

# Dry season diets and habitat use of sympatric Asian elephants (*Elephas maximus*) and greater one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal

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## Abstract

Dry season diets and habitat use of increasing populations of Asian elephants *Elephas maximus* and greater one-horned rhinoceros *Rhinoceros unicornis* in the Babai Valley of Royal Bardia National Park, Nepal, are described, and an assessment is made of the potential for competition between them. The diets, analysed by microhistology, were different, with a similarity index of 37.5%, and with different grass/browse proportions: the rhino diet consisted of 63% grass and 28% browse; that of elephants was 24% grass and 65% browse. A tallgrass floodplain grass, *Saccharum spontaneum*, was the plant most eaten by rhinos, whereas elephants consumed a large proportion of bark of *Bombax ceiba* and *Acacia catechu*, as well as several browse species not eaten by rhino. The habitat use of elephants was determined by dung-counts within 30 km of 20-m wide belt transects, while that of rhino was taken from an earlier study. Elephants used a wider range of habitats than rhino, but two types, the tallgrass floodplain and khair–sissoo forest, were preferred by both species simultaneously. While elephants used the abundant sal forest extensively, rhino strongly avoided this habitat. Densities of both species were low at the time of study (< 0.5 animals/km<sup>2</sup>), but their numbers are expected to increase markedly in coming years. Because available habitats for expansion are limited, this may lead to competition. Rhino might then become the weaker species, as elephants are more flexible in their ranging and foraging activities. The tallgrass floodplain habitat and its important forage grass *S. spontaneum* may then become the critical resources.

**Key words:** competition, *Elephas maximus*, food habits, *Rhinoceros unicornis*, *Saccharum spontaneum*

## INTRODUCTION

Both the Asian elephant *Elephas maximus* L. (hereafter termed ‘elephant’) and the greater one-horned rhinoceros *Rhinoceros unicornis* L. (hereafter termed ‘rhino’) are internationally endangered species (Groombridge, 1993). While poaching is regarded to be the greatest threat to the remaining rhino populations (Bhattacharya, 1993), elephants may be more susceptible to the effects of fragmentation and degradation of their habitats (Sukumar, 1989; Johnsingh & Panwar, 1992; Williams, 2002).

Elephants and rhinos are mixed feeders, with proportions of grass and browse in the diet varying throughout the year (Field & Ross, 1976; Owen-Smith, 1988; Sukumar, 1989; Jnawali, 1995). For the African elephant *Loxodonta africana* L. (which has received far

more attention than the Asian elephant), Laws (1970) postulated that while grasses are probably essential to provide bulk cellulose for energy, the protein requirements of the elephant, especially in dry seasons, can only be met by herbs and browse. This may well apply also to the Asian elephant and rhino. African elephants carry out a substantial part of their browsing below a height of 2 m (Guy, 1976), which is largely the same height to which the Indian rhino is restricted. As megaherbivores with mixed, generalist diets, and probably feeding in the same vegetation layer, rhino and elephants occupy similar ecological niches.

For successful management of sympatric rhino and elephant, it is therefore important to determine whether competition does indeed occur and if so, to what extent. The Babai valley of the Royal Bardia National Park (RBNP), being a relatively contained area with both elephant and rhino present, provided a rare opportunity from which to gain such insights. A diet study was conducted in the hot period of the dry season. A habitat study covered the entire dry season, with a slight emphasis on the hot period.

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## METHODS

### Study area

The study was conducted in central Babai valley (81°30'E, 28°25'N) in the north-eastern part of the 986 km<sup>2</sup> RBNP. The Park is located in lowland Nepal near the Indian border, 390 km west of Kathmandu. The climate is subtropical monsoonal, with between 1550 and 2310 mm rainfall annually, most of it falling between June and September. The rainy season is followed by a dry season lasting from October to June. This season is divided into a cool (October to mid February) and a hot period (mid February to June). Temperatures range from 10 °C in January to 41 °C in May (Dinerstein, 1979a).

The vegetation is sub-tropical, consisting of a mosaic of early successional floodplain communities along the Babai river and its tributaries, and with large areas of climax sal *Shorea robusta* L. forest on the upper, drier land. Intermingled in the latter are patches of grassland, locally known as *phantas*. They originated from cultivated areas around villages, which were abandoned before the Park was extended in 1984 (Upreti, 1994).

Dinerstein (1979b) gave a detailed description of the vegetation types of the Karnali floodplain area in the south-western part of the Park, 20 km south-west of the Babai valley. Jnawali & Wegge (1993) extended this vegetation map, with a few modifications in nomenclature. Using Jnawali & Wegge's (1993) classification system, Fjellstad & Steinheim (1996) estimated the proportions of different vegetation types in the 48 km<sup>2</sup> study area (Table 1).

Rhinos have been reintroduced to RBNP since 1986. Thirteen animals were then released in the Karnali Floodplain, followed in 1990 by 25 rhino released in the Babai Valley. Owing to poaching and stochastic events, the population increases have been slow, but habitat quality is suitable as indicated by successful breeding after releases. In 1994, the Karnali population consisted of 15 individuals (Jnawali, 1995), whilst the Babai population in early 1996 numbered between 20 and 24 (G. Singh, pers. comm.). Until the late 1980s, only a few elephants visited the Park seasonally. In 1994, some 30–40 elephants migrated into the Park, presumably from India (Velde, 1997) and became more or less permanent residents. At the time of this study, at least 18 of these used the Babai valley regularly.

Large herbivores, other than rhino and elephant, observed in the study area were sambar *Cervus unicolor* Kerr, spotted deer *Axis axis* Erxleben, four-horned antelope *Tetracerus quadricornis* Blainville, and barking deer *Muntiacus muntjak* Zimmermann.

### Microhistological analysis

Microhistological analysis of faeces has been used to study the diets of several taxonomic groups, and has been confirmed as a reliable method for estimating diet composition for grazing herbivores (Stewart, 1967; Todd & Hansen, 1973; Johnson & Pearson, 1981; Larter & Gates, 1991; Alipayo *et al.*, 1992; Jnawali, 1995), but

**Table 1.** Vegetation types in the study area in Babai Valley, with some of the important and dominating plant species in each. Data from Fjellstad & Steinheim (1996)

Vegetation type	Cover (%)	Dominating plant species
Tallgrass floodplain	7.8	Grasses: <i>Saccharum spontaneum</i> , <i>Saccharum bengalensis</i> , <i>Phragmites karka</i>
Khair–sissoo forest	7.8	Trees: <i>Acacia catechu</i> , <i>Dalbergia sissoo</i>
Moist riverine forest	16.1	Shrubs: <i>Callicarpa macrophylla</i> , <i>Colebrookia oppositifolia</i> Trees: <i>Mallotus philippinensis</i> , <i>Ficus glomerata</i> , <i>Syzgium cuminii</i>
Phanta	14.3	Grasses: <i>Imperata cylindrica</i> Trees: <i>Bombax ceiba</i>
Wooded savannah	7.1	Grasses: <i>I. cylindrica</i> , <i>Vetiveria zizanioides</i> Trees (sparse): <i>Bombax ceiba</i> , <i>M. philippinensis</i> , <i>Adina cordifolia</i>
Mixed hardwood forest	9.1	Trees: <i>Terminalia tomentosa</i> , <i>Schleicheria trijuga</i> Shrubs: <i>C. oppositifolia</i>
Sal forest	26.6	Trees (canopy): <i>Shorea robusta</i> (sal), <i>Terminalia tomentosa</i> Understorey: sal, <i>Buchanania latifolia</i>
Rivers and river beds	11.3	Sandy and stony areas along the river and its tributaries

correction factors must be applied to provide a suitable degree of quantification for ruminant herbivores (Dearden, Pegau & Hansen, 1975; Holechek, Vavra & Pieper, 1982; Mofareh, Beck & Schneberger, 1997; but see Alipayo *et al.*, 1992). The method is considered particularly useful for comparative studies (Butet, 1985) and is believed to be more accurate for non-ruminant, monogastric animals than for ruminants (Jnawali, 1995). This is probably especially true for bulk feeders such as rhino and elephant, where a large proportion of the food passes through the digestive tract virtually undigested (Owen-Smith, 1988).

Fresh faecal samples were collected from 40 individual rhino dung piles and 50 elephant dung piles during March and April 1996. From tracks and direct sightings it became clear that 2 groups of elephants and a few stray individuals inhabited the study area. Dung was sampled both from stray individuals and from the 2 groups. To ensure that samples were taken from a wide range of individuals, the weight of boli (individual faeces) was used as a guideline, assuming a fixed relationship between boli weights and elephant size (Jachmann & Bell, 1984). As rhino establish latrines for defecation (Laurie, 1978), the 40 samples were collected from 20 different latrines distributed throughout the study area to ensure a total representation of the population's diet. Only fresh dung (< 24 h old) was used. Each pile was mixed thoroughly before samples were taken.

A reference collection was made from plants collected in the study area. Jnawali (1995), in his study in the nearby

Karnali flood plain area, ranked the rhino food plants according to their relative importance in the diet. Owing to limited resources, our reference collection was chosen to consist of those plant species present in our study area that Jnawali (1995) had found to be most important for rhino in the Karnali area. In addition, *Litsea monopetala* and *Murraya paniculata* were included, which, although not present in the Karnali floodplain (Jnawali, 1995), were found to be important rhino food in Royal Chitwan National Park (RCNP) (Laurie, 1978). Aquatic plants are also reported to be important food for rhino (Laurie, 1978; Sinha & Sawarkar, 1991), and 2 common species, *Hydrilla* spp. and *Paspallum* spp., were included in the reference collection.

For the microhistological analyses, a method was adopted that mainly followed Sparks & Malechek (1968) and Anthony & Smith (1974), as modified by Vavra & Holechek (1980) and Jnawali (1995). After air-drying, grinding and sieving, the individual samples were pooled at random into 5 of each species. Detailed drawings were made of species-specific cell characteristics of the reference plants. Before reading, the observer went through training and testing as recommended by Holechek & Gross (1982).

The faecal slides were read at 200× magnification. Following transects across the slide, only non-overlapping fragments, identifiable at least to the categories 'grass', 'browse' or 'herbs', and intercepted by the transects, were recorded. Fragments with good identifying features but not present in the reference collection, and fragments identifiable to category but too damaged to determine whether or not they matched any reference sample, were classified as 'unidentified', e.g. 'unidentified grass' etc. A special category, 'woody remnants', was made for all fragments of bark and wood. Two grasses, *Phragmites karka* and *Arundo donax*, could not be distinguished from each other, and were thus grouped. Four hundred fragments were classified from each pooled sample.

#### Analysis of habitat use

Logistics did not allow a radio-telemetry study to monitor habitat use, and dense vegetation in most of the area precluded direct observation as a mode of data collection. The habitat use of elephants was, therefore, determined by counting dung piles along transects, a method recommended by Dawson & Dekker (1992) for surveying Asian elephants, after being widely used in African forests (Jachmann & Bell, 1979, 1984; Fay, 1991; Barnes & Barnes, 1992; Barnes *et al.*, 1995). Dung count surveys are based on the assumption that defecation rates of elephants are independent of vegetation type, as is indicated in the literature; elephants defecate regularly at least 13 times each day (McKay, 1973; Ratnasooriya *et al.*, 1994), and there is no apparent synchronization in defecation (Ratnasooriya *et al.*, 1994). Hence, dung count surveys give information on movements of elephants during the whole 24-h cycle.

A team of 4 observers searched 20-m wide transects for elephant dung piles. The speed of the team was adjusted

according to visibility to ensure 100% dung detection, e.g. the speed had to be considerably slower in tallgrass floodplain than in sal forest. Transects were designated in a systematic random manner: from a randomly placed starting point, 14 transects were laid perpendicular to the Babai river, and equidistant from one another. The total length of transects was *c.* 30 km.

For every dung pile encountered, vegetation type was recorded. Each dung pile was classified according to degradation stage, following the method of Dawson & Dekker (1992), where stage 1 is fresh dung and stage 5 is old, nearly completely degraded dung. Dung was divided into 2 age classes; 'new' dung, comprising degradation stages 1 and 2; and 'old' dung, comprising degradation stages 3–5. The division was done such that most of the 'new' dung was from the hot period of the dry season. The bulk of the 'old' dung originated from the cool period of the dry season: little is believed to remain from the monsoon and hot period of the previous dry season owing to rapid degradation under humid conditions (Barnes & Barnes, 1992).

Because rhinos deposit their dung in latrines shared by several individuals (Dinerstein, 2003), counting dung is unsuitable for surveys of rhino habitat. Data on rhino habitat use were extrapolated from a recent telemetry study of 8 female rhino, conducted during the same season in the nearby Karnali floodplain area (Jnawali, 1995). Composition of habitat types in Babai was similar to that in Karnali, with slight differences in relative proportions.

#### Statistical analyses

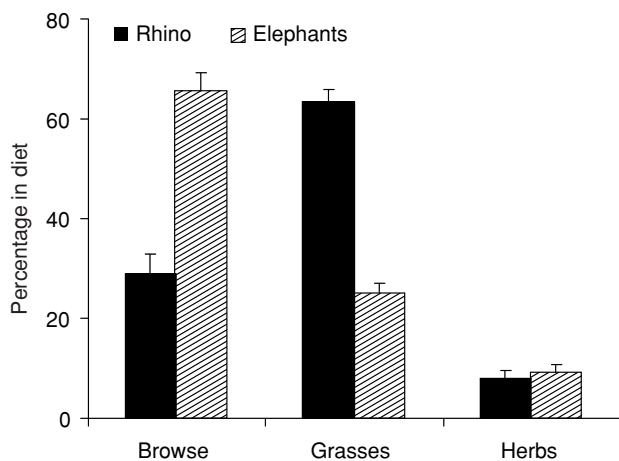
A chi-square test was carried out to test if the proportions of grasses, browse and herbs were the same for rhino and elephant. Chi-square tests were used to determine the significance of any differences found within each category. A chi-square test was also performed to test the null hypothesis that the 2 species had the same overall diets, in terms of quantities of individual food plant species and categories.

A percentage similarity index (Gauch, 1973) was calculated as a measure of overall diet similarity between the rhino and elephants:

$$\text{PSI} = \frac{2 \times \sum \min(x, y)}{\sum(x + y)} \times 100\%$$

where *x* and *y* are the frequencies of each food species in rhino and elephant diets, respectively, and  $\min(x, y)$  is the lesser of the 2 frequencies.

A chi-square goodness-of-fit test was carried out to determine whether vegetation types were used according to their abundance. To determine which vegetation types were preferred or avoided, Bonferroni simultaneous confidence intervals (Byers, Steinhorst & Krausman, 1984) were calculated for the usage proportions. The proportions of different vegetation types within the study area (Table 1) were taken to represent the expected proportions



**Fig. 1.** Proportions of browse, grasses and herbs in the dry season diets of rhinos *Rhinoceros unicornis* and elephants *Elephas maximus*. Fragments identified only to category and not to species level are included. Error bars denote 1 SD.

of elephant usage, to which the confidence intervals were compared.

The Bonferroni approach does not give information on the strength of preference/avoidance. Therefore, to determine the magnitude of the preferences, Ivlev's electivity indices (Ivlev, 1961) were calculated:

$$IEI = \frac{a - b}{a + b}$$

where  $a$  is the proportion of use of a vegetation type and  $b$  is the availability of that type. Thus, an IEI of 1.0 denotes maximum preference of a vegetation type, 0 denotes use exactly according to availability and a value of  $-1.0$  denotes total avoidance. To determine whether the habitat preferences of elephants changed during the year, IEI was also calculated separately for the cool period (old dung) and the hot period (new dung) of the dry season.

Information on habitat use of rhino was adopted from Jnawali's (1995) study in the Karnali area. When males and females differed in their preferences, data on females was used, this being more reliable, as only 2 males were radio-collared. The strength of rhino preferences (IEIs) was calculated from the proportion of radio-telemetry locations in different vegetation types.

Average absolute values of IEIs for the whole dry season (i.e. from both 'new' and 'old' dung classes for elephants) were computed to determine to what degree the 2 megaherbivores were habitat specific.

## RESULTS

### Diet

An overview of the distribution of fragments between categories (including 'unidentified' fragments) shows that the dominant category in the diet of rhino was the grasses (Fig. 1), comprising 63%, followed by

browse (29%) and herbaceous plants (8%). The diet of elephant was significantly different from that of rhino for grass/browse/herbs proportions ( $\chi^2 = 620.7$ , d.f. = 2,  $P < 0.01$ ); the browse plants dominated strongly with 66%, while grasses made up 25% and herbaceous plants 9% of the diet. Chi-square tests showed that the differences between elephant and rhino were significant for the proportions of browse ( $\chi^2 = 543.0$ , d.f. = 1,  $P < 0.01$ ) and grass ( $\chi^2 = 591.4$ , d.f. = 1,  $P < 0.01$ ). Remnants of aquatic plants were not found in either the elephant or the rhino samples.

The elephant and rhino did not have the same diets in terms of quantity of individual food species ( $\chi^2 = 1129.3$ , d.f. = 20,  $P < 0.01$ ). By far the most abundant plant species in rhino faecal samples was *Saccharum spontaneum* (Fig. 2). This grass species alone accounted for 35% of the diet. Other frequently found grasses were *Phragmites karka/Arundo donax* (8%), *Imperata cylindrica* (6.4%) and *Cynodon dactylon* (5%). The most abundant browse species was *Mallotus philippinensis* with 8%, while *Dalbergia sissoo* and *Litsea monopetala* were represented with 6% and 5%, respectively. Woody remnants contributed 8%.

By contrast, in the elephant dung samples, 'other browse' formed the largest single component of the diet with 40%. Woody remnants contributed 26%, and the thorny bush *Ziziphus mauritiana* 7%. As for rhino, *Saccharum spontaneum* was the most common grass species in the elephant diet, contributing 10%, followed by *Phragmites karka/Arundo donax* (4%).

The overall similarity between the diets of elephant and rhino, as represented by the percentage similarity index (PSI), was 37.5%.

### Habitat use

According to the distribution of elephant dung, elephants did not use the vegetation types according to availability during the dry season ( $\chi^2 = 63.9$ , d.f. = 7,  $P < 0.001$ ). Bonferroni analyses showed that elephants consistently preferred three habitat types during the two periods of the dry season (Table 2). Looking at the strength of preferences throughout the dry season, the most preferred vegetation type was wooded savannah (IEI = 0.32), closely followed by tallgrass floodplain (IEI = 0.24) and khair-sissoo forest (IEI = 0.23). Rivers and riverbeds (IEI =  $-0.69$ ), followed by sal forest (IEI =  $-0.22$ ) were the vegetation types most strongly avoided by elephants.

An overview for the Karnali rhinos during the dry season (Jnawali 1995) shows that moist riverine forest was the most strongly preferred vegetation type (IEI = 0.49), followed by khair-sissoo forest (IEI = 0.36) and tallgrass floodplain (IEI = 0.23). Rhino showed almost total avoidance of sal forest (IEI =  $-0.98$ ) and phanta (IEI =  $-1.00$ ).

A chi-square test, comparing locations of dung of the two different age classes showed that the habitat use of elephants varied significantly between the cool and

**Table 2.** Habitat use of elephants during the dry season, with expected and actual use (%), and significance of deviation from expected use. Results for the cool period are calculated from counts of 'old' dung stages (stage 3–5, see text), results for the hot period from 'new' dung (stages 1–2). Significance of deviation from expected habitat use for rhino is calculated from radio-telemetry data from Jnawali (1995), collected in the nearby Karnali area

Vegetation types	Expected use <sup>a</sup>	Period	Actual use ( <i>P</i> )	Bonferroni confidence intervals (habitat use) <sup>b</sup>	Significance for elephant <sup>c</sup>	Significance for rhino <sup>d</sup>
Tallgrass floodplain	7.8	Cool	12.0	$8.3 \leq P \leq 15.8$	++	ns
		Hot	15.6	$11.4 \leq P \leq 19.8$	++	+
Khair–sissoo forest	7.8	Cool	11.1	$7.5 \leq P \leq 14.7$	+	+
		Hot	17.6	$13.2 \leq P \leq 22.0$	++	+
Moist riverine forest	16.1	Cool	17.0	$12.6 \leq P \leq 21.3$	ns	+
		Hot	16.1	$11.8 \leq P \leq 20.3$	ns	+
Mixed hardwood forest	9.1	Cool	9.4	$6.0 \leq P \leq 12.8$	ns	ns
		Hot	8.8	$5.5 \leq P \leq 12.1$	ns	ns
Wooded savannah	7.1	Cool	12.2	$8.4 \leq P \leq 15.9$	++	–
		Hot	19.5	$14.9 \leq P \leq 24.1$	++	–
Phanta	14.3	Cool	17.9	$13.5 \leq P \leq 22.3$	ns	0
		Hot	8.8	$5.5 \leq P \leq 12.1$	– –	0
Sal forest	26.6	Cool	18.0	$13.6 \leq P \leq 22.5$	– –	0
		Hot	12.7	$8.8 \leq P \leq 16.5$	– –	–
Rivers and river beds	11.3	Cool	2.4	$0.6 \leq P \leq 4.1$	– –	–
		Hot	1.0	$-0.2 \leq P \leq 2.1$	– –	–

<sup>a</sup> Proportions of vegetation types in the study area.

<sup>b</sup> 99% overall significance level.

<sup>c</sup> ++ / – –, significant preference/avoidance at 99% level; +, significant preference at 95% level; NS, not significant.

<sup>d</sup> Preferences tested at 95% level of confidence; +, significant preference; –, significant avoidance; 0, no telemetry locations.

the hot periods of the dry season ( $\chi^2 = 26.2$ , d.f. = 7,  $P < 0.001$ ). Jnawali's (1995) telemetry study in Karnali showed that rhinos also changed their habitat use between these periods. Both species used tallgrass floodplain more during the hot than during the cool period. While the rhino's use of khair–sissoo forest decreased in the hot period, elephants increased their use of this habitat. The elephants also increased their use of wooded savannahs, whilst the rhino spent more time in mixed hardwood forest during the hot period (Fig. 3).

## DISCUSSION

### Diet

In other comparative studies of large sympatric herbivores (Garcia-Gonzalez & Cuartas, 1989; Cuartas & Garcia-Gonzalez, 1992), a diet similarity index (PSI) below 50% has been considered low. Thus, the overall similarity between rhino and elephants in our study area was, at 37%, very low, indicating a substantial degree of niche separation. The grass and browse proportions of the diets of the two species were quite different. The proportions in the diet of rhinos show a close similarity to the results obtained in the Karnali floodplain area by Jnawali (1995), while Laurie (1978) found rhino in RCNP to consume much more grass, a discrepancy probably explained by the poorer floodplains in RBNP. The grass/browse/herb proportions of the diet of elephants in Babai valley are similar to those of elephants in southern India (Sukumar, 1989).

Reinforcing the general impression of niche separation, the statistical tests showed that the diets were also different in terms of the relative use of individual food plants. The game scouts in RBNP believe that elephants prefer several species of *Ficus* (G. Singh, pers. comm.), as has been documented by Williams (2002) from northern India. Moreover *Ficus* spp. are among the most important browse fodder for domestic elephants (Lemkuhl, 1989; Thorsrud, 1997). Additional reference slides of four *Ficus* species were compared with the elephant samples. A relatively large proportion of the 'other browse' fragments resembled the *Ficus* references, however, the fragments in question consisted only of naked leaf nerves, and neither species nor genus determination of adequate certainty could be made. The large proportion of 'other browse' may also have included several climber species, as these are believed to be important fodder plants for elephants (M. B. Lama & G. Singh, pers. comm.).

*Mallotus philippinensis* was the most common browse species for rhino in our study area. In Corbett National Park in India, Williams (2002) found this species to be an important food item for elephants as well. Yet, interestingly, *Mallotus philippinensis* was not detected in the faecal samples of the Babai elephants.

As for the 'woody remnants' category, the elephants ate considerable amounts (26.2%) of bark and wood, as also found in northern (Williams, 2002) and southern India (Sukumar, 1989). Bark eating is probably common for the same reasons as proposed for African elephants, namely to obtain minerals (Laws, Parker & Johnstone, 1975; Dougall & Drysdale, 1978) and essential fatty acids (McCullagh, 1973). African elephants have been shown to spend up to 80% of their foraging time feeding on

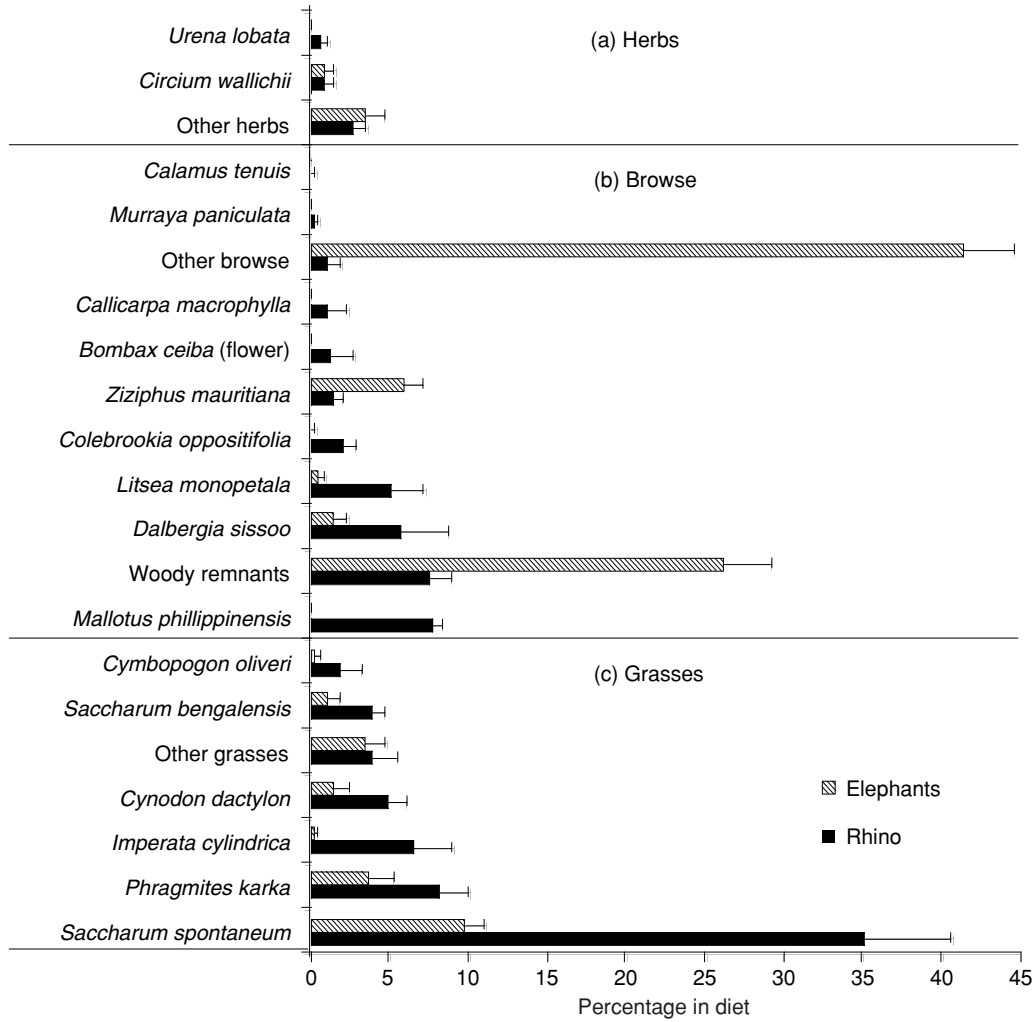


Fig. 2. The contribution of different food items to the dry season diets of rhinos *Rhinoceros unicornis* and elephants *Elephas maximus*. Error bars denote 1 SD. In addition to species found in the diets, the plant reference collection included aquatic plants *Hydrilla* spp. and *Paspallum* spp., and four *Ficus* species.

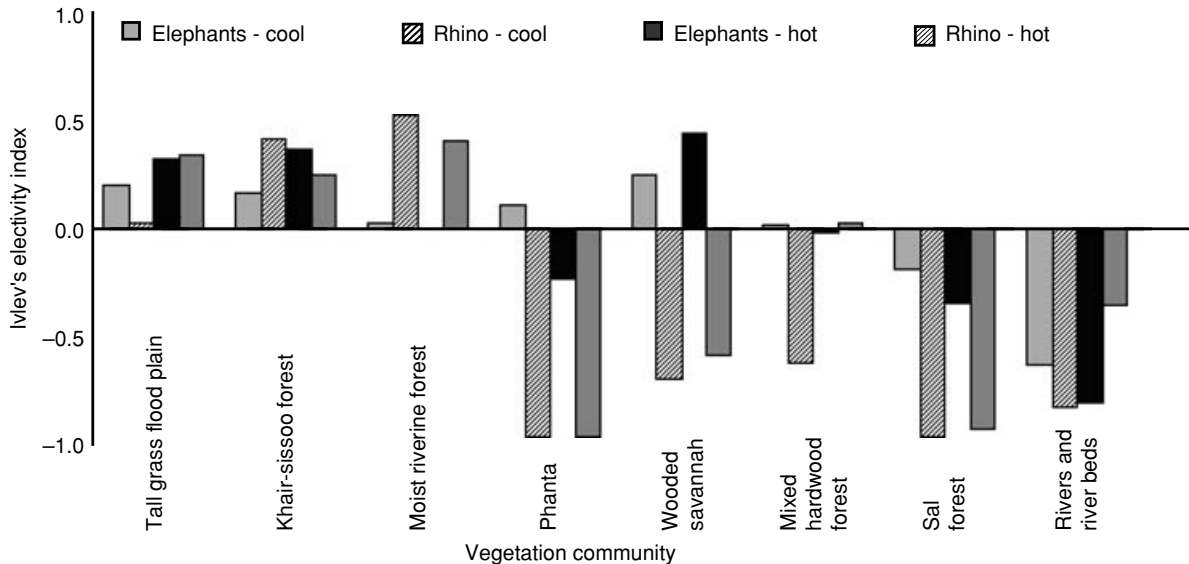


Fig. 3. Strength of habitat selection, measured by Ivlev's (1961) electivity index, by elephants *Elephas maximus* and rhino *Rhinoceros unicornis*, during the October to mid February cool, and the mid February to June hot period of the dry season.

bark, wood and roots during droughts (Owen-Smith, 1988). Elephants were observed in the study area feeding on wood and bark of *Acacia catechu* and bark from *Bombax ceiba*. This was also confirmed by large, easily identifiable remnants in the fresh elephant dung, and signs of debarking on a number of these trees. Compared with the elephants, the rhino ate small amounts of bark and wood. However, the rhino in our study area consumed more woody remnants (7.5%) than reported from other studies in Nepal (Laurie, 1978; Jnawali, 1995).

*Saccharum spontaneum* contributed most, quantitatively, to the grass proportions of the diets of both species. This similarity is important since *S. spontaneum* was the plant species contributing most to the diet of the rhino. *Saccharum spontaneum* is the dominating species in the tallgrass floodplain. Unlike most other grasses, this species sprouts during the dry season, providing food of relatively good quality.

### Habitat use

Both species preferred vegetation types of relatively early seral stages, as is also indicated in the literature (Mueller-Dombois, 1972; Laurie, 1982; Ishwaran, 1983). However, the two species differed in their degrees of preference; the rhino had a stronger tendency to avoid several vegetation types than elephants did, and the complex of tallgrass floodplain/moist riverine forest/khair–sissou forest seemed to be a critical habitat feature for rhino.

Elephants used sal forest less than expected. However, statistical avoidance, or negative IEI, does not mean that the habitat is unsuitable. Where a vegetation type is superabundant, as sal forest was in the study area, animals may spend a considerable amount of time in that vegetation type, yet still 'avoid' it in terms of use in proportion to availability. Although sal forest was not used according to its availability, it was nevertheless the habitat most used by elephants during the cool period. In the hot period, however, sal forest dropped from first to fifth in ranked importance. This can be explained by sal forest only having a sparse grass and shrub layer during the hot period (Dinerstein, 1979a). The remnant hot-period use of sal forest may in part be explained by the elephants seeking shade from the sun and heat during the hottest hours of the day.

The overall strength of habitat selection, both for rhino and elephant, differed between the cool and hot periods. Rhino preferred two vegetation types in the cool period, i.e. khair–sissou forest and moist riverine forest, and were scarcely found in the other vegetation types. During the hot period, food quality declines in these preferred habitats, so the tallgrass floodplain, with sprouting, high quality *S. spontaneum*, becomes important. Habitat use was thus spread over three vegetation types rather than two, resulting in lower overall preferences during the hot period.

For elephants, the situation was different. Preferences and avoidances became more pronounced, leading to a

more clumped distribution of animals in the hot part of the dry season. Such habitat use contraction during the driest periods, and widening during the rest of the year has also been observed for African elephants by Leuthold (1970), who suggested that elephants, by this behaviour, avoid unnecessary depletion of food reserves. It seems, then, that rhinos have a rather confined choice of vegetation types, among which they exploit the tallgrass floodplain more intensively during the hot period. Their relative use of the floodplain increases even further in the rainy season, when the growth of *S. spontaneum* reaches its peak (Jnawali, 1995). Elephants, on the other hand, use a variety of habitat types in the cool period but restrict their range during the hot period when good quality food is only available in some areas.

The fact that the average absolute value of IEI for the dry season as a whole was 140% higher for rhino than elephants indicates that rhino had more pronounced preferences and avoidances than elephants throughout the dry season. Simply looking at time expenditure reveals that rhino spent 85% of their time in only three vegetation types (tallgrass floodplain, moist riverine forest and khair–sissou forest), whilst elephants used none of the vegetation types > 19.5% of the time. To reach 85% habitat occupancy for elephants, six vegetation types had to be included in the calculation. The rhino can therefore be said to have a narrower niche in the habitat dimension than the elephants.

### Potential competition

The diet of rhino was strongly dominated by grasses, whilst elephants relied mostly on browse. Bearing in mind the gut anatomy and digestive physiology of the two species, the adaptations underlying these differences are apparent. As reported by Owen-Smith (1988), the food intake of rhino is limited by its slow rate of digestive throughput. This long retention time results in a fairly effective fermentation of cellulose; hence the rhino depends upon a relatively high concentration of fermentable fibres in the food. This makes grasses suitable forage for rhino. The elephant, on the other hand, has a comparatively rapid digestive throughput rate. Feeding on browse is favourable owing to the suitable mix of easily digestible carbohydrates and indigestible fibres of the woody plants (Owen-Smith, 1988), the latter enhancing the throughput rate. Quickly digested carbohydrates are absorbed, and the remainder is passed out of the gut to make way for more food.

Furthermore, the elephant's trunk gives opportunities for browsing from a higher layer than accessible for any other ground-dwelling herbivores. Data on African elephants show that this species browses mostly from the 0–2 m layer (Guy, 1976), but the possibility of reaching higher is still there. Elephants are also prone to push over trees (Croze, 1974; Williams, 2002), thus gaining access to otherwise inaccessible browse, although Asian elephants may be less inclined to do this than African elephants (Ishwaran, 1983).

Another difference between rhino and elephants is the scale of their spatial strategies. Elephants occupy annual home ranges far larger than those of rhino. Recent telemetry studies by Fernando & Lande (2000) and Williams (2002) showed annual ranges varying between 61 to 121 km<sup>2</sup> in Sri Lanka to between 188 and > 400 km<sup>2</sup> in Rajaji National Park in northern India, respectively. Extensive movements of elephants were observed in our study area, with individuals walking up to 18 km, straight-line distance, in < 20 h. Rhinos, on the other hand, do not seem to move widely. In RCNP they have annual home ranges of c. 3 km<sup>2</sup> while in Karnali their ranges were larger (c. 30 km<sup>2</sup>), probably owing to low animal density shortly after reintroduction and/or poorer floodplain quality than RCNP (Jnawali, 1995).

The overall picture is that elephants have the capacity for wide roaming, opportunistic and flexible behaviour (Leuthold, 1977; Sukumar, 1989; Williams, 2002), whilst rhinos occupy smaller, fixed home ranges in which their specific habitat demands are met (Laurie, 1978; Sinha & Sawarkar, 1991; Jnawali, 1995; Dinerstein, 2003).

At the time of study, numbers of rhinos and elephants were low, estimated at roughly 0.4 and 0.5 animals/km<sup>2</sup>, respectively. From tracks and direct sightings it was clear that the populations of both species included several juveniles, indicating good recruitment. With virtually no habitat available for rhinos outside the Babai valley, and restricted areas within the national park for the elephants, densities of both species are expected to increase markedly in the years to come. Their different spatial strategies might then influence the outcome of any competition for resources. Since rhino are restricted to relatively small home ranges throughout the dry season while elephants roam over much larger areas, rhino might then be at a disadvantage.

Although their diets and habitat preferences were found to be substantially different, there were similarities that could lead to interspecific competition at higher animal densities. Both species ate considerable amounts of *S. spontaneum*. If this species is over-exploited, the rhino in particular would suffer, as more than one-third of their diet during the hot period of the dry season consisted of *S. spontaneum*. Dinerstein (2003) considers available *S. spontaneum* areas as a key factor determining rhino population growth. Also, *Phragmites karka*/*Arundo donax* were the second most important species in the grass diets of both elephants and rhinos. All three grasses are confined to the tallgrass floodplain, making this the critical habitat for the two megaherbivores at increased population densities. Protecting the tallgrass floodplain areas, and monitoring their use by both elephants and rhinos for early detection of competition, are thus key elements to ensure sustainable management of the two endangered megaherbivores in Nepal.

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