



Feeding ecology of two endangered sympatric megaherbivores: Asianelephant *Elephas maximus* and greater one-horned rhinoceros *Rhinoceros unicornis* in lowland Nepal

Authors: Pradhan, Narendra M. B., Wegge, Per, Moe, Stein R., and Shrestha, Anil K.

Source: *Wildlife Biology*, 14(1) : 147-154

Published By: Nordic Board for Wildlife Research

URL: [https://doi.org/10.2981/0909-6396\(2008\)14\[147:FEOTES\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2008)14[147:FEOTES]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

SHORT COMMUNICATION

Short communication articles are short scientific entities often dealing with methodological problems or with byproducts of larger research projects. The style is the same as in original articles

Feeding ecology of two endangered sympatric megaherbivores: Asian elephant *Elephas maximus* and greater one-horned rhinoceros *Rhinoceros unicornis* in lowland Nepal

Narendra M.B. Pradhan, Per Wegge, Stein R. Moe & Anil K. Shrestha

Pradhan, N.M.B., Wegge, P., Moe, S.R. & Shrestha, A.K. 2008: Feeding ecology of two endangered sympatric megaherbivores: Asian elephant *Elephas maximus* and greater one-horned rhinoceros *Rhinoceros unicornis* in lowland Nepal. - Wildl. Biol. 14: 147-154

We studied the diets of low-density but increasing populations of sympatric Asian elephants *Elephas maximus* and greater one-horned rhinoceros *Rhinoceros unicornis* in the Bardia National Park in lowland Nepal. A microhistological technique based on faecal material was used to estimate the seasonal diet composition of the two megaherbivores. Rhinos ate more grass than browse in all seasons, and their grass/browse ratio was significantly higher than that of elephants. Both species ate more browse in the dry season, with bark constituting an estimated 73% of the elephant diet in the cool part of that season. Diet overlap was high in the resource-rich monsoon season and lower in the resource-poor dry season, indicating partitioning of food between the two species in the period of resource limitation. Both species consumed large amounts of the floodplain grass *Saccharum spontaneum*, particularly during the monsoon season. As the numbers of both species increase, intraspecific and interspecific competition for *S. spontaneum* in the limited floodplains is likely to occur. Owing to their higher grass diet and more restricted all-year home ranges within the floodplain habitat complex, rhinos are then expected to be affected more than elephants.

Key words: competition, diet, elephant, *Elephas maximus*, food habits, megaherbivores, rhino, *Rhinoceros unicornis*, *Saccharum spontaneum*

Narendra M.B. Pradhan, Per Wegge, Stein R. Moe & Anil K. Shrestha, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Ås, Norway - e-mail addresses: narendrapradhan@hotmail.com (Narendra M.B. Pradhan); per.wegge@umb.no (Per Wegge); stein.moe@umb.no (Stein R. Moe); savetiger2002@yahoo.com (Anil K. Shrestha)

Corresponding author: Per Wegge

Received 27 January 2006, accepted 10 July 2006

Associate Editor: Johan T. du Toit

Asian elephant *Elephas maximus* (henceforth elephant) and greater one-horned rhinoceros *Rhinoceros unicornis* (henceforth rhino) are both internationally endangered species (World Conservation Union 2004). Loss and fragmentation of habitat, poaching and other human disturbances commonly cause these megaherbivores to compress into small protected areas (Owen-Smith 1988, Sukumar 1989). Compression in limited areas results in high densities even though their absolute population sizes are decreasing (Croze et al. 1981).

Megaherbivores need more food and space than do smaller herbivores (Owen-Smith 1988), but space and food are common constraints in areas of high population pressure. For large herbivores, for which population regulation through natural predation is not common, it is likely that food is the limiting resource (Sinclair 1975, Owen-Smith 1988, Sukumar 1989). In the world of today, the most productive habitats, like the floodplain areas in which rhinos are commonly found, are severely impacted by an ever-increasing human population, and they are therefore among the most threatened ecosystems (Dinerstein 2003).

As mixed feeders, elephant and rhino have considerable seasonal variation in consumed food items (rhino: Laurie 1982, Jnawali 1995; elephant: Sukumar 1989, Williams 2003). At present, in most parts of the world, elephants and rhinos no longer exist together. Little is known, therefore, about their diet and space overlap. Except for a recent dry season study (Steinheim et al. 2005), to our knowledge no comprehensive diet study has yet been made on sympatric elephants and rhinoceros, neither in Africa nor in Asia. The Bardia National Park in Nepal provides a unique opportunity to compare their diets, because in this park they exist sympatrically in a comparatively small area. Besides, both species are increasing in numbers, elephants because of immigration, probably from India (Velde 1997), and rhinos due to re-introduction to the park since 1986 (Department of National Parks and Wildlife Conservation 2002).

As mixed feeders, and because they derive their food from the same vegetation layers (Guy 1976), these species occupy similar ecological niches. Increasing numbers of such large mammals in a

small area may cause reduction of food and space for one of them. Therefore, information regarding diets is essential for long-term conservation management.

Methods

Study area

Bardia National Park (28°35' N, 81°20' E) is the largest national park in the southwestern lowland (Terai) of Nepal covering an area of 968 km². The climate is subtropical monsoonal type with three distinct seasons: cool-dry (November-February), hot-dry (March-June) and monsoon (July-October). Average yearly temperature ranges from a minimum of 10°C in January to a maximum of 41°C in May (Dinerstein 1979a). Most of the rain (1,560-2,230 mm) falls during June-September, somewhat later than in the rest of the country (Bolton 1976).

The vegetation is subtropical, ranging from early successional floodplain communities along the Karnali and Babai rivers to a mature climax Sal *Shorea robusta* forest on the upper, drier area. Dinerstein (1979b) described six distinct vegetation types for the Karnali floodplain area in the southwestern part of the park and later on Jnawali & Wegge (1993) extended this to seven types (Table 1).

Due to recent immigration, the elephant population has increased from two males in 1992 to about 80 individuals at present (N.M.B. Pradhan, unpubl. data). Altogether 83 rhinos have been translocated to the area since 1986. At the time of our study, some 70-80 animals were estimated to be inside the park (N.M.B. Pradhan, unpubl. data). Other large herbivores in the park are spotted deer *Axis axis*, hog deer *Axis porcinus*, swamp deer *Cervus duvauceli*, sambar deer *Cervus unicolor*, nilgai antelope *Boselaphus tragocamelus* and four-horned antelope *Tetracerus quadricornis*.

Microhistological analysis

To study the diets, we used a microhistological technique based on faecal material (Sparks & Malechek 1968, Dawson & Ellis 1979). This method is considered reliable for estimating the diet composition of herbivores (Stewart 1967, Tood & Hansen 1973,

Table 1. Vegetation types in Bardia National Park in lowland Nepal.

Vegetation Type	Description
Tall grassland	Consists of a mixture of perennial tall grasses in the floodplain where <i>Saccharum spontaneum</i> is the dominant species; other associate grass species are <i>S. bengalensis</i> , <i>Phragmites karka</i> and <i>Arundo donax</i> .
Khair-sissoo forest	The pioneer association on riverside gravel dominated by <i>Sissoo Dalbergia sissoo</i> and Khair <i>Acacia catechu</i> tree.
Mixed hardwood forest	Comprises of <i>Terminalia tomentosa</i> , <i>Schleicheria trijuga</i> , <i>Adina cordifolia</i> and <i>Mitragyna parviflora</i> . These species intermingle in the forests, resembling wooded savannah vegetation, but with a denser tree layer and a more distinct shrub layer such as <i>Colebrookia oppositifolia</i> .
Riverine forest	Distributed in patches along the watercourse and in Riverine forest depression; consists mostly of evergreen trees like <i>Syzizium cumini</i> , <i>Ficus racemosa</i> and <i>Mallotus philippinensis</i> and species able to withstand water logging. <i>Callicarpa macrophylla</i> and <i>Colebrookea oppositifolia</i> are common shrubs found in this vegetation type.
Phanta	Short, open grasslands in previously cultivated field; <i>Imperata cylindrica</i> is the dominating grass species.
Wooded savannah	Characterised by short grasses such as <i>Imperata cylindrica</i> and <i>Vetivria zizanoides</i> with sparsely distributed tree species such as <i>Bombax ceiba</i> , <i>Mallotus philippinensis</i> and <i>Adina cordifolia</i> .
Sal forest	Dominated by <i>Shorea robusta</i> with associated species such as <i>Terminalia tomentosa</i> and <i>Lagerstroemia parviflora</i> .

Johnson & Pearson 1981, Holechek & Gross 1982, Alipayo et al. 1992, Jnawali 1995). The technique is believed to be especially suitable for comparative studies of non-ruminant, monogastric bulk-feeding species (Butet 1985), where a large proportion of the food passes through the digestive tract virtually undigested (Owen-Smith 1988).

Fresh dung samples of elephants (N = 296) were collected from February 2003 to March 2004. Samples were selected on the basis of their bolus size to ensure a wide range of individuals and age representation. Due to the habit of rhino to defecate in latrines (Laurie 1982), samples of variable bolus sizes were collected from widely spaced latrines. Laboratory procedure and slide preparation for analysis followed Jnawali (1995) and Wegge et al. (2006).

A total of 71 potential food species were collected for the preparation of reference slides. The collection was made on the basis of previous diet studies of rhino (Jnawali 1995) and elephant (Steinheim et al. 2005) and from plants that we observed to be eaten in the field.

The fragments of the plant reference material were photographed using a Leica DFC camera mounted microscope. Altogether 1,250 reference photographs were taken using 100-400 x lenses.

Two transects per slide were randomly chosen and the first 20 non-overlapping fragments intercepted by the transect lines, identifiable at least to category level (i.e. grass, browse and others) were compared with the reference slides. Whenever possible, the fragments were identified to species level. If species or genus could not be determined, then the category level and plant part level (bark, leaf and unknown) were recorded. The fragments which could not be identified to species or genus

level but to category were classified into 'unidentified grass', 'unidentified browse' or 'unidentified others'. A total of 200 fragments per animal species per season were recorded.

The relative frequency of a plant species in the faecal material was calculated. Diet overlap was calculated using the percentage overlap index (Renkonen index; Renkonen 1938, Krebs 1999). We carried out χ^2 tests to compare the seasonal and yearly frequencies of grasses and browse within and between elephant and rhino. We also used χ^2 statistics to examine for differences between main plant species and the parts of browse eaten by the two megaherbivores.

Results

We recorded a total of 31 species of elephant food plants (15 browse species and 16 grass species) and 28 species of rhino food plants (13 browse species, 13 grass species, and two other plants) from the dung (Table 2).

The proportions of consumed browse and grass differed between the two species ($\chi^2 = 110.8$, $df = 1$, $P < 0.0001$). On an annual basis, browse dominated the elephant diet (60.2%), whereas rhinos were mainly grazers (69.5%). Elephants ate mainly browse in the cool-dry season (83.5%) and in the hot-dry season (58.0%), whereas they were mainly grazers (61.0%) during the monsoon season. Grasses made up the bulk of the rhino diet during all seasons, but the proportion was highest during the monsoon season (see Table 2).

Bark turned out to be a very important food item for elephants (Fig. 1). On an annual basis elephants consumed 51.5% bark, and in the cool-dry

Table 2. Percentage representation of plant species in the diet of Asian elephant and greater one-horned rhino in Bardia National Park in lowland Nepal.

Species	Rhino						Elephant					
	Cool dry		Hot dry		Monsoon		Cool dry		Hot dry		Monsoon	
	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD
Browse												
<i>Acacia catechu</i>	-	-	-	-	-	-	-	-	1.5	3.4	0.5	1.6
<i>Aegle marmelos</i>	-	-	-	-	-	-	2.5	3.5	1.0	2.1	-	-
<i>Bauhinia</i> spp.	-	-	-	-	-	-	8.0	5.9	4.0	5.2	3.0	2.6
<i>Bauhinia vahlii</i>	-	-	-	-	-	-	-	-	-	-	0.5	1.6
<i>Bombax ceiba</i>	3.0	3.5	3.5	4.1	-	-	-	-	-	-	-	-
<i>Bridelia stipularis</i>	-	-	-	-	-	-	-	-	1.0	2.1	0.5	1.6
<i>Caesalpinia decapetala</i>	0.5	1.6	0.5	1.6	-	-	-	-	-	-	0.5	1.6
<i>Calamus tenuis</i>	0.5	1.6	1.0	2.1	-	-	1.0	3.2	2.0	2.6	-	-
<i>Callicarpa macrophylla</i>	10.0	4.7	2.0	3.5	0.5	1.6	-	-	-	-	-	-
<i>Colebrookea oppositifolia</i>	1.0	2.1	1.0	2.1	0.5	1.6	-	-	-	-	-	-
<i>Dalbergia sissoo</i>	7.0	5.9	6.0	7.7	4.5	3.7	4.0	5.7	1.5	2.4	0.5	1.6
<i>Desmodium oojeinense</i>	-	-	-	-	-	-	2.5	2.6	1.5	2.4	1.0	3.2
<i>Dillenia pentagyna</i>	-	-	-	-	-	-	-	-	-	-	0.5	1.6
<i>Ehretia laevis</i>	5.0	4.1	4.0	5.7	2.0	3.5	1.5	3.4	0.5	1.6	3.5	4.1
<i>Ficus glomarata</i>	0.5	1.6	-	-	-	-	-	-	-	-	-	-
<i>Holarrhena antidysentrica</i>	-	-	-	-	-	-	-	-	-	-	0.5	1.6
<i>Litsea monopetala</i>	-	-	-	-	0.5	1.6	-	-	-	-	-	-
<i>Mallotus philippinensis</i>	8.0	6.7	5.0	4.7	2.0	3.5	3.0	3.5	0.5	1.6	1.5	2.4
<i>Millettia auriculata</i>	-	-	-	-	-	-	-	-	-	-	0.5	1.6
<i>Spatholobus parviflorus</i>	-	-	0.5	1.6	-	-	1.5	2.4	1.5	3.4	3.0	2.6
<i>Trewia nudiflora</i>	1.0	2.1	-	-	1.0	2.1	-	-	-	-	-	-
<i>Ziziphus mauritiana</i>	1.0	2.1	1.0	2.1	0.5	1.6	-	-	-	-	-	-
Unidentified browse	9.0	6.1	4.0	4.6	1.5	2.4	59.5	16.4	43.0	11.7	23.0	13.0
Total browse	46.5		28.5		13.0		83.5		58.0		39.0	
Grass												
<i>Apluda mutica</i>	-	-	-	-	-	-	-	-	-	-	0.5	1.6
<i>Arundo donax</i>	3.0	3.5	1.5	3.4	8.5	5.3	1.0	3.2	2.5	3.5	3.0	3.5
<i>Cyperus</i> spp	-	-	0.5	1.6	-	-	-	-	-	-	-	-
<i>Cymbopogon</i> spp	3.0	4.8	3.0	4.2	2.0	3.5	-	-	1.5	2.4	-	-
<i>Cynodon dactylon</i>	2.0	2.6	2.5	2.6	7.0	3.5	-	-	0.5	1.6	-	-
<i>Dendrocalamus</i> spp -	-	-	-	-	-	0.5	1.6	1.5	3.4	1.5	3.4	-
<i>Desmostachia bipinnata</i> -	-	0.5	1.6	2.0	2.6	0.5	1.6	5.0	5.3	1.5	2.4	-
<i>Imperata cylindrica</i> -	-	4.5	5.0	4.5	3.7	-	-	2.0	2.6	2.0	3.5	-
<i>Narenga porphyrocoma</i>	3.0	3.5	1.0	2.1	5.5	3.7	-	1.5	3.4	3.0	4.2	-
<i>Panicum</i> spp	-	-	-	-	-	-	-	-	3.0	4.2	-	-
<i>Phragmites karka</i>	-	-	0.5	1.6	1.0	2.1	2.5	5.4	-	-	1.0	3.2
<i>Saccharum bengalensis</i>	3.5	4.1	2.5	2.6	3.0	3.5	-	-	2.5	3.5	4.0	5.2
<i>S. munja</i>	-	-	-	-	-	-	-	-	1.0	2.1	0.5	1.6
<i>S. spontaneum</i>	18.5	9.4	31.5	9.1	28.0	10.9	1.5	3.4	10.5	6.0	25.0	13.5
<i>Themeda arundinarea</i>	6.5	6.3	-	-	4.0	3.9	-	-	1.0	2.1	-	-
<i>Typha elephantiana</i>	-	-	-	-	0.5	1.6	-	-	-	-	0.5	1.6
<i>Vetiveria zizanioides</i>	-	-	0.5	1.6	6.5	7.8	-	-	-	0.5	1.6	-
Unidentified grass	13.0	11.1	20.5	7.2	14.5	8.3	10.5	8.0	9.5	6.4	18.0	8.6
Total grass	52.5		69.0		87.0		16.5		42.0		61.0	
Others												
<i>Cirsium wallichii</i>	0.5	1.6	-	-	-	-	-	-	-	-	-	-
Water herb	0.5	1.6	2.5	4.2	-	-	-	-	-	-	-	-
Total others	1.0		2.5									
Total	100.0		100.0		100.0		100.0		100.0		100.0	

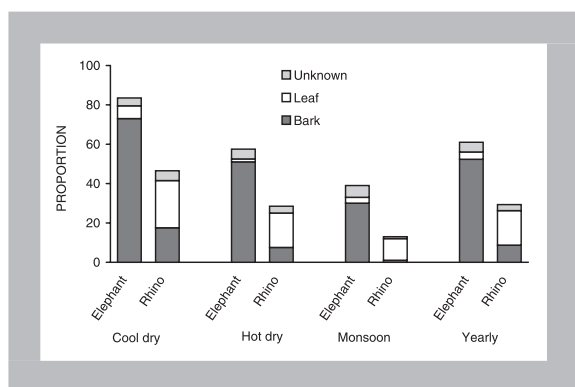


Figure 1. Proportions of bark (■), leaves (□) and unknown plant parts (□) in the browse diets of Asian elephant and greater one-horned rhino in Bardia National Park in lowland Nepal.

season the proportion of bark was as high as 73% (see Fig. 1). Annually, the rhinos consumed only 8.7% bark, and in contrast to elephants, leaves (17.5%) comprised a proportionally higher part of their browse diet than bark did ($\chi^2 = 197.6$, $df = 1$, $P < 0.0001$; see Fig. 1).

The woody species *Dalbergia sissoo*, *Mallotus philippinensis*, *Ehretia laevis* and *Calamus tenuis* were common food species for both the elephant and the rhino. *Callicarpa macrophylla* and *Bombax ceiba* were other important browse species for rhino, but not for elephant. *Aegle marmelos*, *Bauhinia* spp., *Desmodium oojeinense* and *Spatholobus parviflorus* were found frequently in the elephant browse diet, but were either quite rare or absent in the rhino diet. A large proportion of the woody species consumed by elephants was bark and could not be identified to species or genera (see Table 2).

The tall grass *Saccharum spontaneum* was a very important species in the rhino diet during all three seasons comprising 18.5-31.5%. The same species also comprised 10.5 and 25% of the elephant diet during the hot-dry and monsoon seasons, respectively (see Table 2). Both the rhino and the elephant differed in their seasonal consumption of tall grass ($\chi^2 = 16.3$, $df = 2$, $P = 0.003$ for rhino and $\chi^2 = 12.1$, $df = 2$, $P = 0.002$ for elephant). Other frequently found grasses in both the elephant and rhino diets were *Arundo donax*, *Desmostachia bipinnata*, *Imperata cylindrica*, *Narenga porphyrocoma* and *Saccharum bengalensis*. Among other grasses, *Vetiveria zizanioides*, *Themeda arundinacea*, *Cynodon dactylon* and *Cymbopogon* spp. were important food plants for rhino whereas *Panicum* spp. was important only for elephant.

Table 3. Percentage diet overlaps between Asian elephant and greater one-horned rhino in Bardia National Park in lowland Nepal.

Diet category	Cool dry	Hot dry	Monsoon	Yearly
Browse	0.37	0.22	0.30	0.33
Grass	0.33	0.56	0.67	0.77
All species	0.33	0.45	0.61	0.60

Diet overlap between elephant and rhino, as represented by the percentage overlap index, was 33% in the cool-dry season, 45% in the hot-dry season and 61% in the monsoon season. Diet overlap was relatively small for browse species but much higher for grass species, particularly in the hot-dry (56%) and monsoon seasons (67%; Table 3).

Discussion

Both herbivore species consumed more grass during the monsoon season than during the two dry seasons, but rhinos consumed consistently more grass than elephants all year around. An increase in browse from the wet to the dry season has also been recorded in various studies of the African savanna elephant *Loxodonta africana* (Wing & Buss 1970, Field & Ross 1976, Guy 1976, Barnes 1982), the Asian elephant (Sukumar 1989, Williams 2003) and the rhino (Laurie 1982, Jnawali 1995). When grasses dry up and become senescent, their nutritive quality declines rapidly to less than that of browse (Pellew 1984, Sukumar 1989). The elephant, being more mobile and having a flexible trunk, is then able to exploit the more dispersed browse sources at less energetic cost than rhino. Conversely, as the digestive passage throughput rate is slower in rhino than in elephant (Owen-Smith 1988), leading to longer retention time and more effective cellulose fermentation (Demment & van Soest 1985), rhinos can subsist upon a relatively higher concentration of fermentable fibre, i.e. graminoids, than elephants (Owen-Smith 1988).

During the monsoon season, the diet overlap between rhinos and elephants was 61% while it decreased to 45 and 33% in the hot-dry and cool-dry season, respectively. Hence, there was considerable diet niche separation between the two species during the dry season. Resource partitioning in the dry season occurred not only in food species (see Table 2); it also occurred in plant parts eaten. In the cool-dry season, an estimated 83% of the elephants' diet consisted of browse, of which as much as 73% was bark.

Comparable figures in rhino were 47 and 18%, respectively. The high proportion of bark in the elephant diet could be due to differential digestion (Vavra & Holechek 1980), where bark fragments pass more or less undigested compared to leaves. Bark-feeding by elephants might occur because of the sap content in the cambium layer, particularly during the dry season (Owen-Smith 1988, Sukumar 1989). From Africa, McCullagh (1973) and Short (1981) suggested that elephant feeding on bark might be a response to fatty acid deficiency and higher concentration of calcium, respectively. African savanna elephants may spend up to 80% of their foraging time feeding on bark, wood and roots (Owen-Smith 1988). In contrast to elephant, most of the rhino browse was leaves. With its prehensile upper lip the rhino is probably better adapted to select leaves than elephants, whereas the specialised trunk of the elephant facilitates debarking.

Systematic sampling along fresh elephant tracks disclosed that about 42% of the elephant food trees were *M. philippinensis* (N.M.B. Pradhan, unpubl. data), and Williams (2003) reported that this species was the most important woody food plant for elephants during the dry season in northern India. Similarly, Thorsrud (1997) reported that *Ficus* spp. were the most important food trees of domestic elephants during the dry season. Surprisingly, no *Ficus* species and a negligible amount of *M. philippinensis* were recorded in the elephant faecal samples. This is probably due to the elephant's preference for the cambium layer of the woody stems and general avoidance of leafy material (A. Chaudhary, pers. comm.). Holdo (2003) also reported elephants feeding only on the bark and never on the leaves of *Guibourtia coleosperma*. Hence, the large proportion of unidentified bark material in the elephant faecal material in our study was probably *M. philippinensis* and *Ficus* spp.

Our study documented that tall grass is the most important grass for rhino all year around, as also reported by Laurie (1982) and Jnawali (1995). The high contribution of *Saccharum* to the rhino diet was probably because of its unique nature of sprouting throughout the year (Dinerstein 1979a, Lehmkuhl 1989), and its high standing biomass (Jnawali 1995). Elephant also fed extensively on this species during the hot-dry and monsoon seasons. Their switch to more grass may in part have been triggered by a change in food quality. The first rain in the pre-monsoon season stimulates new grass growth, and the intercalary meristem growth of monocots is

more nutritious food than apical growth in browse plants (Jarman 1974).

The density of rhino was quite low in the study area, estimated at 0.5 animals/km² of riverine/tallgrass habitat (Department of National Parks and Wildlife Conservation 2002), compared to 3.3 animals/km² of same habitat in the Chitwan National Park (Department of National Parks and Wildlife Conservation 2005). Hence, high diet overlap in the monsoon season in Bardia was probably due to low animal densities and enough food for both species. Population trends in the park show that the densities of both species are increasing. Thus, densities may reach levels where competition could occur. In such a circumstance, being more of a generalist feeder with a large home range, the elephant might be less affected than rhino. Tall grass was the main food plant for rhino, and the availability of this species probably determines the upper limit of rhino abundance (Dinerstein 2003). Furthermore, presence of elephants in the study area may lower the upper limit of rhino abundance compared with Chitwan National Park. With smaller home ranges, and being confined to the restricted areas of floodplain habitat, the rhino will probably be at a disadvantage compared to elephants, when animal numbers increase. Therefore, at higher densities of the two megaherbivores, we predict rhino to be affected first.

Acknowledgements - our study was funded by the Norwegian Agency for Development Cooperation (NO-RAD) as part of a collaborative research programme between the Department of National Parks and Wildlife Conservation/Nepal and the Agricultural University of Norway (now the Norwegian University of Life Sciences). The Bardia National Park (BNP) and the Nepal Trust for Nature Conservation (NTNC) provided technical support. In particular, we want to thank P.B. Shrestha, R. Thapa, A. Bhandari, L.B. Thapa, N. Tharu (BNP), S.R. Jnawali, N. Subedi, M.B. Lama, M.S. Lama and S. Malla (NTNC) for their assistance in the fieldwork. Special thanks go to R. Shrestha for his guidance in microhistological laboratory work.

References

- Alipayo, D., Valdez, R., Holechek, J.L. & Cardenas, M. 1992: Evaluation of microhistological analysis for determining ruminant diet botanical composition. - *Journal of Range Management* 45: 148-152.
- Barnes, R.F.W. 1982: Elephant feeding behaviour in Ruaha National Park, Tanzania. - *African Journal of Ecology* 20: 123-136.

- Bolton, M. 1976: Royal Karnali Wildlife Reserve Management Plan, 1976-1981. - FAO/NEP/Project document number 72/002, 70 pp.
- Butet, A. 1985: Methode d'étude du regime alimentaire d'unrongeur polyphage (*Apodemus sylvaticus* L., 1758) par l'analyse microscopique des feces. - *Mammalia* 49: 455-483. (In French).
- Croze, H., Hillman, A.K.K. & Lang, E.M. 1981: Elephants and their habitats: How do they tolerate each other. - In: Fowler, C.W. & Smith, T.D. (Eds): Dynamics of large mammal populations. John Wiley & Sons, New York, pp. 297-314.
- Dawson, T.J. & Ellis, B.A. 1979: Comparison of the diets of Yellow-footed Rock wallabies and sympatric herbivores in Western New South Wales. - *Australian Wildlife Resources* 6: 245-254.
- Demment, M.W. & Van Soest, P.J. 1985: A nutritional explanation for body-size patterns of ruminants and non-ruminant herbivores. - *American Naturalist* 125: 641-672.
- Department of National Parks and Wildlife Conservation 2002: Rhino count 2002 in and around Royal Chitwan National Park, a brief report. - Department of National Parks and Wildlife Conservation, Babarmahal, Kathmandu, Nepal, 12 pp.
- Department of National Parks and Wildlife Conservation 2005: Report on rhino count 2005 in and around Royal Chitwan National Park. - Department of National Parks and Wildlife Conservation, Babarmahal, Kathmandu, Nepal, 18 pp.
- Dinerstein, E. 1979a: An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part I: vegetation, modifying factors, and successional relationships. - *Biological Conservation* 15: 127-150.
- Dinerstein, E. 1979b: An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part II: habitat/animal interactions. - *Biological Conservation* 16: 265-300.
- Dinerstein, E. 2003: The return of the unicorns: the natural history and conservation of the greater one-horned rhinoceros. - Columbia University Press, 316 pp.
- Field, C.R. & Ross, I.C. 1976: The savanna ecology of Kidepo Valley National Park. II Feeding ecology of elephant and giraffe. - *East African Wildlife Journal* 14: 1-16.
- Guy, P.R. 1976: The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa Area, Rhodesia. - *South African Journal of Wildlife Resource* 5: 55-63.
- Holdo, R.M. 2003: Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. - *Journal of Tropical Ecology* 19: 189-196.
- Holechek, J.L. & Gross, B. 1982: Training needed for quantifying simulated diets from fragmented range plants. - *Journal of Range Management* 35: 644-647.
- Jarman, P.J. 1974: The social organization of antelope in relation to their ecology. - *Behavior* 48: 215-266.
- Jnawali, S.R. 1995: Population ecology of greater one-horned rhinoceros (*Rhinoceros unicornis*) with particular emphasis on habitat preference, food ecology and ranging behavior of a reintroduced population in Royal Bardia National Park in lowland Nepal. - PhD thesis, Agricultural University of Norway, 129 pp.
- Jnawali, S.R. & Wegge, P. 1993: Space and habitat use by a small re-introduced population of greater one-horned rhinoceros (*Rhinoceros unicornis*) in Royal Bardia National Park in Nepal - a preliminary report. - In: Ryder, A.O. (Ed.); Rhinoceros biology and conservation. Proceedings of an international conference of Zoological Society of San Diego, San Diego, pp. 208-217.
- Johnson, M.K. & Pearson, H.A. 1981: Esophageal, fecal and enclosure estimates of cattle diets on a long leaf pine-bluestem range. - *Journal of Range Management* 34: 232-234.
- Krebs, C.J. 1999: Ecological methodology. - Benjamin/Cummings, Menlo Park, California, 620 pp.
- Laurie, W.A. 1982: Behavioral ecology of the greater one horned rhinoceros (*Rhinoceros unicornis*). - *Journal of Zoology (London)* 196: 307-341.
- Lehmkuhl, J.F. 1989: The ecology of a south Asian tall grass community. - PhD thesis, University of Washington, 195 pp.
- McCullagh, K.G. 1973: Are African elephants deficient in essential fatty acids? - *Nature* 242: 267-268.
- Owen-Smith, R.N. 1988: Megaherbivores: the influence of very large body size in ecology. - Cambridge University Press, Cambridge, 369 pp.
- Pellew, R.A. 1984: The feeding ecology of a selective browser, the giraffe (*Giraffa camelopardalis tippelskirchi*). - *Journal of Zoology (London)* 202: 57-81.
- Renkonen, O. 1938: Statisch-Ökologische Untersuchungen über die terrestrische Kaferwelt der finnischen Bruchmoore. - *Annales Zoologici Societatis Zoologicae Botanicae Fennicae Vanamo* 6: 1-226. (In German).
- Short, J. 1981: Diet and feeding behaviour of the forest elephant. - *Mammalia* 45: 177-185.
- Sinclair, A.R.E. 1975: The resource limitation of tropic levels in tropical grassland ecosystems. - *Journal of Animal Ecology* 44: 497-520.
- Sparks, D.R. & Malechek, J.C. 1968: Estimating percentage dry weight in diets using a microscopic technique. - *Journal of Range Management* 21: 264-265.
- Steinheim, G., Wegge, P., Fjellstad, J.I., Jnawali, S.R. & Weladji, R.B. 2005: Dry season diets and habitat use of sympatric Asian elephants (*Elephas maximus*) and greater one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal. - *Journal of Zoology (London)* 265: 377-385.
- Stewart, D.R.M. 1967: Analysis of plant epidermis in feces: A technique for studying the food preferences

- of grazing herbivores. - *Journal of Applied Ecology* 4: 82-111.
- Sukumar, R. 1989: *The Asian elephant: ecology and management*. - Cambridge University Press, Cambridge, 255 pp.
- Thorsrud, K. 1997: Ecological impacts of domestic Asian elephants *Elephas maximus* on vegetation and wildlife during the dry season in Royal Bardia National Park in lowland Nepal. - M.Sc. thesis, Agricultural University of Norway, 71 pp.
- Todd, J.W. & Hansen, R.M. 1973: Plant fragment in the feces of bighorn as indicator of food habits. - *Journal of Wildlife Management* 37: 363-365.
- Vavra, M. & Holecek, J.L. 1980: Factors influencing microhistological analysis of herbivore diets. - *Journal of Range management* 33: 371-374.
- Velde, P.F. 1997: A Status report of Nepal's wild elephant population. - Unpubl. report, WWF Nepal, Kathmandu, 55 pp.
- Wegge, P., Shrestha, A.K. & Moe, S.R. 2006. Dry season diets of sympatric ungulates in lowland Nepal; competition and facilitation in alluvial tall grasslands. - *Ecological Research*, DOI: 10.1007/s11284-006-0177-7.
- Williams, A.C. 2003: Elephants, their habitats in Rajaji-Corbett National Parks. - PhD thesis, Saurashtra University, Rajkot, India, 91 pp.
- Wing, L.D. & Buss, I.O. 1970: Elephant and forests. - *Wildlife Monograph* 19: 92 pp.
- World Conservation Union 2004: IUCN Red List of threatened species. - Gland, Switzerland. Available at <http://www.iucnredlist.org> (accessed December 2005).