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A comparative study of the diets of tiger (*Panthera tigris tigris* Linnaeus, 1758) and leopard (*Panthera pardus fusca* Linnaeus, 1758) in relation to human- wildlife conflicts in and around Chitwan National Park, Nepal

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Abstract

This study compares the diet and prey preference of tiger (*Panthera tigris tigris*) and leopard (*Panthera pardus fusca*) in Chitwan National Park, Nepal in an attempt to link differences in diet and prey dynamics to human- wildlife conflicts. Tiger and leopard diets were compared between three areas under different management regimes including core area (CA), buffer zone (BZ) and corridor forest (CO). Diets were assessed utilizing microscopic hair morphology and gross hair morphological features, including bones and skin present in scats collected during transects. Prey availability was estimated through reports of previous surveys. Most common prey items in tiger diet (N=135) were chital (*Axis axis*) (36.50%), sambar (*Rusa unicolor*) (22.63%) and wild boar (*Sus scrofa*) (16.79%). Chital (49.06%), muntjac (*Muntjakus vaginalis*) (13.21%) and birds (9.43%) made up the main share of leopard diet (N=53). Our statistical analysis suggests that tigers prefer medium to large sized prey such as wild boar, sambar and gaur (*Bos gaurus*) while leopards prefer small to medium sized prey like muntjac and hog deer (*Axis porcinus*). The contribution of wildlife to the diet was maximal in the core area (98%) and minimal in the corridor forest (83%). Birds were only found in the buffer zone and corridor forest. A larger portion of the leopard diet consisted of livestock (14%) compared to tiger (3%). Livestock depredation (mainly goats) has decreased slightly between 2009 and 2017. The results suggest that leopards are more abundant in areas with higher degrees of disturbance and more involved in livestock raiding compared to tigers in areas where both species are sympatric. Therefore, conflict mitigating measures should prioritize the corridor forest and buffer zone over core area and leopard over tiger to reduce the economic loss inflicted by livestock depredation.

Public summary

The increased pressure of growing human populations on wild habitats has resulted in an increase in human- carnivore conflict. In densely populated areas where carnivores live in close proximity to humans, depredation of livestock results in significant economic losses. Many subpopulations of leopard and tiger, both carnivores at the top of the food chain, are threatened by loss of habitat, changes in prey species dynamics, human disturbance and climate change. Retaliatory killings by locals in areas with intensive conflict poses an extra threat towards their conservation and may have cascading effects on ecosystem functioning.

In Chitwan National Park (CNP) in Nepal, human- wildlife conflicts have intensified over the past few decades. The park consists of a core area and a buffer zone. There is also a corridor forest (Barandabhar Corridor) which connects CNP to the Hill forest in the North. Tiger and leopard abundance, prey species dynamics and levels of human disturbance differ between these three areas. This research compared the diets of tiger and leopard in an attempt to prioritize species and areas for conflict mitigating measures. Insights in their interaction and the identification of factors that contributed to the intensification of conflict in recent years is essential for tiger and leopard conservation.

The results indicate that leopard and tiger diets have a significant overlap, with differences in prey species preferences and occurrences. Livestock is mainly depredated by leopard and more in areas which experience higher levels of human disturbance. The data suggest that leopard density is highest at the periphery of the park.

This study contributes to the PhD research of Babu Ram Lamichhane and is supervised by the University of Antwerp (UA), Leiden University (LEI) and the NTNC Biodiversity Conservation Center in Nepal. The results of this study are implemented in Chitwan National Park (CNP) in Nepal.

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1. Introduction

1.1. General introduction

The recent human induced extinction of species has often been proclaimed to be the 6th mass extinction in the history of life (Barnosky *et al.*, 2011; Chapin *et al.*, 2000). Many species on the planet are threatened by local and even global extinction while most others have shown a decline in distribution and abundance over the last few centuries (Butchart *et al.*, 2010; Dirzo & Raven, 2003). These trends can be linked to the exponential growth of the global human population and the associated habitat destruction and species exploitation, especially after industrialization (McKee, Sciulli, Fooce, & Waite, 2004; Ripple *et al.*, 2014). This resulted in an alarming decline in species and an increase in human- wildlife conflicts (Baillie, Hilton-Taylor, & Stuart, 2004; Vié, Hilton-Taylor, & Stuart, 2009). Many wildlife species are now forced to live in close proximity to people which enhances the probability of conflict (Inskip & Zimmerman, 2009). Many of the larger mammals are confined to protected areas, often creating isolated populations that lost their connection with others, making these populations more vulnerable to inbreeding depression, stochastic changes and the increasing pressures on their habitat (Brüner, Gullison, Rice, & Da Fonsesca, 2001; Naughton-Treves, Holland, & Brendon, 2005; Woodroffe & Ginsberg, 2005).

Southeast Asia (SE Asia) is a global hotspot for biodiversity and endemism (Hughes, 2017). This region reflects the issues that the tropics face on a global scale (Hughes, 2017). Many ecosystems are threatened by a large array of drivers, which increases the probability of extinction for many species (Hughes, 2017). The greatest threats to regional biodiversity in SE Asia are deforestation, tree plantation (e.g. palm oil), (illegal) hunting and mining (Hughes, 2017). Many populations of large carnivores such as tiger (*Panthera tigris* Linnaeus, 1758) and leopard (*Panthera pardus* Linnaeus, 1758) are threatened as a result of these pressures (IUCN, 2016; Woodroffe, 2000). As top predators they play an important role in ecosystems and their extinction may result in cascading effects (Ripple *et al.*, 2014). Large carnivores are often used as umbrella species for conservation purposes (Karanth & Sunquist, 1995; Ripple *et al.*, 2014). Because of the high metabolic demands of large carnivores which are a result of large body size and endothermy, these carnivores often require large prey and large territories (Carbone, Teacher, & Rowcliffe, 2007; Ripple *et al.*, 2014). Due to these ecological requirements, leopards and tigers have been involved in human- wildlife conflict for centuries (Ripple *et al.,* 2014; Woodroffe & Ginsberg, 2005). Retaliatory killing of large carnivores by local communities is a severe threat towards already vulnerable subpopulations of these species. It poses one of the most important challenges for their conservation (Woodroffe & Ginsberg, 2005).

1.2. Tiger

The tiger (*Panthera tigris*) is the largest feline in the world (Seidensticker, Christie, & Jackson, 1999). There are six extant subspecies of tiger, including the Amur tiger (*P. t. altaica*), Northern Indochinese tiger (*P. t. corbetti*), Malayan tiger (*P. t. jacksoni*), Sumatran tiger (*P. t. sumatrae*), Bengal tiger (*P. t. tigris*) and the possibly extinct South China tiger (*P. t. amoyensis*) (Luo *et al.*, 2004). Tigers occupy a diversity of habitats, ranging from semi- arid deserts in India to the tropical rain forests of Sumatra (Indonesia) to the coniferous forests of Russia (Sunquist, M., Karanth, & Sunquist, F., 1993).

The range of the Bengal tiger, the studied subspecies, covers the majority of the Indian subcontinent, including Nepal (IUCN, 2016). Historically, tigers were widespread in most of Asia with an estimated population of 100,000 in the early 1900s (Dinerstein *et al.*, 2007). The species is listed as Endangered on the IUCN Red List of Threatened Species and has been pushed back to less than 7 percent of its original range with an estimated 3150 individuals left in the wild (IUCN, 2016). Main threats are habitat loss, human- wildlife conflicts and poaching (IUCN, 2016).

Tigers are territorial, solitary hunters, well equipped to ambush and capture large prey, sometimes even up to five times their own weight (Karanth & Sunquist, 1995). The Bengal tiger measures an average of 3m from head to tail, with adult males weighing 200-260 kg and adult females 100-160 kg (Sunquist, 2009). Their diet consists mainly of medium (50- 100 kg) to large (>100 kg) sized prey such as sambar (*Rusa unicolor* Kerr, 1792), chital (*Axis axis* Erxleben, 1777), wild boar (*Sus scrofa* Linnaeus, 1758), barking deer (*Muntjakus vaginalis* Boddaert, 1758) and others (Bhattarai & Kindlmann, 2012; Karanth & Sunquist, 1995). Prey density is the most important factor influencing tiger density, territory size, breeding performance and survival of cubs and juveniles (Karanth, Nichols, Kumar, Link, & Hines, 2004). The lower limit of female territory size in Chitwan National Park (CNP) is around 15-

20 km² (MCP), set by social intolerance (Smith 1993; Sunquist, 2009). Males have larger territories which overlap the territories of multiple females (Sunquist, 1981). Territory size may change during the breeding season as males try to acces female territories, often leading to violent confrontations with other males (Smith, 1993; Sunquist, 2009).

Tigers are prolific breeders with a short gestation period of 103 days and an average litter size of 3 cubs (Sunquist, 2009). Females first breed at the age of three years with an interbirth interval of around 20 months (Sunquist, 2009). In CNP, sub adults disperse at the age of 19-28 months old, 1 or 2 months after the mother gives birth to new cubs (Smith, 1993). The average dispersal distance of females is smaller than for males who often settle in territories of lower quality (Smith, 1993). Territories of young females are often found adjacent to their mothers. Dispersal movement can take from a few weeks up to 8 months (Smith, 1993). Dispersing sub- adults, older tigers and tigers with physical abnormalities that have been pushed out from core habitats are most often associated with human- wildlife conflict (Gurung, Smith, McDougal, Karki, & Barlow, 2008; Lamichhane *et al.*, 2017).

The tiger population in CNP has been estimated to be around 120 individuals (Table 1) (DOF, 2013). In recent years (1979- 2014) there has been a significant increase in human casualties (from 1.2/year to 7.2/year) as a result of intensifying conflict and habitat degradation (Dhungana *et al.*, 2017; Gurung *et al.*, 2008).

Table 1. Estimated tiger population size in Chitwan National Park and Nepal (Source: Department of Forestry (DOF), 2013; Karki *et al.*, 2015).

Year	**Chitwan**	**Nepal**	**Source**
1996	48-49	93-97	DOF (2013)
2000	50-60	106-133	DOF (2013)
2008	91 (71-147)	121 (100-194)	DOF (2013)
2010	125(95-183)	N/A	Karki *et al.* (2015)
2013	120 (98-139)	198 (163-235)	DOF (2013)

1.3. Leopard

The leopard (*Panthera pardus*), is the most widely distributed and adaptable large cat of the genus Panthera (Nowell & Jackson, 1996). Its range extends across much of Africa and Asia, from the Middle East to the Pacific Ocean (Jacobson *et al.*, 2016). The leopard has a large adaptability to different habitats which can result in genetic differentiation due to increased habitat fragmentation (Dutta *et al.*, 2013). A study carried out on the African subcontinent found that leopards occupy a diverse variety of habitats, ranging from tropical rain forests to semi-deserts, and from alpine mountains to the edges of urban areas (Balme, Hunter, & Slotow, 2007). Their ability to inhabit such a variety of landscape types is largely due to their highly adaptable foraging strategy (Balme *et al.*, 2007). Nine subspecies are recognized according to genetic analysis. These include *P. p. pardus* (Africa), *P. p. nimr* (Arabia), *P. p. saxicolor* (SW Asia), *P. p. melas* (Java), *P. p. kotiya* (Sri Lanka), *P. p. fusca* (Indian sub-continent), *P. p. delacouri* (SE Asia- S China), *P. p. japonensis* (N China) and *P. p. orientalis* (SE Russia, Korean peninsula & NE China) (Uphyrkina *et al.*,2001). *Panthera pardus fusca* is the subspecies present in the study area.

Leopards are visual hunters, relying heavily on sight and to a lesser extent on hearing to detect prey (Sunquist & Sunquist 2002). Leopards are considered to be catholic predators of more than a hundred small (<50 kg) to medium (50- 100 kg) sized prey species, but their common kill is between 10 and 40 kg, with an optimum weight of 23 kg (Hayward *et al.* 2006).

The age at first reproduction in CNP was estimated to be 2-3 years and young leopards dispersed from their mother when they were 12-18 months old (Sunquist, 1981). Leopards are territorial and males mark their territory with urine (Ahlbom & Jackson, 1986). Acquiring a territory is related to breeding, individuals without a territory do not breed, even when they are sexually mature (Sunquist & Sunquist, 2002). The home ranges (Fixed kernel, 95%) of three leopards in the subtropical forest of Bardia National Park (BNP) were estimated with the help of VHF radio-telemetry and found to be around 47.4 km² for two males and around 17 km² for one female (Odden & Wegge, 2005). Male home ranges often overlap with those of several females (Odden, 2007). Home range is also related to the reproductive status of the female and was found to be smallest when the female leopard was with cubs less than 6 months old (Odden, Wegge, & Fredriksen, 2010). Males of polygynous species such as leopards have been found to more frequently cause conflicts with humans compared to females due to inherent higher risk-taking behavior (Sukumar, 1991).

The Indian leopard (*Panthera pardus fusca*) is only found on the Indian sub- continent. Ngoprasert, Lynam and Gale (2007) found that human activity influences the diurnal activity and habitat use of the Indian leopard which poses a threat to leopard population persistence.

The subspecies is globally listed as Vulnerable on the IUCN Red List of Threatened Species and only occupies 25- 37% of its historic range (Jacobson *et al.*, 2016). Poaching, habitat loss, human- wildlife conflicts and the negative effects of the interaction with tigers have resulted in a decline of most subpopulations across their range (IUCN, 2017). Several subspecies and regional populations are considered Critically Endangered (Jacobson *et al.,* 2016) It is estimated that there are less than 10,000 individuals left in the wild (IUCN, 2017).

The leopard population in and around CNP is estimated to be around 57 individuals (Table 2) (Thapa, 2011). The data suggest that leopard numbers have slightly increased in CNP from 2008 to 2010 (Thapa, 2011).

Table 2. Leopard population size estimates in and around Chitwan National Park (Source: Thapa, 2011).

Year	Population size
2008- 2009	37±5.49
2010	57±9.94

1.4. Interaction between tiger and leopard

Tiger and leopard are known to be sympatric carnivores across most of their range, meaning they are present in the same geographic area and may encounter one another. However, in some areas the nature of their co-existence is conflicting (Bhattarai & Kindlmann, 2012; Odden *et al.*, 2010). Tiger and leopard have substantial dietary overlap, both predating on small to large sized ungulates but there are differences in prey selection (Karanth & Sunquist, 1995; Odden, 2007) . While tiger prefers medium (50- 100 kg) to large (>100 kg) sized prey, leopards show a preference towards small (<50 kg) to medium (50- 100 kg) sized prey resulting in an overlap of preference for medium sized prey (Bhattarai & Kindlmann, 2012). Harihar, Pandav and Goyal (2011) reported that the reintroduction of tigers in Rajaji National Park, India caused a shift in the diet of leopards towards a significantly higher intake of domestic prey as well as a sharp decline in leopard density. They argue that it is important for conservation initiatives that aim to restore tiger populations to first carefully examine the local interspecific interactions between sympatric carnivores (Harihar *et al.*, 2011).

Leopards in CNP and Bardia National Park, Nepal (BNP) are primarily nocturnal and their activity pattern is influenced by the presence of tigers in the sense that leopards tend to avoid tigers (Odden *et al.*, 2010; Seidensticker, 1990). Støen and Wegge (1996) reported that in spite of the high prey biomass and diversity, leopards are displaced to the borders of BNP, suggesting that interspecific predation rather than food competition excluded coexistence with tigers. In a later study, Odden *et al.* (2010) argue that interference competition is the main reason why leopards show a preference for the periphery of the park in BNP. Leopards are also less active than tigers in the same area, both during day time as well as during night time (Seidensticker *et al.*, 1990; Sunquist, 1981). Interference competition is stronger between both species when the abundance of prey species is low and the overlap in diets increases (Odden *et al.,* 2010). A recent study on tiger diets in CNP suggests that predation of medium sized domestic animals is higher when abundancy of large prey species is low (Bhandari, Chalise, & Pokharel, 2017). The leopard predates more on livestock, small mammals and birds in areas where both species are present (Bhattarai & Kindlmann, 2012; Odden *et al.,* 2010).

1.5. Diet study

Understanding the diet of sympatric tiger and leopard populations is useful for long term population management because it may explain the drivers of increasing conflict with humans (Bhandari *et al.,* 2017). Kolipaka *et al.* (2017) found that the preference of tiger for domestic prey in areas with free roaming cattle in Panna NP (Madya Pradesh), depends on distance from core area, tiger age- group, tiger sex and season. Free-for-all livestock grazing has a negative impact on large carnivore conservation in reserves where tigers are reintroduced as it increases human- wildlife conflict (Kolipaka *et al.,* 2017). Herding cattle is not allowed in the core area of CNP in Nepal, but it is allowed under certain conditions in both the buffer zone and the Barandabhar corridor forest (Gurung, Nelson, & Smith, 2009; Gurung *et al.,* 2008; Nepal & Weber, 1994). As this could have an impact on the incidence of conflict (i.e. the occurrence of human encounters and livestock depredation), these areas should get extra attention for conservation efforts. A diet study can give insight in the diet composition and preferred prey species of tiger and leopard. The results of a diet study may support future conservation practices to reduce conflict. Keeping cattle inside corrals or setting up a strict seasonal grazing pattern for these areas can contribute to reduce conflict (Gurung *et al.,* 2009; Kolipaka *et al.,* 2017). Another option is to enhance natural prey populations of tiger and leopard (Bhattarai & Kindlmannn, 2012; Gurung *et al.*, 2008). This may give carnivores less incentives to move outside of the reserve in search of other prey such as livestock. The overall diet and prey preference of tiger and leopard have been studied in the past (Bhattarai &

Kindlmann, 2012). However, in cases of human wildlife conflicts it is advised to use strategies for an area that are situation specific (Inskip & Zimmerman, 2009). In order for conflict prevention and mitigation efforts to be effective, the study area and all its aspects which are involved in the intensifying conflict need to be identified (Inskip & Zimmerman, 2009). In combination with diet data from previous years, data on the spatial dynamics of tiger and leopard, previous conservation efforts and sociological surveys, this study intends to contribute to an up-to-date assessment of the conflict and its potential solutions.

1.6. Research questions and hypothesis

The aim of this research is to analyse the diet and prey preference of tigers and leopards in and around Chitwan National Park and identify potential competition. The factors which explain differences in diet such as interaction effects, prey species density/availability effects, and other spatial and temporal change effects are determined by comparing three areas under different management regimes.

1.6.1. Research questions:

1) What is the overall diet composition of tigers and leopards and is there a difference between the two species in space (core area, buffer zone & corridor) and time (months, years)?
2) What is the contribution of wildlife, livestock and small prey (birds, rodents) in the diet of tiger and leopard in time and space?
3) What is the density of the prey and do tiger and leopard show a preference for certain prey species in time and space?
4) Which factors contribute to changes in time and space in the diets of leopard and tiger?

1.6.2. Hypothesis:

i) Because of a high density of tigers inside the core area, leopards are pushed to the buffer zone and corridor forest and become more involved in livestock raiding.

ii) Scat of both leopard and tiger collected in the core area contains a smaller proportion of domestic animals compared to scat collected in the buffer zone and corridor forest.

2. Methods and materials

2.1. Study area

This study was conducted in Chitwan National Park (CNP) and its buffer zone in Nepal (Fig. 1), including the Barandabhar Corridor Forest (Fig. 2). The latter bisects the Chitwan District in East and West Chitwan (Lamichhane *et al.*, 2018). Chitwan National park is a World Heritage Site with a unique assemblage of species , both flora and fauna (UNESCO, 2009). It is located in the lower Terai region in Nepal, close to the border with India. The park covers a large diversity of habitats varying from ‘Sal’ forest (80%) and grasslands (12%) to alluvial flood plains (5%) and water bodies (3%) (Thapa, 2011). The deciduous and semi- deciduous forests on the higher elevations are dominated by Sal (*Shorea robusta* G. f.) whilst the riverine forest in the lowland areas mostly consists of *Bombax ceiba* L. and *Trewia nudiflora* L. (Bhattarai & Kindlmann, 2012). It is one of the major national parks where tigers are still present on the Indian subcontinent with a viable population of around 125 individuals (Karki *et al.*, 2015). Due to the presence of this population, CNP is considered an important area for tiger conservation globally (Wikramanayake *et al.*, 1998). CNP holds the second largest population of greater one-horned rhinoceros (*Rhinoceros unicornis* Linnaeus, 1758) in the world with the latest estimate of around 600 individuals (CNP, 2015). Other important species present are the Indian elephant (*Elephas maximus indicus* Linnaeus, 1758), Gaur (*Bos gaurus* C. H. Smith 1827), Sloth bear (*Melursus ursinus* Shaw, 1791), Great hornbill (*Buceros bicornis* Linnaeus, 1758) and Gharial crocodile (*Gavialis gangeticus* Gmelin in Linnaeus, 1789) (Bhattarai & Kindlemann, 2012; CNP, 2015). In total there are about 70 mammal species, over 600 bird species, 49 species of reptiles and amphibians, 156 butterfly species and 120 species of fish present in the park (CNP, 2015). The park consists of a core area with a total surface area of 932 km², surrounded by a buffer zone which covers a surface area of about 750 km² (Bhattarai & Kindlmann, 2012). The buffer zone is made up of 55% agricultural land and 45% community forest. The buffer zone on the north side of the park lies adjacent to the Barandabhar Corridor Forest, dominated by Sal forest, grassland and a few large water bodies (Lamichhane *et al.*, 2018). This wildlife corridor connects CNP to the Mahabharat Mountain Range in the North and is partly protected as a Ramsar Site due to the presence of 328 species of birds that live in proximity of the large waterbodies (Lamichhane *et al.*, 2018).

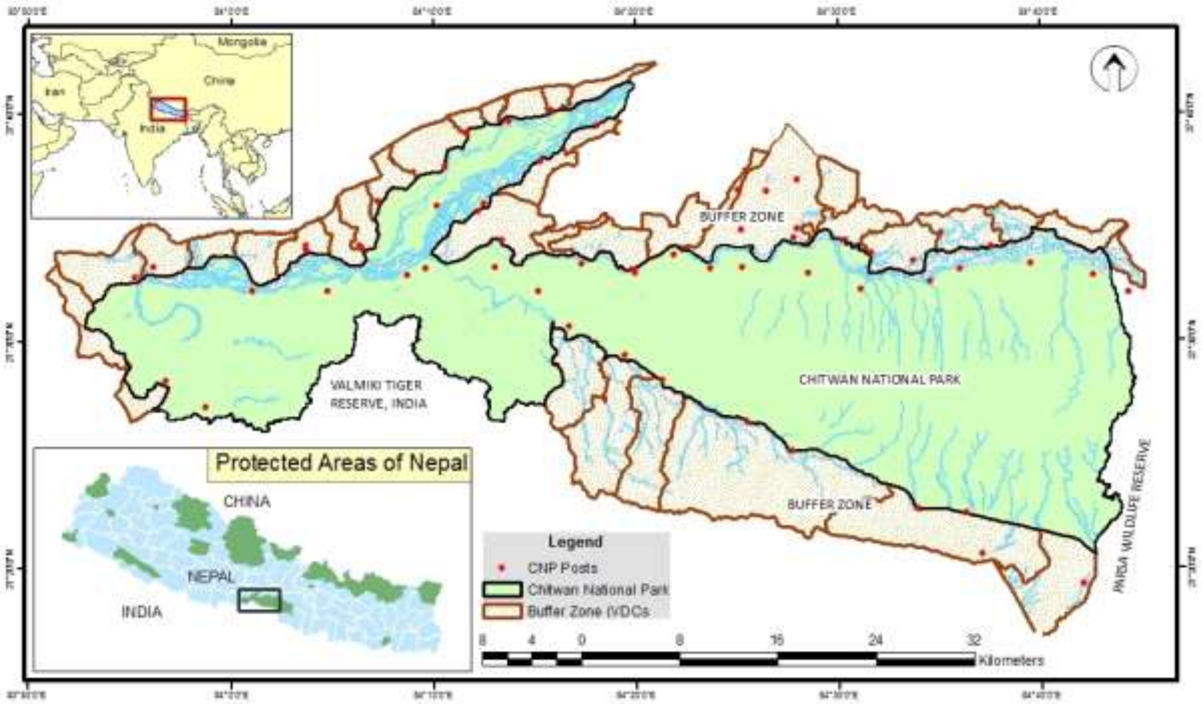

Figure 1. Map indicating Chitwan National Park and buffer zone (Source: NTNC, 2017).

In this study, the corridor forest (CO) is considered that part of the Barandabhar corridor forest that lies outside of the buffer zone (Fig. 2). Core area (CA), buffer zone (BZ) and corridor forest (CO) are assumed to experience different degrees of human disturbance. The core area only experiences a small degree of human disturbance in the form of tourism and is completely surrounded by the buffer zone. Guided walking tours and car tours only cover a small proportion of the park, resulting in almost no disturbance in the majority of the core area. Grazing practices and fodder collection are prohibited (some exceptions: e.g. elephant owners). The buffer zone is meant as a transition area which connects the core area to the villages surrounding the park. Sustainable livestock grazing and fodder collection is allowed in this area under certain conditions (Gurung *et al.*, 2009; Nepal & Weber, 1994). The buffer zone is assumed to be under a mediocre degree of human disturbance. The corridor forest is bisected by a busy highway. It is surrounded by villages on all sides, except for two small sections in the North and South (Fig. 2) and sustainable grazing practices as well as fodder collection are allowed (Gurung *et al.*, 2009). The corridor forest is assumed to experience a high degree of human disturbance.

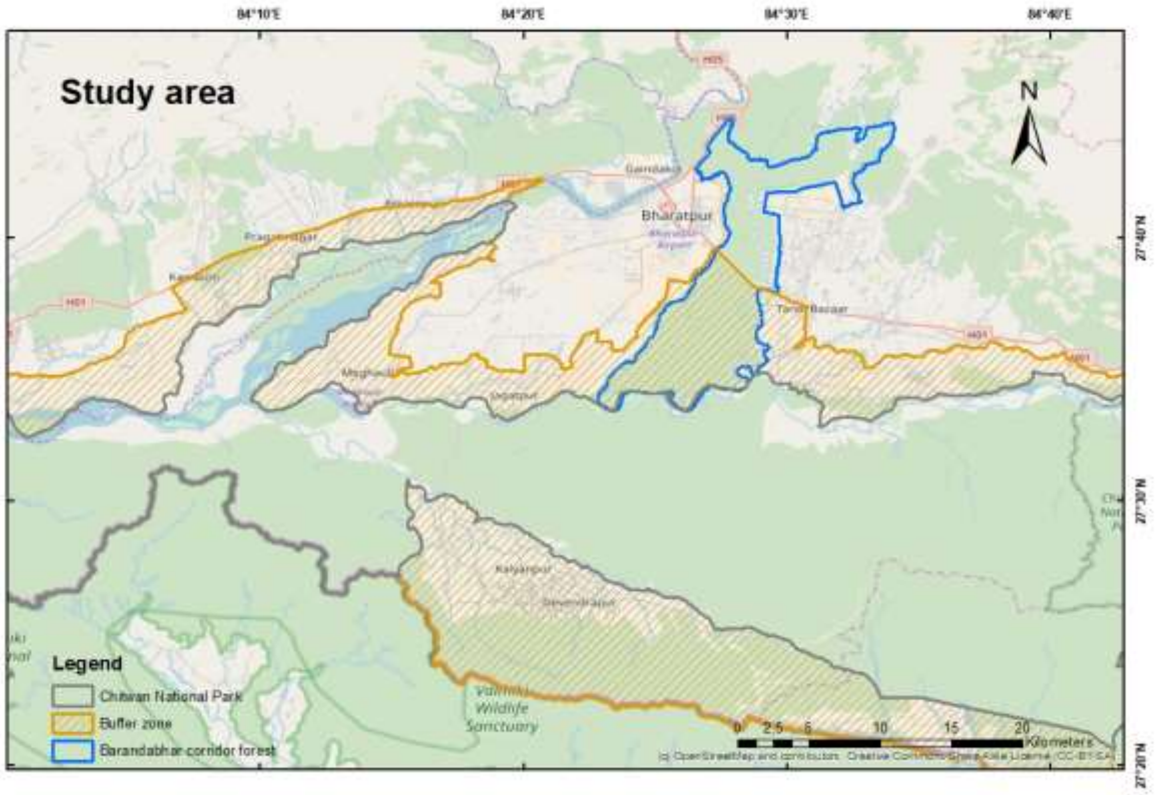

Figure 2. Map indicating the study area including the core area (map: Chitwan National Park), buffer zone and the Barandabhar corridor forest.

2.2. Data collection

For this study, microscopic analysis of prey hair morphology from scat was used to determine the diets of leopard and tiger (Ramakrishnan, Coss, & Pelkey, 1999). This is a noninvasive method (see also Bhattarai & Kindlmann, 2012). Scats were collected and analysed over a period of almost four months (12 January until 4 May 2017) in three different areas, namely core area (CA), buffer zone (BZ) and corridor forest (i. e. the part of the Barandabhar corridor forest that lies outside of the buffer zone) (CO) (See Fig. 2). Transects of different length were walked or covered by motorcycle. Differentiation between tiger and leopard scats was based on the signs in proximity (<20m) of the scat and the identification by expert technicians (Odden *et al.*, 2010). Signs include length of scratch marks, other deposits, pugmarks and smell. Collected scats were dried and then washed using a sieve (pore size: 0.5 mm ø) until only hair, feathers and bones remained. These samples were then dried in open air and inserted in an envelope for further drying.

2.3. Scat analysis

Next, scat samples were analysed according to the method of Ramakrishnan *et al.* (1999). First, the gross morphological features of the prey hairs including colour, texture and basal shape were determined and photographed with a Canon Digital Camera (model: IXUS 85 IS). Signs of birds or rodents such as feathers and small skulls were noted. Second, from each envelope 20-30 hairs were randomly selected and analysed using the reference guide by Bahuguna, Sahajpal, Goyal, Mukherjee and Thakur (2010) and the hair reference collection available at NTNC. This reference collection includes photographs of hair cuticular patterns of 8 wild prey species and 7 domesticated prey species. Hairs were first briefly washed in ethanol for about five minutes and afterwards dried on filter paper. Next, a thin layer of clear nail polish was applied to clean glass slides and the hairs were mounted on the slide. After the nail polish had dried (about 10 min.), the hairs were removed, leaving an imprint. The slides were then placed under the microscope at x400 magnification where the medullary pattern was matched with the available patterns on the reference slides. Additionally, pictures were taken of the apical, medial and basal part of the medullary pattern with a Coslab Digital Camera (model: MDCE- 5C) for each hair imprint. For all hair samples both the gross morphological features and the cuticular pattern were used in the analysis. The majority of the prey species determination was done afterwards using the pictures.

Prey species were classified in different categories based on their weight (Bhattarai & Kindlemann, 2012; Tuqa, 2015). Weight classes differed slightly from previous studies, but the methodology is similar. Very small prey (<10 kg) (vs) including birds, rodents and rhesus macaque (*Macaca mulatta* Zimmerman, 1780) were considered as a separate category. Small prey (10-50 kg) (s) include the indian muntjac, nepal gray langur (*Semnopithecus schistaceus* Hodgson, 1840) and domestic dog (*Canis lupus* Linnaeus, 1758). Chital, Indian hog deer (*Axis porcinus* Zimmerman 1780), domestic goat (*Capra hircus* Linnaeus, 1758) and wild boar are considered medium sized prey (50- 100 kg) (m). Sambar, sloth bear, domestic buffalo (*Bos bubalis* Linnaeus, 1758), cattle (*Bos indicus* Linnaeus, 1758) and gaur are considered large sized prey (>100 kg) (l).

2.4. Prey species density

Prey species densities where estimated using data from reports available at NTNC. For the comparison between the three different areas, data of previous years from these areas has been used (2016-2017) with the assumption that prey composition had not changed significantly during 2016 and 2017. The latest survey of prey species density for the core area was conducted in April 2016 (Appendix A). NTNC implements annual prey density surveys in parts of the core area, buffer zone and corridor forest on elephant back through distance sampling based line transects (Khadka, Lamichhane, & Aryal, 2016). For the corridor area data were collected during May 2017 using a similar method (Appendix B). The raw dataset of this survey was used to estimate relative prey species availability in both buffer zone and corridor forest. Not enough data were available to calculate exact prey species density values or available prey biomass for most species. Count data gathered during the surveys was therefore used to calculate the prey availability along the transects. Prey availability is here defined as the number of counts of a single prey species divided by the total of prey species counted during the survey. It was assumed that prey availability along the transects did not differ significantly from prey availability in the whole park and corridor. Thus, relative prey availability from the surveys was used as a proxy for prey availability across the entire area.

2.5. Data analysis and statistics

All statistical analysis was performed using the software Rstudio version 3.0.2 (R foundation, Vienna). Data were tested on normality using Shapiro tests, where $W>0.9$ means that the data follow a normal distribution. Test results were assumed significant for significance levels of ($p<0.05$).

Jacobs indices were calculated to look for prey species preference for both tiger and leopard in the three different areas (i) core area (CA), (ii) buffer zone (BZ) and (iii) corridor forest (CO) (Jacobs, 1974). The relative proportion of prey species sightings along the transect was used as a prey population index for the area.

$$E = \frac{r - p}{r + p}$$

E= Jacobs Index, indicates whether there is a preference for the considered prey species

r= % prey species in diet

p= % available prey in the environment of the predator

The outcome of a Jacobs index is a value between -1 and 1, where the first represents a strong dislike and the latter represents a strong preference for the considered prey species (Jacobs, 1974). Livestock was excluded from the prey species preference calculations in the core area, as grazing of livestock is illegal and no domestic animals were seen during the transect counts. However, Sharma and Shaw (1993) found that practices such as illegal livestock grazing and fodder collection do occur inside CNP. In a more recent study, Gurung *et al.* (2009) reported that even with stricter grazing regulations, illegal grazing is still an issue in and around CNP probably due to the fact that poorer households with insufficient agricultural land are pushed to meet their resource needs in protected areas. Although no livestock was recorded during the transect counts in the wildlife corridor, grazing is allowed under certain conditions in both BZ and CO (Gurung *et al.*, 2009; Nepal & Weber, 1994) . Therefore, livestock was included in the prey species preference calculations for these areas. For birds, it was not possible to distinguish between livestock or wild species. Additionally, the transect counts only included large bird species. Because of this, birds were also left out of the prey preference calculations.

Chi square tests and Fisher's exact tests (for tables that contained cells with counts <5, simulated p-value with >=2000 replicates) were used to find out differences in the overall diet between tiger and leopard and in the distribution of prey items for different prey species between years.

Generalized linear models (GLM, family='binomial') were used to test for significant differences in the contribution of wildlife, livestock and birds to the diet between the three areas as well as between tiger and leopard. Two by two comparisons were done utilizing post-hoc Tukey tests to find significant differences. The diet data matrix was split up to obtain four dependent factors consisting of wildlife, livestock, birds and other. All prey species presences and absences in the data matrix where assigned to one of these four classes. Species (tiger or leopard) and location (core area, buffer zone or corridor) were considered as independent factors explaining the variation in the model.

3. Results

3.1. Data collection

In total 207 scats were collected of which 2 were discarded because of uncertainty of the carnivore species. Out of the remaining 205 scats, 57 were identified to belong to leopard and 148 to tiger (Table 3). For tiger, a total of 79 scats were collected in the core area. In the buffer zone and corridor together 69 scats were collected. For leopard, most scats were collected in the buffer zone and corridor together (47 scats) and only 10 leopard scats were found in the core area of the park. The small sample sizes for leopard in both core area and corridor are a limiting factor for statistical analysis. Distribution of scats found across the different areas differed significantly between tiger and leopard (Chi-squared, $\chi^2=26.04$, df=2, p- value= 2.21*10^-6) (Table 3).

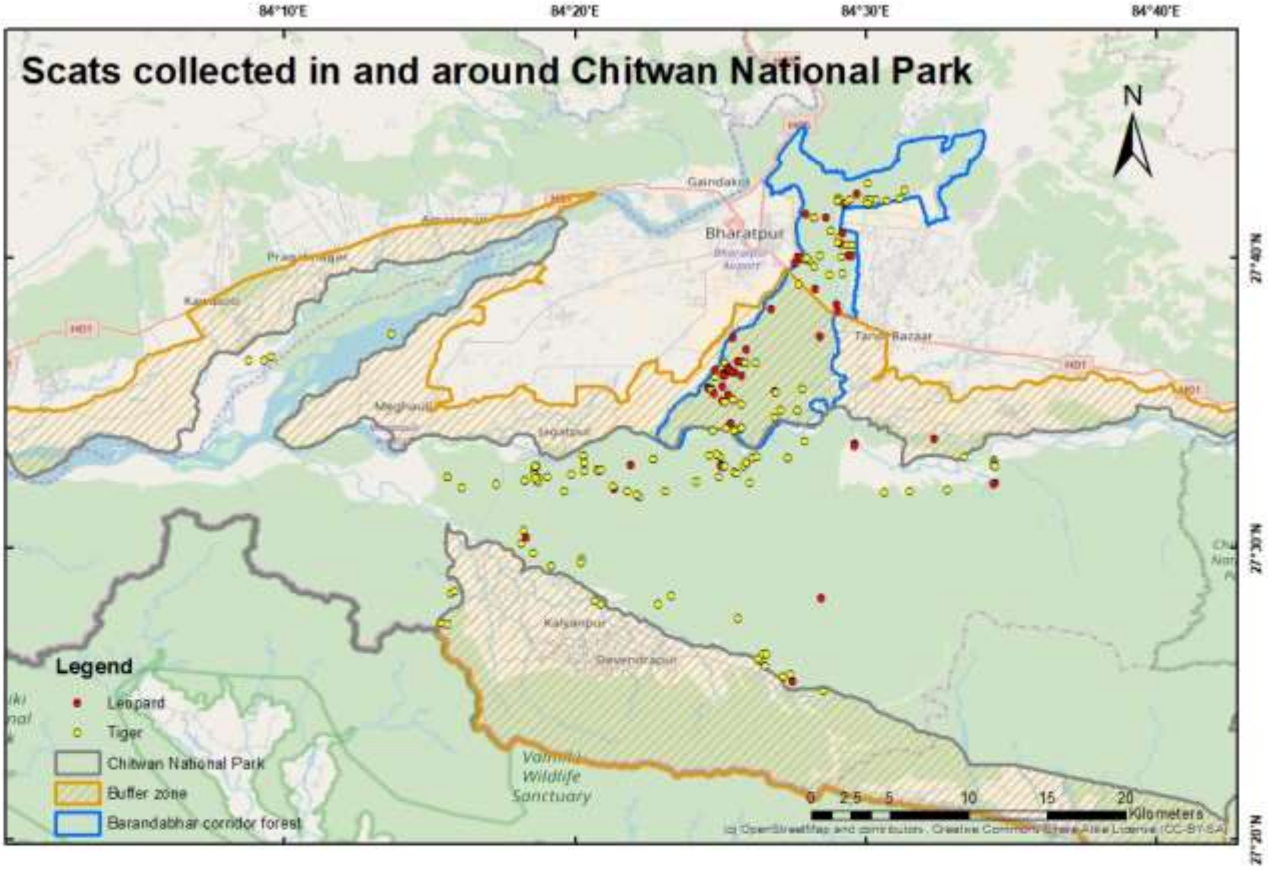

Figure 3. Map showing the location of all scats collected in 2017. Scats were collected across three areas: core area, buffer zone and corridor forest.

Table 3. Total of scats collected for tiger and leopard per area.

	Tiger	Leopard	**Total per area:**
Core area	79	10	89
Buffer zone	36	33	69
Corridor forest	33	14	47
Total per species	148	57	205
Total used	129	52	181

Some samples (n=24) could not be analyzed due to the lack of hairs and other material after washing. Prey species present in 129 of the 148 tiger scats and 52 out of the 57 leopard scats were properly identified.

3.2. Diet comparison

Most samples (>90%) contained a single prey species. Only 6 samples (5%) of tiger and 1 sample (2%) of leopard scats had two prey items. To determine the prey species present in the unidentified samples, DNA analysis has to be performed which is a relatively expensive and time consuming process. For logistical reasons, hair samples could not be exported from Nepal to Belgium. Because of this, these samples were not used in further statistical analysis.

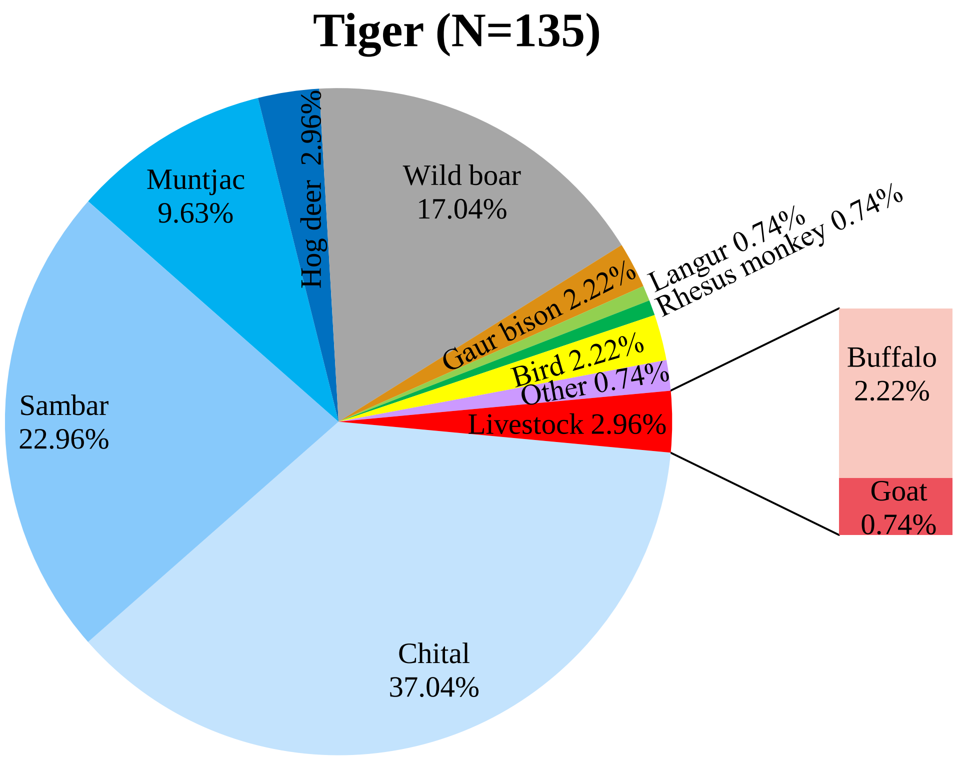

Figure 4. Diversity of tiger diet across CA, BZ and CO combined (blue= deer, green= primates, yellow= birds, red= livestock).

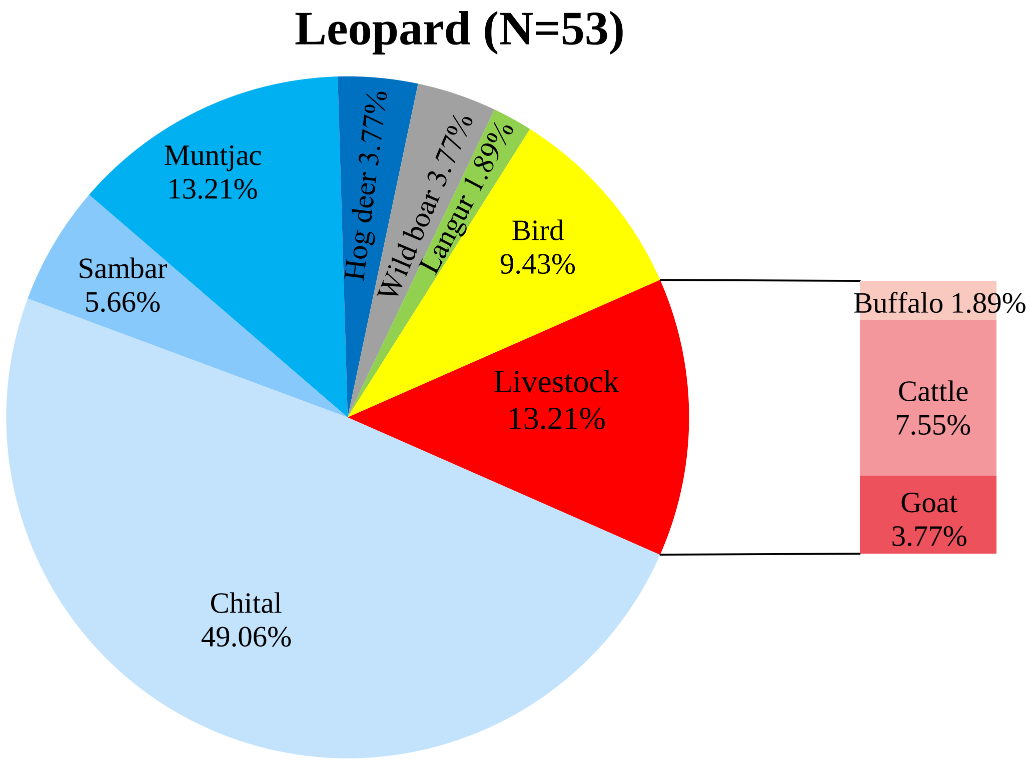

Figure 5. Diversity of leopard diet across CA, BZ and CO combined (blue= deer, green= primates, yellow= birds, red= livestock).

Table 4. Total counts and relative frequency of occurrence of prey items in the diet of leopard and tiger across all three areas.

	Tiger	Tiger (%)	Leopard	Leopard (%)	Sum	Sum (%)
Chital	50	37.04	26	49.06	76	40.43
Sambar	31	22.96	3	5.66	34	18.09
Muntjac	13	9.63	7	13.21	20	10.64
Hog deer	4	2.96	2	3.77	6	3.19
Wild boar	23	17.04	2	3.77	25	13.30
Gaur bison	3	2.22	0	0.00	3	1.60
Langur	1	0.74	1	1.89	2	1.06
Rhesus monkey	1	0.74	0	0.00	1	0.53
Bird	3	2.22	5	9.43	10	4.26
Buffalo	3	2.22	1	1.89	4	2.13
Cattle	0	0.00	4	7.55	4	2.13
Goat	1	0.74	2	3.77	3	1.60
Other	2	1.48	0	0.00	2	1.06
Total:	135	100	53	100	190	100

A total of 12 prey species were found and 2 samples were not identified to species level due to the lack of reference material and classified as ‘other’ (Fig. 4). A significant difference was found in the overall diet between tiger and leopard (Fisher’s Exact Test, p- value=0.005). The results suggest that the relative contribution of wild boar (17.04%) and sambar deer (22.96%) to the tiger diet is larger compared to the leopard diet (3.77% and 5.66%). Chital (49.06%) and muntjac (13.21%) make up a bigger percentage of the leopard’s diet compared to tiger (37.04% and 9.63%). Cattle was only found in leopard diet (7.55%) and rhesus monkey only in tiger diet (0.74%). All other prey species make up a similar amount of both diets (Table 4).

Table 5. Counts and relative frequency of occurrence of very small (vs), small (s), medium (m) and large (l) prey size classes for tiger and leopard across all three areas. The category ‘other’ (2 prey items) was left out of this table resulting in a total of 135 prey items for tiger.

		Tiger	Tiger (%)	Leopard	Leopard (%)
Prey class	Very small (<10 kg)	4	4.44	5	9.43
	Small (10-50 kg)	14	10.37	8	15.09
	Medium (50-100 kg)	78	57.78	32	60.40
	Large (>100 kg)	37	27.41	8	15.09
	Total:	133	100	53	100

No significant difference in the distribution of prey items in different prey classes between both species was found although the data suggest that the diet of tigers contains relatively less small prey and more large prey compared to leopard (Table 5).

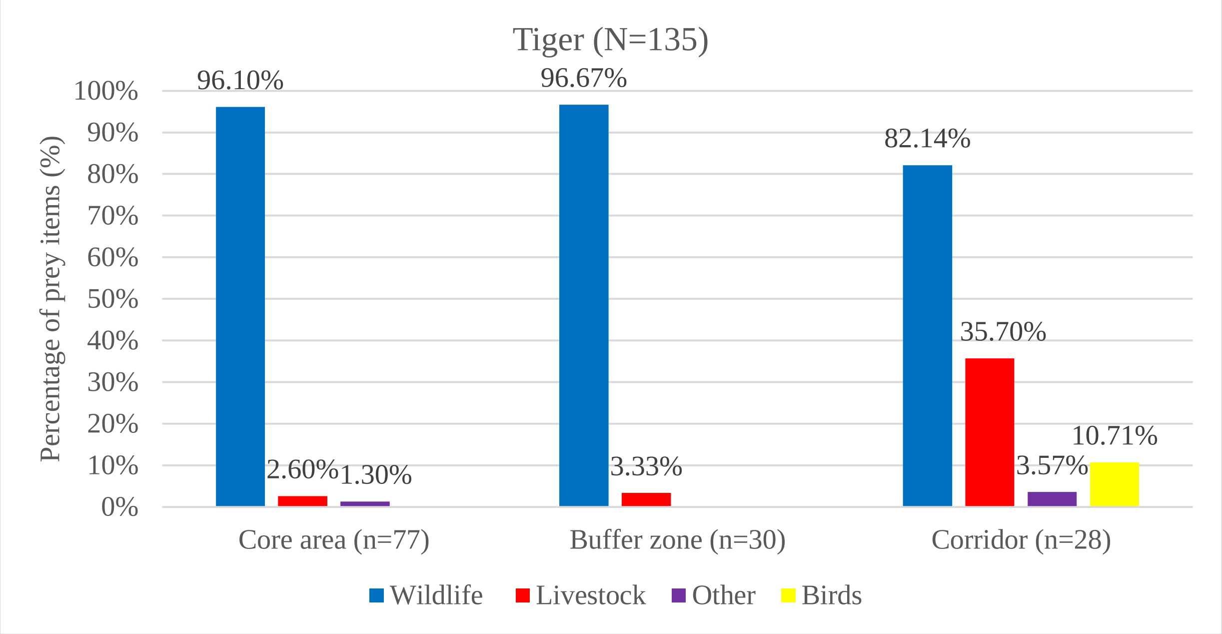

Figure 6. Relative frequencies of prey items expressed as percentage of wildlife, livestock, birds and other present in tiger scat.

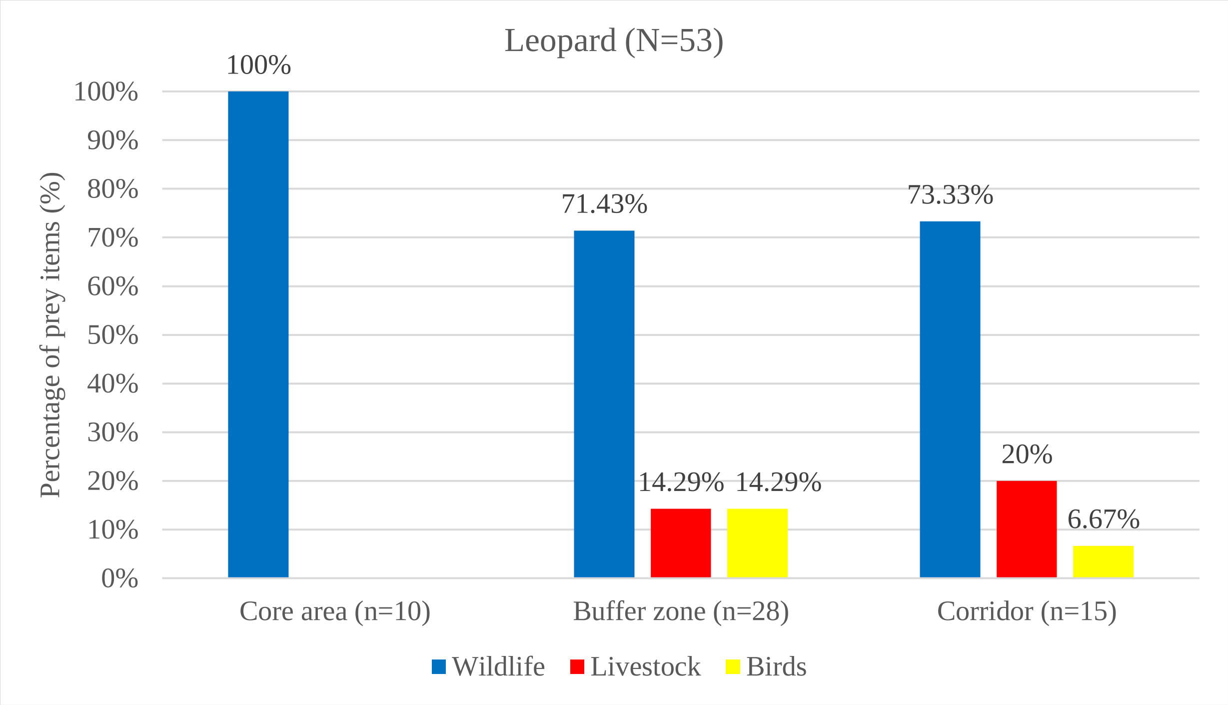

Figure 7. Relative frequencies of prey items expressed as percentage of wildlife, livestock and birds present in leopard scat.

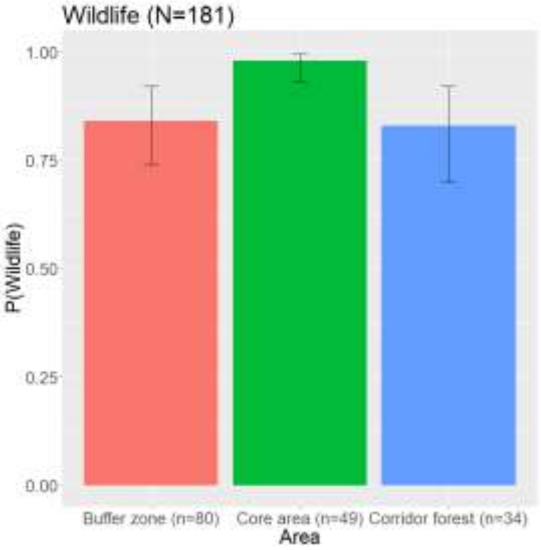

Figure 8. Differences in the proportion of wildlife found in scats of tiger plus leopard between the three different areas. Scats in the core area (green) (0.98) contain a significantly higher amount of wildlife than those found in the buffer zone (red) (0.84) and corridor forest (blue) (0.83) (source: GLM, R version 3.4.1, package 'ggplot2'). Error bars represent 95% confidence intervals on the estimates.

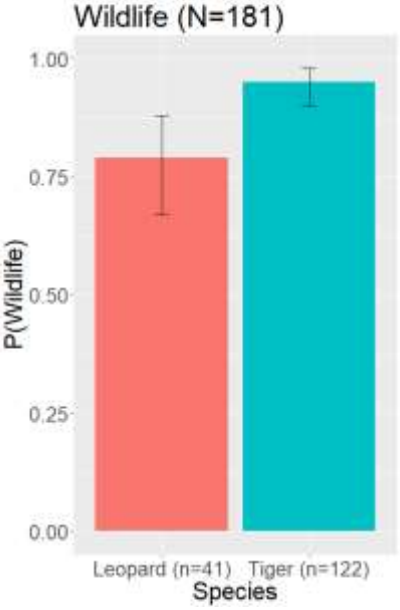

Figure 9. Differences in proportion of wildlife found in scats of tiger versus leopard. Scats of tiger (blue) contain a significantly higher amount of wildlife (0.95) compared to leopard (red) (0.79) (Source: GLM, R version 3.4.1, package (ggplot2'). Error bars represent 95% confidence intervals on the estimates.

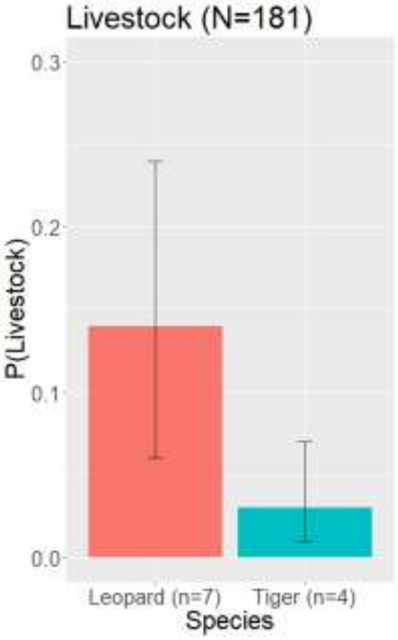

Figure 10. Difference in contribution of livestock to the diet between tiger and leopard. A significant difference between both species was found, with the leopard having significantly more livestock in its diet compared to the tiger (source: GLM, R version 3.4.1, package ‘ggplot2’). Error bars represent 95% confidence intervals on the estimates.

There is some variation in the contribution of livestock, wildlife and birds to the diet of tiger versus leopard as well as between the different areas (Fig. 6 & 7). To find if any of these variations are statistically significant, p-values were computed using the GLM’s. For neither wildlife, livestock nor birds a significant interaction between species and location was found. Scats found in the core area contain a significantly higher proportion of wildlife (0.98) than those found in the corridor forest (0.83) (GLM, df=2, z-value=-2.48, p- value =0.028) (Fig. 8). Scats found in the core area (0.98) contain significantly more wildlife than in the buffer zone (0.84) (GLM, df=2, z-value= -2.548, p- value= 0.033) (Fig. 8). No significant difference between CO and BZ was found in the occurrence of wildlife prey items in scats. Tiger scats (0.95) contain a significant larger share of wildlife prey compared to leopard scats (0.79) (GLM, df= 1, z-value = 2.989, p-value= 0.0028) (Fig. 9). A significantly larger proportion of leopard scats contains livestock (0.14) compared to tigers (0.03) (GLM, df= 1, z-value = -2.43, p-value =0.015) (Fig. 10). No significant difference in contribution of livestock to the diet between the three areas was found. No birds were found in the core area and there is no significant difference in the relative proportion of birds or ‘other’ prey items between areas or species.

3.3. Prey species availability and preference

In the core area, the density estimate was 132 ± 19 animals per km² for all prey species combined (chital, sambar, hog deer, muntjac, wild boar, birds and others) whereas the density of chital and hog deer was 88 ± 26 and 45 ± 20 per km² respectively. Due to a smaller number of detections for other species, the density could not be estimated. Thus, counts (number of animals detected during survey) were used and extrapolated to the whole core area to represent the relative prey availability (Table 7 & 8). Chital (70%), Hog deer (22%) and species under the category 'other' are the most available prey (Table 7 &8). Similarly, prey species counts from transect surveys were used for buffer zone and corridor forest. Chital (91%), sambar (3.7%) and wild boar (3%) show the highest prey availability (Table 9, Table 10, Table 11 and Table 12).

Table 6. Species availability (April 2016), diet contribution and Jacob index calculations for tiger in core area. Total of 'Diet contribution in %' is not 100 due to the finding of cattle and birds in some samples which make up the missing 2.59% of the diet .

Tiger (CA)					
Species	**Count**	**Availability in %**	**Diet contribution in %**	**Jacobs index**	**Preference**
Chital (m)	353	70.32	29.87	-0.40	No
Sambar (l)	3	0.60	31.17	0.96	Yes
Hog deer (m)	109	21.71	3.90	-0.70	No
Muntjac (s)	8	1.59	7.79	0.66	Yes
Gaur (l)	0	0	1.30	1	Yes
Wild boar (m)	7	1.39	19.48	0.87	Yes
Rhesus monkey(s)	0	0	1.30	1	Yes
Langur (s)	0	0	1.30	1	Yes
Other	17	3.39	1.30	-0.45	No
Total	502	100	97.41		

Table 7. Species availability (April 2016), diet contribution and Jacob index calculations for leopard in core area.

Leopard (CA)					
Species	**Count**	**Availability in %**	**Diet contribution in %**	**Jacobs index**	**Preference**
Chital (m)	353	70.32	60	-0.08	No
Sambar (l)	3	0.60	20	0.94	Yes
Hog deer (m)	109	21.71	0	-1	No
Muntjac (s)	8	1.59	0	-1	No
Gaur (l)	0	0	0	0	Neutral
Wild boar (m)	7	1.39	10	0.76	Yes
Rhesus monkey(s)	0	0	0	0	Neutral
Langur (s)	0	0	10	1	Yes
Other	17	3.39	0	-1	No
Total	502	100	100		

Table 6 and Table 7 show that tiger and leopard have a pronounced preference for sambar (T: 0.96, L: 0.94), wild boar (T: 0.87, L: 0.76) and langur (T:1, L:1) in the core area. Chital, although abundant, is not preferred by either feline but this avoidance effect is much stronger in tiger (T: -0.40, L:-0.08) (Table 6 & 7). Hog deer are not preferred by either species (Table 6 & 7) Rhesus monkey, gaur and muntjac are preferred by tiger but not by leopard (Table 6 & 7).

Table 8. Species availability (May 2017), diet contribution and Jacob index calculations for tiger in buffer zone. Birds make up the missing 6.24% in the total of diet contribution.

Tiger (BZ)					
Species	**Count**	**Availability in %**	**Diet contribution in %**	**Jacobs index**	**Preference**
Chital (m)	513	91.12	46.67	-0.32	No
Sambar (l)	21	3.73	13.33	0.56	Yes
Hog deer (m)	2	0.36	0	-1	No
Muntjac (s)	9	1.60	16.67	0.82	Yes
Gaur (l)	0	0	0	0	Neutral
Wild boar (m)	17	3.02	20	0.74	Yes
Rhesus monkey(s)	1	0.18	0	-1	No
Langur (s)	0	0	0	0	Neutral
Buffalo (l)	0	0	0	0	Neutral
Goat (m)	0	0	3.33	1	Yes
Cattle (l)	0	0	0	0	Neutral
Other	0	0	0	0	Neutral
Total	563	100	93,76		

Table 9. Species availability (May 2017), diet contribution and Jacob index calculations for leopard in buffer zone. Birds make up the missing 7.69% in the total diet.

Leopard (BZ)					
Species	**Count**	**Availability in %**	**Diet contribution in %**	**Jacobs index**	**Preference**
Chital (m)	513	91.12	43.86	-0.35	No
Sambar (l)	21	3.73	3.57	-0.02	No
Hog deer (m)	2	0.36	3.57	0.82	Yes
Muntjac (s)	9	1.60	17.86	0.84	Yes
Gaur (l)	0	0	0	0	Neutral
Wild boar (m)	17	3.02	3.57	0.08	Yes
Rhesus monkey (s)	1	0.18	0	-1	No
Langur (s)	0	0	0	0	Neutral
Buffalo (l)	0	0	3.57	1	Yes
Goat (m)	0	0	3.57	1	Yes
Cattle (l)	0	0	7.14	1	Yes
Other	0	0	0	0	Neutral
Total	563	100	86.71		

Some results found in the buffer zone are similar to those of the core area. Both species show a preference for wild boar (T: 0.74, 0.08) although this preference is much stronger for tiger (Table 8 & 9). Chital is not preferred by either tiger or leopard (Table 8 & 9). Both species show a strong preference for muntjac and a strong avoidance of rhesus monkey (Table 8 & 9). Sambar is strongly preferred by tiger but avoided by leopard (T:0.56, L:-0.02). Hog deer is preferred by leopard but strongly avoided by tiger. Both species show a strong preference for goats. Cattle and buffalo are also strongly preferred by leopard but not by tiger (Table 8 & 9).

Table 10. Species availability (May 2017), diet contribution and Jacob index calculations for tiger in corridor forest. Birds make up the missing 10.71% of the tiger diet total.

Tiger (CO)					
Species	**Count**	**Availability in %**	**Diet contribution in %**	**Jacobs index**	**Preference**
Chital (m)	513	91.12	46.43	-0.32	No
Sambar (l)	21	3.73	10.71	0.48	Yes
Hog deer (m)	2	0.36	3.57	0.82	Yes
Muntjac (s)	9	1.60	7.14	0.63	Yes
Gaur (l)	0	0	7.14	1	Yes
Wild boar (m)	17	3.02	7.14	0.41	Yes
Rhesus monkey(s)	1	0.18	0	-1	No
Langur (s)	0	0	0	0	Neutral
Buffalo (l)	0	0	3.57	1	Yes
Goat (m)	0	0	0	0	Neutral
Cattle (l)	0	0	0	0	Neutral
Other	0	0	3.57	1	Yes
Total	563	100	89.29		

Table 11. Species availability (May 2017), diet contribution and Jacob index calculations for leopard in corridor forest. Birds make up the missing 6.67% in the total diet contribution.

Leopard (CO)					
Species	**Count**	**Availability in %**	**Diet contribution in %**	**Jacobs index**	**Preference**
Chital (m)	513	91.12	53.33	-0.26	No
Sambar (l)	21	3.73	0	-1	No
Hog deer (m)	2	0.36	6.67	0.90	Yes
Muntjac (s)	9	1.60	13.33	0.79	Yes
Gaur (l)	0	0	0	0	Neutral
Wild boar (m)	17	3.02	0	-1	No
Rhesus monkey(s)	1	0.18	0	-1	No
Langur (s)	0	0	0	0	Neutral
Buffalo (l)	0	0	0	0	Neutral
Goat (m)	0	0	6.67	1	Yes
Cattle (l)	0	0	13.33	1	Yes
Other	0	0	0	0	Neutral
Total	563	100	93.33		

In the corridor forest, tiger and leopard avoid Chital and show a strong avoidance for rhesus monkey (Table 10 & 11). Both species show a strong preference for hog deer and muntjac (Table 10 & 11). Sambar and wild boar are preferred by tiger but strongly disliked by leopard

(Table 10 & 11). Tiger shows a strong preference for buffalo and leopard shows a strong preference for cattle and goats (Table 10 & 11).

4. Discussion

4.1. Tiger and leopard distribution

The results suggests that leopards are more active in the periphery of the park and more involved in livestock raiding than tigers. These results are in agreement with Bhattarai & Kindlmann (2012), who found that tiger and leopard predate more livestock in areas with a higher degree of habitat disturbance with a stronger effect for the latter. As the relative presence of leopard scats compared to tiger scats increases for corridor forest and buffer zone, this seems to confirm the findings of Odden *et al.* (2010) who suggested that tigers displace leopards to the edge zones of parks. The total of scats collected for tiger (148) is almost three times the number of scats collected for leopard (57). This results in a scat ratio of slightly less than 3:1 for tiger compared to leopard. Assuming that there are no factors other than abundancy that influence the chance of detecting tiger and leopard scats and that transects covered an area representative for the park, this may indicate that tiger abundance is 2-3 times as high as leopard abundance in and around CNP. However, several studies have suggested that other factors such as interspecific avoidance are also a determinant in tiger and leopard activity patterns and distribution (Bhattarai & Kindlmann, 2012). Wegge, Odden, Pokharel and Storass (2009) reported that leopard density is 3-4 times lower than tiger density with extensive interspecific dietary overlap in areas where both species are sympatric. Thapa (2011) found that leopard density in and around CNP is 2-3 times lower than tiger density which is slightly higher than expected. The overall diet results and distribution of leopard and tiger scats seem to support this finding.

4.2. Diets in space

Prey species preferences differ between species across the different areas. Although chital is the most abundant species in all three areas, it is not preferred by either tiger or leopard. This is in accordance with previous findings (Bhattarai & Kindlmann, 2012). Both species show a preference for sambar across core area and buffer zone. Sambar is preferred by tiger only in the corridor forest. Wild boar and Gaur are preferred by tiger in the core area. In this study, livestock, small (e.g. muntjac) and very small prey (birds) are relatively more consumed by leopard. This was also found by Odden *et al.* (2010) in BNP. Birds were only found in buffer zone and corridor forest, and more prominently present in Leopard diet (T:2.22%, L:9.43%). Comparatively higher numbers of livestock were detected in the corridor, less in the buffer zone and the least in the core area. This indicates that tiger and leopard consume more livestock and birds in disturbed areas. It may however also indicate that natural prey densities are lower in areas with higher disturbance which in turn results in a shift in leopard and tiger diet towards other more available prey, including livestock. Bhattarai & Kindlmann (2012) suggested that the abundance of mainly large natural prey species in the buffer zone is low due to their high sensitivity for human disturbance. Relative frequencies of prey species occurrence in this study are similar to earlier studies, suggesting that tiger diet consists mainly of large to medium sized prey and leopard diet mainly of medium to small sized prey (Bhattarai & Kindlmann, 2012; Karant & Sunquist, 1995; Odden *et al.,* 2010; Sunquist, 1981). The distribution of scat and the higher relative frequency of livestock in leopard diet confirms that leopards are more active in the buffer zone and corridor forest and as a consequence get more involved in livestock raiding than tigers (Bhattarai & Kindlmann, 2012; Odden, 2010; Sunquist, 1981).

Interspecific differences in prey species preference and occurrence in the diets indicate that there is some degree of dietary overlap and potential competition between tiger and leopard, but that this is partly avoided by having a stronger preference for different prey. Maintaining substantial populations of highly preferred wild prey species populations of both tiger and leopard is therefore essential to maintain viable populations of wild cats in this area. Maintaining wild prey populations will also reduce the economic losses as a result of human-carnivore conflicts due to the fact that stronger competition between tiger and leopard as well as the loss of wild prey results in higher livestock depredation (Bhandari *et al.*, 2017; Harihar *et al.*, 2011). Karanth & Sunquist (1995) found that although leopard and tiger both eat chital, wild boar and sambar, tigers show a bias towards adult males in these prey species whereas leopard kills younger and smaller individuals. These findings suggest that even within prey species, tiger and leopard have a preference for different age/stage classes. In this study, it was not possible to distinguish between different age or stage groups of the same species. However, it is important to keep in mind that actual competition for the same prey may be lower than portrayed here due to differences in intraspecific prey selectivity.

Many studies have looked at the diets of tiger and leopard in Chitwan National Park (Bhattarai & Kindlmann, 2012; Bhandari *et al.*, 2017; Hayward *et al.*, 2006; Lamichhane & Jha, 2015; Sunquist, 1981). However, only Bhattarai and Kindlemann (2012) linked prey species preference to the degree of habitat disturbance. This study is the first that makes a comparison between three different areas that receive different degrees of anthropogenic pressure. Overall contribution of livestock to tiger and leopard diet was small (5.86%, N=188) and there is no significant difference between the three areas.

The results of this study suggests that the main bulk of tiger diet consists of chital (36.50%) and sambar (22.63%) in CNP. However, out of these two species only sambar is preferred. Comparatively, Bagchi, Goyal and Sankar (2003) found that the main bulk of the diet of tigers constitutes of chital (31%) and sambar (47%) and that both species are preferred in Ranthambhore National Park, India. As most studies do not show a preference for chital (Lamichhane & Jha, 2015; Sunquist, 1981), this indicates that tiger diet and prey preference may differ between different areas according to the available prey and other local differences. Sambar, for example, has the highest density in forests where visibility is low while chital prefers both grasslands and open forest types (Kushwaha, Khan, Habib, Quadri, & Singh, 2004; Mishra, 1982). Because of this, sambar density may be underestimated while surveying. In the diet analysis however, this species is not missed, which can lead to a pseudo preference for sambar.

The results suggest that livestock makes up 3.57% of the tiger diet in the corridor forest although the difference with other areas was not significant. Presence of livestock in tiger diet was found to be substantially higher in the Khata corridor, Nepal compared to buffer zone and core area with 12– 15% of the diet consisting of livestock (Wegge, Yadav, & Lamichhane, 2018). The contribution of livestock to tiger diet for the corridor area in this study is significantly lower, but the overall leopard diet shows similar results (13.2%). For tiger, the highest contribution of livestock was found in the buffer zone (9.38%). The data suggest that leopard diet contained most livestock in the corridor forest (20%). The presence of livestock in the diet of tiger in the core area may indicate that illegal grazing activities are still occurring or that some tigers migrate out of the core area to feed .

4.3. Diets in time

Table 12. Comparison of the relative frequency of occurrence for different prey species between tiger and leopard in 2017 (N=190, tiger=137, leopard=53), 2014 (Tiger only; N=109 after Bhandari *et al.*, 2017) and 2009 (N=326, tiger= 229, leopard= 97 after Bhattarai & Kindlmann, 2012).

	Relative frequency of occurrence (%)				
	Tiger			Leopard	
	2009[1]	**2014[2]**	**2017[3]**	**2009[1]**	**2017[3]**
Chital	33.41	44.94	37.04	10.82	49.06
Sambar	22.27	22.92	22.96	1.55	5.66
Muntjac	3.49	3.63	9.63	15.98	13.21
Hog deer	7.21	9.16	2.96	2.58	3.77
Wild boar	18.12	14.65	17.04	8.76	3.77
Gaur bison	1.09	1.82	2.22	0	0.00
Langur	6.55	0	0.74	17.01	1.89
Rhesus monkey	3.71	0	0.74	13.40	0.00
Bird	0.87	0	2.22	3.09	9.43
Buffalo	0.87	1.82	2.22	0	1.89
Cattle	0.87	0.9	0.00	0	7.55
Goat	0.22	0	0.74	22.68	3.77
Other	1.32	0	1.48	4.12	0.00
Total:	100	100	100	100	100

[1] Bhattarai & Kindlmann, 2012 [2] Bhandari *et al.*, 2017 [3] Current data

Distribution of prey items differs significantly for leopard between 2009 and 2017 (Fisher's Exact Test, p- value=0.0005). Table 6 indicates that the contribution of chital towards the diet of the leopard has increased over time (from 10.82% to 49.06%). The contribution of langur (from 17.01% to 1.89%) and rhesus monkey (from 13.40% to 0%) to the overall diet of leopard is suggested to be lower in 2017. The results from 2017 suggest that the contribution of livestock, i. e. mainly goats (from 22.68% to 3.77%) to leopard diet has decreased over time. The contribution of birds has also increased from 3.09% to 9.43%. Cattle and buffalo were only found in the diet in 2017.

For tiger, the distribution of prey items differs significantly between 2009 and 2017 (Fisher's Exact Test, p- value=0.006). Table 6 suggests a decrease in the contribution of langur (from 6.55% to 0.74%), rhesus monkey (from 3.71% to 0.74%) and hog deer (from 7.21% to 2.96%) to the diet. The contribution of buffalo (from 0.87% to 2.22%), birds (from 0.87 to 2.22%), and muntjac (from 3.49% to 9.63%) has increased. Distribution of prey items also differs significantly between 2009 and 2014 (Fisher’s Exact Test, p-value= 0.026). No monkeys were found in the tiger diet in 2014. The proportion of chital in the diet increased considerably (from 33.41% to 44.94%) and the percentage of wild boar decreased slightly (from 18.12% to 14.65). The contribution of all other prey items was similar between both years. No significant differences in the distribution of prey items were found between 2014 and 2017.

Distribution of prey items differed significantly between 2009 and 2017 for both tiger and leopard. The underrepresentation of langur and rhesus monkey in both diets in 2017 may indicate that the sampled area in the CA is not representative for the whole park or that preferences have changed over time. For tigers, the contribution of livestock to the diet found in 2017 was similar to 2009. Other differences, such as the increase of muntjac, bird prey items as well as a decrease in hog deer contribution to the diet are relatively small. The frequency of occurrence of chital in leopard diet has increased by 39%. This could indicate that chital populations have increased or that the availability of other prey for leopards (including livestock) has decreased. The proportion of goat in leopard diet has decreased with 19%. This suggests that livestock depredation by leopards has decreased over time (from 23% of prey items in the diet to 14%). The most depredated livestock prey changed from goat to cattle. Dhungana *et al.* (2017) found a significant increase in livestock depredation in and around CNP from 2009- 2014, with goat (55%) as the main depredated livestock prey. The overall observed decrease of livestock depredation by tiger and leopard combined (from 12.32% in 2009 to 5.86% in 2017) must therefore mainly have occurred between 2014 and 2017. Long term data of sociological surveys (1998- 2016) suggests a decreasing trend of wildlife attacks on humans and livestock due to decreased forest dependency and conflict mitigating measures (e.g. stall feeding, more secure livestock corrals), although this trend was not statistically significant (Lamichhane *et al.*, in prep.).

However, differences in methodology may also have contributed towards significant differences in prey composition between the two years. Bhattarai & Kindlmann (2012) collected scats during 2008 and 2009 all year round. Data of this study were only collected over a period of four months during the dry season. Prey abundance and density fluctuates according to the seasons in climates that have pronounced wet and dry seasons (Davidson *et al.*, 2013; Ogutu & Dublin, 2002). Some carnivores sympatric with tiger and leopard (including dhole, snow leopard and lion) show seasonal differences in livestock depredation in the sense that they predate more livestock during the wet season (Oli, Taylor, & Rogers, 1993; Thinley *et al.*, 2011; Van Bommel, Bij de Vaate, De Boer, & De Iongh, 2007). The overall lower contribution of domestic animals to the diet of both tiger and leopard in 2017 compared to 2012 may not only be due to a smaller sample size, but also due to the fact that data in my study were only collected during the dry season and thus do not represent the overall diet of both species. This is unlikely though, because Dhungana *et al.* (2017) did not find a significant correlation between livestock depredation and rainfall or temperature in and around CNP.

4.4. On the methodology of the study

In a previous study, the field identification of carnivore species by technicians was found to be ‘fairly accurate’ (96%, N=101) (Upadhyaya *et al.*, in prep.). This indicates that results based on morphological scat identification are reliable, even without the use of DNA analysis techniques for carnivore identification.

Determining the abundance of livestock in the study area has proven to be difficult. Although free livestock grazing has reduced in recent years, both BZ and CO are still continuously used as grazing grounds where cattle roam around freely (Gurung *et al.*, 2008; Lamichhane *et al.*, in prep.; Sharma & Shaw, 1993). This is not reflected in the data collected through transect counts during this study. This may be due to the small temporal scale of the data as measurements were only performed once for each transect. It must be considered that the high prey species preference for cattle in both buffer zone and corridor may be due to the lack of enough data instead of reflecting an actual preference. This problem can partly be solved by improving the method used for transect counts. This can be achieved by increasing efforts on both a temporal and spatial scale, resulting in more realistic estimates of available prey in the buffer zone and corridor forest.

Overall, results of this research are similar to previous studies although some differences were found, especially for leopard. The very small sample size (N=10) in the core area for example, may have resulted in a smaller contribution of langur and rhesus monkey, thus not reflecting their actual contribution to the overall leopard diet in CNP. If scats were only collected in areas where langur and rhesus monkey densities are low, this could have resulted in lower frequencies than expected which is seen in both tiger and leopard. It is impossible to determine how many individual tigers and leopards were involved in this research, thus whether the diet represents the entire population. As scats were collected in three areas in relative close proximity and tiger and leopard have large territories, there may be a bias towards preference of only a few individuals. Most samples were collected on roads, which are less frequently used by leopards compared to tigers in CNP (Sunquist, 1981). The difference in scats found between tiger and leopard may be a direct result of the methodology used during scat collection. A cautious approach must therefore be maintained when extrapolating these findings towards the entire tiger and leopard population in CNP or when using these results to suggest interaction effects. Significant differences between species or areas may be very well due to chance effects as the sample sizes, especially for leopard (N=53), are relatively small.

The origin or prey species present could not be determined in a relatively large amount of the collected scat (N=29, 14.1%). The use of DNA analysis techniques can improve the accuracy at which the correct species are identified, especially in cases where the samples lack a sufficient amount of material (hairs, bones, skin and/or feathers) used for morphological analysis. Although the species present in samples which contain a sufficient amount of material can be determined, a certain degree of uncertainty remains for some samples when utilizing hair morphology characteristics to analyze diets.

5. Conclusions and recommendations

i) I conclude that the diet and distribution of tigers and leopards changes according to the available prey and level of human disturbance in and around CNP. Although both carnivore species eat similar prey, interspecific differences in prey species preferences allow coexistence. Leopards are more abundant at the periphery of the park and consume more small to medium sized prey and livestock compared to tigers.

ii) Conservation actions in and around CNP have been implemented and enforced in recent years and are currently being evaluated and adapted to reduce the conflict with large carnivores (Lamichhane *et al.*, in prep.). Future conservation measures should focus on the corridor forest and buffer zone, where the combined data suggest that conflict is the most intense. Mitigating conflict with leopards instead of tigers is also of higher priority, especially when it aims at reducing economic damage inflicted by livestock depredation.

iii) The majority of leopard and tiger diet in CNP consists of wild prey. Proper management of wild prey populations plays a major role in keeping the conflict within an acceptable range (Bhandari *et al.*, 2017). Earlier studies prove that even when a certain amount of livestock depredation cannot be avoided, educating and informing local communities can result into a positive attitude towards large carnivores, reducing the chance of aggressive retaliation in reaction to livestock depredation (Wegge *et al.*, 2018). Therefore it is advised to mainly focus on the social aspects of the conflict when management plans of wild prey populations are already in place and proven relatively successful. In addition, proper grazing and fodder collection regulations in these areas are of major importance for the reduction of conflict and the conservation of these carnivores. Lamichhane *et al.* (in prep.) found that most livestock depredation in recent years happened within the stall, indicating a shift in livestock practices and conflict dynamics which brings new challenges. Positive attitudes towards tiger and leopard cannot be achieved solely through enforcement of regulations. Conservation actions on the long term can only be effective if enforcement of regulations is combined with education and the active involvement of local communities in decision making (Inskip & Zimmerman, 2009). The importance of a more inclusive and integrated approach towards conflict mitigation in and around CNP cannot be underestimated.

iv) Although based on a limited amount of data, this study suggests that livestock depredation may have decreased over the last eight years, indicating that previous conservation actions contributed to conflict mitigation. However, more diet data across a larger spatial and temporal scale is required to confirm this finding.

v) The interaction between tiger and leopard in CNP, as well as their specific role in human- wildlife conflicts is by now quite well understood. Future studies that assess the effectiveness of implemented conservation strategies are necessary to guide the decision making that contributes to the mitigation of human- wildlife conflicts and ultimately the long term conservation of tiger and leopard.

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7. References

Ahlbom, G. C., & Jackson, R. M. (1986). Marking in free-ranging snow leopards in west Nepal: a preliminary assessment. *Proceedings of the 5th lnternational Snow Leopard Symposium, 1&15 October* (pp. 25-49). Seattle, Washington DC: ISLT.

Balme, G., Hunter, L., & Slotow, R. (2007). Feeding habitat selection by hunting leopards Panthera pardus in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*, *74*(3), 589-598.

Bagchi, S., Goyal, S. P., & Sankar, K. (2003). Prey abundance and prey selection by tigers (Panthera tigris) in a semi-arid, dry deciduous forest in western India. *Journal of Zoology*, *260*(3), 285-290.

Bahuguna, A., Sahajpal, V., Goyal, S. P., Mukherjee, S. K., & Thakur, V. (2010). *Species identification from guard hair of selected Indian mammals: A reference guide (ed. 1).* Dehradun, India: Wildlife Institute of India.

Baillie, J. E. M., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2004). *2004 IUCN red list of threatened species: a global species assessment*. Gland, Switzerland and Cambridge, UK: IUCN.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived?. *Nature*, *471*(7336), 51.

Bhandari, S., Chalise, M. K., & Pokharel, C. P. (2017). Diet of Bengal Tigers (Panthera tigris tigris) in Chitwan National Park, Nepal. *European Journal of Ecology*, *3*(1), 80-84.

Bhattarai, B. P., & Kindlmann, P. (2012). Interactions between Bengal tiger (Panthera tigris) and leopard (Panthera pardus): implications for their conservation. *Biodiversity and conservation*, *21*(8), 2075-2094.

Brüner, A. G., Gullison, R. E., Rice, R. E., & Da Fonseca, G. A. (2001). Effectiveness of parks in protecting tropical biodiversity. *Science*, *291*(5501), 125-128.

Butchart, S. H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, R., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeogh, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear. D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrell, T. D., Vié,, J. C., & Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science*, *328* (5982), 1164- 1168.

Carbone, C., Teacher, A., & Rowcliffe, J. M. (2007). The costs of carnivory. *PLoS biology*, *5*(2), e22. Retrieved from https://doi.org/10.1371/journal.pbio.0050022.

Chapin Iii, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., & Diaz, S. (2000). Consequences of changing biodiversity. *Nature*, *405*(6783), 234.

Chitwan National Park Office. (2015). Biodiversity. Retrieved from http://www.chitwannationalpark.gov.np/index.php/biodiversity.

Goodrich, J., Lynam, A., Miquelle, D., Wibisono, H., Kawanishi, K., Pattanavibool, A., Htun, S., Tempa, T., Karki, J., Jhala, Y., & Karanth, U. (2015). *Panthera tigris*. Retrieved from The IUCN Red List of Threatened Species website: http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T15955A50659951.en

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F., & Macdonald, D. W. (2013). Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PLoS One*, *8*(2), e55182. Retrieved from https://doi.org/10.1371/journal.pone.0055182

Dhungana, R., Savini, T., Karki, J. B., Dhakal, M., Lamichhane, B. R., & Bumrungsri, S. (2017). Living with tigers Panthera tigris: patterns, correlates, and contexts of human–tiger conflict in Chitwan National Park, Nepal. *Oryx*, *52*(1) , 55-65.

Dinerstein, E., Loucks, C., Wikramanayake, E., Ginsberg, J., Sanderson, E., Seidensticker, J., Forrest, J., Bryja, G., Heydlauff, A., Klenzendorf, S., Leimgruber, P., Mills, J., O'Brien, T. G., Shrestha, M., Simons, R. & Songer, M. (2007). The fate of wild tigers. *AIBS Bulletin*, *57*(6), 508-514.

Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and loss. *Annual Review of Environment and Resources*, *28*(1), 137-167.

DNPWC & DOF (Department of National Parks and Wildlife Conservation & Department of Forests). (2013). *Status of Tigers and Prey-base in Terai Arc Landscape, Nepal Summary Report*. Kathmandu, Nepal: Department of National Parks and Wildlife Conservation & Department of Forests.

Dutta, T., Sharma, S., Maldonado, J. E., Wood, T. C., Panwar, H. S., & Seidensticker, J. (2013). Fine-scale population genetic structure in a wide-ranging carnivore, the leopard (*Panthera pardus fusca*) in central India. *Diversity and Distributions*, *19*(7), 760-771.

Gurung, B., Nelson, K. C., & Smith, J. L. (2009). Impact of grazing restrictions on livestock composition and husbandry practices in Madi Valley, Chitwan National Park, Nepal. *Environmental Conservation*, *36*(4), 338-347.

Gurung, B., Smith, J. L. D., McDougal, C., Karki, J. B., & Barlow, A. (2008). Factors associated with human-killing tigers in Chitwan National Park, Nepal. *Biological Conservation*, *141*(12), 3069-3078.

Wickham, H. (2009). *Elegant Graphics for Data Analysis (ggplot2).* New York, NY: Springer.

Harihar, A., Pandav, B., & Goyal, S. P. (2011). Responses of leopard Panthera pardus to the recovery of a tiger Panthera tigris population. *Journal of Applied Ecology*, *48*(3), 806-814.

Hayward, M. W., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G., & Kerley, G. I. H. (2006). Prey preferences of the leopard (Panthera pardus*). Journal of Zoology*, *270*(2), 298-313.

Hüfner, K. (2009). UNESCO–United Nations Educational, Scientific And Cultural Organization. In *A Concise Encyclopedia of the United Nations* (pp. 715-718). The Netherlands: Brill.

Hughes, A. C. (2017). Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere*, *8*(1), e01624. Retrieved from https://doi.org/10.1002/ecs2.1624

Huqa, T. J. (2015). *The impact of climate variability on the ecology of a lion (Panthera leo Linnaeus 1758) population and lion livestock conflicts in the Amboseli ecosystem–Kenya* (Unpublished doctoral dissertation). Faculty of Science, Leiden University, Leiden, The Netherlands.

Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: a review of patterns and priorities worldwide. *Oryx*, *43*(1), 18-34.

Jacobson, A. P., Gerngross, P., Lemeris Jr, J. R., Schoonover, R. F., Anco, C., Breitenmoser-Würsten, C., Durant, S. M., Farhadinia, M. S., Henschel, P., Kamler, J. F., Laguardia, A., Rostro-Garcia, S., Stein, A. B., & Dollar, L. (2016). Leopard (Panthera pardus) status, distribution, and the research efforts across its range. *PeerJ, 4*, e1974. Retrieved from https://doi.org/10.7717/peerj.1974

Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia, 14*(4), 413-417.

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*(14), 4854-4858.

Karanth, K. U., Sunquist, M. E. (1995). Prey Selection by Tiger, Leopard and Dhole in Tropical Forests. *Journal of Animal Ecology, 64*(4), 439-450.

Karki, J. B., Pandav, B., Jnawali, S. R., Shrestha, R., Pradhan, N. M. B., Lamichane, B. R., Khanal, P., Subedi, N. & Jhala, Y. V. (2015). Estimating the abundance of Nepal's largest population of tigers Panthera tigris. *Oryx*, *49*(1), 150-156.

Khadka, B. B., Lamichhane, B. R., & Aryal, N. (2016). High prey density observed in village evacuated area: A case study from Padampur of Chitwan National Park. Retreived from http://www.chitwannationalpark.gov.np/index.php/news/doc_download/41-prey-base-in-padampur-13-02-2017

Kolipaka, S. S., Tamis, W. L. M., van‘t Zelfde, M., Persoon, G. A., & de Iongh, H. H. (2017). New insights into the factors influencing movements and spatial distribution of reintroduced Bengal tigers (Panthera tigris tigris) in the human-dominated buffer zone of Panna Tiger Reserve, India. *Mammalia.* Retrieved from https://doi.org/10.1515/mammalia-2016-0126

Kushwaha, S. P. S., Khan, A., Habib, B., Quadri, A., & Singh, A. (2004). Evaluation of sambar and muntjak habitats using geostatistical modelling. *Current Science, 86*(10), 1390-1400.

Lamichhane, B. R. (2016, 1 November). Study of Big Cat's Diet and Livestock Depredation Pattern in Chitwan National Park to Reduce Human Carnivore Conflict. Retreived from https://www.rufford.org/projects/babu_ram_lamichhane

Lamichhane, B. R., Persoon, G. A., Leirs, H., Musters, C. J. M., Subedi, N., Gairhe, K. P., ... & Smith, J. L. D. (2017). Are conflict-causing tigers different? Another perspective for understanding human-tiger conflict in Chitwan National Park, Nepal. *Global Ecology and Conservation*, *11*, 177-187.

Lamichhane, B. R., Persoon, G. A., Leirs, H., Poudel, S., Subedi, N., Pokheral, C. P., Bhattarai, S., Thapaliya, B. S., & de Iongh, H. (2018). Spatio- temporal patterns of attacks on human and economic losses from wildlife in Chitwan National Park, Nepal. *In preparation.*

Lamichhane, S., & Jha, B. R. (2015). Prey selection by Bengal Tiger Panthera tigris tigris (Mammalia: Carnivora: Felidae) of Chitwan National Park, Nepal. *Journal of Threatened Taxa*, *7*(14), 8081-8088.

Lamichhane, S., Gurung, A., Pokheral, C. P., Rayamajhi, T., Gotame, P., Regmi, P. R., & Lamichhane, B. R. (2018). First record of the Dhole Cuon alpinus (Mammalia: Carnivora: Canidae) in Barandabhar Corridor Forest, Chitwan, Nepal. *Journal of Threatened Taxa*, *10*(1), 11243-11244.

Luo, S. J., Kim, J. H., Johnson, W. E., Van Der Walt, J., Martenson, J., Yuhki, N., ... & Tilson, R. (2004). Phylogeography and genetic ancestry of tigers (Panthera tigris). *PLoS biology*, *2*(12), e442. Retrieved from https://doi.org/10.1371/journal.pbio.0020442.

McKee, J. K., Sciulli, P. W., Fooce, C. D., & Waite, T. A. (2004). Forecasting global biodiversity threats associated with human population growth. *Biological Conservation*, *115*(1), 161-164.

Mishra, H. R. (1982). Ecology and behaviour of Chital (Axis, axis) in the Royal Chitwan National Park, Nepal (with comparative studies of hog deer (Axis porcinus), sambar (Cervus unicolor) and Barking deer (Muntiacus muntjak)) (Unpublished doctoral dissertation). University of Edinburgh, Edinburg, UK.

Naughton-Treves, L., Holland, M. B., & Brandon, K. (2005). The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annual Review of Environment and Resources*, *30*, 219-252.

Nepal, S. K., & Weber, K. E. (1994). A buffer zone for biodiversity conservation: viability of the concept in Nepal's Royal Chitwan National Park. *Environmental Conservation*, *21*(4), 333-341.

Ngoprasert, D., Lynam, A. J., & Gale, G. A. (2007). Human disturbance affects habitat use and behaviour of Asiatic leopard Panthera pardus in Kaeng Krachan National Park, Thailand. *Oryx*, *41*(3), 343-351.

Nowell, K., & Jackson, P. (Eds.). (1996). *Wild cats: status survey and conservation action plan* (Vol. 382). Gland, Switserland: IUCN.

Odden, M. (2007). Tigers, leopards and their prey in Bardia National Park, Nepal (Unpublished doctoral dissertation). Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Norway.

Odden, M., & Wegge, P. (2005). Spacing and activity patterns of leopards Panthera pardus in the Royal Bardia National Park, Nepal. *Wildlife Biology*, *11*(2), 145-152.

Odden, M., P. Wegge & T. Fredriksen (2010). Do tigers displace leopards? If so, why? *Ecological Research 25*(4): 875–881.

Ogutu, J. O., & Dublin, H. T. (2002). Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology*, *40*(2), 120-129.

Oli, M. K., Taylor, I. R., & Rogers, D. M. (1993). Diet of the snow leopard (Panthera uncia) in the Annapurna Conservation Area, Nepal. *Journal of Zoology, 231*(3), 365-370.

Ramakrishnan, U., Coss, R. G., & Pelkey, N. W. (1999). Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biological Conservation*, *89*(2), 113-120.

RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. Retrieved from http://www.rstudio.com/.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. Retrieved from http://dx.doi.org/10.1126/science.1241484

Seidensticker, J. (1990). Leopards living at the edge of the Royal Chitwan National Park, Nepal. *Conservation in developing countries: Problems and prospects* (pp 415-423). Bombay, India: Bombay Natural History Society.

Seidensticker, J., Christie, S., & Jackson, P. (Eds.). (1999). *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge, UK: Cambridge University Press.

Sharma, U. R., & Shaw, W. W. (1993). Role of Nepal's Royal Chitwan National Park in meeting the grazing and fodder needs of local people. *Environmental Conservation, 20*(2), 139-142.

Smith, J. L. D. (1993). The role of dispersal in structuring the Chitwan tiger population. *Behaviour, 124*(3), 165-195.

Stein, A.B., Athreya, V., Gerngross, P., Balme, G., Henschel, P., Karanth, U., Miquelle, D., Rostro-Garcia, S., Kamler, J.F., Laguardia, A., Khorozyan, I., & Ghoddousi, A. (2016).

Panthera pardus. Retrieved from The IUCN Red List of Threatened Species website: http://dx.doi.org/10.2305/IUCN.UK.2016- 1.RLTS.T15954A50659089.en

Støen, O. G., & Wegge, P. (1996). Prey selection and prey removal by tiger (Panthera tigris) during the dry season in lowland Nepal. *Mammalia*, *60*(3), 363-374.

Sukumar, R. (1991). The management of large mammals in relation to male strategies and conflict with people. *Biological Conservation, 55*(1), 93-102.

Sunquist, M. (2009). What is Tiger? Ecology and Behaviour. In Tilson , R., & Nyhus, P. J., (Eds.). *Tigers of the world: The Science, Politics and Conservation of Panthera tigris* (pp 19-35). Amsterdam, The Netherlands: Academic Press.

Sunquist, M. E. (1981). *The social organization of tigers (Panthera tigris) in Royal Chitawan National Park, Nepal.* Washington, DC:Smithsonian Institution Press.

Sunquist, M., & Sunquist, F. (2002). *Wild cats of the world.* Chicago, Illinois: University of Chicago Press.

Sunquist, M., Karanth, K.U., & Sunquist, F. (1993). Ecology, behaviour and resilience of the tiger and its conservation needs. In White, G. (1993). *Riding the tiger: The politics of economic reform in post-Mao China* (Vol. 994). Palo Alto, California: Stanford University Press.

Thapa, T. B. (2011). *Habitat suitability evaluation for Leopard (Panthera pardus) using remote sensing and GIS in and around Chitwan National Park, Nepal* (Doctoral dissertation). Saurashtra, India: Saurashtra University.

Thinley, P., Kamler, J. F., Wang, S. W., Lham, K., Stenkewitz, U., & Macdonald, D. W. (2011). Seasonal diet of dholes (Cuon alpinus) in northwestern Bhutan. *Mammalian Biology-Zeitschrift für Säugetierkunde, 76*(4), 518-520.

Upadhyaya, S. K., Musters, C. J. M., de Snoo, G. R., Thapa, P., Dhakal, M., Lamichhane, B. R., Karmacharya, D., Shrestha, P. M., & de Iongh, H. H. (2017). An insight into the diets of male and female tigers and leopards in Bardia National Park, Nepal. *In preparation.*

Uphyrkina, O., Johnson, W. E., Quigley, H., Miquelle, D., Marker, L., Bush, M., & O'Brien, S. J. (2001). Phylogenetics, genome diversity and origin of modern leopard, Panthera pardus. *Molecular ecology*, *10*(11), 2617-2633.

Van Bommel, L. B. D. V., Bij de Vaate, M. D., De Boer, W. F., & De Iongh, H. H. (2007). Factors affecting livestock predation by lions in Cameroon. *African journal of ecology*, *45*(4), 490-498.

Vié, J. C., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2009). *Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species*. Gland, Switzerland: IUCN.

Wegge, P., Odden, M., Pokharel, C.P., & Storass, 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*(1), 189–202.

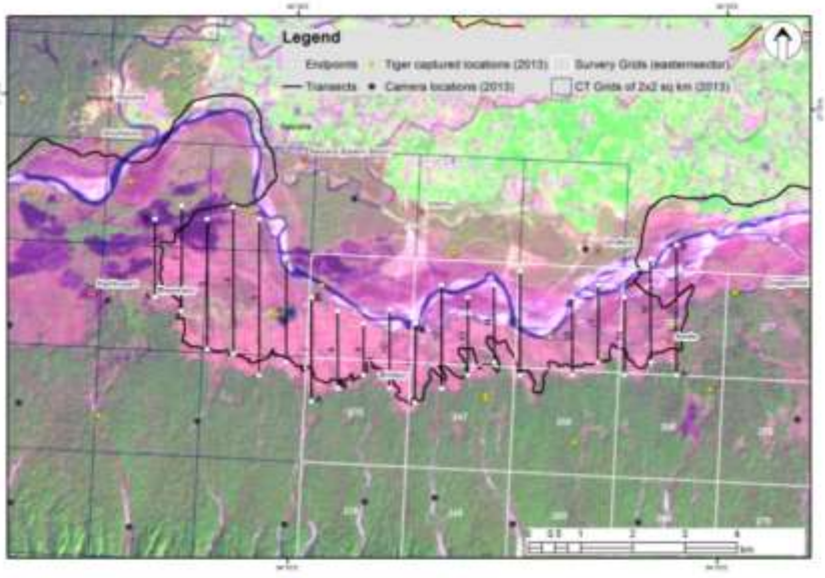
Wegge, P., Yadav, S. K., & Lamichhane, B. R. (2018). Are corridors good for tigers Panthera tigris but bad for people? An assessment of the Khata corridor in lowland Nepal. *Oryx, 52*(1), 35-45.

Wikramanayake, E. D., Dinerstein, E., Robinson, J. G., Karanth, U., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Conner, M., Hemley, G. & Bolze, D. (1998). An ecology-based method for defining priorities for large mammal conservation: the tiger as case study. *Conservation Biology, 12*(4), 865-878.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation forum*, *3*(2), 165-173.

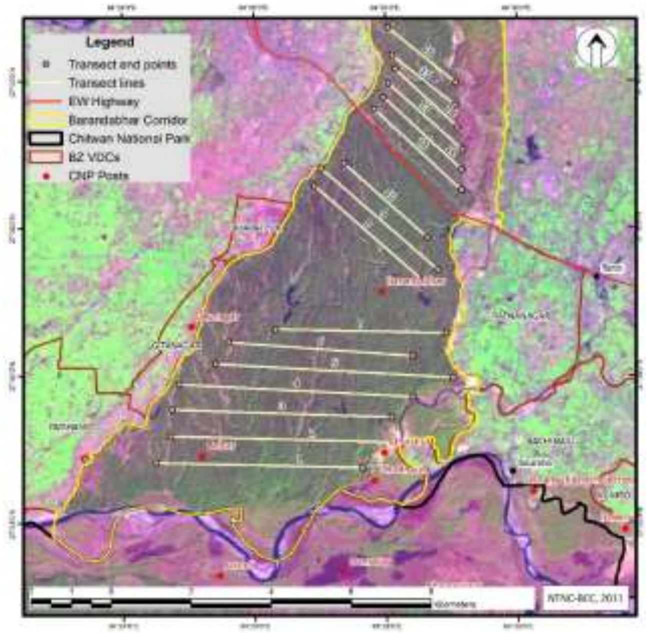
Woodroffe, R., & Ginsberg, J. R. (2005). King of the beasts? Evidence for guild redundancy among large mammalian carnivores. In Ray, J., Redford, K. H., Steneck, R., & Berger, J. (Eds.). *Large carnivores and the conservation of biodiversity.* Washington, D.C.: Island Press.

8. Appendix A



Appendix A. Map indicating the line transects walked on elephant back to estimate prey availability in the core area (Source: Khadka *et al.*, 2016).

9. Appendix B



Appendix B. Map indicating the line transects walked on elephant back to estimate prey availability in the Barandabhar corridor forest (Source: NTNC, 2017).