Human-wildlife interactions in the Western Terai of Nepal. An analysis of factors influencing conflicts between sympatric tigers (Panthera tigris tigris) and leopards (Panthera pardus fusca) and local communities around Bardia National Park, Nepal

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Diet composition and prey preference of tigers

"**An insight into the diet and prey preference of tigers in Bardia National Park, Nepal**"
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Abstract

We studied the diet composition and prey preferences of tigers (*Panthera tigris tigris* Linnaeus, 1758) in Bardia National Park, Nepal using DNA based techniques from their scat samples. Remains of prey species in scats were identified through microscopic hair morphology analysis. Out of 101 scats, DNA was extracted from 84 samples and 75 were assigned to tigers (34-males and 41-females). We found seven and six prey species in the diet of male tiger and female tiger, respectively. The diet of male and female tigers did not differ significantly, with chital (*Axis axis* Erxleben, 1777) as the most abundant prey species. The Jacobs index suggested a preference of male tigers for sambar deer (*Cervus unicolor* Kerr, 1792) and wild pig (*Sus scrofa* Linnaeus, 1758) and of the female tigers for wild pig and chital. Bardia National Park has the highest density of tiger prey species (92.6 animals/km^2) among the national parks of Nepal. Still, the density of larger prey species is relatively low. Increasing the density of larger prey like sambar and re-introduction of larger prey species like gaur (*Bos gaurus* Smith, 1827) can further enhance the tiger population in the park. Our study demonstrates that tigers mostly preyed on wild species, indicating a low level of tiger-livestock interaction. Hence, this park seems to be a prospective area for tiger conservation in the long run.

Keywords

Bardia, diet, DNA analysis, prey preference, tiger.

3.1 Introduction

The density of carnivores depends on the availability of prey biomass (Fuller & Sievert, 2001; Karanth et al., 2004; Hayward et al., 2007; Simcharoen et al., 2014). Prey species composition in the diet of predators is important in knowing prey-predator interactions as well as for studying the role and impact of predation (Odden & Wegge, 2009). Increased prey density helped in increasing the population of Amur tiger (*Panthera tigris altaica* Temminck, 1844) (Jiang et al., 2017). Thus, understanding the diet of flagship species like tiger (*Panthera tigris tigris* Linnaeus, 1758) will contribute to better conservation planning, especially for habitat prioritization, protection and restoration (Kapfer et al., 2011).

The diets of elusive species like tigers are generally assessed by identification of prey species in scats through microscopic hair morphology analysis (Mukherjee et al., 1994; Ramakrishnan et al., 1999). Kerley (2010) reported the use of scat detection dogs for the collection of tiger scat from the Russian Far-east. Field identification of scats based on size, shape or smell is sometimes inconsistent and unreliable, as body size of a carnivore can vary greatly within a species. Moreover, the same individual can leave scats of different sizes (Farrell et al., 2000). Sometimes leopard (*Panthera pardus* Linnaeus, 1758) scat can be mistaken for tiger scat. This ambiguity can be overcome by using mitochondrial DNA obtained from scats to distinguish a tiger from a leopard (Bhagavatula & Singh 2006; Mondol et al., 2009). The sex of felids can also be determined using genomic DNA obtained from scats (Pilgrim et al., 2005).

Tigers are the largest living felids, with an average body weight of 175-260 kg for males and 100-160 kg for females in South Asia (Sunquist, 1981; Karanth, 2003). On average, tigers are estimated to consume 10% of the available prey within their territories per year (Sunquist 1981; Karanth et al., 2004). An adult male requires 4,000 kg of meat per year (55-60 ungulates) whereas females without cubs consume 3,000 kg/year (40-45 ungulates) (Sunquist, 1981). Females raising three cubs roughly consume >4500kg/year (60-75 ungulates) (Sunquist, 1981; Karanth, 2003). The home ranges of female tigers are primarily determined by the abundance of prey whereas the territories which can be defended by a male is a function of the number of female home ranges that can be covered by a male (Karanth, 2003). Throughout most of the year, an adult female is with cubs and in the last six months before her young are independent, she provides food for three to four adult sized animals, and in the last six months before a female's cub is independent she is killing more prey than a male (Smith, 1993). In social organization of solitary felids, the limiting resource for a female is the availability of food and that for a male is access to females (Odden & Wegge, 2005). With higher prey abundance the home range of female decreases leading to the increase in density (Simcharoen et al., 2014). Kolipaka et al. (2017) reported from Panna Tiger Reserve, Madhya Pradesh, India, that female tigers are mostly confined to the core zone of the park and preferentially target wild prey.

The overall aim of this study was to investigate the diet of tigers in Bardia National Park with following objectives:

1. To analyze prey species composition in the diet of tigers.
2. To assess the diet composition and prey preferences of male and female tigers.

Since male and female tigers may have different dietary requirements and the presence of prey also differs in different habitats, knowing the diet on the basis of sex can be helpful in better conservation planning. Optimal foraging theory formulated by MacArthur & Pianka (1966) discussed a graphical method that allows a specification of a specific diet of a predator in terms of the net amount of energy gained from a capture of prey as compared to the energy expended in searching of the prey. Carbone et al. (2007) predicted that the transition between diet types in relation to predator's mass may be predicted through the maximization of net energy gain and this can be achieved by larger prey feeding strategy. Based on this we assume that male tigers may be targeting large size prey species than female tigers. Our study relates sex of the tiger to its diet and is the first of its kind in Nepal. We believe that it will contribute to the conservation of endangered and important flagship species.

3.2 Methods

3.2.1 Study area

Bardia National Park (IUCN, Category II) is the largest national park (968 km^2) in the lowland Terai-Bhabar tract, located in the South-western part of Nepal (N: 28.2630 to 28.6711; E: 80.1360 to 81.7645) (Figure 3.1). The park was established in 1976 with an area of 368 km^2 as the Royal Karnali Wildlife reserve and extended to its current size in 1984. The park was established originally to protect the representative ecosystems as well as to conserve the tiger and its prey species (DNPWC, 2017). The Karnali and Babai rivers drain through the park. The floodplain grasslands of these rivers support high prey and tiger densities. The park is home to more than 30 species of mammals and > 230 bird species. Bardia is a part of the Terai Arc Landscape (TAL), a trans-boundary tiger conservation landscape in India and Nepal, identified as a level-1 tiger conservation unit (Wikramanayake et al., 1998). The density of tigers in Bardia is 3.3/100 km^2 and the prey density is 92.6 animals/km^2 (Dhakal et al., 2014). The main prey species of tigers in Bardia are chital (*Axis axis* Erxleben, 1777), hog deer (*Axis porcinus* Zimmermann, 1780) and wild pig (*Sus scrofa* Linnaeus, 1758), supplemented by barking deer (*Muntiacus vaginalis* Boddaert, 1785), barasingha (*Cervus duvauceli* Cuvier, 1823) and nilgai (*Boselaphus tragocamelus* Pallas, 1766) (Wegge & Storaas, 2009). Leopards are present in a lower density compared to tigers and are found primarily in the periphery of the park (Wegge et al., 2009; Odden et al., 2010). The park has a sub-tropical monsoonal climate with three distinct seasons: winter (October to February), summer (February to June) and monsoon (June to October). During summer, temperatures could rise to 45°C. About

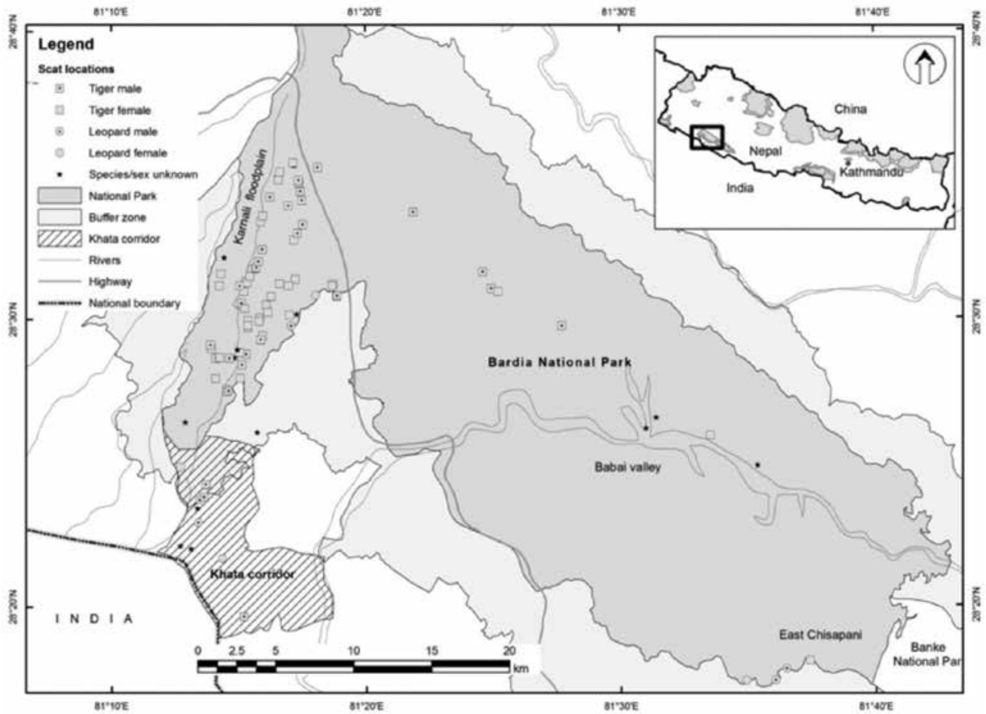

Figure 3.1
Study area showing the location of scat collection with identification of scat to species and sex level. The rectangle in the inset shows the location of Bardia National Park in Nepal.

70% of the forest consists of Sal (*Shorea robusta* Gaertn, *1805*) with a mixture of grassland and riverine forests (DNPWC, 2017).

3.2.2 Sample collection

During January - February and May-June 2015, we systematically searched for scats along forest roads and trails, which are often used by tigers and leopards. We did not collect scats in the summer because the outer mucosal layer from scat required for DNA extraction was readily eaten up by insects (May-June 2015). Hence, we limited our study to samples collected during the winter months only. Fresh scats were identified, on the basis of the state of the mucosal outer layer of the faces (Wasser et al., 2009). Surveys were repeated once a week in the Karnali floodplain and in the Khata corridor where tiger density is high (Stoen & Wegge, 1996; Dhakal et al., 2014). We also surveyed the Babai valley, East Chisapani and buffer zones of the national park (Figure 3.1). Two samples were collected from each scat, one for genetic analysis and another for prey identification. For the genetic analysis, the mucosal layer of the scat, which contains sloughed-off intestinal cells from the host animal, was collected in vials containing DET (Dithiothreitol EDTA Tris-hydrochloride) buffer (Wultsch et al., 2014). The remaining part of the scat was collected in a paper bag to assess the prey species composition. GPS coordinates of the site of sample collection were also recorded. The distinction between tiger and leopard scats in the field was done following earlier studies: Karanth & Sunquist (1995); Biswas & Sankar (2002); Edgaonkar & Chellam (2002) and Lovari et al. (2015). A total of 101 scat samples were collected and 92 were used for the diet analysis of tigers.

3.2.3 DNA extraction and species and sex identification

The scats were pre-treated using an Inhibit-EX buffer to adsorb PCR inhibitors. After pre-treatment, DNA was extracted using the Qiagen QIAamp DNA Mini Fast Stool Kit (Qiagen, Germany) following the manufacturer's protocol and finally 150 μl of DNA was eluted. Identification of tiger's and leopard's scats was done by specifically amplifying the mitochondrial DNA regions (Bhagavatula & Singh 2006; Mondol et al., 2009). Sex identification of tiger and leopard samples was done by amplifying the Amelogenin area on sex chromosomes based on sequencing data available for a domestic cat (Pilgrim et al., 2005).

3.2.4 Diet analysis

The scat samples were sun-dried and then washed through a one mm sieve, using hot water to separate hair from other organic material. Separated hair was washed in acetone hydrated in 100% ethanol and dried on filter paper (Ramakrishnan et al., 1999; Breuer, 2005). The analysis of predator diets is based upon indigestible remains of prey species, particularly hairs, bones, quills and feathers. Guard hair is often used for the identification of prey species. From each scat, a predefined minimum of 20 hairs was sampled and hairs were identified on the basis of general appearance, color, relative length, relative width, cortex pigmentation, medullary width and the ratio of medulla to cortex in a cross-section following Mukherjee et al. (1994). The cortex and medullary pattern of guard hairs as observed under a trinocular microscope (200X), was compared with photographs from the reference guide prepared by Bahuguna et al. (2010). The frequency of occurrence of food items in scats was also recorded following Mukherjee et al. (1994). We used genetic analysis to determine if the scat was deposited by a tiger or a leopard and we only used scat deposited by tigers in this paper.

3.2.5 Data analysis and statistics

The frequency and relative frequency of occurrence were estimated as defined by Lyngdoh et al. (2014). When scats have either a single prey species or just two prey species, the frequency of occurrence and relative frequency of occurrence of prey items give similar results (Bagchi et al., 2003). Therefore, we used the frequency of occurrence of prey species in our analysis. If prey species differ in their body size then the frequency of occurrence cannot give a proportion of the prey species consumed by predators. We used the non-linear (asymptotic) model developed by Chakrabarti et al. (2016) to calculate biomass consumed per collectable scat/predator weight. The relative biomass (D) and relative number of prey species consumed (E) were calculated following Andheria et al. (2007). We used the Fisher's exact test to compare the diet composition of male and female tigers as well as prey preferences. A binomial logistic regression was used to determine the probability of finding a positive DNA result in relation to forest type and the age of the scat. All the above tests were performed in software program R (R Core Team, 2015). The density of prey species was obtained from Dhakal et al. (2014) who used a line transect method. The data were analyzed under the distance sampling framework using DISTANCE program version 6. Although density estimation was done in 2013, we assumed that the species density had been stable. Preferences of tigers for prey species was estimated using the Jacobs Index (Jacobs, 1974). The value ranges from +1 (for preference) to -1 (for avoidance).

3.3 Results

From the 101 scat samples collected, 84 were confirmed as tiger or leopard scats with PCR-based genetic species identification, whereas DNA could not be extracted from the others. The amplified PCR product size was 162 bp for tiger and 130 bp for leopard. The amplified PCR product of nuclear DNA of the male had two bands measuring 194 bp and 214 bp, whereas, females had one band of 214 bp. The site for scat collection in comparison to results of species and sex identification is shown in Figure 3.1. The results showed that tiger scats were mostly confined to the core area of the park and in the corridor, while leopard scats were more often found near the park boundary in the buffer zone and in the hills.

The older the scat, the more difficult it was to assess the species and sex using DNA (p= 0.009) (Figure 3.2). The habitat of the scat collection was not significantly related to the results (p = 0.450) (Table 3.1).

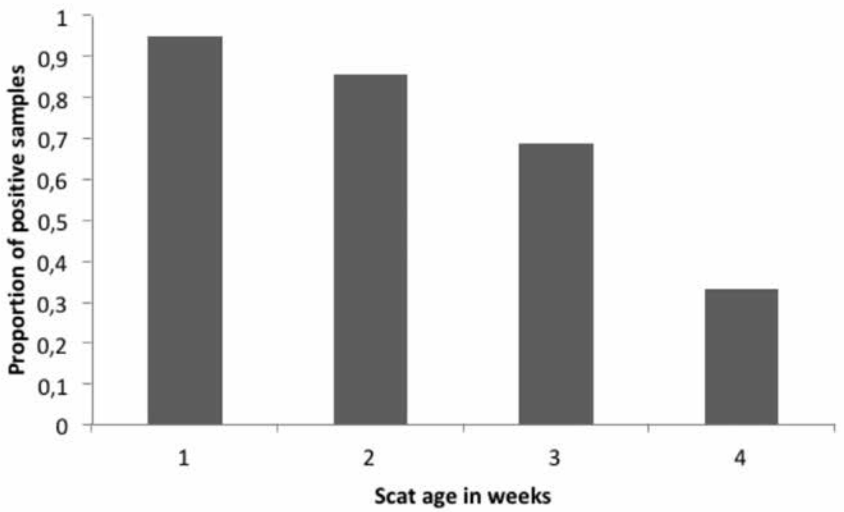

Figure 3.2
Positive results in DNA tests related to age of scat.

Table 3.1
Logistic model showing the positivity of DNA test depending on age of scat and habitat (forest type).

	Df	Deviance	AIC	LRT	Pr(>Chi)	
Full Model		79.402	91.402			
Scat Age	1	86.261	96.261	6.8591	0.008819	**
Forest Type	4	83.089	87.089	3.6874	0.449964	

Note: AIC= Akaike information criterion; LRT= likelihood ratio test.

Among the 101 scat samples, we used 92 samples for the analysis of tiger's diet because nine samples were of leopard, which was confirmed by DNA analysis. Of the 92 tiger scat samples, eight had no guard hair. From the remaining scats, nine wild prey species and two domestic animals (water buffalo and goat) were identified. A single prey species was detected in 32 male and 38 female tiger scats (93.3%), whereas two male and three female tiger scats had two prey species (6.7%). One unidentified scat sample also contained two prey species in the scat. Detection of single prey species in the scat was regarded as one animal killed and that of two species was regarded

Table 3.2
The frequency of occurrence of prey in the diet of male and female tigers, denoted in brackets as percentage, NI= Species and sex not identified by DNA analysis.

Prey Species	Tiger		NI	Total
	Male	Female		
Sambar	3(8.6)	1(2.2)	5(27.8)	9(9.2)
Chital	14(40)	23(51.1)	3(16.7)	40(40.8)
Langur	0(0)	1(2.2)	1(5.6)	2(2)
Hog deer	4(11.4)	9(20)	2(11.1)	15(15.3)
Wild pig	6(17.1)	5(11.1)	1(5.6)	12(12.2)
Four horned antelope	2(5.7)	1(2.2)	0(0)	3(3)
Swamp deer	1(2.9)	0(0)	0(0)	1(1)
Goat	0(0)	0(0)	1(5.6)	1(1)
Barking deer	0(0)	0(0)	1(5.6)	1(1)
Buffalo	1(2.9)	0(0)	0(0)	1(1)
No guard hair	2(5.7)	2(4.4)	4(22.2)	8(8.1)
Unknown	2(5.7)	3(6.7)	0(0)	5(5.1)
Total	35(100)	45(100)	18(100)	98(100)

as two animals killed (Stoen & Wegge, 1996). Plant materials were found in 14.9 % of the scat samples. We observed that both males and females preyed most frequently upon chital (M-40%, F -51%). The other prey species found in the male tiger scat were wild pig (17%), hog deer (11%), sambar (*Cervus unicolor* Kerr, 1792), (9%) and four-horned antelope (*Tetracerus quadricornis* de Blainville, 1816). In the diet of female tigers, chital was followed by hog deer (20%), wild pig (11%), sambar, four-horned antelope and langur (*Semnopithecus schistaceus* Hodgson, 1840) (Table 3.2).

Table 3.3
Relative biomass and relative number of prey consumed by male (M) and female (F) tigers.

Prey	X (Kg)	Predator	Z (Kg)	X/Z	Y	Y_C	A (%)	D (%)	E (%)
Sambar	212	TigerM	235	0.902	0.329	77.42	8.6	9.98	2.21
		TigerF	140	1.514	0.330	46.19	2.2	2.53	0.47
Chital	53	TigerM	235	0.226	0.320	75.31	40.0	45.17	39.92
		TigerF	140	0.379	0.325	45.50	51.1	57.86	43.19
Hog deer	33	TigerM	235	0.140	0.316	74.33	11.4	12.71	18.03
		TigerF	140	0.236	0.321	44.92	20.0	22.35	26.80
Wild pig	38	TigerM	235	0.162	0.317	74.61	17.1	19.13	23.58
		TigerF	140	0.271	0.322	45.10	11.1	12.46	12.97
Four horned antelope	20	TigerM	235	0.085	0.313	73.47	5.7	6.28	14.71
		TigerF	140	0.143	0.316	44.30	2.2	2.42	4.80
Swamp deer	160	TigerM	235	0.681	0.329	77.23	2.9	3.36	0.98
		TigerF	140	1.143	0.330	46.17	0	0	0
Buffalo	275	TigerM	235	1.170	0.330	77.51	2.9	3.37	0.57
		TigerF	140	1.964	0.330	46.19	0	0	0
Langur	8	TigerM	235	0.034	0.308	72.47	0	0	0
		TigerF	140	0.057	0.310	43.46	2.2	2.38	11.77

A = Frequency of occurrence of the prey species in scats; X = Mean body mass of the prey (Karanth & Sunquist, 1992; Bhattarai & Kindlman, 2012); Z = Mean body mass of the predator (Smith et al., 1983) Y = Biomass consumed; ($Y = 0.033\text{-}0.025\exp^{-4.284X/Z}$, Chakrabarti et al., 2016); Y_C= Y corrected for predator weight (Y*Z); D= Relative Biomass, (A × Yc)∑(A × Yc) * *100*; E = Relative number of each prey species consumed, (D/x)∑(D/x) * *100*.

Swamp deer and water buffalo (*Bubalus bubalis* Linneaus 1758) were found only in the male tiger scat, and langur in the diet of a female tiger. We recorded only one instance of livestock predation, where a male tiger preyed upon buffalo. The diet of male and female tigers was not significantly different (Fisher's exact test, p=0.363). Chital made the most abundant relative biomass of the prey species consumed by both male (45.17%) and female (57.86%) tigers (Table 3.3).

Table 3.4
Female and male tiger prey preference of major prey species in Bardia National Park.

Prey	Frequency of occurrence in Diet	Proportion in Diet -r	Prey density*	Proportion in field-p	Jacobs index
Female tiger					
Chital	23	0.767	53.99	0.638	0.301
Sambar	1	0.033	4.45	0.053	-0.234
Wild pig	5	0.167	4.79	0.057	0.538
Langur	1	0.033	21.35	0.252	-0.814
Total	30	1	84.58	1	
Male tiger					
Chital	14	0.609	53.99	0.638	-0.063
Sambar	3	0.130	4.45	0.053	0.460
Wild pig	6	0.261	4.79	0.057	0.709
Langur	0	0	21.35	0.252	-1
Total	23	1	84.58	1	
Combined					
Chital	37	0.698	53.99	0.638	0.134
Sambar	4	0.075	4.45	0.053	0.190
Wild pig	11	0.208	4.79	0.057	0.627
Langur	1	0.019	21.35	0.252	-0.890
Total	53	1	84.58	1	

*Dhakal *et al.* (2014); Jacobs index (Jacobs, 1974).

The Jacobs index for prey preference of female and male tigers suggested a preference towards wild pig. Sambar deer seem to be preferred by male tigers, and chital by female tigers. Langur seemed to be not a preferred species for either sex. When we combined both male and female together, a preference for wild pig was suggested, followed by sambar and chital (Table 3.4).

However, testing showed no significant difference between prey occurrence in the diet and prey density in the field for males, females and both combined (Fisher's exact test, p=1).

3.4 Discussion

The freshness of scat samples affected the assessment of species and sex positively. We got valid results for 83.16% of the scat samples used for the identification of species and sex of both tiger and leopards, as expected (Bhagavatula & Singh 2006; Mondol et al., 2009). Our results are comparable to those of Borthakur et al. (2011) who reported 84.21% success. So, although field identifications are usually correct, the chance of misidentification can always be corrected by DNA analysis.

Five prey species (viz. chital, sambar, wild pig, hog deer and four-horned antelope) contributed to the diet of tigers. Our findings are similar to the findings of Andheria et al. (2007), who reported that chital, sambar, gaur and wild pig constituted 96% of the diet of the tiger from Bandipur Tiger Reserve, India (gaur was not available in our study site). We found that chital was the most common prey species of tigers, as Stoen & Wegge (1996) and Wegge et al. (2018) reported from Bardia. Our results are different to those of Chitwan National Park where sambar was reported as the main prey species (Kapfer et al., 2011).

Prey availability and body mass were the key determinants of prey preference of tigers in Bardia National Park (Stoen & Wegge, 1996). In our study also, we found that the number of large-sized prey species (sambar) consumed by male tigers was higher than that for female tigers, although not statistically significant. Similarly, female tigers had relatively more medium-sized prey species (chital) in comparison to a male tigers. Male tigers mainly killed bigger prey species and females killed slightly smaller prey animals, according to their body size (Hayward et al., 2012). However, in Bardia, large prey are scarce and patchily distributed which makes it energetically costly to search for them, whereas medium sized prey like chital is very abundant and makes up >80 % of the available wild herbivore prey (Stoen & Wegge, 1996).

The Jacobs index for prey preference suggested a positive preference of male tigers towards wild pig and sambar and female tigers towards wild pig and chital. However, the chi-square test comparing the diet of male and female tigers was not significant. In the absence of larger prey the tigers are non-selective (Stoen & Wegge, 1996). Although chital was found to be the most abundant prey in the diet of both male and female tigers, it is too small to be an optimal prey for tigers (Hayward et al., 2012). Because of the yarding behavior of chital at night in open areas, they tend to become less vulnerable to stalking predators like tiger and leopard (Johnsingh, 1992).

In our study, livestock was present in a very small proportion of tiger scats, which is comparable to Biswas & Sankar (2002) in Pench National Park and Bhattarai & Kindlmann (2012) in Chitwan National Park. This is a remarkable finding since many other studies report livestock raiding by both tigers and leopards (Seidensticker, 1976; Wang & Macdonald, 2009; Kolipaka et al., 2017). One scat of a male tiger collected from Khata corridor that links Bardia National Park with Katarniaghat Wildlife Sanctuary in India had buffalo in the diet. In contrast, Basak et al. (2018) reported from the Katarniaghat Wildlife Sanctuary that the frequency of occurrence of large cattle in the diet of tiger was 17.5%, which is much larger than in our study. Livestock which mainly consisted of cattle and buffalo also contributed to 10.4% of the tiger's diet in the Sariska Tiger Reserve (Sankar et al., 2010). Kolipaka et al. (2017) also found that male tigers were killing more livestock in the buffer zone, whereas female tigers mostly relied upon wild prey in the core zone of the Panna Tiger Reserve, India. We also found plant materials in the scat. The presence of plant material in 15% of our scat samples may be due to accidental consumption of plants along with the main prey (Rajaratnam et al., 2007). It is also believed that plant materials aid in the digestion and the fibers present makes it easy for the animals to defecate. Plant materials were also reported from the scat of leopards and tigers of Sariska Tiger Reserve (Sankar & Johnsingh, 2002).

The density of large ungulates is low in Bardia. It is possible to have high densities of large ungulates in successional and disturbed forests if poaching is under control (Karanth & Sunquist, 1992). Tigers cannot sustain and reproduce in large numbers in the absence of large prey species even when small prey species are quite abundant (Sunquist, 1981; Karanth & Sunquist, 1995). Seidensticker (1986) reported from Java that one of the main reasons for the decline of Javan tiger was a decline in the abundance of larger prey. Thus, to increase the carrying capacity of tigers (Walston et al., 2010), Bardia should focus on increasing the density of large-sized prey species along with the re-introduction of gaur in the near future as well as maintain the chital and wild pig population.

Understanding the diet of tiger has great implications for tiger conservation. However, the present study is short as it covers just one season. Prey density estimation data were taken from the study carried out by park authority however, we assume that there is no significant variation in the predator diet and the prey density because it was taken during the same season. Simultaneous study of prey density and predator diet should be done in the near future to come up with a clear picture in multiple prey-predator environments. The home range of the tiger as well as the prey preferences changes with the season, therefore a thorough study covering all seasons is needed along with regular scientific monitoring of the prey and predator population. This will provide crucial information required for a better management and help in the long-term conservation of tigers in Nepal.

3.5 Implications for Conservation

The population of tigers has declined worldwide as a result of prey depletion. Prey density is important for the maintenance of large carnivore populations (Sankar et al., 2010). Accurate knowledge of the diet of a species is important for effective conservation and is important for conservation initiatives like habitat prioritization, protection and restoration (Kapfer et al., 2011). The diet of tigers can be helpful in knowing about the home range and carrying capacity of a park. Nepal is one of the 13 countries to ratify the Global Tiger Recovery Plan at the meeting of world leaders held in St. Petersburg in 2010 which aims at doubling the number of wild tiger by 2022. Bardia National Park is regarded as one of the global source sites for tigers. Therefore, to increase the carrying capacity of the park we need to focus on increasing the number of larger prey species. On the basis of our results we suggest that future studies of tiger diet should be of longer duration and cover a wide area in order to understand the spatiotemporal variation of tiger diet (Kapfer et al., 2011).

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