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# 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

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## ABSTRACT

Interactions among sympatric large predators and their prey and how they respond to conservation measures are poorly known. This study examines predictions concerning the effects of establishing a protected area in Nepal on tigers (*Panthera tigris*), leopards (*Panthera pardus*), and their ungulate prey. Within a part of the park, after 22 years the total density of wild ungulates had increased fourfold, to ca. 200 animals/km<sup>2</sup>, almost exclusively due to a remarkable increase in chital deer (*Axis axis*). Tiger density also increased markedly to nearly 20 animals/100 km<sup>2</sup>, whereas leopard density did not and was ca. 5 animals/100 km<sup>2</sup>. The prediction that grazers should increase more than browsers was only partially supported. The prediction of positive density dependence in prey selection was not supported. Instead, the most abundant species (chital and hog deer, *Axis porcinus*) were killed less frequently than expected, whereas the lower-density wild boar (*Sus scrofa*) was preferred. Predictions that (i) initially rare species suffer highest predation was partially supported, and that (ii) predation is highest among the most abundant prey was not supported, and that (iii) predation is highest among the most preferred prey independently of their densities was supported. Clearly, the conservation efforts adopted in Bardia were successful, as both tigers and their natural prey base increased. However, the positive numerical response of tigers limited and depressed the abundance of some prey species. Thus, conservation activities aimed at restoring large predators are likely to change in the composition of the overall mammal community, potentially eliminating rare but preferred prey species.

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## 1. Introduction and objectives

The literature provides a wide range of examples of single-species management strategies producing unpredicted ef-

fects both on the target species and on other species (Sinclair and Byrom, 2006). Changes in the population density of a single species may produce marked effects on entire ecological communities and, as a consequence, conservation threats

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to a species often originate through complex interactions at different trophic levels (see review by Sinclair and Byrom, 2006). Our ability to predict the fate of threatened or endangered species therefore depends upon recognizing the relative strength and interactions among several population-regulating factors that operate in the ecosystem. These include intrinsic factors (Wynne-Edwards, 1962; Chitty, 1987), i.e., behavioural or physiological factors, including density-dependent dispersal, territoriality or reproductive inhibition, and extrinsic regulating factors (Nicholson, 1933; Lack, 1954), such as disease, interspecific competition, or trophic interactions acting either from below (bottom-up) or above (top-down).

Facing the escalating conservation threats from habitat loss due to human population growth and land-clearing, the government of Nepal passed the National Parks and Wildlife Conservation Act in 1973. The act initiated the establishment of an increasing number of protected areas, which currently cover more than 15% of the country's total area. Two national parks and three wildlife reserves are situated in the densely populated and highly productive lowland (Terai) along the Indian border. In 1976, a thorough ecosystem study was conducted in a part of present Bardia National Park, just prior to it being established as a protected area (Dinerstein, 1979a,b, 1980). Twenty years later, a collaborative research program in the same area between the Department of National Parks and Wildlife Conservation/GoN, the Norwegian University of Life Sciences and the Nepal Trust for Nature Conservation provided an opportunity to assess the effects of the adopted conservation efforts.

In this paper, we examine various predictions about population responses of tigers (*Panthera tigris*), leopards (*Panthera pardus*) and their ungulate prey, and about their trophic interactions, since the protected area was established (Table 1). We assess our predictions by modeling the influence of habitat on the densities and distribution of ungulates, and by comparing their current densities with those obtained in 1976 by Dinerstein (1980). Furthermore, we investigate prey selection patterns and predation impact by combining data on prey densities and distribution, predator densities, their diets and food consumption rates, and mortality patterns of radio-collared deer.

### 1.1. Population responses

The influence of livestock grazing on native wildlife has been a matter of considerable debate (e.g. Saberwal, 1996; Mishra and Rawat, 1998; Voeten, 1999; Prins, 2000). However, studies conducted in somewhat similar habitat types in tropical forests in India have documented substantial increases in wild ungulate populations following reductions in livestock grazing (Khan et al., 1996; Madhusudan, 2004). Both studies attributed the increases to a release from resource competition with domestic stock. Livestock grazing was high in Bardia prior to 1976. Dinerstein (1980) estimated densities of 136 domestic cattle and 55 buffalo/km<sup>2</sup> in a smaller part of the study area, whereas the total density of wild ungulates averaged 46 per km<sup>2</sup>. Following the banning of livestock grazing in 1976, it is assumed that the densities of wild ungulates would have increased as a result of absence of competition from livestock.

**Prediction 1: Grazers have increased more than browsers.** The ungulates in Bardia can be grouped into three main classes based on previous studies of their diets (Dinerstein, 1979b; Khatri, 1993; Pokharel, 1996; Wegge et al., 2006): (i) grazers, those with a grass-dominated diet: barasingha (swamp deer, *Cervus duvauceli*) and hog deer (*Axis porcinus*); (ii) mixed feeders: nilgai antelope (*Boselaphus tragocamelus*) and chital deer (*Axis axis*); and (iii) browsers, those feeding mainly on woody plants: muntjac (barking deer, *Muntiacus muntjak*) and sambar deer (*Cervus unicolor*). Grazers overlap more in diet with domestic ungulates than browsers (Khan et al., 1996; Madhusudan, 2004). Thus, following the ban on livestock grazing, populations of grazers should have increased more than browsers. Furthermore, the adopted management practice of cutting and burning of the grasslands should have arrested succession and maintained the habitat quality for grazers (Moe and Wegge, 1994).

**Prediction 2: Densities of tiger and leopard have increased as a consequence of a larger natural prey base.** Predators are known to track the densities of their main prey (Karanth et al., 2004). Hence, with an increasing abundance of natural prey following the virtual elimination of livestock and other human disturbances, numbers of tigers and leopards should also have increased.

**Table 1 – Predictions concerning predator–prey relationships and changes in the abundance of tigers and leopards and their natural ungulate prey species after 22 years of protection in Bardia National Park, Nepal.**

	Prediction	Support
1	Grazers increased more than browsers	<i>Partially supported:</i> chital and hog deer increased dramatically; wild boar and nilgai decreased; barasingha, sambar and muntjac unchanged
2	The densities of tiger and leopard have increased	<i>Partially supported:</i> large increase in tigers, no apparent change in leopards
3	Predation is positively density dependent and levels out interspecific differences in prey abundance	<i>Not supported:</i> removal rate lowest on densest prey
4	Predation is independent of the density of the prey species; impact is highest on the larger and preferred species	<i>Supported:</i> highest impact on medium and low density, preferred species (wild boar and sambar) and lowest on most abundant species (chital and hog deer)
5	Predation impact is inversely density dependent and may limit the abundance of secondary, low-density prey species	<i>Partially supported:</i> highest impact on medium and low-density, but preferred, wild boar and sambar

## 1.2. Trophic interactions

The impact of predation on prey populations depends to a great extent on the shape of the predator's functional response (Holling, 1959), i.e., on how consumption rates vary with prey density. The traditional functional response relates to use of a prey species at different densities of that prey. In this paper we examine predictions of how the functional response varies with the density of different prey species, assuming similar underlying ecological relationships. The functional responses shown by tigers and leopards to changes in prey densities are poorly understood and, thus, several contrasting scenarios can be theorized.

*Prediction 3: Prey preference is positively density dependent, leveling out differences in abundance among prey species* (Chesson and Rosenzweig, 1991). If predators show a Type III functional response, and preferentially kill the more abundant species, differences in original abundances of prey species will be reduced.

*Prediction 4: Prey preference by predators is independent of prey species densities.* Tigers and leopards prefer the larger sized among the available prey species that they are able to kill (Gittleman, 1989; Karanth and Sunquist, 1995; Sankar and Johnsingh, 2002). If predators show a Type II functional response, i.e., exhibits a constant preference for a prey species independently of its density above a threshold density, the larger and commonly preferred prey will be affected more by predation than smaller and medium-sized prey of lower preference.

*Prediction 5: Predation is inversely density dependent; higher predation on the least abundant species increases interspecific differences in prey abundance.* In this scenario, a predator

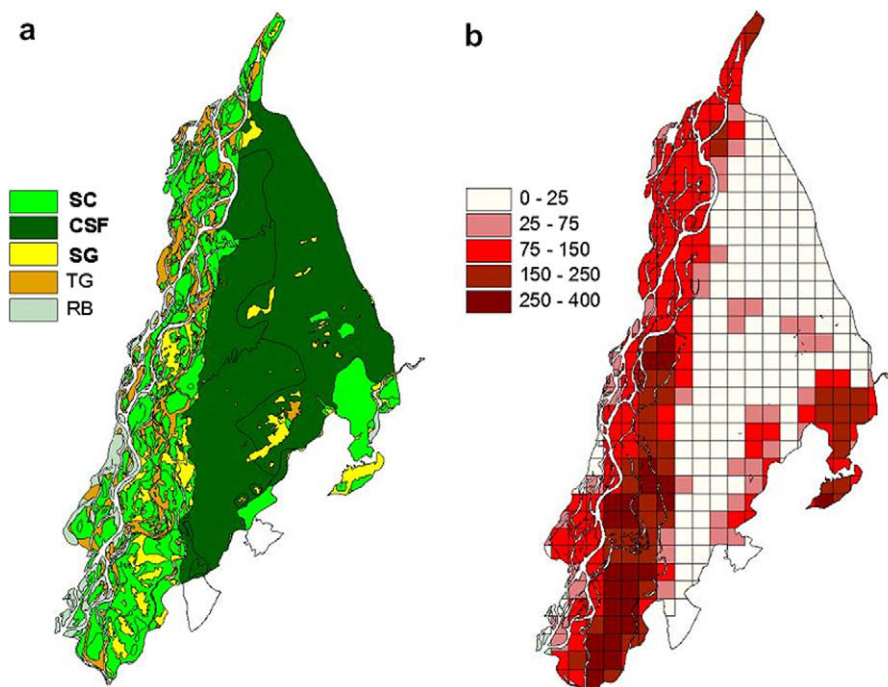
exhibits a positive numerical response to increased abundance of a primary prey species, which, in turn, leads to elevated predation pressure on secondary, less preferred prey (Sinclair et al., 1998; Wittmer et al., 2005). This may occur when the secondary prey is initially rare, in which case the secondary prey may be driven to extinction (Sinclair et al., 1998).

## 2. Materials and methods

### 2.1. Study area

We conducted our research within a 105-km<sup>2</sup> area in the south-western corner of Bardia National Park (986 km<sup>2</sup>). The study area is bordered by the large Geruwa river in the west, the east-west highway in the north, and by human settlements and cultivated land in the east and south. The climate is subtropical monsoonal with heavy rains from June to September/October. The habitat types within the study area were first described by Dinerstein (1979a), and later mapped by Sharma (1999): the floodplain consists of a mosaic of *Saccharum*-dominated tall grasslands interspersed with patches of early forest successional stages, consisting mainly of sissoo (*Dalbergia sissoo*) (Fig. 1a). Moving east from the river, on less disturbed soils, later successional forests dominate. These have a dense overstory of several hardwood trees (*Trewia nudiflora*, *Ficus* spp., *Mallotus philippinensis*, *Syzigium cumini*), and are interspersed with patches of Savannah grasslands dominated by *Imperata cylindrica*. Sal (*Shorea robusta*) forest covers the eastern part of the study area.

In our analysis we grouped the habitats into four types, two forest types and two grassland types: (i) climax Sal forest



**Fig. 1** – Distribution of habitat types (a) and estimated total densities (no./km<sup>2</sup>) of chital, hog deer, muntjac, wild boar, barasingha and nilgai (b) in a 105-km<sup>2</sup> study area in the south-western part of Bardia National Park, Nepal, in 1997/99. SC = successional forest, CSF = climax forest, SG = Savannah grasslands, TG = tall floodplain grasslands and RB = riverbeds. The square sizes are 33 ha.

(CSF) consisted of Sal forests with small, interspersed patches of *Terminalia* forest, (ii) successional forest (SF) consisted of all forest types other than Sal forest, (iii) Savannah grasslands (SG) included all *Imperata*-dominated vegetation types, (iv) tall floodplain grasslands (TG) were dominated by *Saccharum spontaneum*.

The main management routines in the Park included preventing poaching, livestock grazing and other human disturbance. Although poaching has been documented, it is uncommon, and cattle grazing and other human impacts have diminished markedly (Yonzon and Heinen, 1997). A complete barring of human impact entails a trend of the vegetation towards climax forests (Dinerstein, 1979a). In order to maintain early successional stages, which are considered key habitats for a range of ungulate species, controlled cutting and burning of grasslands has been allowed during a two-week period in the early dry season. Since the mid-1990s, prevention of bush encroachment into the grasslands has been intensified by uprooting fire-resistant woody plants (Bhatta, 2000).

## 2.2. Species

Tigers and leopards were the main large predators in the park. The medium-sized chital (50–60 kg) was the most abundant ungulate (Støen and Wegge, 1996). Although classified as a mixed feeder, graminoids make up the bulk of its diet (Schaller, 1967; Martin, 1982; Johnsingh and Sankar, 1991). The smaller and more solitary hog deer (ca. 30–40 kg) is confined to the tall grasslands in the floodplains throughout the year (Odden et al., 2005). The forest-dwelling Indian muntjac is a small (15–20 kg) and solitary browser with a dispersed distribution (Ilyas and Khan, 2003; Odden and Wegge, 2007). The internationally endangered, large-sized barasingha (>150 kg) occurred in low numbers, associated mainly with grasslands both in terms of habitat use and food habits (Pokharel, 1996; Wegge et al., 2006). The nilgai is the largest of the Asian antelopes (>150 kg). It is group-living and mixed feeder, rarely found in Sal forest (Dinerstein, 1979b; Subedi, 2001). Wild boar (*Sus scrofa*, 35–40 kg) was quite common, except in the floodplain, whereas the forest-dwelling, large sized sambar (ca. 200 kg) was rarely observed in the southwestern part of the park where our study was conducted.

## 2.3. Ungulate densities

### 2.3.1. Field methods

Density estimates of ungulates were obtained by counting animals that were flushed out from patches of vegetation surrounded by either roads or dry riverbeds, where it was easy to count them. During 1997–1999, 169 counts were conducted in 46 different habitat blocks with an average size of 33.7 ha. To ensure that we counted all animals within the patch, we employed a large number of beaters (~65 people/block), walking in a line 10–20 m apart.

Approximately one third of the people counted animals, and two thirds beat through the blocks. We took care not to disturb the animals before starting the counts, and not to flush animals into areas where counts were to be conducted later. On 33 occasions, we monitored the movements of

radio-collared hog deer ( $N = 19$ ) and muntjacs ( $N = 14$ ) inside the blocks prior to the counts. The beaters, who did not know in advance in which blocks the deer were located, detected all the collared hog deer and 12 of the 14 muntjacs. Owing to the very intensive sampling, and that we recorded the deer known to be in the blocks on nearly all occasions, we assume that we counted all the ungulates inside the blocks. However, because the number of muntjacs was slightly underestimated, due to their habit of freezing instead of fleeing when approached by the beaters, we multiplied their density estimates by 1.17 (14 muntjacs in block counts/12 observed).

### 2.3.2. Data analyses

The habitats and the blocks where we did the ungulate counts were digitized using the ArcView GIS 3.2. First, we transformed all habitat polygons to point themes by overlaying evenly distributed points every 50 m. Next, we extracted all points that were situated in a specific habitat type and, based on the x-y coordinates of these points, we conducted fixed 95% kernel analyses (Worton, 1989) with a smoothing factor of 200 m. This procedure was done separately for each of the four habitat types, producing  $50 \times 50$  m grid cells for each habitat type, with specific kernel values for each grid cell. Cells situated near the center of large habitat patches received high kernel values ( $\leq 100$ ). These values decreased gradually moving towards the edge of the habitat patches, and reached zero 200 m outside of the patch. Next, we calculated average habitat specific kernel values for all grid cells within each ungulate census block. Hence, each block received four kernel values, one for each of the habitat types. This procedure enabled us to assess how habitats situated in close vicinity of a census block affected the density of animals inside the block.

Considering the average densities of animals within each of the blocks as dependent variables and habitat specific kernel values as predictors, we modeled the influence of habitat on the densities of each ungulate species (Eq. (1)) by using generalized linear models (GLM)

$$\text{Density} = \text{TG} + \text{SG} + \text{SF} + \text{CSF} \quad (1)$$

where TG is the tall grass, SG is the Savannah grassland, SF is the successional forests, CSF is the climax Sal forest.

In addition to the full model, we made a set of models including all simpler combinations of main effects, rendering a total of 15 candidate models for each ungulate species. Absence of the habitat types listed above would only occur in areas that were unsuitable for the ungulates, such as rivers and sandbanks. Hence, the intercept was excluded from the models. The most parsimonious models describing ungulate densities were selected by comparing the Akaike information criterion corrected for small samples ( $AIC_c$ ) and the  $\Delta AIC_c$  ( $AIC_c$  for the model of interest minus the smallest  $AIC_c$  for the set of model considered (Burnham and Anderson, 2002)). In addition, the Akaike weights, i.e., the normalized likelihood of the models,  $\omega_i$ , were calculated to show the relative difference in performance of each suitable model (Burnham and Anderson, 2002). The best models were used to produce probabilistic ungulate density maps for the whole 105-km<sup>2</sup> study area (SA, Fig. 1b), and the 11.8 km<sup>2</sup> part that was censused by Dinerstein (1980) in 1976. We hereafter refer to densi-

ties in 1976 as DIN 1976, and to densities within the same area during our study as DIN 1998.

## 2.4. Predator densities

### 2.4.1. Field methods

Prior to the establishment of the protected area, the abundance of tigers and leopards was not known from systematic census methods. Instead, indirect information based on frequency of observing animals and their signs, including pugmarks, and human–carnivore interactions (livestock losses and human injuries), indicated that tigers were more common than leopards and that the former occurred at a lower density than in the mid-1990s when the first systematic pugmark census was conducted (K.M. Shrestha, first Park Warden, pers. comm.; Bolton, 1976; Dinerstein, 1979b; Støen and Wegge, 1996).

In the early dry seasons of 1998/99 and 2000/01 we sampled tigers and leopards by the camera trapping technique (Karanth, 1995; Karanth and Nichols, 1998; O'Brien et al., 2003; Wegge et al., 2004). During the two seasons, 50 and 54 camera stations were distributed in a rough grid pattern spaced 0.8–2.2 km apart, each monitored for an average of 14 and 11 successive nights, respectively. With  $\leq 12$  stations in operation per sampling event, stations were successively moved to new locations across the study area; thus sampling over the whole study area was completed within eight weeks. Only three photographs of two different leopards were obtained during the two sampling periods. Radio telemetry data and the distribution of leopard scats and pugmarks collected in another ongoing study (Odden and Wegge, 2005) indicated that more leopards resided in the study area. We adjusted the density estimate of leopards based on this information (see Results).

### 2.4.2. Data analyses

Capture–recapture models estimate population size ( $N$ ) with the assumption of geographic closure (closure by a boundary) for both demographically closed and open populations (White et al., 1982). Demographic closure assumes that the size of the population is constant over the period of trapping, i.e., no recruitment or losses occur during the sampling period. We analyzed the capture history data with the software CAPTURE (Otis et al., 1978; White et al., 1982), which computes closure test and model selection, and estimates the number of animals present within the sampling grid under different assumptions about capture probability. The abundance estimate was then converted to a density estimate according to Karanth and Nichols (1998); a buffer strip around the sampling area was calculated and added to the area covered by the camera traps, after subtracting unsuitable tiger habitat. The strip width was estimated from the mean maximum distance moved (MMDM) by animals photographed more than once (Karanth and Nichols, 1998).

## 2.5. Prey selection and removal rates

### 2.5.1. Field methods

During the dry seasons (November–June) in 1999–2000, tiger and leopard scats were collected opportunistically when

doing other fieldwork. From January to April 2001, scats were collected systematically by surveying roads and trails within the study area. Date, location, relative age and presence of associated signs (tracks, markings) were recorded for each collection. Excess scats were removed from the trails to prevent repeated sampling in the next sampling period. Scats of tigers ( $N = 365$ ) were distinguished from those of leopards ( $N = 95$ ) by their larger size, and by examining the size and shape of associated tracks and markings. This method of separating tiger and leopard scats was shown to be appropriate by Andheria et al. (2007) in a study where scat identification based on associated signs was compared with a “true” identification obtained by DNA analysis. We omitted scats from further analyses whenever in doubt of the predator species.

### 2.5.2. Scat analyses

We collected 20–30 hairs from each scat sample (Mukherjee et al., 1994a,b), and compared them with a reference collection (Johnsingh, 1992; Karanth and Sunquist, 1995; Støen and Wegge, 1996). We excluded scats from further analysis if they contained too few intact hairs to make a reliable identification. The reference collection included hair from all potential wild and domestic ungulate, primate, and carnivore prey species. We used Koppikar and Sabnis' (1976a,b) descriptions of hairs from different Indian mammals whenever identification was uncertain.

### 2.5.3. Prey selection analyses

Small prey species produce more scats per unit prey weight consumed than large prey. Thus, the frequency of occurrence (FO) of different prey items in scats misrepresents the relative numbers of prey species killed (Ackerman et al., 1984). In order to convert FO of different species in the scats into relative biomass and numbers of individuals killed, we used the formula given by Ackerman et al. (1984), Eq. (2). This formula was originally developed for cougar (*Felis concolor*), and has been used in studies of other large cats (Karanth and Sunquist, 1995; Hart et al., 1996; Støen and Wegge, 1996; Farrell et al., 2000; Biswas and Sankar, 2002; Sankar and Johnsingh, 2002)

$$Y = 1.980 + 0.035X \quad (2)$$

where  $Y$  is the weight of prey consumed per scat and  $X$  is the prey body weight (kg).

We used the software SCATMAN (Hines and Link, 1994) to analyze prey selection by tigers and leopards. In this software, one specifies the FO of different prey items in the scats, and the means and standard deviations of the prey density estimates. The program then estimates the relative number of scats produced per kill (Eq. (2)), and compares observed and expected proportions of prey species in the scats by using likelihood ratio tests (G tests, Zar, 1984), based on a parametric bootstrapping procedure. In these analyses, we performed 1000 bootstrap simulations, and if two prey items were found in a scat we counted each as 0.5, as suggested by Karanth and Sunquist (1995). Live weights of prey were obtained from our own data from radio-collared muntjacs and hog deer (Odden et al., 2005; Odden and Wegge, 2007), and from Schaller (1967), Dinerstein (1980), Karanth and Sunquist (1995) and Fleagle (1999).

#### 2.5.4. Prey removal analyses

The annual removal rate of different ungulates by predators was defined as the number of animals killed of each species divided by the total number of animals in the study area. Firstly, we converted the FO of each prey species in the scats into relative biomasses (proportions) by using Eq. (3), and, secondly, we used Eq. (4) to convert these relative biomass estimates into relative numbers of individuals killed.

$$RB_i = \frac{FO_i \times CF_i}{\sum_{i=1}^n FO_i \times CF_i} \quad (3)$$

$$RN_i = \frac{RB_i/LW_i}{\sum_{i=1}^n RB_i/LW_i} \quad (4)$$

where RB is the relative biomass each species that were killed, i.e., the relative contribution of species *i* to the total biomass of all killed animals ( $0 \leq RB_i \leq 1$ ), FO is the frequency of occurrence in scats, CF is the correction factor specified in Eq. (2), RN<sub>*i*</sub> is the relative proportion of individuals of species *i* that was killed ( $0 \leq RN_i \leq 1$ ), and LW is the average live weight.

We estimated the total food consumption by different methods. For leopards, we estimated a food consumption rate of 4.0 kg/day for a radio-collared female with cubs in our study area and 4.3 kg for two male leopards (Odden and Wegge, in press). Assuming an equivalent difference in food consumption among leopard categories as shown by Stander et al. (1997), single females probably consumed about 3.3 kg/day. Stander et al. (1997) reported that the proportion of a prey consumed by leopards varied with prey size, i.e., 95% consumption of prey <20 kg, and 70% consumption of prey >20 kg. In our estimates, we assume that the proportions of the live weight of prey consumed by tigers and leopards were similar to that reported by Stander et al. (1997). We estimated the total weight of all animals killed by leopards from Eq. (5):

$$BCL_i = RB_i \times \left( \frac{NL_{sf} \times FC_{sf} + NL_{fc} \times FC_{fc} + NL_m \times FC_m}{CR_i} \right) \quad (5)$$

where BCL<sub>*i*</sub> is the total biomass of all ungulates of species *i* that were killed by all the leopards in the study area, RB<sub>*i*</sub> is specified in Eq. (5), NL is the number of leopards, FC is the annual meat consumption, sf is single females, fc is females with cubs and m is the males.

Annual prey removal by tigers was estimated by the following two methods:

M1: Sunquist (1981) estimated daily meat consumption to be 5–6 kg/day for adult female tigers and 6–7 kg/day for adult males, resulting in an annual meat consumption of 1825–2190 kg and 2190–2555 kg, respectively. Tamang (1982) assumed that daily food consumption was somewhat higher, i.e., on average 7 kg/day for all adult tigers. For our purposes we used the highest values of food requirements of tigers from Sunquist (1981), 6 kg of meat/day for adult females and 7 kg/day for males. This rate compares closely with consumption predicted on the basis of body weights of large cats (Emmons, 1987). We assumed that each female, on average, had 1 cub <6 months of age, and that the food consumption of cubs was of the requirement of adult females (Tamang, 1982; Støen and Wegge, 1996). We used Eq. (6) to estimate food consumption based on these assumptions:

$$BCT_i = RB_i \times \left( \frac{NT_f \times FC_f + NT_m \times FC_m + NT_c \times FC_c}{CR_i} \right) \quad (6)$$

where BCT<sub>*i*</sub> is the total biomass of prey species *i* killed by tigers in the study area, NT is the number of tigers, FC is the annual food consumption, f is females, c is cubs, m is males and CR<sub>*i*</sub> is the average proportion consumed by tigers of species *i*.

M2: During 1998/2000, we captured and radio marked 53 hog deer and monitored them weekly, as described in Odden and Wegge (2007). We used a Kaplan–Meier model to estimate annual predation rates of these deer (Kaplan and Meier, 1958). We estimated the total number of hog deer killed by tigers in the study area by multiplying their density estimate with their estimated predation rate. We then subtracted the estimated predation by leopards (Eq. (5)). Lastly, assuming that the ratios between the estimated relative numbers killed of the different species derived from scats (Eq. (4)) equals the ratios between their actual predation rates, we estimated the numbers of ungulates killed with Eq. (7):

$$NKT_i = NK_h \times \left( \frac{RN_i}{RN_h} \right) \quad (7)$$

where NKT<sub>*i*</sub> is the total number of ungulates of species *i* killed by tigers, NK<sub>*h*</sub> is the total number of hog deer killed in the study area, RN<sub>*i*</sub> is the relative numbers of species *i* killed by tigers and RN<sub>*h*</sub> is the relative number of hog deer killed by tiger.

## 3. Results

### 3.1. Vegetation development

The spatial composition of the vegetation types within the 11.8 km<sup>2</sup> area that was surveyed by Dinerstein (1979a) in 1976 changed during the 22 years after it became part of the protected area. In 1976, the estimated proportion of tall floodplain grasslands was 8.5%; in 1998 they covered 4.6%. Imperata-dominated Savannah grasslands decreased from 22.9% to 18.8%, successional forests increased from 44.9% to 51.6%, and the proportion of Sal forest remained constant (from 23.7% to 25.0%). Hence, Dinerstein's (1979a) estimate of grassland coverage was 8% higher than in this study, indicating a development of the vegetation towards later successional stages.

### 3.2. Ungulate abundance

The estimated density of six wild ungulates in DIN 1998 was 201.9/km<sup>2</sup>, four times higher than in DIN 1976 (Table 2). This increase was caused almost exclusively by a remarkable increase in chital. The errors of the estimates varied among the different species, but were quite small for the ones that contributed the most to the density change.

### 3.3. Grazers increased more than others? (prediction 1)

The density of chital, and to a lesser extent hog deer, increased markedly (Table 2 and Fig. 2). Because no error estimates were presented for the density of barasingha in

**Table 2 – Set of the best performing generalized linear models expressing the influence of habitat on densities of ungulates in Bardia National Park, Nepal, 1997–1999. TG = tall grasslands, SG = Savannah grasslands, CSF = climax Sal forests, SF = successional forests. Significant terms are in bold.  $\Delta$ AICc = the Akaike information criterion corrected for small samples (AICc) of the model of interest minus the smallest AICc among all models,  $\omega$  = Akaike weight. The columns on the right show predicted densities according to the best models in terms AICc. DIN 1976 = Densities within an 11.8 km<sup>2</sup> fraction of our 105 km<sup>2</sup> study area that was surveyed in 1976 (derived from Dinerstein, 1980), DIN 1998 = densities in the same area in 1998. Note that the standard errors (SE) of DIN 1976 were obtained by combining information from two different tables in (Tables 1 and 2) in Dinerstein (1980). Live weights of the ungulates were obtained from own data from radio-collared Indian muntjacs and hog deer (Odden and Wegge, 2007), and from Schaller (1967), Dinerstein (1980) and Karanth and Sunquist (1995).**

Species (weight)	No.	Models				Predicted densities (no./km <sup>2</sup> ± SE)		
		Terms	$\Delta$ AICc	$\omega$	R <sup>2</sup>	DIN 1976	DIN 1998	Whole study area
Muntjac (17 kg)	1	CSF <sup>***</sup> + SF <sup>***</sup> – TG	0.00	0.38	0.46	1.7 [-]	2.6 ± 0.4	2.3 ± 0.4
	2	CSF <sup>***</sup> + SF <sup>***</sup>	0.03	0.37	0.43			
	3	CSF <sup>***</sup> + SF <sup>***</sup> – SG – TG	2.25	0.12	0.47			
	4	CSF <sup>***</sup> + SF <sup>**</sup> – SG	2.44	0.11	0.43			
Hog deer (27 kg)	1	TG <sup>***</sup>	0.00	0.27	0.65	3.2 ± 1.2	6.9 ± 0.8	13.2 ± 1.5
	2	SF + TG <sup>***</sup>	0.17	0.25	0.66			
	3	SF – SG + TG <sup>***</sup>	1.12	0.16	0.67			
Wild boar (38 kg)	1	CSF <sup>***</sup>	0.00	0.29	0.46	4.2 ± 0.6	1.0 ± 0.2	2.2 ± 0.4
	2	CSF <sup>***</sup> + SF	0.62	0.21	0.48			
	3	CSF <sup>***</sup> + SG	0.98	0.18	0.48			
Chital (53 kg)	1	SF <sup>**</sup> + SG <sup>***</sup> – TG	0.00	0.37	0.77	31.8 ± 3.7	190.8 ± 16.6	84.7 ± 7.9
	2	SF <sup>***</sup> + SG <sup>***</sup>	0.09	0.35	0.76			
	3	–CSF + SF <sup>**</sup> + SG <sup>***</sup>	2.21	0.12	0.76			
	4	–CSF + SF <sup>**</sup> + SG <sup>***</sup> – TG	2.22	0.12	0.77			
Barasingha (159 kg)	1	CSF <sup>**</sup>	0.00	0.38	0.17	0.5 [-]	0.2 ± 0.1	0.4 ± 0.1
	2	CSF <sup>**</sup> + SG	1.59	0.17	0.18			
	3	CSF <sup>**</sup> + SF	2.09	0.13	0.17			
	4	CSF <sup>**</sup> + TG	2.23	0.12	0.17			
Nilgai (169 kg)	1	CSF <sup>†</sup>	0.00	0.34	0.12	5.0 ± 0.3	0.1 ± 0.1	0.3 ± 0.1
	2	CSF <sup>†</sup> + SF	1.46	0.17	0.14			
	3	CSF <sup>†</sup> + SG	2.18	0.12	0.12			
	4	CSF <sup>†</sup> + TG	2.30	0.11	0.12			

\* P < 0.05.  
 \*\* P < 0.01.  
 \*\*\* P < 0.001.

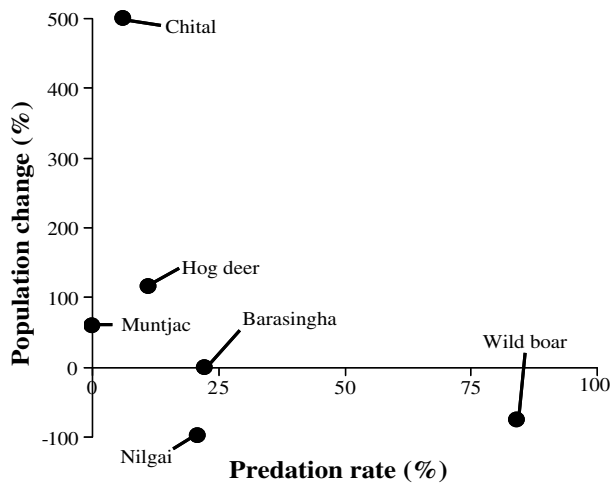
1976, it is difficult to assess the temporal change in abundance of this species. According to our initial model, the total number within our 105-km<sup>2</sup> area was 42 ± 10.4 animals. A study that was conducted within the same area a few years earlier estimated the number of barasingha to nearly twice that number (Ghimre, 1996). The barasingha is group-living and was quite rare in Bardia. Hence, we suspect that the discrepancy in barasingha numbers was due to sampling bias, i.e. some groups were missed during the block counts. We therefore adjusted our barasingha density estimate by multiplying the means and standard errors with 1.79, i.e. the ratio between Ghimre's (1996) and our density estimates for the whole study area. The adjusted density estimate in DIN 1998 was similar to that in DIN 1976, suggesting that their abundance had not changed (Table 2 and Fig. 2). Numbers of muntjac seemed to have increased, but the error estimate was high, whereas wild boar and nilgai had clearly decreased since the census in 1976 (Table 2). In conclusion, only two of the species had increased (hog deer and chital), while the other species had either decreased (nilgai and wild boar), or their densities had remained more or less unchanged (barasingha and muntjac). According to prediction 1, we expected increases not only in chital and hog deer

but also in barasingha and nilgai. Hence, prediction 1 was only partially supported.

### 3.4. Increased predator densities? (prediction 2)

During 1998/99, we obtained 30 photographs of 14 different tigers (4 males, 9 females and 1 of unknown sex) within the study area (Table 3). Two years later, we obtained 40 photographs of 22 different tigers. Program CAPTURE selected the models M<sub>h</sub> and M<sub>bh</sub> (capture probability varies among individuals and also with behavioural responses, respectively) as the best models for the data sets, which gave estimates of 13.3 ± 2.08 (SE) tigers/100 km<sup>2</sup> in 1998/99 and 19.3 ± 2.18 (SE) in 2000/01. Since the first camera trapping period was conducted during the same period as when the ungulates were censused (1997–1999), we used the data from 1998/99 in the subsequent analyses of prey removal. We assumed that the sex ratio among photographed tigers in 1998/99 was representative for the population, rendering 9.7 females and 4.3 males within the 105-km<sup>2</sup> study area.

We only obtained three photographs of two different leopards during the two camera trapping periods (Table 3). However, additional data indicated that there were more



**Fig. 2** – Annual predation of wild ungulates by tiger in the south-western part of Bardia National Park, Nepal, during 1997–1999, and changes in ungulate population densities from 1976 to 1997–99. Predation rates were estimated by combining information on mortality patterns of radio marked hog deer, predator scats and annual food consumption of tigers and leopards combined. We estimated population changes by comparing densities reported in [Dinerstein \(1980\)](#) and our own data.

leopards in the area. The camera-trapped animals, a male and a female, were both radio marked, and their movements were monitored intensively ([Odden and Wegge, 2005](#)). Their territories were spatiotemporally stable, overlapped each other, and were situated along the park border in the eastern part of the study area. We frequently observed pugmarks of female leopards to the north and south of the territory of the marked female, but no signs on the western side ([Odden, 2008](#)). Furthermore, the territory of the camera-trapped male bordered the territory of another radio marked male on the northern side, whose territory was mainly outside the study

area ([Odden and Wegge, 2005](#)). In addition, we frequently observed pugmarks of a male south of the radio-collared males. The territory sizes of the marked males were both nearly 50 km<sup>2</sup>. Assuming a similar range size of the unmarked male, it is likely that only a part of his territory was inside our study area. Hence, we counted the two male leopards that were not photographed as one, resulting in a total number of two adult males and three adult females within the study area.

### 3.5. Patterns of predation and prey removal (predictions 3, 4, and 5)

In the tiger scats, wild ungulates and other prey occurred at a frequency of 93.4% and 6.6%, respectively ([Table 4](#)). The equivalent numbers in leopard scats were 56.9% wild ungulates and 43.1% other prey. Chital was the most important food resource of both predators. Among the prey whose densities were not estimated, the remains of big domestic animals, i.e., cows and buffalos, occurred most frequently in tiger scats. Hairs of smaller domestic animals (goats, pigs and sheep) were frequently found in leopard scats. Furthermore, a relatively large proportion of leopard scats contained remains of birds and smaller mammals (classified as “other” in [Table 4](#)). The frequency of sambar in tiger scats was high, considering that the density of this species was very low. In fact, we never recorded sambar during the ungulate censuses, and this species was therefore not included in the ungulate density analyses.

Non-random selection of wild ungulate prey was evident among both tigers ( $X^2 = 302.5$ ,  $DF = 5$ ,  $P < 0.001$ ) and leopards ( $X^2 = 45.8$ ,  $DF = 5$ ,  $P < 0.001$ ). In the tiger scats, the frequencies of chital, and muntjacs were significantly lower and that of wild boar and barasingha significantly higher than expected ([Table 5](#)). In the leopard scats, wild boar occurred significantly more often and hog deer significantly less frequently than expected. Hence, our results show an opposite pattern than expected from prediction 3, as the more common species, chital

**Table 3** – Results from camera trapping of tigers conducted during 1998/99 and 2000/01 in Bardia National Park, Nepal. Distance units are in km and area units are in km<sup>2</sup>. Mean maximum distance moved (MDMM) is the average among the longest distances between two different captures of the same tiger. Strip width equals MDMM/2, and expresses the width of a buffer that is added to the sampling area (minimum convex polygon around trapping locations) to obtain an estimate of the area actually sampled with camera trapping (effective area).

	1998/99	2000/01
No. of trap stations	50	54
Distance between traps (min–max)	0.8–2.2	0.8–2.2
No. of trap nights	720	563
No. of leopard photographs	2	1
No. leopard photos/100 trap nights	0.28	0.18
No. of different leopards (male, female, unknown sex)	1/1/0	1/0/0
No. of tiger photographs	30	40
No. of tiger photos/100 trap nights	6.94	7.10
No. of different tigers (male, female, unknown sex)	4/9/1	8/13/0
Mean maximum distance moved	2.6 ± 0.57	4.1 ± 0.54
Strip width	1.35 ± 0.29	2.00 ± 0.27
Sampling area	81.0	88.3
Effective area	120.7	129.4
Tiger density (no/100 km <sup>2</sup> ± SE)	13.3 ± 2.08	19.3 ± 2.18

**Table 4 – Removal rates of ungulate prey by tigers and leopards in the south-western part of Bardia National Park, Nepal, 1997–1999. Removal rates by tigers were estimated with two methods: M1 assumes an annual meat consumption of 2190 kg for adult females, 2555 kg for adult males and 547 kg for cubs (Sunquist, 1981; Støen and Wegge, 1996), and M2 is based on mortality data of radio-collared hog deer. The prey removal estimates by leopards is based on the assumption that females with cubs consume 1460 kg of meat annually, whereas single females and males consume 1204 and 1570 kg, respectively (Odden and Wegge, in press). Live weights of prey were obtained from own data from radio-collared Indian muntjacs and hog deer, and from Schaller (1967), Dinerstein (1980), Fleagle (1999) and Karanth and Sunquist (1995). Relative numbers in scats were converted to relative numbers killed by using a formula given by Ackerman et al. (1984).**

Species	Prey		Tiger				Leopard		
	Live weight	Rel. abundance (%)	Rel. no. in scats (%)	Rel. no. killed (%)	M1 Removal rate (%)	M2 Removal rate (%)	Rel. no. in scats (%)	Rel. no. killed rate (%)	Removal rate (%)
Chital	53.0	69.1	59.0	52.1	5.9	6.2	46.7	21.7	1.9
Hog deer	27.0	24.1	11.1	14.7	10.7	11.1	1.1	0.8	0.2
Muntjac	16.6	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wild boar	38.0	2.9	17.4	18.5	80.7	84.1	10.0	5.6	12.0
Barasingha	159.0	1.0	2.7	1.6	21.5	22.4	2.2	0.7	4.2
Nilgai	169.0	0.3	1.1	0.6	20.0	20.8	0.0	0.0	0.0
Sambar deer <sup>a</sup>	212.0	0.0	2.1	1.3	–	–	0.0	0.0	0.0
Langur	6.5	–	1.4	5.7	–	–	9.0	21.8	–
Big domestic	167.0	–	4.4	2.5	–	–	1.0	0.3	–
Small domestic	27.5	–	0.3	0.4	–	–	20.0	15.3	–
Other	5.0	–	0.5	2.9	–	–	11.0	33.8	–

a Very rare and never recorded in ungulate censuses, thus no estimate of removal rate.

**Table 5 – Selection among wild ungulates by tigers and leopards in the south-western part of Bardia National Park, Nepal, 1997–1999, based on likelihood ratio tests (Program Scatman, Hines and Link, 1994). Obs. = frequency of occurrence of prey species in scats (%), Exp. = expected frequency of prey species in scats (%). Signs + and – indicate preference and avoidance, respectively.**

	Tiger				Leopard			
	Obs. (%)	Exp. (%)	X <sup>2</sup>	P	Obs. (%)	Exp. (%)	X <sup>2</sup>	P
Chital	64.6	83.1	80.83	<0.001–	77.8	83.1	1.08	0.299
Hog deer	12.1	11.0	0.47	0.583	1.9	10.9	4.59	0.032–
Muntjac	0.0	1.6	5.26	0.022–	0.0	1.5	0.85	0.356
Wild boar	19.0	2.4	402.09	<0.001+	16.7	2.4	47.89	<0.001+
Barasingha	3.0	1.4	6.57	0.010+	3.7	1.3	2.18	0.139
Nilgai	1.2	0.7	1.38	0.240	0.0	0.7	0.37	0.545

and hog deer, were killed less frequently, not more, than expected.

The removal rates by tigers were high for three of the least abundant species; barasingha (21.5–22.4%), nilgai (20.0–20.8%) and wild boar (80.7–84.1%) (Table 4). The removal rate of sambar deer could not be quantified due to its very low abundance, but was undoubtedly also quite high. Thus, prediction 5 of inverse density dependent predation was partly supported.

Muntjac and wild boar occurred at intermediate densities in the study area, but their removal rates differed markedly; muntjacs were never recorded in the scats, whereas the removal rates of wild boar were the highest among all the natural prey species, by both predators (Table 4). Except for muntjac, the lowest removal rates by tigers were recorded among the most abundant prey species, chital and hog deer (between 5.9% and 6.2% and 10.7% and 11.1%, respectively). There was no clear relationship between predation impact by tigers across the wide range of prey densities. Instead,

the very high predation rates on wild boar and sambar and relatively low rates on chital and hog deer give support to prediction 4, i.e. that predation is related to prey preference independently of their densities.

Leopards had a much lower impact on wild ungulates than tigers. Highest removal rates by leopards were recorded for wild boar (12%). Among the other species, leopards killed a larger proportion of the chital population than of hog deer and muntjac (Table 4).

## 4. Discussion

### 4.1. General change in the large mammal community

Within the smaller part of the overall study area, the total number of wild ungulates increased by a factor of 4.3 during the 22 years of protected area management, to about 200 animals/km<sup>2</sup> in 1997/99. The change in abundance was due to a remarkable increase in chital and hog deer, as the other four

ungulates declined (nilgai and wild boar) or remained more or less unchanged (muntjac and barasingha) (Fig. 2). Of the two predators, only tiger responded positively to the increased prey base. With an estimated high density of nearly 20 animals/100 km<sup>2</sup>, territorial behaviour seems to have had limited effect in regulating tiger numbers, as recapture locations during camera trapping indicated substantial intrasexual overlap. Instead, limited dispersal due to surrounding farmland and unsuitable habitat may have acted to pack animals densely together on restricted, optimum space. The tiger and prey density estimates in this study are well within the 95% prediction intervals of the model describing the relationship between tiger and prey densities proposed by Karanth et al. (2004). Our data therefore support the conclusion of Karanth et al. (2004) that prey density is a suitable predictor of tiger abundance. Better protection from poaching probably contributed only marginally to the increase in tigers; prior to establishment, the area was used as a royal *shikari* (hunting) reserve with deployed forest guards to prevent killing of tigers (Bolton, 1976).

The mean capture frequency of leopards was 0.25/100 trap nights and, thus, far lower than for tigers (7.02/100 trap nights). Much higher capture frequencies of leopards have been observed in other studies; 5.44/100 trap nights in Nagarhole National Park, India, and 2.28 in Pench National Park, India (Karanth and Nichols, 1998). Also, in a recent study in Malaysia leopards were camera-trapped more frequently than tigers (Kawanishi and Sunquist, 2004). Hence, leopards are readily sampled by camera traps, and their low capture success in our study therefore suggests a low density. The lack of a positive density response among leopards, like that seen among tigers, may be due to suppression by the expanding tiger population; Karanth and Sunquist (1995) suggested that when large-sized prey are scarce, like in our study area, tigers may displace leopards due to interspecific competition for the same food resources. However, the bulk of the diet of both species was made up by the abundant chital, from which removal rates were modest and low, respectively. This suggests that competition for food was not a determinant factor. Instead, social dominance is a more likely explanation, as inferred from their spacing behaviour and food habits (Odden, 2008).

#### 4.2. Have grazers increased more than browsers? (prediction 1)

The remarkable increase in number of ungulate prey was due to the positive response of two species. Hog deer, a true grazer, increased by a factor of 2.2, and chital, a mixed feeder but with a grass-dominated diet, increased by a factor of 6. Barasingha is a true grazer, but did not increase, and nilgai, a mixed feeder, decreased markedly and was heading towards extirpation. Hence, the prediction was only partly supported. In spite of management actions aimed at maintaining the tall and short grasslands, succession has led to constriction of grasslands and an increased relative coverage of forest. This should have favoured muntjac, wild boar and sambar. Only muntjac may have responded positively, if at all.

The initial large increase in chital and hog deer, in spite of some loss of preferred habitat, was probably mediated by the release of food competition from domestic livestock concur-

rent with a low predation pressure from tigers and leopards. Also, the practice of cutting and burning the short grasslands has greatly improved the habitat and food quality for chital (Moe and Wegge, 1994, 1997). The lack of a similar positive response in barasingha may be explained by their small initial density, and that they are large-bodied and thus more attractive prey for tigers than the smaller chital and hog deer.

#### 4.3. Patterns of predation (predictions 3–5)

Remains of hog deer occurred less frequently than expected in leopard scats, and that of chital less than expected among tigers. Hence, neither of the two predators selected for the most abundant prey. Both predators selectively killed wild boar, and muntjac was avoided. Nilgai and barasingha were recorded more often than expected. Hence, except for muntjacs, prey species of low density were not avoided. Accordingly, the predators did not exhibit a Type III functional response, i.e., they did not direct their predation at the more abundant species. Hence, prediction 3 was not supported.

According to predictions 4 and 5, predation should be a limiting factor for some of the ungulate species, either for those that initially occurred in low densities (prediction 5), or for those that are commonly preferred by the predators independently of their abundance (prediction 4). Removal rates were quite high for wild boar, nilgai and barasingha, and much lower for muntjac, hog deer and chital (Table 4). Hence, except for muntjac, the commonly preferred large-sized species (barasingha and nilgai), both occurring at low densities, and the selectively killed wild boar at medium density, had highest removal rates, which supports prediction 4.

According to prediction 5, initially rare species should have declined due to an increasing predation pressure. The population development of nilgai did not follow this prediction, as they showed the most pronounced decrease even though they were the second most abundant ungulate in 1976 (Dinerstein, 1980). However, their decline may be related to prediction 5, albeit in an indirect way: after area protection, tiger numbers increased, tracking the rapid increase in chital and hog deer. Concurrently, as livestock grazing ceased, the vegetation responded by proliferating new shrubs and tree seedlings (Sharma, 1999), which virtually closed the visibility in the lower strata in the forested habitats. Nilgai rely on sight for detecting predators (Sheffield et al., 1983). Thus, a much denser shrub layer probably made the nilgai more vulnerable to predation by tiger. Although not a primary food species, by representing prey of optimum size (Karanth and Sunquist, 1995), nilgai may therefore have been subject to unsustainable losses from predation by an increasing number of tigers.

Does predation by tigers and leopards limit the abundance of their prey in the study area? Predators may have a regulating effect on their prey species (i.e., maintain their densities within narrow bounds) if their predation rate varies with the density of the prey species. Conversely, predators may limit the density of their prey if their removal constitutes a large proportion of the total mortality of the prey and the density of the prey species is relatively constant or decreasing. In other words, regulation implies density dependence, whereas limitation implies that predation is a main factor for slowing down, halting, or reversing population growth. The two dom-

inating ungulates, hog deer and chital, increased 2.2–6-fold during the 22-year period, presumably due to improved habitat quality. Their total estimated annual removal rates by tiger and leopard were about 11% and 8%, respectively (Table 4). Both species are monotocus, seasonal breeders. To balance their recruitment rates, annual mortalities should not exceed 20–25%. Thus, predation accounted for a relatively large proportion of their annual mortalities. The abundance of chital was censused in 1993 (Andersen and Næss, 1993), yielding a slightly higher density than our 1997–1999 estimate, which suggests that the combined predation by both cats may have had a limiting effect on this species since the early 1990s.

The continued increase in hog deer implies that predation has had little limiting effect on this species. Instead, hog deer may have benefited from the re-introduction of greater one-horned rhinoceros (*Rhinoceros bicornis*) in the late 1980s. This species now shares the floodplain habitat with hog deer, and through their feeding and trampling it probably facilitates the sprouting of *Saccharum spontaneum*, thereby improving the habitat quality for hog deer (Wegge et al., 2006).

Despite the very low density of sambar, this species occurred in the tiger scats more frequently than barasingha. This indicates that sambar was a selected prey by tiger, as have been documented in other studies (Biswas and Sankar, 2002; Bagchi et al., 2003). The fact that this species has remained quite rare within the study area in spite of suitable habitat, and that they are relatively abundant in the adjoining Sal forests (Dinerstein, 1979b; pers. obs.) suggests that tiger predation on potential colonizers is a main reason for preventing this species from becoming established within the study area. Thus, tiger predation is probably exerting strong limitation on this species, which lends support for both predictions 4 and 5.

High removal rates were recorded on wild boar, nilgai and barasingha, and their abundances had decreased or not changed notably since 1976 (Fig. 2). The reproductive capacity of wild boar is extremely high (Nahlik and Sandor, 2003), and this species can therefore sustain high predation losses. Our results show that this species is also a preferred prey by tiger, as was also concluded in an earlier study (Støen and Wegge, 1996). Nilgai and barasingha are within the preferred size range for tigers. Among both species, field observations indicated high recruitment of young (Subedi, 2001; pers. obs.), implying that food and habitat conditions were not limiting. Thus, the decreasing and stabilizing trends of abundance were likely caused by the predation from the expanded tiger population; in nilgai mediated through structural vegetation changes after the exclusion of livestock. Predation was therefore clearly a limiting factor on these three prey species.

The density of muntjacs appeared to have increased, and predation by tigers and leopards was almost nil. Muntjac is known to be prey of leopards elsewhere (see review by Hayward et al., 2006), but in our study area other species, especially chital, were more readily available and attractive prey. Hence, predation was not a limiting factor on this species. Instead, muntjac may have benefited from the increase in forest cover. Also, in this species density is probably stabilized through a site-specific dominance system (Odden and Wegge, 2007), whereby animal numbers are regulated mainly by spacing behaviour (Davies and Houston, 1984; Lomnicki, 1988).

## 5. Conclusions and implications for management

Following 22 years of protected area management, three of six wild ungulates increased (chital, hog deer and muntjac), wild boar and nilgai decreased, and barasingha remained unchanged. Tiger numbers increased remarkably, whereas leopard abundance did not change. High and skewed impact from tiger predation on the different ungulates largely explains their patterns of population developments.

Our findings do not exclude the influence of other potential factors, such as interspecific competition. Theory states that the importance of this form of competition tends to decrease when the heterogeneity of the environment increases, due to the enhanced opportunities for niche separation (Chesson and Rosenzweig, 1991; Cromsigt and Olff, 2006). The ungulate species that were included in our analyses showed pronounced differences in the influence of habitat on their densities (Table 2), and they did not overlap extensively in diets (Dinerstein, 1979b; Wegge et al., 2006). Hence, considering the marked habitat heterogeneity of the study area in Bardia (Odden and Wegge, 2007), the influence of interspecific competition should be relatively low. Nevertheless, this factor may have had an additive effect on the population development of some of the ungulates in the area.

The large mammal community has certainly not reached any stable balance or “dynamic equilibrium” among its members. Tiger numbers increased from 1989 to a record high of ca. 19 animals/100 km<sup>2</sup> in 1999. Karanth et al. (2006) showed that tiger numbers may locally fluctuate markedly over short periods. Thus, predation impacts will vary with such temporal variation. Owing to progressively denser habitat that makes them more vulnerable to tiger predation, nilgai appeared to be heading for extinction. A prolific breeder, wild boar is likely to fluctuate notably from year to year, its high reproductive capacity and immigration from surrounding Sal forests buffering its very high predation rate. Chital, the staple food supply of both tigers and leopards, is likely to be negatively affected by the ongoing succession towards later seral stages with denser undergrowth. A pronounced decline of this species is apt to have cascading effects on the composition of the whole mammal community, both on the two main predators and the other ungulates.

Our analyses show that the establishment of a protected area and the subsequent conservation efforts initiated by the wildlife conservation authority in Nepal have been successful; ungulate densities have increased to levels higher than in most other tropical and sub-tropical areas (e.g. Schaller, 1967; Eisenberg and Seidensticker, 1976). As a consequence, the south-western part of Bardia National Park supports one of the densest tiger populations ever recorded (Karanth et al., 2004; Kawanishi and Sunquist, 2004; Wegge et al., 2004). The ban on livestock grazing, and predation by an expanding tiger population, has played a major role in shaping the current ungulate community, with predation becoming a limiting factor for several species. Hence, conservation did not benefit all members of the large mammal community, especially not the nilgai and the endangered barasingha. Potentially negative effects on ungulate populations from an increased large carnivore guild need therefore

to be taken into account in conservation planning. This statement contrasts with the conclusions of numerous previous studies, which emphasize the importance of large carnivores for maintaining biodiversity. Large carnivores are often portrayed as ecosystem janitors that stabilize the system, for instance by their ability of inhibiting meso-predator release, or by preventing over-abundance among their prey (e.g. Terborgh et al., 1999).

Improving the habitat conditions for prey species and providing full protection to both predators and their prey within a small area will affect neighbouring fauna through source-sink processes. In the case of our study area in Bardia, where people and farmland that restrict animal dispersal occupy much of the surrounding land, wildlife conflicts are apt to increase. Typically, the level of crop damage and frequencies of livestock predation and human injuries and death from tigers have increased in recent years (DNPWC, 2005). Prevention of genetic exchange with other populations may have negative effects on the genetic composition and long-term viability of isolated populations like that in Bardia National Park (Smith et al., 1998). Thus, a recently initiated landscape program (MFSC, 2006), aimed at restoring habitats outside the Park and establishing connectivity to other tiger populations, is a timely and well-founded management initiative, provided it does not impose hardships on local people. Balancing the needs and aspiration of poor farmers living next to the Park and the need for conserving endangered, large and dangerous animals is a difficult and challenging task in any developing country, including Nepal.

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