A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India

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Abstract The ecology and predator–prey dynamics of large felids in the tropics have largely been studied in natural systems where wild ungulates constitute the majority of the prey base. However, human-dominated landscapes can be rich in potential prey for large carnivores because of the high density of domestic animals, especially in tropical countries where pastoralism is an important livelihood activity. We report the almost complete dependence of leopards *Panthera pardus* on domestic animals as prey in the crop lands of Ahmednagar district, Maharashtra, India. From analysis of 85 confirmed leopard scats, 87% of the leopard's prey biomass consisted of domestic animals, with 39% consisting of domestic dogs *Canis lupus familiaris* alone. The only wild species that occurred in the leopard's diet were rodents, small indian civet *Viverricula indica*, bonnet macaque *Macaca radiata* and other primates *Semnopithecus* spp., mongoose *Herpestes* spp., and birds. Interviews conducted in 77 households distributed randomly in the study area documented a high density of domestic animals: adult cattle *Bos taurus*, calves, goats *Capra aegagrus*, dogs and cats *Felis catus* occurred at densities of 169, 54, 174, 24 and 61 per km^2, respectively. Ivlev's electivity index indicated that dogs and cats were over-represented in the leopard's diet, given the higher densities of goats and cattle. The standing biomass of dogs and cats alone was sufficient to sustain the high density of carnivores at the study site. Our results show that the abundance of potential domestic prey biomass present in human-use areas supports a relatively high density of predators, although this interaction could result in conflict with humans.

Keywords Conflict, diet, domestic dog, human-dominated landscape, leopard, *Panthera pardus*

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Introduction

Studies have shown that the density of carnivores is related to the availability of prey biomass (Fuller & Sievert, 2001; Carbone & Gittleman, 2002; Karanth et al., 2004; Khorozyan et al., 2008; Carbone et al., 2010). These analyses are based largely on studies of prey and predator species in natural or semi-natural ecosystems (Fuller & Sievert, 2001; Carbone & Gittleman, 2002; Andheria et al., 2007; Karanth & Nichols, 2010). However, more recent studies have found that large carnivores can also persist in human-dominated areas (Yirga et al., 2012; Athreya et al., 2013) by relying fully or partially on food resources associated with humans (Gehrt et al., 2010). The potential carrying capacity of human-dominated landscapes for large carnivores must therefore be investigated in terms of the abundance and availability of domestic prey species as well as wild prey (Boitani & Powell, 2012).

The biomass of domestic animals in human-use landscapes can be higher than that of wild prey, as seen in Brazil, Nepal and Kenya (Schaller, 1983; Seidensticker et al., 1990; Mizutani, 1999). Anthropogenic food sources such as garbage and pet food can also contribute to the diet of wild carnivores (Gehrt et al., 2010). These food resources can be abundant, leading to densities of wild carnivores comparable to, or even greater than, their densities in the wild. For example, densities of urban red foxes *Vulpes vulpes* were 15 times higher (Bino et al., 2010), and of black bear *Ursus americanus* three times higher (Beckmann & Berger, 2003), in semi-urban areas than in natural habitats because of better foraging opportunities from crops, garbage, livestock and artificial feeding.

In India several carnivore species, such as wolves *Canis lupus* (Jhala & Giles, 1991), Asiatic lions *Panthera leo persica* (Vijayan & Pati, 2002; Meena et al., 2011) and striped hyaenas *Hyaena hyaena* (Shilpi et al., 2009; Singh et al., 2010), also occur in human-dominated landscapes and feed on livestock. Tigers *Panthera tigris* are also known to attack livestock in and around protected areas (Sekhar, 1998; Karanth & Gopal, 2005; Woodroffe et al., 2005). Leopards *Panthera pardus* are adaptable, using a variety of habitats and feeding on a range of wild and domestic prey (Seidensticker et al., 1990; Daniel, 2009; Hunter, 2011), which enables them to live close to human settlements (Nasik Gazetteer, 1883; Daniel, 2009). A high density of

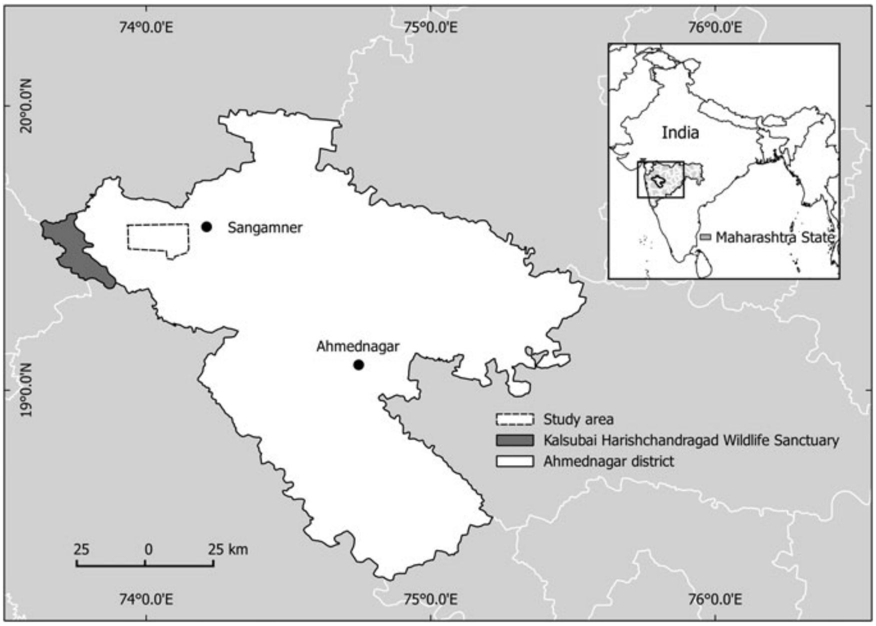

FIG. 1 The Ahmednagar district of western Maharashtra, India, where leopard *Panthera pardus* scats were collected during December 2007–April 2009 in a human-dominated agricultural landscape. The rectangle on the inset indicates the location of the main figure in India.

domestic animals (Thornton et al., 2002; FAO, 2005) could therefore constitute a stable and abundant prey base, facilitating the persistence of leopard populations in human-dominated landscapes far from protected conservation areas (Athreya et al., 2013).

Although widespread occurrence of leopards across India has been documented (Vijayan & Pati, 2002; Daniel, 2009; Athreya et al., 2013), few studies have assessed the leopard's diet and availability of prey in human-dominated landscapes (Punjabi et al., 2012). To improve our understanding of resource usage by leopards in a rural, human-dominated landscape, we analysed the diet of leopards, and estimated prey densities and biomass, in an agricultural landscape in western Maharashtra.

Study area

The study was conducted in an irrigated valley (238 km²), dominated by crop lands, around the town of Akole (human population c. 20,000) in the Ahmednagar district of western Maharashtra, India (Fig. 1). The mean population density reported for Ahmednagar district in 2011 was 266 people per km² (Census of India, 2011). Approximately 80% of the human population in the district is rural, with farming of millet, sugar cane and vegetables being the major sources of livelihood. Annual rainfall is 1,000–2,000 mm. The nearest protected area is the Kalsubai Harishchandragarh Wildlife Sanctuary (299 km²), 18 km from the western edge of the study area. There are no patches of natural forest within the study area.

Camera-trapping surveys have recorded leopard, striped hyaena, golden jackal *Canis aureus*, Bengal fox *Vulpes bengalensis*, jungle cat *Felis chaus* and rusty-spotted cat *Prionailurus rubiginosus* (Athreya et al., 2013) in the area. No wild ungulate species were recorded in this study, nor have any been reported by the Forest Department. There are various occupational groups in the area, the dominant one being settled farmers who own land and livestock. Pastoral, migratory shepherds arrive annually in the dry season, with herds of sheep and goats (each herder has >100 animals), to pasture on crop-residues in the fields.

Methods

Government records indicate an overall livestock density of 176 head of livestock per km² across the district (Livestock Census, 2003). This includes domestic and feral/semi-feral dogs *Canis familiaris*, pigs *Sus scrofa* and cats, which may also constitute part of the leopard's diet. To get a more detailed overview of the prey available in the study area we interviewed a random sample of 77 households of resident farmers to assess the number and species of domestic animals owned. The density of houses was obtained by digitally mapping all residential houses, using 2007 imagery from *Google Earth v. 6.1.0.5001* (Google, Mountain View, USA), and then ground-truthing a sample of 200 homesteads to obtain the percentage of houses (as distinct from shops, schools and other buildings). The interview data and estimated density of houses were used to estimate densities of domestic animals in the study area. Although the urban area of Akole has a large number of pigs, they are restricted to the town area and are not present in the wider crop-land landscape. The Wadhari people, who claim ownership of the feral pigs, state that there are at least several hundred pigs in the town of Akole.

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Initial scat surveys in the region indicated that leopards used trails such as foot paths, edges of fields, paved roads and dry stream beds. These trails were identified using *Google Earth* and surveyed using three methods: (1) 130 km of trails that were marked across the entire study area were walked a total of three times each during December 2007–April 2008, with a 3-week interval between each sampling session, (2) 85 randomly selected 1-km² grid cells were overlaid on a *Google Earth* map and a mean of 2.37 ± SD 0.86 km of road/path within each cell was searched, on foot, for scats, and (3) scats were collected opportunistically during December 2007–April 2009. We used all three methods because we lacked a priori information on where to locate leopard scats in a human-dominated landscape. The scats represent a sample from the dry season.

Two trained surveyors walked on either side of the trail and collected all scats judged to be of carnivore origin, based on size, shape and ancillary evidence such as scrape signs and tracks. The scats were measured and stored in zip-lock bags, and the geographical coordinates of each location were recorded using a geographical positioning system. The scats were later transferred to polythene bags and part of each scat was transferred into vials for storage in absolute alcohol for subsequent DNA analysis to identify leopard scats (Mondol et al., 2009, 2011; Navya et al., unpubl. data). Visual identification of scats is not always reliable (Farrell et al., 2000), and therefore diet analysis was conducted only on scats confirmed to be of leopard origin, either using DNA methods or having been collected from scrapes characteristic of those made by large felids (as the leopard is the only large felid present in the study area).

The scat analysis was carried out as described by Mukherjee et al. (1994), Mukherjee & Mishra (2001) and in other diet studies of large felids (Karanth & Sunquist, 1995; Andheria et al., 2007; Khorozyan et al., 2008; Odden & Wegge, 2009). The scats were washed and dried and the prey species were identified from the presence of claws, hoofs or hair. For hair, we used a microscope to identify the origin of 25 randomly selected hair samples per scat. Prey species were identified based on comparison with reference slides of hair samples from domestic animals in the study area and from reference slides of hair samples from wild prey, from collections at the Centre for Wildlife Studies, Bangalore, and the Bombay Natural History Society, Mumbai. Scats that were highly degraded or had too few identifiable prey remains were not used in the analysis.

We calculated the frequencies of occurrence of the various prey species (the percentage of the total number of scats that contained a specific prey item). However, this variable can be misleading because smaller prey species contribute more to a scat than larger species (Karanth & Sunquist, 1995; Klare et al., 2011). Based on feeding trials on captive mountain lions *Puma concolor*, Ackerman et al. (1984) derived a regression equation to calculate the relative biomass of different prey species consumed, based on their relative proportions in scats. Mountain lions are similar in size to leopards and this method has been used previously for leopards (Karanth & Sunquist, 1995; Andheria et al., 2007; Khorozyan et al., 2008; Odden & Wegge, 2009; Wegge et al., 2009).

The regression equation is in the form:

$$Y = 1.98 + 0.35x$$

where Y is the mass of prey consumed per scat and x is the mean mass of the prey. The relative biomass (D) and the relative numbers of each prey species consumed (E) were obtained using the equations

$$D = (A \times Y)/\Sigma(A \times Y) \times 100$$
$$E = (D/x)/\Sigma(D/x) \times 100$$

where A is the frequency of occurrence of the prey item in the scats. The prey biomass ($B_{\text{prey}} = D_{\text{prey}} \cdot W_{\text{prey}}$; Khorozyan et al., 2008) in the study area was calculated using density estimates (D_{prey}) for the four most common prey species (domestic goats, dogs, calves and cats), based on interview data. The mean weight of the domestic animal species (W_{prey}) was estimated by a livestock veterinarian working in the region. Adult cattle were not included because compensation records indicate that only one cow was attacked in the study area in 3 years, whereas calves were preyed on in relatively higher numbers (Forest Department records).

We used Ivlev's (1961) electivity index to assess prey selection:

$$E = \frac{r_i - p_i}{r_i + p_i}$$

where r_i is the relative proportion of prey item i in the diet and p_i is the relative proportion of prey item i in the environment. E is in the range −1–+1, where negative values indicate that the prey item is avoided or inaccessible and positive values indicate that it is selected for.

Results

Leopard scats, confirmed using DNA analysis, were found throughout the sampled area, including close to houses, and on a variety of trail types, including dirt and paved roads. The mean distance from leopard scats to the nearest house was 213 m (range 10–850 m), and 140 m (range 0–815 m) from roads. Two scats were found on the main street of Akole town.

Of the 265 scats collected 80 were confirmed as leopard scats based on DNA analysis and 43 were identified based on the presence of tracks or scrapes. Of these 123 leopard scats 85 had usable remains for diet analysis. Thirty-eight scats could not be used because the remains were degraded

TABLE 1 Prey species identified in the diet of leopards *Panthera pardus* in the Ahmednagar district of western Maharashtra, India (Fig. 1), from analysis of 85 scats collected from a human-dominated landscape during December 2007–April 2009. *Y* is the correction factor from Ackerman et al. (1984).

Prey species	Frequency of occurrence in scats (%)	Mean mass (kg)	*Y* (kg per scat)	Relative biomass in leopard diet (%)	Relative no. of individuals consumed
Primate spp.	0.8	10.0	2.3	0.7	0.3
Small Indian civet *Viverricula indica*	2.3	2.0	2.1	1.9	3.6
Mongoose *Herpestes* spp.	3.1	2.0	2.1	2.5	4.8
Pig *Sus scrofa*	3.1	20.0	2.7	3.2	0.6
Bird spp.	3.9	1.0	2.0	3.0	11.8
Sheep *Ovis aries*	5.4	30.0	3.0	6.4	0.8
Rodent spp.	6.9	0.5	2.0	5.4	42.3
Goat *Capra aegagrus*	10.0	25.0	2.9	11.2	1.7
Cow *Bos taurus*	10.8	40.0	3.4	14.2	1.4
Cat *Felis catus*	15.4	2.0	2.1	12.3	24.1
Dog *Canis lupus*	38.5	18.0	2.6	39.2	8.5

and, although they contained hair and bone, they could not be identified visually or under the microscope. Of 110 intact leopard scats the mean diameter at the thickest section was 25.15 ± SD 5.2 mm (range 11.5–38.3 mm). The scats contained a total of 131 prey items, comprising 11 prey species (Table 1). Fifty-six percent of the scats contained one prey species, 21% two species, 8% three species, 3% four species and only one scat contained five species. Domestic animals (pig, sheep, cat, dog, goat, cow) constituted 87% of the prey biomass consumed by leopards. The wild prey present in the scats were civet *Viverricula indica*, rodent, primate, bird and mongoose *Herpestes* spp. (Table 1). In the case of rodents a mean mass of 500 g (Table 1) was considered because of the presence of the bandicoot rat *Bandicota* spp. in the crop lands. Dogs were the most significant constituent of the leopard's diet, accounting for 39% of the biomass consumed. Ivlev's index indicates that despite the higher biomass of goats and calves available, dogs and cats were preyed upon to a greater extent than expected, which could be attributable to preference or greater accessibility (Fig. 2; Table 2).

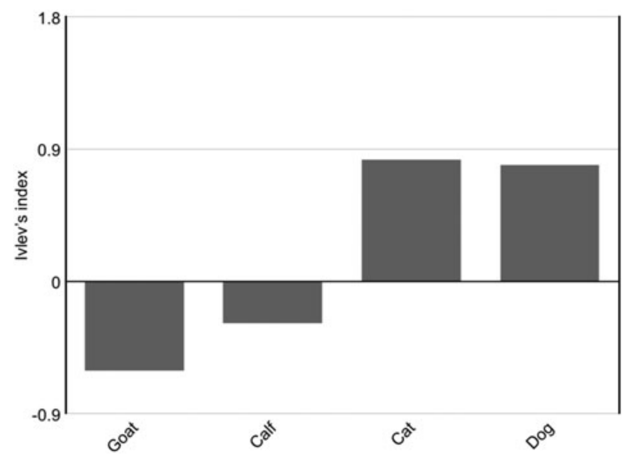

FIG. 2 Ivlev's index (Ivlev, 1961) for goat *Capra aegagrus*, calf *Bos taurus*, cat *Felis catus* and dog *Canis lupus familiaris*, based on scat analysis of leopard prey in Ahmednagar district of western Maharashtra. The index is based on the frequency of prey species in scats relative to the availability of these species in the area. Species with positive index values are more selected for/more available than species with negative values.

Discussion

The relationship between large felids and humans is complex and the spectrum of interactions ranges from fascination to fear (Boomgaard, 2001; Loveridge et al., 2010). Large felids are often portrayed as flagship species for conservation (Treves & Karanth, 2003) but conflict occurs at the local level, where the presence of a large carnivore can result in damage to property and loss of human life (Treves et al., 2006). Retaliatory killings are a significant cause of mortality of large felids, and studies have focused on human–felid conflict (Inskip & Zimmermann, 2009). Although depredation of livestock is a widespread occurrence (Linnell et al., 2012), domestic livestock usually constitute only a small part of the diet of large felids and complete dependency on domestic species has rarely been observed. The biomass of livestock can be high in human-dominated areas, exceeding that of wild prey in surrounding forest areas in Brazil, Nepal and Kenya (Schaller, 1983; Seidensticker et al., 1990; Mizutani, 1999). Domestic animals are easier to attack because they lack anti-predatory behaviour, unlike their wild counterparts (Diamond, 2002). However, availability does not always indicate accessibility as livestock may be guarded by day and enclosed in predator-proof enclosures at night.

TABLE 2 Density (km^{-2}) of domestic animals in the study area, from interviews of a random sample of households (n = 77) in the town of Akole in the Ahmednagar district of western Maharashtra (Fig. 1). The interviews were conducted during September 2007–September 2009.

	Buffalo	Cow (adult)	Calf	Goat	Sheep	Dog	Cat	Chicken
Mean no. per household (range)	0.11 (0–1)	2.7 (0–18)	0.9 (0–8)	2.9 (0–40)	0.06 (0–1)	0.40 (0–5)	1 (0–6)	1.8 (0–50)
Density (km^{-2})	7	162	54	174	4	24	61	109
Biomass (kg per km^2)	2,450	56,700	2,440	4,350	120	432	108	109

Our results show that a large predator such as a leopard can attain relatively high densities in a rural landscape (Athreya et al., 2013) while subsisting almost entirely on a diet of domestic animals. Despite the density of goats being seven times that of domestic dogs, goats constituted only 11% of the prey biomass of leopards, whereas dogs constituted 39%. This is probably because goats are less accessible than dogs, being actively herded by day and enclosed in sheds at night. The results show that dogs are an important food resource for leopards and they occur at high density in the study area. The proclivity of leopards towards killing and eating dogs has been noted in anecdotal, historical literature (Daniel, 2009). Two studies carried out within protected areas in the states of Maharashtra and Jammu & Kashmir have reported the importance of dogs as prey for leopards (Edgaonkar & Chellam, 2002; Shah et al., 2009).

Domestic dogs are ubiquitous in the Indian landscape and density estimates from an adjoining human-use landscape in Maharashtra range from 23 (farmland) to 113 km^{-2} (village area; Punjabi et al., 2012; Hughes & Macdonald, 2013). Domestic cats also appear to be an important component of the leopard's diet in our study area, contributing 12% of the biomass consumed. Based on interviews, the densities of goats and cows in the study area were 174 and 162 km^{-2}, respectively. Thus, rural landscapes in India can be prey-rich areas for wild carnivores because of the importance of animal husbandry in the livelihoods of rural people.

In natural ecosystems predator density is correlated with prey biomass (Carbone & Gittleman, 2002; Karanth et al., 2004; Marker & Dickman, 2005; Beckmann & Lackey, 2008; Khorozyan et al., 2008; Bino et al., 2010). If we consider the density of the four common prey species (goats, calves, cats and dogs) identified in the scat analysis, the potential prey biomass for leopards in the study area is 733,000 kg per 100 km^2 (Table 2). The regression equation of Carbone & Gittleman (2002) estimates that 10,000 kg of prey is required per 90 kg of predator, irrespective of predator size. Based on this equation the total amount of prey biomass (including goats and cattle) in our study area could, in theory, support >10 times the number of leopards that are present. The biomass of the owned dogs and cats alone constitutes c. 54,000 kg per 100 km^2, which would be predicted to support a 45 kg predator at a density of 10.8 individuals per 100 km^2, which is close to the combined density of leopards and striped hyaenas in the study area, based on estimates from a camera-trap study (Athreya et al., 2013). The reason for the relatively low density of leopards despite the high biomass of prey is probably related to the low availability of domestic stock because they are protected by farmers (Athreya et al., unpubl. data) and the fact that large stock are not predated by leopards. Most cattle in the study area are hybrid varieties that are larger than the indigenous breeds.

The selection of domestic dogs and cats as prey means that the economic impact of predation by the leopard on valuable livestock is lower than expected. Thus human–leopard conflict is largely driven by people's fear of leopards foraging in the proximity of their houses, and the sentimental value of dogs as pets.

Our findings are similar to those of studies on rural and urban carnivores in western Europe and North America, where wild carnivores reside in modified human-dominated landscapes and are totally dependent on anthropogenic sources of food (Gehrt et al., 2010). Our work contributes to a growing awareness of the potential conservation value of private lands and non-protected areas in the tropics (Negrões et al., 2011).

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References

ACKERMAN, B.B., LINDZEY, F.G. & HEMKER, T.P. (1984) Cougar food habits in southern Utah. *The Journal of Wildlife Management*, 48, 147–155.

ANDHERIA, A.P., KARANTH, K.U. & KUMAR, N.S. (2007) Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology*, 273, 169–175.

ATHREYA, V., ODDEN, M., LINNELL, J.D.C., KRISHNASWAMY, J. & KARANTH, K.U. (2013) Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS ONE*, 8(3), e57872.

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

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

Bino, G., Dolev, A., Yosha, D., Guter, A., King, R., Saltz, D. & Kark, S. (2010) Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology*, 47, 1262–1271.

Boitani, L. & Powell, R.A. (eds) (2012) *Carnivore Ecology and Conservation: A Handbook of Techniques*. Oxford University Press, New York, USA.

Boomgaard, P. (2001) *Frontiers of Fear: Tigers and People in the Malay World, 1600–1950*. Yale University Press, New Haven, USA.

Carbone, C. & Gittleman, J.L. (2002) A common rule for the scaling of carnivore density. *Science*, 295, 2273–2276.

Carbone, C., Pettorelli, N. & Stephens, P.A. (2010) The bigger they come, the harder they fall: body size and prey abundance influence predator–prey ratios. *Biology Letters*, 7, 312–315.

Census of India (2011) Http://censusindia.gov.in/ [accessed 24 May 2014].

Daniel, J.C. (2009) *The Leopard in India: A Natural History*. Natraj Publishers, Dehradun, India.

Diamond, J. (2002) Evolution, consequences and future of plant and animal domestication. *Nature*, 418, 700–707.

Dickman, A.J. (2010) Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation*, 13, 458–466.

Edgaonkar, A. & Chellam, R. (2002) Food habit of the leopard, *Panthera pardus*, in the Sanjay Gandhi National Park, Maharashtra, India. *Mammalia*, 66, 353–360.

FAO (Food and Agriculture Organization of the United Nations) (2005) *Livestock Sector Brief: India*. http://www.fao.org/ag/againfo/resources/en/publications/sector_briefs/lsb_IND.pdf [accessed 15 January 2013].

Farrell, L.E., Roman, J. & Sunquist, M.E. (2000) Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology*, 9, 1583–1590.

Fuller, T.K. & Sievert, P.R. (2001) Carnivore demography and the consequences of changes in prey availability. In *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 163–178. Cambridge University Press, Cambridge, UK.

Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (eds) (2010) *Urban Carnivores: Ecology, Conflict and Conservation*. The Johns Hopkins University Press, Baltimore, USA.

Hughes, J. & Macdonald, D.W. (2013) A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation*, 157, 341–351.

Hunter, L. (2011) *Carnivores of the World* (Princeton Field Guides). Princeton University Press, Princeton, USA.

Inskip, C. & Zimmermann, A. (2009) Human–felid conflict: a review of patterns and priorities worldwide. *Oryx*, 43, 18–34.

Ivlev, V.S. (1961) *Experimental Ecology of the Feeding of Fishes*. Yale University Press, New Haven, USA.

Jhala, Y.V. & Giles, R.H. (1991) The status and conservation of the wolf in Gujarat and Rajasthan, India. *Conservation Biology*, 5, 476–483.

Karanth, K.U. & Gopal, R. (2005) An ecology-based policy framework for human–tiger coexistence in India. In *People and Wildlife: Conflict Or Co-existence?* (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 373–387. Cambridge University Press, Cambridge, UK.

Karanth, K.U. & Nichols, J.D. (2010) Non-invasive survey methods for assessing tiger populations. In *Tigers of the World: The Science, Politics and Conservation of* Panthera tigris (eds R.L. Tilson & P.J. Nyhus), pp. 241–262. Elsevier, New York, USA.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. (2004) Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 4854–4858.

Karanth, K.U. & Sunquist, M.E. (1995) Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology*, 64, 439–450.

Khorozyan, I.G., Malkhasyan, A.G. & Abramov, A.V. (2008) Presence–absence surveys of prey and their use in predicting leopard (*Panthera pardus*) densities: a case study from Armenia. *Integrative Zoology*, 3, 322–332.

Klare, U., Kamler, J.F. & Macdonald, D.W. (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review*, 41, 294–312.

Linnell, J., Odden, J. & Mertens, A. (2012) Mitigation methods for conflicts associated with carnivore depredation on livestock. In *Carnivore Ecology and Conservation: A Handbook of Techniques* (eds L. Boitani & R.A. Powell), pp. 314–332. Oxford University Press, Oxford, UK.

Livestock Census (2003) Directorate of Economics and Statistics, Planning Department, Government of Maharashtra, Mumbai, India.

Loveridge, A.J., Wang, S.W., Frank, L.G. & Seidensticker, J. (2010) People and wild felids: conservation of cats and management of conflicts. In *The Biology and Conservation of Wild Felids* (eds D.W. Macdonald & A.J. Loveridge), pp. 161–198. Oxford University Press, Oxford, UK.

Marker, L.L. & Dickman, A.J. (2005) Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *South African Journal of Wildlife Research*, 35, 105–115.

Meena, V., Jhala, Y.V., Chellam, R. & Pathak, B. (2011) Implications of diet composition of Asiatic lions for their conservation. *Journal of Zoology*, 284, 60–67.

Mizutani, F. (1999) Biomass density of wild and domestic herbivores and carrying capacity on a working ranch in Laikipia District, Kenya. *African Journal of Ecology*, 37, 226–240.

Mondol, S., Ramesh, N., Athreya, V., Sunagar, K., Selvaraj, V.M. & Ramakrishnan, U. (2009) A panel of microsatellites to individually identify leopards, and its application to leopard monitoring in human-dominated landscapes. *BMC Genetics*, 10, 79–85.

Mondol, S., Thatte, P., Yadav, P. & Ramakrishnan, U. (2011) A set of mini STRs for population genetic analyses of tigers (*Panthera tigris*) with cross-species amplification for seven other Felidae. *Conservation Genetics Resources*, 4, 63–66.

Mukherjee, S., Goyal, S.P. & Chellam, R. (1994) Standardisation of scat analysis techniques for leopard (*Panthera pardus*) in Gir National Park, Western India. *Mammalia*, 58, 139–143.

Mukherjee, S. & Mishra, C. (2001) Predation by leopard *Panthera pardus* in Majhatal Harsang Wildlife Sanctuary, W. Himalayas. *Journal of the Bombay Natural History Society*, 98, 267–268.

Nasik Gazetteer (1883) Https://cultural.maharashtra.gov.in/english/gazetteer/Nasik/004%20General/006%20WildAnimalsAndBirds.htm [accessed June 2014].

Negrões, N., Revilla, E., Fonseca, C., Soares, A.M.V.M., Jácomo, A.T.A. & Silveira, L. (2011) Private forest reserves can aid in preserving the community of medium and large-sized vertebrates in the Amazon arc of deforestation. *Biodiversity Conservation*, 20, 505–518.

Odden, M. & Wegge, P. (2009) Kill rates and food consumption of leopards in Bardia National Park, Nepal. *Acta Theriologica*, 54, 23–30.

Punjabi, G.A., Athreya, V. & Linnell, J.D.C. (2012) Using natural marks to estimate free-ranging dog *Canis familiaris* abundance in a MARK–RESIGHT framework in suburban Mumbai, India. *Tropical Conservation Science*, 5, 510–520.

Schaller, G.B. (1983) Mammals and their biomass on a Brazilian ranch. *Arquivos de Zoologia*, 31, 1–36.

Seidensticker, J., Sunquist, M. & McDougal, C. (1990) Leopards living at the edge of the Royal Chitwan National Park, Nepal. In *Conservation in Developing Countries: Problems and Prospects* (eds J.C. Daniel & J.S. Serrao), pp. 415–423. Oxford University Press, Bombay, India.

Sekhar, N.U. (1998) Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India. *Environmental Conservation*, 25, 160–171.

Shah, G.M., Jan, U., Bhat, B.A., Ahmad, F. & Ahmad, J. (2009) Food habits of the leopard *Panthera pardus* in Dachigam National Park, Kashmir, India. *Journal of Threatened Taxa*, 1, 184–185.

Shilpi, G., Krishnendu, M., Shankar, K. & Qamar, Q. (2009) Estimation of striped hyaena *Hyaena hyaena* population using camera traps in Sariska Tiger Reserve, Rajasthan, India. *Journal of the Bombay Natural History Society*, 106, 284–288.

Singh, P., Gopalaswamy, A.M. & Karanth, K.U. (2010) Factors influencing densities of striped hyenas (*Hyaena hyaena*) in arid regions of India. *Journal of Mammalogy*, 91, 1152–1159.

Thornton, P.K., Kruska, R.L., Henninger, N., Kristjanson, P.M., Reid, R.S., Atieno, F. et al. (2002) *Mapping Poverty and Livestock in the Developing World*. Http://www.ilri.org/InfoServ/Webpub/fulldocs/InvestAnim/Book2/media/PDF_chapters/B2_Front.pdf [accessed 15 January 2013].

Treves, A. & Karanth, K.U. (2003) Human–carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, 17, 1491–1499.

Treves, A., Wallace, R.B., Naughton-Treves, L. & Morales, A. (2006) Co-managing human–wildlife conflicts: a review. *Human Dimensions of Wildlife*, 11, 383–396.

Vijayan, S. & Pati, B.P. (2002) Impact of changing cropping patterns on man–animal conflicts around Gir Protected Area with specific reference to Talala Sub-District, Gujarat, India. *Population and Environment*, 23, 541–559.

Wegge, P., Odden, M., Pokharel, C.P. & Storaas, T. (2009) Predator–prey relationships and responses of ungulates and their predators to the establishment of protected areas: a case study of tigers, leopards and their prey in Bardia National Park, Nepal. *Biological Conservation*, 142, 189–202.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005) The impact of human–wildlife conflict on natural systems. In *People and Wildlife: Conflict or Co-Existence?* (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 1–12. Cambridge University Press, Cambridge, UK.

Yirga, G., De Iongh, H.H., Leirs, H., Gebrihiwot, K., Deckers, J. & Bauer, H. (2012) Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia. *Journal of Animal Ecology*, 81, 1052–1055.

Biographical sketches

Vidya Athreya's research has focused on understanding the ecology of large carnivores when they reside in human-use landscapes, and translating her findings into informed management actions. Morten Odden has worked on large carnivores in Nepal and on human–leopard interactions in India. He is interested in predator–prey interactions and in space use of large carnivores. John Linnell conducts multi-disciplinary research on the relationships between wildlife and humans, with a focus on large carnivores and herbivores. He works in Europe, South America, India and South-east Asia. Jagdish Krishnaswamy is interested in ecohydrology, landscape ecology and applications of Bayesian statistics in ecology and environmental science. Ullas Karanth studies the ecology of large carnivores, focusing on population modelling and estimation, and applies the results to practical conservation efforts.