciplines, including economics, public health, sociology, ethics, psychology and planning. It is only through such an integrative approach that we can advance our understanding of how to live successfully alongside wildlife in an increasingly urbanised world.

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