REVIEW ARTICLE

Big city life: carnivores in urban environments

P. W. Bateman[1,2] & P. A. Fleming[2]

1 Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
2 School of Veterinary and Biomedical Sciences, Murdoch University, Murdoch, WA, Australia

Abstract

Cities may represent one of the most challenging environments for carnivorous mammals. For example, cities have a dearth of vegetation and other natural resources, coupled with increased habitat fragmentation and an abundance of roads as well as altered climate (e.g. temperature, light, rainfall and water runoff). It is therefore intriguing that several carnivore species have become established in cities across the globe. Medium-sized carnivores such as the red fox, coyote, Eurasian badger and raccoon not only survive in cities but also have managed to exploit anthropogenic food sources and shelter to their significant advantage, achieving higher population densities than are found under natural conditions. In addition, although they may not live permanently within cities, even large carnivores such as bears, wolves and hyaenas derive significant benefit from living adjacent to urbanized areas. In this review, we examine the history of urban adaptation by mammalian carnivores, explore where they are living, what they eat, what kills them and the behavioural consequences of living in urban areas. We review the biology of urban carnivores, exploring traits such as body size and dietary flexibility. Finally, we consider the consequences of having populations of carnivores in urbanized areas, both for humans and for these charismatic mammals. In conclusion, in a time of massive environmental change across the globe, the continuing encroachment of urbanization upon wilderness areas is substantially reducing the availability of natural habitats for many species; therefore, understanding the biology of any taxon that is able to adapt to and exploit anthropogenically disturbed systems must aid us in both controlling and developing suitable conservation measures for the future of such species.

Introduction

Wild carnivores have doubtless been entering human settlements for millennia, either by mistake, as scavengers or as predators, or through deliberate encouragement by humans to control pests or aid hunting. For example, grey wolves *Canis lupus* started developing a close association with humans ~100 000 years ago (Vilà *et al.*, 1997) with a 'formal' domestication of dogs *Canis familiaris* around 12 000–14 000 years ago (Savolainen *et al.*, 2002). Similarly, cats *Felis catus* may have started to feed upon rodents dwelling around human food stores around 9500 years ago (Driscoll *et al.*, 2007) and thus become habituated to people. At this time, human settlements may have represented an altered but perhaps not significantly challenging habitat. As human societies have grown, however, landscapes have been increasingly altered through anthropogenic activities (Baker & Harris, 2007; Gehrt, 2010).

For the first time in history, the majority of the human population resides within urban areas, with over 3 billion people living in cities across the world (UNFPA, 2007; Gehrt, 2010). Gehrt (2010) defines 'urban' as an area of human residence, activity and associated land area developed for those purposes, usually defined by a threshold human density. These large groupings of people and associated structures comprise at least one town or city (Gehrt, 2010) and include a wide range of anthropogenic disturbances, including buildings and associated infrastructure, for example, gardens, roads, waste ground and parkland (Baker & Harris, 2007). However, the definition of what is classified as 'urban' varies greatly depending on geographic location, which, in part, may reflect population density present in the country. Furthermore, while city centres may represent the extreme of anthropogenically altered environments, city suburbs, villages and small towns or even rural farmland also represent challenges in terms of altered landscapes (Fig. 1).
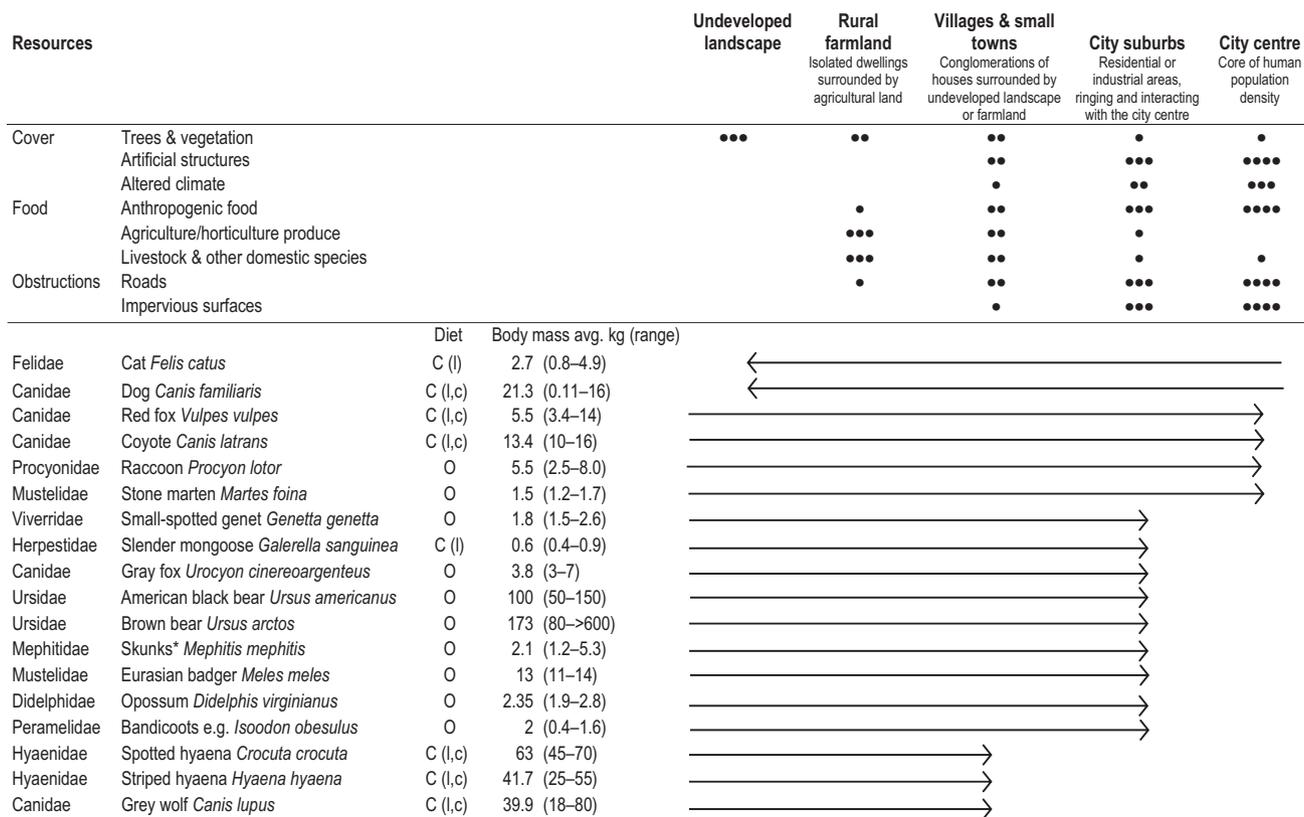
Resources		Undeveloped landscape	Rural farmland Isolated dwellings surrounded by agricultural land	Villages & small towns Conglomerations of houses surrounded by undeveloped landscape or farmland	City suburbs Residential or industrial areas, ringing and interacting with the city centre	City centre Core of human population density
Cover	Trees & vegetation	●●●	●●	●●	●	●
	Artificial structures			●●	●●●	●●●●
	Altered climate			●	●●	●●●
Food	Anthropogenic food		●	●●	●●●	●●●●
	Agriculture/horticulture produce		●●●	●●	●	
	Livestock & other domestic species		●●●	●●	●	●
Obstructions	Roads		●	●●	●●●	●●●●
	Impervious surfaces			●	●●●	●●●●

Family	Species	Diet	Body mass avg. kg (range)
Felidae	Cat *Felis catus*	C (l)	2.7 (0.8–4.9)
Canidae	Dog *Canis familiaris*	C (l,c)	21.3 (0.11–16)
Canidae	Red fox *Vulpes vulpes*	C (l,c)	5.5 (3.4–14)
Canidae	Coyote *Canis latrans*	C (l,c)	13.4 (10–16)
Procyonidae	Raccoon *Procyon lotor*	O	5.5 (2.5–8.0)
Mustelidae	Stone marten *Martes foina*	O	1.5 (1.2–1.7)
Viverridae	Small-spotted genet *Genetta genetta*	O	1.8 (1.5–2.6)
Herpestidae	Slender mongoose *Galerella sanguinea*	C (l)	0.6 (0.4–0.9)
Canidae	Gray fox *Urocyon cinereoargenteus*	O	3.8 (3–7)
Ursidae	American black bear *Ursus americanus*	O	100 (50–150)
Ursidae	Brown bear *Ursus arctos*	O	173 (80–>600)
Mephitidae	Skunks* *Mephitis mephitis*	O	2.1 (1.2–5.3)
Mustelidae	Eurasian badger *Meles meles*	O	13 (11–14)
Didelphidae	Opossum *Didelphis virginianus*	O	2.35 (1.9–2.8)
Peramelidae	Bandicoots e.g. *Isoodon obesulus*	O	2 (0.4–1.6)
Hyaenidae	Spotted hyaena *Crocuta crocuta*	C (l,c)	63 (45–70)
Hyaenidae	Striped hyaena *Hyaena hyaena*	C (l,c)	41.7 (25–55)
Canidae	Grey wolf *Canis lupus*	C (l,c)	39.9 (18–80)

Figure 1 Anthropogenically altered landscapes vary along a gradient from rural farmlands through to the centres of cities, the ultimate urban habitat. Urban environments have significantly altered cover and food resources, and also present challenges in the forms of obstructions (shown by increasing number of ● symbols). Diet is listed as O: omnivore C: carnivore (l: live prey, c: carrion). Urban environments may offer substantial anthropogenic food sources for carnivores, and although there is likely to be little natural habitat available for cover, there are plenty of artificial structures, for example, road culverts, abandoned buildings, etc. While domestic cats and dogs have become feral in undeveloped landscapes, most other carnivore species illustrated demonstrate increased use of anthropogenically altered landscapes. The degree to which individual carnivore species are found living among human built-up areas is demonstrated by the relative length of the arrows for each species (e.g. red foxes are present within the centres of cities across the globe). *Skunks: Principally striped skunk, *Mephitis mephitis*, also less commonly spotted skunk, *Spilogale putorius*, hog-nosed skunk, *Conepatus leuconotus*, and hooded skunk *Mephitis macroura*.

With the spread of urban environments (e.g. McKinney, 2002; Radeloff *et al.*, 2005), many terrestrial species have withdrawn into reduced ranges; this response is particularly noticeable in mammalian carnivores (Woodroffe & Ginsberg, 1998; Woodroffe, 2000; Cardillo *et al.*, 2004). Many carnivore species actively avoid urban areas, rapidly disappearing from encroaching urban spread ('urbanophobes', *sensu* Witte, Diesing & Godde, 1985, 'urban avoiders', *sensu* McKinney, 2006). A number of other species, however, can be described as truly urban dwellers, maintaining varying levels of intimacy with humans, residing within cities and built-up areas across the globe, despite the significantly artificial environment. For some, cities have grown up around their preferred habitat; their presence close to human societies therefore represents continuation of a somewhat altered lifestyle (e.g. Radeloff *et al.*, 2005), and they usually do not make extensive use of anthropogenic resources, largely still relying on natural resources ('urban adapters', *sensu* McKinney, 2006). By con-

trast, fully synanthropic species ('urban exploiters', *sensu* McKinney, 2006) may actively invade city environments, make use of anthropogenic food and shelter, and often attain population densities far above those found for rural habitats. In this paper, we have reviewed available information on carnivores dwelling in urban environments (either as 'urban adapters' or 'urban exploiters') and compare these with species that have not successfully adapted to the urban environment ('urban avoiders').

Why review the biology and ecology of urban carnivores? Firstly, as cities grow, we are removing alternative habitat for these animals. With increasing loss of undeveloped landscape, urban resources are likely to become more important for conservation of wild animals. City-dwelling is becoming more important for wildlife as the global human population grows (Baker & Harris, 2007). Secondly, it is evident that increasing numbers of carnivores are using urban areas. For example, during the 1990s, there was a 15-fold increase in the numbers

of nuisance coyotes *Canis latrans* removed annually from the Chicago metropolitan area (Gehrt, 2011); similarly, there has been a 10-fold increase in complaints about black bears *Ursus americanus* in urban Nevada (Beckmann & Lackey, 2008). Thirdly, it is biologically interesting that some species, but not others, do so well in urban environments. Understanding more about the biology of these animals is likely to aid our management and conservation of carnivores as a group. Finally, as Gehrt, Riley & Cypher (2010) pointed out, carnivores elicit strong feelings in people (e.g. fascination, admiration, fear and hate), which may be a manifestation of our ancestral predator–prey relationships and which certainly mould and direct our interactions with these animals.

In this review, we summarize the history of terrestrial mammalian carnivore species as urban dwellers in a taxonomic framework (section: '*History of carnivore urban adaptation*'). We then examine how the ecology of carnivores is influenced by urban living, addressing their habitat utilization and diet (section: '*How is the ecology of mammal carnivores influences by urban living?*'). We explore the causes of mortality and the effects of increased density on carnivore behavior and sociality. In the following section ('*Which species make the best urban adapter/exploiter?*'), we investigate features that may allow a species to become adapted to urban environments (i.e. taxonomy, body size, diet and phylogenetic history). Finally, we explore the consequences of carnivore presence within cities for humans, and, in turn, what a future in urban areas may hold for carnivores.

History of carnivore urban adaptation

Carnivores have demonstrated a range of adaptation to living with humans (Fig. 1). Dogs and cats have lived in close association with humans for millennia, and as human populations have spread, these animals have travelled with them, gaining access to some of the most remote locations on the globe. Their extremely adaptable nature has allowed dogs and cats to move out from human habitation to exploit new environments. A key example of this has been the establishment of the dingo *Canis lupus dingo* in Australia. Dingoes entered the continent with human settlers some 3500–4000 years ago (Corbett, 1995) and have since become established over the entire continent. Arguably, the cat is even more successful in its exploitation of habitats. Its high mobility and flexible biology makes the cat robust to habitat fragmentation (Crooks, 2002) and, coupled with transportation by humans (McKinney, 2006), these animals have spread largely unchecked over new landscapes (e.g. islands such as Australia and New Zealand) where they are an important and numerous predator (Schmidt, Lopez & Pierce, 2007). While domestic dogs and cats have moved out from human settlements to become feral in wild areas (Fig. 1), other carnivore species have encroached to varying degrees into human habitation (Fig. 1).

Red foxes *Vulpes vulpes* may be one of the most adaptable of the wild carnivores, inhabiting 'the most expansive geographical range of any wild carnivore using habitats as varied as arctic tundra, arid deserts, and metropolitan centres' (Macdonald, 1987; Voigt, 1987). The first unequivocal documenta-

tion of non-domestic predators dwelling in large cities is records of red foxes in British cities in the 1930s, although they may have been present much earlier (Teagle, 1967; Soulsbury *et al.*, 2010). The urban red fox was regarded as a 'British phenomenon' for a long time, but subsequent records indicate significant numbers of red foxes residing within an estimated 114 cities across the globe, including 56 cities in the UK, 40 European cities, 10 North American cities and 6 Australian cities (reviewed by Soulsbury *et al.*, 2010). Red foxes appear to actively colonize urban areas (Macdonald & Newdick, 1982; Harris & Rayner, 1986b; Wilkinson & Smith, 2001); this is particularly true for countries where this species is introduced, where there is a noted spread into a variety of habitats, including cities (Adkins & Stott, 1998; Marks & Bloomfield 1999b and references therein).

Raccoons *Procyon lotor* have been living in and around cities since the turn of the 20th century and are arguably one of the most common carnivores in modern North American cities (Seton, 1929; Hadidian *et al.*, 2010). The raccoon was introduced into Japan where it is now regarded as a pest in both urban and rural areas (Ikeda *et al.*, 2004) and has also spread in Germany where it was introduced ~70 years ago (Frantz, Cyriacks & Schley, 2005).

Their 'plasticity in behaviour, social ecology, and diet allows coyotes to not only exploit, but to thrive, in almost all environments modified by humans' (Gese & Bekoff, 2004). Despite the success of coyotes in colonizing urban areas (Gese & Bekoff, 2004), little is known of their ecology in comparison with rural populations (Curtis, Bogan & Batcheller, 2007). This is partly due to difficulties inherent in such studies, but also because 20 years ago, there was little need for such studies (Gehrt & Prange, 2007), indicating a recent accession of coyotes to an urban-adapted niche. Coyotes may have always existed in and around cities in south-western North America, although their presence in midwestern and eastern cities has indicated their increases in population presence and size over the past ~100 years (Gehrt & Riley, 2010). Sizable populations now exist in urban areas across North American cities (Gehrt, 2011). At least in some areas, coyotes became urbanized through the enclosure of undisturbed patches of environment within the urban matrix (Quinn, 1997b), although more recently they appear to be actively colonizing urban areas (Grinder & Krausman, 2001a; Gehrt, 2011). Andelt & Mahan (1980) provided one of the first descriptions of an urban coyote interacting with people and dogs in Lincoln, Nebraska, US, in 1975 before its death at the hands of a hunter. Coyotes have apparently increased in abundance, spreading across New York State at an estimated rate of 78–90 km decade^{-1} over the past 60 years, culminating in the report of a coyote running through the streets of New York city in 2007 (Fener *et al.*, 2005; Berchielli, 2007; Curtis *et al.*, 2007).

Other carnivore species show less utilization of anthropogenic food sources and may still depend on expanses of native vegetation and resources. Often these species are found within suburban areas where the lower density of human living allows the retention of more natural environments compared with city centres.

Urban badgers *Meles meles* have been studied in several countries across Europe and Asia (reviewed in Roper, 2010). Badgers appear to have originally become urbanized through the enclosure of relicts of undeveloped habitat within an urban matrix, although there is also some evidence for active colonization (Harris, Baker & Soulsbury, 2010b). Teagle (1969) states that badgers in London, UK, 'could *still* be found in Richmond Park and Wimbledon Common and in nearby parks, golf courses and other private property' (emphasis added). Once established, animals will also spread within the urban matrix (Harris, 1984). Huck, Davison & Roper (2008a) and Delahay *et al*. (2009) note that complaints by people of damage to property by urban badgers is currently increasing in the UK, possibly implying an active increase in the badger population.

Striped skunks *Mephitis mephitis* and eastern spotted skunks *Spilogale putorius* are less well-studied as urban animals, but due to their defence behaviour of spraying, encounters with them can be dramatic and traumatic for humans and their pets (skunks represented 51% of total urban problem wildlife trapped in California up to 1990; Maestrelli, 1990). Reports of skunks in urban areas can therefore be out of proportion to their urban densities (Prange & Gehrt, 2004).

Apart from the red fox and coyote, other canid species have been less successful in urban areas. Gray foxes *Urocyon cinereoargenteus* (Harrison, 1997; Iossa *et al*., 2010) and kit foxes *Vulpes macrotis* (Cypher, 2010) can be found in suburbs of some North American towns, but little is known about the biology of these urban populations at present.

Slender mongooses *Galerella sanguinea* have been observed in urban and suburban Pretoria and Johannesburg, South Africa, and small-spotted genets *Genetta genetta* have been observed in urban Johannesburg (PWB pers. obs.; R. Morley pers. comm.), around a town in Ethiopia (Admasu *et al*., 2004) and urban areas in southern France (Gaubert *et al*., 2008). Stone or beech martens *Martes foina* have been recorded as making extensive use of urban environments, at least in central Europe (Herr, 2008), and records date as far back as 1949 (Nicht 1969). More interestingly, the same species is noted as almost completely absent from urban areas in Iberia (Virgós & Casanovas, 1998; Virgós & García, 2002).

Of marsupial carnivores, Virginia opossums *Didelphus virginianus* are familiar urban animals over much of the US, both colonizing new areas and being introduced outside of their natural, increasing range (Maestrelli 1990 and references therein). Opossums also appear to show a preference for developed areas (Kanda, Fuller & Sievert, 2006; Markovchick-Nicholls *et al*., 2008). In Australia, southern brown bandicoot or quenda *Isoodon obesulus* and long-nosed bandicoot *Peremeles nasuta* populations have become enclosed by urban spread of a number of Australian cities (e.g. Dowle & Deane, 2009). Within this matrix, bandicoots may persist, benefiting from urbanization in terms of control of predators (e.g. red fox; Harris, Mills & Bencini, 2010a). In many cities, bandicoots become habituated to people (pers. obs.) and may benefit from deliberate or inadvertent feeding.

Finally, a number of carnivore species visit upon the fringes of cities or towns. Their home ranges may include some urban area or they may use urban areas for foraging, but they do not live exclusively within urban areas (Iossa *et al*., 2010).

Apart from domestic cats, very few felids can be considered established urban dwellers. Bobcats *Lynx rufus* (e.g. George & Crooks, 2006; Riley, 2006; Riley *et al*., 2010) and pumas *Puma concolor* (e.g. Beier, 1995; Markovchick-Nicholls *et al*., 2008; Beier, Riley & Sauvajot, 2010) have been reported from parks and large gardens in suburbs on the edge of the urban-undeveloped land interface in the US, but they do not appear to reside within built-up parts of the cities.

Grey wolves were persecuted by humans, resulting in their extermination from Britain and Ireland by 1773 and significant reduction in numbers on the European continent, driving the few survivors into remote areas far away from human settlement (Cosmosmith, 2011). However, protection of the species has led to increasing numbers of wolves over mainland Europe over recent years, and they are occasionally reported foraging on garbage dumps near towns (see the section: '*Refuse*').

American black bears have been reported in urban areas of North America (Gunther, 1994; Beckmann & Lackey, 2008) and brown bears *Ursus arctos* will forage for foods in some European towns, notably Brazov, Romania (Pasitschniak-Arts, 1993; Quammen, 2003). Spotted hyaenas *Crocuta crocuta* famously enter the streets of Harar, Ethiopia (Kruuk, 2002), and striped hyaenas *Hyaena hyaena* forage in and around towns in Israel (Yom-Tov, 2003).

How is the ecology of mammal carnivores influenced by urban living?

Perhaps the best way of understanding how carnivores are influenced by living in an urban environment is to compare these animals with populations living in rural locations. This sounds simple in principle; however, it is remarkable how few comparative studies exist. Three key variables are believed to influence a species' adoption of new environments (Shea & Chesson, 2002): resources, natural enemies and the physical environment. Cities may provide hospitable niches for carnivores due to reliable, non-seasonal food and water resources, reduced threat of natural enemies and/or altered physical environment (e.g. temperature, providing shelter) (Fig. 1). We discuss these aspects below.

Within cities, where are carnivores living?

The presence of natural vegetation within cities is important for supporting significant numbers of carnivores (Baker & Harris, 2007). Therefore, proximity to large expanses of connected habitat ('green zones') within cities would provide refuge that may act as resources for animals. Garden size and garden structure are also important factors: Baker & Harris (2007) reported that urban carnivores in the UK are variously negatively affected by the increased fragmentation and reduced proximity of natural and semi-natural habitats, decreasing garden size and garden structure. The presence of

flood channels or drainage lines, powerline corridors, beach strands and railroad corridors running through suburbs allow connectivity between habitat patches (Lewis, Sallee & Golightly, 1993) and would support populations of species that will not walk across open areas. The dispersal of food resources within a city is also likely to influence exploitation of these habitats by carnivores. Availability of soil types suitable for drainage and digging burrows is likely to limit utilization by burrowing species (see discussion by Kaneko, Maruyama & Macdonald, 2006). Finally, some urban carnivores make use of anthropogenic structures for shelter and do so even when natural alternatives are available, while other species appear to be completely adverse to using anthropogenic structures. For example, bandicoots show no obvious use of manmade structures, but are dependent on dense vegetation for cover: they are likely to withdraw from manicured or cleared urban gardens (Chambers & Dickman, 2002; FitzGibbon, Putland & Goldizen, 2007).

Foxes require both secure daytime rest sites and breeding sites (earths) to ensure their permanent presence (Baker et al., 2000). Even in urban environments, red foxes still seem to rely on areas to dig earths for denning, so that concentrated housing with small gardens discourages breeding (Harris & Rayner, 1986b). However, many British cities provide ideal habitat for red foxes, for example, inter-war housing with established gardens including hedges and shrubs for daytime cover, together with older residents, fewer children and hence less disturbance (Harris, 1981a; Harris & Rayner, 1986b). Harris (1981a) also recorded breeding foxes making earths under the floorboards of occupied houses and derelict buildings in Bristol, UK. In the US, small road culverts, old barns and other refugia are likely to provide important shelter for red foxes, particularly in the presence of coyote predators (Gosselink et al., 2007). In Australian cities, red foxes often reside in reserves or parklands (pers. obs.). Removing thickets of non-native plants (e.g. lantana, blackberry), which are preferred diurnal rest sites, has been proposed as one means of reducing red fox density in Australia (Marks & Bloomfield, 2006).

Coyotes do not appear to make direct use of buildings for shelter, but within built-up areas, patches of natural forest and scrub, even undeveloped plots amongst housing, are vital as protective cover (Atwood, Weeks & Gehring, 2004; Atwood, 2006; Baker, 2007). For example, all recorded dens in Cape Cod, US, were naturally dug and >300 m from houses (Way et al., 2001). Kit foxes also make use of undeveloped lands (e.g. vacant lots, fallow crop fields), industrial areas (e.g. manufacturing and shipping yards) and open spaces (e.g. parks, canals, railroad and powerline corridors), but will use manmade structures in addition to digging dens (Cypher, 2010).

In contrast with these species, many other carnivore species readily exploit anthropogenic structures for habitat. While badgers in Europe rarely seem to use buildings (Delahay et al., 2009; Roper, 2010), in the suburbs of Tokyo, Japanese badgers *Meles anakuma* make use of under-floor spaces of empty buildings as resting places (Kaneko et al., 2006). Where available, hollow trees seem to be preferred den sites for raccoons (Stuewer, 1943); however, in urban areas, raccoons favour parks and avoid major roads and the most built-up areas, but do enter houses and make use of sewers, chimneys and other structures as alternative denning sites where hollow trees are in short supply (Hoffmann & Gottschang, 1977; Prange, Gehrt & Wiggers, 2003, and references therein, Hadidian et al., 2010). Striped skunks survive in highly modified urban environments, including 'single family homes on adjacent lots with manicured lawns and yards' (Engeman et al., 2003) and can den in crawl spaces under houses (Clark, 1994), while eastern spotted skunks can enter attics (Maestrelli, 1990). Opossums find human habitation extremely suitable as shelter and 'a penchant for building malodorous nests inside or beneath occupied buildings give the opossum an unwelcome reputation in urban areas' (Maestrelli, 1990). Finally, according to Delibes (1983), European stone martens live 'almost exclusively in the human dwellings and their immediate surroundings' and they prefer inhabited buildings, particularly in winter, presumably because of warmth (Herr et al., 2010). They tend to be absent from grassland and large areas of arable land, probably due to the lack of tree-hollow shelters (Virgós & García 2002 and references therein).

What do they eat?

A diversity of food resources are available to urban carnivores and the majority of well-established urban carnivores include a wide range of items in their diet (see further discussion in the section: *'Diet'*). Food resources available in urban areas include human refuse, crops (i.e. fruit and vegetables), synanthropic rodents and birds, pets, livestock and road-kill, or food made available through deliberate feeding. For example, more than half of the stomach contents of red foxes in Zürich, Switzerland, was anthropogenic, and 85% of surveyed households provided food for foxes (through rubbish bins, compost heaps, garden fruit and food for pets and wild birds) (Contesse et al., 2004). Consequently, urban carnivores have access to an increased range of high nutrition food as well as a greater degree of seasonal food security than do their rural counterparts. With the exception of coyotes (which have been reported to hunt singly in urban environments, not in groups), urban carnivore species are not generally group hunters (Iossa et al., 2010). This may reflect the generalist nature of the successful urban dwelling species, as well as the rich, easily accessible anthropogenic food that does not necessitate cooperative hunting behaviour.

Refuse

Carnivores can benefit by utilizing sources of high-energy food from human refuse. Even in rural areas, there may be huge amounts of anthropogenic waste. For example, Yom-Tov, Ashkenazi & Viner (1995) estimated that 1208 tons of meat was disposed of by farmers in the Golan Heights, Israel, in 1 year; many carnivore species take advantage of such resources. In urban areas, carnivores may forage at tip sites and often turn over bins in backyards, streets and parks.

Red foxes are both generalist and eclectic in their diet choice, that is, they eat a broad range of food types and also can adapt to substantial local variation in food types available (Harris, 1981*b*; Reynolds & Tapper, 1995). In addition to items that rural foxes consume (i.e. small mammals, fruit, earthworms, etc.), urban red foxes may rely heavily on scavenged anthropogenic food (Baker *et al.*, 2000), and scavenged food can make up to 60% of an adult urban fox's diet (Doncaster, Dickman & Macdonald, 1990; Saunders *et al.*, 1993). For example, in Zürich, over 50% of fox stomachs examined contained anthropogenic food and this increased from suburban to city centre zones (Contesse *et al.*, 2004). Refuse and discarded fast food is of such abundance that the Zürich fox population is still increasing (Contesse *et al.*, 2004). In Orange County, California, remains of human food and food packaging were present in 62% of fox scats, particularly during winter months (Lewis *et al.*, 1993).

The faeces of raccoons from a primarily urban site (Glendale, Ohio, US) contained seeds from 46 species of plants including human food (e.g. grapes, corn and watermelon) that probably came from raided bins (Hoffmann & Gottschang, 1977). Prange *et al.* (2003) recommended reduction or elimination of anthropogenic food as the best control method for problem urban raccoons. Yom-Tov (2003) reported that around Israeli settlements, badgers do not feed on garbage dumps but rather feed on vegetables in agricultural fields. However, of questionnaires returned by Bristol residents, 16.4% of complaints were due to badgers disrupting bins (Harris, 1984). Striped skunks will raid bins and bee hives in urban areas (Clark, 1994) with up to 18% of the diet of eastern striped skunks living near humans sourced from trash (Hamilton, 1936), while bin-raiding by opossums make them one of the most commonly reported pest species (Clark, 1994).

Inadvertently enticing animals closer to human settlements through the provision of refuse is likely to be the first step towards these animals becoming habituated to human presence. For example, banded mongooses *Mungos mungo* have been recorded feeding at tips in Uganda (Gilchrist & Otali, 2002) as have red foxes in Saudi Arabia (Macdonald *et al.*, 1999) and brown bears in Europe (Quammen, 2003). Wolves make use of refuse dumps in Israel (Yom-Tov, 2003), Canada (Geist, 2007), Italy (Cosmosmith, 2011) and Romania (Promberger *et al.*, 1998). Such feeding behaviour has resulted in increased habituation to humans to the extent that they have little fear of people. In Canada, wolves are reported to approach the dump truck carrying refuse to the tip (timing their arrival to that of the truck) and thus have come to associate human smell with the provision of food (Geist, 2007).

Animals that raid human refuse for food are likely to also ingest substantial quantities of non-food material, which might become detrimental to their health. In addition to anthropogenic food items, the faeces of raccoons from urban sites include a variety of non-food items (e.g. plastic, rubber bands) that probably came from raided bins (Hoffmann & Gottschang, 1977). Even though coyotes (Gehrt, 2007) and stone martens (Eskreys-Wójcik & Wierzbowska, 2007) are not noted as bin raiders, 2% of Chicago coyotes' scats have evidence of human refuse, for example, fast food wrappers, pieces of rubber, sweet wrappers, plastic, string and aluminum foil (Morey, Gese & Gehrt, 2007), and 17% of stone marten scats from urban areas contained rubber and plastic, etc. (Eskreys-Wójcik & Wierzbowska, 2007).

Crops (fruit, vegetables and grain)

Fruit is of major seasonal importance to badgers, making up 48–61% of the diet (stomach contents and faeces) of Bristol badgers (Harris, 1984), and persimmons are found in 100% of autumn-collected Japanese badger scats in urban Tokyo. Stone martens also rely heavily on fruit (present in 43% of scats, Baghli, Engel & Verhagen, 2002; Lanszki, 2003). Even species such as coyotes and foxes may use fruit as a significant food source. Fruit is present in 23% of Chicago coyote scats (Morey *et al.*, 2007), and 43% of urban Washington State coyote scats (Quinn, 1997*a*). Lewis *et al.* (1993) reported seeds of >44 plant genera (from >28 plant families) present in 73% of the scats of red foxes from Orange County, California (with seasonal differences: greater occurrence in autumn). Contesse *et al.* (2004) recorded wild fruit in the stomachs of 23% of urban Zürich red foxes examined, and cultivated fruit and crops in 49%. These carnivore species may therefore significantly benefit from orchards and market gardens around towns and cities, and the badger, for example, appears to take less scavenged food at the time of year that seasonal fruit is available (Harris, 1984).

Synanthropic prey – rodents and birds

The rich resource of rodents in urban areas is likely to have encouraged the first cats into close association with humans, as discussed earlier. Rodents and birds (especially synanthropic species, e.g. sparrows, pigeons) are also a major food source for a number of other carnivore species, most notably coyotes, red foxes, stone martens and badgers. Rodents are present in 42% of Chicago coyote scats (Morey *et al.*, 2007) and 26% of Zürich red fox stomachs (where they make up 11% of total stomach content; Contesse *et al.*, 2004). Rodent remains are present in 14.3% of Tokyo Japanese badger scats in spring (Kaneko *et al.*, 2006).

Although they only make up 5% of stomach volume, bird prey were present in 24% of Zürich red fox stomachs (Contesse *et al.*, 2004). In California, bird remains are present in 70% of fox scats in built-up areas including extensive amounts of duck and passerine remains, with egg shell in 5% of scats (Lewis *et al.*, 1993). 6.2% of badger samples collected in Bristol (Harris, 1984), but 29% of urban Tokyo Japanese badger scats (Kaneko *et al.*, 2006) include bird remains during spring (when birds are breeding).

In urban Luxembourg, stone martens prey principally on synanthropic birds and mammals (Herr, 2008). Lanszki (2003) compared stone marten scats from a small village and surrounding agricultural area in Hungary. Stone martens from both areas relied heavily on fruit (cultivated fruit for village animals, more wild fruit in rural animals), while village martens included a high proportion of birds (e.g. house spar-

rows) in their diet (20% for village compared with 11% for rural animals) but fewer mammals (13% for village compared with 35% for rural animals).

Pets, livestock and road-kill

Urban carnivores may also make use of domestic animals as prey. For example, three studies report that between 1 and 13% of the diet of urban coyotes is made up of cats (Mac-Cracken, 1982; Quinn, 1997b; Morey et al., 2007). Urban areas may also provide food for scavenging in that the numbers of road kills around towns and cities is likely to be higher than it is for rural areas. For example, in a park surrounded by urbanization in Ohio, US, coyotes eat a primarily 'natural' diet of small to large mammals, but they also take advantage of the many white-tailed deer road-kill carcasses (Cepak, 2004), a resource that would normally be rare. Pets and livestock (including hens, cats, dogs, rabbits and cattle) make up 4.5% of the gut volume of Zürich red foxes (Contesse et al., 2004) and a small proportion of the diet of Californian red foxes (Lewis et al., 1993). In Europe, grey wolf and brown bear numbers have been increasing, which is likely to result in increased interaction with humans at the rural-urban interface: because of the decline in the number of wild game, they have begun to prey on domestic horses, cattle and dogs (and will also take fruit and vegetables, e.g. potatoes) (Pasitschniak-Arts, 1993; Cosmosmith, 2011).

Deliberate feeding

In many urban areas across developed countries, households may regularly put out food for urban carnivores such as badgers and even foxes. Roper (2010) reported that 29% of householders surveyed in Brighton deliberately provided food for foxes, badgers and other mammals, and over half of these households were providing food every night. Lewis et al. (1993) reported an individual person regularly feeding red foxes within a Californian urban park, providing an average ($\pm$SD) of 7.12 ± 0.23 kg day^{-1} of beef, chicken, turkey and fish (measured over a 48-day period) to the ~40 foxes present in the park (~0.177 kg per fox per day). Even if the food is not left deliberately, many wild carnivores will regularly take dog or cat food left accessible. For example, in Zürich, when pet food was present in a fox stomach, it made up the majority of the stomach contents (Contesse et al., 2004). With the high energy content of anthropogenic food, one or two households leaving out food may have a significant effect on the foraging behaviour of these animals.

Food security in urban areas

One of the greatest advantages of anthropogenic food sources may be that they are more reliable compared with natural food sources. For example, urban coyotes show a seasonal pattern in some dietary foods (e.g. fruit) but also eat refuse (as do those in more rural areas if they can access it) (Quinn, 1997a), which is less likely to be seasonally affected. Similarly, although red foxes are eclectic feeders and can easily adapt to

variation in food types available (Reynolds & Tapper, 1995), seasonal variation of London fox diet appears to be less pronounced than in rural foxes (Harris, 1981b). Even so, some seasonal variation in diet has still been demonstrated for certain urban red fox populations (Oxford: Doncaster et al., 1990, e.g. Zürich: Contesse et al., 2004).

In rural areas of Britain and Ireland, the most favoured badger habitats are broad-leaf woodlands and meadows (Feore & Montgomery, 1999) that provide them with access to large numbers of earthworms (Kruuk, 1978, 1989). However, in an urban environment, badgers seem to avoid open grass-lands (lawns, playing fields, etc.) within their home ranges (supporting the contention that they are opportunistic generalists rather than earthworm specialists; Roper, 1994). Instead, urban badgers expand their diet range to include more anthropogenic food sources (e.g. refuse and garden crops) to the extent that earthworms are seasonally only a minor dietary component (Harris, 1984; Huck et al., 2008b).

What kills urban carnivores?

Review of the literature indicates many anecdotal statements (but few records) regarding causes of mortality in urban carnivores. Causes of mortality can also be dynamic, with principal causes shifting over time, making it difficult to carry out direct comparison between urban and rural environments. For example, the principal cause of mortality in red foxes in the US has shifted away from hunting due to an over 10-fold fall in fur prices making hunting less profitable (Gosselink et al., 2007). Additionally, avoidance of an encroaching competitor/predator (the coyote) has resulted in increased road mortality in red foxes because they are utilizing habitat that brings them closer to human habitation (Gosselink et al., 2007). Waves of disease have also resulted in significant mortality in carnivores. In dense urban populations, where individuals live in closer proximity to each other, it is intuitive that the likelihood of an infectious disease spreading may be increased (but see also White, Harris & Smith, 1995, who predicted that heterogeneity of urban habitats meant lower frequency of contact between rabies infected and uninfected British foxes than in rural populations of a similar density).

We summarized 29 studies that included cause of death statistics for red fox, coyote, badgers, bobcats and raccoon to investigate whether the causes of death differed between urban and rural areas (Fig. 2). We identified the absolute numbers of animals where cause of death was identified as due to motor vehicles ('cars' or 'road-kill'), hunting/euthanasia, toxicity, predation/aggression, disease, starvation/emaciation and unknown/other.

Road accident has been listed as a major cause of mortality in carnivores, killing a large proportion of badgers (57%), red foxes (40%), coyotes (31%), bobcats (38%) and skunks (30%), with little difference evident between urban and rural habitats where these data are available (Fig. 2). Road death is likely to be biased towards individuals that disperse further, for example, males and juveniles (Baker et al., 2007). Of the 151 recorded deaths of black bears in urban environments (over a 10-year period), all were due to humans, and 89 of 151 (59%)
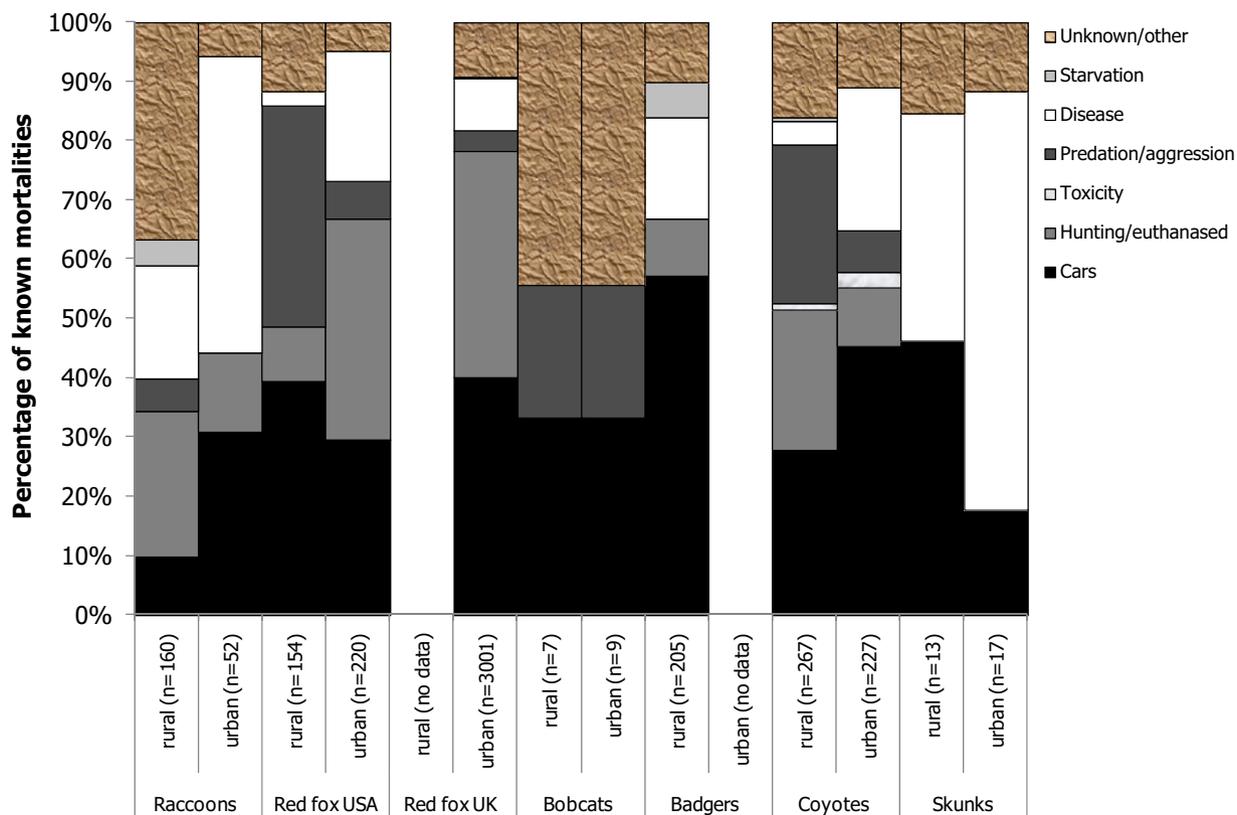
Figure 2 Causes of mortality in rural and urban populations of badgers *Meles meles*, red foxes *Vulpes vulpes*, coyotes *Canis latrans*, raccoons *Procyon lotor*, bobcats *Lynx rufus* and skunks *Mephitis mephitis*. Data have been extracted from various sources and percentages have been calculated from the total absolute number of animal deaths across all studies inclusive: coyote (Andelt & Mahan, 1980; Atkinson & Shackleton, 1991; Holzman, Conroy & Davidson, 1992; Chamberlain & Leopold, 2001; Way *et al*., 2001; Grinder & Krausman, 2001*a*; Tigas, Vuren & Sauvajot, 2002; Riley *et al*., 2003; Van Deelen & Gosselink, 2006; Berger & Gese, 2007; Gosselink *et al*., 2007; Schrecengost *et al*., 2009; Gehrt, 2011); red fox (Harris & Smith, 1987; Lewis *et al*., 1993; Gosselink *et al*., 2007; Soulsbury *et al*., 2007); skunks (Gehrt, 2005); badgers (Cheeseman, Wilesmith & Stuart, 1989; Kowalczyk *et al*., 2003); and raccoons (Mech, Barnes & Tester, 1968; Glueck, Clark & Andrews, 1988; Clark *et al*., 1989; Hasbrouck, Clark & Andrews, 1992; Riley *et al*., 1998; Chamberlain *et al*., 1999; Gehrt & Fritzell, 1999; Prange *et al*., 2003; Gehrt & Prange, 2007; Urbanek, Nielsen & Wilson, 2009). *Data for 1636 red foxes in Bristol, UK, were assumed to include data collected previously by the same researchers (1978–80, *n* = 87 Harris 1981a, 1977–86, *n* = 564, Harris & Trewhella 1988).

were killed by vehicles (Beckmann & Lackey, 2008). In urban areas, deaths exceeded recruitment meaning urban areas were sinks for this species (Beckmann & Lackey, 2008). Notably, an estimated 50 000 badgers are believed to die on British roads each year (Harris *et al*., 1992, 1995), which equates to 49% of all adult and post-emergence cub fatalities. We could not find published mortality statistics specifically for urban badgers for comparison. Road accident is a major cause of death in urban raccoons (31%), but less so for rural animals (8%). Roads can act as barriers to dispersing wildlife (e.g. pumas Beier, 1995; bobcats and coyotes; Riley *et al*., 2003), although this can be mitigated by culverts and underpasses (Grilo, Bissonette & Santos-Reis, 2008; Harris *et al*., 2010*a*), while Bristol red foxes change their activity patterns, avoiding roads prior to midnight when traffic volume is higher (Baker *et al*., 2007).

Hunting and destruction (i.e. euthanasia) are the next most common causes of death among carnivores (Fig. 2). Hunting/ destruction is the major cause of death for raccoons (61% of mortalities), especially for rural raccoons (64%), while almost a quarter (22%) of rural coyotes die at the hands of hunters (compared with 9% in urban environments). Thirty-eight per cent of deaths of red foxes in European cities are due to animals being destroyed. Similar figures exist for urban areas in the US (35%), but in rural US, hunting is a minor cause of death in foxes (9%), where predation (38%) and death on roads (40%) are the major causes of mortality.

Pollutants (e.g. motor oil and antifreeze) and poisons (particularly anticoagulant rodenticides, directly poisoning the animal or where the carnivore takes poisoned rodents) are likely to be a significant cause of mortality in urban carnivores. However, our literature review indicated that toxicity is listed as a cause of death for only a few urban and rural coyotes (Riley *et al*., 2003; Van Deelen & Gosselink, 2006) (Fig. 2) and for kit foxes (Cypher, 2010). The lack of reports

may be related to difficulty in ascertaining poisoning as a cause of death, particularly when carcasses are located some time after death. Organochlorines (Dip *et al.*, 2003) and lead (Dip *et al.*, 2001) are found in higher concentrations in urban than rural red foxes in Zürich. Organochlorine levels increase in adult male foxes but not vixens, which appear to pass the compounds to their offspring through lactation.

Protection from predators is likely to play an important role in selection of urban habitats. Predation or aggression is responsible for the death of only 10% of urban coyotes compared with 25% for rural populations, where they conflict with wolves (Fig. 2) and it has been suggested that the massive increase in coyote numbers over recent decades is likely due to reduction in the numbers of grey wolf across North America (Gese & Bekoff, 2004). In turn, coyotes tend to avoid landscapes with extensive human presence, and their conflict with red foxes means that foxes end up being relegated to areas with relatively more intense human activity (e.g. roads, farmsteads) (Gosselink *et al.*, 2007). An estimated 38% of red foxes in rural US die due to predation/aggression, largely due to conflict with coyotes, compared with only 12% in urban US (Gosselink *et al.*, 2007). In the UK, the absence of a natural predator for the fox results in less predation. Nevertheless, even in urban UK (London and Bristol), a high proportion of red foxes die due to wounds incurred during aggression, principally from stray dogs or conspecifics (Harris & Smith, 1987; Soulsbury *et al.*, 2007). Recent control of stray dog numbers, however, has reduced the incidence of aggression as a cause of death (S. Harris, pers. comm. 2010).

Disease has been recorded as the major cause of mortality for urban raccoons, accounting for an average of 50% of deaths in urban areas compared with only 19% of rural raccoons (Fig. 2). High levels of sarcoptic mange have been recorded in urban red foxes in Britain, causing population crashes (Baker *et al.*, 2000; Soulsbury *et al.*, 2007) and to a lesser extent in urban coyotes (Grinder & Krausman, 2001*a*). Disease outbreaks may be important factors affecting populations of other carnivore species; however, we note that not all authors indicate a breakdown for disease that would allow comparison – for example, disease and starvation/emaciation are often not distinguished.

Consequences of increased food and water, protection from predation

As a consequence of increased food and water availability in urban habitats, coupled with protection from predators, growth rate, body condition, survival and population densities of carnivores are predicted to be favoured.

Accelerated growth rates and reduced weight loss over winter

The presence of abundant, high-energy, non-seasonal food sources in urban areas may have a significant effect on the growth of carnivore species. Yom-Tov (2003) examined museum specimens collected from Israel over 60 years (from 1945 to 2005), a time span when human population in the country increased approximately eightfold, resulting in a significant increase in anthropogenic food sources (Yom-Tov, 2003). He recorded that, over this time, species that do not use anthropogenic food (the caracal *Caracal caracal* and jungle cat *Felis chaus*) did not significantly change in mass or size; however, wolves, golden jackals *Canis aureus* and striped hyaenas, which all feed from garbage dumps and make use of livestock carcasses, increased in body mass. The larger species appeared to be more capable of exploiting the extra food provided by humans (Yom-Tov, 2003). A similar pattern of size increase in skull measurements was also recorded for badger and red fox populations in Denmark from 1862 to 2000, which again could be related to altered human agriculture and therefore food sources (Yom-Tov, Yom-Tov & Baagøe, 2003).

Starvation due to substantial weight loss over winter is a significant cause of death in skunks, but urban skunks fare better over winter than their rural counterparts (Rosatte *et al.*, 2010). Similarly, urban raccoons exhibit better physical condition than rural ones, possibly due to anthropogenic food (Rosatte, Power & Macinnes, 1991). Black bears in urbanized Nevada average 30% heavier than bears in rural areas due to a diet heavily supplemented by garbage (Beckmann & Lackey, 2008). Urban kit foxes demonstrate greater body mass compared with non-urban individuals (especially for juveniles) and also demonstrate different haematological characteristics (Cypher, 2010). Urban Eurasian badgers can be heavier than nearby rural badgers, presumably due to the availability of anthropogenic food (Roper 2010 and references therein). More research in this area is needed.

Increased reproduction and survival in urban habitats

Increased survivorship has been recorded for a number of urban carnivore species (**Table 1**). Opossums are recognized as bin-raiders *par excellence* (Clark, 1994), and their reliance on anthropogenic sources of food is such that, in areas where one would expect their range to have been limited by the winter cold and lack of natural food, they are, in fact, well-established (Kanda, 2005). Similarly, in addition to their better physical condition, urban raccoons demonstrate increased survival and higher annual recruitment compared with rural animals and subsequently increased site fidelity and higher population densities (Hoffmann & Gottschang, 1977; Rosatte *et al.*, 1991; Riley, Hadidian & Manski, 1998; Smith & Engeman, 2002; Prange *et al.*, 2003).

Although most coyotes in urban Chicago die before reaching their second year (Gehrt, 2011), urban coyote populations nevertheless show higher survival compared with rural studies, where coyotes are exposed to wolf predation, as well as hunting and trapping by humans (Gehrt, 2007 and references therein). Female black bears in urban areas of Nevada give birth much earlier (between 4 and 5 years of age, some as early as 2–3 years of age) than rural bears (7–8 years; Beckmann & Lackey, 2008). Urban black bear survival was, however, so much lower that this higher fecundity does not

translate to higher recruitment and urban areas act as sinks. The evidence for reproductive rate and survival in red foxes seems to be mixed: even if urban animals do exhibit higher reproductive rates, this may, however, be countered by lower survivorship (e.g. Harris, 1977; Doncaster & Macdonald, 1991).

In their taxonomic review of urban carnivores, Iossa et al. (2010) indicated that although juvenile and adult survivorship for urban carnivore species tends to be higher than for their rural counterparts, the pattern is not statistically significant across taxa (n = 4 species for juvenile survivorship and n = 8 species for adult survivorship).

Increased population density

Carnivore species that are able to exploit additional food resources are likely to exhibit higher population densities in urban compared with rural environments. For example, coyotes, red foxes, eastern striped skunks, stone martens, badgers, raccoons and opossums, all may reach higher densities in cities compared with rural areas (**Table 1**) (Iossa et al., 2010). Carnivores may reach extremely high densities in urban areas. For example, Fedriani, Fuller & Sauvajot (2001) reported densities of 3 coyotes km^{-2} in urban southern California, which is approximately seven times higher than that in rural locations. The highest badger density may be 33 adults km^{-2} recorded for Brighton, UK (Huck et al., 2008a). The highest density recorded for raccoons is an astonishing 333 individuals km^{-2} (estimated for an urban park in Fort Lauderdale, Florida), which is ~4 to ~400 times the density recorded for rural populations (Riley et al., 1998; Smith & Engeman, 2002).

Although 87% of the total British red fox population may be located in rural areas (Webbon, Baker & Harris, 2004), foxes may reach much higher densities in urban than rural locations. In Bristol, red fox densities of up to 37 indivi-

duals km^{-2} have been recorded (Baker et al., 2001), while 16 individuals km^{-2} were recorded for Melbourne, Australia (White et al., 2006). Town councils and local mammal groups across Great Britain record either stability in numbers or more often an increase in urban fox populations, with more cities in the south-east and coast areas hosting foxes (Wilkinson & Smith, 2001, and references therein). Foxes are also now present in cities that earlier models of population growth (Harris & Smith, 1987) predicted would not host foxes. Although the most common reason given for perceived increases in urban fox numbers is increased food availability, Harris (1981b) found that, at least in some urban areas, waste food formed a small part of a fox's diet, suggesting that other variables are involved.

In contrast with the species listed earlier, there seem to be conflicting data for opossums. Prange & Gehrt (2004) suggested that opossum densities are not increased in urban areas, with opossums being relatively more common in rural than urban parts of north-eastern Illinois, US. Kanda et al. (2006), however, reported that road-killed opossums in Massachusetts, US, are more common in areas of low forest cover and more human development, and the authors considered them urban generalists. Similarly, striped skunks can be regarded as generalists par excellence, being found in nearly all habitats across North America (Verts, 1967). Densities, however, do not generally seem to differ between urban and rural locations (Gehrt, 2004; Prange & Gehrt, 2004), suggesting either an inability to make extensive use of anthropogenic resources as successfully as other carnivore species or some other constraints.

Social systems and territorial behaviour

Greater resource availability and increased population density for urban carnivores are likely to determine their social behav-

Table 1 As a consequence of abundant aseasonal food resources and protection from predation, many carnivore species demonstrate increased survival in urban habitats compared with their rural counterparts, consequently reaching higher population densities and exhibiting smaller home range sizes.? indicates that comparative data for urban and rural locations do not appear in the literature

	Survival	Density	Territory size	Reference
Coyote	Higher	Higher	Larger, smaller	Fedriani et al., 2001; Riley et al., 2003; Atwood et al., 2004; Gehrt, 2007, and references therein, Gehrt & Riley, 2010
Red fox	Higher	Higher	Not different, smaller	Lyoyd, 1980; Harris, 1981a; Harris & Rayner, 1986a; Adkins & Stott, 1998; Marks & Bloomfield, 1999a; Heydon, Reynolds & Short, 2000, data cited by Contesse et al., 2004; Webbon et al., 2004; Iossa et al., 2010
Eastern striped skunks	?	Equal or higher	Smaller, not different	Verts, 1967; Bixler & Gittleman, 2000; Gehrt, 2004; Prange & Gehrt, 2004; Rosatte et al., 2010
Stone martens	?	Higher	Not different	Herr, 2008; Herr et al., 2009a
Eurasian badger	?	Equal or higher	Larger, smaller	Harris, 1982; Cresswell & Harris, 1988a; Cheeseman et al., 1988b; Feore & Montgomery, 1999; Kowalczyk et al., 2000; Davison et al., 2009; Huck et al., 2008a
Raccoon	Higher	Higher	Smaller	Hoffmann & Gottschang, 1977; Riley et al., 1998; Smith & Engeman, 2002; Prange et al., 2003; Prange, Gehrt & Wiggers, 2004; Hadidian et al., 2010
Opossums	Higher	Equal or higher	?	Prange & Gehrt, 2004; Kanda, 2005

Table 2 Prediction table describing how the factors influencing sociality in carnivores (*sensu* Creel & Macdonald, 1995) are influenced by living in the urban environment

	Mechanism for action	Prediction for urban environment
Resource dispersion	Abundant prey, or rich or highly variable resource patches result in conspecifics being more tolerated	Reduced competition would result in reduced aggression, overlapping home ranges and the formation of larger groups.
Dispersal costs	High numbers of mates, plenty of suitable habitat and reduced intra-specific competition	Reduced competition for resources would encourage dispersal.
Resource acquisition	Groups needed to acquire and retain resources, e.g. through hunting	Largely negated by the abundance of 'easily captured' food
Defence against predators	Groups less vulnerable than solitary animals	Largely negated by the absence of natural predators
Reproductive advantages	Groups better at feeding and protecting young than are solitary animals	Largely negated by abundant food resources year round

iour. The corollary of having more animals resident in urban areas is that either the individuals have smaller exclusive territories or that their home ranges overlap with more individuals, implying considerable changes in sociality and behaviour. Creel & Macdonald (1995) discussed five selective pressures that appear to influence sociality in carnivores (**Table 2**). Examining the potential action of these factors in the urban environment suggests that resource dispersion and dispersal costs are likely to have the greatest influence on carnivore sociality, and we predict reduced territoriality or aggression for urban carnivores, reduced home range area for individuals, increased group sizes, greater dispersal of individuals from their natal sites and altered mating systems (**Table 2**). Reviewing the literature suggests that there is evidence to support these predictions of social plasticity (e.g. for foxes and coyotes), although we need more direct comparisons between rural and urban using standard methods to make general conclusions regarding these aspects of carnivore biology.

Generally, red foxes appear to have smaller home ranges and shorter dispersal distances under higher population densities (Macdonald, 1980; Adkins & Stott, 1998). However, red foxes are so behaviourally plastic that it is often difficult to demonstrate any overt territorial and social behaviour (Cavallini, 1996). This plasticity is demonstrated upon release from population pressures. For example, an outbreak of sarcoptic mange in Bristol foxes caused a population crash that resulted in the remaining foxes increasing their home range size, even though food availability did not change (Baker *et al.*, 2000). Additionally, in Oxford and Toronto, Canada, suburban populations have more stable territories than foxes closer into the cities (Doncaster & Macdonald, 1991; Adkins & Stott, 1998). Diet and home range were not different between red foxes in the two areas in Oxford, and the shifting territories were likely to be due to a higher turnover of the fox population in the more disturbed city centre (Doncaster & Macdonald, 1991). Changes in the distribution of food has a rapid effect on social structure: Macdonald *et al.* (1999) found that otherwise sparsely distributed red foxes in Saudi Arabia centred their activities around often ephemeral but important food resources such as camel carcasses and shifting human camps and were tolerant of the presence of other foxes. Most major cities in Switzerland support red fox populations, most

likely due to the anthropogenic food supplies available; as rural foxes are shy, Contesse *et al.* (2004) suggested that this colonization must have entailed 'behavioural ontogenetic adaptations'.

Like red foxes, raccoons appear to have a plastic social system. Generally thought to be solitary and asocial, there is some evidence that loose groups of males maintain territories that overlap with those of solitary females (Chamberlain & Leopold, 2002). Territoriality collapses in urban areas with concentrated sources of food, where raccoons can reach extraordinary densities (Smith & Engeman, 2002).

Badger society is based around their setts (Kruuk, 1989) and badger distribution in urban areas seems to be partly dependent on suitable areas for digging setts (Huck *et al.*, 2008a). In urban areas, distribution of suitable soil (with appropriate drainage) is patchy, and it has been noted that zones of intermediate human population density are apparently favoured (Huck *et al.*, 2008a; Davison *et al.*, 2008). Badger setts in some urban UK sites are smaller than nearby rural setts, possibly indicating their more recent provenance and therefore an active colonisation process (Davison *et al.*, 2008). Bristol and Brighton (UK) urban badgers demonstrate less territorial behaviour (e.g. no scent marking of boundaries) and higher rates of dispersal than rural populations (Harris, 1982; Cheeseman *et al.*, 1988a; Cresswell & Harris, 1988b; Davison *et al.*, 2009), but while Bristol badgers had larger but more overlapping home ranges, the Brighton badgers had small non-contiguous territories typical of low density rural populations (Davison *et al.*, 2009). The Brighton population had extremely high population density, however (Huck *et al.*, 2008a), with much dispersal between groups, suggesting that differences between Bristol and Brighton are less to do with badger population density than the nature of the urban environment itself (Roper, 2010). The presence of solitary animals in urban environments, not obviously affiliated with any particular group, reflects the diverse range of social organization in badgers (Kowalczyk, Bunevich & Jedrzejewska, 2000).

In general, coyote densities are higher for urban compared with rural areas. Urban coyotes demonstrate both smaller (Andelt & Mahan, 1980; Atwood *et al.*, 2004; Gehrt, 2007, and references therein) and larger (Riley *et al.*, 2003) home ranges than their rural counterparts. Home range size may

largely be driven by resources available rather than population densities as coyotes avoid the most built-up areas, preferring wooded/shrubby areas to open areas (Quinn, 1997b) and need areas of 'natural' cover (vegetation) within their urban territories, which influences dispersal patterns (Grinder & Krausman, 2001b). Water, which may limit coyote distribution and density in deserts (Gese & Bekoff, 2004), is not likely to be a limiting factor in urban areas. Gehrt and colleagues (Gehrt & Prange, 2007; Gehrt, Anchor & White, 2009; Gehrt, 2011) refer to urban coyotes forming packs and suggest that, although coyotes prefer to hunt alone, they form packs to defend territories, with roughly half of all urban coyotes living in territorial packs that consist of five to six adults and their pups that were born that year.

This pattern of altered territories does not, however, hold true for all carnivore species in an urban area. Despite reaching moderately higher population densities in urban compared with rural locations, stone martens show no significant differences in territory size between the two habitats, even though the territories of urban martens fell entirely within built-up areas (Herr, Schley & Roper, 2009a).

Which species make the best urban adapter/exploiter?

Understanding the biology of urban adapters and exploiters may enable us to explain their role in cities and also allow predictions regarding their future and the abilities of other carnivores to establish within urban areas. It is possible that some 'non-adapted' species (i.e. 'urban avoiders', *sensu* McKinney, 2006) may adapt to the urban environment sometime in the future or even come to exploit human resources in and around cities. What, though, are the features that make some species better than others at becoming urban dwellers?

Geographic location

Although we have reviewed literature from all continents across the globe, we note that there is a bias towards 'western' societies in terms of the reporting rate for urban carnivores: we found few or no reports of urban dwellers other than anecdotal information outside of Europe, North America, Japan and Australia. We suggest that this bias may, firstly, reflect differences in human population densities. Higher human population density results in an increased proportion of 'urbanized' land and reduced availability of undeveloped landscape, pressurizing or enticing animals to use urban habitat. Secondly, the nature of cities will influence whether carnivores reside there. Compared with densely populated city centres, suburbs and towns support greater natural resources and therefore provide more opportunity for urban carnivores. Thirdly, Iossa *et al.* (2010) pointed out that there is a high prevalence of populations of feral and stray dogs in developing countries, which might limit the presence of carnivore species (e.g. Vanak & Gompper, 2009; Vanak, Thaker & Gompper, 2009). Finally, across the globe, people will

respond differently to carnivores entering urban environments, which may contribute to differences in reporting ratio. In India, culturally based tolerance towards carnivores allows many small carnivores and even leopards *Panthera pardus*, wolves, sloth bears *Melursus ursinus* and striped hyaenas to persist among high human population densities, albeit in agricultural landscapes (Karanth & Chellam, 2009). In south China, large and small carnivore species have been extirpated or greatly reduced in numbers; ironically, it is in mostly highly urbanized Hong Kong, with strong legal protection, where surviving species can be most easily encountered (Lau, Fellowes & Chan, 2010). Outside of anecdotal information, we could find no reports of carnivores living in African cities, despite a vast array of carnivore species on the continent. This may reflect the nature of urbanization or the nature of predator guilds in Africa: large expanses of adjacent rural or undeveloped habitat may provide sufficient alternative resources, while human self-preservation or protection of livestock may preclude the establishment of some carnivore species close to urban areas.

The role of taxon

All major terrestrial carnivore families have representatives that show some degree of association with human settlement (Fig. 3a). There appears to be no taxonomic restriction in terms of an ability to exploit urban environments. The major restrictions may therefore be in terms of body size and dietary flexibility.

Body size

Body size plays an important part in determining whether a carnivore species uses the urban environment. The proportion of species that utilize human habitat – from villages through to cities – is not spread evenly across the range of eutherian terrestrial carnivore body masses (Fig. 3b; $\chi^2_6 = 12.60$, $P = 0.05$). Both small and large carnivores are under-represented in the urban environment.

Body size is important in terms of how a species is able to deal with the habitat fragmentation implicit with urban environments. Larger body size is a benefit in human-fragmented agricultural landscapes if it aids the animals' ability to move in and out of the fragment matrix (e.g. coyotes), but body size should not be too large that viable populations cannot survive in small habitat fragments (Gehring & Swihart, 2003). Crooks (2002) reported that of 11 predator species in southern California, the four largest (puma, coyote, bobcat and American badger, *Taxidea taxus*) and two smallest (western spotted skunk *Spilogale gracilis* and long-tailed weasel *Mustela frenata*) species were most sensitive to fragmentation of natural habitat. The medium-sized species (raccoon, gray fox, cat, opossum and striped skunk) were the best at adapting to fragmented and anthropogenically modified habitats. Gehring & Swihart (2003) found a similar result for eight carnivore species at Indiana, US (coyote, red fox, gray fox, raccoon, striped skunk, opossum, cat and long-tailed weasel).
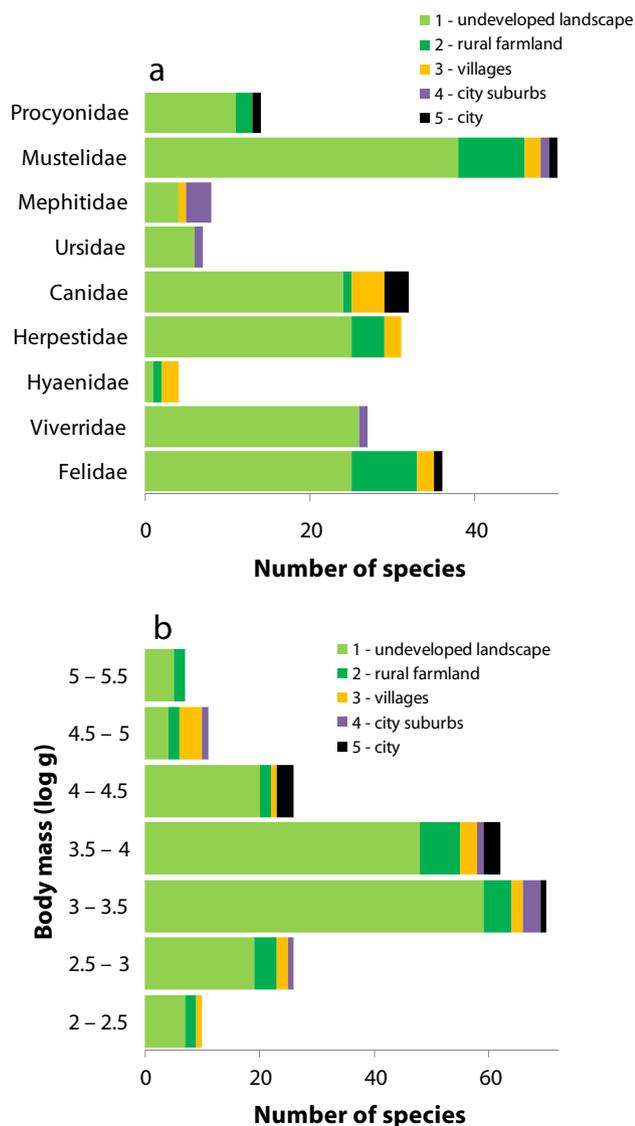
Figure 3 There are no clear phylogenetic determinants of whether a species will show some adaptation to anthropogenically disturbed habitat (a), although body mass (b) does appear to be relevant: most eutherian Carnivora species that are known to associate with towns and cities are in the range of 1–30 kg. Data do not include non-terrestrial carnivores or vegetarian diet specialists (e.g. red panda, *Ailurus fulgens*; Ailuridae).

In addition to compromised mobility, small carnivores are also likely to conflict with domestic cats and dogs. For example, Harris (1981*a*) reported that 15% of red fox cubs were killed by animals; in most cases, these were known to have been stray dogs. The British cat population (total ~9 million cats) killed an estimated 92 million prey items over a period of 5 months (from April to August), of which 57 million were mammals (Woods, Macdonald & Harris, 2003). Although only 0.1% of this mammal prey could be identified as other carnivores, 9 million cats is 20

times the population of weasels *Mustela nivalis* and stoats *M. erminea* and 38 times the population of red foxes in Britain (Woods *et al.*, 2003), implying the possibility of intense competition.

Despite their size, some large carnivores have managed to maintain an uneasy truce at some urban interfaces by moving in and out of the urban matrix, for example, brown bears (Swenson *et al.*, 2000; Kaczensky *et al.*, 2003; Rauer, Kaczensky & Knauer, 2003), black bears (Witmer & Whittaker, 2001; Beckmann & Berger, 2003; Beckmann & Lackey, 2008) and spotted hyaenas (Patterson *et al.*, 2004; Kolowski & Holekamp, 2006). Although they are also active killers of live prey, these species scavenge, making use of the rich resources available around cities. Wolves can also come into surprisingly close contact with humans in rural (Bangs & Shivik, 2001; Musiani *et al.*, 2003; Wydeven *et al.*, 2004) and urban (Promberger *et al.*, 1998) areas.

Although their size is an advantage in terms of accessing resources over a wide area, it can also make large carnivores a greater threat to humans and, clearly, human tolerance is a limiting factor for some species (Iossa *et al.*, 2010). Most large (>20 kg, Carbone, Teacher & Rowcliffe, 2007) carnivores have given way before humans (Woodroffe, 2000; Cardillo *et al.*, 2004), generally avoiding built-up areas. On average, felids (23.1 ± 39.7 kg, range 1.3–164 kg, $n = 36$ species) are larger than other carnivores (average 9.1 ± 22.8 kg, range 0.104–173, $n = 173$ species, $t_{207} = 2.90$, $P = 0.004$; analysed from raw data presented by Meiri, Simberloff & Dayan, 2005); and their trend to hypercarnivory (> 70% meat in the diet) and propensity for killing rather than scavenging prey seems to preclude large felids from residing comfortably with humans. A greater proportion of the largest carnivores are felids, which include some of the most dangerous carnivores that have, or occasionally still do, live in close association with humans (e.g. lions *Panthera leo* and tigers *Panthera tigris*; Löe & Röskaft, 2004). In the Sundarbans region of Bangladesh, 392 people were killed by tigers between 1956 and 1970 (Hendrichs, 1975), and 79 people from villages close to the mangrove jungle were killed by tigers between 2002 and 2006 (Khan, 2009). Löe & Röskaft (2004) cited over 12 000 human deaths reported globally in the 20th century due to tigers (in the same period only 313 deaths from brown bears were recorded).

For carnivores, a body mass of 20 kg marks where a shift from small prey to large vertebrate prey occurs (Carbone *et al.*, 2007). With the exception of the occasional coyote, all the well-established urban dwellers are well below this mass (average 4.60 ± 4.56, $n = 11$, min eastern spotted skunk: 0.34 kg, max coyote: 13.4 kg; Fig. 1). The coyote's success in urban environments appears to be due to their movements between urban and undeveloped areas, and switching between live prey and scavenging (Gehring & Swihart, 2003). Smaller (≤20 kg) carnivore species may be successful as urban dwellers due to release from competition with larger species ('mesopredator release', *sensu* Crooks & Soulé, 1999). Species with the most potential competitors (e.g. generalist diet species) may therefore have the greatest release from competition (Caro & Stoner, 2003) in urban zones.

Diet

Nearly all the well-established urban carnivores are generalists that are able to make use of carrion and human waste food (Fig. 1) (Crooks, 2002). The majority of these species are omnivorous, taking a wide range of diet items, including fruit, small mammals, invertebrates, lizards, and scavenged food (as discussed in the section: '*What do they eat?*'). McKinney (2006) terms these animals 'edge' species as they do well in the biodiverse and food-rich gardens and natural fragments that make up much of the urban landscape. Many carnivores that do not succeed in human-dominated landscapes (e.g. bobcats, American badgers, weasels and eastern spotted skunks) are hypercarnivore hunters of live prey or specialists (e.g. American badgers rely on digging out burrow-dwelling small mammals). For example, even when cohabiting with humans in farmland, the eastern spotted skunk relies on commensal rats and mice and takes no anthropogenic food (Crabb, 1941).

The most notable exception to this trend to omnivory is the domestic cat. While felids are adapted to hypercarnivory and can take prey as large as or larger than themselves (Kok & Nel, 2004), domestic cats may be exceptional in that, across multiple studies, they seem to subsist on prey averaging 1.1% their own mean body mass (Pearre & Maass, 1998), which is smaller than predicted based on their body mass (13%, Peters, 1983, 11%, Vézina, 1985) but larger than expected if they were considered specialist 'small-prey eaters' (Peters, 1983) or reliant on invertebrates (Vézina, 1985). Domestic cats appear to break the mould of 'specialised' felids and, like red foxes, are eclectic feeders that can adapt to local prey availability. We analysed data presented by Pearre & Maass (1998) and found that cats sampled from sites close to human habitation (farms, suburban and urban studies) take significantly smaller prey (23.2 ± 8.3 g; $n = 16$ studies) than cats in rural areas (72.6 ± 92.1 g, $n = 28$ studies). These data suggest that cats living close to human habitation modify their diet, which may explain how these hypercarnivores deal so well in anthropogenic environments.

Behavioural and biological flexibility

The 'ideal' urban carnivore should be highly adaptable in terms of diet, movement patterns and social behaviour (in the section: '*How is the ecology of mammal carnivores influenced by urban living?*'). However, there are some exceptions to this premise. For example, Herr *et al.* (2009*a*) found that stone martens in Luxembourg were almost entirely urban (their territories falling within the extent of the study towns), and their presence suggests that they successfully deal with the challenges of this environment. Their socio-spatial distribution, however, is almost exactly the same as recorded in non-urban habitats, and stone martens do not make much use of anthropogenic food sources (implying both social and dietary inflexibility). While stone martens are well-established urban carnivores, the congeneric pine marten *Martes martes* avoids human habitation (Baghli *et al.*, 2002; Herr, 2008). This difference appears to be due to pine martens being less omnivorous than stone martens, and while pine martens are diurnal,

the crepuscular stone marten is less susceptible to clashes with humans (Herr, 2008; Herr, Schley & Roper, 2009*b*).

Cardillo *et al.* (2004) demonstrated how biological features (e.g. geographic range, population density, reproductive rates and dietary requirements) explain 45% of variation in risk of extinction for carnivore species, or 80% when combined with high levels of exposure to human populations. Biological 'inflexibility' (small geographic ranges, low population density, low reproductive rates, need for large hunting areas or specific prey) in the face of increasing human populations and urbanization means potential extinction, while 'flexible' species (wide geographic range, potential high population density, high reproduction and generalist trophic niche) are more likely to adapt to increasing urbanization.

What are the consequences of carnivore presence in cities?

Although urban carnivores may be valued by large sectors of society (Baker & Harris, 2007) and even encouraged (e.g. through deliberate feeding section: '*What do they eat?*'), these animals can also clash with their human neighbours to a greater or lesser degree through disease transmission to humans and pets, damage to houses and gardens, general nuisance value (e.g. bin-raiding) or direct attack of humans or pets (Baker & Harris, 2007).

Disease

The risk of zoonoses is a significant cause for concern. The public health issues of carnivore presence in cities have therefore been the focus of much research as well as the drive for extensive control measures. For example, the potential transmission of rabies, tuberculosis and parasites are potential dangers for humans, pets or livestock. Rabies control measures have seen significant numbers of carnivores killed (e.g. Tischendorf *et al.*, 1998; Guerra *et al.*, 2003; Bourhy *et al.*, 2005) at substantial economic cost (Curtis & Hadidian, 2010). The greatest fear has been that rabies presence in established urban species is likely to increase the chance of transmission to pets or humans. Parasite transmission is also a significant risk. For example, raccoons carry a roundworm *Baylisascaris procyonis*, which causes no symptoms in the primary host but can be fatal to intermediate hosts (including humans) through visceral, neural or ocular larva migrans. As raccoons leave faeces in latrines in the open, risk of infection can be high for small children. Roussere *et al.* (2007) recorded that almost half of California residences surveyed had least one raccoon latrine containing *B. procyonis* eggs. Similarly, there is a high prevalence of *Echinococcus multilocuralis* in foxes in Zürich; this might be a source of infection for domestic carnivores and urban inhabitants (Stieger *et al.*, 2002). Carnivores carry many other parasite diseases (see review by Soulsbury *et al.*, 2010), which may have economic importance through transmission to domestic pets in urban environments.

Damage and nuisance

Carnivores may damage houses and gardens due to their diggings and residing in locations that may be problematic (e.g. roof spaces, where their movements are noisy and defecation or urination can cause damage) (e.g. Herr et al., 2010). Stone martens in Luxembourg climb into car engine compartments and, as part of territorial behaviour, destroy cables and rubber components and scent mark them (Herr et al., 2009b). In terms of general nuisance value, bin-raiding is a commonly reported problem with urban carnivores (Harris, 1984; Clark, 1994) (discussed in the section: 'Refuse'). Digging activities may also cause damage; for example, badger setts can be extensive (e.g. have 80 entrance holes and 360 m of tunnels, Delahay et al., 2009, and references therein), and while badgers in Europe do not often use buildings, their excavations cause significant damage to roads, buildings and waterways (Delahay et al., 2009).

Pet mortality, nuisance and direct attacks

Larger carnivores using urban areas might also increase the chance of direct attacks upon humans and companion animals (e.g. Gehrt & Riley, 2010). Löe & Röskaft (2004) suggested that tiger attacks on humans are more likely when there is less natural prey (a situation typical of urban areas). Also, as some carnivores become used to human presence, they lose their fear, resulting in direct attacks. Non-threatening behaviour by humans and the presence of anthropogenic waste food may have contributed to the death of a geologist in Canada, allegedly due to grey wolves (Geist, 2007). Many people also seem to avoid acting aggressively when they encounter large carnivores in the hope this will prevent or stop an attack; at least for wolves (Geist, 2007) and for pumas (Beier, 1991) shouting and throwing objects is more effective. A recent account of a red fox attack on infant twins in London indicated that even screaming and lunging at the fox was not sufficient to scare it off (Anon, 2010). Rabid carnivores, particularly, act aggressively and this may increase their encounters with humans (Anon, 2008).

Arguably, the coyote may be the most directly dangerous carnivore to humans due to its reasonably large body size (10–16 kg), potential for hybridization with wolves in some part of its range (Curtis et al., 2007; Gehrt & Riley, 2010) and close association with urban areas. Urban coyotes show reduced fear of humans, even biting or acting aggressively towards them (Carrillo et al., 2007; Farrar, 2007; Schmidt & Timm, 2007; Shivik & Fagerstone, 2007). Potential hybridization with wolves may increase the incidence of this type of aggressive interaction.

The future of urban carnivores

As the human population grows and urban areas expand, it is likely that a growing number of animal species will come into contact with anthropogenically altered landscapes; the concomitant reduction in wilderness areas will make this inevitable. The availability of food and shelter resources within these landscapes will also entice species in. Beckmann & Lackey's (2008) study of black bears is a good example: bear numbers in urban areas of Nevada have increased more than three times the recorded historical baseline, and there has been a 10-fold increase in complaints about urban bears. The bears become fatter on anthropogenic food and breed younger, but mortality is so high that urban areas are sinks, particularly as urban black bears do not appear to be able to recolonize undeveloped areas. Consequently, bears are becoming concentrated around urban areas and rare in undeveloped areas. The pattern of increasing numbers of carnivore species present in towns and cities over recent decades (e.g. coyotes in the US: Gehrt, 2011; bears in the US: Beckmann & Lackey, 2008; and Europe: Quammen, 2003) may mark the future for the coexistence of carnivores with man. Understanding the biology of these animals is therefore going to become more important if we are to make the best of these unfolding circumstances towards the conservation of the carnivores as well as mitigating their potential impacts upon our lives.

We predict that on the outskirts of cities, more large species are likely to make use of urban resources (bears, wolves, possibly cougars and bobcats in America and Europe, and hyaenids in Africa and Asia). This may, however, be short-lived as cities become more intensively urban, the urban/wildland interface of suburbs becomes more blurred, and the extent of undeveloped land diminishes. Within cities themselves, if sufficient patches of vegetation remain, carnivores may continue to use urban habitats, as long as they are not outcompeted by established urban exploiters (e.g. cats, dogs) or destroyed through control measures due to disease concerns.

Although we predict the continuing increase in incidence of carnivores in urban areas, other authors have suggested that overall carnivore diversity is likely to decrease in the future due to human action. For example, although genets Genetta genetta are common and widely distributed, Cardillo et al. (2004) identify genets (along with several other viverrids) as likely to become endangered by 2030 due to their overlap in distribution with areas of high human population density. However, genets have been observed living alongside humans in urban habitats in Africa (PWB pers. obs.) and Europe (Larivière & Calzada, 2001 and references therein). The perseverance of carnivores such as genets in significantly anthropogenically disturbed habitats is likely to rely on physiological and behavioural adaptability of these charismatic animals.

Acknowledgements

References

Adkins, C.A. & Stott, P. (1998). Home ranges, movements and habitat associations of red foxes Vulpes vulpes in suburban Toronto. J. Zool., Lond. **244**, 335–346.

Admasu, E., Thirgood, S.J., Bekele, A. & Laurenson, M.K. (2004). A note on the spatial ecology of African civet *Civettictis civetta* and common genet *Genetta genetta* in farmland in the Ethiopian highlands. *Afr. J. Ecol.* **42**, 160–162.

Andelt, W.F. & Mahan, B.R. (1980). Behavior of an urban coyote. *Am. Midl. Nat.* **103**, 399–400.

Anon (2008). Untamed and uncut: rabid fox attacks man. Animal Planet Videos, 4 September 2008. http://animal. discovery.com/videos/untamed-and-uncut-rabid-fox-attacks-man.html. Accessed: October 2011.

Anon (2010). Mother's 'nightmare' after baby twins 'mauled' by fox. BBC News, 7 June 2010. http://www.bbc.co.uk/news/10251349. Accessed: October 2011.

Atkinson, K.T. & Shackleton, D.M. (1991). Coyote, *Canis latrans*, ecology in a rural-urban environment. *Can. Field-Nat.* **105**, 49–54.

Atwood, T.C. (2006). The influence of habitat patch attributes on coyote group size and interaction in a fragmented landscape. *Can. J. Zool.* **84**, 80–87.

Atwood, T.C., Weeks, H.P. & Gehring, T.M. (2004). Spatial ecology of coyotes along a suburban-to-rural gradient. *J. Wildl. Mgmt.* **68**, 1000–1009.

Baghli, A., Engel, E. & Verhagen, R. (2002). Feeding habits and trophic niche overlap of two sympatric Mustelidae, the polecat *Mustela putorius* and the beech marten *Martes foina*. *Z. Jagdwiss.* **48**, 217–225.

Baker, P.J., Dowding, C.V., Molony, S.E., White, P.C.L. & Harris, S. (2007). Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. *Behav. Ecol.* **18**, 716–724.

Baker, P.J., Funk, S.M., Harris, S. & White, P.C.L. (2000). Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Anim. Behav.* **59**, 127–146.

Baker, P.J. & Harris, S. (2007). Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. *Mammal Rev.* **37**, 297–315.

Baker, P.J., Harris, S., Robertson, C.P.J., Saunders, G. & White, P.C.L. (2001). Differences in the capture rate of cage-trapped red foxes *Vulpes vulpes* and an evaluation of rabies control measures in Britain. *J. Appl. Ecol.* **38**, 823–835.

Baker, R.O. (2007). A review of successful urban coyote management programs implemented to prevent or reduce attacks on humans and pets in southern California. In *Proceedings of the 12th wildlife damage management conference*: 382–392. Nolte, D.L., Arjo, W.M. & Stalman, D.H. (Eds). University of Nebraska: Lincoln.

Bangs, E. & Shivik, J. (2001). Managing wolf conflict with livestock in the Northwestern United States. *Carnivore Damage Prevention News*. **3**, 2–5.

Beckmann, J.P. & Berger, J. (2003). Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *J. Zool. (Lond.)* **261**, 207–212.

Beckmann, J.P. & Lackey, C.W. (2008). Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. *Hum.-Wildl. Confl.* **2**, 168–174.

Beier, P. (1991). Cougar attacks on humans in the United States and Canada. *Wildl. Soc. Bull.* **19**, 403–412.

Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *J. Wildl. Mgmt.* **59**, 228–237.

Beier, P., Riley, S.P.D. & Sauvajot, R.M. (2010). Mountain lions (*Puma concolor*). In *Urban carnivores*: 141–155. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Berchielli, L.T. (2007). Impacts of urban coyotes on people and pets in New York state. In *Proceedings of the 12th wildlife damage management conference*: 332–333. Nolte, D.L., Arjo, W.M. & Stalman, D.H. (Eds). University of Nebraska: Lincoln.

Berger, K.M. & Gese, E.M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *J. Anim. Ecol.* **76**, 1075–1085.

Bixler, A. & Gittleman, J.L. (2000). Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). *J. Zool. (Lond.)* **251**, 525–533.

Bourhy, H., Dacheux, L., Strady, C. & Mailles, A. (2005). Rabies in Europe in 2005. *Euro Surveill.* **10**, 575.

Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007). The costs of carnivory. *PLoS Biol.* **2**, e22.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Macel, G.M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biol.* **2**, 909–914.

Caro, T.M. & Stoner, C.J. (2003). The potential for interspecific competition among African carnivores. *Biol. Conserv.* **110**, 67–75.

Carrillo, C., Schmidt, J., Bergman, D. & Paz, G. (2007). Management of urban coyotes and attacks in Green Valley, Pima County, Arizona. In *Proceedings of the 12th wildlife damage management conference*: 324–331. Nolte, D.L., Arjo, W.M. & Stalman, D.H. (Eds). University of Nebraska: Lincoln.

Cavallini, P. (1996). Variation in the social system of the red fox. *Ethol. Ecol. Evol.* **8**, 323–342.

Cepak, J.D. (2004). Diet composition of coyotes in the Cuyahoga Valley National Park. *Ohio J. Sci.* **104**, 60–64.

Chamberlain, M. & Leopold, B.D. (2002). Spatio-temporal relationships among adult raccoons (*Procyon lotor*) in Central Mississippi. *Am. Midl. Nat.* **148**, 297–308.

Chamberlain, M.J., Hodges, K.M., Leopold, B.D. & Wilson, T.S. (1999). Survival and cause-specific mortality of adult raccoons in central Mississippi. *J. Wildl. Mgmt.* **63**, 880–888.

Chamberlain, M.J. & Leopold, B.D. (2001). Survival and cause-specific mortality of adult coyotes (*Canis latrans*) in central Mississippi. *Am. Midl. Nat.* **145**, 414–418.

Chambers, L.K. & Dickman, C.R. (2002). Habitat selection of the long-nosed bandicoot, *Perameles nasuta* (Mammalia, Peramelidae), in a patchy urban environment. *Aust. Ecol.* **27**, 334–342.

Cheeseman, C.L., Cresswell, W.J., Harris, S. & Mallinson, P.J. (1988a). Comparison of disperal and other movements in two badger (*Meles meles*) populations. *Mammal Rev.* **18**, 51–59.

Cheeseman, C.L., Wilesmith, J.W. & Stuart, F.A. (1989). Tuberculosis: the disease and its epidemiology in the badger, a review. *Epidemiol. Infect.* **103**, 113–125.

Cheeseman, C.L., Wilesmith, J.W., Stuart, F.A. & Mallinson, P.J. (1988b). Dynamics of tuberculosis in a naturally infected badger population. *Mammal Rev.* **18**, 61–72.

Clark, K.D. (1994). Managing raccoons, skunks, and opossums in urban settings. *Sixt. Vert. Pest Conf.* **317**: 319. Vertebrate Pest Conference Proceedings collection, University of Nebraska – Lincoln.

Clark, W.R., Hasbrouck, J.J., Kienzler, J.M. & Glueck, T.F. (1989). Vital statistics and harvest of an Iowa raccoon population. *J. Wildl. Mgmt.* **53**, 982–990.

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F. & Deplazes, P. (2004). The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mamm. Biol.* **69**, 81–95.

Corbett, L.K. (1995). *The dingo in Australia and Asia*. Sydney: University of NSW Press.

Cosmosmith (2011). European wolves. wolves of the world. http://www.cosmosmith.com/european_wolves.html. Accessed: November 2011.

Crabb, W.D. (1941). Food habits of the prairie spotted skunk in southeastern Iowa. *J. Mammal.* **22**, 349–364.

Creel, S.R. & Macdonald, D.W. (1995). Sociality, group size and reproductive suppression among carnivores. *Adv. Study Behav.* **24**, 203–257.

Cresswell, W.J. & Harris, S. (1988a). The effects of weather conditions on the movements and activity of badgers (*Meles meles*) in a suburban environment. *J. Zool. (Lond.)* **216**, 187–194.

Cresswell, W.J. & Harris, S. (1988b). Foraging behaviour and home-range utilization in a suburban Badger (*Meles tneles*) population. *Mammal Rev.* **18**, 37–49.

Crooks, K.R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv. Biol.* **16**, 488–502.

Crooks, K.R. & Soulé, M.E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**, 563–566.

Curtis, P.D., Bogan, D.A. & Batcheller, G. (2007). Suburban coyote management and research needs: a northeast perspective. In: Wildlife Damage Management, Internet Center for Wildlife Damage Management Conferences – Proceedings. University of Nebraska – Lincoln.

Curtis, P.D. & Hadidian, J. (2010). Responding to human-carnivore conflicts in urban areas. In *Urban carnivores*:

201–211. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Cypher, B.L. (2010). Kit foxes (*Vulpes macrotis*). In *Urban carnivores*: 49–60. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008). Urban badger setts: characteristics, patterns of use and management implications. *J. Zool. (Lond.)* **275**, 190–200.

Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2009). Restricted ranging behaviour in a high-density population of urban badgers. *J. Zool. (Lond.)* **277**, 45–53.

Delahay, R.J., Davison, J., Poole, D.W., Matthews, A.J., Wilson, C.J., Heydon, M.J. & Roper, T.J. (2009). Managing conflict between humans and wildlife: trends in licensed operations to resolve problems with badgers *Meles meles* in England. *Mammal Rev.* **39**, 53–66.

Delibes, M. (1983). Interspecific competition and the habitat of the stone marten *Martes foina* (Erxleben 1777) in Europe. *Acta Zool. Fenn.* **174**, 229–231.

Dip, R., Hegglin, D., Deplazes, P., Dafflon, O., Koch, H. & Naegeli, H. (2003). Age- and sex-dependent distribution of persistent organochlorine pollutants in urban foxes. *Environ. Health Perspect.* **111**, 1608–1612.

Dip, R., Stieger, C., Deplazes, P., Hegglin, D., Müller, U., Dafflon, O., Koch, H. & Naegeli, H. (2001). Comparison of heavy metal concentrations in tissues of red foxes from adjacent urban, suburban, and rural areas. *Arch. Environ. Contam. Toxicol.* **40**, 551–556.

Doncaster, C.P., Dickman, C.R. & Macdonald, D.W. (1990). Feeding ecology of red foxes (*Vulpes vulpes*) in the city of Oxford, England. *J. Mammal.* **71**, 188–194.

Doncaster, C.P. & Macdonald, D.W. (1991). Drifting territoriality in the red fox *Vulpes vulpes*. *J. Anim. Ecol.* **60**, 423–439.

Dowle, M. & Deane, E.M. (2009). Attitudes to native bandicoots in an urban environment. *Eur. J. Wildl. Res.* **55**, 45–52.

Driscoll, C.A., Menotti-Raymond, M., Roca, A.L., Hupe, K., Johnson, W.E., Geffen, E., Harley, E.H., Delibes, M., Pontier, D., Kitchener, A.C., Yamaguchi, N., O'Brien, S.J. & Macdonald, D.W. (2007). The Near Eastern origin of cat domestication. *Science* **317**, 519–523.

Engeman, R.M., Christensen, K.L., Pipas, M.J. & Bergman, D.L. (2003). Population monitoring in support of a rabies vaccination program for skunks in Arizona. *J. Wildl. Dis.* **39**, 746–750.

Eskreys-Wójcik, M. & Wierzbowska, I. (2007). The food habits of stone marten (*Martes foina*) inhabiting the city of Krakow. In *Abstract booklet of the 25th mustelid colloquium. Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic; Ministry of the Environment of the Czech Republic; Agency for Nature Conservation and Landscape Protection of the Czech Republic; Czech Otter*

Foundation Fund, Trebon, Czech Republic: 49. Hajkova, P. & Ruzickova, O. (Eds). 49.

Farrar, R.O. (2007). Assessing the impact of urban coyote on people and pets in Austin, Travis County, Texas. In *Proceedings of the 12th wildlife damage management conference*: 334–341. Nolte, D.L., Arjo, W.M. & Stalman, D.H. (Eds). University of Nebraska: Lincoln.

Fedriani, J.M., Fuller, T.K. & Sauvajot, R.M. (2001). Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* **24**, 325–331.

Fener, H.M., Ginsberg, J.R., Sanderson, E.W. & Gompper, M.E. (2005). Chronology of range expansion of the coyote, *Canis latrans*, in New York. *Can. Field-Nat.* **119**, 1–5.

Feore, S. & Montgomery, W.I. (1999). Habitat effects on the spatial ecology of the European badger (*Meles meles*). *J. Zool. (Lond.)* **247**, 537–549.

FitzGibbon, S.I., Putland, D.A. & Goldizen, A.W. (2007). The importance of functional connectivity in the conservation of a ground-dwelling mammal in an urban Australian landscape. *Landsc. Ecol.* **22**, 1513–1525.

Frantz, A.C., Cyriacks, P. & Schley, L. (2005). Spatial behaviour of a female raccoon (*Procyon lotor*) at the edge of the species' European distribution range. *Eur. J. Wildl. Res.* **51**, 126–130.

Gaubert, P., Jiguet, F., Bayle, P. & Angelici, F.M. (2008). Has the common genet (*Genetta genetta*) spread into southeastern France and Italy? *Ital. J. Zool.* **75**, 43–57.

Gehring, T.M. & Swihart, R.K. (2003). Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. *Biol. Conserv.* **109**, 283–295.

Gehrt, S. (2011). Urban Coyote Ecology and Management, The Cook County, Illinois, Coyote Project. http://urbancoyoteresearch.com/. Accessed: October 2011.

Gehrt, S.D. (2004). Ecology and management of striped skunks, raccoons, and coyotes in urban landcscapes. In *People and predators: from conflict to conservation*: 81–104. Fascione, N., Delach, A. & Smith, M. (Eds). Washington: Island Press.

Gehrt, S.D. (2005). Seasonal survival and cause-specific mortality of urban and rural striped skunks in the absence of rabies. *J. Mammal.* **86**, 1164–1170.

Gehrt, S.D. (2007). *Ecology of coyotes in urban landscapes*. In: 12th Wildlife Damage Management Conference. D. L. Nolte, W. M. Arjo & D. H. Stalman (Eds.). Wildlife Damage Management, Internet Center for USDA National Wildlife Research Center.

Gehrt, S.D. (2010). The urban ecosystem. In *Urban carnivores*: 3–11. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Gehrt, S.D., Anchor, C. & White, L.A. (2009). Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *J. Mammal.* **90**, 1045–1057.

Gehrt, S.D. & Fritzell, E.K. (1999). Survivorship of a nonharvested raccoon population in South Texas. *J. Wildl. Mgmt.* **63**, 889–894.

Gehrt, S.D. & Prange, S. (2007). Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. *Behav. Ecol.* **18**, 204–214.

Gehrt, S.D. & Riley, S.P.D. (2010). Coyotes (*Canis latrans*). In *Urban carnivores*: 79–95. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (2010). *Urban carnivores*. Baltimore, MD: The John Hopkins University Press.

Geist, V. (2007). Statement by Valerius Geist pertaining to the death of Kenton Carnegie, http://wolfcrossing.org/blog/wp-content/uploads/2007/11/dr-valarius-geist-re-carnegie-ii.pdf Accessed: September 2007

George, S.L. & Crooks, K.R. (2006). Recreation and large mammal activity in an urban nature reserve. *Biol. Conserv.* **133**, 107–117.

Gese, E.M. & Bekoff, M. (2004). Coyote *Canis latrans* say, 1823. In *Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan*: 81–87. Sillero-Zubiri, C., Hoffmann, M., Macdonald, D.W. & IUCN/SSC Canid Specialist Group (Eds). Cambridge: IUCN Publications Services Unit, SSC Species Action Plans.

Gilchrist, J.S. & Otali, E. (2002). The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. *Can. J. Zool.* **80**, 1795–1802.

Glueck, T.F., Clark, W.R. & Andrews, R.D. (1988). Raccoon movement and habitat use during the fur harvest season. *Wildl. Soc. Bull.* **16**, 6–11.

Gosselink, T.E., Van Deelen, T.R., Warner, R.E. & Mankin, P.C. (2007). Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. *J. Wildl. Mgmt.* **71**, 1862–1873.

Grilo, C., Bissonette, J.A. & Santos-Reis, M. (2008). Response of carnivores to existing highway culverts and underpasses: implications for road planning and mitigation. *Biodivers. Conserv.* **17**, 1685–1699.

Grinder, M. & Krausman, P.R. (2001a). Morbidity-mortality factors and survival of an urban coyote population in Arizona. *J. Wildl. Dis.* **37**, 312–317.

Grinder, M.I. & Krausman, P.R. (2001b). Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *J. Wildl. Mgmt.* **65**, 887–898.

Guerra, M.A., Curns, A.T., Rupprecht, C.E., Hanlon, C.A., Krebs, J.W. & Childs, J.E. (2003). Skunk and raccoon rabies in the eastern United States: temporal and spatial analysis. *Emerg. Infect. Dis.* **9**, 1143–1150.

Gunther, K.A. (1994). Bear management in Yellowstone National Park, 1960–93. *International Conference on Bear Research and Management*. **9**, 549–560.

Hadidian, J., Prange, S., Rosatte, R., Riley, S.P.D. & Gehrt, S.D. (2010). Racoons (*Procyon lotor*). In *Urban carnivores*:

35–47. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Hamilton, W.J. (1936). Seasonal food of skunks in New York. *J. Mammal.* **17**, 240–246.

Harris, I.M., Mills, H.R. & Bencini, R. (2010a). Multiple individual southern brown bandicoots (*Isoodon obesulus fusciventer*) and foxes (*Vulpes vulpes*) use underpasses installed at a new highway in Perth, Western Australia. *Wildl. Res.* **37**, 127–133.

Harris, S. (1977). Distribution, habitat utilization and age structure of a suburban fox (*Vulpes vulpes*) population. *Mammal Rev.* **7**, 25–39.

Harris, S. (1981a). An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol, and some possible factors affecting their distribution. *J. Appl. Ecol.* **18**, 455–465.

Harris, S. (1981b). The food of suburban foxes (*Vulpes vulpes*), with special reference to London. *Mammal Rev.* **11**, 151–168.

Harris, S. (1982). Activity patterns and habitat utilization of badgers (*Meles meles*) in suburban Bristol: a radio tracking study. *Symp. Zool. Soc. Lond.* **49**, 301–323.

Harris, S. (1984). Ecology of Urban badgers *Meles meles*: distribution in Britain and habitat selection, persecution, food and damage in the city of Bristol. *Biol. Conserv.* **28**, 349–375.

Harris, S., Baker, P.J. & Soulsbury, C.D. (2010b). Eurasian badgers (*Meles meles*). In *Urban carnivores*: 109–119. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: John Hopkins University Press.

Harris, S., Cresswell, W., Reason, P. & Cresswell, P. (1992). An integrated approach to monitoring badger (*Meles meles*) population changes in Britain. In *Wildlife 2001: populations*: 945–953. McCullough, D.R. & Barrett, R.H. (Eds). London: Elsevier Applied Science.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995). *A review of British mammals: population estimates and conservation status of British mammals other than cetaceans*. Peterborough: Joint Nature Conservation Committee.

Harris, S. & Rayner, J.M.V. (1986a). Models for predicting urban fox (*Vulpes vulpes*) numbers in British cities and their application for rabies control. *J. Anim. Ecol.* **55**, 593–603.

Harris, S. & Rayner, J.M.V. (1986b). Urban fox (*Vulpes vulpes*) population estimates and habitat requirements in several British cities. *J. Anim. Ecol.* **55**, 575–591.

Harris, S. & Smith, G.C. (1987). Demography of two urban fox (*Vulpes vulpes*) populations. *J. Appl. Ecol.* **24**, 75–86.

Harris, S. & Trewhella, W.J. (1988). An analysis of some of the factors affecting dispersal in an urban fox (*Vulpes vulpes*) population. *J. Appl. Ecol.* **25**, 409–422.

Harrison, R.L. (1997). A comparison of gray fox ecology between residential and undeveloped rural landscapes. *J. Wildl. Mgmt.* **61**, 112–122.

Hasbrouck, J.J., Clark, W.R. & Andrews, R.D. (1992). Factors associated with raccoon mortality in Iowa. *J. Wildl. Mgmt.* **56**, 693–699.

Hendrichs, H. (1975). The status of the tiger *Panthera tigris* (Linnaeus 1758) in the Sundarbans Mangrove Forest. *Saugetierk. Mitt.* **23**, 161–199.

Herr, J. (2008). *Ecology and behaviour of urban stone martens (Martes foina) in Luxembourg*, Doctor of Philosophy. School of Life Sciences: University of Sussex.

Herr, J., Schley, L., Engel, E. & Roper, T.J. (2010). Den preferences and denning behaviour in urban stone martens (*Martes foina*). *Mamm. Biol.* **75**, 138–145.

Herr, J., Schley, L. & Roper, T.J. (2009a). Socio-spatial organization of urban stone martens. *J. Zool. (Lond.)* **277**, 54–62.

Herr, J., Schley, L. & Roper, T.J. (2009b). Stone martens (*Martes foina*) and cars: investigation of a common human–wildlife conflict. *Eur. J. Wildl. Res.* **55**, 471–477.

Heydon, M.J., Reynolds, J.C. & Short, M.J. (2000). Variation in abundance of foxes (*Vulpes vulpes*) between three regions of rural Britain, in relation to landscape and other variables. *J. Zool. (Lond.)* **251**, 253–264.

Hoffmann, C.O. & Gottschang, J.L. (1977). Numbers, distribution, and movements of a raccoon population in a suburban residential community. *J. Mammal.* **58**, 623–636.

Holzman, S., Conroy, M.J. & Davidson, W.R. (1992). Diseases, parasites and survival of coyotes in south-central Georgia. *J. Wildl. Dis.* **28**, 572–580.

Huck, M., Davison, J. & Roper, T.J. (2008a). Predicting European badger *Meles meles* sett distribution in urban environments. *Wildl. Biol.* **14**, 188–198.

Huck, M., Frantz, A.C., Dawson, D.A., Burke, T. & Roper, T.J. (2008b). Low genetic variability, female biased dispersal and high movement rates in an urban population of badgers (Meles meles). *J. Anim. Ecol.* **77**, 905–915.

Ikeda, T., Asano, M., Matoba, Y. & Abe, G. (2004). Present status of invasive alien raccoon and its impact in Japan. *Glob. Environ. Res.* **8**, 125–131.

Iossa, G., Soulsbury, C.D., Baker, P.J. & Harris, S. (2010). A taxonomic analysis of urban carnivore ecology. In *Urban carnivores*: 173–180. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Kaczensky, P., Knauer, F., Krze, B., Jonozovic, M., Adamic, M. & Gossow, H. (2003). The impact of high speed, high volume traffic axes on brown bears in Slovenia. *Biol. Conserv.* **111**, 191–204.

Kanda, L.L. (2005). Winter energetics of Virginia opossums *Didelphis virginiana* and implications for the species' northern distributional limit. *Ecography* **28**, 731–744.

Kanda, L.L., Fuller, T.K. & Sievert, P.R. (2006). Landscape associations of road-killed Virginia opossums (*Didelphis virginiana*) in Central Massachusetts. *Am. Midl. Nat.* **156**, 128–134.

Kaneko, Y., Maruyama, N. & Macdonald, D.W. (2006). Food habits and habitat selection of suburban badgers (*Meles meles*) in Japan. *J. Zool. (Lond.)* **270**, 78–89.

Karanth, K.U. & Chellam, R. (2009). Carnivore conservation at the crossroads. *Oryx* **43**, 1–2.

Khan, M.M.H. (2009). Can domestic dogs save humans from tigers *Panthera tigris*? *Oryx* **43**, 44–47.

Kok, O.B. & Nel, J.A.J. (2004). Convergence and divergence in prey of sympatric canids and felids: opportunism or phylogenetic constraint? *Biol. J. Linn. Soc.* **83**, 527–538.

Kolowski, J.M. & Holekamp, K.E. (2006). Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biol. Conserv.* **128**, 529–541.

Kowalczyk, R., Bunevich, A.N. & Jedrzejewska, B. (2000). Badger density and distribution of setts in Białowieza Primeval Forest (Poland and Belarus) compared to other Eurasian populations. *Acta Theriol.* **45**, 395–408.

Kowalczyk, R., Zalewski, A., Jedrzejewska, B. & Jedrzejewska, W. (2003). Spatial organization and demography of badgers (*Meles meles*) in Bialowieza Primeval Forest, Poland, and the influence of earthworms on badger densities in Europe. *Can. J. Zool.* **81**, 74–87.

Kruuk, H. (1978). Spatial organization and territorial behaviour of the European badger *Meles meles*. *J. Zool. (Lond.)* **184**, 1–19.

Kruuk, H. (1989). *The social badger*. Oxford: Oxford University Press.

Kruuk, H. (2002). *Hunter and hunted: relationships between carnivores and people*. Cambridge: Cambridge University Press.

Lanszki, J. (2003). Feeding habits of stone martens in a Hungarian village and its surroundings. *Folia Zool.* **52**, 367–377.

Larivière, S. & Calzada, J. (2001). *Genetta genetta*. Mammalian species account No. 680. http://www.science.smith.edu/departments/Biology/VHAYSSEN/msi/msiaccounts.html. Accessed: October 2011.

Lau, M.W., Fellowes, J.R. & Chan, B.P.L. (2010). Carnivores (Mammalia: Carnivora) in South China: a status review with notes on the commercial trade. *Mammal Rev.* **40**, 247–292.

Lewis, J.C., Sallee, K.L. & Golightly, R.T.J. (1993). *Introduced red fox in California*. In: Nongame Bird and Mammal Section Report: 74. The Resources Agency, State of California. Department of Fish and Game, Wildlife Management Division.

Löe, J. & Röskaft, E. (2004). Large carnivores and human safety: a review. *Ambio* **33**, 283–288.

Lyoyd, H.D. (1980). *The red fox*. London: Batsford.

MacCracken, J.G. (1982). Coyote foods in a southern California suburb. *Wildl. Soc. Bull.* **10**, 280–281.

Macdonald, D.W. (1980). *Rabies & wildlife: a biologist's perspective*. Oxford: Oxford University Press.

Macdonald, D.W. (1987). *Running with the fox*. London: Unwin Hyman.

Macdonald, D.W., Courtenay, O., Forbes, S. & Mathews, F. (1999). The red fox (*Vulpes vulpes*) in Saudi Arabia: loose-knit groupings in the absence of territoriality. *J. Zool. (Lond.)* **249**, 383–391.

Macdonald, D.W. & Newdick, M.T. (1982). The distribution and ecology of foxes, *Vulpes vulpes* (L.), in urban areas. In *Urban ecology: proceedings of the second European ecological symposium, Berlin, September 8–12, 1980*: 123–135. Bornkamm, R., Lee, J.A. & Seaward, M.R.D. (Eds). Oxford: Blackwell Scientifc Publications.

Maestrelli, J.R. (1990). Urban animal damage control in California. In *Proceedings of the 14th Vertebrate Pest Conference*: 156–159. Davis, L.R. & Marsh, R.E. (Eds). University of Nebraska: Lincoln.

Markovchick-Nicholls, L., Regan, H.M., Deutschman, D.H., Widyanata, A., Martin, B., Noreke, L. & Ann Hunt, T. (2008). Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conserv. Biol.* **22**, 99–109.

Marks, C.A. & Bloomfield, T.E. (1999a). Bait uptake by foxes (*Vulpes vulpes*) in urban Melbourne: the potential of oral vaccination for rabies control. *Wildl. Res.* **26**, 777–787.

Marks, C.A. & Bloomfield, T.E. (1999b). Distribution and density estimates for urban foxes (*Vulpes vulpes*) in Melbourne: implications for rabies control. *Wildl. Res.* **26**, 763–775.

Marks, C.A. & Bloomfield, T.E. (2006). Home-range size and selection of natal den and diurnal shelter sites by urban red foxes (Vulpes vulpes) in Melbourne. *Wildl. Res.* **33**, 339–347.

McKinney, M.L. (2002). Urbanization, biodiversity and conservation. *BioScience* **52**, 883–890.

McKinney, M.L. (2006). Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247–260.

Mech, L.D., Barnes, D.M. & Tester, J.R. (1968). Seasonal weight changes, mortality, and population structure of raccoons in Minnesota. *J. Mammal.* **49**, 63–73.

Meiri, S., Simberloff, D. & Dayan, T. (2005). Insular carnivore biogeography: island area and mammalian optimal body size. *Am. Nat.* **165**, 505–514.

Morey, P.S., Gese, E.M. & Gehrt, S. (2007). Spatial and temporal variation in the diet of coyotes in the Chicago metropolitan area. *Am. Midl. Nat.* **158**, 147–161.

Musiani, M., Mamo, C., Boitani, L., Callaghan, C., Gates, C.C., Mattei, L., Visalberghi, E., Breck, S. & Volpi, G. (2003). Wolf depredation trends and the use of fladry barriers to protect livestock in western north America. *Conserv. Biol.* **17**, 1538–1547.

Nicht, M. (1969). Ein Beitrag zum Vorkommen des Steinmarders, *Martes foina* (Erxleben 1770), in der Grostadt (Magdeburg). *Z. Jagdwiss.* **15**, 1–6. cited in Herr 2008.

Pasitschniak-Arts, M. (1993). *Ursus arctos*. Mammalian species account No. 439. http://www.science.smith.edu/departments/Biology/VHAYSSEN/msi/msiaccounts.html. Accessed: October 2011.

Patterson, B.D., Kasiki, S.M., Selempo, E. & Kays, R.W. (2004). Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Park S. Kenya. *Biol. Conserv.* **119**, 507–516.

Pearre, S. & Maass, R. (1998). Trends in the prey size-based trophic niches of feral and house cats *Felis catus* L. *Mammal Rev.* **28**, 125–139.

Peters, R.H. (1983). *The ecological implications of body size*. Cambridge: Cambridge University Press.

Prange, S. & Gehrt, S.D. (2004). Changes in mesopredator-community structure in response to urbanization. *Can. J. Zool.* **82**, 1804–1817.

Prange, S., Gehrt, S.D. & Wiggers, E.P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *J. Wildl. Mgmt.* **67**, 324–333.

Prange, S., Gehrt, S.D. & Wiggers, E.P. (2004). Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *J. Mammal.* **85**, 483–490.

Promberger, C., Ionescu, O., Mertens, A., Minca, M., Predoiu, G., Promberger-Fürpa, B., Sandor, A., Scurtu, M. & Sürth, P. (1998). *Carpathian large carnivore project*. In: Annual Report 1997/98.

Quammen, D. (2003). *Monster of god: the man-eating predator in the jungles of history and the mind*. London: Pimlico, Random House.

Quinn, T. (1997a). Coyote (*Canis latrans*) food habits in three urban habitat types of western Washington. *Northwest Sci.* **71**, 1–7.

Quinn, T. (1997b). Coyote (*Canis latrans*) habitat selection in urban areas of western Washington via analysis of routine movements. *Northwest Sci.* **71**, 289–297.

Radeloff, V.C., Hammer, R.B., Stewart, S.I., Fried, J.S., Holcomb, S.S. & Mckeefry, J.F. (2005). The wildland-urban interface in the United States. *Ecol. Appl.* **15**, 799–805.

Rauer, J., Kaczensky, P. & Knauer, F. (2003). Experiences with aversive conditioning of habituated brown bears in Austria and other European countries. *Ursus* **14**, 215–224.

Reynolds, J.C. & Tapper, S.C. (1995). The ecology of the red fox *Vulpes vulpes* in relation to small game in southern England. *Wildl. Biol.* **1**, 105–109.

Riley, S.P.D. (2006). Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. *J. Wildl. Mgmt.* **70**, 1425–1435.

Riley, S.P.D., Boydston, E.E., Crooks, K.R. & Lyren, L.M. (2010). Bobcats (*Lynx rufus*). In *Urban carnivores*: 121–138. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Riley, S.P.D., Hadidian, J. & Manski, D.A. (1998). Population density, survival, and rabies in raccoons in an urban national park. *Can. J. Zool.* **76**, 1153–1164.

Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C. & Wayne, R.K. (2003). Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conserv. Biol.* **17**, 566–576.

Roper, T.J. (1994). The European badger *Meles meles*: food specialist or generalist? *J. Zool. (Lond.)* **234**, 457–482.

Roper, T.J. (2010). *Badger*. London: Harper Collins Publishers.

Rosatte, R., Sobey, K., Dragoo, J.W. & Gehrt, S.D. (2010). Striped skunks and allies (*Mephitis* spp.). In *Urban carnivores*: 99–106. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Rosatte, R.C., Power, M.J. & Macinnes, C.D. (1991). Ecology of urban skunks, raccoons, and foxes in metropolitan Toronto. In *Wildlife conservation in metropolitan environments.* National institute for urban wildlife symposium series 2: 31–38. Adams, L.W. & Leedy, D.L. (Eds). Columbia, MD: National Institute for Urban Wildlife.

Roussere, G.P., Murray, W.J., Raudenbush, C.B., Kutilek, M.J., Levee, D.J. & Kazacos, K.R. (2007). Raccoon roundworm eggs near homes and risk for larva migrans disease, California communities. *Emerg. Infect. Dis.* **9**, 1516–1522.

Saunders, G., White, P.C.L., Harris, S. & Rayner, J.M.V. (1993). Urban foxes (*Vulpes vulpes*): food acquisition, time and energy budgeting of a generalized predator. *Symp. Zool. Soc. Lond.* **65**, 215–234. Cited by Baker *et al*. 2000.

Savolainen, P., Jing Luo, Y.-P.Z., Lundeberg, J. & Leitner, T. (2002). Genetic evidence for an east Asian origin of domestic dogs. *Science* **298**, 1610–1613.

Schmidt, R.H. & Timm, R.M. (2007). Bad dogs: why do coyotes and other canids become unruly? *12th wildlife damage management conference*: 287–302. Nolte, D.L., Arjo, W.M. & Stalman, D.H. (Eds). University of Nebraska: Lincoln.

Schmidt, P.M., Lopez, R.R. & Pierce, B.L. (2007). Estimating free-roaming cat densities in urban areas: comparison of mark-resight and distance sampling. *Wildl. Biol. Pract.* **3**, 18–27.

Schrecengost, J.D., Kilgo, J.C., Ray, H.S. & Miller, K.V. (2009). Home range, habitat use and survival of coyotes in Western South Carolina. *Am. Midl. Nat.* **162**, 346–355.

Seton, E.T. (1929). *Lives of game animals*. Cited in Hoffman & Gottschang 1977. Garden City, NY: Doubleday & Co.

Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* **17**, 170–176.

Shivik, J.A. & Fagerstone, K.A. (2007). A broad perspective on current and future research on urban coyotes. In *Proceedings of the 12th wildlife damage management conference*: 418–420. Nolte, D.L., Arjo, W.M. & Stalman, D.H. (Eds). University of Nebraska: Lincoln.

Smith, H.T. & Engeman, R.M. (2002). An extraordinary raccoon, *Procyon lotor*, density at an urban park. *Can. Field-Nat.* **116**, 636–639.

Soulsbury, C.D., Baker, P.J., Iossa, G. & Harris, S. (2010). Red foxes (*Vulpes vulpes*). In *Urban carnivores*: 63–75. Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (Eds). Baltimore, MD: The John Hopkins University Press.

Soulsbury, C.D., Iossa, G., Baker, P.J., Cole, N.C., Funk, S.M. & Harris, S. (2007). The impact of sarcoptic mange *Sarcoptes scabiei* on the British fox *Vulpes vulpes* population. *Mammal Rev.* **37**, 278–296.

Stieger, C., Hegglin, D., Schwarzenbach, G., Mathis, A. & Deplazes, P. (2002). Spatial and temporal aspects of urban transmission of *Echinococcus multiloculalis*. *Parasitology* **124**, 631–640.

Stuewer, F.W. (1943). Raccoons: their habits and management in Michigan. *Ecol. Monogr.* **13**, 203–258.

Swenson, J.E., Gerstl, N., Dahle, B. & Zedrosser, A. (2000). Action plan for the conservationof the brown bear (*Ursus arctos*) in Europe. In: Convention on the Conservationof European Wildlife and Natural Habitats (Bern Convention) Nature and environment, No. 114. Council of Europe Publishing.

Teagle, W.G. (1967). The fox in the London suburbs. *Lond. Nat.* **46**, 44–68.

Teagle, W.G. (1969). The badger in the London area. *Lond. Nat.* **48**, 48–75.

Tigas, L.A., Vuren, D.H.V. & Sauvajot, R.M. (2002). Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biol. Conserv.* **108**, 299–306.

Tischendorf, L., Thulke, H.-H., Staubach, C., Muller, M.S., Jeltsch, F., Goretzki, J., Selhorst, T., Muller, T., Schluter, H. & Wissel, C. (1998). Chance and risk of controlling rabies in large-scale and long-term immunized fox populations. *Proc. Roy. Soc. Lond. Ser. B* **265**, 839–846.

UNFPA (2007). 2007 State of World Population (UNFPA).

Urbanek, R.E., Nielsen, C.K. & Wilson, S.E. (2009). Survival of unexploited raccoons on a rural refuge in Southern Illinois. *Trans. Ill. State Acad. Sci.* **102**, 3–4.

Van Deelen, T.R. & Gosselink, T.E. (2006). Coyote survival in a row-crop agricultural landscape. *Can. J. Zool.* **84**, 1630–1636.

Vanak, A.B. & Gompper, M.T. (2009). Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition. *Mammal Rev.* **39**, 265–283.

Vanak, A.B., Thaker, M. & Gompper, M.T. (2009). Experimental examination of behavioural interactions between free-ranging wild and domestic canids. *Behav. Ecol. Sociobiol.* **64**, 279–287.

Verts, B.J. (1967). *The biology of the striped skunk*. Urbana, IL: University of Illinois Press.

Vézina, A.F. (1985). Empirical relationships between predator and prey size in terrestrial vertebrates. *Oecologia* **67**, 555–565.

Vilà, C., Savolainen, P., Maldonado, J.E., Amorim, I.R., Rice, J.E., Honeycutt, R.L., Crandall, K.A., Lundeberg, J. & Wayne, R.K. (1997). Multiple and ancient origins of the domestic dog. *Science* **276**, 1687–1689.

Virgós, E. & Casanovas, J.G. (1998). Distribution patterns of the stone marten (*Martes foina* Erxleben, 1777) in Mediterranean mountains of central Spain. *Z. Saugetierkd* **63**, 193–199.

Virgós, E. & García, F.J. (2002). Patch occupancy by stone martens *Martes foina* in fragmented landscapes of central Spain: the role of fragment size, isolation and habitat structure. *Acta Oecologica* **23**, 231–237.

Voigt, D.R. (1987). Red fox. In *Wild furbearer management and conservation in North America*: 379–392. Novak, M., Baker, J., Obbard, M.E. & Malloch, B. (Eds). Ontario: Ontario Ministry of Natural Resources.

Way, J.G., Auger, P.J., Ortega, I.M. & Strauss, E.G. (2001). Eastern coyote denning behavior in an anthropogenic environment. *Northeast Wildl.* **56**, 18–30.

Webbon, C.C., Baker, P.J. & Harris, S. (2004). Faecal density counts for monitoring changes in red fox numbers in rural Britain. *J. Appl. Ecol.* **41**, 768–779.

White, J.G., Gubiani, R., Smallman, N., Snell, K. & Morton, A. (2006). Home range, habitat selection and diet of foxes (*Vulpes vulpes*) in a semi-urban riparian environment. *Wildl. Res.* **33**, 175–180.

White, P.C., Harris, S. & Smith, G.C. (1995). Fox contact behaviour and rabies spread: a model for the estimation of contact probabilities between urban foxes at different population densities and its implications for rabies control in Britain. *J. Appl. Ecol.* **32**, 693–706.

Wilkinson, D. & Smith, G.C. (2001). A preliminary survey for changes in urban Fox (*Vulpes vulpes*) densities in England and Wales, and implication for rabies control. *Mammal Rev.* **31**, 107–110.

Witmer, G.W. & Whittaker, D.G. (2001). *Dealing with nuisance and depredating black bears*. Wildlife Damage Management, Internet Center for USDA National Wildlife Research Center – Staff Publications. University of Nebraska, Lincoln: Western black bear workshop **7**, 73–81.

Witte, R., Diesing, D. & Godde, M. (1985). Urbanophobe, urbanoneutral, urbanophile – behavior of species concerning the urban habitat. *Flora* **177**, 265–282.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Anim. Conserv.* **3**, 165–173.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and extinction of populations inside protected areas. *Science* **280**, 2126–2128.

Woods, M., Macdonald, R. & Harris, S. (2003). Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Rev.* **2**, 174–188.

Wydeven, A.P., Treves, A., Brost, B. & Wiedenhoeft, J.P. (2004). Characteristics of wolf packs in Wisconsin: identification of traits influencing depredation. In *People and predators: from conflict to coexistence*: 28–57. Fascione, N., Delach, A. & Smith, M.E. (Eds). Washington: Island Press.

Yom-Tov, Y. (2003). Body sizes of carnivores commensal with humans have increased over the past 50 years. *Funct. Ecol.* **17**, 323–327.

Yom-Tov, Y., Ashkenazi, S. & Viner, O. (1995). Cattle predation by the golden jackal *Canis aureus* on cattle in the Golan Heights, Israel. *Biol. Conserv.* **73**, 19–22.

Yom-Tov, Y., Yom-Tov, S. & Baagøe, H. (2003). Increase of skull size in the red fox (*Vulpes vulpes*) and Eurasian badger (*Meles meles*) in Denmark during the twentieth century: an effect of improved diet? *Evol. Ecol. Res.* **5**, 1037–1048.