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

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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

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*

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Corresponding author: Per Wegge
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,
leaf and unknown) were recorded. The fragments then the category level and plant part level (bark, possible, the fragments were identified to species compared with the reference slides. Whenever接纳 by the transect lines, identifiable at least to a category level (i.e. grass, browse and others) were collected from widely spaced latrines. 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. 2006). We carried out 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 \( \chi^2 \) tests to compare the seasonal and yearly frequencies of grasses and browse within and between elephant and rhino. We also used \( \chi^2 \) 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 1. Vegetation types in Bardia National Park in lowland Nepal.

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

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 reference of 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 100-400x 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.

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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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Rhino</th>
<th></th>
<th></th>
<th>Elephant</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Cool dry</td>
<td>Hot dry</td>
<td>Monsoon</td>
<td>Cool dry</td>
<td>Hot dry</td>
</tr>
<tr>
<td></td>
<td>%</td>
<td>%</td>
<td>%</td>
<td>%</td>
<td>%</td>
<td>%</td>
</tr>
<tr>
<td><strong>Browse</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia catechu</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Aegle marmelos</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2.5</td>
<td>3.5</td>
<td>1.0</td>
</tr>
<tr>
<td>Bauhinia spp.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>8.0</td>
<td>5.9</td>
<td>4.0</td>
</tr>
<tr>
<td>Bauhinia sutili</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bombax ceiba</td>
<td>3.0</td>
<td>3.5</td>
<td>3.5</td>
<td>4.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bridelia stipularis</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.0</td>
<td>2.1</td>
</tr>
<tr>
<td>Cassalia decapetala</td>
<td>0.5</td>
<td>1.6</td>
<td>0.5</td>
<td>1.6</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Calamus tetum</td>
<td>0.5</td>
<td>1.6</td>
<td>1.0</td>
<td>2.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Callicarpa macrophylla</td>
<td>10.0</td>
<td>4.7</td>
<td>2.0</td>
<td>3.5</td>
<td>0.5</td>
<td>1.6</td>
</tr>
<tr>
<td>Colebrookea oppositifolia</td>
<td>1.0</td>
<td>2.1</td>
<td>1.0</td>
<td>2.1</td>
<td>0.5</td>
<td>1.6</td>
</tr>
<tr>
<td>Dalbergia sissoo</td>
<td>7.0</td>
<td>5.9</td>
<td>6.0</td>
<td>7.7</td>
<td>4.5</td>
<td>3.7</td>
</tr>
<tr>
<td>Desmodium osojenense</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2.5</td>
<td>2.6</td>
</tr>
<tr>
<td>Dillenia pentagyna</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ethretia laevis</td>
<td>5.0</td>
<td>4.1</td>
<td>4.0</td>
<td>5.7</td>
<td>2.0</td>
<td>3.5</td>
</tr>
<tr>
<td>Ficus glomarata</td>
<td>0.5</td>
<td>1.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Holarrhena antidysenterica</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Lannea monteatala</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.5</td>
<td>1.6</td>
<td>-</td>
</tr>
<tr>
<td>Mallotus philippinensis</td>
<td>8.0</td>
<td>6.7</td>
<td>5.0</td>
<td>4.7</td>
<td>2.0</td>
<td>3.5</td>
</tr>
<tr>
<td>Millettia auriculata</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Spathophyllum parviflorus</td>
<td>-</td>
<td>0.5</td>
<td>1.6</td>
<td>-</td>
<td>1.5</td>
<td>1.5</td>
</tr>
<tr>
<td>Trewia nudiflora</td>
<td>1.0</td>
<td>2.1</td>
<td>-</td>
<td>1.0</td>
<td>2.1</td>
<td>-</td>
</tr>
<tr>
<td>Ziziphus mauritiana</td>
<td>1.0</td>
<td>2.1</td>
<td>1.0</td>
<td>2.1</td>
<td>0.5</td>
<td>1.6</td>
</tr>
<tr>
<td><strong>Unidentified browse</strong></td>
<td>9.0</td>
<td>6.1</td>
<td>4.0</td>
<td>4.6</td>
<td>1.5</td>
<td>2.4</td>
</tr>
<tr>
<td><strong>Total browse</strong></td>
<td>46.5</td>
<td>28.5</td>
<td>13.0</td>
<td>83.5</td>
<td>58.0</td>
<td>39.0</td>
</tr>
<tr>
<td><strong>Grass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apluda mutica</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Arundo donax</td>
<td>3.0</td>
<td>3.5</td>
<td>1.5</td>
<td>3.4</td>
<td>8.5</td>
<td>5.3</td>
</tr>
<tr>
<td>Cynodon dactylon</td>
<td>2.0</td>
<td>2.6</td>
<td>2.5</td>
<td>2.6</td>
<td>7.0</td>
<td>3.5</td>
</tr>
<tr>
<td>Dendrocalamus spp.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.5</td>
<td>1.6</td>
<td>1.5</td>
</tr>
<tr>
<td>Desmostachia bipinnata</td>
<td>0.5</td>
<td>1.6</td>
<td>2.0</td>
<td>2.6</td>
<td>0.5</td>
<td>1.6</td>
</tr>
<tr>
<td>Imperata cylindrica</td>
<td>4.5</td>
<td>5.0</td>
<td>4.5</td>
<td>3.7</td>
<td>-</td>
<td>2.0</td>
</tr>
<tr>
<td>Narenga porphyrocoma</td>
<td>3.0</td>
<td>3.5</td>
<td>1.0</td>
<td>2.1</td>
<td>5.5</td>
<td>3.7</td>
</tr>
<tr>
<td>Panicum spp</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3.0</td>
<td>4.2</td>
</tr>
<tr>
<td>Phragmites karka</td>
<td>-</td>
<td>0.5</td>
<td>1.6</td>
<td>1.0</td>
<td>2.1</td>
<td>2.5</td>
</tr>
<tr>
<td>Saccharum bengalensis</td>
<td>3.5</td>
<td>4.1</td>
<td>2.5</td>
<td>2.6</td>
<td>3.0</td>
<td>3.5</td>
</tr>
<tr>
<td>S. munja</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.0</td>
<td>2.1</td>
</tr>
<tr>
<td>S. spontaneum</td>
<td>18.5</td>
<td>9.4</td>
<td>31.5</td>
<td>9.1</td>
<td>28.0</td>
<td>10.9</td>
</tr>
<tr>
<td>Themeda arundinata</td>
<td>6.5</td>
<td>6.3</td>
<td>-</td>
<td>4.0</td>
<td>3.9</td>
<td>-</td>
</tr>
<tr>
<td>Themeda arundinata</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.5</td>
<td>1.6</td>
<td>-</td>
</tr>
<tr>
<td>Vetiveria zizanioides</td>
<td>-</td>
<td>0.5</td>
<td>1.6</td>
<td>6.5</td>
<td>7.8</td>
<td>-</td>
</tr>
<tr>
<td><strong>Unidentified grass</strong></td>
<td>13.0</td>
<td>11.1</td>
<td>20.5</td>
<td>7.2</td>
<td>14.5</td>
<td>8.3</td>
</tr>
<tr>
<td><strong>Total grass</strong></td>
<td>52.5</td>
<td>69.0</td>
<td>87.0</td>
<td>16.5</td>
<td>42.0</td>
<td>61.0</td>
</tr>
<tr>
<td><strong>Others</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cirsium waltchii</td>
<td>0.5</td>
<td>1.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Water herb</td>
<td>0.5</td>
<td>1.6</td>
<td>2.5</td>
<td>4.2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Total others</strong></td>
<td>1.0</td>
<td>2.5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
</tbody>
</table>
The woody species *Dalbergia sissoo*, *Mallotus phillippinensis*, *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 bipinata*, *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.

### 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.

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

<table>
<thead>
<tr>
<th>Diet category</th>
<th>Cool dry</th>
<th>Hot dry</th>
<th>Monsoon</th>
<th>Yearly</th>
</tr>
</thead>
<tbody>
<tr>
<td>Browse</td>
<td>0.37</td>
<td>0.22</td>
<td>0.30</td>
<td>0.33</td>
</tr>
<tr>
<td>Grass</td>
<td>0.33</td>
<td>0.56</td>
<td>0.67</td>
<td>0.77</td>
</tr>
<tr>
<td>All species</td>
<td>0.33</td>
<td>0.45</td>
<td>0.61</td>
<td>0.60</td>
</tr>
</tbody>
</table>

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).
the intercalary meristem growth of monocots is
monsoon season stimulates new grass growth, and
a change in food quality. The first rain in the pre-
to more grass may in part have been triggered by
ing the hot-dry and monsoon seasons. Their switch
Elephant also fed extensively on this species dur-
1989), and its high standing biomass (Jnawali 1995).
important grass for rhino all year around, as also
and
pinensis
were reported by Laurie (1982) and Jnawali (1995). The
forage time feeding on bark, wood and roots
(Owen-Smith 1988). In contrast to elephant, most of
the rhino browse was leaves. With its prehensile up-
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. phillipppinensis (N.M.B. Pradhan, unpubl.
data), and Williams (2003) reported that this species
was the most important woody food plant for ele-
dphants during the dry season in northern India.
Similarly, Thorsrud (1997) reported that Ficus spp.
were the most important food trees of domestic ele-
phants during the dry season. Surprisingly, no Ficus
species and a negligible amount of M. phillippinen-
sis 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 gener-
al avoidance of leafy material (A. Chaudhary, pers.
comm.). Holdo (2003) also reported elephants feed-
ing only on the bark and never on the leaves of
Guibourtia coleosperma. Hence, the large propor-
tion of unidentified bark material in the elephant
faecal material in our study was probably M. phillip-
phinensis 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 Na-
tional Park (Department of National Parks and
Wildlife Conservation 2005). Hence, high diet
overlap in the monsoon season in Bardia was proba-
bly 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 abun-
dance compared with Chitwan National Park.
With smaller home ranges, and being confined to
the restricted areas of floodplain habitat, the rhi-
no will probably be at a disadvantage compared to
elephants, when animal numbers increase. There-
fore, at higher densities of the two megaherbivores,
we predict rhino to be affected first.

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References
Alipayo, D., Valdez, R., Holechek, J.L. & Cardenas,
M. 1992: Evaluation of microhistological analysis
for determining ruminant diet botanical composition.
Barnes, R.F.W. 1982: Elephant feeding behaviour in Ru-
aha National Park, Tanzania. - African Journal


Stewart, D.R.M. 1967: Analysis of plant epidermis in feces: A technique for studying the food preferences