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Abstract

There is increasing evidence of large carnivores using human-use areas, but our understanding of their ecology in such landscapes is limited. The role of wild and domestic prey in sustaining populations of carnivores in human-use landscapes could be significant but is currently poorly documented. We studied the prey composition and diet selection of leopards (*Panthera pardus*) in a forest and tea-garden landscape in north-eastern India where the population density is greater than 700 people per km² and average domestic animal density is 340 animals per km². Wild prey density in the landscape was 56 animals per km². Both wild and domestic prey were used by leopards in proportion to their availability with no selectivity toward either ($\chi^2 = 87.17$, p = .99, SE = 0.001). Among wild prey, Rhesus macaque (*Macaca mulatta*) was found in high densities (24 animals per km²) and was preyed by leopards more frequently that the proportional availability. High use of domestic prey by leopard, with 60% of the prey biomass comprising cattle and goats has the potential for negative impact on conservation support for the species. While on one hand, there is great scope for the persistence of large cats in dense human-use landscapes due to the availability of domestic prey, on the other hand, the study highlights the problems of livestock loss especially to poorer sections of the society which need to be reconciled for achieving long-term and sustainable conservation goals.

Keywords

human-dominated landscapes, human-wildlife conflict, livestock, prey-selection, feeding ecology

Introduction

There is increasing evidence of the presence and persistence of large carnivores in human-use areas across the world; however, little is known about their ecology in these shared space areas (Gehrt, Riley, & Cypher, 2010; Kshettry, Vaidyanathan, & Athreya, 2017; Ripple et al., 2014; Takahata, Nielsen, Takii, & Izumiyama, 2014). Often the idea of 'wilderness' precludes us from easily accepting that a large wild cat can make a human-use landscape its habitat (Cronon, 1995). Furthermore, the lack of detailed information on the feeding and habitat ecology of large carnivores in dense human-use landscapes also hinders science-based conservation and management of such populations (Ghosal, Athreya, Linnell, & Vedeld, 2013; Odden, Athreya, Rattan, & Linnell, 2014).

Availability of prey is one of the most important drivers of large carnivore distribution, but wild prey may occur at very low densities in human-use areas (K. Ullas Karanth, Nichols, Kumar, Link, & Hines, 2004; Khorozyan, Ghoddousi, Soofi, & Waltert, 2015). However, all human-use landscapes, be it cold northern Europe or sparsely inhabited South America have very high densities of domestic animals (Schaller, 1983; Woodroffe, Thirgood, & Rabinowitz, 2005) which are used by the large

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carnivores as prey (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2014; Shehzad et al., 2014).

Usage of anthropogenic food sources by large carnivores has been documented across a wide range of species, thereby exposing the immense variation in dietary habits between species of the same guild and even between populations of same species (Gehrt et al., 2010). Usage of livestock by carnivores could also potentially lead to conflict of interest between carnivore conservation goals and livestock owners. Such conflicts become severe when livestock forms a considerable portion of the carnivores' diet and also if livestock contributes to substantial income for local people.

This is particularly true in a country like India where human density is extremely high along with one of the highest density of livestock in the world (Robinson et al., 2014) and where wide range of wild carnivores co-occur with humans (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2013; Bauer, Müller, Van Der Goes, & Sillero-Zubiri, 2015; Suryawanshi et al., 2017). Among the large carnivores, especially felids, leopards are widely spread across India, overlapping with humans in much of its distribution (Kshettry et al., 2017). They are also known to be generalists in their diet which can consist of rodents and amphibians to large bovids (Hayward et al., 2006). Studies have also shown that leopards mostly feed on feral dogs and livestock when they persist in human-dominated landscapes (Athreya et al., 2014; Shehzad et al., 2014). However, studies that assess their prey requirements and selectivity in human-use landscapes are scarce in India with most studies restricted to protected areas (Jathanna, Karanth, & Johnsingh, 2003; K. U. Karanth & Sunquist, 1995; Ramakrishnan, Coss, & Pelkey, 1999).

In the present study, we investigated the diet usage and selectivity of leopard in a landscape consisting of small patches of protected forests interspersed within larger areas of tea estates and human settlements. Specifically, we (a) assessed the availability of prey by estimating densities of wild prey and obtaining livestock density from available records and (b) investigated prey usage by leopards by analyzing prey remains from scat (faces). This study provides us with greater information on the feeding ecology of leopards in a high-conflict, human-use landscape.

Methods

Study Area

The study was conducted in a 408-km² area located in the Jalpaiguri District of the state of West Bengal in north eastern India (Figure 1). The habitat of this region used to consist of moist deciduous and Sal (Shorea sp) forests which were converted to tea plantations by the British during the colonial period in the late 1800s (Chatterjee, 2001). The forests occur in Gorumara National Park (80 km²) and Territorial forests (60 km²) of Jalpaiguri Division. Now, tea gardens cover a large part of the area with more than 70 tea estates in the district and the human population density of the district is 700 per km² (http://jalpaiguri.gov.in, accessed March 2017). The people of this region belong to marginal communities with a daily per capita income of less than 1 USD (http://www.macroscan.com/fet/may08/print/ prnt120508West Bengal.htm, accessed on October 20, 2015).

There is considerable conservation conflict as leopards injure more than 50 people per year in the region and also cause livestock loss (Kshettry et al., 2017). The landscape hosts a thriving population of greater one-horned rhinoceros (*Rhinoceros unicornis*); the Indian elephant

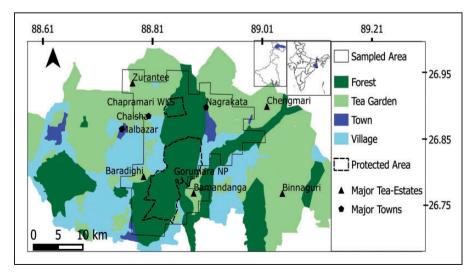


Figure 1. Map showing location of the study area and the land-use types in northern West Bengal, India.

(*Elephas maximus*); and other wildlife including sambar (*Rusa unicolor*), gaur (*Bos Gaurus*), chital (*Axis axis*), barking deer (*Muntiacus muntjak*), rhesus macaque (*Macaca mulatta*), and wild pig (*Sus scrofa*) (Kshettry et al., 2017). A detailed description of the study area is provided in Kshettry et al. (2017).

Estimating Prey Availability

The abundance and the proportion of different prey species in the diet of a carnivore can provide information on the prey selection (K. U. Karanth & Sunguist, 1995). The study site has both wild and domestic prey species. We estimated wild prey density in the forested area using standard distance sampling method, namely, line transects (Burnham, Anderson, & Laake, 1980). The transect design was created using program DISTANCE 6.0 (Thomas et al., 2010); a total of 12 transects within the forest patches, each 2.5 km long, was walked five times between 6:30 and 8:00 hr and 15:30 and 17:00 hr. Data were collected between November 2013 and March 2014. Data from the temporal replicates of each transect were pooled for analysis with a total walk effort of 150 km. The data were analyzed using program DISTANCE 6.0 (Thomas et al., 2010). Half Normal and Hazard Rate models were run for all prev species using Cosine Function and was compared with the Uniform function. The best model was selected using Akaike Information Criterion (AIC) and AIC corrected for small sample size (AICc; Burnham et al., 1980; Johnson & Omland, 2004). After Comparison, the Half Normal model was used for all prey species (sambar, gaur, and peafowl) except rhesus macaque for which the Hazard Rate model was used.

Estimates of domestic prey abundance in the nonforested areas were obtained from the livestock census data 2007 (http://dahd.nic.in/dahd/reports/compendiumof-schemes/livestock-census, accessed October 2013). The total number of livestock in each village or tea estate was divided by its area to arrive at the density. The densities of all units were used to estimate the mean density and standard error. We used livestock data from 2007 since the latest Livestock census data (2011) was not freely available. However, the overall results are unlikely to change, data from the animal husbandry department show an overall decrease in goat (Capra sp.) populations by 3.8% between 2007 and 2011 and the cattle (Bos sp.) holding also decreased by 8.9% in the same period (http://pib.nic.in/newsite/PrintRelease.aspx?relid = 109280, accessed August 21, 2017).

Estimating Diet Composition of Leopard

To understand the diet selection of leopards, we identified prey species based on the hair found in the leopard scats (Alberts et al., 2017; Bagchi & Mishra, 2006; Harihar, Panday, & Goyal, 2011). We walked all available roads or trails inside the forest areas to collect leopard scats, in the non-forested areas; we walked village roads and tea-garden roads and collected all the fresh scats encountered during the survey. Scats were also collected opportunistically whenever encountered in the study area between November 2013 and March 2014. The scats were analyzed for prey remains based on methods described in Mukherjee, Goyal, and Chellam (1994) and Bagchi, Goyal, and Sankar (2003). The hair specimens were identified to the species level based on difference in medullary patterns (Bahuguna, Sahajpal, Goyal, Mukherjee, & Thakur, 2010), and the frequency of occurrence was computed for each species across all scats that were examined. All large felid scats encountered during the survey were attributed to leopards since there are no similar-sized sympatric felids in the study area including the tiger, which was last reported from the landscape more than three decades ago. To determine the adequacy of sample size, we also plotted a species accumulation curve based on the scat samples. To distinguish leopard scats from canid scats, we analyzed only those scats which has associated secondary leopard signs such as pugmark, claw mark (on trees), and scrape.

Estimating Diet Selection

Diet selectivity has been defined as consumption of prey types in frequencies that are different from those expected, based on their availability in the environment (Chesson, 1978). The frequency of occurrence of prey types in scat was related to prey biomass using generalized model developed by Chakrabarti et al. (2016). This equation relates the prey biomass to the estimated number field collectible scats that the prey type can produce (Chakrabarti et al., 2016). We used prey body weights from literature but used the body weights of calves and subadults for gaur and cattle because we found mostly subadult and calf carcasses in field fed by leopards and also since it is highly unlikely that leopards will kill an adult gaur. Frequency of occurrence of prey species in the scat was computed and when more than one prey species was found in a scat, each was given a fractional weightage. For example, if there were two species then each one would get weight of 0.5 in the frequency calculation (Bagchi & Mishra, 2006; Link & Karanth, 1994). The expected frequencies of prey species in scat were estimated using a parametric bootstrap method corrected for over dispersion; the program SCATMAN (Hines & Link, 1995) was used for this purpose with 1,000 simulations and subsequently multinomial likelihood ratio tests were performed to assess selection (Link & Karanth, 1994).

Results

A total search effort of 370 km, spread across the 408 km² of the study site, yielded 120 leopard scats. However, for the diet analyses, we used only 70 scats which we could confirm as leopard scats because they had associated secondary signs such as scrape marks, pugmark, or claw marks. Of these, 56 were collected within the forested

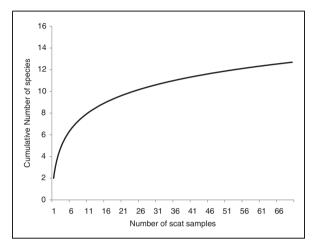


Figure 2. Cumulative frequency of occurrence of various prey species of leopard in the study area in northern West Bengal, India.

areas and 14 were collected in human-dominated landscapes. In our study, the cumulative species occurrence saturated before 70 scats and hence there is adequate sample size to perform statistical analyses (Figure 2).

Prey Availability in the Landscape

A total of 150 km walk effort was equally distributed among 12 transects. The surveys yielded 45 detections of gaur, 47 detections of peafowl, 49 detections of rhesus macaque, and 34 detections of sambar within the protected area. The domestic prey density in the study area was found to be 342 (SE=65.61) per sq km and that of wild prey at 56 (SE=16.93) per sq km. Rhesus macaque was the most common wild prey recorded during the transects, and cattle and goat were the most abundant among the domestic species (Figure 3).

Prey Usage by Leopards

A total of 14 different prey species were found in the scats with varying frequencies. Of the 70 leopard scats that were analyzed, 85% had multiple prey species. Seventy-five percent of the scats had more than one prey species. Ninety-four percent of the scats had presence of at least one domestic prey, 75% of the scats had presence of at

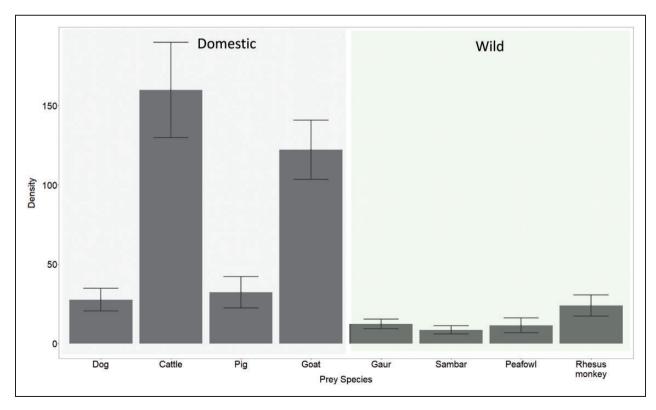


Figure 3. Density of available prey species in the study area in northern West Bengal, India.

Table 1. Frequency of Prey Species Found in Scats $(n = 70)$ of Leopards, Relative Biomass of Prey Consumed, and
Relative Number of Prey Consumed in the Study Area in Northern West Bengal, India.

	Prey species	A (%)	x (kg)	Y (kg/scat)	D (%)	Ε
Domestic	Cattle (Bos sp.)	27.03	60.00	1.80	48.22	7.07
	Goat (Capra sp.)	8.58	25.00	1.62	13.75	4.84
	Pig (Sus sp.)	6.24	40.00	1.75	10.83	2.38
	Dog (Canis familiaris)	5.13	18.00	1.48	7.50	3.66
Wild	Rhesus macaque (Macaca mullata)	10.49	6.00	0.95	9.90	14.51
	Rodent species	5.25	0.50	0.49	2.56	45.01
	Bird species	1.70	2.00	2.05	1.07	15.17
	Gaur (Bos gaurus)	18.0	60.00	1.80	1.44	0.21
	Muntjac (Muntiacus muntjac)	1.08	20.00	1.53	1.63	0.72
	Jungle cat (Felis chaus)	1.20	6.00	0.95	1.13	1.66
	Viverrid sp.	1.00	2.00	0.64	0.63	2.78
	Chital (Axis axis)	0.41	55.00	1.80	0.73	0.12
	Hare species	0.65	2.00	0.64	0.41	1.81
	Leopard (Panthera pardus)	0.20	40.00	1.80	0.36	0.08

Note. A = frequency of occurrence; x = average body weight; Y = correction factor relating prey body weight to number of field collectible scats (Chakrabarti et al., 2016); D = Relative biomass found to be consumed by leopards; E = Relative number of prey animals consumed.

least one wild prey, and 21% had only domestic prey while 4% had only wild prey.

Eighty percent of the biomass in the leopard diet was contributed by domestic prey (Table 1). Cattle were the most frequent prey species encountered in the scat (Table 1) contributing 48% of prey biomass. The results of this study indicate that the leopards' diet consisted mostly of livestock (cattle and goat). Among the wild prey, rhesus macaque contributed the highest relative biomass (10%) in the diet of the leopard followed by rodents (2.56%).

Both wild and domestic prey were found in scats irrespective of whether it was collected from the forests or human-use areas.

Diet Selection

We tested for selectivity in leopard diet for the major prey species, both wild and domestic, that are present in the landscape. We restricted our analysis to prey species which were represented in more than 25% of the scat samples. The analyses were conducted for cattle, goat, pig, and dog among domestic prey and gaur and rhesus macaque among wild prey. Chi-squared tests showed no overall selectivity in diet ($\chi^2 = 87.17$, p = .99, SE = 0.001). Rhesus macaques were predated upon more than proportional availability ($\chi^2 = 80.92$, p = .001, SE = 0.0001) despite their low relative biomass in the scat (10%). In spite of having high percentage of domestic prey biomass in the diet (80%), there was no significant selectivity for cattle ($\chi^2 = 3.61$, p = .08, SE = 0.001) or goats ($\chi^2 = 2$,

p = .19, SE = 0.001) and they were used in proportion of their availability (Table 2).

Discussion

Human-use landscapes generally have a high density of domestic animals, especially in countries which depend heavily on animal protein and dairy products (Robinson et al., 2014). In addition, pet animal densities can also be very high and all these form food resources for carnivores (Bruskotter et al., 2017; Gehrt et al., 2010). India, for example, has one of the highest livestock and domestic animal densities in the world (Robinson et al., 2014), and livestock is a crucial component of the livelihood of farmers. If other factors, such as social, cultural, and legal, allow the presence of wild carnivores outside wilderness areas, then domestic animals do form an important food resource allowing for the co-occurrence of humans and large carnivores. This was seen in our study area where the density of domestic animals was higher by more than a factor of 6 compared with the wild species.

While livestock can subsidize the persistence of large carnivores in human-use landscapes, it could also give rise to conservation conflicts due to the loss of livelihood to the people and can form a major hurdle to the conservation of large felids (Patterson, Kasiki, Selempo, & Kays, 2004; Shehzad et al., 2014; Treves & Karanth, 2003).

The leopard is one such large carnivore which has the ability to persist in human-use areas throughout its global range, especially in India (Athreya et al., 2013; Kshettry et al., 2017; Navya, Athreya, Mudappa, & Raman, 2014).

	Species	Observed scat frequency	Expected scat frequency	Chi squared	p value	Standard error
Domestic	Cattle (Bos sp.)	27.03	34.18	3.61	.080.	0.001
	Goat (Capra sp.)	8.59	13.09	2.00	.190	0.001
	Pig (Sus sp.)	6.24	4.89	0.41	.540	0.001
	Dog (Canis familiaris)	5.13	2.40	3.24	.070	0.000
Wild	Gaur (Bos gaurus)	0.81	2.62	1.31	.260	0.001
	Rhesus macaque (Macaca mullata)	10.49	1.11	80.92	.001 ^a	0.000
	Composite			87.17	.990	0.001

Table 2. Expected Frequency of Prey Based on Prey Densities and Observed Frequencies Based Prey Usage for Major Prey Species Used by Leopards in the Study Area in Northern West Bengal, India.

The adaptability of the leopard, the availability of suitable habitat along with high density of potential prey species in the form of domestic animals, favorable legal conditions, and other social and cultural factors could facilitate its persistence in human-use areas (Gehrt et al., 2010; Ghosal et al., 2013; Odden et al., 2014).

Our research underscores the adaptability of the leopard (Hayward et al., 2006) in a high-density human-use landscape, where we recorded more than 14 prey species in 70 leopard scats. Seventy-five percent of the scats had more than one prey species which varied from rodents to gaur. There was no overall selectivity in the diet, indicating the generalist nature of the leopard in relation to its diet which has also been seen in other studies (Hayward et al., 2006; Mondal, Gupta, Bhattacharjee, Qureshi, & Sankar, 2012; Ramesh, Snehalatha, Sankar, & Qureshi, 2009). There was a positive selection toward rhesus macaques, despite their densities being one sixth that of goats. Herbivores such as gaur and sambar occurred at very high densities within forested habitats, but they did not form a major proportion of the leopards' diet possibly because these are much larger than their ideal prey size for leopards (Hayward et al., 2006).

Livestock comprised a large portion of the diet of the leopard (80% relative biomass in scat) with cattle being the most frequent prey species followed by goats and pigs. The diet selection study did have a limitation as domestic pigs could not be distinguished from wild pigs based on hair in leopard scat; hence, all the analysis has been carried out without distinguishing between wild and domestic pigs. Furthermore, the small number of scats collected from the human-use areas (14) precluded any comparison of the diet between the forested areas and human-use areas. However, since the forest patches are small in size, we do not expect any variation in the diet between the forests and human-use areas. This was substantiated by the fact that we found livestock remains even from the scats collected from the forested areas. Livestock, along with dogs, has been found to form a major portion of leopard's diet in other parts of subcontinent (Athreya et al., 2014; Shehzad et al., 2014). In our study area, although density of dogs was high (27 per km²), the density of cattle and goats was much higher (280 per km²). The leopard showed no selectivity toward livestock indicating that they are used in proportion to their availability. Globally, large carnivores are known to predate on livestock at varying intensities depending on the type of habitat, density of livestock, and its accessibility (Ghoddousi et al., 2016; Miller, Jhala, Jena, & Schmitz, 2015). In our study area, the livestock are not protected and are in the open making them very accessible to leopards.

The presence of such a high biomass of domestic prey has allowed the persistence of leopards in this landscape which also has a lot of vegetation cover in terms of tea gardens set among a mosaic of forest patches (Kshettry et al., 2017). However, it also creates conservation problems. For instance, in this landscape, the tea-garden laborers are not allowed to keep livestock in the plantations but do so because of severe economic conditions (Bhattacharjee & Parthasarathy, 2013). As a result, they are also not compensated for the loss. Furthermore, there is no space for planning better protection of livestock because they are "illegally maintained." The social conditions here (Chatterjee, 2001) also have made it difficult for them to protect their livestock. The huge quantum of livestock that is present in an area where free land is not available makes the management of this issue a great challenge. There also might be inherent acceptance of these species, in which case integrated damage mitigation as suggested by Bauer, Müller, Van Der Goes, and Sillero-Zubiri (2017) would be a better model compared with separation of spaces or compensation (Gebresenbet, Baraki, Yirga, Sillero-Zubiri, & Bauer, 2017). The results from this work provides an opportunity to engage with local communities to develop a way forward which will reduce the damage caused to their livestock by leopards.

^aSignificant p value.

Implications for Conservation

Conserving large bodied wild felids in human-use areas faces considerable conservation challenges. Human life loss and economic damage are the prime hurdles to big cat conservation in such diverse landscapes. In this article, we analyzed one such root of the conflict which may arise due to high usage of domestic prey by leopards in the region. We did not find any evidence of selective predation toward domestic livestock which implies that leopards are using both wild and domestic prey in proportion to their availability. This implies that domestic prey is more widespread and accessible to leopards in the region and proactive measures for livestock protection is urgently needed and should be the focus of future research in the region. At the global scale, the study adds to the growing body of literature on large wildlife residing in peri-urban landscapes. Such studies are vital for the effective management of "potentially dangerous" wildlife in human-use areas. The study also highlights the broad diet width of leopards as reported from other studies but rarely investigated in human-use areas. At the regional scale, the study focuses on the feeding ecology of leopards in a high-conflict landscape where more than 50 people are injured by leopards annually on an average. While a previous study has found that the incidents are largely accidental in nature, the current study finds that the high dependence of leopards on domestic prey could be a reason behind the persistence of leopards in the human-use areas such as tea gardens. The tea-garden landscape provides opportunities for large carnivore conservation outside protected areas but also throws up conservation challenges. Livestock protection measures such as active guarding and predator proof livestock enclosures may be useful in reducing livestock predation by leopards if they are found to be economically viable. Furthermore, livestock insurance schemes may help negate the losses faced by local residents due to leopards; however, the success of such programs needs to be tested first before implementation. Moreover, holistic understanding of leopard ecology and human-leopard interactions are required to solve conservation conflicts in shared-space areas. Knowledge of dietary and habitat requirements of other wildlife in "non-wild" lands is urgently needed for the conservation of such threatened species across multiple land-use types.

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