
**PREY SELECTION BY TIGERS (*PANTHERA TIGRIS*
TIGRIS) IN THE KARNALI FLOODPLAIN OF
BARDIA NATIONAL PARK, NEPAL**

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LIST OF ACRONYMS

BCP	Bardia Conservation Programme
BNP	Bardia National Park
BTR	Bandipur Tiger Reserve
CNP	Chitwan National Park
DNA	Deoxyribonucleic acid
IUCN	International Union for Conservation of Nature
KTR	Kanha Tiger Reserve
NGO	Non-Governmental Organisation
NNP	Nagarahole National Park
NSTR	Nagarjunasagar Srisaïlam Tiger Reserve
NTNC	National Trust for Nature Conservation
PCR	Polymerase Chain Reaction
PNP	Pench National Park
RBNP	Royal Bardia National Park Management Plan
RNP	Rathambore National Park
SE	Standard Errors

ABSTRACT

Populations of the tiger (*Panthera tigris*) are declining worldwide. Continued depletion of tiger prey base seems to be the current leading threat to tigers' survival. Increased knowledge of tiger food habits under ever-changing prey base availability in increasingly human-modified ecological systems is then essential to recognise this endangered species' conservation needs.

Food habits of tigers were studied in the Karnali floodplain of Bardia National Park, Nepal, during the dry season of 2009. The diet of tigers was determined by analyses of 67 scats collected opportunistically from the study area between February and May 2009. The scats were analysed for undigested prey hairs, with hair features, such as scale patterns of the cuticula and configuration of the medulla analysed and compared to a reference hair library. A regression equation originating from earlier studies was used to convert frequency of occurrence of prey items in scats to relative biomass and relative number of individuals killed. Defining prey selectivity as taking of prey types in frequencies that were different from those expected, based on prey density estimates, prey selection by Karnali tigers was determined. Results showed that two species, chital (*Axis axis*) and hog deer (*Axis porcinus*), constituted the bulk of the diet of tigers comprising 78.75% of all prey killed. Overall, wild prey comprised 96.44% of the total biomass consumed by tigers, with domestic livestock contributing 3.56%. Karnali tigers showed significant selectivity among a number of prey species. Despite the scarcity of sambar (*Cervus unicolor*) and barasingha (*Cervus duvauceli*) in the study area, tigers showed significant selectivity for these optimum-sized prey. Tigers also showed significant selectivity for medium-sized species, preferentially consuming chital and wild boar (*Sus scrofa*) but avoiding muntjac (*Muntiacus muntjac*). Hog deer (*Axis porcinus*) and rhesus (*Macaca mulatta*) were preyed upon less than their availability, however, this was not considered as significant. No remains of other potential tiger prey, such as nilgai (*Bosephalus tragocamelus*), Indian porcupine (*Hystrix indica*), langur (*Presbytis entellus*) and domestic buffalo (*Bubalis bubalis*) were found in the samples. The presence of sheep (*Ovis sp.*) in the diet of Karnali tigers indicates that although livestock make up a relatively small component of the tiger's

diet (3.56%), domestic animals are illegally grazed in BNP and/or that tigers may be frequenting the buffer zones surrounding the park.

The results from this study suggest that in areas with low densities of large prey, tigers show significant selection for medium-sized prey thus potentially leading to the spatial exclusion of sympatric carnivores through food competition. Significant selectivity for sambar and barasingha suggests that tigers will select for these optimum-sized prey when they are available and that prey vulnerability can strongly influence prey selection by tigers. The continuing decline in prey and tiger densities in BNP highlights the urgent need for increased enforcement of strict protection and management rules if BNP is to realize its potential of becoming an important and much needed conservation area for tigers and their prey in Nepal.

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1. INTRODUCTION

1.1 Problem statement

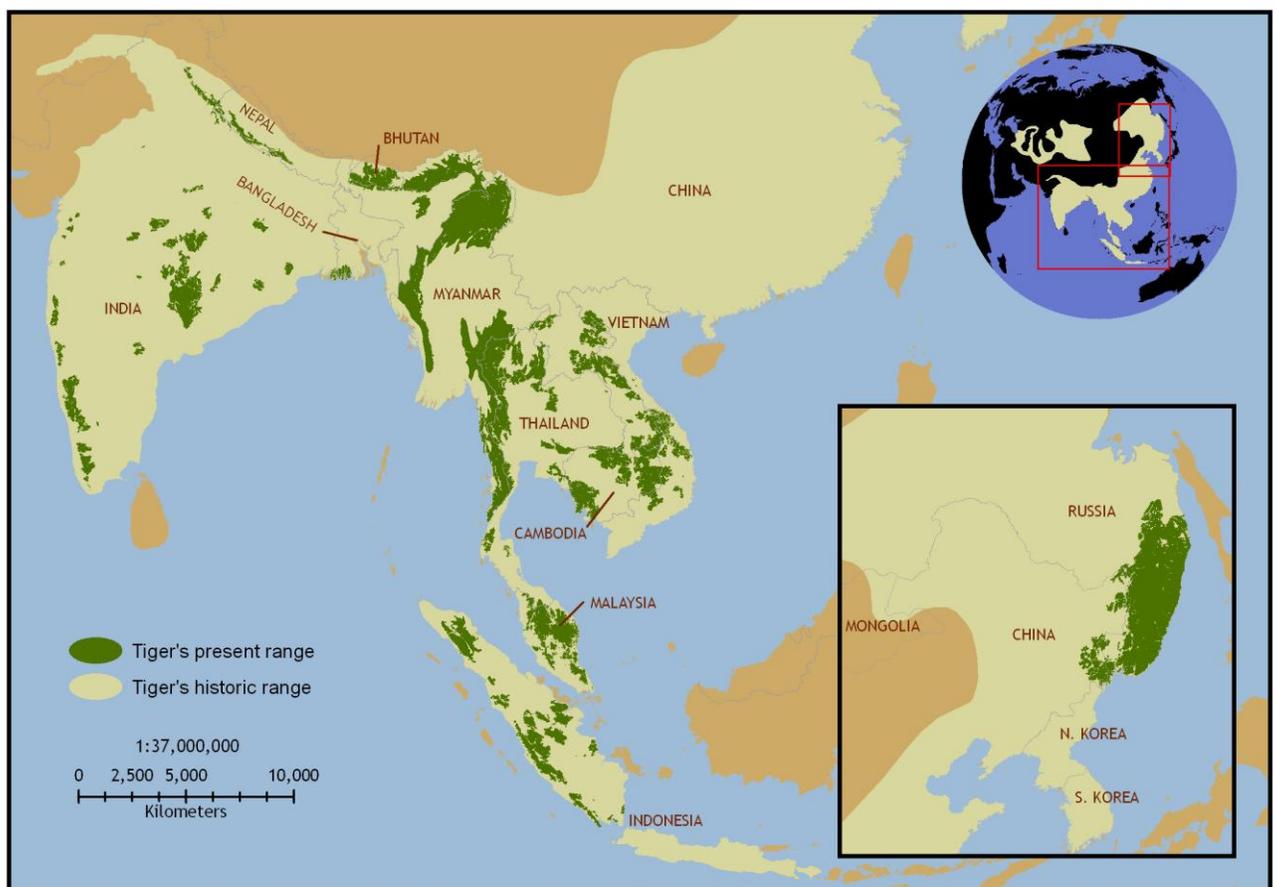
The tiger (*Panthera tigris*), the largest of all living cats and Asia's largest predator (Seidensticker & McDougal, 1993), is widely considered to be one of the most charismatic species on Earth. Throughout centuries, the tiger has been revered as a cultural icon over much of its range (Jackson, 1999). This has not, however, afforded the species much, if any, protection. The tiger is now listed as endangered on the International Union for Conservation of Nature (IUCN) Red List (2007) and despite extensive conservation efforts this iconic species continues its relentless decline (IUCN, 2007).

A total of eight tiger subspecies are commonly recognised: Bengal tiger (*Panthera tigris tigris*), Sumatran tiger (*P. t. sumatrae*), Amur tiger (*P. t. altaica*), Indo-China tiger (*P. t. corbetti*), South China tiger (*P. t. amoyensis*), Caspian tiger (*P. t. virgata*), Javan tiger (*P. t. sondaica*) and Bali tiger (*P. t. balica*) (Luo *et al.*, 2004; IUCN, 2007). Three of these, the Caspian, Javan and Bali tiger, went extinct in the last fifty years. The last Bali tiger was killed in 1937, the Caspian tiger went extinct in the 1950s and the last wild Javan tiger was seen in 1972. The wild South China tiger has not been directly observed since the 1970s and is now believed to be extinct in the wild too (Sunquist *et al.*, 1999; IUCN, 2007).

At the beginning of the last century an estimated 100,000 wild tigers roamed the Asian continent. Their geographical distribution spanned widely from eastern Turkey to the sea of Okhotsk in the Russian Far East, with tiger territories overlapping with those of lions in a wide region stretching across north-western India (Schaller, 1967; Sunquist & Sunquist, 1988; IUCN, 2007). Over the past 100 years tigers have lost 93% of their range and their numbers have declined by more than 95%. Between 3,402 and 5,140 individuals remain in the wild at present, with a total effective population size estimated at mere 1,361 to 2,056 mature breeding individuals (IUCN, 2007). Unfortunately, tigers' unrelenting decline

continues, and fast too. Within the past decade alone, the estimated area known to be occupied by tigers has declined by 41%. Tigers persist now in increasingly fragmented and often degraded habitats in parts of India, South-east Asia, Sumatra and the Russian Far East, with a negligible number in China (IUCN, 2007) (Figure 1).

Figure 1. Historic (circa 1850) and present distribution of tigers. From www.worldwildlife.org



Throughout centuries, various factors have contributed to the decline in tiger populations worldwide (Chundawat *et al.*, 1999). The hunting of tigers for sport, coupled with retaliatory killings by discontented farmers, played a major role in the predator's historical decline (Chundawat *et al.*, 1999; IUCN, 2007). Between 1860 and 1960, for example, approximately 93,000 tigers were killed for sport or bounties in parts of British India (Karanth, 2003). Poaching (to satisfy the demands for oriental medicine and for costume decoration of Tibet's growing middle-class), habitat loss and most importantly continued depletion of prey base are considered the current leading threats to tigers. It is widely recognized that these factors will determine tigers' survival in the future (Karanth & Stith, 1999; Sunquist *et al.*, 1999; Dinerstein *et al.*, 2006). Although this is undoubtedly alarming, tigers have proved to be a remarkably resilient species (Sunquist *et al.*, 1999; Biswas & Sankar, 2002). Tigers have the ability to live in very diverse habitats, where they tolerate a wide range of temperatures and rainfall regimes. They produce relatively large litters with relatively short interbirth intervals. They can take prey differing considerably in size and their hunting tactics will vary based on prey size, prey species and habitat (Karanth, 2003). Tiger predatory behaviour can also change with experience (Sunquist *et al.*, 1999). Owing to such outstanding resilience, tigers are able to relatively swiftly recover from substantial losses, providing their habitat and prey populations remain intact (Sunquist *et al.*, 1999; Biswas & Sankar, 2002).

1.2 Introduction to this study

In 1994 the Karnali floodplain of Bardia National Park (BNP), Nepal, was supporting a higher density of tigers than anywhere else in the park (Støen, 1994). Støen (1994) suggests that this was directly influenced by a relatively high density biomass of wild prey in the area at that time. Extensive poaching of wild prey, however, has led to a dramatic decrease in prey density in the floodplain over the past 15 years, with a corresponding significant reduction in tiger density (BCP report, 2006). Studies, such as this one, which look into the food habits of tigers are then essential to gain a comprehensive understanding

of the predator's ability to adapt to ever-changing prey base availability and habitat and are vital to effectively address conservation needs of this endangered species (Biswas & Sankar, 2002; Bagchi *et al.*, 2003).

Direct observation of the tiger's feeding ecology, however, is greatly hindered by the cryptic, solitary and nocturnal nature of the predator. Dense habitats in which the species preferentially hunts further hamper the observation (Schaller, 1967; Sunquist & Sunquist, 1989). Although the use of radiotelemetry, for example, makes kill data collection at kill sites a relatively efficient method of determining the food habits of carnivores, the collected data are generally biased towards bigger prey, as smaller carcasses are usually consumed in their entirety, thus leaving no evidence behind (Schaller, 1967; Sunquist, 1981; Nunez *et al.*, 2000; Schwarz & Fischer, 2006). In addition, since scavengers quickly scatter remains and dense vegetation makes it difficult to locate the kill, radiotelemetry is not completely satisfactory when used alone (Sunquist, 1981; Schwarz & Fischer, 2006).

Instead, the diet of tigers can be determined by scat analysis for undigested prey hairs (Reynolds & Aebischer, 1991; Mukherjee *et al.*, 1994a, 1994b; Melville *et al.*, 2004; Gazzola *et al.*, 2005; Schwarz & Fischer, 2006; Bodendorfer *et al.*, 2006; van Dijk *et al.*, 2007). As the method is non-invasive and relatively time and cost efficient (Schaller, 1967; Sunquist, 1981; Mukherjee *et al.*, 1994b; Karanth & Sunquist, 1995; Gonzales-Esteban *et al.*, 2006), it is a widely used field technique for assessing the food habits of large carnivores, including tigers (Karanth & Sunquist, 1995; Støen & Wegge, 1996; Ramakrishnan *et al.*, 1999; Biswas & Sankar, 2002; Bagchi *et al.*, 2003; Bodendorfer *et al.*, 2006). Tiger scats are collected opportunistically in locations known to be frequented by tigers (Sunquist, 1981; Johnsingh, 1983; Schwarz & Fischer, 2006). Prey hairs removed from the scats are examined macroscopically and microscopically, with features, such as hair colour, width, cuticular scalation and medullar structure examined and compared to a reference library of prey hairs (Amerasinghe, 1983; Teerink, 1991; Karanth & Sunquist, 1995; Støen & Wegge, 1996; Bodendorfer *et al.*, 2006; De Marinis & Asprea, 2006). To obtain accurate quantification of the diet of tigers, advanced analytical methods is applied

to scat data (Ackerman *et al.*, 1984; Karanth & Sunquist, 1995). The computer programme Scatman developed by Hines & Link (1994) is used to determine tiger prey selection.

Prey selection by large felids is a result of complex interactions of various ecological parameters, which in case of the tiger can greatly differ across the predator's distributional range (Sunquist & Sunquist, 1989). Karanth & Sunquist (1995), for example, showed that in the absence of large prey tigers would remove non-selectively medium-sized prey. In contrast, Støen & Wegge (1996) demonstrated that when large prey were scarce, tigers showed significant selection among medium-sized prey. Biswas & Sankar (2002), on the other hand, provided data which suggested that tigers would select for medium-size prey regardless the existence of an ample supply of large prey in the area.

1.3 Aims and objectives

In view of the continuing decline of BNP tigers and their prey densities this study set out to:

1. Determine what species constitute the diet of Karnali tigers.
2. Establish what species Karnali tigers are presently selecting, by testing the null hypothesis that frequencies of prey species in a predator's diet are proportional to their availability.
3. Ascertain what proportion of the diet of Karnali tigers is composed of livestock.

2. BACKGROUND

Since the early 1970s tigers have been used as an umbrella species for wildlife conservation in South Asia. As a result, thousands of sq. km of natural habitat have been proclaimed as protected areas (Karanth, 2003). Although we lack baselines to adequately assess tigers' role in structuring the communities in which they occur (Seidensticker & McDougal, 1993), it is widely accepted that these predators play a relatively major role in shaping prey communities in the stable environment of tropical forests (Karanth & Sunquist, 1995). Field studies of prey selection by tigers, however, have been scarce (Schaller, 1967; Johnsingh, 1983; Rabinowitz & Nottingham, 1986). What is more, Karanth & Sunquist (1995) argue that even the existing studies' inferences on prey selection patterns are somewhat undermined by continually diminishing prey-predator assemblages, simultaneous poaching of prey species by humans and the use of crude methods of measuring prey selectivity. Still, a number of studies over the past 15 years (Karanth & Sunquist, 1995; Støen & Wegge, 1996; Nunez, Miller & Lindzey, 2000; Biswas & Sankar, 2002; Bagchi *et al.*, 2003; Bodendorfer *et al.*, 2006) have offered us some valuable insights into the complex phenomenon of prey selection by tigers (Bonnin, 2008).

2.1 Feeding ecology of tigers

Although over the last 100 years the tiger's range has been greatly reduced, tigers are still found in a diverse array of habitats of varying altitudes, temperatures and rainfall patterns (Sunquist *et al.*, 1999). Within the Indian subcontinent they inhabit tropical dry and moist deciduous forests, evergreen and mangrove forests, terai grasslands and mixed conifer-broadleaf forests in the Himalayan foothills. Tigers are also found in mangrove swamps of the Sunderbans, tropical rainforests of Sumatra and Malaysia and the coniferous-deciduous forests of eastern Russia. Tiger tracks have even been found in Himalayan winter snow at 3,000 metres (Prater, 1971). The fact that tigers are found in such a diversity of habitats and

climates indicates that habitat as such was not a critical element in the evolutionary history of this predator. Rather, it was the Pleistocene radiation of large-bodied cervids and bovids in South-east Asia, an episode which opened up an ecological niche for a large-bodied, forest-edge predator that prompted the divergence of the *tigris* line from the *Panthera* stock (Biswas & Sankar, 2002). It was then the need to kill large ungulate prey that has been the driving force behind the evolution of this solitary hunter (Sunquist *et al.*, 1999). In fact, tigers' distribution seems to be determined primarily by availability of large ungulates (Karanth, 2003) which tigers preferentially select for in all of the ecosystems across the predator's range (Biswas & Sankar, 2002; Karanth, 2003).

Prey selectivity can be defined as the killing of prey types in frequencies that are different from those expected, based on their availability in the environment (Chesson, 1978). Prey choice by large felids, which ultimately determines the food habits of these predators, plays a key part in determining their life history strategies, including movement, habitat selection, social structure, geographical distribution and reproductive success (Sunquist & Sunquist, 1989). Several hypotheses have been proposed to explain prey selection by predators (Taylor, 1976; Temple, 1987; Stephens & Krebs, 1987). The optimal foraging theory, for example, originally developed in an attempt to explain why, out of the wide range of foods available, animals often restrict themselves to a few preferred types (MacArthur & Pianka, 1966), predicts that predators should choose the most profitable prey, which in case of tigers would seem to be the largest prey they can safely kill (Sunquist & Sunquist, 1989; Støen, 1994). Although tigers kill prey ranging in size from amphibians to 1000-kg gaur (*Bos gaurus*), the bulk of their diet is obtained predominantly from deer species, which contribute up to 75% of the prey biomass requirement of the tiger in most parts of its range (Sunquist *et al.*, 1999; Sunquist, 1981; Støen & Wegge, 1996; Biswas & Sankar, 2002). Apart from livestock, the principal wild prey of tigers in India and Nepal include: chital (*Axis axis*), hog deer (*Axis porcinus*), barasingha (*Cervus duvauceli*), nilgai (*Bosephalus tragocamelus*), muntjac (*Muntiacus muntjac*) and wild boar (*Sus scrofa*) (Schaller, 1967). In addition, tigers will take Indian porcupine (*Hystrix indica*), langur (*Presbytis entellus*) and rhesus monkey (*Macaca mulatta*) (Schaller, 1967; Dinerstein, 1980; Sunquist, 1981).

The mean weight of species hunted by tigers ranges between 82 kg and 114 kg (Sunquist, 1981; Karanth & Sunquist, 1995; Bagchi *et al.*, 2003; Goyal & Sankar, 2003). Tigers also take larger prey such as sambar (*Cervus unicolor*) (212 kg) and domestic buffalo (*Bubalis bubalis*) (400 kg), clearly displaying a preference for large prey when they are available (Biswas & Sankar, 2002).

2.2 Is there enough for everyone?

A tigress requires 5-6 kg of meat a day, which amounts to 1825-2190 kg of meat a year. As 30% of each kill is inedible, a tigress in effect needs to kill some 2373-2847 kg a year of meat on the hoof. An adult male needs around 1,000 kg more meat a year. Hypothetically, the required amount of food could come from an ungulate of any size. A tigress could take one 20-kg muntjac every 2-3 days or one 200-kg sambar every few weeks (Sunquist *et al.*, 1999). Although tigers' plasticity in prey capture and killing behaviour allow them to hunt a wide range of prey types and sizes, as mentioned earlier, tigers preferentially prey on the largest available ungulates in most parts of their geographic range (Biswas & Sankar, 2002). Unfortunately, there are not many areas remaining where large ungulate populations remain intact. In Thailand, for example, four of the six species of deer that occurred there in recent times have already been lost. Cambodia has lost its great assemblages of gaur, banteng (*Bos javanicus birmanicus*), kouprey (*Bos sauveli*), water buffalo and sambar. Similarly, large body prey such as water buffalo and barasingha no longer occur in Chitwan National Park (CNP), Nepal (Sunquist *et al.*, 1999). Foraging theory models predict that if large prey is uncommon, other factors such as search time and encounter rates may increase to a point where selecting for the optimum-sized prey becomes too energetically costly and smaller and more abundant prey species may become more profitable (Stephens & Krebs, 1987). Sunquist *et al.* (1999) suggest that in many parts of the tiger's range, where large cervids and bovids are heavily poached, tigers may be approaching a situation the authors call 'muntjac-only scenario'. Sunquist *et al.* (1999) offer a hypothetical scenario, where the only prey available is a 20-kg muntjac. At this species' highest recorded density of 7

individuals per km², a 100 km² area of forest would contain 700 adult muntjac. Assuming that half of the population were females, and that each female produced one young per year, 350 young would be added to the population each year, ultimately amounting to 1050 new individuals. The hypothetical tigress killing muntjac at a rate of one every 2-3 days would remove 122-183 individuals per year from this population. This would remove 2440-3660 kg of meat on the hoof a year, which, minus the aforementioned 30% of inedible portion, yields 1708-2562 kg of meat a year. However, this figure covers only a maintenance diet of a tigress. A tigress feeding two large young needs approximately 50% more food. To meet this demand a tigress would need to kill one muntjac every 1-2 days, or 183-365 individuals a year. At this level of cropping, the authors suggest, there is no recruitment among the prey, and the muntjac population declines. Consequently, under the hypothetical ‘muntjac-only scenario’, which according to Sunquist *et al.* (1999) approximates the situation in many parts of true tropical rainforests, muntjac density would provide a maintenance diet for a relatively low-density of tigers of approximately 1 tiger per km². In comparison, data from a landscape-scale long term (1995-2003) field study estimate tiger densities in eleven ecologically diverse sites across India to range between 3.2 and 16.8 tigers per 100 km² (Karanth *et al.*, 2004). As the muntjac population continues to decline, Sunquist *et al.* (1999) conclude, an increasing number of tiger populations will come to exist at very low densities, with a depleted prey base supporting only occasional reproduction.

2.3 Studies of prey selection by tigers

Griffiths (1975) suggests that in habitats with a large range in size of prey, vertebrate predators are ‘energy maximisers’, preying selectively upon large species, but are non-selective ‘number maximisers’ in habitats where large prey are scarce. In concurrence with this hypothesis, Karanth & Sunquist (1995) provide scat analysis data from their study in Nagarahole National Park (NNP), India, where the resident tigers were shown to select for gaur and male sambar, the two largest available prey species, whereas chital, muntjac and

wild boar, the medium-sized prey, were underrepresented in the diet. Tigers' selectivity towards different species in NNP was thought to be related to a number of factors. Selectivity for gaur indicated a preference for large prey size that is strong enough to override the possible risk of injury during capture. Karanth & Sunquist (1995) suggest that the preference of gaur for open clearing in the forest, their crepuscularity (active before sunrise) and relatively poor eyesight make the species easier prey to locate and stalk. This would seem to suggest that anti-predator behaviour, rather than size, may be more effective defense against ambush predators (Karanth & Sunquist, 1995). The underrepresentation of chital and muntjac in the diet was thought to reflect avoidance of smaller prey or be the result of the diurnal activity patterns of these two species (Karanth & Sunquist, 1995). Similarly, tigers in CNP were shown to select for sambar, illustrating that when present, large prey will be selected for by these predators (Sunquist, 1981).

In contrast to the prediction of Griffiths (1975) and findings of Karanth & Sunquist (1995) and (Sunquist, 1981), Støen & Wegge (1996) demonstrated that when large prey were scarce, tigers in the Karnali floodplain of BNP showed significant selection for medium-sized prey. It was shown that when large prey such as nilgai and barasingha were in short supply, wild boar were preyed upon significantly more than expected, while muntjac were underrepresented in the diet. The fact that nilgai and barasingha were scarce and patchily distributed, making them energetically costly to search for, was thought to be the reason for non-selection of these optimum-sized prey species. In addition, the frequented by nilgai types of habitats, such as open jungle near human settlements, are generally avoided by tigers. Sambar, which are commonly taken by tigers in other areas, were also not preyed upon by Karnali tigers. This was thought to be due to scarcity of sambar and their confinement to the hill sides mainly outside the study area (Støen & Wegge, 1996). Støen & Wegge (1996) found that other medium-sized prey species such as chital were killed in accordance to their proportion in the study area. The difference in the selection among medium-sized prey was thought to be the result of differences in their vulnerability. In the dry season, during which the study of Støen & Wegge (1996) was undertaken, wild boar are mostly solitary or live in small groups, whereas chital live in relatively large groups and

gather together on cut and burned areas. Since remaining in large groups facilitates easier detection of predators, thus lessening the chance of an individual being taken, large congregations of chital were hypothesized to be the main reason why proportionately fewer chital were killed by tigers than expected (Støen & Wegge, 1996). Highly localized distribution of wild boar and distinct foraging areas, on the other hand, made the species more vulnerable to predation than chital (Støen & Wegge, 1996). Hog deer, also solitary or living in small groups, were not selected by Karnali tigers, however. It was suggested that the diurnal activity pattern of this medium-sized prey species made it less susceptible to tiger predation compared to the predominantly nocturnal wild boar (Støen & Wegge, 1996). A similar response of tigers to scarcity of optimum-sized prey has also been observed in other carnivore studies (Sunquist, 1981; Rabinowitz & Nottingham, 1986; Henschel *et al.*, 2005; Bodendorfer *et al.*, 2006).

Biswas & Sankar (2002), on the other hand, found that tigers in Pench National Park (PNP), India, selected for medium-size prey regardless an ample supply of large prey in the area. In fact, selective predation by tigers in PNP, an area with a large range in size of prey, was directed towards prey species with both medium and large body mass. PNP tigers killed sambar and wild boar more than their availability, with chital taken in proportion to their availability. Biswas & Sankar (2002) found that the predation rate on sambar in PNP was relatively lower when compared to studies undertaken in Bandipur Tiger Reserve (BTR), India, in 1983, NNP in 1995, CNP in 1977 and 1981 and in BNP in 1996. All these sites, however, indicated a correspondingly lower degree of predation on chital. The authors did not comment on the observed potential correspondence. They were also unable to offer an explanation on the reported low, yet selective predation of sambar by PNP tigers. With regards to wild boar, which were taken in excess of their availability, Biswas & Sankar (2002) referred to a study by Miquelle *et al.* (1991) undertaken in the Sikhote-Alin mountain area in Russia, which suggested that high overlap of habitat use between tigers and wild boar may facilitate a high level of tiger predation on this prey. Unfortunately, no information on habitat use of wild boar in the Indian subcontinent exists to see whether a

similar overlap in habitat use is influencing tiger predation on wild boar in the region (Biswas & Sankar, 2002).

Valuable comparison between sites with different prey availability located in the same park was made by Harsha *et al.* (2004). The researchers, who examined prey selection in two different areas within Nagarjunasagar Srisailam Tiger Reserve (NSTR), India, found that the mean mass of prey killed by tigers in one of the examined areas was 78.6 kg, while in the other it was only 43.9 kg. It was concluded that this spatial variation in the diet of NSTR tigers was attributable to different prey availability in respective areas (Harsha *et al.*, 2004).

A number of studies (Sunquist & Sunquist, 1988; Johnsingh, 1992; Karanth & Sunquist, 1995; Farrell *et al.*, 2000; Karanth *et al.*, 2004) have also increased our knowledge of the inter- and intra-guild competition and co-existence among sympatric carnivores such as tigers, leopards (*Panthera pardus*) and dholes (*Cuon alpinus*). As Asia's largest predator, the tiger is socially dominant over leopards and dholes (Sunquist & Sunquist, 1988; Farrell *et al.*, 2000; Karanth *et al.*, 2004). Although various studies (Sunquist & Sunquist, 1988; Johnsingh, 1992; Karanth & Sunquist, 1995; Farrell *et al.*, 2000; Karanth *et al.*, 2004) provide evidence of a substantial diet overlap among tigers, leopards and dholes, thus highlighting the potential for high intra-guild competition among them, they also suggest that when a wide range of prey size is available, these predators would preferentially hunt different prey. Tigers preferentially hunt large-sized prey while leopards and dholes preferably select for medium-sized prey species (Sunquist & Sunquist, 1988; Johnsingh, 1992; Karanth & Sunquist, 1995; Farrell *et al.*, 2000; Karanth *et al.*, 2004). Karanth & Sunquist (1995), for example, showed that in NNP, gaur and adult sambar, the largest available prey species, were the main prey of tigers, while leopards and dholes preferentially selected for chital. Although leopards avoided wild boar, which presumably resulted from the inability of this relatively light predator to tackle agile and aggressive prey of comparable weight, they preyed upon langur more than the other two carnivores, which was thought to be linked to the leopard's greater arboreality and crypticity. Dholes,

in turn, due to their hunting technique of chasing prey in packs, were least likely to capture langur. It was suggested that such prey partitioning facilitate coexistence of sympatric predators (Karanth & Sunquist, 1995). Similarly, a study in BTR showed that 42% of tigers' kills were comprised of prey weighing over 100 kg, whereas 69% of leopard kills weighed less than 50 kg (Johnsingh, 1992). As human activities are causing drastic reductions in ungulate abundance and distribution, however, studies such as those of Sunquist (1981) and Karanth & Sunquist (1995) suggest that the increasingly common switching to smaller prey by tigers, due to prey base depletion, can in fact lead to reduced densities of leopards and other sympatric carnivores through food competition, thus significantly reducing the diversity of predator communities.

Further challenges to conservation efforts may come from the inherent predisposition of tigers to cause substantial livestock depredation if natural prey species are depleted (Sunquist, 1981; Tamang, 2000; Bagchi *et al.*, 2003). Increasing livestock densities within protected areas are also believed to increase the chances of domestic animals being preyed upon (Sekhar, 1998). Sekhar (1998) informs that domestic livestock, whose population in Sariska Tiger Reserve, India, increased by 45% from 1977 to 1992, have become a part of the regular food source for large carnivores. Furthermore, in contrast to the speculations of Dinerstein (1979) that tigers will not take livestock if wild ungulate prey is abundant, Bagchi *et al.* (2003) found that in Rathambore National Park (RNP), India, livestock accounted for 10 to 12% of tigers' diet despite the park's high wild prey densities. This was most likely a direct result of extensive livestock grazing in the park as reported by Bagchi *et al.* (2003). This shows that when livestock are available, tigers will readily prey on them (Sunquist 1981). To similar conclusions came Biswas & Sankar (2002), who observed that although livestock were not grazed in PNP, they accounted for 8.2% of all prey consumed by the park's tigers. It was thought that the tigers killed domestic animals in the areas outside the boundaries of the park, which were subjected to a high level of grazing (Biswas & Sankar, 2002).

Although humans are the most available food source across the tiger's range, they are not taken in numbers proportionate to their availability and apparent vulnerability (Schaller, 1967; Seidensticker & McDougal, 1993). Still, man-eating tigers are a serious problem especially that tiger attacks on people have increased dramatically over the years across much of the tiger's range (Gurung *et al.*, 2006). In Nepal, for example, where, to address the issue of tiger habitat loss and fragmentation, the government has initiated an ambitious Terai Arc Landscape project aiming at increasing land base for tigers and restoring connectivity between protected areas, the marked increase in habitat use by these predators in multiple-use buffer zone community forests has unfortunately resulted in dramatic increase in conflict between humans and tigers (Gurung *et al.*, 2006). The number of humans killed by tigers in the vicinity of CNP, for instance, has increased from an average of 1.5 persons per year (1979-1998) to 8.25 per year since 1999. The increasing trend of people killed was significant in the buffer zone of the park. A total of 37 tigers were thought to be responsible for killing 88 people, of which 17 were removed because of their man-eating habits. The number of problem tigers removed per year in the area has been increasing over the years. Although the fact that tigers are using the buffer zones of CNP and dispersing beyond into the national forests is good news for conservation of this endangered species, the increasing number of human deaths due to man-eating predators can certainly erode local communities' support for tiger conservation (Gurung *et al.*, 2006).

2.4 Study area and species

The study was conducted in the south-western part of the 968 km² BNP (28°30'N, 81°15'E), the largest protected area in the Terai zone of lowland Nepal (Støen & Wegge, 1996). The 91.7 km² large study area, the Karnali floodplain, is bounded in the west by the Geruwa river, in the north by the East West Highway between Amreni and Chisapani and in the east and south by cultivation along Orai river (Støen, 1994) (Fig. 2). The Karnali floodplain is surrounded by cultivated land and villages on all sides except for the north

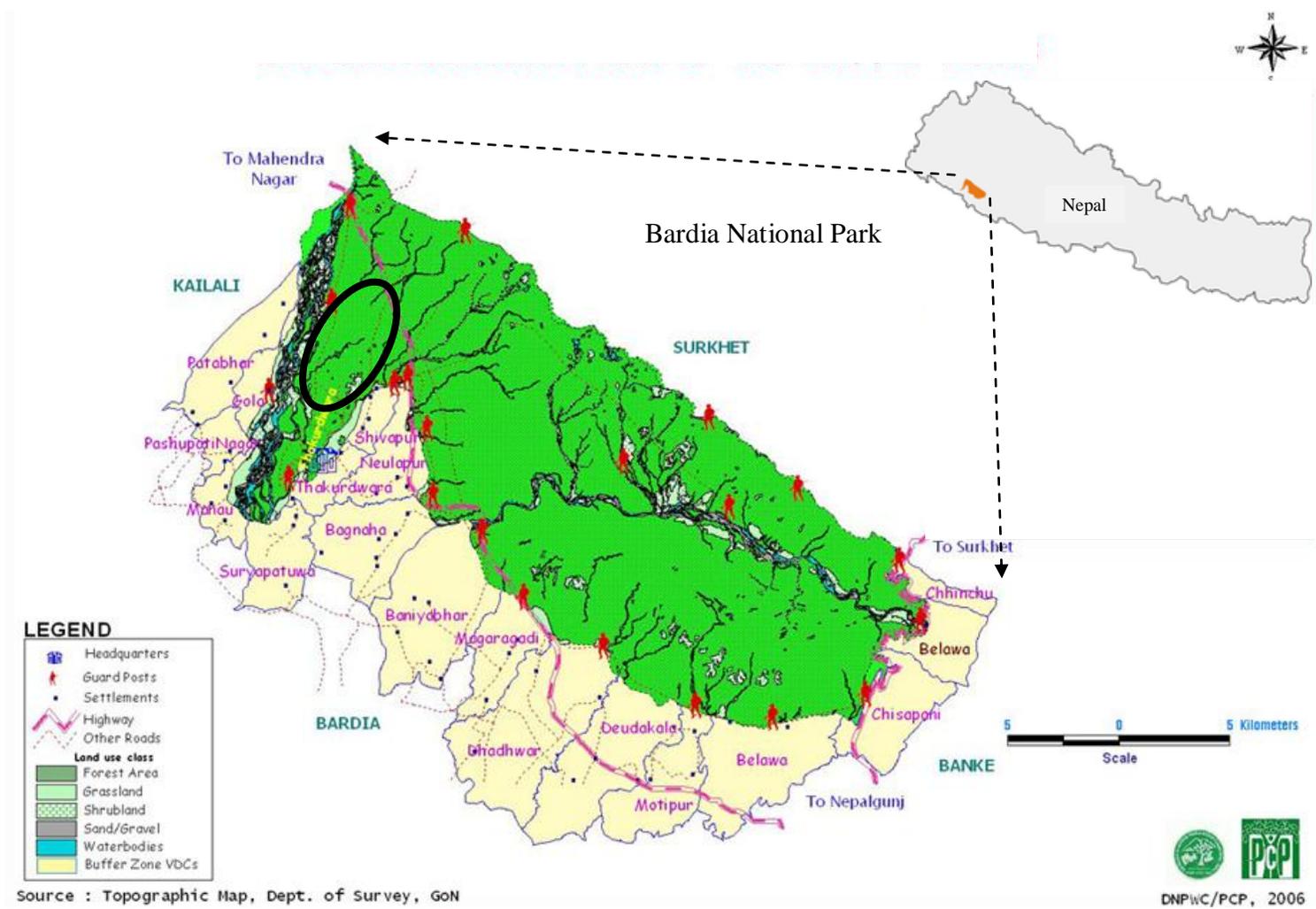
where sal (*Shorea robusta*) forest, which covers approximately 70% of the whole park area, extends into the Siwalik mountain range (Støen, 1994).

BNP has a subtropical monsoonal climate with annual rains falling mainly between June and September. The rainy season is followed by a relatively cool dry season from mid October to mid February and a hot period from mid February to June. Temperatures in the park range between 10° C in January and 41° C in May (Tamang, 2000).

The vegetation of the park is sub-tropical, with the western part of the study area consisting of a mosaic of grassy islands with diverse floodplain communities in early succession stages. The eastern part of the study area is dominated by the sal forest with small pockets of grassland locally known as phantas, which originated from previously cultivated lands that had to be abandoned after the area was established as a royal hunting reserve in 1846. A total of six different habitat types make up the Karnali floodplain: sal forest (66%); khair sissoo forest (11%), wooded grasslands (7%), floodplain grasslands (6%), riverine forest (5%) and phantas (< 1%) (Jnawali & Wegge, 1993).

Such combination of different habitats combined with the abundant water supply from the Karnali river provides first-rate conditions for a rich and diverse fauna. BNP is home to 53 mammal species, 400 avifauna, 25 species of reptiles and amphibians and 121 fish species (RBNP report, 2005; Upadhyay, 2005). The dominant carnivores are tigers, but leopards, sloth bears (*Melursus ursinus*) and jackals (*Canis aureus*) are also present, with transient dholes visiting the area periodically (Støen & Wegge, 1996). Potential prey of Karnali tigers include chital, hog deer, wild boar, sambar, barasingha, muntjac, nilgai, Indian porcupine, langur and rhesus monkey (Schaller, 1967; Dinerstein, 1980; Sunquist, 1981).

Figure 2. Map of Bardia National Park, Nepal, and its buffer zone (the 91.7 km² study area encircled in black).



3. METHODS

3.1 Reconstruction of the diet of tigers by scat analysis

The diet of Karnali tigers was determined by scat analysis.

3.1.1 Collection and treatment of scats

Tiger scats were collected by BNP rangers for a period of four months during the dry season between February and May 2009. The scats were collected opportunistically along forest roads and trails, or on grass immediately bordering them, in locations known to be frequented by tigers. Tiger scats were distinguished from those of leopards based on their size (scats of tigers are larger), appearance (tigers scats have a lower degree of coiling) and other supplementary evidence in the form of associated pugmarks and scraps. The fact that tigers deposit their scats at relatively larger distances between two successive constrictions within a single piece of scat was also used to distinguish between scats of these two felid species (Biswas & Sankar, 2002). Faecal DNA tests confirmed the accuracy of these field classifications (Andheira *et al.*, 2007). Scats not clearly identifiable in the field were disregarded. Each collected scat was air dried, then stored in paper envelopes and individually labeled, with collection date and location, including latitude and longitude obtained from Global Positioning System, recorded.

3.1.2 Reference hair library

As the existing and belonging to National Trust for Nature Conservation (NTNC), Nepal, reference library of hairs of the mammals preyed upon by tigers was found to be partly damaged, with some slides no longer useful, a new set of reference slides was prepared by the author using hairs from known species obtained from Zoological Society of London, UK (see Fig. 3 for examples of such reference slides). For good quality permanent slides, the hairs were washed in tepid water containing detergent, rinsed in distilled water followed by a bath in absolute alcohol. A fine-meshed sieve (1-3 mm) was used to transport the hairs from one bath to another. Thus treated hairs were used to prepare cuticular and medullar slides, which ultimately formed a part of NTNC reference hair library. The slides were prepared following the methodology of Teerink (1991) and De Marinis & Asprea (2006).

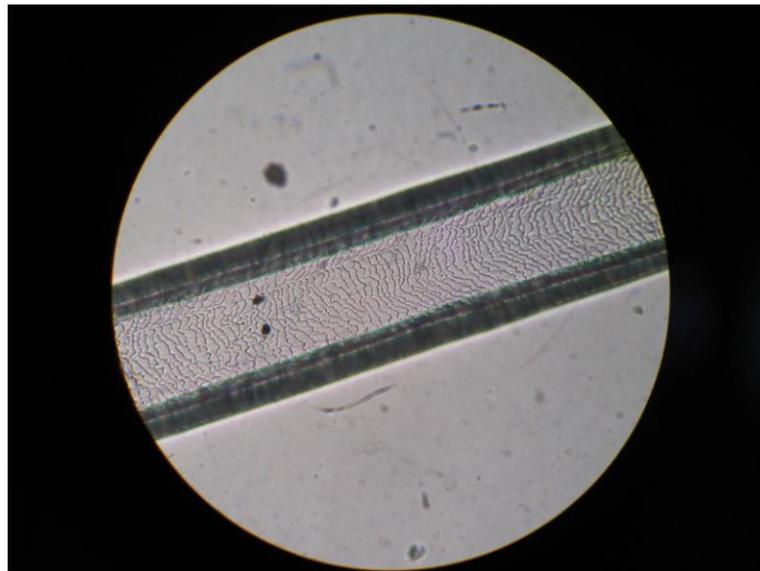
Figure 3. Some of the reference slides (prepared by the author), which now comprise part of NTNC reference library of hairs of BNP mammals potentially preyed upon by tigers.



3.1.3 Cuticular slides

As the scale pattern of the hairs' cuticula can not be properly observed without the use of special techniques, cuticular slides were prepared by creating casts of the hairs in gelatin (see Fig. 4 for an example of a cuticular slide). This method allowed for the shape of the hairs' cuticular scales to be transferred to the medium, where it could be observed with a microscope. To make such slides, a gelatine stock was prepared by dissolving granular gelatine in cold, distilled water until saturated followed by gently heating the solution over a kitchen stove flame. A few crystals of phenol were added to the solution as preservative. A thin layer of thus prepared warm gelatine was applied onto a slide and smoothed over using a thin brush. Gelatine was allowed to cool for about five minutes after which the hairs were placed on the gel side by side, with two to four hairs of the same species per slide depending on the size of the individual hairs. At times some pressure had to be applied with tweezers to allow the hairs to properly adhere to the solution. The gel was allowed to set for approximately one hour after which a pair of tweezers was used to carefully remove the hairs. Each removed from the gel hair was then again rinsed in detergent, distilled water and absolute alcohol before being used in the preparation of medullar slides.

Figure 4. Microphotograph (taken by the author) of a cuticular slide showing cuticular scale pattern in the tip region of a chital hair (400x).



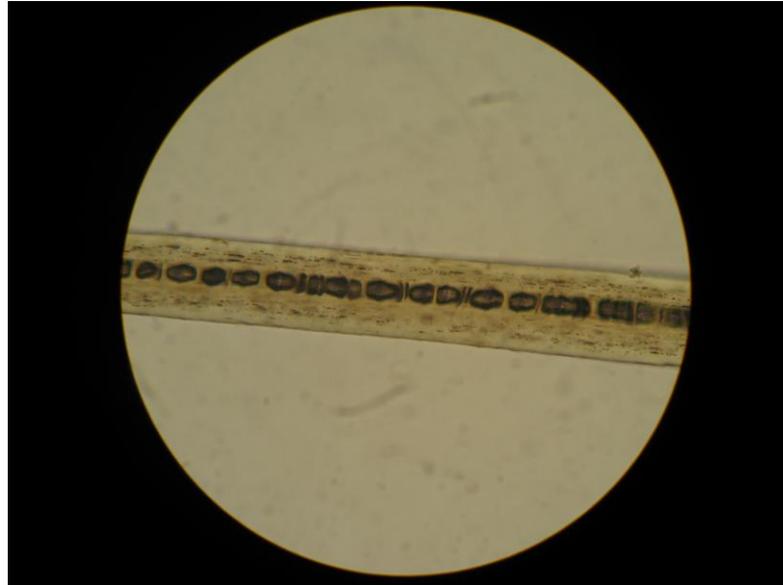
3.1.4 Medullar slides

Each hair was fixed in place with small drops of white book binder's glue (polyvinyl chloride acetate) at a number of points along the hair. After the glue was hardened, the hair was cut between the glue drops with a razor blade. It was important to include a cut at the widest part of the hair. Three to four hairs of the same species were mounted on each slide. Next, small drops of Canada balsam were applied onto the hairs and the slides were covered by a cover slip. The slides was then left for thirty minutes for the oil to completely or partially replace the air in the intercellular chambers of medulla, which greatly improved observation of the structure and position of the cells (see Fig. 5 to observe the effect of a Canada balsam application and Fig. 6 for an example of a medullar slide).

Figure 5. Microphotograph (taken by the author) of a medullar slide showing the result of a Canada balsam penetration, with the effect of the oil replacing the air in the intercellular chambers (dark medulla becomes transparent) clearly noticeable in the region of the cut (100x).



Figure 6. Microphotograph (taken by the author) of a medullar slide showing the tip region of a rhesus hair (400x).

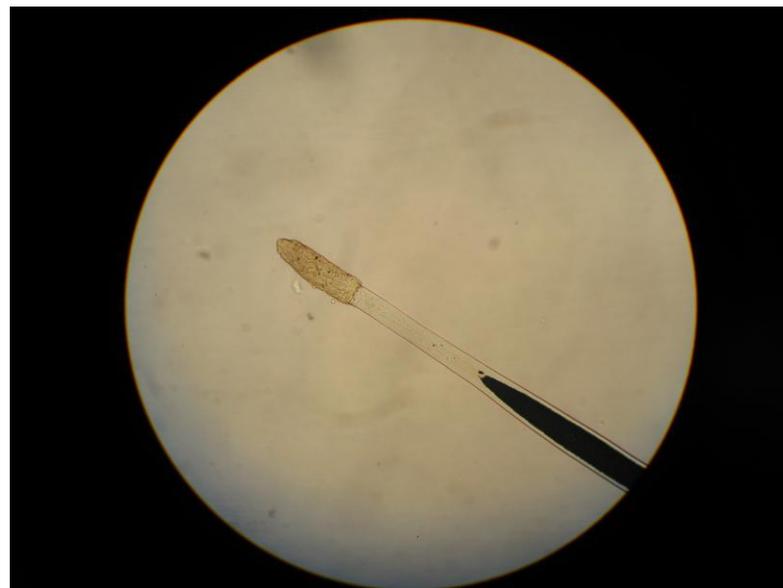


3.1.5 Scat analysis

With NTNC reference hair library augmented with new reference slides, analysis of the collected scats was then carried out. Each scat was placed in a plastic container filled with warm water containing detergent. Each, well soaked scat was then carefully washed through a fine-meshed sieve to separate hairs from other organic matter. Each scat sample was washed separately. Remains such as bones, hooves and teeth were separated from the scats too. Those were stored in ziplock bags and labelled accordingly. The separated from the scats hairs were washed in the same manner as for the reference hairs. Thus cleaned and dried hairs were stored in ziplock bags. All the time great care was taken to avoid cross-contamination of samples. This was achieved by thoroughly rinsing all equipment between each sample.

Next, following Mukherjee *et al.* (1994a), twenty prey hairs were randomly sampled from each scat. Cuticular and medullar slides were prepared in the same manner as for the reference hair library, with paraffin oil used instead of Canada balsam to prepare medullar slides. Paraffin oil serves the same function as Canada balsam, but instead produces non-permanent slides (Teerink, 1991). Medullar and cuticular slides were prepared for eight hairs per sample, with the remaining twelve hairs used to prepare hair profile slides. For this, each hair was placed on a glass slide without the use of any mounting medium and covered by a cover slip. This way the hairs were examined under a microscope with root structure, colour and pigment recorded (see Fig. 7 for an example of a microphotograph showing a root of a hair). If hair profile analysis revealed a different hair type to the other eight analysed in that sample, medullar and cuticular slides were prepared for further identification.

Figure 7. Microphotograph (taken by the author) showing the root region of a chital hair (100x).



All prepared cuticular and medullar slides were examined microscopically under 400 x magnification. Cuticular patterns of the hairs left in the gel were compared to those of the reference hairs included in NTNC reference hair library, with identification supported by a hair reference table obtained from Bonnin (2008) (Table 1).

Table 1. Reference hair library table for tigers, their main prey and domestic livestock in BNP. Leopard hairs (only rarely eaten by tigers) were also referenced as a differential for tiger hairs (Bonnin, 2008).

Species	Hair width (mean, range)	Medullar % width (mean, range)	Colour Pigment	Cuticular scale position	Cuticular scale pattern	Cuticular margin	Cuticular scale distance	Medullar structure	Medullar pattern	Medullar margin
Chital	86.6µm (87.5- 95µm)	80.9% (71- 92%)	R/Bn.; Bn.; W Streaky	Transversa 1	Irreg. wave (sd) Reg. wave (st)	Rippled (sd) Smooth (st)	Near	Cloisonné	C	Scalloped
Hog deer	146µm (100-237µm)	79.7% (66-95%)	O/Bn.; O; Bn. Streaky, granular	Transversa 1	Irreg. wave (sd) Reg. Wave (st)	Rippled(sd) Smooth (st)	V. near (sd) Near (st)	Cloisonné	C	Scalloped
Muntjac	128µm (120-135µm)	91% (90-92%)	G/Bn.; Bn.; O; W Grainy	Transversa 1	Reg./irreg. wave (sd) Reg. wave (st)	Smooth/rippled (sd) V. smooth (st)	Near	Cloisonné	C	Scalloped
Sambar	115µm (90-138µm)	36.4% (14-53%)	Dk. R/Bn.; G/Bn. Streaky, ovoid bodies	Transversa 1	Reg. wave	Rippled (sd) Smooth (st)	V. near (sd) Near (st)	Cloisonné	C (sd) F (st)	Irregular
Barasingha	90.4µm (60-135µm)	46% (33-63%)	O/Bn.; R/Bn.; W Streaky (light)	Transversa 1	Reg/irreg. wave (sd) Reg. wave (st)	Rippled (sd) Smooth/rippled (st)	V. near (sd) Near (st)	Cloisonné	C	Scalloped
Nilgai	70µm (68-73µm)	75.3% (66-85%)	G/Bn.; R/Bn.; Cr. Streaky	Transversa 1	Irreg. wave (sd) Reg. wave (st)	Smooth/rippled (sd) Smooth (st)	Near	Amorphous	C	Straight to fringed
Wild boar	221µm (180-258µm)	Not clear	Bk.; dk. R/Bn. Streaky, ovoid bodies	Transversa 1	Irreg. wave (sd) Irreg. wave (st)	Rippled	Near (sd) V. near (st)	Amorphous	C/F	Irregular
Indian Porcupine	557.5µm (370-640µm)	41.5% (32-51%)	Dk. Bn./Bk. Grainy	Transversa 1	Reg. wave (sd) Irreg. wave (st)	Rippled	V. near (sd) Near (st)	Multicellular	C	Straight
Rhesus	68.5µm (53-85µm)	17.7% (12-29%)	Gr.; O/Bn. Small brown granules	Transversa 1	Reg. wave	Rippled	V.near (sd) Near (st)	Unicellular, regular	F	Irregular
Langur	66.8µm (47-100µm)	25% (22-32%)	S; Bk. Streaky/absent	Transversa 1	Reg/irreg wave	Rippled	Near	Amorphous	F	Irregular
Cattle	63.8µm (55-70µm)	80% (77-83%)	Bk.; Bn.; W Streaky, ovoid bodies	Transversa 1	Irreg. wave	Smooth/rippled (sd) Smooth (st)	Near	Amorphous	C	Irregular
Buffalo	106.25µm (90-123µm)	41.3% (32-51%)	Bk.; Bn.; R/Bn.; Gr. Streaky, ovoid bodies	Transversa 1	Irreg. wave	Rippled	Near	Amorphous	C/F	Irregular
Sheep	66.25µm (37.5-85µm)	77.3% (66-82%)	W Granular	Transversa 1	Irreg. wave	Smooth	Near to distant	Multicellular	C	Scalloped
Goat	108.8µm (73-130µm)	90% (83-96.1%)	Bk; Bn; W Clear/streaky	Transversa 1	Irreg. wave	Rippled	Near	Multicellular /cloisonné	C	Scalloped
Tiger	91.3µm (80-105µm)	69% (64-73%)	O/Bn.; Dk. Bn.; W Streaky	Transversa 1	Reg. wave	Rippled (sd) Smooth (st)	Near	Amorphous	C	Irregular
Leopard	67.5µm (55-78µm)	53% (50-57%)	Dk. Bn.; W Clear/streaky	Transversa 1	Reg. wave	Rippled (sd) Smooth (st)	Near (sd) Distant (st)	Amorphous	F	Fringed

Bk. = black; Bn. = brown; O = orange; R = red; G = gold; W = white; Cr. = cream; S = silver; Gr. = grey
(sd) = shield / tip region; (st) = shaft / root region; C = continuous; F = fragmental

Identification of the hairs using medullar slides was based on the general appearance and medullary configuration of the hairs, with the help from both NTNC reference hair library and the hair reference table obtained from Bonnin (2008) (Table 1). Hair width and medullar width (expressed as a percentage of total hair) were measured using a calibrated eyepiece graticule. A 21 mm eyepiece micrometer (graticule) was calibrated in the Olympus CH-2 microscope used in this study. The eyepiece micrometer calibration was carried out using a stage micrometer under 400 x magnification (x40 objective and x10 eyepiece). It was determined that 24.5 stage micrometer divisions of 0.01 mm (=2.45 mm) were equivalent to 100 eyepiece divisions. Based on the following calculation: $0.245 \div 100 = 0.00245 = 2.45 \mu\text{m}$, each eyepiece division was multiplied by 2.45 to obtain measurements in micrometers (μm). For example, at 400 x magnification, a hair with a width of 34 eyepiece divisions measured $34 \times 2.45 = 83.3 \mu\text{m}$ (Thienpont *et al.*, 1979). As the hairs of wild boar were easily distinguished from all other prey by their coarse and thick appearance, with hairs always split at the top, their microscopic identification was not necessary.

3.2 Occurrence of prey, relative biomass and relative number of prey consumed

To quantify the diet of tigers, frequency of occurrence (percentage of total scats in which an item was found) and percent occurrence (number of times a specific item was found as a percentage of all items found) were calculated. If two prey items were found in a scat, each scat was counted as 0.5 prior to calculating frequency of occurrence (Karanth & Sunquist 1995; Biswas & Sankar, 2002).

As high variability in body sizes of tiger prey species inevitably leads to an overestimation of smaller prey in the diet (smaller prey species have more hair per unit body weight than larger prey and thus produce relatively more scats per unit prey weight consumed), the calculated frequency of occurrence did not adequately represent the proportion of different prey species consumed (Karanth & Sunquist, 1995). To overcome this problem, a

regression equation developed by Ackerman *et al.* (1984) was used to relate the average live weight of a prey animal consumed (X) to the weight of that prey represented in one field collectable scat (Y):

$$Y = 1.980 + 0.035X$$

Although originally developed for cougars (*Felis concolor*), the above equation was successfully adopted for dietary studies of tigers following the assumption of Karanth & Sunquist (1995) that the digestive system of tigers is comparable to that of cougars. Mean live weights of different prey species were obtained from Karanth & Sunquist (1995), Dinerstein (1980), Schaller (1967), Bonnin (2008) and Subedi (2009). From the above equation, scat production ($\lambda_i = X_i/Y_i$, the average number of collectable scats produced by a given predator from an individual animal of each prey species i), relative biomass and numbers of each prey killed were calculated.

3.3 Prey selection

Prey selectivity by tigers was estimated by comparing the observed number of scats associated with each species to the expected numbers of scats associated with that species in the environment using multinomial likelihood tests (Link & Karanth, 1994; Karanth & Sunquist, 1995). The expected proportion of scats containing a particular species i based on the null hypothesis of random, non-selective predation is calculated as:

$$\pi_i = d_i \lambda_i / \sum_i d_i \lambda_i$$

where prey species i has a population density of d_i , and λ_i is the average number of field collectable scats produced by the tiger from a single species i ($\lambda_i = X_i/Y_i$) (Hines & Link, 1994; Bagchi *et al.*, 2003).

Next, to arrive at the expected proportions of prey species in the scats, the computer programme Scatman developed by Hines & Link (1994) was used. It was suggested that variability in both the density estimates of each prey species (d_i) and the number of scats produced from a single species (λ_i) may increase the likelihood of the Type 1 error (observing a difference when in truth there is none) (Link & Karanth, 1994). To alleviate this problem, thus providing more reliable P values, parametric bootstrapping implemented in Scatman was used as suggested by Link & Karanth (1994). Two hundred bootstrap replications were consequently performed, with the coefficient of variation in scat production rates set at 40% of the mean level. Each prey item was given equal weighting (i.e. if two prey items were found in a scat, each scat was counted as 0.5) for scat frequency values (Karanth & Sunquist 1995; Biswas & Sankar, 2002).

Domestic livestock were not included in prey selection calculations as no density data were available for livestock in BNP. Density estimates for the seven remaining wild prey species identified in the collected scats were obtained from Støen (1994) and Subedi (2009). Because the recently collected density data for ungulates in BNP have not yet been analysed, prey density estimates for this study were obtained from Støen (1994). These were reduced by 30% following a dramatic decrease in prey densities over the past decade (Subedi, 2009). Consequently, standard errors (SE) were set at a conservative 50% of the estimated densities. Selectivity was considered significant at P values less than 0.05.

4. RESULTS

4.1 Species composition of the tiger diet

A total of 67 scats were collected. Although tiger scats composed entirely of grass or soil were found in previous studies (Bonnin, 2008) and are suggested to be a relatively common occurrence (Schaller, 1967; Sunquist, 1981), all scats in this study, in spite of some containing varying amounts of soil and/or grass, contained prey items. All prey items found in the scats could be readily identified, the results of which, including percentage occurrence, frequency of occurrence, relative biomass killed and estimates of relative number of individuals consumed by tigers, are presented in Table 2. A total of eight species were identified in the 67 scats analysed. Tiger hairs were found in four of the samples. As the numbers of individual tiger hairs within these scats were negligible in comparison with other species present, however, the hairs were assumed to be grooming hairs and were excluded from further analysis. Remains of bones and hooves were found in seven scats (10.44% of the total scats collected).

The 67 scats analysed contained 78 prey items. Eleven scats (16%) contained two prey items, while the remaining 56 scats (84%) contained one item. No scats contained more than two prey items. The estimated relative number of different prey species killed showed that although tigers consumed a wide variety of prey, two species (chital and hog deer) constituted the bulk (78.75%) of the tiger diet, with the remaining wild species and domestic livestock contributing 15.46% and 5.80% of all prey killed respectively (Table 2). Overall, wild prey constituted 96.44% of the total biomass consumed by tigers, while domestic livestock contributed 3.56%. The average weight of all the prey species consumed by Karnali tigers was 50.73 kg. No remains of other potential tiger prey such as nilgai, porcupine, langur and buffalo were found in the samples.

Table 2. Prey species composition in tiger scats ($n = 67$) and their percentage occurrence, frequency of occurrence and calculation of relative biomass and relative number of prey individuals killed by tigers, based on the scats collected in the Karnali floodplain of BNP, during the dry season between February and May 2009.

Prey	No. of Prey Items	Percentage Occurrence (%)	(A) Frequency of Occurrence (%)	(B) Estimated Weight X (kg)	(C) Correction Factor Y (kg of prey/scat)	(D) Relative Biomass Killed (%)	(E) Relative No. Inds. Killed (%)
Chital	46.00	58.98	61.94	55.00	3.90	63.40	55.56
Hog deer	15.00	19.24	21.64	40.00	3.38	19.20	23.19
Wild boar	6.00	7.69	5.97	38.00	3.31	5.19	6.76
Sambar	1.00	1.28	1.49	212.00	9.40	3.68	0.97
Barasingha	1.00	1.28	1.49	159.00	7.55	2.95	0.97
Muntjac	2.00	2.56	2.24	20.00	2.68	1.58	3.86
Rhesus	1.00	1.28	0.75	8.00	2.26	0.44	2.90
Sheep	6.00	7.69	4.48	30.00	3.03	3.56	5.80
Total	78.00	100.00	100.00			100.00	100.00

$$D = (A \times C) / \Sigma (A \times C); E = (D / B) / \Sigma (D / B)$$

4.2 Prey selection

Results of prey selectivity in this study relate only to wild species, which comprise 96.44% of the total biomass killed by tigers. Sambar ($P = 0.001$), barasingha ($P = 0.0089$), chital ($P = 0.0193$) and wild boar ($P = 0.0003$) were preyed upon significantly more than expected from their availability, indicating positive selection. Muntjac ($P = 0.0049$) were preyed upon significantly less than their availability, indicating negative selection. Hog deer and rhesus were preyed upon less than their availability, however, this was not considered as significant ($P = 0.1775$ and $P = 0.8441$ respectively).

Table 3. The observed number of scats associated with each species (scat frequency), the average number of collectable scats produced by a given predator from an individual animal of each prey species (scat production) and estimates of prey densities with associated standard errors (SE) for each prey species. This data was used in the computer programme Scatman to estimate prey selectivity by Karnali tigers.

Prey	Scat Frequency	Scat Production ($\lambda_i = X/Y$)	Density (individuals/km ²)	SE Density (individuals/km ²)
Chital	41.50	14.10	86.41	43.21
Hog deer	14.50	11.83	73.30	36.65
Sambar	1.00	22.55	0.10	0.05
Barasingha	1.00	21.06	0.22	0.11
Muntjac	1.50	7.46	62.08	31.04
Wild boar	4.00	11.48	2.80	1.40
Rhesus	0.50	3.54	7.50	3.75

$$D = (A \times C) / \Sigma (A \times C); E = (D \square B) / \Sigma (D \square B) \text{ (Støen \& Wegge, 1996).}$$

Table 4. Results of testing for prey selectivity from scat data in Table 3. Bootstrap replications were set at 200 and the variability in scat production rates was set at 40% of the mean level.

Prey	Observed scat frequency	Expected scat frequency	Chi squared	Unadjusted P-value	Adjusted P-value	(SE)
Chital	41.50	30.08	8.11	0.004	0.0193	0.0015
Hog deer	15.05	21.41	2.83	0.093	0.1775	0.0070
Sambar	1.00	0.06	16.03	<0.001	0.001	<0.001
Barasingha	1.00	0.11	6.87	0.009	0.0089	<0.001
Muntjac	1.50	11.44	10.49	0.001	0.0049	0.0006
Wild boar	4.00	0.79	13.11	<0.001	0.0003	<0.001
Rhesus	0.50	0.66	0.04	0.847	0.8441	0.0042

5. DISCUSSION

5.1 Composition of the tiger diet and prey selection

It has been suggested that a minimum of 60 tiger scats should be analysed to understand the pattern of prey use by tigers (Biswas, 2002). The 67 scats collected in this study satisfy this recommendation thus allowing valid conclusions. For the purpose of this study, prey species were classified into small (<20 kg), medium (20-50 kg) and large (>50 kg), based on their body mass (Karanth & Sunquist, 1995).

The diet of Karnali tigers was quantified by calculating frequency of occurrence (percentage of total scats in which an item was found) and percent occurrence (number of times a specific item was found as a percentage of all items found) (Ackerman *et al.*, 1984; Karanth & Sunquist 1995; Biswas & Sankar, 2002). Generally, percent occurrence is considered a more appropriate method of quantifying the diet of carnivores than frequency of occurrence as it accounts for more than one of a given item being found in a scat (Ackerman *et al.*, 1984). Since the majority of the scats in this study had either a single (84%) or just two prey (16%) species, however, both approaches gave similar results (Table 2). Biswas & Sankar (2002) inform that multiple prey items are rare in scats of large predators, such as tigers, but are relatively common in smaller carnivores such as the canids (Reynolds & Aebischer, 1991; van Dijk *et al.*, 2007).

As reported by a number of studies (McDougal, 1977; Sunquist, 1981; Johnsingh, 1983; Karanth & Sunquist, 1995; Stoen & Wegge, 1996; Karanth & Sunquist, 1999; Biswas & Sankar, 2002) the cervids (chital, hog deer, sambar, barasingha and muntjac) formed the bulk (84.55% of all individual prey species killed) of the Karnali tigers' diet.

In contrast to suggestions that tigers would be non-selective 'number maximisers' in areas with low densities of larger prey (Griffiths, 1975; Sunquist, 1981; Karanth & Sunquist,

1995) and in agreement with studies by Støen & Wegge (1996) and Biswas & Sankar (2002), Karnali tigers showed significant selection for medium-sized prey, with the predators significantly selecting for chital and wild boar, but avoiding muntjac. Selective predation by Karnali tigers was also significantly directed towards large-sized prey, with sambar and barasingha taken significantly more than their availability. Consequently, comparison of the observed and expected proportions of prey species in the Karnali tiger scats rejected the hypothesis of non-selective predation. Hog deer and rhesus were preyed upon less than their availability, however, this was not considered as significant.

The found differences in the selection amongst various prey species, apart from prey availability, were probably due to differences in their vulnerability, which apparently strongly influences prey selection by large felids (Sunquist & Sunquist, 1989). According to Taylor's (1976) model of predation, which predicts that aggregation of prey constrains the predator, gregarious nature of chital makes the species less vulnerable to predation than other solitary prey (Schaller, 1967; Sunquist & Sunquist, 1989). Chital habitually associate in aggregations of 20 to 100 individuals on forest edges and grasslands and are considered to be the most gregarious among wild ungulates (Dinerstein, 1980; Schaller, 1967; Sunquist & Sunquist, 1988). Karnali tigers preyed upon chital ($P = 0.0193$) significantly more than expected from their availability, however, indicating positive selection. Cases of tigers positively selecting for chital were also shown in earlier studies (Karanth & Sunquist, 1995; Bagchi *et al.*, 2003). It is hypothesised that relatively high density of chital in an area may increase their encounter rate with the tiger, ultimately increasing the chance of predation (Karanth & Sunquist, 1995). In agreement with this, chital have the highest density (43.21 individuals per km²) of all principal prey in BNP. But, chital have also been shown to be taken in proportion to their availability (Biswas & Sankar, 2002) as well as less than their availability (Støen & Wegge, 1996) despite their relatively high densities. This suggests that other factors may also determine prey selection by tigers and that these may vary under different environmental conditions (Sunquist, 1981).

Wild boar ($P = 0.0003$) were another medium-sized species significantly selected for by Karnali tigers. Wild boar are common prey of tigers in India and Nepal and have been shown to be significantly selected for by the predator (Støen & Wegge, 1996; Biswas & Sankar, 2002). Unlike chital, wild boar are mostly solitary or live in small groups making them more vulnerable to predation than gregarious species (Støen & Wegge, 1996).

Sambar ($P = 0.001$) and barasingha ($P = 0.0089$) were the two large-sized prey species which were consumed by Karnali tigers in excess of their availability. It is worth mentioning, however, that out of the 78 prey items found in the 67 scats examined in this study only one item was that of sambar and one of barasingha. It would seem that the extremely low densities of both prey species (0.05 individuals per km² for sambar and 0.11 individuals per km² for barasingha) resulted in multinomial likelihood tests calculating their selection by Karnali tigers as significantly positive. Nevertheless, regardless rather usual low densities and patchy distribution of sambar and barasingha in recent times, tigers do regularly take these two species clearly displaying a preference for large prey when they are available (Biswas & Sankar, 2002; Bagchi *et al.*, 2003). Furthermore, nocturnal habits and solitary nature of sambar (Johnsingh, 1992) make the species additionally vulnerable to predation by tigers (Sunquist, 1981).

Muntjac ($P = 0.0049$) were preyed upon significantly less than their availability, indicating negative selection. A number of earlier studies have shown that muntjac do not form a significant part of the diet of tigers (Schaller, 1967; Sunquist, 1981; Sunquist & Sunquist, 1988). It is thought that the animal's small size (20 kg) and diurnal nature play an important part in the negative selection of this prey species (Karanth & Sunquist, 1995).

Hog deer ($P = 0.1775$), although the second most abundant prey in BNP (36.65 individuals per km²), were preyed upon less than their availability, however, this was not considered as significant. Although normally solitary, or occurring in groups containing two or three individuals (Schaller, 1967), during the dry season hog deer associate in small herds to feed on growing new shoots following the annual cutting and burning of grasslands (Sunquist &

Sunquist, 1988). These recurring gregarious habits may explain why fewer hog deer were taken between February and May 2009 (dry season) than were available.

Rhesus have not been reported to date to be selected for by tigers, and this study found that rhesus ($P = 0.8441$) were preyed upon less than their availability, however, as with hog deer, this was not considered as significant.

The absence of nilgai remains in the Karnali tiger scats was probably due to the combined effect of nilgai low density in the study area (0.10 individuals per km²) (Subedi, 2009) and their habitat use (nilgai are found mostly in open areas near human settlements or relocated village sites, the types of habitat greatly unsuitable for tigers to hunt) (Schaller, 1967; Støen & Wegge, 1996; Karanth & Sunquist, 1995).

With regards to the mean mass of the prey killed, the average weight of prey species consumed by Karnali tigers (50.73 kg) was considerably less than that reported from Kanha Tiger Reserve (KTR), India, (66.0 kg), CNP (61.8 kg), NNP (65.5 kg), PNP (82.1 kg) and the first of the two examined sites in NSTR (78.6 kg) (Schaller, 1967; Sunquist, 1981; Karanth & Sunquist, 1995; Biswas & Sankar, 2002; Harsha *et al.*, 2004). It was, however, more than in the second of the two examined sites in NSTR (43.9 kg), where the major proportion of the prey biomass came from species weighing less than 50 kg (Harsha *et al.*, 2004). Harsha *et al.* (2004) suggest that the substantial difference between the average weights (78.6 kg vs. 43.9 kg) of prey species taken by NSTR tigers in the two examined areas was attributable to different prey availability in respective studied parts of the park. Similarly, the considerable differences between the average weights of prey species consumed in KTR, CNP, NNP and PNP could be attributed to significant differences in prey biomass density in the examined areas. CNP, for example, had the lowest average weight of prey species consumed (61.8 kg) and also the lowest prey biomass density (2933 kg/km²), with PNP having the second highest prey biomass density (6013 kg/km²) and the highest average weight of prey species consumed (82.1 kg) (Biswas & Sankar, 2002).

5.2 Prey availability and co-existence of predators

Resource partitioning in a multi-predator guild is achieved mainly by selection for different size classes of prey, and has been used to explain co-existence among sympatric carnivores (Wang & Macdonald, 2009). Karanth & Sunquist (1995) found that tigers, leopards and dholes preyed selectively upon different prey species, with adequate availability of prey of varying sizes facilitating co-existence among these carnivores. Decreasing prey numbers, however, can intensify sympatric competition for food and space in predator guilds (Wang & Macdonald, 2009), potentially leading to competitive exclusion of leopards and dholes by socially dominant tigers (Karanth & Sunquist, 1995).

The reported dramatic decrease in prey densities in BNP (BCP report, 2008), coupled with the apparent scarcity of large-bodied ungulates in the park (Støen & Wegge, 1996) and the reported by this study significant selection for medium-sized prey by Karnali tigers could consequently reduce the diversity of the park's predator community (Sunquist, 1981). Such competitive spatial exclusion has been shown to occur in areas where large prey are scarce (Karanth & Sunquist, 1995). Although Støen & Wegge (1996) reported that very few leopards or other large predators were present during their study in BNP, they also showed that Karnali tigers removed only 3.1% of the total available ungulate prey biomass annually, suggesting that there should be an adequate supply of food available for other large predators. Instead, the authors hypothesised, leopards may avoid areas occupied by tigers due to interspecific predation. Prey densities have decreased dramatically in BNP (BCP report 2008; Subedi, 2009) over the years, however, and it has been shown by other studies (Sunquist; 1981; Karanth & Sunquist, 1995) that switching to smaller prey by tigers, following prey base depletions, can in fact lead to reduced densities of leopards through food competition. As suggested by Støen & Wegge (1996), further studies are needed to clarify the mechanisms that affect the coexistence of these predators.

5.3 Livestock depredation

During the monsoon of 1975 tigers killed at least 20 buffalos and cattle in communal grazing areas bordering BNP (Dinerstein, 1979). It was believed that low densities of sambar, chital and wild boar as well as illegal livestock grazing inside the park boundaries were the reasons for such a high level of livestock depredation (Dinerstein, 1979). For the same reasons BNP tigers were shown to be the primary predators of domestic livestock in 2000, when they were reported to take 67% of the livestock lost to carnivores (Tamang, 2000). In 2003/04 BNP tigers were reported to kill 182 goats, 31 pigs and 9 buffalos (AWELY, 2009).

The results of this study reveal that livestock make up a relatively small proportion (5.80% of individuals killed) of Karnali tigers, however. Similarly, Harsha *et al.* (2004) provided data suggesting that regardless low densities of wild prey in NSTR and high densities of livestock (60% of the ungulate density within the reserve), the total contribution of domestic livestock in the diet of the park's tigers was only 6.2%. Similar pattern was found in Panna Tiger Reserve, India, by Chundawat *et al.* (1999). Harsha *et al.* (2004) suggested that in the absence of large prey species, NSTR tigers have adapted to smaller prey (<50 kg) and take domestic livestock only on rare occasion.

Regardless the relatively low contribution of livestock to the diet of Karnali tigers found in this study, the continuing decline of natural prey in BNP (BCP report, 2008; Subedi, 2009) and the apparent illegal grazing of domestic animals in the park cannot be ignored as a potential source of human-predator conflict.

5.4 The neglected factor of prey depletion

Despite millions of tiger conservation dollars spent by non-governmental organisations (NGO) and governments, causes of the continuing decline of the tiger are still poorly

understood (Karanth & Stith, 1999). It is habitat loss and poaching of tigers that are usually indicated as the major factors driving the predator's decline (Karanth & Stith, 1999). Habitat loss has been a historically well-known factor responsible for declines of tiger populations. But, recent maps of forest-cover reveal that extensive stretches of potentially suitable tiger habitats still exist in most range countries. Presence-absence data, however, show that tigers are either extinct or in decline in most of these habitats (Karanth & Stith, 1999). Clearly, as Karanth & Stith (1999) suggest, additional causal factors must be at work.

Poaching of tigers is widely considered to be the major causal factor responsible for the current decline of tiger populations (Karanth & Stith, 1999). The issue has been consequently attracting considerable media attention and substantial financial support for some years now, with conservationists focusing a great deal on reducing the demand for tiger body parts (Karanth & Stith, 1999). However, there is empirical evidence that hunting of tigers may not depress their densities if less than 10-25% of their total population is removed annually. In fact, Karanth & Stith (1999) suggest that effect of hunting mortality in tigers is likely to be largely compensatory rather than additive. The authors suggest that generally about 10-25% tigers which are older than a year die annually as a result of intraspecific aggression, hunting injuries or starvation. Consequently, the authors continue, tiger poaching may actually substitute some of these deaths. Furthermore, removing of a tiger can improve survival probabilities of other tigers if there is intense competition for limited territorial slots (Karanth & Stith, 1999). This argument seems to be supported by historical evidence of large scale tiger hunting in India and Nepal, where tiger populations managed to withstand heavy off-takes for long periods of time, with remaining tiger populations quickly recovering from such episodic slaughters (Karanth & Stith, 1999; IUCN, 2007).

Consequently, Karanth & Stith (1999) suggest that low densities or absence of tigers in many regions with extensive and potentially suitable tiger habitats may be largely due to dramatic decreases in prey base densities. It is prey depletion rather than physical shrinkage

of habitat or poaching of tigers that may be the predominant constraint on tiger population recovery in most areas, the authors advise. A stochastic demographic model of ‘typical’ wild tiger populations in Asia developed by Karanth & Stith (1999) seems to support their hypothesis. The model provides data suggesting that even small, insular populations of tigers have a low probability of extinction. It also implies that modest-sized tiger populations can sustain low levels of poaching indefinitely. Such capacity for population persistence is suggested to be a function of tigers’ remarkable resilience (Karanth & Stith, 1999; Sunquist *et al.*, 1999; Biswas & Sankar, 2002). When Karanth & Stith (1999) simulated the effect of prey depletion, however, tigers declined rapidly and extinction risks were substantial for nearly all prey depletion scenarios considered in the study. The authors concluded by strongly advising to recognise prey depletion as a threat distinct from loss of tiger habitat (Karanth & Stith, 1999).

5.5 Limitations of the study, ways forward and recommendations

The analysis of scats is a widely used field technique for assessing the food habits of tigers and a good alternative to data collection at kill sites. The methodology, however, is not without its limitations.

To start with, although scats not clearly identifiable in the field were discarded in this study, it was still possible to confuse tiger scats with those of leopards. Generally, tiger scats are distinguished from those of leopard by their larger size, shape (less coiling) and the presence of supplementary evidence in the form of pugmarks and scrapes (Biswas & Sankar, 2002). A full-grown tiger (135 kg) weighs over three times more than a full-grown leopard (45 kg) and as such produces larger scats (Karanth & Sunquist, 1995). A particularly large leopard can produce larger scats than a relatively small tiger, however (Subedi, 2009). It is also suggested that scats from a tiger cub less than six months of age could be misclassified as those of a leopard (Schwarz & Fischer, 2006). Next, although associated tiger pugmarks and scrapes can facilitate identification of scats, this

supplementary evidence was found on very few occasions along with the scats in this study (Subedi, 2009). It is also worth noting that, as in most studies, the scats of Karnali tigers were collected along forest roads and trails in the study area, which are believed to be favoured by the predator for scat deposition. However, do tigers really prefer forest roads and trails or are tiger scats simply easier to detect there? Schwarz & Fischer (2006) were concerned with such issue during their study of the food habits of leopards. The authors concluded in the end that even if leopards have actually not preferred to defecate on hiking trails and paths, where their scats are usually collected, it wouldn't introduce bias since it is highly unlikely that faeces on paths and trails would contain substantially different prey items from scats left in other locations (Schwarz & Fischer, 2006).

As indicated earlier, one of the disadvantages of direct observations of the food habits is that the method tends to over-represent bigger prey. Contrary to this, scat analysis is biased towards small prey items (small prey species produce more scats per unit prey weight consumed than large prey) (Karanth & Sunquist, 1995). This problem can be overcome (as it was done in this study) by applying a regression equation developed by Ackerman *et al.* (1984), following the assumption of Karanth & Sunquist (1995) that the digestive system of tigers is comparable to that of cougars. Karanth & Sunquist (1995) came to this assumption by observing that the degree of carcass utilization by predators in NNP appeared generally comparable to the utilization rates observed in the food habits studies conducted by Ackerman *at al.* (1984). However, the hypothesis of Karanth & Sunquist (1995), although now widely adopted for dietary studies of tigers, has apparently never been tested thoroughly by the authors or other researchers for that matter. If so, it would appear that further studies might be necessary to confirm that the digestive system of tigers is indeed comparable to that of cougars.

One of the considerable limitations in this study was the inability to determine whether all Karnali tigers contributed equally to the scat samples collected in the floodplain (Støen & Wegge, 1996; Bonnin, 2008). Individual differences in prey selection or differences in densities of prey in the individual territories of tigers could lead to a bias (Støen & Wegge,

1996). This could be the case with barasingha, for example, which live in tall swampy grasslands in a very small area in the middle part of the Karnali floodplain (Schaller, 1967; Støen & Wegge, 1996). Collection of scat samples from the whole study area could potentially lead to underestimation of barasingha in the diet of Karnali tigers, even if the species was generally preferred by the tigers (Støen & Wegge, 1996). Taking an advantage of recently introduced DNA techniques, such as molecular scatology and the use of polymerase chain reaction (PCR) techniques, could match the analysed prey items in scats to individual tigers (Bonnin, 2008). This could not only reduce such biases but by being able to identify tigers individually, it would be possible to determine the tigers' population size, composition and spatial use of habitat (Symondson, 2002; Schwarz & Fischer, 2006). This would be of considerable importance for endangered species such as tigers, which survive in increasingly isolated, scattered and often very small populations that are prone to inbreeding (Schwarz & Fischer, 2006).

Although thanks to a strict adherence to hair identification procedures and relatively small sample size it was possible to identify all hairs in this study, identification of hairs was occasionally found to be challenging. To start with, the terminology used in the literature reviewed (Koppikar & Sabnis, 1975; Koppikar & Sabnis, 1976; Amerasinghe, 1983; Teerink, 1991; De Marinis & Asprea, 2006; Bonnin, 2008) varied at times considerably, and since on several occasions it was necessary to consult different works, some confusion did arise during identification. As suggested by Bonnin (2008), a hair key would benefit future prey selection studies.

Next, as the cervids all possess a cloisonné medullar structure (Bonnin, 2008), identification of prey items within this family turned out to be at times problematic. Hairs of chital and hog deer, for example, were so alike that the only clearly distinguishing feature was the width of their hairs. Accordingly, any hairs measuring more than 100µm in width were identified as hog deer and any hairs measuring less than 100µm in width were identified as chital, with the help of other identification features (Bonnin, 2008). However, as hairs may have been altered during the digestive process (Teerink, 1991), potential

misclassification between these two species was still possible. Variations in medullar and cuticular features within hairs of the same prey species, between guard- and under-hairs as well as potentially high degree of observer variability in the literature, further complicated identification of a considerable number of the prey items examined in this study (Bonnin, 2008).

Although the shape and dimensions of hair in cross-sections can prove very useful for hair identification, cross-sectioning is the most complicated type of hair analysis. This is because the shapes of cross-sections change along the hair and only the sequence of the shapes along the hair, rather than the shape at any particular point, can be used for the identification. In addition, cross-sections of hairs of closely related species appear very similar to each other, and as a result have no diagnostic value (Mukherjee *et al.*, 1994a; Bodendorfer *et al.*, 2006). Consequently, due to time constraints and the fact that a number of researchers have not found cross-sectioning to be necessary for hair identification (Mukherjee *et al.*, 1994a; Bodendorfer *et al.*, 2006), this procedure was not included in this study. Cross-sectioning was successfully used by Palmer & Fairall (1988) to confirm identification of hairs, however, and could prove valuable in future studies of prey selection by Karnali tigers (Bonnin, 2008).

Unfortunately, due to the absence of reference material, the separated from the Karnali scats bones, hooves and teeth could not be used to assist in identification of prey items. As such organic remains were shown useful in identification of prey species in earlier studies (Norton *et al.*, 1986; Biswas & Sankar, 2002; Bodendorfer *et al.*, 2006; Schwarz & Fischer, 2006), the compilation of such reference material for BNP would certainly facilitate species identification in future studies (Bonnin, 2008).

The lack of current estimates of BNP prey densities was another substantial limitation in this study. First of all, the obtained from Støen (1994) density estimates did not contain SE and it was impossible to get hold of Andersen & Nees' (1993) original study from which the data originated. Next, setting the current prey densities at 30% less than those in 1994,

as recommended by Subedi (2009), was a potentially substantial source of error. It would be highly advisable to re-analyse this data with more accurate density data and corresponding SE values, which are currently being compiled at BNP (Subedi, 2009).

Like many other studies of the food habits of tigers by scat analysis (Karanth & Sunquist, 1995; Støen & Wegge, 1996; Biswas & Sankar, 2002; Bagchi *et al.*, 2003; Harsha *et al.*, 2004; Bonnin, 2008), this study was undertaken during the dry season. However, changes in the utilisation of different vegetation types by different prey species influenced by seasonal variations in the environment cause variation in prey availability on seasonal scale (Haugo & Hoem, 1999). As such seasonal factors are likely to influence the diet of predators, a study of prey selection by Karnali tigers during other seasons would generate important information on any corresponding changes in the food habits of these predators (Bonnin, 2008).

Also, like other studies (Biswas & Sankar, 2002; Bagchi *et al.*, 2003; Bonnin, 2008), this study did not consider selectivity in age and sex classes of prey species. Schwarz & Fischer (2006) propose that combining scat analysis, direct observation and radio-tracking would bring the best results in comprehensive studies of the food habits of predators. The authors suggest that combining scat analysis with other techniques would bring the following advantages: (1) scat analysis would prevent over-representation of both large and small prey, (2) direct observation would answer questions about the predator's mode of feeding and provide information on sex, age and condition of the predator and its prey, (3) radio-tracking would provide data on spatial and temporal habitat use.

5.6 Conclusions

It would appear that there are still several areas in Asia, such as CNP, NNP, KTR, Kaziranga National Park, India, Gunung Leuser National Park, Indonesia, Taman Negara National Park, Malaysia, Huai Kha Khaeng, Thailand, PNP and Ranthambore National

Park, India, that could support demographically viable populations of tigers (Karanth & Stith, 1999; Biswas & Sankar, 2002; Bagchi *et al.*, 2003). BNP, being the largest protected area in the Terai region of Nepal (RBNP report, 2005), has the potential to accommodate a relatively high density of tigers, making the park comparable to these few of the best remaining tiger habitats in Asia. However, as the capacity for sustaining productive tiger populations depends primarily on maintaining high prey densities (Karanth & Stith, 1999), current low prey densities in BNP could prevent the park from realising its full potential for becoming an important and much needed conservation area for tigers and their prey in Nepal (Bonnin, 2008).

The significant selection by Karnali tigers for smaller prey observed in this and earlier studies (Støen & Wegge, 1996; Bonnin, 2008) may also prevent other carnivores such as leopards and dholes from thriving in BNP without any behavioural and habitat segregation, thus disturbing the park's carnivore community (Sunquist, 1981; Karanth & Sunquist, 1995; Støen & Wegge, 1996; Biswas & Sankar, 2002). This, in turn, may adversely affect the biodiversity of the entire ecosystem (Bonnin 2008).

Although Karnali tigers, unlike tigers in many areas of the Indian subcontinent (Biswas & Sankar, 2002), depend mostly on wild prey rather than domestic livestock for food, the revealed in this study presence of livestock remains in tiger scats suggests that illegal grazing is continuing in BNP. This, coupled with the drastic decline of prey base in the park, could in due course lead to human-predator conflicts, thus further complicating management of the park (Oli *et al.*, 1994; Mishra, 1997; Tamang, 2000; Schiess-Meier *et al.*, 2007). Furthermore, although BNP does not seem to harbour any man-eating tigers at present, the number of human deaths due to human-tiger conflict is increasing worldwide (IUCN, 2007). Man-eating is the ultimate manifestation of human-predator conflict and even a single case of human death caused by tigers could lead to intolerance of these predators by local communities and consequently jeopardise efforts to build local support for tiger conservation (Gurung *et al.*, 2006).

Given the chronic scarcity of resources for conservation of tigers across the predator's range, it is essential to prioritise areas where the probability of tigers' survival is highest in the future (Biswas & Sankar, 2002). BNP is among those areas that have the potential to harbour relatively high prey densities. Uncontrolled poaching of tiger prey species, however, continues to threaten biodiversity conservation in this area (Upadhyay, 2005). Reduction of hunting pressure on tiger prey base should therefore become the central component of tiger population recovery efforts (Karanth & Stith, 1999).

Our understanding of the food habits of tigers, although vital to effectively address conservation needs of this endangered species, is still far from complete (Biswas & Sankar, 2002; Bagchi *et al.*, 2003). Further prey selection studies, such as this one, can therefore contribute valuable information on the factors influencing selectivity by tigers and on this species' ability to adapt to human-modified landscapes. Furthermore, further research of the diet of tigers can assist in keeping the diversity of predator communities intact and help to demonstrate the impact of management strategies aiming at reducing human pressures on protected areas by revealing the extent of livestock depredation (Bagchi *et al.*, 2003).

Almost four decades ago, during the 1969 IUCN General Assembly, Indira Gandhi, then prime minister of India, assertively declared that her government would save the tiger, which was on the brink of extinction in India and elsewhere at the time. Initially, dramatic recovery of India's tigers did actually follow. Over the years, however, governmental inefficiency put back India's tigers to their present dire state (Johnsingh & Goyal, 2005). Much has changed since the early 1970s when conservationists were first making plans to save wild tigers (Dinerstein *et al.*, 2007). Then the dialogue involved a few dedicated conservationists and national park officials on a country-by-country basis. Over the years, however, it has become apparent that the matter of saving the tiger from extinction is transnational (Dinerstein *et al.*, 2007). Ultimately, without full support, lasting commitment and competency of all of the governments throughout the tiger's range (Dinerstein *et al.*, 2007), the grim predictions that wild tigers could become 'virtually extinct' in our lifetime (Karanth & Stith, 1999) may come true after all.

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