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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^2, almost exclusively due to a remarkable increase in chital deer (*Axis axis*). Tiger density also increased markedly to nearly 20 animals/100 km^2, whereas leopard density did not and was ca. 5 animals/100 km^2. 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, 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 effects 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^2 in a smaller part of the study area, whereas the total density of wild ungulates averaged 46 per km^2. 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	*Partially supported*: 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	*Partially supported*: large increase in tigers, no apparent change in leopards
3	Predation is positively density dependent and levels out interspecific differences in prey abundance	*Not supported*: 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	*Supported*: 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	*Partially supported*: highest impact on medium and low-density, but preferred, wild boar and sambar

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