

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

Upadhyaya, S.K.

Citation

Upadhyaya, S. K. (2019, April 16). *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*. Retrieved from https://hdl.handle.net/1887/71374

Note: To cite this publication please use the final published version (if applicable).

Human-wildlife Interactions in the Western Terai of Nepal

This research is funded by the Netherlands Fellowship Program of NUFFIC (Netherlands Universities Foundation for International Cooperation).

© 2019, Subodh Kumar Upadhyaya subodh@ku.edu.np; subodhu@gmail.com

ISBN 978-90-5191-190-9

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**

proefschrift

ter verkrijging van de graad van Doctor aan de Universiteit Leiden op gezag van de Rector Magnificus prof. mr. C.J.J.M. Stolker volgens besluit van het College voor Promoties te verdedigen op dinsdag 16 april 2019 klokke 15.00 uur

door

Subodh Kumar Upadhyaya

Geboren te Khanchikot, Arghakhanchi, Nepal in 1965

Table of Contents

6 Synthesis 101

1

General Introduction

1.1 Introduction

1.1.1 Carnivore conservation worldwide

The evolution of cats (*Felidae*) started only relatively recently with several species diverging within a time span of c. 28.5 to 35 million years (Sunquist & Sunquist 2002). It has been estimated that the group of large 'roaring' cats, including tigers and leopards, have diverged around 2-3 million years ago (Turner, 1987).

Historically, the conservation of large cats has been motivated on a.o. aesthetic, symbolic, spiritual, ethical, utilitarian and ecological considerations (Loveridge et al., 2010). Nowadays, the threats for the conservation of tigers and leopards are generally grouped into five main categories: 1) habitat destruction, 2) poaching for illegal trade, 3) decline of prey populations, 4) retaliatory killing after conflicts with local communities, and 5) genetic isolation and inbreeding depression (Mills & Allendorf, 1996; Inskip & Zimmermann, 2009; Karanth & Chellam, 2009; Ripple et al., 2014; Nyhus, 2016).

As human populations are increasing, natural habitat continues to be exploited, leading to considerable alterations to the global landscape (Lambin & Meyfroidt, 2011). Tigers and leopards are now regarded as conservation dependent species because their habitat is facing increasing threats from human developmental activities (Thapa et al., 2017). Loss of highly suitable habitats is generally attributed to unauthorized resource extraction, coupled with natural processes such as flooding and forest succession (Wegge et al., 2009; Carter et al., 2012). Across much of the leopard range, land has been converted to agriculture for producing crops in order to support the growing human population (Jacobson et al., 2016).

Poaching and illegal trade of skin, bones and other body parts of large carnivores has also greatly contributed to their decline in certain areas (Goodrich et al., 2008; Kolipaka et al., 2017). Tigers, more so than leopards, require large populations to persist and are susceptible to modest increases in mortality, and less likely to recover quickly after a population decline (Chapron et al., 2008). Knowledge on rates of decline and causes of mortality among tiger and leopard populations is crucial in order to understand their population dynamics and hence to formulate effective conservation measures (Caughley & Sinclair, 1994; Goodrich et al., 2008). When prey levels are very low, a minor increase in poaching could result in the local extinction of the tiger (Damania et al., 2003). Mortality rates of more than 15% of adult female tigers can lead to their extinction (Chapron et al., 2008). For Amur tigers (*Panthera tigris altaica*) poaching was regarded as the main cause of death in Silhote-Alin Biosphere Zapovednik of Russia (Goodrich et al., 2008). Goodrich et al. (2008) even found that all dispersing Amur tigers that had been collared were poached before they got a chance to settle or reproduce. The threat posed to tigers by the illegal trade in wildlife parts is considered to be greater in Asia than anywhere else (Nowell & Jackson, 2006).

In a study on the effects of humans poaching on prey species of carnivores in the Northern part of Bardia, Bhattarai et al. (2017) found that decreased prey numbers led to a decrease in tiger, leopard, fox (*Vulpes vulpes*) and jackal (*Canis aureus*) population. After the area was included under the buffer zone in 2010 and due to regular patrolling by armed forces, poaching in this area had however dropped drastically (Bhattarai et al., 2017), and as a consequence carnivore populations have recovered recently.

Retaliatory killing by humans in areas where livestock or occasionally even humans are attacked by large carnivores has increasingly contributed to large carnivore population declines over the past decades (Inskip et al., 2014). When in the early 1950s tigers were declared a pest in China, this quickly resulted in uncontrolled killing of tigers, especially in areas where they were causing problems (Seidensticker et al., 2009). But also leopards have long been persecuted as a retribution measure to real and perceived livestock losses (Ray et al., 2005; Shehzad et al., 2015). In the Annapurna Conservation Area in Nepal there have been records of snow leopards killed in retaliation to the killing of sheep (Oli et al., 1991). Numerous studies have reported this same threat to cause great declines in population numbers of tigers in Asia (Inskip et al., 2014; Lamichhane et al., 2017), lions in Africa and South West Asia, and mountain lion (*Puma concolor*) populations in North America (Nowell & Jackson, 1996).

Several studies have found inbreeding among isolated populations of large carnivores to negatively impact their long-term viability (Smith et al., 1998; Perez et al., 2006). Reduced genetic exchange rates between populations could compromise genetic variation and long-term viability of populations (Smith et al., 1998). Furthermore, as a consequence of high inbreeding rates, small population sizes and long-term population isolation, genetic variability could become alarmingly low, potentially leading to increased susceptibility to contagious lethal diseases (e.g. Arabian leopards in Israel; Perez et al., 2006). To maintain demographic and genetic viability of low density and wide-ranging species such as the tiger, it is essential to extend conservation actions beyond protected area boundaries, i.e. at the landscape level (Waltson et al., 2010). In addition, promoting protected area connectivity is suggested to positively influence the conservation status of wide ranging large carnivores (Mills & Allendorf, 1996, Wikramanayake et al., 2004).

Morrison et al. (2007) compared the historical (1500 AD) range map of large mammals with their current distributions to determine which areas today retain complete assemblages of large mammals and reported that at the time of his assessment, leopards inhabited 65% of their historical range while tiger populations have shrunk to a mere 18% of their historical range. This indicates a significant global decline in distribution of these large carnivores. Since tiger and leopard densities are naturally limited by energetic constraints, their numbers could significantly impact the community structure of herbivores through resource facilitation and trophic cascades (Ripple et al., 2014).

1.1.2 Human-wildlife conflicts

While large cat species worldwide generally serve as an umbrella and flagship species for ecosystem conservation (Loveridge et al., 2010), the relationship between humans and wild felids has historically been a complex and often paradoxical one (Loveridge et al., 2010). In certain cultural beliefs wild cats have since long been considered as valuable assets, cultural icons or to carry a significant symbolic value (Bhattarai & Fischer, 2014; Kolipaka et al., 2015). In terms of their economic value, a clear shift has taken place over the past century or so, from being the main target as a valuable hunting trophy to generating income as a key tourist attraction (Mehta & Heinen, 2001; Bhattarai & Fischer, 2014).

But just like their larger carnivorous relatives around the world, large cats are also known to cause serious problems if their activities coincide with those of humans (Woodroffe et al., 2005; Treves et al., 2006; Inskip & Zimmerman, 2009). Due to a global increase in land resource use, numerous wildlife species have lost vital habitat and are forced to live in close proximity to humans, thereby competing for space and food (Inskip & Zimmerman,

2009). Conflicts arising from this competition could pose a serious threat on both the wildlife species involved, especially if it is considered threatened with extinction, and the people that are trying to defend themselves or their livestock (Saberwal et al., 1994). Particularly wide ranging species, such as leopards and tigers, could trigger a conflict situation at great distances from protected areas (Bhattarai & Fischer, 2014; Acharya et al., 2016). At the same time, retaliatory actions taken by local communities that suffered losses due to attacks by such predators could extend far into protected areas. Such species are therefore prone to being killed by people (Woodroffe et al., 2005; Kolipaka et al., 2017). The methods used by local inhabitants to kill large carnivores are numerous, and vary to a great extent including shooting, poisoning of livestock kills, electrocution, snaring and trapping (Karanth & Gopal, 2005). Local villagers around Chitwan National Park, Nepal have been reported to put out poisoned livestock carcasses to kill tigers (Sunquist, 1981).

But conflicts with large carnivores not only arise as a consequence of direct interactions with humans, expanding human habitation, loss of natural habitat, the local and international trade in wildlife parts and in some regions growing wildlife populations resulting from successful conservation programs are also important contributing factors (Saberwal et al., 1994; Treves & Karanth, 2003; Wang & Macdonald, 2006).

Inskip & Zimmerman (2009) define a human-wildlife conflict (HWC) as the situation that arises when behavior of a non-pest, wild animal species poses a direct and recurring threat to the livelihood or safety of a person or a community and in response, persecution of the species ensues. The use of the term 'human-wildlife conflict' is usually misleading as it portrays wildlife as an antagonist with conscious intent to interfere with people's lives and livelihoods, whereas the real conflict is between conservation and other human interests (Peterson et al., 2010; Redpath et al., 2015; Fisher, 2016). The phrase 'human-wildlife conflict' is now commonly used to describe a situation that involves any negative interactions between humans and wildlife (Messmer, 2009).

1.1.3 Tiger ecology

The tiger (*Panthera tigris,* Linnaeus, 1758) is one of the world's most iconic predator species. Unfortunately, it is also one of the most endangered species (Seidensticker, 2010). The tiger is regarded as a top predator and a flagship or umbrella species for their role in biodiversity conservation and maintaining a healthy ecosystem (Morrison et al., 2007; Ripple et al., 2014). According to the IUCN global Red list, the tiger is considered Endangered (IUCN, 2018).

In 2011 a Tiger Summit was organized in St. Petersburg, Russia, to discuss on a global action plan for tiger conservation (GTRP, 2011). In the St. Petersburg declaration which resulted from this meeting, the member states have recognized that in the past century, tiger numbers have plummeted from 100,000 to below 3,500, and are still declining (GTRP, 2011). While tigers were once widely distributed across Central, East and South Asia (Figure 1.1, Mazak, 1981) the declaration indicates that tiger numbers and habitat surface area had shrunk by 40 percent in the last decade alone, largely due to habitat loss, poaching, illegal wildlife trade, and human-tiger conflicts (GTRP, 2011). A study by Waltson (2010) has identified 42 tiger source sites representing 6 % of their existing range, and holding 70% of the tiger population.

There are nine sub-species of tigers identified of which four are already extinct (Seidensticker, 2010). Wilting et al. (2015) supports the recognition of two distinct evolutionary groups of sub-species of tiger: the Sunda tiger (*P. tigris sondaica*) and the continental tiger (*P. tigris tigris*) (Table 1.1).

Table 1.1

Sub-species of tigers, with their distribution and status

(Reference: Seidensticker, 2010; Wilting et al., 2015)

Tigers maintain large home ranges and exhibit intra-sexual territoriality (Smith et al., 1989). A study carried out by Smith & McDougal (1991) in Chitwan National Park, Nepal on reproductive patterns in the local tiger population showed that the mean age of reproduction for female tigers was 3.4 years and for male tigers 4.8 years. Adult male tigers are about 1.3 to 1.6 times larger than female tigers (Seidensticker & McDougal, 1993). Tiger litter size varies from 2-5, with an average of 3 cubs, and a gestation period of 103 days (Sunquist, 1981; Smith & McDougal, 1991). Female tigers vocalize and scent mark extensively during the week prior to estrous. In response, male tigers could track an estrous female, possibly marking the onset of a period in which the male and female remain in close proximity and frequently mate (Smith & McDougal, 1991). Smith & McDougal (1991) suggested that on two occasions an estrous female was located near the territorial boundary of two males. This resulted in a fight between the two males and the winner successfully mated with the female while the other male left the area permanently (Smith & McDougal, 1991).

The size of a tiger's home range can vary from 20 to over 400 km $^{\rm 2}$ depending on the availability of prey (Smith, 1993; Seidensticker & McDougal, 1993). In

Chitwan National Park, tiger home ranges varied in size from 60-70 $\mathrm{km^2}$ for adult males and from $16-20 \text{ km}^2$ for adult females, with the smallest home ranges recorded in the wet season, for both males and females (Sunquist, 1981). The distance a female tiger covers at night in this study area was estimated at 10-20 km/night (Sunquist, 1981). In general, dispersing tigers may travel over 100 km in search for a suitable new home range, with males dispersing three times more often than females (Smith, 1993). Female philopatry is frequently observed in tigers, with sub-adult females often inheriting a portion of their natal home range and males generally dispersing longer distances than females (Smith, 1993; Goodrich et al., 2010). Male and some female tigers leave their natal areas when they are 19-28 months old.

The tiger is the largest of all living felids. Its morphology reflects adaptations for killing large and potentially dangerous prey either by concealment, stealth or by sudden attack (Seidensticker & McDougal, 1993; Karanth & Sunquist, 2000). Prey is killed using throat bites, leading to strangulation in 70% of the kills, followed by a neck twist in 14% of the kills, resulting in a cerebral fracture (Karanth & Sunquist, 2000). A tigress requires 5-6 kg of meat per day as a maintenance diet to fulfill her metabolic requirements (Sunquist, 1981). Tiger densities are positively correlated to prey densities, and under optimal conditions 10% of the available prey within a tiger territory will be annually consumed (Karanth et al., 2004). The density of tigers in Chitwan National Park has been estimated at 3.8 tigers/100 km2 through camera trap studies (Dhakal et al., 2014). This is higher than the tiger densities found in other protected areas, such as Bardia (3.3 tigers/100 km²) and Suklaphanta (3.4 tigers/100 km2) (Dhakal et al., 2014). Wegge & Storaas (2009) reported that the tigers' main prey species in Bardia were chital *Axis axis*, hog deer *Axis porcinus* and wild pig *Sus scrofa*, supplemented by fewer barking deer *Muntiacus muntjac*, barasingha *Cervus duvauceli* and nilgai antelope *Boselaphus tragocamelus*. Tigers in Chitwan National Park were found to prey heavily on medium- to large-sized large cervids (Kapfer et al., 2011).

In Nepal, three distinct populations of tigers have been identified: the Chitwan population, the Bardia population and the Suklaphanta population (Smith et al., 1998). In a recent study carried out on the status of the tiger's prey base in Nepal, it was estimated that the tiger population had increased by 63% over a 5-year period, with an annual growth rate of 12.7% (Dhakal et al., 2014). In Bardia, the tiger population was estimated at 18 individuals in 2008/2009 (Karki et al., 2009), growing to an estimated 87 tigers in 2018 (unpublished results).

1.1.4 Leopard ecology

The leopard (*Panthera pardus,* Linnaeus, 1758) is the most widely distributed wild felid, with a distribution ranging from sub-Saharan Africa, the Middle-East, the Far-East, extending northwards to Siberia and southwards to Sri Lanka and Malaysia (Figure 1.2, Nowell & Jackson, 1996). According to the IUCN Red list, the leopard is considered Vulnerable (IUCN, 2018). The Indian leopard (*P. p. fusca*), with its distributional range restricted to the Indian subcontinent, is listed as near-threatened (IUCN, 2018). The leopard is a habitat generalist, ranging from tropical rainforest to arid savanna and from Alpine mountains to the edges of urban settlements (Nowell & Jackson, 1996; Dutta et al., 2013). In India and Southeast Asia, leopards are found in all forest types, from tropical rainforest to temperate deciduous and alpine coniferous forest (up to 5,200 m in the Himalaya), as well as in dry scrub and grasslands (Nowell & Jackson, 1996). Their ability to inhabit such a variety of landscape types is largely due to their highly adaptable foraging strategy (Balme et al., 2007).

Figure 1.2

Present and historic range of the leopard in Africa and Eurasia [Source: Peter Gerngross, IUCN (2016)].

The leopard now occupies 25-37% of its historic range, but there are differences between different sub-species (Jacobson et al., 2016). There are nine sub-species of leopard known (Table 1.2) of which three (*P. pardus pardus*, *P.p. fusca*, and *P.p. saxicolor*) account for 97% of the leopard's entire distribu-

tional range, while another three (*P. pardus orientalis*, *nimr*, and *P.p. japonensis*) have each lost 98% of their historical range (Jacobson et al., 2016).

Table 1.2

(References: Miththapala et al., 1996; Upriyanka et al., 2001; Jacobson et al., 2016).

Leopards are considered as a catholic predator, generally preying on over a hundred prey species with an average weight of 10 to 40 kg (peaking at 23 kg; Hayward et al., 2006). A leopard weighs 38 kg (females) to 58 kg (males) (Bailey, 1993; Nowell & Jackson, 1996). The average food intake for a male leopard is 4.3 kg/day and for a female 4.9 kg/day (Odden & Wegge, 2009). Leopards are nocturnal hunters, relying heavily on their good vision and to a lesser extent on hearing to detect their prey (Sunquist & Sunquist, 2002). Leopards kill most of their prey (90%) using throat bites, with the nape bite or a napeand-throat bite often being used to kill medium-sized prey, such as barking deer (*Muntiacus muntjac*) or chital fawns (Karanth & Sunquist, 2000).

Young leopards disperse from their mother when they are 12-18 months old, becoming reproductively active at the age of 2-3 years (Sunquist, 1983) and only acquiring a home range when they start breeding (Sunquist & Sunquist, 2002).

In India, leopard densities are highest inside protected areas, e.g. with a density estimate of 14.99 leopards/100 km² in the Chilla range of Rajaji National Park (Harihar et al., 2009) and of 23.5 leopards/100 km2 in the Sariska Tiger Reserve (Chauhan et al., 2005).

Leopard home range sizes vary greatly throughout their distributional range and depend mostly on prey availability (Simcharoen et al., 2008; Odden et al., 2010). In sub-Saharan Africa, home range sizes of 15-16 km² have been reported in prey rich areas but could cover up to $2,182 \ \mathrm{km^2}$ in areas with very low prey densities (Bailey, 1993; Bothma & Le Riche, 1984). The home ranges of three leopards in subtropical forest of Bardia National Park was estimated using radio-telemetry techniques and was found to be 47.4 km² for two males and $16.9 \mathrm{~km^2}$ for one female (Odden & Wegge, 2005). Home range size also depends on the reproductive status of the female. The smallest home ranges have been reported for female leopards having cubs of less than 6 months old (Odden & Wegge, 2005).

1.1.5 Tiger-leopard interactions

Tigers and leopards are sympatric, normally inhabiting the same habitat with a substantial overlap in the prey species they catch (Seidensticker, 1976; Lovari et al., 2015). Tigers prefer habitats with more grassland and higher landscape connectivity compared to leopards (Carter et al., 2012). The size of the prey they kill, does differ however, (Seidensticker, 1976), with leopards generally focusing their foraging efforts on the prey items that are too small for tigers (Odden et al., 2010). Tigers are mostly ground-dwelling while leopards also frequently use trees as a resting, feeding or venturing point (Seidensticker, 1976). Interspecies competition between tigers and leopards where they occupy the same habitat, can lead to the displacement of leopards (Odden & Wegge, 2005; Harihar, et al., 2011; Mondal et al., 2012). Leopards are generally less active when tigers are around, both during the day and night (Sunquist, 1981). Tigers are more susceptible to heat than leopards and tend to be more active during early mornings, when it is cooler. Leopards do not avoid activity during the day, but generally become more active after sunset (Seidensticker, 1976). When there is sufficient prey to sustain both tigers and leopards in a certain area, they can co-exist, provided that competitive interactions are limited through spatial and/or temporal partitioning (Lovari et al., 2015). Although there are several studies covering interactions between sympatric tigers and leopards, only few study cover the impact of such interactions on human-wildlife conflicts (Bhattarai & Kindlmann, 2012). In general, tigers prefer less disturbed areas located further away from human settlements, while leopards seem to be more resilient to disturbances; in some areas (e.g. Maharashtra in India) leopards are surviving despite spending a considerable part of their daily activities inside or around human settlements (Athreya et al., 2013).

Nevertheless, whenever both species are ranging in close proximity to local human communities and their livestock the risks of conflicts arising from this are higher (Harihar et al., 2011). Such inter-species dynamics thus not only influence population numbers of the interacting species, they could alsoplay a significant role in the onset of conflicts with humans.

In a study carried out over a period of four years in the Chilla range of Rajaji National Park, India, increasing numbers of tigers (from 3.31 per 100 km $^{\rm 2}$ to 5.81 per 100 km2 ; Harihar et al., 2011) not only caused the leopard population to decrease (from 9.76 per 100 km² to 2.07 per 100 km²), it also initiated a shift in diet of leopards towards more domestic prey (from 6.8% to 31.8%) and towards smaller prey (from 9% to 36%) (Harihar et al., 2011).

Figure 1.3 shows different types of interactions in a protected area of a human dominated landscape. In order to better understand the extent to which interactions between tigers and leopards are causing conflict situations, we will be taking a broad set of independent factors into consideration.

Conceptual research framework describing the conflict situation in Bardia National Park.

1.2 Research aims and objectives

1.2.1 Research aims

The overall aim of my research is to investigate and analyze to what extent interactions between sympatric tigers and leopards contribute to conflicts with humans. I chose the Bardia National Park and its surroundings as my study area, since preliminary results there suggest that tiger numbers are increasing as a result of recent conservation efforts (Dhakal et al., 2014). With respect to interactions with humans I expect to find similar results as in Chitwan National Park, where conflicts increased in response to a rise in tiger numbers.

1.2.2 Objectives

The specific objectives are:

- **1** To determine the spatial and temporal overlap in the activity of tigers and leopards.
- **2** To assess the diet composition and prey preferences of tigers and leopards.
- **3** To assess spatial and temporal patterns in conflict incidences around Bardia National Park.
- **4** To examine the perception and attitudes of local communities towards conservation in general and towards big wild cats in particular, and the implications thereof for the long-term conservation of tigers and leopards.

1.2.3 Research Questions

This study seeks to answer the following questions:

- **1** To what extent do activity patterns of tigers and leopards overlap in space and time?
- **2** What type of prey do tigers and leopards prefer, and is this related to conflicts with humans?
- **3** Do human-wildlife interactions around Bardia National Park change in space and time?
	- **a** What wildlife species are causing conflicts?
	- **b** How much money is spent on compensation schemes (compensation paid on real price)?
	- **c** What is the perception of local communities on how to manage the conflict situation?
- **4** How can risks of predatory attacks around protected areas be defined and what are the implications for their conservation status?

1.3 Study area

1.3.1 Nepal

Nepal is a landlocked country that lies between 80°4' to 88°12' East longitude and 26°22' to 30°27' North latitude, surrounded by the two most densely populated countries of the world: India (along the Eastern, Western and Southern border) and China (along the Northern border). Covering 147,181 km2 , Nepal is located in the central Himalayan region. It extends roughly 885 km from East to West and between 145-241 km from North to South. The climate varies with topography and altitude to include tropical, mesothermal, microthermal, taiga and tundra types of climate. The extensive altitudinal range (70-8,848m) is the main contributing factor to the great variety of habitats and the very rich biodiversity, all within a relatively short horizontal range of about 200 km (Acharya et al., 2016). Nepal includes twenty protected areas, largely situated in the Terai region and high Himalayas (Figure 1.4).

Figure 1.4

Protected areas of Nepal (DNPWC, 2017).

1.3.2 Bardia National Park

Bardia National Park (IUCN, Category II) is located in the South-western part of Nepal (N: 28.2630 to 28.6711; E: 80.1360 to 81.7645), in Province 5. It is the largest park in the lowland Terai, covering an area of $968 \mathrm{~km^2}$. The park was originally established as a hunting reserve in 1969. In 1976 an area of 368 km2 was officially named the Royal Karnali Wildlife Reserve and renamed in 1982 as Bardia Wildlife Reserve. In 1984 the park was expanded to the current size with the inclusion of Babai valley. Finally, the park was upgraded to the status of National Park in 1998 (Brown, 1998). The park consists of two distinct units: the Karnali flood plain and the Babai valley. The Karnali flood plain covers the western side of the park and is rich in biodiversity, whereas Babai valley is a wilderness zone comprised of alluvial grassland and forests, covering more than 50% of the park (Chanchani et al., 2014). The Bardia National Park is part of the Terai Arc Landscape (TAL), one of the most important landscapes for tiger conservation, and was recognized as such in 2001 when it was designated as the number one tiger conservation unit by the Government of Nepal and WWF Nepal (Wikramanayake et al., 2004). The park was however identified as a poaching hot spot, when DNA forensic analysis from seized tiger parts revealed that six out of fifteen tiger parts originated from the Bardia tiger population (Karmacharya et al., 2018).

Bardia National Park is home to several flagship species, including tiger and leopard but also Asian elephant and Indian rhinoceros. It has been estimated that the tiger population of Bardia has increased from 18 in 2009 to 87 in 2018. The current prey base of Bardia is suggested to be sufficiently large to support a population of 100 tigers, assuming 10% removal per year (Karki et al., 2016). The current estimated population of 87 tigers in Bardia is therefore expected to grow, provided that other conditions for their survival remain optimal. Although information on leopard population dynamics for Bardia are lacking, other studies in similar habitat suggest that leopards occur at densities of approximately 14.99 individuals/km2 (Harihar et al., 2009). Studies in other protected areas also showed that when both tigers and leopards share the same habitat, leopards are often displaced to the fringe of the protected area (Harihar et al., 2011; Mondal et al., 2012). Whether this is also the case for Bardia National Park, where prey is generally abundant, is part of the main objectives of the present research. I have chosen Bardia National Park for this study because the numbers of tigers are increasing as a result of implementation of better management practices.

1.3.3 Geomorphology and climate

The park consists of three ecological zones, on the southern flank of the Himalayas: *siwalik* hills, *bhabhar* zone and the Terai plains (Shrestha, 2004). The *siwalik* hills are an uplifted ridge system formed from the debris brought down from the main Himalayas and runs along the base of the Himalayas. It is composed of coarsely bedded stone, crystalline rocks, clays and conglomerates. The soils are young and very shallow and exposed to greater erosion levels (Bhattarai, 2009). The *bhabar* is formed by the deposit of coarse material brought down by the Himalayan rivers along the foothills of Siwalik. The *bhabar* is characterized by a low ground water table because the deposits are primarily boulders which make them porous. This zone is not suitable for agriculture and is characterized by large tracts of forests (Bhattarai, 2009). The *Terai* plains, which are situated South of bhabar, hold a river basin and consists of fine alluvial soil with a high ground water table (Shrestha, 2004).

The climate of Bardia National Park is subtropical monsoonal, with rain from June to early October, a cool dry season from late October to late February and a hot and dry season from March to mid- June. The temperature ranges from 10°C in January to 41°C in May, with an average rainfall of 1500mm (Dinerstein, 1979). The altitude of the park ranges from 152m to 1441m above sea level (Dinerstein, 1979).

1.3.4 Flora and fauna of Bardia

Seven major vegetation types have been identified in Bardia National Park, four of which are forests and three are grasslands. The forest vegetation types include: Sal forest, Khair-Sisso forest, Riverine forest and Hardwood forest (Dinerstein, 1979). The grasslands include: Wooded grassland, *Phanta* and Tall floodplain grassland (Dinerstein, 1979). The *Phanta* (grassland) of Bardia includes: Baghaura, Khauraha, Lamkauli, Sanoshree, Thuloshree, Chepang and Guthi (Chanchani et al., 2014). About 70% of the forest consists of Sal forest, with a mixture of riverine forest and grassland (DNPWC, 2018).

More than 30 different mammals and 230 species of birds have been recorded in the park (DNPWC, 2018), among which are the iconic, endangered tiger, Asian elephant, Indian rhinoceros, swamp deer and black buck (*Antilope cervicarpa*). Species that have been identified in the park as major prey species for tigers and leopards include chital (*Axis axis*) which is the most abundant medium-sized prey, followed by hog deer (*Axis pornicus*), muntjac (*Muntaicus muntjak*) and wild boar (*Sus scrofa*) (Wegge et al., 2009). The larger species of prey ungulates include barasingha (*Cervus duvauceli*), nilgai (*Boselaphus tragocamelus*) and sambar (*Cervus unicolor*) which are present in lower densities (Wegge et al., 2009). The tiger prey base density in Bardia National Park was estimated at 92.6 animals/km², which is the highest in Ne- $\,$ pal as compared to other national parks (Dhakal et al., 2014).

1.3.5 The buffer zone of Bardia National Park

The buffer zone of Bardia National Park was established in 1996 with an area of 327 km², which was later on extended by adding 180 km² of the Surkhet district, finally expanding its surface area to 507 km^2 in 2010. It now includes forest patches, agricultural land, river and water bodies, settlements, a cultural heritage village and other forms of land use (Budathoki, 2003). The buffer zone provides benefits to both villagers and wildlife: villagers harvest forest products from the buffer zone community forests and wildlife uses it as extended habitat, as a refuge, and as a movement corridor (Budathoki, 2004). The buffer zone encompasses three districts: Bardia, Banke and Surkhet (DNPWC, 2018). Approximately 30 to 50% of the revenue generated by the protected area is invested in local communities residing in the buffer zone (Baral & Heinen, 2007). These investments are intended to support conservation and alternative livelihood activities, and are based on the priorities that have been established through an approved management plan (Heinen & Mehta, 2000; Baral & Heinen, 2007).

1.4 Structure of the thesis

This PhD dissertation is based on articles and is divided into six chapters. The individual chapters two to five are either published or in the process of publication in scientific journals. References of all the chapters are grouped together and presented at the end of the thesis.

Chapter one mainly focuses on the theoretical background of my study, stressing the need to fill theoretical gaps. The literature review in the introduction provides a basis for the description of the aim of my study and my research questions, which are followed by a description of the study area.

Chapter two mainly focuses on spatial and temporal interactions between leopards and tigers. Camera trap data from 2013 and 2016 are used to study the level of interaction between the two species. The 'overlap' package is used to determine temporal overlap between the two species. This article is currently under review in the Journal of Tropical Ecology.

Chapter three describes the diet and prey preference of male and female tigers. DNA analyses were performed to confirm the individual's species and sex. Microscopic hair analysis of prey species was done to determine the prey species that had been consumed. This study has been published as journal article in Tropical Conservation Science, 2018, Vol 11, DOI: 10.1177/1940082918799476.

Chapter four describes the spatial and temporal patterns of human-wildlife conflicts in Bardia National Park over a period of five years. We looked at variations in conflict incidence over time and in relation to moon phase. We also studied spatial patterns of conflict in different sub-regions of the buffer zone. This article is submitted to the Journal of Wildlife Management.

Chapter five provides an overview of the probabilities of livestock loss using a general linear model. The perceptions and attitudes of people living in the different sectors of the buffer zone of Bardia National Park are investigated by means of a questionnaire survey. This article is accepted for publication in the journal Oryx (13 November, 2018).

Chapter six covers the synthesis and integrates all chapters of this study. It also formulates strategies and suggestions for the successful management of co-existing tigers and leopards, and general recommendations for managing the human-wildlife conflict in the region as a whole, and for Bardia National Park specifically.

2 Activity patterns of co-existing tigers and leopards

"Interaction between sympatric tiger and leopard in Bardia National Park, Nepal." Subodh K. Upadhyaya, Babu Ram Lamichhane, C.J.M. Musters, Naresh Subedi, Geert R. de Snoo, Panna Thapa, Maheshwar Dhakal, Laxman Prasad Paudyal, Shailendra K. Yadav, Hans H. de Iongh.

(Submitted to the Journal of Tropical Ecology)

Abstract

We studied spatiotemporal activity patterns between tigers (*Panthera tigris*) and leopards (*Panthera pardus*) in Bardia. For this we used camera trap data from 2013 and 2016 which were placed inside grid cells of 2×2 km. We divided the park surface into a core zone and a boundary zone. We hypothesized that leopards are pushed towards the park boundary, which could be caused by the increase in tiger abundance in the core zone of the park. First, we tested if there is spatial avoidance between the two species. Second, we analyzed the temporal overlap and temporal activity between different time periods of the day to detect temporal avoidance. We found that there was a significant level of spatial avoidance between the two species in the core zone grid cells whereas in the boundary zone grid cells no such avoidance was detected. The overall temporal overlap was around 0.8 in both core zone and boundary zone grid cells, which is substantial. When all grid cells for the entire park were incorporated, the Fisher's test showed that temporal presence of leopards in grid cells where both leopard and tiger are present is significantly different from the activity of leopards in grid cells where tigers are absent. For the core zone specifically however, the presence of tigers was not significantly different in grid cells with the leopard in the core zone. The activity of the tigers in the boundary zone was significantly different when the leopard was present, while the activity of leopards did not change. Our findings suggest that leopards avoid tigers spatially and that leopards avoid tigers temporally in the core zone, but this pattern is different near the human-dominated area i.e. in the boundary zone.

Keywords

avoidance, boundary zone, camera traps, competition, core zone, species interaction, top predators.

2.1 Introduction

2.1 Introduction

Top predators have been described as a flagship or umbrella species for their role in biodiversity conservation and maintaining a healthy ecosystem (Morrison et al., 2007; Ripple et al., 2014). The species interactions responsible for maintaining ecological integrity are eroding as animal populations are declining due to over-exploitation or habitat loss (Steinmetz et al., 2013). Managing populations of large carnivore species that are threatened, but in competition with each other, presents a conservation challenge over species prioritization (Rayan & Linkie, 2016).

Some studies pointed out that in optimal habitat, with sufficient prey, in combination with low densities of leopards and tigers, both predators can successfully co-exist, even with a certain overlap in spatiotemporal activity (Amarasekare, 2008; Lovari et al., 2015; Ramesh et al., 2012). In areas of high tiger density, tigers generally out-compete leopards and in extreme cases, tigers have been observed to attack and kill leopards (McDougal, 1988; Mondal et al., 2012b). Karanth & Sunquist (2000) reported leopards showing behavioral avoidance of tigers by hunting at different times of the day. Harmsen et al. (2009) pointed out from their study on puma (*Panthera concolor*) and jaguar (*Panthera onca*) that there was spatial overlap but no temporal overlap among them.

Some other studies also indicate that leopards avoid tigers in time and space (Odden et al., 2010; Steinmetz et al., 2013). Spatial segregation between tigers and leopards could be attributed to a general ecological dominance of tiger over leopard (Steinmetz et al., 2013). Intra-guild competition over prey has been reported to result in a change in feeding behavior (McDougal, 1988; Mondal et al., 2012b; Palomares & Caro, 1999; Ramesh et al., 2017). In this process, subordinate members of the guild have evolved activity patterns that minimize overlap with dominant predators (Hayward & Slotow, 2009). Seidensticker (1976) and Seidensticker et al. (1990) suggested that leopards consequently avoid areas frequented by tigers and often occupy the periphery of parks close to human settlements. As a catholic predator with a large prey base, leopards can adapt to a wide range of habitats, even in close proximity to human settlements (Athreya et al., 2013).

In Bardia National Park (henceforth Bardia) the number of tigers has been increasing since 2009, when about 18 tigers had been recorded. In 2014 their number had increased to 50 individuals (Dhakal et al., 2014) and to 87 in 2018 (unpublished results).

In the present study we test the hypothesis that leopards would actively avoid tigers in Bardia as a consequence of this increase in tiger numbers. Due to the elusive nature of the tiger and leopard, which makes research based on direct observations impracticable, we used a presence and absence record in grid cells by compiling camera trap data from 2013 and 2016. We tested the following hypotheses: (1) activities of tigers and leopards show distinct patterns when comparing the year 2013 to 2016; (2) activity patterns of tigers and leopards are characterized by spatiotemporal variation; and (3) populations of tigers and leopards show different levels of overlap in the core zone versus the boundary zone of Bardia.

We expected that with the increase of tigers inside the park leopards are pushed towards the park edges. The results of this study are expected to provide a scientific basis for ecological restoration efforts for tigers and leopards. They could be used by e.g. park officials to formulate actions which would promote successful co-existence of these two apex predators in a human-dominated landscape.

2.2 Methods

2.2.1 Study Area

This study was carried out in Bardia which covers a surface area of 968 km². The buffer zone of the park covers an area of 507 square km (Figure 2.1). This park is one of the major sites for the conservation of large carnivores and is designated under category II by IUCN. The park is part of the Terai Arc Landscape (TAL), a trans-boundary tiger conservation landscape in India and Nepal, and is regarded as a level-1 tiger conservation unit (Wikramanayake et al., 2008). Carnivorous mammals present in the park include large carnivores (tiger and leopard) and meso-carnivores: grey wolf (*Canis lupus*), striped hyena (*Hyaena hyaena*), golden jackal (*Canis aureus*) and fox (*Vulpes vulpes*). The two major rivers flowing inside the park, Karnali river in the west and Babai river in the east, have created an alluvial floodplain grassland that is rich in biodiversity (Bhattarai & Fischer, 2014). Prey species in the park include chital (*Axis axis*), which is most abundant followed by hog deer (*Axis pornicus*), muntjac (*Muntaicus muntjak*) and wild boar (*Sus scro-* *fa*) (Wegge et al., 2009). Larger prey ungulates which occur in lower densities include barasingha (*Cervus duvauceli*), nilgai (*Boselaphus tragocamelus*) and sambar (*Cervus unicolor*) (Wegge et al., 2009). The overall density of prey species is $92.6/\text{km}^2$ with chital at $53.99/\text{km}^2$, sambar at $4.45/\text{km}^2$, wild boar at 4.79/km2 , muntjac at 1.97/km2 , rhesus monkey (*Macaca mulatta*) at 5.47/ km2 and langur (*Semnopithecus entellus*) at 21.35/km2 (Dhakal et al., 2014).

The vegetation in Bardia National Park, mainly consists of Sal forest *Shorea robusta* and patches of grasslands dominated by *Imperata cylindrica*. Along the river alluvial tall grassland and variety of successional forest type is dominating (Odden, 2004). The forest types included: Sal forest, Khair-Sisso forest, Riverine forest and Hardwood forest (Dinerstein, 1979).

The land included forest patches, river and water bodies, agricultural lands, settlements, cultural heritages, village open space and other types of land use (Budhathoki, 2003). Subsistence farming is practiced by villagers in which crop production is supplemented by the use of forests and grasslands for livestock grazing (Studsrød & Wegge, 1995).

2.2.2 Study species

Tigers and leopards are sympatric in most of their shared habitat type, which mainly includes woodland and grassland with patches of thick vegetation (Seidensticker, 1976). Tigers and leopards coexist in the riverine forest and tall-grass vegetation of the Terai (Seidensticker et al., 2015). Co-existence of tigers and leopards are often associated with low densities of both species (Linnell & Strand 2000)

Leopards generally feed on small $(< 50 \text{ kg})$ to medium-sized $(50-100 \text{ kg})$ prey and other smaller prey items that are too small for tigers (Odden et al., 2010). Tigers generally feed on medium to larger (>100 kg) prey species. Nonetheless, tigers and leopards can prey on different size classes of the same species (Seidensticker et al*.*, 2015). Where large prey occurs at very low densities, tigers have been observed to switch to smaller prey species, which could lead to more intense competition with leopards over prey (Støen & Wegge, 1996; Odden et al., 2010).

2.2.3 Data collection

Our study is based on camera trap data collected during 2013 and 2016 by the Department of National Parks and Wildlife Conservation (DNPWC) in technical collaboration with the National Trust for Nature Conservation (NTNC) and World Wildlife Fund (WWF), Nepal. In 2013, the camera trapping survey covered 72 days (17 February - 28 April 2013) with cameras placed at 238 locations, or the equivalent of 3570 trap nights. In 2016, the camera trapping survey covered 71 days (18 January- 28 March 2016) during which cameras were placed at 264 locations, or equivalent of 4215 trap nights.

The survey area was selected based on intensive sign survey prior to the deployment of camera in order to identify potential survey sites to increase probability of a tiger or a leopard being photographed. The study was done in the dry season mostly due to better accessibility of the study area and better visibility as a result of reduced vegetation cover. The survey area covered the whole park area including part of the buffer zone as well as the corridors, and was divided into grid cells of 2×2 km. A total of 238 grid cells were surveyed in 2013, with 175 grid cells in the core zone and 63 grid cells in the boundary zone. Grid cells which were at least partly extending beyond the park boundary were marked as boundary zone (henceforth BZ) grid cells. Grid cells which were located entirely inside the park boundaries were assigned as core zone (henceforth CZ) grid cells. In 2016, 264 grid cells were surveyed, of which 175 grid cells in the core area and 89 grid cells in the boundary zone. A pair of motion sensor digital cameras (Bushnell Trophy Cam HD, Reconyx HC500 and HC550) facing each other, spaced at a distance of 6-8 m, was placed in each cell. The cameras were mounted on trees or wooden poles 45 cm above the ground, and placed on either side of the game trails, forest roads, and riverbeds without using a lure, for a period of 15 days at each grid cell (Dhakal et al., 2014). The CZ grid sample size was 175 for both 2013 and 2016 whereas 63 grids and 89 grids were sampled in the BZ in 2013 and 2016 respectively.

2.2.4 Spatial overlap

The presence of tigers and leopards in the designated grid cells was analyzed by camera capture records. Presence was scored for each tiger or leopard captured by the camera. To determine the presence of any spatial overlap we analyzed the data presented in Table 2.1. We performed a Chi-square test to analyze the level of spatial overlap between tigers and leopards.

2.2.5 Temporal overlap

Temporal overlap between tigers and leopards was calculated by comparing the times at which individual leopards and tigers had been captured on camera in the CZ versus the BZ. For estimations of inter-specific temporal interactions between tigers and leopards, two strategies were followed. For the first strategy, the temporal activity (diel time scale) was estimated using the non-parametric circular kernel-density function of activity derived from the camera trap captures and the coefficient of overlap (Dhat) to measure the extent of overlap between two kernel-density estimates (Carter et al., 2015; Linkie & Ridout 2011; Ridout & Linkie, 2009). The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap). Overlap was defined as the area under the curve, taking the minimum of two kernel-density estimates at each point in time (Carter et al., 2015). As per the recommendation by Meredith & Ridout (2018), we used a coefficient of overlap estimator Dhat1 when the sample size was less than 50 and Dhat4 when the sample size was more than 75. For estimating the overlap, the time span for each independent detection was pooled to 30 minutes (only photographs taken at an interval of at least 30 minutes at one camera trap location were used) (Linkie & Ridout, 2011). We calculated the 95% confidence interval index using smoothed bootstrap with 10,000 resamples (Carter et al., 2015; Linkie & Ridout 2011; Meredith & Ridout, 2018). We performed a density overlap test with (1) all grids of 2013 and 2016 combined, (2) grids of CZ of 2013 and 2016 combined, (3) grids of BZ of 2013 and 2016 combined. Temporal overlap analysis was performed in R using the '*overlap*' package (Meredith & Ridout, 2018).

For the second strategy, we combined 2013 and 2016 data and compared the temporal activity of tigers and leopards within certain periods of the day. Grid cells were marked as 'overlap grids' whenever both tiger and leopard were present and 'non-overlap grids' when either tiger or leopard was present. We did this comparison also for grid cells of CZ and BZ separately. For testing the temporal overlap, we divided the 24 hours of a day into dawn (05h01-08h00), day (08h01-17h00), dusk (17h01-20h00) and night (20h01- 05h00), and counted the number of grid cells in which either tiger or leopard was caught on camera trap during these periods. We tested differences in activity with the Fisher's exact test. All statistical tests were performed in R.

2.3 Results

Table 2.1 provides a summary of tiger and leopard presence. We observed an increase in camera trap captures of tigers and a decrease in captures of leopards in 2016 compared to 2013.

Table 2.1

Number of camera trap grid cells showing tiger and leopard presence or absence during 2013 and 2016.

Leopards were captured in 18.9% of the grid cells in 2013 and in 14.8% of the grid cells in 2016. Tigers were captured in 47.5% of the grid cells in 2013 and in 48.9% of the grid cells in 2016. Concurrent presence of both tiger and leopard was recorded for 6.7% and 5.3% of the grid cells in 2013 and 2016, respectively. In 40.3% and 41.6% of the grid cells in 2013 and 2016, respectively, neither tiger nor leopard had been captured.

2.3.1 Spatial overlap of activity between tigers and leopards

After classifying grid cells as either core zone (CZ) or boundary zone (BZ), a significant level of spatial avoidance was found between tigers and leopards in the CZ grid cells of the park, but not in the BZ grid cells. In 2013, spatial overlap between tigers and leopards was recorded in five CZ grid cells (2.9%) and in 11 BZ grid cells (17.5%). In 2016, spatial overlap was observed in six CZ grid cells (3.4%) and eight BZ grid cells (9.0%).

Table 2.2

Spatial overlap between tigers and leopards in 2013 versus 2016 and for each zone (T1: tiger presence, T0: tiger absence, L1: leopard presence, L0: leopard absence, df: degree of freedom; p-value of Chi-square test shown).

There was spatial overlap between tigers and leopards in both years, with greater overlap $(p=0.219)$ in the BZ grid cells compared to the CZ grid cells $(p=0.451)$. There was no difference between years in the number of presence/ absence grid cells for leopards and tigers in the CZ and BZ (Table 2.2). When testing how the presence of leopards is different when tigers are present and vice versa, we found a significant difference between 2013 and 2016 for the CZ grid cells ($p = 0.005$, $p = 0.023$, Table 2.2).

Figure 2.2

Temporal overlap with smoothed bootstrap confidence interval (95%) in all grid cells combined.

We found a considerable temporal overlap in tiger and leopard activity in both 2013 and 2016. Although the overlap estimator shows that the overlap in temporal activity between tigers and leopards had slightly $(\Delta=0.82)$ decreased in 2016 as compared to 2013 (Δ =0.87) for both zones combined, it showed an increase for the BZ in 2016 (Δ =0.83). The lowest temporal activity overlap between tigers and leopards was recorded in overlap grids during 2016 (Δ =0.69) and the highest in combined grids during 2013 and 2016 $(\Delta=0.88)$ (Table Appendix 2.1).

2.3 Results

Figure 2.3

a) Activity curves of tigers in the absence of leopards, b) Activity curves of leopards in the absence of tigers, c) Activity curves of leopards and tigers in combined grid cells of 2013 and 2016, d) Activity curves of tigers in the CZ in the absence of leopards, e) Activity curves of leopards in the CZ in the absence of tigers, f) Activity of leopards and tigers when both were present in combined grid cells of the CZ for 2013 and 2016, g) Activity curves of tigers in the BZ in the absence of leopards, h) Activity of leopards in the BZ in the absence of tigers and i) Activity of leopards and tigers when both were present in combined grid cells of the BZ for 2013 and 2016. The coefficient of overlap is equal to the area below both curves, shaded grey in the diagram.

The activity of tiger in the 'tiger only' grid cells shows that they were most active during dawn and dusk, with less activity during the daytime for both zones combined (Figure 2.3a) as well as in the CZ (Figure 2.3d) while they were most active at night with less activity during the daytime in the BZ (Figure 2.3g). The activity of leopards in 'leopard only' grid cells shows that leopards were also active at dawn while less activity was seen during the dusk period for both zones combined (Figure 2.3b) and in the CZ (Figure 2.3e), and that leopards were more active than tigers during dawn and dusk but slightly less active during the daytime in the BZ (Figure 2.3h).

In general, leopards were more active during the daytime compared to tigers (Figure 2.3b). There was no significant difference in activity between tigers and leopards for grid cells where both tigers and leopards were present (Figure 2.3c); both tigers and leopards were more active during the night. There was a marked difference in activity between tigers and leopards in the overlap grid cells of the CZ, with leopards being more active during the day (Figure 2.3f). In the overlap grid cells of the BZ, leopards were more active during dawn and dusk and tigers were more active during the night (Figure 2.3i).

Table 2.3

Fisher's exact probability test comparing the number of times leopards and tigers were captured on camera in different time periods (dawn, day, dusk and night) between overlap grids and non-overlap grids and between CZ and BZ. More detailed data on each specific Fisher's test is provided in Table Appendix 2.2.

Leopard activity during dawn, day, dusk and night was significantly different in overlap grid cells versus non-overlap grid cells of the CZ ($p= 0.02$, Table 2.3). The temporal presence of tigers was significantly different when comparing overlap and non-overlap grid cells of the BZ ($p = 0.07$, Table 2.3). None of the other comparisons of temporal activity data showed any significant differences.

2.4 Discussion

2.4 Discussion

Our findings suggest that with the increasing number of tigers, especially in the core zone of the park, leopards may have started to show a certain level of avoidance by moving towards the park boundary, which is in support of our hypothesis (Harihar et al., 2011; Mondal et al., 2012b; Odden & Wegge, 2005). Our results are comparable with those of Rayan & Linkie (2016) who found that leopards avoided tigers on a fine spatial scale in areas with high tiger and prey density, mainly in the central area of a park in Malaysia. Linnell & Strand (2000) confirmed that certain species of carnivores may be forced to avoid habitats used by a more dominant carnivore. In our study leopard seemed to avoid tigers in the CZ, which is in accordance with earlier findings from Bardia (Odden et al., 2010) and Chitwan National Park (Carter et al., 2015). Although we did not find any changes in this avoidance between 2013 and 2016, the lower camera capturing rate for leopards in combination with the higher capturing rate for tigers between both years do suggest a general negative presence correlation between both species. Most of the temporal overlap in activity pattern between tigers and leopards in both 2013 and 2016 took place at night in both the CZ and BZ of the park. Tigers showed a bimodal peak of activity, with a peak from midnight until early morning and a peak just after sunset (Azlan & Sharma, 2006). This finding calls for further investigation, as it is different from results presented by e.g. Kawanishi & Sunquist (2004), who found that tigers and leopards in Taman Negara National Park, Malaysia were more diurnal than nocturnal and their activity pattern overlapped with crepuscular/diurnal prey species. Our finding that leopards in Bardia were more diurnal compared to tigers is in accordance with earlier findings (Azlan & Sharma 2006; Steinmetz et al., 2013) from leopards and tigers in Malaysia and Thailand. This suggests that leopards can co-exist with tigers by shifting their activity pattern (Seidensticker, 1976). Further, leopards become less active when tigers are around, both during the day as well as during the night time (Sunquist, 1981).

The temporal overlap between tigers and leopards we found, could have been facilitated by the abundant prey of various sizes present in Bardia, as was also suggested to be the case in Chitwan (Carter et al., 2015). Mondal et al. (2012a) suggest that when tigers and leopards are present in the same habitat, leopards would target the smaller females or fawns of large ungulate prey, while tigers would more often hunt the adult males of such larger ungulate species. However, in areas of low prey density leopard closely track prey as well as avoid tiger (Steinmetz et al., 2013).

We found that the level of temporal overlap near the park boundary was higher in 2016 compared to 2013. This may be a result of the growing tiger population in Bardia. The high temporal overlap in activity between the two cat species (Dhat4 >0.7) suggests that if tigers and leopards share the same forested habitat, their temporal activity is not driven by behavior aimed at avoidance (Karanth & Sunquist, 2000). Mondal et al. (2012a) also suggested that in order to co-exist with tigers, leopards either decreased their niche breadth or shifted to areas where tigers were absent.

Our research suggests that at least some mutual avoidance between tigers and leopards occurs, although not visible from the overlap coefficient (Dhat4). The proximity of human settlements in the BZ grids may have contributed to the avoidance we found for tigers. Another explanation could be that the tigers that were captured on camera in the BZ were mainly sub-adult tigers that may have been displaced from their core home range or could be too young and inexperienced to compete with leopards (e.g. Kolipaka et al. 2017).

As home ranges and prey availability change with season for both tigers and leopards (Odden & Wegge, 2005; Kapfer et al., 2011), the spatiotemporal activity pattern of the two sympatric carnivores could change accordingly if captured during a different time of the year. Although our study only covered the dry season, mostly due to better accessibility of the study area and better visibility as a result of reduced vegetation cover, a year-round study could help to determine whether or not spatiotemporal activity patterns are seasonally dependent.

The camera traps were primarily used for estimating the number of tigers in the national park and therefore were put in places where there was a frequent movement of tigers. This may have resulted in an underestimation of leopard presence and may have enhanced the 'avoidance effect' we found for leopards.

For park management to be effective and for top predators to successfully co-exist, effective protection measures, targeted at both the predator species and its habitat, should be formulated and enforced. In order to achieve this, the effects of interspecific interactions, such as described in this chapter, should be taken into consideration. The knowledge that leopards, at least to some extent, are being displaced by tigers in Bardia could help to predict the effect of top predators on each other, especially when certain populations are increasing (Sunarto et al., 2015).

Acknowledgements

We are grateful to the Department of National Parks and Wildlife Conservation (DNPWC), Kathmandu, Nepal for providing us the camera trap data. We thank Mr. Ramesh Thapa and Mr. Ashok Bhandari for their support and permission to work in BNP. We are also thankful to the National Trust for Nature Conservation, Bardia Conservation Program for their technical support in gathering the information. And finally we would like to express our gratitude to all the technicians and team members who participated in the camera trapping for their contribution.

Appendix

Table Appendix 2.1

Temporal overlap estimates for different years and grids. Approximate 95% bootstrap confidence interval of overlap estimates are also shown (OL-overlap grids; NOL-non-overlap grids).

Table Appendix 2.2

Temporal overlap between tigers and leopards in the overlap and non-overlap grids of park, CZ and BZ over different periods of the day (dawn, day, dusk and night).

3 Diet composition and prey preference of tigers

"**An insight into the diet and prey preference of tigers in Bardia National Park, Nepal**" Subodh K. Upadhyaya, C.J.M. Musters, Babu Ram Lamichhane, Geert R. de Snoo, Panna Thapa, Maheshwar Dhakal, Dibesh Karmacharya, Purna Man Shrestha, Hans H. de Iongh. (Published in Tropical Conservation Science, 2018, Vol 11, p 1-9)

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/km²) 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

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 Fareast. 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 km²) 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 $3.3/100 \mathrm{~km^2}$ and the prey density is 92.6 animals/ km2 (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).

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

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

Table 3.1

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		ΝI	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.

A = Frequency of occurrence of the prey species in scats; $X = M$ ean 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 = 0.033-0.025exp^{-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

*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).

Acknowledgments

We are grateful to the Department of National Parks and Wildlife Conservation (DNPWC), Kathmandu, Nepal for necessary permits to conduct this study. We are indebted to Mr. Ram Chandra Kandel, Mr. Ramesh Thapa and Mr. Ashok Bhandari from BNP. We are also grateful to Mr. Ambika Prasad Khatiwada, Mr. Rabin Kadariya, Mr. Shailendra Kumar Yadav and Mr. Shree Ram Ghimire from NTNC, Bardia Conservation Program. Our sincere thanks go to the technicians of CMDN, Kathmandu for DNA analysis. We are also grateful to our field assistants Phiru Lal Tharu, Indra Prasad Jaisee, Khushi Ram Chaudhary, Prasun Ghimire and Mohan Lal Tharu. We would also like to thank anonymous reviewers who helped in improving the earlier version of this manuscript.

Declarations of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: Netherlands fellowship program (Nuffic, NFP PhD fellowship).

4 Spatiotemporal patterns of human-wildlife interactions

"Spatiotemporal patterns of human-wildlife interactions in the buffer zone of Bardia National Park, Nepal"

Subodh K. Upadhyaya, C.J.M. Musters, Ashok Bhandari, Babu Ram Lamichhane, Geert R. de Snoo, Panna Thapa, Maheshwar Dhakal, Hans H. de Iongh. (Submitted to the Journal of Wildlife Management)

Abstract

The spatiotemporal pattern of conflict incidences in the buffer zone of Bardia National Park over the period 2013-2017 was studied based on compensation paid to the victims. The majority of conflict incidences reported, included (fatal) human injury, crop damage and property damage, as well as livestock predation. Elephants and leopards were responsible for the majority of conflict incidences, followed by tigers and wild boars. The elephant was responsible for killing 14 people during the study period, while wild boar killed one person. Neither tigers nor leopards had been reported to have contributed to human fatalities around Bardia. The conflicts caused by elephants peaked during the autumn season when their favored matured crop. Livestock predation by leopards peaked during the rainy season, whereas predation frequency by tigers was relatively constant throughout the year. There was a significant relationship between livestock predation and moon phase, with most predation incidences taking place during the new moon phase. Moon phase was not significantly related to conflict incidences caused by elephants. When comparing the conflict patterns in different sub-regions of the buffer zone, elephant, leopard and wild boar, but not tiger, showed significant differences between these sub-regions. In terms of monetary loss, most of the losses were attributed to elephants. A total of \$ 61,085 was paid to villagers as compensation. Villagers living in the buffer zone mostly preferred electric fencing and improved enclosures in order to minimize human-wildlife conflicts.

Key words

buffer zone, carnivores, compensation, conflict, herbivores, moon-phase.

4.1 Introduction

4.1 Introduction

Farmers in developing and biodiversity rich countries experience economic loss through the loss of their resources by negative interactions with wild predators and herbivores (Thinley et al., 2018). For this phenomenon the term 'human-wildlife conflict' is usually used, but this is misleading as it portrays wildlife as an antagonist with the conscious intent to interfere with people's lives and livelihoods, whereas the real conflict is between conservation and other human interests (Peterson et al., 2010; Redpath et al., 2015; Fisher, 2016). In this study we therefore only use the term 'conflict' to describe negative interactions between people and wildlife.

Besides the previously discussed conflict situations which arise from large predators attacking livestock or even people, other large mammals such as the elephant and rhinoceros may also cause conflicts by destroying agricultural crops or personal properties and by sometimes even fatally injuring people (Sukumar, 1991). Wherever conflicts with wild animals occur, they may cause a certain antipathy and negative attitude among people living in the periphery of natural reserves (Sukumar, 1991). As a result, the conservation of such 'high-risk' species near human settlements often generates a lot of debate as to what extent humans should tolerate the negative impact of these conflict causing species and what could be done to mitigate conflicts and prevent the locals from initiating retaliatory measures (Manral et al., 2016; Carter & Linnell, 2016; Lamichhane et al., 2018). Balancing the needs and aspirations of the often poor farmers living close to protected areas and the need of conserving endangered, large and dangerous animals is a challenging task in developing countries like Nepal (Wegge, et al., 2009).

Human intolerance towards conflict causing mammals is often based on misconceptions about the potential risk these animals pose to property, livestock and humans (Oli et al., 1994; Treves & Karanth, 2003; Pant et al., 2016). A poor understanding of the ecological role they play may also induce a certain resentment against conservation in general (Nyhus, 2016; Thinley et al., 2018). Human-wildlife conflict is one of the most critical threats faced by many wildlife species today, and the topic is receiving increasing attention from conservation biologists (Dickman, 2010). A good understanding of the patterns of human-wildlife conflict and identifying the causes is therefore key to formulating effective conservation strategies (Acharya et al., 2016). One aspect of conflict causing activities of large carnivores and herbivores that needs urgent attention is the spatial and temporal pattern of conflict and how this conflict differs between conservation areas (Wilson et al., 2013; Lamichhane et al., 2018a). For example, moon phase is reported to have an effect on conflict incidence in Africa and Nepal (Tumenta, 2012; Packer et al., 2011; Gunn et al., 2014; Lamichhane et al., 2018a). Crop raiding by African elephants was lower during the full moon phase (Gunn et al., 2014) whereas Lamichhane et al. (2018a) reported more incidents by Asian elephants during the full moon phase. Incidence of attacks on humans and livestock by large carnivores were shown to be lower during the full moon phase in some studies (e.g. Packer et al., 2011; Lamichhane et al., 2018a) while Tumenta (2012) did not report a significant effect of full moon phase on livestock depredation. Traill et al. (2016) reported that the proximity of lions and not the moon phase affects the behavior of prey animals such as zebra and wildebeest. The effect of moon phase on predatory events by large carnivores thus differs between geographical regions and could be influenced by other local factors as well.

People living around the buffer zone of Bardia are using both traditional and modern means to guard their crops against wild animals (Thapa, 2010). Conflict mitigation measures include providing monetary compensation to the victims, construction of electric fences and trenches along the forest edges and construction of predator proof corrals to minimize damage to livestock (Acharya et al., 2016). In order to prevent damage caused by elephants, electric fencing and beehives are used as means of protection (King et al., 2009; Sapkota et al., 2014). In other areas, cultivation of unpalatable cash crops such as capsicum is effective in reducing human elephant conflict (Parker & Osborn, 2006). Chili smokes and spotlights are also sometimes used for reducing crop raiding by elephants (Davies et al., 2011).

The main aim of this chapter is to provide an overview of spatiotemporal factors affecting human-wildlife conflicts around Bardia National Park. The research questions which were addressed include:

- **1** What are the main conflict causing wildlife species?
- **2** Are there any spatiotemporal patterns found in conflict incidences?
- **3** How much money is spent on compensation schemes?
- **4** What is the perception of local communities on how to manage conflicts?

4.2 Study area

Bardia National Park (henceforth BNP) (28°15' to 28°35.5' N and 80°10' to 81°45' E, 968 km², altitudinal range 152-1440m) was established in 1969 and is situated in the Bardia and Banke districts of Nepal, south west of Kathmandu. The park is designated under IUCN category II (DNPWC, 2018). It is part of the western Terai Arc Landscape (TAL), providing important habitat for large carnivores, including tigers and leopards. BNP is one of the largest protected areas in the Terai lowland. BNP has undergone a series of shifts in terms of property rights and changes in conservation status. The area was first declared as a Royal Hunting Reserve in 1969, but since established rules and regulations were not strictly enforced, access to resources inside the reserve was basically free to the local community. In 1976, an area of 368 km² was officially declared as the Royal Karnali Wildlife Reserve and in 1982 renamed as the Bardia Wildlife Reserve. After discovery of the Babai valley with its higher wildlife densities, suitable plains for habitats and the main river course flowing to the far west, the size of the reserve was extended in 1984. Finally, in 1988 the reserve was upgraded to the National Park status (Brown, 1998).

The buffer zone of BNP was established in 1996, when an area of 327 km^2 was added to the park. In 2010 an additional 180 km^2 of the Surkhet district was added to expand the buffer zone to arrive at a final surface area of 507 km2 . The area of the buffer zone is designated as IUCN category-VI (DN-PWC, 2018). Buffer zones have been instated in most of the national parks and wildlife reserves throughout Nepal and also in Bardia by government to create areas around national parks which are both of natural value, e.g. including forest patches, river and water bodies, and of cultural or economic importance, e.g. agricultural lands, human settlements, cultural heritages, open meeting spaces and other forms of land use (Budhathoki, 2004). A buffer zone serves the dual purpose of providing an opportunity for local people to collect and use forest products from the community forest on a regular basis, and as extended natural habitat serving as wildlife refuges and corridors (Budhathoki, 2004). Buffer zones are managed by both the park authorities and the local communities through jointly organized community development and natural resource management initiatives (DNPWC, 2018). For this purpose 19 Buffer Zone User Committees (BZUC) have been created in BNP (Figure 4.1).

For BNP, approximately 30 to 50% of the revenue generated by the protected area is invested in local communities residing in the buffer zone. These investments are intended to support conservation and alternative livelihood activities, and are based on the priorities that have been established through an approved management plan (Heinen & Mehta, 2000; Baral & Heinen, 2007). The communities living in the BNP buffer zone are a heterogeneous society comprising indigenous Tharu people and migrants from the hills (Bhattarai et al., 2016).

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) with an annual rainfall of 1500 mm. During summer temperatures could rise to 45°C. About 70% of the forest consists of Sal (*Shorea robusta*) with a mixture of grassland and riverine forest (DNPWC, 2018).

Figure 4.1

Study area showing the buffer zone user committees (BZUC) with conflict incidents.

4.3 Methods

Yearly data on human-wildlife conflict cases were collected from existing park records, based on compensations paid to the victims as per the recommendations of the BZUC for the loss or damage of property between 2013 and 2017. We used the data to identify the main conflict causing wildlife species and the major spatial and temporal factors affecting conflict incidences. We performed chi-square to know about the predation event of tigers and leopards. We divided the BZUC into East, West, North and South sub-regions according to their location. We performed a single factor ANOVA to test the spatial pattern of conflict over different sub-regions of the buffer zone. The response variable was number of conflicts per year per sub-region, and the single factor tested was sub-region.

Seasons were defined as follows: Winter: December to February, Spring: March to May, Summer: June to August and Autumn: September to November.

Lunar days were assigned using the Gregorian-Lunar calendar conversion table of the Hong Kong Observatory (www.hko.gov.hk/gts/time/conversion. html). Day 1 was assigned New moon day and Day 15 Full moon day. Days 28, 29, 1, 2, 3 or 29, 30, 1, 2, 3 were assigned as New moon phase (dark phase) and days 13, 14, 15, 16, 17 as Full moon phase (light phase) (following Traill et al., 2016). A waxing moon is defined as the period after the new moon and before the full moon, whereas a waning moon is defined as the period after the full moon and before the new moon. We performed a two tailed, paired t- test to compare the conflicts during new moon and full moon and during the waxing and waning moon phase over a period of five years.

In order to calculate spent compensations (compensations spent on real price), annual fluctuations in inflation rate were taken into account. We calculated the real price that has been adjusted with an inflation rate over the five years of our study period. We used the real price of 2017 as the amount of compensation paid. Inflation rate figures for Nepal were taken from www. statista.com/statistics/422594/inflation-rate-in-nepal.

Data on perceptions of local inhabitants on conflict-prone wildlife was collected during a questionnaire survey among 290 households in the buffer zone (Supplementary material 4.1). The selection of villages and household heads took place according to Upadhyaya et al. (2018) (accepted). The household heads were asked to rate several aspects of human-wildlife conflicts by giving a preference score from 1 to 6 (where 6 is most preferred and 1 least preferred). All statistical analyses were done in Microsoft Excel 2010 (Microsoft Redmond, USA).

4.4 Results

A total of 3,283 conflict incidences were reported over a period of five years. Eleven species were found to cause conflicts during the study period: Elephant (*Elephas maximus*) (60%), Leopard (*Panthera pardus*) (24%), Wild boar (*Sus scrofa*) (6%), Tiger (*Panthera tigris*) (6%), Rhinoceros (*Rhinoceros unicornis*) (0.6%), Sloth bear (*Melursus ursinus*) (0.06%), Chital (*Axis axis*) (0.5%), Nilgai (*Boselaphus tragocamelus*) (2%), Crocodile (*Crocodylus palustris*) (0.3%), Python (*Python bivitattus*) (0.06%) and Porcupine (*Hystrix indica*)(0.03%). Elephant, leopard, wild boar and tiger were responsible for conflicts during each of the five years of the study period whereas the other seven species caused conflicts in some years only.

Elephants were responsible for most conflicts, resulting from damage to crops, stored grains, houses as well as injuries inflicted to human beings which were even fatal on 14 occasions (Figure 4.2). Although no human beings had been killed by tigers or leopards, wild boar was reported to have caused one fatality among local residents. Tigers and leopards were mainly involved in killing livestock such as goats, pigs, sheep and cattle (Figure 4.4).

Figure 4.2

Average number of conflict incidences from 2013 to 2017 caused by different wildlife species. The error bars indicate standard deviations.

Figure 4.3 (a-b)

The conflict incidence frequency caused by predators and herbivores over five years.

Over the entire study period, livestock predation rates were higher for leopards than for tigers (χ^2 = 27.391, df= 4, p< 0.001) (Figure 4.3a). Leopards mainly killed goats and pigs (731 and 234 respectively), whereas tigers also killed cattle (100), in addition to goats and pigs (147 and 23 respectively) (Figure 4.4). The overall livestock predation rate was higher in 2014 and 2016 compared to the other years. The damage caused by elephants was highest during 2016 (Figure 4.3b).

Property damage caused by wildlife mainly comprised damage to housing and raiding of stored grain, followed by damage to kitchen facilities and wall structures (Figure 4.5a). Paddy was the major crop damaged by elephant, followed by wheat and maize (Figure 4.5b). Maize was the major crop damaged by wild boar, followed by paddy and wheat (Figure 4.5c).

Figure 4.5 (a-c) Crop and property damage caused by elephants and wild boar.

Livestock predation occurred more often during the new moon phase compared to the full moon phase (Figure 4.6) by leopards ($p=0.006$) and tigers (p=0.046), whereas no significant relation was found between conflict incidence and new moon/full moon phase for any of the herbivore species. No effect of waxing/waning moon phase was found for any of the four studied species.

a) Monthwise conflict incidence for herbivores

b) Monthwise conflict incidence for predators

Figure 4.7 (a-b) Monthly variations in conflict incidence by wildlife group.

The month-wise conflict incidence showed that elephants and wild boars were damaging more crops during the monsoon season (Figure 4.7a). Among the predators, leopards showed a peak in predation incidences during July, whereas predation incidences by tigers remained relatively constant throughout the year (Figure 4.7b).

Figure 4.8 (a-d)

Average number of conflict incidences in different sub-regions of the buffer zone for elephants, tigers, leopards and wild boars.

Elephants were responsible for the majority of conflict incidences in the west followed by the southern sub-region of the park (Figure 4.8a). Conflicts caused by leopards and wild boars were also higher in the southern and western part of the buffer zone (Figure 4.8b, d). Conflict incidences caused by tigers were spread relatively evenly over the park (Figure 4.8c).

The results of a single factor ANOVA only showed significantly different conflict incidence rates between different sub-regions for elephants (p<0.001), leopards ($p=0.006$) and wild boars ($p=0.003$).

A total of NRs (Nepali Rupees) 6,719,420 (\$ 61,085; 1\$=NRs 110) were paid to villagers as compensation for conflicts over the five year study period. Although compensation fees for each of the species did not change over the years (Table 4.1), there was a marked increase in the average amount paid to each household in 2017 compared to other years.

Table 4.1

Compensation paid (in Nepali Rupees) for damages caused by four major species, adjusted as per the real price of 2017.

*Inflation rate is calculated based on price change over previous year.

CPI= Commodity price index.

Figure 4.9

Effectiveness scores for six wildlife damage prevention methods according to the questionnaire survey of respondents. The Y-axis shows average preference scores, with the highest score (6 points) for the most preferred measure and the lowest score (1 point) for the least preferred method.

Improved enclosures which are mainly used to prevent livestock depredation and electric fencing, mainly used to keep elephants away from human settlements and crop fields were rated as the most preferred damage prevention methods among the respondents (Figure 4.9).

4.5 Discussion

This study examined the conflict incidences around Bardia on the basis of compensation paid to the villagers for the loss of crops or livestock attributed by different wildlife. The use of human dominated zones by elephants was highest during the autumn season when crops like paddy and maize mature (Pant et al., 2016; Lamichhane et al., 2017). Crop raiding incidences were higher during the cool autumn season which may be due to the low quality of the forage available in the forest during the late part of the autumn season (Pradhan & Wegge, 2007). A high level of crop raiding was also reported for Assam in India (Wilson et al., 2015) during the cooler months between August and December. Similar to our findings, Dublin & Hoare (2004) reported that agricultural loss due to African elephants is mainly due to loss of food crops, cash crops and even crops stored inside houses.

Our results on tiger and leopard conflict incidences in relation to moon phase are comparable to those presented by Packer et al. (2011) on lions in Tanzania, Africa and Lamichhane et al. (2018a) and on tigers and leopards in Nepal, with significantly more attacks on livestock taking place during the new moon phase. The reason for this may be as tigers and leopards are nocturnal predators and dark nights of the new moon make them easy for predation because they are not detected. However, since our data lacks the time period of the incidence a detailed study in future with time of the incident would be helpful to understand the effect of moon phase.

In terms of livestock predation, leopards in our study area were responsible for more conflicts than tigers, which was also the case all over Nepal mainly in the protected areas and community and government forests (Acharya et al., 2016) and in Chitwan NP, Nepal (Lamichhane et al., 2018a). Sangay & Vernes (2008) also documented more killings of livestock by leopards (70%) than by tigers (19%) in Bhutan. The relatively high rate (67.8%) of attacks on goats in our study area is supported by findings from e.g. Chitwan NP where 87.7% of the livestock killed by leopards were goats (Dhungana et al. 2018). Goats are ideal food items for leopards because of their medium size and relatively high availability around the study area. Kabir et al. (2014) also reported significant killing of goats by leopards from in and around the Machiara National Park, Pakistan.

Leopards caused significantly more conflicts and killed more livestock than tigers around Bardia, tiger attacks could potentially lead to greater damages because they more frequently attack larger livestock such as cattle (32% as opposed to 3% for leopards), which per head are considered much more valuable than goats. Tigers generally kill larger prey in order to meet their energy requirement (Hayward et al., 2012; Upadhyaya et al., 2018). Livestock predation by leopards peaked during the monsoon season which was also found for leopards in Bhutan (Sangay & Vernes 2008). One of the causes for this peak could be a more random dispersal pattern of wild prey, away from water sources, which reduces hunting success during this time of the year (Moe & Wegge, 1994). Decreased visibility due to high standing grasses and shrubs inside the park is also considered as an important factor contributing to lower hunting success rates by large predators on wild prey (Dinerstein, 1979). As a consequence, leopards could become more tempted to attack livestock that is often poorly protected against predatory attacks (Acharya et al., 2016).

In order to minimize financial damages, respondents mostly preferred electric fencing and improving enclosures. This was a direct consequence of the damage caused by elephants and leopards, which contributed to most damages suffered. Since electric fencing and improved enclosures have been reported to effectively control damages caused by elephants (e.g. Davies et al., 2011 in Assam, India) and leopards, damages inflicted by these two species are expected to decrease over time (King et al., 2009; Sapkota et al., 2014). Plantation of cash crops like chili *Capsicum sp.* has effectively reduced damages by elephants in Zimbabwe (Parker & Osborn, 2006).

Cases for Nepal in which humans are injured or even killed in wildlife encounters mainly involve four wildlife species: tiger, leopard, elephant and rhinoceros (Acharya et al., 2017). Most of the human fatalities in our study were caused by elephants, which are known for their unpredictable behavior, like males elephants have been found to more frequently cause conflicts with humans than females due to their inherent higher risk-taking behavior (Sukumar, 1991). Combined with their exceptional force, elephants are likely to kill anyone who gets in their way. This is reflected in the figures from all over the elephants' distributional range, where they are responsible for the majority of human fatalities in conflict situations (e.g. in India and Nepal) (Wilson et al., 2015; Acharya et al., 2016). Although wild boars are generally shy and not likely to spontaneously attack humans, when provoked they could attack ferociously with their sharp tusks, leading to serious and occasionally fatal injuries (Manipady et al., 2006). The single fatal casualty caused by wild boar from our study is in line with this, and other reports on wild boar attacks in the region (e.g. India, (Manipady et al., 2006; Chauhan et al., 2009)

4.6 Management Implications

Our study is the first comprehensive study on human-wildlife conflicts conducted around Bardia National Park. The conflict 'hot spot' in the southern and western sub-region of the buffer zone we identified, could serve as a primary focal point for which to develop and implement conflict prevention measures. Such measures should take into account that certain prevention techniques are more effective than others, e.g. the use of alternative cropping patterns and electric fencing could effectively deter elephants. Improved livestock husbandry techniques and predator proof corals could be helpful in protection against predators. Promotion of livestock insurance schemes could also help to reduce the financial burden on the government and thus help in maintaining sustainability.

Acknowledgements

We are grateful to the Department of National Parks and Wildlife Conservation (DNPWC), Kathmandu, Nepal for providing permission to carry out this research. We also thank the officials of Bardia National Park for their support and permission to work in BNP. We are grateful to Mr. Shyam Thapa, Incharge and other members of the Bardia Conservation Program of National Trust for Nature Conservation for their support during the field work. We are also thankful to the Buffer Zone User Committees (BZUC) for their support in data collection.

Supplementary material 4.1

5 Defining the risks of attacks by predators around protected areas

"Defining the risks of attacks by predators around protected areas – the case of Bardia National Park, Nepal". Subodh K. Upadhyaya, C.J.M. Musters, Babu Ram Lamichhane, Geert R. de Snoo, Maheshwar Dhakal, Hans H. de Iongh. (Accepted for publication in Oryx)

Abstract

The present study focused on defining the probability of attacks by predators on livestock in the buffer zone of Bardia National Park, Nepal. Semi-structured interviews were used to explore the patterns and factors affecting livestock losses in four administrative sectors of the park's buffer zone. For this purpose, we developed models to investigate (i) overall probability of livestock loss, (ii) economic damage, and (iii) the attitude of respondents towards wildlife. We observed a higher probability of attacks on livestock by leopards (85%) compared to tigers (8%). Among the four sectors of the buffer zone, the Northern sector experienced the highest loss of livestock (50%). Livestock loss was significantly related to the number of livestock owned, the ethnic group of the respondents, and distance to the national park boundary. Variables contributing to economic damage were study sector, the number of livestock owned, and distance to the national park boundary. The attitude of respondents towards wildlife conservation depended on knowledge about the species (tiger/leopard), educational level, self-sufficiency, and the probability of livestock getting killed by leopards. Higher educational status, male gender and greater self-sufficiency of respondents resulted in a higher positive response rate (80%) for supporting conservation. The higher level of religious tolerance towards tigers and access to conservation benefits by people living in the buffer zone also has a positive role in conservation. Because there are no religious tolerance towards leopards and they are the most damaging predator's strategies should ideally focus on the conservation of leopards in a human-dominated landscape.

Keywords

economic loss, human attitudes towards conservation, leopard, livestock loss, tiger.

5.1 Introduction

Worldwide, large carnivore populations have declined for a variety of reasons, but mostly due to human interventions (Woodroffe & Ginsberg, 1998; Karanth & Chellam, 2009). Poaching for traditional medicine and furs, habitat destruction and depletion of their natural prey are major threats (Smith et al., 1998; Treves & Karanth, 2003).

Several studies reported increased conflicts between people and large carnivores in areas where large carnivore populations have started to increase (Saberwal et al., 1994; Treves & Karanth, 2003; Inskip & Zimmermann, 2009; Seidensticker, 2010; Silwal et al., 2017). This kind of interactions where the needs and behaviour of wildlife has a negative impact on humans or *vice versa* is called human-wildlife conflict (Madden, 2004). However, the use of term human-wildlife conflict is misleading because, in reality, it is a conflict between conservation and other human interests (Peterson et al., 2010; Redpath et al., 2015; Fisher, 2016).

Predatory attacks on livestock are presently one of the most critical challenges faced by livestock owners living near protected areas, with tigers and leopards annually killing 118 livestock in Bardia and 123 livestock in Chitwan National Park (Lamichhane et al., 2018). In spite of these losses, people living around protected areas in Asia have always been relatively tolerant towards wildlife (Dinerstein et al., 2007; Karanth & Nepal, 2012) compared to indigenous people from other regions of the world. Whereas sometimes cultural values and beliefs support wildlife conservation, livestock depredation events often lead to retaliatory killing, as is the case with lions in Africa (Bauer & Iongh, 2005). Trophy hunting also had an adverse effect on the population density of lions (Croes et al., 2011).

As the successful recovery of both leopard and tiger population depends a great deal on their capacity to co-exist with humans, adequate implementation of conflict mitigation measures is key to any protected area in which tiger and leopard are managed in the vicinity of the human population (Treves et al., 2006; Woodroffe et al., 2007; Carter et al., 2012).

In view of this, the aim of our study was (1) to identify the probability of livestock loss due to attacks by predators and due to other factors, such as disease and flooding, in different sectors of the buffer zone of Bardia; (2) to quantify the economic damage to resident communities due to predatory attacks; and (3) to assess the attitude of residents towards the conservation of tigers, leopards and other wildlife, and the factors underlying this attitude.

5.1.1 Study Area

Bardia National Park (henceforth Bardia, IUCN, Category II) established in 1976, is located in South-western Nepal (N: 28.2630 to 28.6711; E: 80.1360 to 81.7645) (Figure 5.1). It is the largest national park in the plains (Terai) of Nepal with a surface area of 968 km² (DNPWC, 2018). It is one of the prime habitats for tiger and leopard in Nepal (Walston et al., 2010). The buffer zone of Bardia was established in 1996 with an area of 327 km². In 2010 an additional 180 km2 of the Surkhet district was included in the buffer zone which mainly consists of hilly terrain. Buffer zone regulations have provisioned 30 to 50% of the revenue generated by the protected area to be invested in measures that should minimize damages caused by wildlife (Baral & Heinen, 2007).

Figure 5.1

Bardia National Park and its buffer zone showing the study sectors, surveyed households and cases of reported livestock loss.

The rapid expansion of human settlements, habitat degradation, and poaching has caused tiger numbers to plummet to 18 individuals inside the park in 2009. In recent years however, the Bardia tiger population has rapidly increased to 50 individuals in 2013 and density of prey is 92.6/km2 (Dhakal et al., 2014). Leopard number has not been recently assessed in Bardia, but Wegge et al. (2009) estimated 5 individuals/ 100 km^2 .

The park has three distinct seasons: winter (late-September to mid-February), summer (mid-February to mid-June) and monsoon (mid-June to September). Temperature could rise to a maximum of 45°C and annual rainfall is 1500 mm (Dinerstein, 1979; DNPWC, 2018). Flooding that took place in 2014 contributed to a significant amount of damage to human and livestock (Bhattarai et al., 2016). However, loss of wildlife was not documented.

Indigenous Tharu people and migrants from the hills (Pahade) inhabit the buffer zone of the park (Bhattarai et al., 2016). The majority of households are involved in subsistence farming supplemented by the use of forest and grassland for grazing livestock (Thapa Karki, 2013). Paddy and maize are grown mainly in the monsoon, whereas wheat, mustard, and lentils are cultivated in winter for domestic consumption (Studsrød & Wegge, 1995). Livestock kept by villagers mainly include cow, buffalo, oxen, sheep, goats, pigs and chickens which are primarily kept for their milk, eggs, meat, manure and draft power (Thapa Karki, 2013).

5.2 Methods

5.2.1 Data collection

We used a semi-structured questionnaire (Supplementary material 5.1) survey (adapted from Sogbohossou et al., 2011 and Bhattarai & Fischer, 2014) of 297 households which were opportunistically selected in each of our four study sectors, taking into account the size and the total number of households in each sector (Table 5.1). The questionnaire was reviewed and we received ethical approval from the Institute of Environmental Science, Leiden University. Between May and August 2015 the heads of each selected household were interviewed taking verbal consent before starting the interview. Interviews were conducted in the Nepali language by native Nepali and Tharu language speaking assistants, who also worked as tourist guides in Bardia. They were trained and instructed on the structure and purpose of the questionnaire before the interview, and during the course of the survey regular assessments were performed to limit any bias which could have resulted from their positive attitude to conservation as professional nature guides.

Table 5.1

The number of households interviewed per sector and village development committee.

*Thapa & Chapman, (2010).

New local bodies have been formed by the Ministry of Federal Affairs and Local Development, Government of Nepal (MoFALD, 2017).

> The surveyed communities were divided into four sectors based on their location inside the park management sectors and taking into account relative densities of livestock and natural prey in these sectors, as contributing factors to the probability of predatory attacks on livestock: The Thakurdwara sector (TK) and Western sector (WS) which were characterized by relatively high densities of both natural prey and livestock, and the Eastern sector (ES) and Northern sector (NS) with relatively low densities of natural prey and high densities of livestock.

5.2.2 Data analyses and statistics

Three logistic models were created to estimate (i) the overall probability of loss of livestock and poultry (including loss due to wildlife attacks and other factors such as disease, natural calamities); (ii) probability of loss due to wildlife; and (iii) the probability of loss due to leopards.

To analyze the economic damage, i.e. the costs of livestock losses due to predatory attacks and other factors, we developed a linear model for economic loss.

We also created logistic models for attitude (which was either positive [1] or negative [0]) towards (i) wildlife in general; (ii) wildlife conservation in general; (iii) wildlife conservation when family members had in some way experienced a negative impact from wildlife; and (iv) wildlife conservation in case of livestock losses due to predatory attacks. All our models were created in R (R Core Team, 2018). The model's likelihood ratio test (LRT) was used to compare all models with and without independent variables (Bolker et al., 2009). All variables are listed in Supplementary Table 5.1.

5.3 Results

Respondents were 16 to 76 years old (40 on average), 254 of whom were male and 43 female. In terms of educational status, 14% of the respondents were illiterate and 86% literate (24% – basic education, 18% – primary level, 23% – lower secondary, 14% – secondary level, and 8% - higher secondary or university level education). 52% of the respondents were able to sustain for 9-12 months, whereas 48% sustained for less than 9 months on their own crop production. Respondents were of several cultural backgrounds, with 37% Brahmin or Chhetri, 46% Tharus, 11% *Dalits* and 6% from another ethnic group. Around 85% of the respondents were farmers. The average household size was 5.13 persons. The average number of livestock kept by respondents was as follows: cow/ox-1.56, sheep/goat-4.49, buffalo-0.95, and pig-0.58. The percentage of livestock in different sectors were as follows: Thakurdwara-23%, Western-21%, Eastern-13%, and Northern-43%.

Around 59% of the respondent households were located within 2 km from the park boundary, 36% between 3-4 km, and 4% at more than 5 km from the park boundary. In total, 131 (44%) household heads reported the loss of livestock and poultry either due to predatory attacks (92 cases, 70%) or due to other factors (disease and flooding) (39 cases, 30%). There were 92 cases of deadly attacks on livestock and poultry reported, of which eight (8%) were due to tiger (which was confirmed by official park records), 78 (85%) due to leopard and six (7%) incidents due to other wildlife, viz. fox (*Vulpes vulpes*), jackal (*Canis aureus*), crocodile (*Crocodylus palustris*), python (*Python bivittatus*), eagle (*Aquila spp.*) and jackal (*Canis aureus*). Tigers kills comprised 94% cattle and 6% water buffalo, whereas leopards kills comprised 68% goats, 12% sheep, 14% pig and 6% cattle. Crocodile and fox killed goats whereas other wildlife killed poultry. Predatory attacks took place more often in summer (46%) and winter (35%) than in the monsoon season (19%). 81% of losses occurred inside the village and 19% away from habitation, in forest habitat. Most respondents were able to distinguish a tiger from a leopard based on photographs (c. 90%). They were able to recognize the predators based on pugmarks at the kill site and bite marks on the livestock carcass, which was verified by a park authority representative during compensation claim verifications.

5.3.1 Probability of loss

The probability of livestock loss per household for each study sector, with their respective causes are shown in Table 5.2. The overall probability of livestock loss was positively related to incidences of livestock grazing inside the community forest ($p = 0.004$), ethnic group ($p = 0.04$), the number of pigs owned by the respondent ($p = 0.02$) and study sector ($p = 0.02$). Attacks on livestock by leopards showed a strong relation with study sector $(p < 0.001)$ (Supplementary Table 5.2). Incidences of livestock grazing inside the government forest (p = 0.04), ethnic group (p = 0.04), number of goats and sheep owned ($p = 0.02$) and number of pigs owned ($p = 0.01$) were significantly related to study sector (Supplementary Table 5.2).

Table 5.2

Probabilities of livestock loss per household in each study sector due to tigers, leopards and other causes.

In all three models, the highest probability of livestock loss was found for the Northern sector (c. 50%), followed by the Eastern sector (c. 30%), and the Thakurdwara sector (c. 20%) (Figure 5.2a).

Figure 5.2

Probability of loss due to leopards, a) according to study sector, b) according to ethnic group.

Our results show that in all three models the probability of loss for the Tharu ethnic group was smaller than for other ethnic groups (Figure 5.2b). Around 79% of the predatory attacks took place when the livestock was held inside their corals and 52% occurred during the night.

5.3.2 Economic loss

The total costs of livestock lost due to predatory attacks and other factors amounted to $$ 22,927$ (1 USD = 105 Nepali Rupees) for the surveyed households, of which \$14,573 (63.5%) was lost due to predatory attacks and \$8,353 (36.5%) due to other factors (Table 5.3). The average cost of each livestock species ranged from \$30 to \$50, depending upon their size.

Table 5.3

Costs (in USD) of overall loss, loss due to predatory attacks and loss due to other factors in each study sector.

The linear model suggests that the most important factors contributing to predation-related economic loss were study sector $(p < 0.001)$ and distance to the national park ($p = 0.003$) (Table 5.4).

Table 5.4

Linear model results for economic loss due to wildlife; results of the likelihood ratio test are shown.

5.3.3 Attitude towards wildlife

Of the 270 responses on questions related to 'attitude towards wildlife', 85% was positive. In addition, 93% of the respondents were positive about the conservation of wildlife in general, even when some of their family members had suffered wildlife-related losses in the past. About 80% of the respondents who had suffered livestock losses from predatory attacks themselves in the past, indicated that they are still in support of wildlife protection and conservation (Table 5.5).

Table 5.5

Attitude towards wildlife in percentage of households for each study sector.

Our logistic model on the attitude towards wildlife showed that of all study sectors, respondents from the Western sector were most positive towards conservation, followed by Thakurdwara, Eastern, and Northern sector respectively ($p = 0.03$). Respondents with a higher level of education were generally more positive towards wildlife in general ($p = 0.004$) and willing to conserve wildlife ($p = 0.02$). Respondents who were generally self-sufficient (i.e. generating crop yields that could sustain their household throughout the year) were more positive about wildlife conservation in general than respondents who were not self-sufficient ($p = 0.03$). With respect to gender, male respondents were more positive about wildlife conservation than females ($p = 0.10$) (Supplementary Table 5.3). Remarkably, respondents who had suffered livestock losses due to tiger attacks had a positive attitude towards wildlife conservation ($p = 0.06$).

The model on attitude towards wildlife conservation shows that self-sufficiency and education level were positively related to a positive attitude ($p =$ 0.01 and 0.02), even when family members had suffered livestock losses from predatory attacks. There is an indication that the overall probability of loss affects the attitude towards conservation ($p = 0.06$) (Supplementary Table 5.3).

The attitude of respondents, who had suffered livestock losses themselves, varied between the study sectors. Around 98% of the respondents of the Thakurdwara and Western sectors, 80% in the Eastern sector and 50% from the Northern sector were positive towards wildlife conservation, despite having suffered livestock losses due to predatory attacks themselves (Table 5.5). The positive response increased with educational level (illiterate-60%, primary level-80%; p < 0.001). Similarly, the overall probability of livestock loss also showed some effect on positive attitude ($p = 0.03$).

5.4 Discussion

Household surveys provide insight into how people live and interact with wildlife. We found that leopard caused most livestock killing, similar to Acharya et al., (2016) who reported that leopards contributed to 21% wildlife-induced livestock losses in Nepal. Signs of leopards were mostly found towards the fringe of park in Bardia (Studsrød & Wegge, 1995; Tamang & Baral, 2008; Upadhyaya et al., 2018) as reported in Chitwan National Park (Bhattarai & Kindlmann, 2012) and Macharia National Park, Pakistan (Dar et al., 2009). Loss of livestock was related to their number which is similar to findings of Tamang & Baral (2008) from Bardia, Oli et al. (1994) from the Annapurna conservation area, Nepal and Wang & Macdonald (2006) from Bhutan. Livestock depredation was higher in the corals as reported by Tamang & Baral, (2008).

Tharu people reported minimal losses, although the number of livestock owned by them was comparable to people of other ethnic groups. This may be related to the Tharu's long experience of living with wildlife as an indigenous group and their adaptation through better livestock husbandry practices (Kolipaka et al., 2017). Distance to the park boundary is an important determinant of predatory attacks on livestock and increased at a distance of 5-12 km in Bardia and Waza National Park, Cameroon (Studsrød & Wegge, 1995; Van Bommel et al., 2007).

Households in the Northern sector suffered considerably higher economic damage compared to other sectors, which may be attributed to the poor husbandry techniques. Poorer respondents substantially lost more livestock compared to wealthier respondents who could afford better protection and husbandry techniques (Saberwal et al., 1994). The lives of people from marginalized groups could be heavily impacted by such financial losses (Manral et al., 2016).

Economic loss due to predatory attacks was comparable to losses due to other causes, which in our study area were related primarily to two natural events: an unexpected flood in 2014, which caused a sudden rise in deaths of livestock, and a bird-flu outbreak which led to great losses among poultry. In other areas where human-carnivore conflicts are considered to be a major cause of economic losses, non-wildlife factors, such as disease and theft, were actually contributing a greater deal to overall economic losses (Dar et al., 2009; Tumenta et al., 2013), compared to predation.

The difference in attitude between respondents from the Western study sector (98% had a positive attitude towards wildlife conservation) and respondents from the Northern sector (around 70% were positive), is very likely to be a consequence of the differences in numbers of livestock lost between these two sectors. In addition, respondents from the Northern sector were generally dissatisfied due to the lack of benefits they are gaining from the Buffer zone program. Pant et al. (2016) showed that a positive attitude is also related to human safety. Although people's attitudes towards wildlife can be influenced by predatory attacks and other wildlife-related financial losses (Røskaft et al., 2007), and that people are more tolerant towards wildlife if they derive benefits from the park (Allendorf et al., 2007; Baral & Heinen, 2007; Romañach et al., 2007; Wegge et al., 2018). Active involvement of local communities in planning, executing and managing small-scale conservation projects, lead to a positive attitude towards conservation (Nepal, 2002).

Despite the differences, we found in attitude towards conservation between the study sectors, overall c. 65% and c. 80% of all our respondents had a positive attitude towards conservation, even when a leopard or tiger, respectively, had killed their livestock. The fact that tigers were 'slightly in favour' by our respondents is a clear reflection of the cultural values of people in this region (Bhattarai & Fischer, 2014; Kolipaka et al., 2015). People from Bardia believe that tigers are the vehicle of the goddess of might and should not be harmed (Bhattarai & Fischer, 2014).

Respondents with a higher level of education and self-sufficiency had a positive attitude towards conservation, which is comparable to other studies (Allendorf et al., 2006; Sarker & Røskaft, 2011; Sogbohossou et al., 2011; Tumenta et al., 2013; Bhattarai & Fischer, 2014). In Bangladesh, wealthy respondents favoured wildlife conservation 7.4 times more than their less wealthy peers (Sarker & Røskaft, 2011). People who have to rely on a single livelihood or few resources are more vulnerable to the impact of depredation (Ogra, 2008; Dickman, 2010). Generally, more educated people are less dependent on natural resources for their sustenance, than their less educated neighbours (Dickman, 2010). Since education can be an important tool in wildlife conservation at the local scale (Nepal & Weber, 1995), conservation authorities in Bardia could use this information to enhance existing indigenous knowledge and technologies in order to reduce risky human-wildlife interactions (Kolipaka et al., 2017). Female respondents had a less positive attitude towards conservation compared to the male respondents, may be linked to the risks women are exposed to due to their involvement in collecting forest resources, making them more vigilant in the vicinity of wildlife than men (Allendorf, 2010; Bhattarai & Fischer, 2014). However, we cannot generalize this because of the low number of female respondents in our study. Carter et al. (2014) also reported that women, less educated persons and people from marginalized groups more often have negative attitudes, specifically towards tigers.

Based on these considerations, we believe our findings could be of great value to Bardia wildlife managers and other conservation authorities in the region. They could help in predicting where interactions with tigers and leopards are likely to lead to problems and to design intervention strategies that could reduce financial losses due to conflicts (Kansky & Knight, 2014). Mitigation measures in and around Bardia should consider the specialized behavioral traits of cat species involved in the conflict. In order to reduce the impact of carnivores on livestock loss we recommend (1) improvements in enclosure and herding practices; (2) reducing the number of livestock kept, by diversifying economy; (3) implementation of a community-based livestock insurance program; and (4) establishing an early warning system.

Acknowledgements

We thank the Department of National Parks and Wildlife Conservation (DN-PWC), Kathmandu, Nepal for providing us permission to conduct the research. Financial support for this study was provided by Nuffic NFP (Netherlands organization for international cooperation in higher education, Netherlands fellowship program). We are grateful to Ram Chandra Kandel, Ramesh Thapa and Ashok Bhandari for their support and permission to work in Bardia. We thank Rabin Kadariya, Ambika Prasad Khatiwada, Shree Ram Ghimire and Shailendra Yadav from the National Trust for Nature Conservation, Bardia for providing logistic support. We are grateful to communities residing in the buffer zone for their active participation in the survey. We wish to thank Hemanta Acharya and his team for conducting the field interviews. We would further like to express our gratitude to two anonymous reviewers whose comments greatly helped in improving our earlier version of this manuscript, and to Barbara Croes for her language editing. This research was carried out in full compliance with the code of conduct for researchers of the Oryx journal.

Conflict of interest:

None

Ethical standards:

Our research complies with journal's code of conduct for authors contributing articles.

Supplementary material 5.1

Questionnaire used for survey

 \overline{a}

- **8** When did you come to stay(Score 1, 2, 3, 4, 5)
	- **a** 0- 5 years
	- **b** 5-10 years
	- **c** 10-20 years
	- **d** 20-30 years
	- **e** Before 30 years
- **9** Why did you come to live here?
- **10** Can differentiate between tiger, leopard and other animals (Yes/No) (Score 0, 1). (Take help of photograph)
- **11** Source of livelihood (Number of months in a year-Score 1, 2, 3, 4, 5)
	- **a** Crop **b** Livestock **c** Employment **d** Business **e** Seasonal labour **f** Others
- **12** What are the activities of other family members?
- **13** How long does the interviewee sustain on own crops and livestock (Select ONLY one-Score 1, 2, 3, 4, 5, 6)
	- **a** Less than 3 months **b** 3 months **c** 3-6 months **d** 6-9 months **e** 9-12 months **f** More than a year

14 Livestock holding (Number)(Score-Big cattles-1, Small cattles-2, Poultry-3)

a Cow/Ox

b Buffalo

- **c** Goat/Sheep
- **d** Pig
- **e** Poultry
- **f** Fishery

15 Which source is utilized for livestock rearing (Give preference from 1 to 4 on the basis of priority)

- **a** National Park **b** Community forest
- **c** Government forest
- **d** Private land

16 Reason for livestock loss last year

- **a** Natural (Number and name of livestock): **b** Disease (Number and name of livestock):
- **c** Theft (Number and name of livestock):
- **d** Wildlife attack (Number and name of livestock):
- **e** Accident (Number and name of livestock):
- **17** Monetary value of loss (in NPR):
- **18** Number of own livestock lost in a tiger/leopard/other wildlife attack within this year (Name of livestock and number)

 $\label{eq:2.1} \frac{1}{\sqrt{2}}\int_{\mathbb{R}^3}\frac{1}{\sqrt{2}}\left(\frac{1}{\sqrt{2}}\right)^2\left(\frac{1}{\sqrt{2}}\right)^2\left(\frac{1}{\sqrt{2}}\right)^2\left(\frac{1}{\sqrt{2}}\right)^2\left(\frac{1}{\sqrt{2}}\right)^2\left(\frac{1}{\sqrt{2}}\right)^2.$

19 Attack on family members or relatives by wildlife within last 20 years (If yes, place, time, date, gender and age of victim, injury or death)

Supplementary Table 2

Logistic models for the probability of loss; results of the likelihood ratio test are shown.

Supplementary Table 3 Logistic models of attitude towards wildlife; results of likelihood ratio test are shown.

6.1 Context

Around the world, wild large mammals have co-existed with humans and their livestock for over ten thousand years (Pereira et al., 2012). Evidence exists from the Pleistocene era of the interactions between large carnivores and early humans, who not only hunted large carnivores for meat, but may have also scavenged on prey killed by large carnivores (Oliver, 1994, Treves & Naughton-Treves, 1999).

Large carnivores require large habitats, and human-induced degradation and fragmentation of habitats over the past decades is regarded as a major threat to their survival. Their large home ranges, low population densities and slow population growth rates further make them vulnerable to extinction (Dickman, 2010). The world's growing human population and the resulting demand for food, space and natural resources hence poses a great threat to large carnivores and their habitats. Several species of large carnivores worldwide have shown strong population declines in the past decades while at the same time the frequency of conflicts with humans has increased (Inskip & Zimmermann, 2009; Karanth & Chellam, 2009). In Nepal, such conflicts have also increased over the past years, as a result of expanding human settlements near buffer zones of protected areas (Bhattarai & Fischer, 2014; Silwal et al., 2017), but possibly also due to increasing wildlife numbers inside some of the national parks following improved wildlife conservation measures.

The majority of wildlife induced fatalities among people for Nepal had been reported from Chitwan National Park (Gurung et al., 2008; Silwal et al., 2017; Dhungana et al., 2017; Lamichhane et al., 2018), where the conflict problem is severe. During 1979-2006 for example, 88 humans were killed by tigers in Chitwan (Gurung et al., 2008). For Bardia National Park cases in which humans were killed by wildlife had also been reported, although average numbers of fatalities were lower than for Chitwan. During 1994 to 2007 tigers had been responsible for 0.93 fatal attacks per year in Bardia (Bhattarai & Fischer, 2014).

Where tigers and leopards occupy the same habitat, interspecies competition could lead to the displacement of leopards towards park edges (Odden & Wegge, 2005; Harihar et al., 2011; Mondal et al., 2012). In order to promote successful management practices in and around BNP that take into account the current human-wildlife conflict situation, the present research focused on tiger and leopard interactions and prey selection in Bardia National Park, and how this is related to the conflict incidences occurring in the area. One objective of my study was to assess whether any spatial and temporal patterns of overlap between the activities of tigers and leopards were present. I also studied the spatiotemporal patterns of conflict incidences and identified the major conflict causing wildlife species in the study area. Finally, I examined the perception and attitudes of local communities towards conservation in general and towards the conservation of big wild cats in particular. As the population of tigers is increasing inside the park, I hypothesized that young tigers and leopards may be pushed out of the park. From my results, I formulated recommendations for the conservation of tigers and leopards in the human dominated landscape of Bardia.

6.2 Interactions between tigers and leopards

In chapter 2, I studied the spatiotemporal interaction between two sympatric carnivores. Tigers and leopards are sympatric in most of their distributional range in Asia, and typically inhabit similar habitat. Both species are regarded as umbrella species because of their function at the top of the ecosystem. Due to their elusive nature and low densities, research based on direct observations is difficult. For this study camera traps were therefore used. The park was divided into a core zone and a boundary zone. I found that there was no significant difference in the activity of tigers and leopards between 2013 and 2016. Spatial avoidance between the two species was evident in the core zone but not in the boundary zone, confirming our hypothesis that leopards may have been forced from the core zone into the boundary zone by tigers. In Bardia, habitat and space use partitioning may thus play an important role in the co-existence of tigers and leopards. Leopards were found to be more active during the daytime whereas tigers were mostly active during dawn and dusk. Leopards appeared to temporally avoid tigers in the core zone, while this was not the case near the human dominated area i.e. in the boundary zone. This could be the result of the fact that tigers in the boundary zone may be sub-adult tigers displaced from their home range. Kolipaka et al. (2017) also mentioned the dispersal of young tigers towards the park boundary.

6.3 Diet and prey preference of tigers and leopards

In chapter 3, I studied the diet composition and prey preferences of tigers in BNP. Knowledge on diet composition and prey preferences could support conservation action plans for both the predator and the prey species. The polymerase chain reaction (PCR) technique was used for the identification of species and sex from scat samples. Prey remains were identified to species level through microscopic hair morphology analysis. Of the 101 scats collected, extraction of DNA and PCR analysis was successful for 84 samples, of which 75 originated from tigers and nine from leopards. From the tiger scat samples 34 were determined to belong to males and 41 to females. The amplified PCR product size was 162 bp for tiger and 130 bp for leopard. The amplified PCR product of nuclear DNA of males had two bands measuring 194 bp and 214 bp, whereas females had one band of 214 bp. Due to the small sample size of leopard scats collected, only tigers were included in the analyses. We found seven and six prey species in the diet of male tigers and female tigers, respectively. The diet of male and female tigers did not differ significantly, with chital as the most abundant prey species for both sexes. Leopards were found to positively select wild boar, hog deer and sheep and goats (Lovari et al., 2015). The Jacobs index did not show any significant prey preference, although male tigers tended to select for sambar deer and wild boar, whereas female tigers more often selected wild boar and chital. The most important difference in diet composition between tigers and leopards was a much higher presence of small mammals and birds in leopard scats as opposed to tiger scats, a larger proportion of domestic animals in leopard scats as opposed to, and more hog deer in tiger scats as opposed to leopard scats (Odden, 2007). Our study demonstrates that tigers mostly preyed on wild species, supporting the relatively low level of tiger-livestock interactions we found for Bardia based on the questionnaire survey. Hence, this park seems to be a prospective area for tiger conservation in the long run. The higher abundance of tiger scats found in the core area of the park versus a higher abundance of leopard scats collected near the edge of the park further supports the assumption that leopards are being displaced by tigers, at least to some extent.

6.4 Spatial and temporal conflict patterns

In chapter 4, I studied the spatial and temporal patterns of conflict in BNP over a period of five years. The study was based on compensation paid to villagers who had been identified as victims of conflict by park officials. The main types of conflict incidences that have been reported were attacks on humans, crop damage, property damage and livestock predation, which is similar to those reported by Peterson et al. (2010). Four wildlife species were responsible for the majority of conflict incidences: elephant, leopard, tiger and wild boar. Elephants were the major conflict causing species responsible for killing 14 humans over a period of five years. Other types of conflict caused by elephants included crop damage and damage to housing along with raiding stored grains. Among the predators, leopards were responsible for most livestock kills. This may have been due to the often poorly constructed sheds and corals in which livestock was kept, offering easy access to leopards (Acharya et al., 2016). Tigers were mainly responsible for killing larger livestock, such as cattle. Other wildlife species that had contributed to at least a certain level of conflict included rhinoceros, chital, sloth bear, nilgai, python, crocodile and porcupine.

In terms of temporal patterns of conflict incidences, most of the predation events took place during dark nights or new moon phase and livestock predation was higher during the monsoon season. The crop damage caused by elephants was higher in the autumn season when the major crop paddy is reaching maturity. Spatial patterns of conflict were reflected in the higher frequency of conflicts which was found for the southern and the western sub-region of the buffer zone, compared to the other zones. This may be due to the presence of a high density of elephants in that zone. The local residents most frequently used electric fencing and improved enclosures in order to prevent conflict incidences. A total of \$ 61,085 was paid to villagers as compensation for conflicts over the study period.

6.5 Defining the risk of attacks by predators

In chapter 5, I focused on defining the probability of predatory attacks on livestock in different regions of the buffer zone of BNP. Large carnivores often cover great distances, thereby sometimes leaving protected areas and roaming into communal lands (Woodroffe et al., 2005). Based on data acquired from a questionnaire survey, I built logistic models to examine the overall probability of livestock losses, economic damage and the attitude of local residents towards wildlife. I found that the Northern sector of the buffer zone, which was recently included in the buffer zone, experienced a larger loss of livestock than any other sector of the buffer zone. The model on livestock loss predicted the number of livestock owned by the respondents and the distance to the national park as important variables contributing to livestock loss. The model on economic damage marked study sector, number of livestock owned, ethnic group of respondents, and distance to the national park as significant variables contributing to economic loss. In the model on the attitude towards wildlife, the variables that resulted in a positive attitude were higher educational status, greater self-sufficiency and male gender. The higher level of religious tolerance towards tigers and the common conservation benefits that people living in the buffer zone share, positively affected their attitude towards conservation (Bhattarai & Fischer, 2014). Although people's attitudes towards wildlife can be influenced by predatory attacks and other wildlife-related financial losses (Røskaft et al., 2007), 85% of all our respondents had a positive attitude towards conservation, even when a leopard or tiger, respectively, had killed their livestock.

6.6 Conclusions

As summarized in Figure 6.1, the main conflict causing animals in Bardia are leopards and elephants. With the increased number of tigers in recent years, it is likely that leopards as well as sub-adult tigers in search for their own home range, will roam into human inhabited areas outside the Bardia National Park. In order to protect these large carnivores, additional habitat should ideally be included into the conservation program. Protection measures could for instance focus on the adjoining community forest or the Government forest. The Banke National Park, which was established in 2010 in continuation with the eastern border of the Bardia National Park, could thereby act as a sink for the Bardia tiger population. In Summary, the following findings have been presented in this thesis:

- **1** Leopards appeared to avoid tigers in and around Bardia National Park, both in time and space. This avoidance behavior is more prominent in the core area of the park than towards the fringe of the park. Leopards were found to be more active during daytime whereas tigers were more active during dawn and dusk.
- **2** The diet of tigers predominantly consisted of wild prey species, with only a single scat sample containing domestic prey. This suggests that tigers around Bardia are generally not involved in direct conflicts with humans. Whereas tigers in Bardia mostly preferred medium-sized prey such as chital and wild boar, other studies suggested that such prey may be energetically suboptimal for tigers as they usually kill larger bodied prey in order to meet their energy demand. Since larger ungulates occur at relatively low densities in Bardia, tigers here are probably trying to compensate this by catching more medium-sized prey. As the prey preference index indeed showed a preference towards large sized prey, future park management efforts should ideally focus on increasing the density of large prey species.
- **3** Elephants were responsible for most of the human fatalities around Bardia whereas tigers and leopards were not involved in any fatal encounters with local people in recent years. Leopards were responsible for more killing of livestock compared to tigers. Livestock predation incidences mostly occurred during the new moon phase. Crop damage mostly occurred during the autumn season when paddy is cultivated.
- **4** Self-sufficiency and education had a positive impact on the attitude of villagers towards conservation and wildlife. Survey respondents with a
negative attitude towards conservation were mostly female, probably due to their involvement in wood collection, requiring women to enter dangerous tiger and leopard habitat more frequently than men. The Northern sector of the buffer zone experienced more conflict incidences, which could be a result of poor animal husbandry techniques. Since the Northern sector has been included in the buffer zone of the National Park only recently, the villagers living in the area have not yet had the opportunity to profit from conservation benefits, such as ecotourism in comparison to other sections of the buffer zone.

6.7 Recommendations

Based on the findings presented in this thesis, I formulated several recommendations for wildlife managers, local communities and for future research:

6.7.1 For wildlife managers

- **1** Habitat management should focus on providing suitable habitat, especially for larger ungulates, as especially tigers could benefit from this and therefore it is expected to positively affect the long term viability of the tiger population in Bardia. The habitat management should focus on providing optimal diversity for the sustenance of a large range of prey species.
- **2** Poaching of tiger/leopard and their prey species needs to be minimized as it is one of the crucial issues in the conservation of tiger/leopard.
- **3** Additional habitat, outside the currently protected areas, should ideally be allocated in order to facilitate the dispersal of sub-adult tigers and leopards. Corridors passing through the adjoining community or government forests could be created for this purpose.

6.7.2 For local communities

1 Local communities should continue to be involved in conservation action planning. Local action groups could for instance encourage youth to join anti-poaching campaigns. Local initiatives could also include education programs, e.g. by introducing study material on wildlife ecology and behavior at primary and secondary school level curricula.

- **2** Initiatives targeted at benefit sharing of park revenues by the local communities could continue to provide incentives to reduce retaliatory actions following conflicts with wildlife. However, current initiatives need to become more practical to execute and compensations after livestock has been lost should be paid with minimum delays. Modernizing and improving existing livestock husbandry techniques and promoting insurance of livestock by livestock owners could reduce the financial burden that may result from the depredation of livestock.
- **3** The reliance of local communities on forest and agricultural resources could be minimized by providing alternative livelihoods. Local initiatives could promote commercial activities in ecotourism, such as involvement in safari tours, home stay and cottage industries. Cultivation schemes targeted at alternative cash crops, such as mentha and chamomile could be implemented in order to reduce the loss of crops by raiding elephants.

6.7.3 Future research

Based on the present thesis, several focal points have been identified for future research on large carnivore interactions and conflicts with local communities (see Figure 6.2):

Figure 6.2

Diagram showing major interaction flows between research focal points, with suggestions for future research questions (indicated by a question mark).

- **1** Continuation of a monitoring program in Bardia National Park, using camera trapping, scat collection and molecular analysis techniques would greatly contribute to detecting long-term trends in population dynamics of leopards and tigers. Especially trends caused by increasing herbivore populations should be further investigated.
- **2** Since our study showed that elephants are responsible for the majority of conflict incidences in which property damage, crop damage or human fatalities occurred, future studies should ideally address possible techniques and measures that could effectively reduce human-elephant conflicts.
- **3** Although the people in Bardia were generally in favor of conservation efforts targeted at both big cat species, their positive attitude is likely to change when conflict incidences are to occur more frequently, possibly as a result of increasing wildlife numbers, in the future. A study on the socio-economic status of villagers could provide valuable insights for this purpose. Indigenous knowledge of local people should be taken into account when defining objectives for this kind of research.

References

- Acharya, K. P., Paudel, P. K., Neupane, P. R., & Köhl, M. (2016). Human-Wildlife Conflicts in Nepal: Patterns of Human Fatalities and Injuries Caused by Large Mammals. *PLOS ONE*, *11*(9), e0161717.
- Acharya, K. P., Paudel, P. K., Jnawali, S. R., Neupane, P. R., & Köhl, M. (2017). Can forest fragmentation and configuration work as indicators of human–wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal. *Ecological Indicators*, *80*, 74–83.
- Allendorf, T., Swe, K. K., Oo, T., Htut, Y., Aung, M., Aung, M., … Wemmer, C. (2006). Community attitudes toward three protected areas in Upper Myanmar (Burma). *Environmental Conservation*, *33*(4), 344–352.
- Allendorf, T. D., Smith, J. L. D., & Anderson, D. H. (2007). Residents' perceptions of Royal Bardia National Park, Nepal. *Landscape and Urban Planning*, *82*(1–2), 33–40.
- Allendorf, T. D. (2010). A framework for the park-people relationship: Insights from protected areas in Nepal and Myanmar. *International Journal of Sustainable Development and World Ecology*, *17*(5), 417–422.
- Amarasekare, P. (2008). Coexistence of intraguild predators and prey in resource-rich environments. *Ecology*, *89*(10), 2786–2797.
- Andheria, A. P., Karanth, K. U., & Kumar, N. S. (2007). Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology*, *273*(2), 169–175.
- Athreya, V., Odden, M., Linnell, J. D. C., Krishnaswamy, J., & Karanth, U. (2013). Big Cats in Our Backyards: Persistence of Large Carnivores in a Human Dominated Landscape in India. *PLoS ONE*, *8*(3).
- Azlan, J. M., & Sharma, D. S. K. (2006). The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. *Oryx*, *40*(1), 36–41.
- 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.* Wildlife Institute of India, Dehradun, India.
- Bailey, T. N. (1993). *The African leopard: ecology and behavior of a solitary felid* (Vol. 430). New York: Columbia University Press.
- 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.
- Baral, N., & Heinen, J. T. (2007). Resources use, conservation attitudes, management intervention and park-people relations in the Western Terai landscape of Nepal. *Environmental Conservation*, *34*(01), 64–72.
- Basak, K., Mandal, D., Babu, S., Kaul, R., Ashraf, N. V. K., Singh, A., & Mondal, K. (2018). Prey Animals of Tiger (Panthera tigris tigris) in Dudhwa Landscape, Terai Region, North India. *Proceedings of the Zoological Society*, *71*(1), 92–98.
- Bauer, H., & Iongh, H. H. (2005). Lion (Panthera leo) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology*, *43*(3), 208– 214.
- Bhagavatula, J., & Singh, L. (2006). Genotyping faecal samples of Bengal tiger Panthera tigris tigris for population estimation: A pilot study. *BMC Genetics*, *7*, 1–12.
- Bhattarai, B. R. (2009). *Human-tiger (Panthera tigris tigris) conflict in Bardia National Park, Nepal*. Ernst Moritz Arndt University of Greifswald.
- 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.
- Bhattarai, B. R., & Fischer, K. (2014). Human–tiger Panthera tigris conflict and its perception in Bardia National Park, Nepal. *Oryx*, *48*(04), 522–528.
- Bhattarai, B., Wright, W., & Khatiwada, A. (2016). Illegal Hunting of Prey Species in the Northern Section of Bardia National Park, Nepal: Implications for Carnivore Conservation. *Environments*, *3*(4), 32.
- Biswas, S., & Sankar, K. (2002). Prey abundance and food habit of tigers (Panthera tigris tigris) in Pench National Park, Madhya Pradesh, India. *Journal of Zoology*, *256*(3), 411–420.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*(3), 127–135.
- Borthakur, U., Barman, R. D., Das, C., Basumatary, A., Talukdar, A., Ahmed, M. F., … Bharali, R. (2011). Noninvasive genetic monitoring of tiger (Panthera tigris tigris) population of Orang National Park in the Brahmaputra floodplain, Assam, India. *European Journal of Wildlife Research*, *57*(3), 603–613.
- Bothma, J., & Le Riche, E. N. (1984). Aspects of the ecology and the behaviour of the leopard Panthera pardus in the Kalahari Desert. *Koedoe: African Protected Area Conservation and Science*, *27*(2), 259-279.
- Breuer, T. (2005). Diet choice of large carnivores in northern Cameroon Diet choice of large carnivores in northern Cameroon. *African Journal of Ecology*, *43*, 97–106.
- Brown, K. (1998). The political ecology of biodiversity, conservation and development in Nepal's Terai: Confused meanings, means and ends. *Ecological Economics*, *24*(1), 73–87.
- Budhathoki, P. (2003). A Category V Protected Landscape approach to buffer zone management in Nepal. *Parks*, *13*(2), 22-30.
- Budhathoki, P. (2004). Linking communities with conservation in developing countries: buffer zone management initiatives in Nepal. *Oryx*, *38*(03), 334–341.
- Carbone, C., Teacher, A., & Rowcliffe, J. M. (2007). The costs of carnivory. *PLoS Biology*, *5*(2), 0363–0368.
- Carter, N. H., Shrestha, B. K., Karki, J. B., Pradhan, N. M. B., & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences*, *109*(38), 15360–15365.
- Carter, N. H., Riley, S. J., Shortridge, A., Shrestha, B. K., & Liu, J. (2014). Spatial assessment of attitudes toward tigers in Nepal. *Ambio*, *43*(2), 125–137.
- Carter, N., Jasny, M., Gurung, B., & Liu, J. (2015). Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Global Ecology and Conservation*, *3*, 149–162.
- Carter, N. H., & Linnell, J. D. C. (2016). Co-Adaptation Is Key to Coexisting with Large Carnivores. *Trends in Ecology and Evolution*, *31*(8), 575–578.
- Caughley, G., & Sinclair, A. R. E. (1994). *Wildlife ecology and management*. Blackwell Science.
- Chakrabarti, S., Jhala, Y. V., Dutta, S., Qureshi, Q., Kadivar, R. F., & Rana, V. J. (2016). Adding constraints to predation through allometric relation of scats to consumption. *Journal of Animal Ecology*, *85*(3), 660–670.
- Chanchani, P., Lamichhane, B. R., Malla, S., Maurya, K., Bista, A., Warrier, R., ... & Dhakal, M. (2014). *Tigers of the Transboundary Terai Arc Landscape: Status, distribution and movement in the Terai of India and Nepal*. National Tiger Conservation Authority, Government of India, and Department of National Park and Wildlife Conservation, Government of Nepal NTNC/DNPWC.
- Chapron, G., Miquelle, D. G., Lambert, A., Goodrich, J. M., Legendre, S., & Clobert, J. (2008). The impact on tigers of poaching versus prey depletion. *Journal of Applied Ecology*, *45*(6), 1667–1674.
- Chauhan, N. P. S., Barwal, K. S., & Kumar, Devender. (2009). Human–Wild Pig Conflict in Selected States in India and Mitigation Strategies. *Acta Silv. Lign. Hung. Acta Silv. Lign. Hung*, *5*(5), 189–197.
- Croes, B. M., Funston, P. J., Rasmussen, G., Buij, R., Saleh, A., Tumenta, P. N., & de Iongh, H. H. (2011). The impact of trophy hunting on lions (Panthera leo) and other large carnivores in the Bénoué Complex, northern Cameroon. *Biological Conservation*, *144*(12), 3064–3072.
- Damania, R., Stringer, R., Karanth, K. U., & Stith, B. (2002). The Economics of Protecting Tiger Populations: Linking Household Behaviour to Poaching and Prey Depletion. *SSRN Electronic Journal*, *79*(2), 198–216.
- Dar, N. I., Minhas, R. A., Zaman, Q., & Linkie, M. (2009). Predicting the patterns, perceptions and causes of human-carnivore conflict in and around Machiara National Park, Pakistan. *Biological Conservation*, *142*(10), 2076–2082.
- Davies, T. E., Wilson, S., Hazarika, N., Chakrabarty, J., Das, D., Hodgson, D. J., & Zimmermann, A. (2011). Effectiveness of intervention methods against crop-raiding elephants. *Conservation Letters*, *4*(5), 346–354.
- Dhakal, M., Karki, M., Jnawali, S. R., Subedi, N., Pradhan, N. M. B., Malla, S., … Oglethorpe, J. (2014). *Status of tigers and prey in Nepal*. Department of National Park and Wildlife Conservation, Kathmandu, Nepal.
- Dhungana, R., Savini, T., Karki, J. B., Dhakal, M., Lamichhane, B. R., & Bumrungsri, S. (2018). Living with tigers Panthera tigris: Patterns, correlates, and contexts of human-tiger conflict in Chitwan National Park, Nepal. *Oryx*, *52*(1), 55–65.
- Dickman, A. J. (2010). Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation*, *13*(5), 458–466.
- Dinerstein, E. (1979). An ecological survey of the Royal Karnali Bardia Wildlife Reserve, Nepal. Part II: Habitat and animal interactions. *Biological Conservation*, *16*(4), 265–300.
- Dinerstein, E., Loucks, C., Wikramanayake, E., Ginsberg, J., Sanderson, E., Seidensticker, J., … Songer, M. (2007). The Fate of Wild Tigers. *BioScience*, *57*(6), 508– 514.
- DNPWC | Department of National Parks and Wildlife Conservation. (2018). Retrieved August 13, 2018, from http://www.dnpwc.gov.np/
- Dublin, H. T., & Hoare, R. E. (2004). Searching for solutions: The evolution of an integrated approach to understanding and mitigating human–elephant conflict in africa. *Human Dimensions of Wildlife*, *9*(4), 271–278.
- Dutta, T., Sharma, S., Maldonado, J. E., Wood, T. C., Panwar, H. S., & Seidensticker, J. (2013). Gene flow and demographic history of leopards (Panthera pardus) in the central Indian highlands. *Evolutionary Applications*, *6*(6), 949–959.
- Edgaonkar, A., & Chellam, R. (2002). in the Sanjay Gandhi National Park , Maharashtra , India. *Mammalia*, *66*, 353–360.
- Farrell, L. E., Roman, J., & Sunquist, M. E. (2000). Dietary separation of sympatric carnivores identified by molecular analysis of scats.pdf. *Molecular Ecology*, *9*, 1583–1590.
- Fisher, M. (2016). Whose conflict is it anyway? Mobilizing research to save lives. *Oryx*, *50*(03), 377–378.
- Fuller, T., & Sievert, P. (2001). Carnivore demography and the consequences of changes in prey availability. *Carnivore Conservation*, (December), 163–179.
- Gilbert, M., Soutyrina, S. V., Seryodkin, I. V., Sulikhan, N., Uphyrkina, O. V., Goncharuk, M., … Miquelle, D. G. (2015). Canine distemper virus as a threat to wild tigers in Russia and across their range. *Integrative Zoology*, *10*(4), 329–343.
- Global Tiger Initiative. (2011). *Global Tiger Recovery Program 2010–2022*. Global Tiger Initiative.
- Goodrich, J. M., Kerley, L. L., Smirnov, E. N., Miquelle, D. G., McDonald, L., Quigley, H. B., … McDonald, T. (2008). Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *Journal of Zoology*, *276*(4), 323–329.
- Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Kerley, L. L., & Howard, B. (2010). Spatial structure of Amur (Siberian) tigers (Panthera tigris altaica) on Sikh ... *Journal of Mammalogy*, *91*(3), 737–748.
- Gross, E. M., Drouet-Hoguet, N., Subedi, N., & Gross, J. (2017). The potential of medicinal and aromatic plants (MAPs) to reduce crop damages by Asian Elephants (Elephas maximus). *Crop Protection*, *100*, 29–37.
- Gunn, J., Hawkins, D., Barnes, R. F. W., Mofulu, F., Grant, R. A., & Norton, G. W. (2014). The influence of lunar cycles on crop-raiding elephants; evidence for risk avoidance. *African Journal of Ecology*, *52*(2), 129–137.
- 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.
- Harihar, A., Pandav, B., & Goyal, S. P. (2009). Density of leopards (Panthera pardus) in the Chilla Range of Rajaji National Park, Uttarakhand, India. *Mammalia*, *73*(1), 68–71.
- 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.
- Harmsen, B. J., Foster, R. J., Silver, S. C., Ostro, L. E. T., & Doncaster, C. P. (2009). Spatial and Temporal Interactions of Sympatric Jaguars (*Panthera onca*) and Pumas *(Puma concolor)* in a Neotropical Forest. *Journal of Mammalogy*, *90*(3), 612–620.
- 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.
- Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, *139*(1–2), 219–229.
- Hayward, M. W., & Slotow, R. (2009). Temporal Partitioning of Activity in Large African Carnivores: Tests of Multiple Hypotheses. *South African Journal of Wildlife Research*, *39*(2), 109–125.
- Hayward, M. W., Jedrzejewski, W., & Jedrzewska, B. (2012). Prey preferences of the tiger P anthera tigris. *Journal of Zoology*, *286*(3), 221–231.
- Heinen, J. T., & Mehta, J. N. (2000). Emerging Issues in Legal and Procedural Aspects of Buffer Zone Management with Case Studies from Nepal. *The Journal of Environment & Development*, *9*(1), 45–67.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., … Stuart, S. N. (2010). The impact of conservation on the status of the world's vertebrates. *Science*, *330*(6010), 1503–1509.
- Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: A review of patterns and priorities worldwide. *Oryx*, *43*(1), 18–34.
- Inskip, C., Fahad, Z., Tully, R., Roberts, T., & MacMillan, D. (2014). Understanding carnivore killing behaviour: Exploring the motivations for tiger killing in the Sundarbans, Bangladesh. *Biological Conservation*, *180*, 42-50.
- Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia*, *14*, 413– 417.
- Jacobson, A. P., Gerngross, P., Lemeris Jr., J. R., Schoonover, R. F., Anco, C., Breitenmoser-Würsten, C., … Dollar, L. (2016). Leopard (Panthera pardus) status, distribution, and the research efforts across its range. *PeerJ*, *4*, e1974.
- Jiang, G., Wang, G., Holyoak, M., Yu, Q., Jia, X., Guan, Y., … Ma, J. (2017). Land sharing and land sparing reveal social and ecological synergy in big cat conservation. *Biological Conservation*, *211*, 142-149.
- Johnsingh, A. J. T. (1992). Prey selection in three large sympatric carnivores in Bandipur insects or lion hunting buffalo , depends on the quality and quantity of its diet time tested strategies against several ecological constraints such as prey size. *Mammalia*, *56*(4), 517–527.
- Kabir, M., Ghoddousi, A., Awan, M. S., & Awan, M. N. (2014). Assessment of human– leopard conflict in Machiara National Park, Azad Jammu and Kashmir, Pakistan. *European Journal of Wildlife Research*, *60*(2), 291–296.
- Kapfer, P. M., Streby, H. M., Gurung, B., Simcharoen, A., McDougal, C. C., & Smith, J. L. D. (2011). Fine-scale spatio-temporal variation in tiger Panthera tigris diet: effect of study duration and extent on estimates of tiger diet in Chitwan National Park, Nepal. *Wildlife Biology*, *17*(3), 277–285.
- Kansky, R., & Knight, A. T. (2014). Key factors driving attitudes towards large mammals in conflict with humans. *Biological Conservation*, *179*, 93–105.
- Karanth, K. K., & Nepal, S. K. (2012). Local residents perception of benefits and losses from protected areas in India and Nepal. *Environmental Management*, *49*(2), 372–386.
- Karanth, K. U., & Sunquist, M. E. (1992). Population Structure, Density And Biomass Of Large Herbivores In The Tropical Forests Of Nagarahole, India. *Journal of Tropical Ecology*, *8*(1), 21–35.
- Karanth, K. U., & Sunquist, M. E. (1995). Prey Selection by Tiger, Leopard and Dhole in Tropical Forests. *The Journal of Animal Ecology*, *64*(4), 439.
- Karanth, K. U., & Sunquist, M. E. (2000). Behavioural correlates of predation by tiger (Panthera tigiris), leopard (Panthera pardus) and dhole (Cuan alpinus) in Nagarahole, India. *Journal of Zoology*, *250*, 255–265.
- Karanth, K. U. (2003). Tiger Ecology and Conservation in the Indian Subcontinent. *Journal of the Bombay Natural History Society, 100*(2&3),169-189.
- 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*, *101*(14), 4854–4858.
- Karanth, K. U., & Gopal, R. (2005). An ecology-based policy framework for human-tiger coexistence in India. *Conservation Biology Series, Cambridge*, *9*, 381.
- Karanth, K. U., & Chellam, R. (2009). Carnivore conservation at the crossroads. *Oryx*, *43*(1), 1–2.
- Karki, J., Jhala, Y., Pandav, B., Jnawali, S., Shrestha, R., Thapa, K., … Barber-Meyer, S. M. (2016). Estimating tiger and its prey abundance in Bardia National Park, Nepal. *Banko Janakari*, *26*(1), 60–69.
- Karmacharya, D., Sherchan, A. M., Dulal, S., Manandhar, P., Manandhar, S., Joshi, J., … Hughes, J. (2018). Species, sex and geo-location identification of seized tiger (Panthera tigris tigris) parts in Nepal—A molecular forensic approach. *PLOS ONE*, *13*(8), e0201639.
- Kawanishi, K., & Sunquist, M. E. (2004). Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation*, *120*(3), 333–348.
- Kerley, L. L. (2010). Using dogs for tiger conservation and research. *Integrative Zoology*, *5*(4), 390-396.
- King, L. E., Lawrence, A., Douglas-Hamilton, I., & Vollrath, F. (2009). Beehive fence deters crop-raiding elephants. *African Journal of Ecology*, *47*(2), 131–137.
- Kolipaka, S. S., Persoon, G. A., De Iongh, H. H., & Srivastava, D. P. (2015). The Influence of People's Practices and Beliefs on Conservation: A Case Study on Human-Carnivore Relationships from the Multiple Use Buffer Zone of the Panna Tiger Reserve, India. *Journal of Human Ecology*, *52*(3), 192–207.
- Kolipaka, S. S., Tamis, W. L. M., Van't Zelfde, M., Persoon, G. A., & De Iongh, H. H. (2017). Wild versus domestic prey in the diet of reintroduced tigers (Panthera tigris) in the livestock-dominated multiple-use forests of Panna Tiger Reserve, India. *PLoS ONE*, *12*(4), 1–15.
- Lambin, E. F., & Meyfroidt, P. (2011). Global land use change, economic globalization, and the looming land scarcity. *Proc Natl Acad Sci U S A*, *108*(9), 3465–3472.
- Lamichhane, B. R., Persoon, G. A., Leirs, H., Poudel, S., Subedi, N., Pokheral, C. P., … de Iongh, H. H. (2018a). Spatio-temporal patterns of attacks on human and

economic losses from wildlife in Chitwan National Park, Nepal. *PLoS ONE*, *13*(4), $1 - 18.$

- Lamichhane, B. R., Pokheral, C. P., Poudel, S., Adhikari, D., Giri, S. R., Bhattarai, S., … Subedi, N. (2018b). Rapid recovery of tigers Panthera tigris in Parsa Wildlife Reserve, Nepal. *Oryx*, *52*(1), 16–24.
- Lamichhane, B. R., Subedi, N., Pokheral, C. P., Dhakal, M., Acharya, K. P., Pradhan, N. M. B., … Yackulic, C. B. (2018). Using interviews and biological sign surveys to infer seasonal use of forested and agricultural portions of a human-dominated landscape by Asian elephants in Nepal. *Ethology Ecology & Evolution*, *30*(4), 331–347.
- Linkie, M., & Ridout, M. S. (2011). Assessing tiger-prey interactions in Sumatran rainforests. *Journal of Zoology*, *284*(3), 224–229.
- Linnell, J. D. C., & Strand, O. (2000). Interference interactions,co-existence and conservation of mammalian carnivores. *Biodiversity Research*, *6*, 169–176.
- Lovari, S., Pokheral, C. P., Jnawali, S. R., Fusani, L., & Ferretti, F. (2015). Coexistence of the tiger and the common leopard in a prey-rich area: The role of prey partitioning. *Journal of Zoology*, *295*(2), 122–131.
- Loveridge, A. J., Wang, S. W., Frank, L. G., & Seidensticker, J. (2010). People and wild felids: conservation of cats and management of conflicts. *Biology and Conservation of Wild Felids*, (January), 161–195.
- Lyngdoh, S., Shrotriya, S., Goyal, S. P., Clements, H., Hayward, M. W., & Habib, B. (2014). Prey preferences of the snow leopard (Panthera uncia): Regional diet specificity holds global significance for conservation. *PLoS ONE*, *9*(2), 1–11.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy Environment. *The American Naturalist*, *100*(916), 603–609.
- Madden, F. (2004). Creating coexistence between humans and wildlife: Global perspectives on local efforts to address Human–Wildlife conflict. *Human Dimensions of Wildlife*, *9*(4), 247–257.
- Madhusudan, M. D. (2003). Living amidst large wildlife: Livestock and crop depredation by large mammals in the interior villages of Bhadra Tiger Reserve, south India. *Environmental Management*, *31*(4), 466–475.
- Manipady, S., Menezes, R. G., & Bastia, B. K. (2006). Death by attack from a wild boar. *Journal of Clinical Forensic Medicine*, *13*(2), 89–91.
- Manral, U., Sengupta, S., Hussain, S. A., Rana, S., & Badola, R. (2016). Human Wildlife Conflict in India: A Review of Economic Implication of Loss and Preventive Measures. *Indian Forester*, *142*(10), 928–940.
- Mazák, V. (1981). Panthera tigris. *Mammalian Species*, *152*, 1–8.
- McDougal, C. (1988). Leopard and tiger interactions at Royal Chitwan National park, Nepal. *Journal Bombay Natural History Society*, *85*(3), 609–610.
- Mehta, J. N., & Heinen, J. T. (2001). Does community-based conservation shape favorable attitudes among locals? An empirical study from Nepal. *Environmental management*, *28*(2), 165-177.
- Meredith, M., & Ridout, M. (2018). Overview of the overlap package. Retrieved from http://cran.radicaldevelop.com/web/packages/overlap/vignettes/overlap.pdf
- Messmer, T. (2009). Human-wildlife conflicts: emerging challenges and opportunities. *Human-Wildlife Conflicts*, *3*(1), 10–17.
- Miller, J. R. B., Jhala, Y. V., Jena, J., & Schmitz, O. J. (2015). Landscape-scale accessibility of livestock to tigers: Implications of spatial grain for modeling predation risk to mitigate human-carnivore conflict. *Ecology and Evolution*, *5*(6), 1354–1367.
- Mills, L. S., & Allendorf, F. W. (1996). The one migrant per generation rule in conservation and management. *Conservation Biology*, *10*(6), 1509–1518.
- Miththapala, S., Seidensticker, J., & O'Brien, S. J. (1996). Phylogeographic subspecies recognition in leopards (Panthera pardus): molecular genetic variation. *Conservation Biology*, *10*(4), 1115-1132.
- Moe, S. R., & Wegge, P. (1994). Spacing behaviour and habitat use of axis deer (Axis axis) in lowland Nepal. *Canadian Journal of Zoology*, *72*(10), 1735-1744.
- Ministry of Federal Affairs and Local Development (MoFALD) (2017). *Gaunpalika and Nagarpalika of Nepal*. Government of Nepal, Kathmandu, Nepal.
- Mondal, K., Gupta, S., Bhattacharjee, S., Qureshi, Q., & Sankar, K. (2012a). Prey selection, food habits and dietary overlap between leopard Panthera pardus (Mammalia: Carnivora) and re-introduced tiger Panthera tigris (Mammalia: Carnivora) in a semi-arid forest of Sariska Tiger Reserve, Western India. *Italian Journal of Zoology*, *79*(4), 607–616.
- Mondal, K., Gupta, S., Bhattacharjee, S., Qureshi, Q., & Sankar, K. (2012b). Response of leopards to re-introduced tigers in Sariska Tiger Reserve, Western India. *International Journal of Biodiversity and Conservation*, *4*(5), 228–236.
- Mondol, S., R, N., Athreya, V., Sunagar, K., Selvaraj, V. M., & Ramakrishnan, U. (2009). A panel of microsatellites to individually identify leopards and its application to leopard monitoring in human dominated landscapes. *BMC Genetics*, *10*.
- Morrison, J. C., Sechrest, W., Dinerstein, E., Wilcove, D. S., & Lamoreux, J. F. (2007). Persistence of Large Mammal Faunas as Indicators of Global Human Impacts. *Journal of Mammalogy*, *88*(6), 1363–1380.
- Mukherjee, S., Goyal, S. P., & Chellam, R. (1994). Standarization of scats analysis technique for leopard (Panthera pardus fusca) in Gir National Park, western India. *Mammalia*, *58*, 139–143.
- Nepal, S. K. (2002). Linking parks and people: Nepal's experience in resolving conflicts in parks and protected areas. *International Journal of Sustainable Development and World Ecology*, *9*(1), 75–90.
- Nepal, S. K., & Weber, K. E. (1995). Managing resources and resolving conflicts: National parks and local people. *International Journal of Sustainable Development and World Ecology*, *2*(1), 11–25.
- Nowell, K., & Jackson, P. (1996). Status Survey and Conservation Action Plan: Wild Cats. (J. P. Kristin Nowell, Ed.), *IUCN*. Gland Switzerland: IUCN.
- Nyhus, P. J. (2016). Human–Wildlife Conflict and Coexistence. *Annual Review of Environment and Resources*, *41*(1), 143–171.
- Odden, M., & Wegge, P. (2005). Spacing and activity patterns of leopards Panthera pardus in the Royal Bardia National Park, Nepal. *Wildlife Biology*, *11*, 145–152.
- Odden, M. (2007). *Tigers, leopards and their prey in Bardia National Park, Nepal*. Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences. PhD thesis.
- Odden, M., & Wegge, P. (2009). Kill rates and food consumption of leopards in Bardia National Park, Nepal. *Acta Theriologica*, *54*(1), 23–30.
- Odden, M., Wegge, P., & Fredriksen, T. (2010). Do tigers displace leopards? If so, why? *Ecological Research*, *25*(4), 875–881.
- Ogra, M. V. (2008). Human-wildlife conflict and gender in protected area borderlands: A case study of costs, perceptions, and vulnerabilities from Uttarakhand (Uttaranchal), India. *Geoforum*, *39*(3), 1408–1422.
- Ogra, M. (2009). Attitudes toward resolution of human Wildlife conflict among forest-dependent agriculturalists near Rajaji National Park, India. *Human Ecology*, *37*(2), 161–177.
- Oli, M. K., Taylor, I. R., & Rogers, M. E. (1994). Snow leopard Panthera uncia predation of livestock-an assessment of local perceptions in the Annapurna Conservation area. *Nepal. Biological Conservation*, *68*, 63–68.
- Oliver, J. S. (1994). Estimates of hominid and carnivore involvement in the FLK Zinjanthropus fossil assemblage: some socioecological implications. *Journal of Human Evolution*, *27*(1–3), 267–294.
- Packer, C., Swanson, A., Ikanda, D., & Kushnir, H. (2011). Fear of darkness, the full moon and the nocturnal ecology of African lions. *PLoS ONE*, *6*(7), 4–7.
- Palomares, F., & Caro, T. M. (1999). Interspecific Killing among Mammalian Carnivores. *The American Naturalist*, *153*(5), 492–508.
- Pant, G., Dhakal, M., Pradhan, N. M. B., Leverington, F., & Hockings, M. (2016). Nature and extent of human-elephant Elephas maximus conflict in central Nepal. *Oryx*, *50*(4), 724–731.
- Parker, G. E., & Osborn, F. V. (2006). Investigating the potential for chilli Capsicum spp. to reduce human-wildlife conflict in Zimbabwe. *Oryx*, *40*(03), 343–346.
- Perez, I., Geffen, E., & Mokady, O. (2006). Critically Endangered Arabian leopards Panthera pardus nimr in Israel: Estimating population parameters using molecular scatology. *Oryx*, *40*(3), 295–301.
- Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: the bad, the good, and the unknown. *Annual Review of Environment and Resources*, *37*, 25-50.
- Peterson, M. N., Birckhead, J. L., Leong, K., Peterson, M. J., & Peterson, T. R. (2010). Rearticulating the myth of human-wildlife conflict. *Conservation Letters*, *3*(2), 74–82.
- Pilgrim, K. L., Mckelvey, K. S., Riddle, A. E., & Schwartz, M. K. (2005). Felid sex identification based on noninvasive genetic samples. *Molecular Ecology Notes*, *5*(1), 60–61.
- Pradhan, N. M. B., & Wegge, P. (2007). Dry season habitat selection by a recolonizing population of Asian elephants Elephas maximus in lowland Nepal. *Acta Theriologica*, *52*(2), 205–214.
- Rajaratnam, R., Sunquist, M., Rajaratnam, L., & Ambu, L. (2007). Diet and habitat selection of the leopard cat (Prionailurus bengalensis borneoensis) in an agricultural landscape in Sabah, Malaysian Borneo. *Journal of Tropical Ecology*, *23*(2), 209–217.
- 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.
- Ramesh, T., Kalle, R., Sankar, K., & Qureshi, Q. (2012). Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. *Journal of Zoology*, *287*(4), 269–275.
- Ramesh, T., Kalle, R., & Downs, C. T. (2017). Staying safe from top predators: patterns of co-occurrence and inter-predator interactions. *Behavioral Ecology and Sociobiology*, *71*(2), 41.
- Ray, J. ., Hunter, L., & Zigouris, J. (2005). *Setting Conservation and Research Priorities for Larger African Carnivores.* Wildlife Conversation Society, New York. *No. 24* (Vol. 267).
- Rayan, D. M., & Linkie, M. (2016). Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. *Biological Conservation*, *204*, 360– 366.
- R Core Team. (2018). R: The R Project for Statistical Computing. Retrieved June 21, 2018, from https://www.r-project.org/
- Redpath, S. M., Bhatia, S., & Young, J. (2015). Tilting at wildlife: Reconsidering human-wildlife conflict. *Oryx*, *49*(2), 222–225.
- Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, *14*(3), 322–337.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, *343*(6167), 1241484-1241484.
- Romañach, S. S., Lindsey, P. A., & Woodroffe, R. (2007). Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. *Oryx*, *41*(2), 185-195.
- Røskaft, E., Händel, B., Bjerke, T., & Kaltenborn, B. P. (2007). Human attitudes towards large carnivores in Norway. *Wildlife Biology*, *13*(2), 172-185.
- Saberwal, V. K., Gibbs, J. P., Chellam, R., & Johnsingh, A. J. T. (1994). Lion-Human Conflict in the Gir Forest, India. *Conservation Biology*, *8*(2), 501-507.
- Sangay, T., & Vernes, K. (2008). Human-wildlife conflict in the Kingdom of Bhutan: Patterns of livestock predation by large mammalian carnivores. *Biological Conservation*, *141*(5), 1272–1282.
- Sankar, K., Johnsingh, A. J. T. (2002). Food habits of tiger (Panthera tigris) and leopard (Panthera pardus) in Sariska Tiger Reserve, Rajasthan, India, as shown by scat analysis. *Mammalia*, *66*(2), 285-289.
- Sankar, K., Qureshi, Q., Nigam, P., Malik, P. K., Sinha, P. R., Mehrotra, R. N., … Gupta, S. (2010). Monitoring of Reintroduced Tigers in Sariska Tiger Reserve, Western India: Preliminary Findings on Home Range, Prey Selection and Food Habits. *Tropical Conservation Science*, *3*(3), 301–318.
- Sapkota, S., Aryal, A., Baral, S. R., Hayward, M. W., & Raubenheimer, D. (2014). Economic Analysis of Electric Fencing for Mitigating Human-wildlife Conflict in Nepal. *Journal of Resources and Ecology*, *55*(533), 237-243.
- Sarker, A. H. M. R., & Røskaft, E. (2011). Human attitudes towards the conservation of protected areas: a case study from four protected areas in Bangladesh. *Oryx*, *45*(03), 391-400.
- Seidensticker, J. (1976). On the Ecological Separation between Tigers and Leopards. *Biotropica*, *8*(4), 225-234.
- Seidensticker, J., Sunquist, M.E., McDougal, C. (1990). *Leopards living at the edge of the Royal Chitwan National Park Nepal.* Conservation in Developing Countries: Problems and Prospects, Bombay Oxford University Press, 415-423.
- Seidensticker, J., & McDougal, C. (1993). Tiger predatory behaviour, ecology and conservation. *Symposium of the Zoological Society of London*, (65), 105–125.
- Seidensticker, J. (2010). Saving wild tigers: A case study in biodiversity loss and challenges to be met for recovery beyond 2010. *Integrative Zoology*, *5*(4), 285–299.
- Seidensticker, J., Dinerstein, E., Goyal, S. P., Harihar, A., Johnsingh, A. J. T., Manandhar, A., ... Wikramanayake, E. (2015). Tiger range collapse at the base of the Himalayas : a case study Tiger range collapse and recovery at the base of the Himalayas. *The Biology and Conservation of Wild Felids*, (September), 784.
- Shehzad, W., Nawaz, M. A., Pompanon, F., Coissac, E., Riaz, T., Shah, S. A., & Taberlet, P. (2015). Forest without prey: livestock sustain a leopard Panthera pardus population in Pakistan. *Oryx*, *49*(2), 248-253.
- Shrestha M. K. (2004). *Relative ungulate abundance in a fragmented landscape: Implications for tiger conservation*. University of Minnesota, PhD thesis.
- Silwal, T., Kolejka, J., Bhatta, B. P., Rayamajhi, S., Sharma, R. P., & Poudel, B. S. (2017). When, where and whom: Assessing wildlife attacks on people in Chitwan National Park, Nepal. *Oryx*, *51*(2), 370–377.
- Simcharoen, S., Barlow, A. C. D., Simcharoen, A., & Smith, J. L. D. (2008). Home range size and daytime habitat selection of leopards in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Biological Conservation*, *141*(9), 2242–2250.
- Simcharoen, A., Savini, T., Gale, G. A., Simcharoen, S., Duangchantrasiri, S., Pakpien, S., & Smith, J. L. D. (2014). Female tiger Panthera tigris home range size and prey abundance: Important metrics for management. *Oryx*, *48*(3), 370–377.
- Smith, J. L. D., Sunquist, M. E., Tamang, K. M., & Rai, P. B. (1983). A Technique for Capturing and Immobilizing Tigers. *The Journal of Wildlife Management*, *47*(1), 255–259.
- Smith, J. L. D., McDougal, C., & Miquelle, D. G. (1989). Scent marking in free-ranging tigers, Panthera tigris. *Animal Behaviour*, *37*(1), 11–27.
- Smith, J. L. D., & McDougal, C. (1991). The Contribution of Variance in Lifetime Reproduction to Effective Population Size in Tigers. *Conservation Biology*, *5*(4), 484–490.
- Smith, J. L. D. (1993). The role of dispersal in structuring the Chitwan tiger population. *Behaviour*, *124*(3), 165–195.
- Smith, J. L. D., Ahearn, S. C., & McDougal, C. (1998). Landscape Analysis of Tiger Distribution and Habitat Quality in Nepal. *Conservation Biology*, *12*(6), 1338– 1346.
- Sogbohossou, E. A., De Iongh, H. H., Sinsin, B., De Snoo, G. R., & Funston, P. J. (2011). Human-carnivore conflict around pendjari biosphere reserve, northern benin. *Oryx*, *45*(4), 569–578.
- Steinmetz, R., Seuaturien, N., & Chutipong, W. (2013). Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biological Conservation*, *163*, 68–78.
- 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.
- Studsrød, J. E., & Wegge, P. (1995). Park-People Relationships: The Case of Damage Caused by Park Animals Around the Royal Bardia National Park, Nepal. *Environmental Conservation*, *22*(2), 133–142.
- Sukumar, R. (1991). The management of large mammals in relation to male strategies and conflict with people. *Biological Conservation*, *55*(1), 93–102.
- Sunarto, S., Kelly, M. J., Parakkasi, K., & Hutajulu, M. B. (2015). Cat coexistence in central Sumatra: Ecological characteristics, spatial and temporal overlap, and implications for management. *Journal of Zoology*, *296*(2), 104–115.
- Sunquist, M. E. (1981). The Social Organization of Tigers (Panthera Tigris) in Royal Chitawan National Park, Nepal. In *Smithsonian Contributions to Zoology* 1–98.
- Sunquist, M., & Sunquist, F. (2002). *Wild Cats of the World*. University of Chicago Press.
- Swanson, A., Arnold, T., Kosmala, M., Forester, J., & Packer, C. (2016). In the absence of a "landscape of fear": How lions, hyenas, and cheetahs coexist. *Ecology and Evolution*, *6*(23), 8534-8545.
- Tamang, B., & Baral, N. (2008). Livestock depredation by large cats in Bardia National Park, Nepal: Implications for improving park-people relations. *International Journal of Biodiversity Science and Management*, *4*(1), 44–53.
- Thapa, S., & Chapman, D. S. (2010). Impacts of resource extraction on forest structure and diversity in Bardia National Park, Nepal. *Forest Ecology and Management, 259*(3), 641-649.
- Thapa, S. (2010). Effectiveness of crop protection methods against wildlife damage: A case study of two villages at Bardia National Park, Nepal. *Crop Protection*, *29*(11), 1297–1304.
- Thapa, K., Wikramanayake, E., Malla, S., Acharya, K. P., Lamichhane, B. R., Subedi, N., … Vattakaven, J. (2017). Tigers in the terai: Strong evidence for meta-population dynamics contributing to tiger recovery and conservation in the terai arc landscape. *PLoS ONE*, *12*(6), 1–15.
- Thinley, P., Rajaratnam, R., Lassoie, J. P., Morreale, S. J., Curtis, P. D., Vernes, K., … Dorji, P. (2018). The ecological benefit of tigers (Panthera tigris) to farmers in reducing crop and livestock losses in the eastern Himalayas: Implications for conservation of large apex predators. *Biological Conservation*, *219*(February), 119– 125.
- Traill, L. W., Martin, J., & Owen-Smith, N. (2016). Lion proximity, not moon phase, affects the nocturnal movement behaviour of zebra and wildebeest. *Journal of Zoology*, *299*(3), 221–227.
- Treves, A., & Naughton-Treves, L. (1999). Risk and opportunity for humans coexisting with large carnivores. *Journal of Human Evolution 36*(3),275–282.
- Treves, A., & Karanth, K. U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology*, *17*(6), 1491–1499.
- Treves, A., Wallace, R. B., Naughton-Treves, L., & Morales, A. (2006). Co-managing human–wildlife conflicts: A review. *Human Dimensions of Wildlife*, *11*(6), 383– 396.
- Tumenta, P. N. (2012). *A Lion Population under Threat*. Leiden University , PhD thesis.
- Tumenta, P. N., de Iongh, H. H., Funston, P. J., & Udo de Haes, H. A. (2013). Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. *Oryx*, *47*(02), 237–242.
- Turner, A. (1987). Megantereon cultridens (Cuvier)(Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on dispersal and the possibility of a New World origin. *Journal of Paleontology*, *61*(6), 1256-1268.
- Upadhyaya, S. K., Musters, C. J. M., Lamichhane, B. R., de Snoo, G. R., Thapa, P., Dhakal, M.,Karmacharya, D., Shrestha, P.M., & de Iongh, H. H. (2018). An Insight Into the Diet and Prey Preference of Tigers in Bardia National Park, Nepal. *Tropical Conservation Science*, *11*, 194008291879947.
- Upadhyaya, S. K., Musters, C. J. M., Lamichhane, B. R., de Snoo, G. R., Dhakal, M. & de Iongh, H. H. (2018). Defining the risks of attacks by predators around protected areas – the case of Bardia National Park, Nepal. *Oryx* (Accepted).
- 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., 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.
- Walston, J., Robinson, J. G., Bennett, E. L., Breitenmoser, U., da Fonseca, G. A. B., Goodrich, J., … Wibisono, H. (2010). Bringing the tiger back from the brink-the six percent solution. *PLoS Biology*, *8*(9), 6–9.
- Wang, S. W., & Macdonald, D. W. (2006). Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological Conservation*, *129*(4), 558– 565.
- Wang, S. W., & Macdonald, D. W. (2009). The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation*, *142*(3), 606–613.
- Wang, S. W., & Macdonald, D. W. (2009). Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. *Journal of Zoology*, *277*(4), 275–283.
- Wasser, S. K., Smith, H., Madden, L., Marks, N., & Vynne, C. (2009). Scent-Matching Dogs Determine Number of Unique Individuals From Scat. *Journal of Wildlife Management*, *73*(7), 1233–1240.
- Wegge, P., Odden, M., Pokharel, C. P., & Storaas, T. (2009). Predator-prey relationships and responses of ungulates and their predators to the establishment of protected areas: A case study of tigers, leopards and their prey in Bardia National Park, Nepal. *Biological Conservation*, *142*(1), 189–202.
- Wegge, P., & Storaas, T. (2009). Sampling tiger ungulate prey by the distance method: Lessons learned in Bardia National Park, Nepal. *Animal Conservation*, *12*(1), 78–84.
- 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*(01), 35–45.
- Wikramanayake, E. D., Dinerstein, E., Robinson, J. G., Karanth, U., Rabinowitz, A., Olson, D., … 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.
- Wikramanayake, E., McKnight, M., Dinerstein, E., Joshi, A., Gurung, B., & Smith, D. (2004). Designing a conservation landscape for tigers in human-dominated environments. *Conservation Biology*, *18*(3), 839-844.
- Wilson, S., Davies, T. E., Hazarika, N., & Zimmermann, A. (2015). Understanding spatial and temporal patterns of human-elephant conflict in Assam, India. *Oryx*, *49*(1), 140–149.
- Wilting, A., Courtiol, A., Christiansen, P., Niedballa, J., Scharf, A. K., Orlando, L., … Kitchener, A. C. (2015). Planning tiger recovery: Understanding intraspecific variation for effective conservation. *Science Advances*, *1*(5) e1400175.
- Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of popualtions inside protected areas. *Science*, *280*, 2126–2128.
- Woodroffe, R., Lindsey, P., Romañach, S., Stein, A., & Ole Ranah, S. M. K. (2005). Livestock predation by endangered African wild dogs (Lycaon pictus) in northern Kenya. *Biological Conservation*, *124*(2), 225–234.
- Woodroffe, R., Frank, L. G., Lindsey, P. A., Ole Ranah, S. M. K., & Romañach, S. (2007). Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: A case-control study. *Biodiversity and Conservation*, *16*(4), 1245–1260.
- Wultsch, C., Waits, L. P., & Kelly, M. J. (2014). Noninvasive individual and species identification of jaguars (Panthera onca), pumas (Puma concolor) and ocelots (Leopardus pardalis) in Belize, Central America using cross-species microsatellites and faecal DNA. *Molecular Ecology Resources*, *14*(6), 1171–1182.

Summary

Large carnivores and humans, along with their livestock, have co-existed for thousands of years. However, human population growth and an increase in economic activities are modifying the landscape for large carnivores and their prey. Large cats, which are regarded as keystone species for maintaining a healthy ecosystem through the balance between predator and prey, are now often locally on the verge of extinction. Large predators are sensitive to human activities and have been actively persecuted from all over the world, because of their conflicts with local people. The number of tigers (*Panthera tigris*) has declined rapidly in the past century and now they are confined to 7 % of their historical range. Similarly the range of leopards (*Panthera pardus*) has also declined significantly, although they are more widespread and adaptive than tigers. Since these carnivores require large habitats, degradation and fragmentation of their habitat over past decades are regarded as the major threats for their survival. The other factors responsible for their decline include poaching for illegal trade of body parts, loss of prey species and conflicts with local communities. Local farmers often face negative interactions with wild predators thereby experiencing economic loss by the killing of livestock. These conflicts in combination with a poor understanding of the ecological role which predators play may lead to local resentment against predators and negative attitude towards predator conservation projects.

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, aims at doubling the number of wild tigers by 2022. In order to achieve this goal the Government of Nepal has focused on better conservation practices in and around tiger conservation landscape. Tigers are found in five National Parks of the lowland plain (Terai). This area is a part of the greater Terai Arc Landscape which is located in India and Nepal. There has been an increase in the tiger population after the end of civil war in Nepal, as well as a decrease in poaching, due to new government policy which included strict protection measures in national parks and the involvement of youths in anti-poaching campaign. As a result of a significant increase in the population of tigers inside Bardia National Park they are now showing more interaction with leopards. As tigers and leopards are elusive species it is difficult to study their interaction in the field. Therefore, using camera trap data obtained during 2013 and 2016, I studied the interaction between tigers and leopards in Bardia National Park. I found that there is a significant level of spatial avoidance of leopards towards tigers in the core zone of the park whereas in the boundary zone the spatial avoidance is not significant. I found that the temporal activities of leopards in grids of the core zone where tigers and leopards both are present are significantly different compared to grids where tigers are absent. The temporal activities of tiger are not significantly different in grids with leopards present in the core zone. However, the temporal activity of tigers is significantly different in the boundary zone when leopards were present, whereas the activity of leopard does not change. This can probably be explained by the suggestion that leopards approach human settlements more easily, while tigers show strong avoidance of human settlements. This also suggests that habitat partitioning and space use may play an important role in the co-existence of tigers and leopards in Bardia National Park. In general leopards show more avoidance to tigers than the other way round.

I also compared the diet and prey preference of tigers and leopards using their scats. However, due to lower number of leopard scats, I could not process it further and had to limit my study to the diet and prey preference of tigers only. I was able to identify male and female tigers based on DNA analysis of scat. I found that both male and female tigers were relying on medium sized prey (10 kg to 40 kg) namely chital (*Axis axis*) and wild pig (*Sus scrofa*) which was the most abundant prey in Bardia. However the Jacobs index for prey preference of male tiger was for sambar (*Cervus unicolor*) and wild pig whereas for female tiger the preference was for chital and wild pig, however the results were not statistically significant. The diet of tigers showed mostly the presence of wild prey species which suggests that they are generally not involved in the killing of livestock. For the long term conservation of the tiger in Bardia National Park we need to focus on increasing the population of larger prey species in the park, so that the available prey species are energetically beneficial for tigers and there is less competition with leopards.

I also looked into the spatiotemporal pattern of the conflict incidence in Bardia NP for a period of five years, on the basis of compensation paid to the villagers for the damage caused by wildlife. I found that four animals were mainly involved in causing damage to local communities, namely elephant (*Elephas maximus*), leopard, tiger and wild boar. The elephant was responsible for most of the damage. During the five years elephants killed 14 people and wild boar killed one person. Elephants also caused serious damage to the crops, destroyed houses and raided store houses for grains. Leopards and tigers particularly caused depredation of livestock. Elephants caused more damage during the autumn season when the crops (mainly paddy) had matured. Leopards killed more livestock during the rainy season compared to dry season, while tigers did not showed seasonal pattern of predation. Tigers and leopards were involved in significantly more killing of livestock during the new moon phase compared to the full moon phase. The conflict incidence for elephants, wild boar and leopards was higher in the southern and the western part of the buffer zone, whereas tigers had a similar level of conflict all over the park.

To know more about the attitude and knowledge of local people living in the buffer zone towards conservation, I conducted a questionnaire survey by dividing the park into four different regions. I found that the loss of livestock was significantly related to number of livestock owned, the distance to the park boundary and the ethnicity of the respondent. The attitude of the respondent towards wildlife conservation was dependent on i) knowledge about the species, ii) (higher) educational level, iii) gender (male/female) and iv) level of self-sufficiency of the respondents, with a positive attitude related to more knowledge, male gender, higher education and higher self-sufficiency level of respondents. The sharing of conservation benefits also resulted in a positive attitude among the people living in the buffer zone.

In conclusion, it can be said that, due to the increase in number of tigers inside the park leopards may be pushed out of the park, where they become involved in conflicts while there may also be a spill-over of young tigers moving to the buffer zone. For future conservation of these large cats, additional habitats need to be sought and the community forest of the buffer zone can provide such habitat. Similarly, Banke National Park which has been established to provide a sink for the Bardia source population, which can help in accommodating the dispersed population of Bardia NP. Therefore, for future conservation programs we need to focus on the conservation of tiger and leopard in human dominated landscape. Due to interaction with tigers, the leopards are living in close proximity with people and thereby get more involved in conflicts with local communities. Tigers enjoy a religious and cultural tolerance among the people living in the buffer zone whereas leopards lack such religious and cultural tolerance.

Samenvatting

Grote carnivoren en mensen, samen met hun vee, leven al duizenden jaren samen in dezelfde gebieden. Bevolkingsgroei en economische ontwikkeling veranderen het landschap van deze gebieden voor carnivoren en hun prooi dieren. Grote katten, die worden beschouwd als sleutel soorten voor gezonde ecosystemen door de wisselwerking predator-prooi, staan nu vaak lokaal op het punt om uit te sterven. Grote carnivoren zijn kwetsbaar voor menselijke activiteiten en worden wereldwijd actief vervolgd, vanwege conflicten met mensen. Het aantal tijgers(*Panthera tigris*) is de afgelopen eeuw sterk afgenomen en tijgers bevinden zich nu slechts in 7% van hun historische leefgebied. Ook het leefgebied van de luipaard (*Panthera pardus*) is sterk afgenomen, alhoewel deze soort meer algemeen en adaptief is dan de tijger. Omdat carnivoren grote leefgebieden nodig hebben, wordt de degradatie van hun habitat over de laatste tientallen jaren gezien als de belangrijkste bedreiging. Andere factoren die van invloed zijn op de afname van carnivoren betreffen stroperij voor de illegale handel in lichaamsdelen van carnivoren, de afname van prooidier populaties en conflicten met lokale gemeenschappen. Lokale boeren ondervinden vaak de negatieve gevolgen van wilde carnivoren, waarbij ze economische schade ondervinden door het doden van vee. Deze conflicten worden verergerd door een beperkt begrip van de ecologische rol van carnivoren en dit kan resulteren in een negatieve houding ten opzichte van carnivoren en gerelateerde projecten voor natuurbescherming.

Nepal is een van de dertien landen die het Global Tiger Recovery Plan hebben getekend op de bijeenkomst van wereldleiders in St Petersburg in 2010, die als doel heeft het aantal wilde tijgers te verdubbelen in 2022. Om dit doel te behalen heeft de regering van Nepal haar aandacht gegeven op verbeterde activiteiten gericht op natuurbescherming in en rond de landschappen waar tijgers voorkomen. Tijgers worden in Nepal nog aangetroffen in vijf nationale parken. In de laagvlakte (Terai). Dit gebied is een onderdeel van het grotere 'Terai Arc' landschap dat zich bevindt in India en Nepal.. De tijger populatie in Nepal is toegenomen sinds het einde van de burgeroorlog, terwijl de stroperij is afgenomen. Dit is een gevolg van het overheidsbeleid, dat strikte natuurbeschermings-activiteiten in nationale parken omvatten e o.m. de deelname van jongeren in anti-stroperij campagnes. Dit heeft geresulteerd in een sterke groei van de tijger populatie in Bardia nationaal park, waar tijgers nu meer interacties hebben met luipaarden dan vroeger. Omdat tijgers en luipaarden schuwe dieren zijn is het moeilijk hun interactie in het veld te onderzoeken. Camera val surveys zijn een goede methode om de aanwezigheid en afwezigheid van tijgers en luipaarden te onderzoeken. Daarom heb ik met behulp van camera val data uit 2013 en 2016 de interacties tussen tijgers en luipaarden bestudeerd in Bardia nationaal park

Ik vond daarbij een significante ruimtelijke ontwijking van luipaarden t.o.v. tijgers in de centrale zone van het park, terwijl in de bufferzone en geen significant patroon van ontwijking was. Ik vond ook dat de activiteiten in de tijd van luipaarden in grids in de centrale zone, waar zowel tijgers als luipaarden aanwezig waren, significant verschilden met grids waar tijgers niet aanwezig waren, maar luipaarden wel. De activiteiten in de tijd van tijgers in grids waar luipaarden ook aanwezig waren in de centrale zone verschillen niet van grids zonder luipaarden. Ik vond echter in de bufferzone een significant verschil wat betreft de activiteiten van tijgers in de tijd in grids met luipaarden vergeleken met grids zonder luipaarden, terwijl de activiteiten van luipaarden in de tijd niet verschilden in grids met en zonder tijgers. Dit kan waarschijnlijk worden verklaard door de suggestie dat luipaarden dichter bij menselijke nederzettingen komen, terwijl tijgers menselijke nederzettingen vermijden Dit geeft ook aan dat het gemeenschappelijk gebruik van habitat en ruimte een belangrijke rol speelt in het samenleven van tijgers en luipaarden in Bardia nationaal park In het algemeen ontwijken luipaarden meer de tijgers dan andersom. Ik heb ook de dieten en prooidier voorkeuren van tijgers en luipaarden willen vergelijken.op basis van uitwerpselen. Echter, vanwege een onvoldoende grote monster-grootte van luipaard uitwerpselen, kon ik deze niet verder gebruiken en heb ik mij beperkt tot het analyseren van de uitwerpselen en prooidier voorkeuren van tijgers. Gebaseerd op het DNA in de uitwerpselen kon ik een onderscheid maken tussen vrouwelijke en mannelijke tijgers. Ik vond dat zowel mannelijke als vrouwelijke tijgers vooral prooidieren eten van medium gewicht (10 tot 40 kg)., namelijk Chital (*Axis axis*)en wild zwijn (*Sus Scrofa*), die de meest algemene prooidieren zijn in Bardia nationaal park. Echter de Jacobs index voor prooidier preferentie van mannelijke tijgers gaf een voorkeur aan voor Sambar hert (*Cervus unicolor*) en wild zwijn, terwijl de Jacobs index voor vrouwelijke tijgers een voorkeur aangaf voor Chital en wild zwijn.

Deze resultaten waren echter statistisch gezien niet significant. Het dieet van tijgers bestond voornamelijk uit wilde prooidier soorten, hetgeen suggereert dat tijgers over het algemeen geen vee consumeren. Voor de lange termijn bescherming van de tijger in Bardia nationaal park moet meer aandacht gegeven worden aan de groei van prooidier populaties in het park, zodat de beschikbare prooidier populaties energetische voordelen bieden voor tijgers en er minder competitie is met luipaarden. Ik heb ook gekeken naar het verloop van conflicten in Bardia nationaal park in ruimte en tijd, over een periode van vijf jaar, op basis van de statistieken van compensatie die is betaald aan dorpelingen voor de schade veroorzaakt door wilde dieren.

Ik vond dat voornamelijk vier soorten dieren betrokken waren bij schade gevallen gemeld door de lokale bevolking; olifant, luipaard, tijger en wild zwijn. Gedurende die vijf jaar werden 14 personen gedood door olifanten en één persoon door een wild zwijn. Olifanten veroorzaakten ook ernstige schade aan gewassen, vernielden huizen en vielen opslag schuren voor graan aan. Luipaarden en tijgers veroorzaakten vooral schade aan vee. Olifanten veroorzaakten meer schade gedurende de herfst wanneer gewassen (vooral rijst) aan het rijpen waren. Luipaarden veroorzaakten meer schade aan vee gedurende het regenseizoen in vergelijking met het droge seizoen, terwijl de schade toegebracht door tijgers geen verschillende vertoonde tussen de seizoenen.. Tijgers en luipaarden veroorzaakten meer schade aan vee gedurende de donkere maan periode vergeleken met de volle maan periode. De frequentie van conflicten met luipaarden was hoger in het zuidelijke en westelijke deel van de bufferzone voor olifanten en wilde zwijnen, terwijl de frequentie van conflicten met tijgers gelijk was over het hele gebied. Om meer te weten te komen over de attitudes en kennis van lokale bewoners die in de bufferzone leven, van belang voor natuurbescherming, heb ik interviews gehouden. Dit heb ik gedaan door het park te verdelen in vier verschillende regio's. Ik vond dat de schade aan vee een significante relatie had met i) de aantallen vee in bezit van bewoners, ii) de afstand tot de park grens en ii) de etnische afkomst van de respondent. De attitude van de respondenten ten opzichte van de bescherming van wilde dieren was gerelateerd aan de volgende factoren; i) kennis over de soort ii) opleidings nivo respondent iii) gender van de respondent (man/vrouw) en iv) nivo van onafhankelijkheid van de respondent. Een positieve attitude was gerelateerd aan meer kennis over de soort, een hoog opleidings nivo, en een hoog nivo van onafhankelijkheid. Het delen van voordelen en inkomsten uit natuurbescherming resulteert ook in een positieve attitude onder de bevolking in de bufferzone. Concluderend kan gezegd worden dat als gevolg van een toename van het aantal tijgers in het park luipaarden waarschijnlijk uitwijken naar de bufferzone, waar ze in conflict komen met bewoners, terwijl ook jonge tijgers het park verlaten. Voor de toekomstige bescherming van deze grote katten is het van belang dat nieuwe habitats worden gezocht en de gemeenschapsbossen in de bufferzone zouden hier aan bij kunnen dragen. Ook kan het nabijgelegen

Banke nationaal park een *sink* vormen voor de bron-populatie in Bardia nationaal park. Dit kan de verdere verspreiding van de tijger populatie in Bardia faciliteren. Voor toekomstige natuurbeschermings programma's is het van belang zich te concentreren op de bescherming van tijger en luipaard in een door mensen gedomineerd landschap. Vanwege de interactie met tijgers leven luipaarden dichter bij mensen en komen ze zo ook vaker in conflict met lokale bewoners. Tijgers genieten een culturele en religieuze tolerantie onder de bevolking die leeft in de bufferzone terwijl luipaarden deze tolerantie niet genieten.

Acknowledgements

I would like to dedicate this work to my parents Puskar Nath Upadhyaya Gyawali and Tamkala Gyawali, who constantly inspired me during my PhD. I also want to thank my wife Hemlata, daughters Simran and Subhani and son Somin for their constant encouragement for my work and to bear with me during the period of my absence from home. I would also like to thank my brother Shyam and sisters Bina, Sarita and Parvata as well as other family members for their support.

I would like to thank my promotor Professor Geert de Snoo and co-promotors Professor Hans H de Iongh and Dr. Kees Musters from Leiden University for their constant supervision, guidance and encouragement. I also would like to thank my co-supervisor at Kathmandu University, Prof. Dr. Panna Thapa for his constant guidance and encouragement. My sincere gratitude go to Prof. Dr. Ram Kantha Makaju Shrestha (Vice Chancellor), Prof. Dr. Subodh Sharma (Registrar), Prof. Dr. Bhola Thapa (Former Registrar) and Prof. Dr. Kanhaiya Jha (Dean of School of Science) of Kathmandu University. I would also like to thank colleagues from my department at Kathmandu University for their support. I would also like to thank the Himalayan Tiger Foundation, especially Cas de Stoppelaar and his team for their support. I would like to thank Dr. Dibesh Karmacharya and his team from the Center for Molecular Dynamics Nepal for helping in carrying out the laboratory work for DNA analysis. My sincere thanks also go to Ms Patricia Chettri, (fellowship officer) of The Netherlands Consulate, Kathmandu for her help in visa processing. I want to thank Nuffic for providing funding for this project through a NFP fellowship. I would also like to thank Cindy Scotte, Marielle van Es and other employees of the department of Student and Educational Affairs (SEA) who helped me with the allotment of funds.

I would also like to thank the Director, and former and present ecologist of the Department of National Parks and Wildlife Conservation (DNPWC), namely Dr. Maheshwar Dhakal, Laxman Poudyal, Rishi Ranabhat and other staff of DNPWC for providing the permit for my research work. I also want to thank former and present senior warden of Bardia National Park, namely Ram Chandra Kandel, Ramesh Thapa, Ashok Bhandari and other staffs for their help. I would like to extend my sincere thanks to Mrs. Sarita Jnawali, Dr. Naresh Subedi and other members of National Trust for Nature Conservation (NTNC) for their support and encouragement. Thanks also go to Rabin Kadariya, Ambika Prasad Khatiwada, Shyam Thapa, Shreeram Ghimire, Shailendra Yadav, Ramji Thapa and other staff of the Bardia Conservation Program of NTNC for providing technical and logistic support during my field work.

I want to thank from my heart Babu Ram Lamichhane for his help and support during the course of my PhD. I also acknowledge the support of friends in Leiden who made my stay comfortable namely Praduman Khayargoli, Prof. Jan Houben, Dr. Saraju Rath, Dr. Bal Gopal Shrestha, Sri Laxmi Shrestha, Dipen Lama, Ranjita Lama and Rogier van de Vorst.

I also want to thank the Scientific Director of the Institute of Environmental Sciences Leiden (CML) Prof. Dr. Arnold Tukker and Head of Environmental Biology department Prof. Dr. Peter van Bodegom. I also want to thank the Institute Manager Paul de Hoog as well as secretaries namely Jory Sjardijn and Susanna van den Oever for their help provided to me during my stay in CML. I am indebted to all staff of CML and my fellow PhD for making my stay at Leiden memorable.

I am grateful to my PhD committee members, Prof. Dr. Arnold Tukker, Prof. Dr. Peter van Bodegom, Prof. Dr. Herwig Leirs and Prof. Dr. Gerard Persoon for evaluation and providing constructive comments and suggestions on an earlier version of the thesis draft. I want to thank Professor Hans de Iongh for the Dutch translation of the summary. I would like to express my gratitude to my friend Sijan Baral for initial correction of the thesis and to Barbara Croes for the final language corrections. I also want to thank Sjoukje Rienks for the layout work. Finally, I am grateful to Sagar Giri for providing the cover photographs and photographs at the beginning of chapter two, four and six.

Curriculum Vitae

Subodh Kumar Upadhyaya was born on the 8th of October 1965 in Khanchikot, Arghakhanchi district of Nepal. He followed his primary and secondary school from 1972 to 1984 in Kendriya Vidyalaya, Shillong, India and attended there the St. Edmund's College affiliated to North Eastern hill University in Shillong, India, where he obtained a Bachelor's degree with Zoology Honours in 1987. He obtained his first Masters degree in Zoology from Tribhuvan University, Kathmandu, Nepal in 1989. and a second Masters degree in Biotechnology from Birla Institute of Technology and Science, Pilani,

India in 2004. Since 1998 he is working as a staff member in the Department of Biotechnology, School of Science, Kathmandu University, Nepal.

Subodh started his PhD at the Institute of Environmental Sciences Leiden (CML) in 2014, when he received a fellowship of the Netherlands Organization for International Cooperation in Higher Education, the Netherlands fellowship program (Nuffic-NFP). His PhD research was on the interaction between tigers and leopards in relation to human-wildlife conflict in Bardia National Park, Nepal. This PhD is part of a collaborative agreement between Leiden University, the Netherlands and Kathmandu University, Nepal and between Leiden University and the National Trust for Nature Conservation Nepal (NTNC).

