Diet and habitat use of Greater Indian one-horned rhinoceros (*Rhinoceros unicornis*) and Asian elephant (*Elephas maximus*) during the dry season in Babai valley, Royal Bardia National Park, Nepal

by

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ABSTRACT

The aim of this study was to assess the niche overlap and potential for competition between Greater Indian one-horned rhinoceros (*Rhinoceros unicornis*) and Asian elephants (*Elephas maximus*) in the Babai valley of Royal Bardia National Park (RBNP) in Nepal, by investigating their diets and habitat use. The rhino of Babai valley were translocated from Royal Chitwan National Park in 1990. For decades, resident elephants have not been reported in RBNP, except for a few individuals, however, during the last two years at least 35 elephants have more or less settled in the area. Of them at least 18 have inhabited the Babai valley on a regular basis.

Plant species consumed and their quantitative contributions to the diets of rhino and elephants were determined by microhistological analysis of faecal samples. To assess food preferences, plant availability data was acquired from a previous study in a similar area nearby (Jnawali 1995). We found the two megaherbivores' diets to be quite different, with a percentage similarity index of 37.5. The proportions of grass and browse were strikingly different in the diets of rhino and elephants; the former consumed of 63% grass and 28% browse, whilst the latter consumed 65% browse and 24% grass. Only in the case of three grass species, *Arundo donax*, *Phragmites karka* and *Saccharum spontaneum*, all mainly growing in tall grass flood plains, did we detect a potential for competition.

The habitat use of elephants was determined by counting dung along transects. Data on rhino habitat use were available from a telemetry study in the nearby Karnali flood plain area (Jnawali 1995). Both species preferred tall grass flood plain and khair-sissoo forest, whilst only elephants preferred wooded savannahs and only rhino preferred moist riverine forest. Preferences differed between the cool and hot periods of the dry season.

Rhino were found to be far more habitat specific than elephants. Rhino spent 85% of their time in only 3 vegetation types, whereas 6 vegetation types were necessary for elephants to reach the same level of habitat occupancy.

As elephants were more flexible and opportunistic in their ranging and foraging behaviour, we predict that rhino will be the weaker part should competition between the two megaherbivores arise. However, at present the low density of animals and the small overlap in diet and habitat use indicated that competition was negligible if existing at all.

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PREFACE

This study was made possible through the co-operation between the Department of Biology and Nature Conservation at the Agricultural University of Norway, the Department of National Parks and Wildlife Conservation/His Majesty's Government of Nepal and the King Mahendra Trust for Nature Conservation in Nepal.

The thesis is submitted to the Agricultural University of Norway in partial fulfillment of the requirements for the degree Cand. Agric./M.Sc. in Nature Conservation and Management of Natural Resources. Our principal supervisor has been Professor Per Wegge at the Department of Biology and Nature Conservation at the Agricultural University of Norway.

Agricultural University of Norway, Ås

December 1, 1996

Jo Inge Fjellstad

Geir Steinheim

02-10-02

Dear Kees,

We hope you, and others, might find parts of the thesis interesting. Thank you for your interest,

Geir S.

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INTRODUCTION

Rhino and elephant status

Both the Greater Indian one-horned rhinoceros (*Rhinoceros unicornis*) and the Asian elephant (*Elephas maximus*) are listed as endangered species by the World Conservation Union (Groombridge 1993).

The Greater Indian one-horned rhinoceros (hereafter termed "rhino") used to be distributed over the flood plains of the Indus, the Ganges and the Brahmaputra (Laurie 1978). Due to a substantial increase in human population during the two last centuries, followed by habitat destruction and extensive hunting, the rhino are now restricted to small, isolated populations in a few protected areas of Nepal and India. Poaching is regarded as the greatest threat to the remaining populations (Bhattacharya 1993).

The majority of the rhino inhabits Kaziranga National Park in India (Fig. 1), where the population has been increasing. However, the annual rate of increase is now low, and the population seems close to the carrying capacity at about 1200 individuals (Bhattacharya 1993, Vigne and Martin 1994). Royal Chitwan National Park (RCNP) in Nepal harbours the second largest population. Following the creation of the park in 1973, the number has increased from about 100 to about 450 (Martin and Vigne 1995).

In order to establish new breeding populations, rhino have been translocated from RCNP to Dudhwa National Park in India (Sale and Singh 1987) and Royal Bardia National Park (RBNP) in Nepal (Jnawali and Wegge 1993). Whilst the establishment of a breeding population in Dudhwa has been troublesome (Sinha and Sawarkar 1991), the reintroduction to RBNP has so far been promising: in 1986, 13 rhino were released in the Karnali flood plain, and in 1990, 25 rhino were released in Babai valley of RBNP. Due to poaching and stochastic events, the population has been slow to increase in RBNP. However, the breeding performance has been high, indicating adequate habitat quality and potential for population increase. 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.).

The Asian elephant (hereafter termed "elephant") numbers between 30,000 and

60,000 (Nuttall 1995, Sukumar 1989), nearly half of which inhabit the Indian sub-continent. Habitat fragmentation and destruction, rather than poaching, are regarded as the major threats to the elephants (Fjellstad and Steinheim 1995, Johnsingh and Panwar 1989, Sukumar 1989).

Elephants occur in relatively low numbers in Nepal, and the only resident ones inhabit Parsa Wildlife Reserve, adjacent to RCNP in central Nepal, numbering 20-30 animals (Smith and Mishra 1992). Two groups of elephants have been sighted on a regular basis in western Nepal, one in the vicinity of RBNP and one in Royal Sukla Phanta National Park 100 km further west (Smith and Mishra 1992). These groups might be part of a larger population of elephants extending to Dudhwa (Sinha and Sawarkar 1991) and Corbett National parks in India (Sukumar 1989). See Fig. 1.

Today approximately 35 elephants inhabit the Bardia area (pers. obs., I. Lama, pers. comm.). Many of them roam into the Babai valley from time to time and at least 18 use the valley regularly (pers. obs., G. Singh, pers. comm.).

Rhino and elephant ecology

Both elephants and rhino can be classified as generalist herbivores, regarding the number of plant species they consume. In Sri Lanka, McKay (1973) recorded elephants consuming a total of 89 plant species, and Ishwaran (1983) found a similar result, with 74 woody plant species being eaten in addition to grass. Sukumar (1989) found, in a study in southern India, that the elephants consumed 112 species of plants. Rhino in RCNP, Nepal, show a similar breadth of diet, feeding on 183 species of plants from 57 botanical families (Laurie 1978).

Elephants and rhino are both reported to be mixed feeders, with proportions of grass and browse in the diet varying throughout the year. Sukumar (1989) found that browse constituted 69% of the elephant diet in southern India during the first dry season (January to April) and only 46% during the wet season. During the second dry season, feeding on browse increased again, to 56%. Similar patterns have also been reported for African elephants (*Loxodonta africana*) (Owen-Smith 1988, Field and Ross 1976).

Similarly, the rhino in Nepal switch from a highly graminoid dominated diet during the wet season, to a diet with increased proportion of browse during the dry seasons

(Jnawali 1995, Laurie 1982).

For herbivores, food quality is generally more limiting than food quantity (Sinclair 1975), and the nutrient value of plants is known to drop during dry seasons (Sukumar 1989). Considering the African elephant[1], Laws (1970) suggested that while grasses probably are 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 also be the case for the Asian elephant and the rhino.

African elephants carry out a substantial part of their browsing below a height of two metres (Guy 1976), i.e. they utilise largely the same layer to which rhino are restricted. As megaherbivores with mixed, generalist diets, probably feeding in the same vegetation layer, there is the possibility that rhino and elephants occupy the same ecological niche. Indeed, where these two species co-exist in high enough densities, there is reason to believe that competition may occur.

Study objectives

For successful management of sympatric rhino and elephant populations, it is important to determine whether competition does indeed occur and if so, to what extent. The Babai valley, being a relatively contained area with present rhino and elephant populations of similar sizes, provides the perfect opportunity from which to gain such insights.

This study aims to determine the degree to which the ecological niches of elephants and rhino overlap, and thus the possibility of inter-specific competition in an area of the Babai valley in RBNP. The fundamental resource dimensions are assumed to be the food resource and, closely linked to this, habitat use. The diet study was conducted in the hot period of the dry season, this being the time of year when food is of poorer quality and thus when potential conflicts may be most apparent. The habitat study covered the entire dry season.

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[1] The ecology of the African elephant has been thoroughly studied, whilst the Asian elephant has received much less attention. Thus, where data is lacking we assume similarities between the two species.

More specifically, we aim to:

- compare the relative proportions of grass, browse and herb species in the diets of rhino and elephants;
- compare the relative importance of food plant species for rhino and elephants, both in terms of their ranked contribution to the diets and the degree to which they are selected (assuming the same availability as in the nearby Karnali flood plain area (Jnawali and Wegge 1993));
- determine the habitat preferences of elephants in the study area, compare those with preferences of rhino (assuming similar preferences for the rhino of our study area as in the Karnali flood plain area (Jnawali 1995, Jnawali and Wegge 1993)) and relate habitat preferences to the availability of food plants; and finally,
- to assess the overall diet similarity and potential for competition between the rhino and elephants of Babai valley during the hot period of the dry season.

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^2 Royal Bardia National Park. The park is located in lowland Nepal (the terai), 390 km west of Kathmandu (Fig. 1). A relatively flat and wide part of the Babai valley was chosen, 46 km^2 in area and lying along the Babai river. The 1,000 feet (305 m) contour lines, which coincide well with the start of the Siwalik hills, were taken to denote the northern and southern boundaries of the study area, except for a few places too steep to be accessible, both for the study objects and the authors. The eastern and western boundaries were set at narrow parts of the valley.

The climate is subtropical monsoonal, with between 1,550 and 2,310 mm rainfall annually, most of which falls 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 period (October to mid February) and a hot period (mid February to June). The temperature ranges from a minimum of 10 °C in January to a maximum of 41 °C in May (Bolton 1976, Dinerstein 1979a).

The vegetation is a sub-tropical type, with a mosaic of early successional flood plain communities along the Babai river and its tributaries. Large areas of climax sal (*Shorea robusta*) forest dominate the upper, drier land, particularly to the north of the river. Intermingled in these areas are patches of grassland, locally known as phantas. The phantas originate from cultivated areas around villages, abandoned during the resettling programme before the park extension in 1984 (Upreti 1994).

Dinerstein (1979b) gave a detailed description of the vegetation types of the Karnali flood plain area in the south eastern part of the park. However, his study covered only a small part of the flood plain, and Jnawali and Wegge (1993) later extended this vegetation map, with a few slight modifications in the nomenclature. Although no vegetation studies have been conducted in Babai valley, we found our study area to be similar enough to the Karnali flood plain area to be described within the same framework. Some small adjustments in nomenclature were considered appropriate (consult "Part 2: Habitat use - results" (p. 28) for relative proportions of vegetation types in our study area):

Rivers and river beds consist of barren, sandy and stony areas along the Babai river and its tributaries.

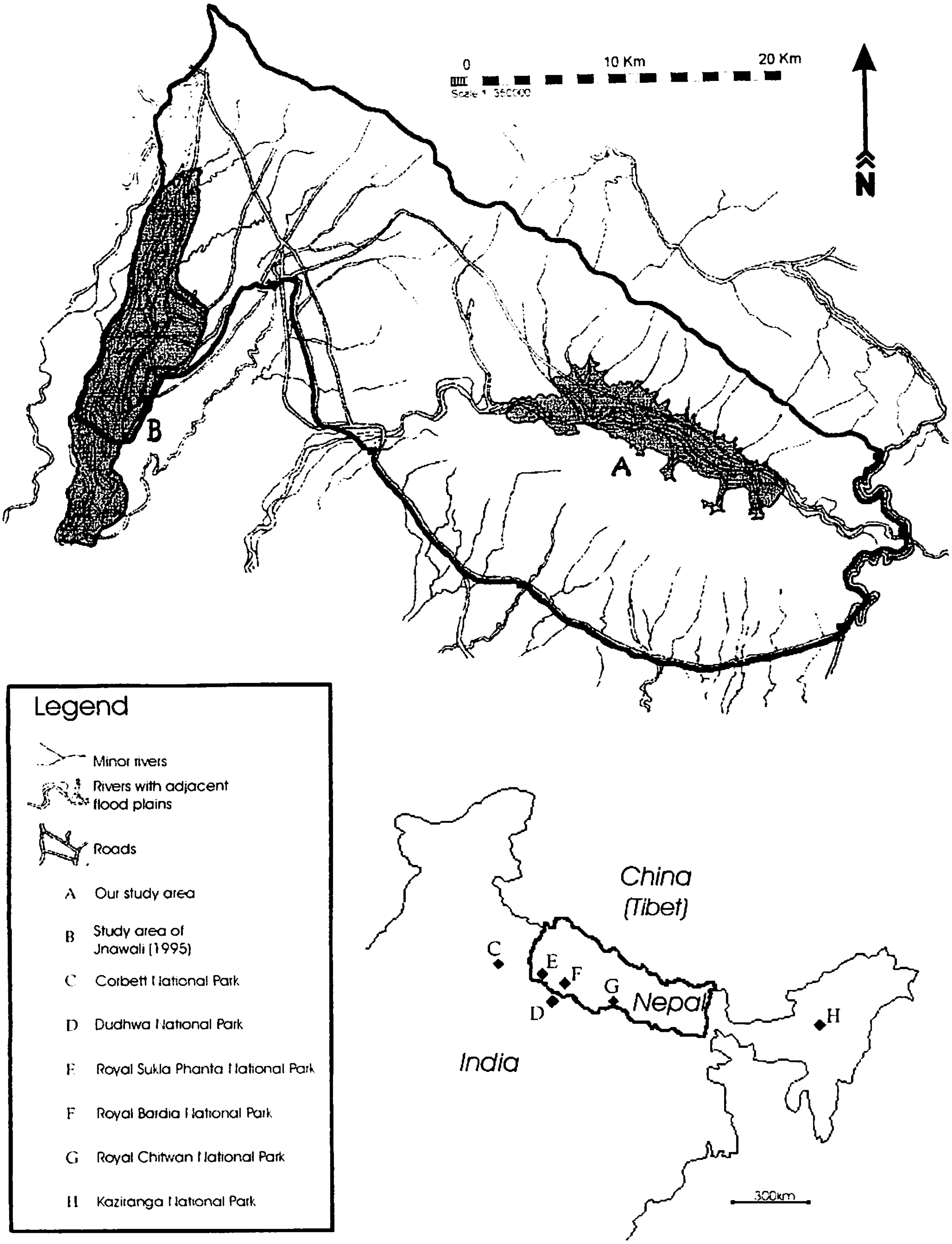

Figure 1: The small map shows national parks mentioned in the main text. The large map shows Royal Bardia National Park, with our study area (A) and the study area of Jnawali (1995) (B) shaded. The RBNP map is adapted from Upreti (1994).

Tall grass flood plains cover alluvial soil deposits along the Babai river and its tributaries, and are flooded during the monsoon season. The dominating species are *Saccharum spontaneum*, *Saccharum bengalensis* and *Phragmites karka*. Jnawali (1995) considers the drier conditions in RBNP compared to RCNP, due to better drained soil, to be an important reason for a less diverse flood plain community, and described (pers. comm.) the flood plains of our study area as even drier and more deficient in species and biomass than the Karnali flood plain.

Khair-sissoo forest is a later seral stage growing in patches on river beds along the Babai river and its tributaries. It is highly dominated by the two tree species *Acacia catechu* (khair) and *Dalbergia sissoo* (sissoo), which form the first seral stand of trees, due to their ability to withstand flooding.

Moist riverine forests grow along water courses and in depressions, and consist of species able to withstand water-logged soil. Grasses and herbaceous plants have difficulty establishing, due to the poor drainage, making the understorey and low layer relatively open. *Callicarpa macrophylla* and *Colebrookia oppositifolia* are common shrubs. The dominating tree species is *Mallotus phillippinensis,* together with *Ficus glomerata* and *Syzigium cuminii.*

Phantas are highly dominated by *Imperata cylindrica*. Most of the phantas in the area experience encroachment by fire resistant *Bombax ceiba* trees.

Wooded savannahs are *Imperata cylindrica* and *Vetiveria zizanoides* dominated grasslands with sparsely distributed tree species, e.g. *Bombax ceiba, Mallotus phillippinensis* and *Adina cordifolia.* Patches of young *Acacia catechu* occur relatively frequently.

Mixed hardwood forests are *Terminalia tomentosa* and *Schleicheria trijuga* intermingled forests, resembling wooded savannah, but with a denser tree layer and a more conspicuous shrub layer, e.g. with *Colebrookia oppositifolia.*

Sal forests are dominated by *Shorea robusta* (sal), which forms the canopy together with *Terminalia tomentosa.* The understorey is formed by *Shorea robusta* seedlings and several other tree species, e.g. *Buchanania latifolia, Mallotus phillippinensis* and *Lagerstroemia parviflora.* During the hot period of the dry season the low vegetation is very sparse.

Thirty-two mammal species were recorded in RBNP by Dinerstein (1979b). There is no specific literature on the fauna of Babai valley. Herbivores other than rhino and elephant observed in the study area were sambar (*Cervus unicolor*), swamp deer (*Cervus duvauceli*), spotted deer (*Axis axis*) and four-horned antelope (*Tetracerus quadricornis*). Barking deer (*Muntiacus muntjak*) were observed within the Babai valley, close to the study area. Nilgai (*Boselaphus tragocamelus*) and hog deer (*Axis porcinus*) were observed in the nearby Karnali flood plain area.

Other large mammals present were tiger (*Panthera tigris*), leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*) and wild boar (*Sus scrofa*).

One dirt road passes through the study area, for the most part parallel to the river. At present the study area is shielded from most human inference. The closest settlements are eight kilometres to the east.

PART 1: DIET COMPOSITION

Methods

Microhistological analysis of faecal samples was considered the most appropriate method of determining the composition of the diets of rhino and elephants. The method is based on recognising plant species remnants in faeces from their cell wall characteristics, and was first used in the analysis of mammal diets by Baumgartner and Martin (1939), when studying the diet of squirrels. Both Storr (1961) and Stewart (1967) have later found the method useful for obtaining accurate qualitative and quantitative measures of herbivores' diets. Other authors state that correction factors must be used to provide a suitable degree of quantification (Dearden *et al.* 1975, Holechek *et al.* 1982, Sparks and Malechek 1968), or that plant species should be merely ranked, according to their abundance in the diet (Vavra *et al.* 1978).

Faecal analysis 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 the case for bulk feeders such as rhino and elephants, where a great proportion of the food passes through the digestive tract virtually undigested (Owen-Smith 1988). This is, to our knowledge, the first study in which the method of microhistological analysis of faeces is used to analyse the diet of elephants.

Sampling

Determining the minimum number of samples necessary to obtain a suitable dietary estimate of a local population has received little attention in the literature. Anthony and Smith (1974) suggested that a minimum of 15 individual samples should be obtained to assess the diet of two deer species (*Odocoileus* spp.) in a particular season. In our study, fresh faecal samples from 40 rhino dung piles and 50 elephant dung piles were collected during March and April 1996.

Rhino establish latrines (Plate 1, p. 15) for defecation (Laurie 1978). To ensure a total representation of the rhino's diet, we collected dung samples from 20 different latrines distributed throughout the study area, as advised by Jnawali (1995 and pers. comm.).

From tracks and direct sightings it became clear that two groups of elephants and a few stray individuals inhabited the study area. We sampled dung both from stray individuals and from the two groups. To ensure that samples were taken from a wide representation of individuals, we used the weight of boli (individual faeces) as a guideline, assuming a fixed relationship between the boli weights and the sizes of elephants (Jachmann and Bell 1984). The whole range of boli weights were represented in the sample.

None of the dung piles from which samples were taken was judged to be more than 24 hours old. Each pile was mixed thoroughly, and samples of approximately 400 g (wet weight) were taken.

To enable interpretation of the faecal samples, 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 relative importance value (RIV). Due to limited time and resources, we chose our reference collection to consist of those plant species present in our study area which Jnawali had found to be most important for rhino in the Karnali area, with the lower limit of RIV set at 0.5 (see Appendix 1). In addition we included *Litsea monopetala* and *Murraya paniculata* which, although not occurring in the Karnali flood plain area (Jnawali 1995), were found to be important rhino food in RCNP (Laurie 1978). Aquatic plants are also reported to be important food for rhino (Laurie 1978, Sinha and Sawarkar 1991), and we included two common species, *Hydrilla* spp. and *Paspallum* spp., in the reference collection.

Slide preparation

We adopted a method which mainly followed Sparks and Malechek (1968) and Anthony and Smith (1974), as modified by Vavra and Holechek (1980) and Jnawali (1995).

The faecal samples were air dried (Plate 1, p. 15) and ground to pass through a 1 mm screen. The ground material was sieved through Endecotts sieves of 595 and 210 microns mesh size, to remove large unidentifiable particles and dust respectively. The samples were pooled at random into 5 pools from each species. The pooled samples werethoroughly mixed, and from each pool two spatulas of material were transferred to test tubes. Warm 5% sodium hydroxide (NaOH) solution was added, and the test

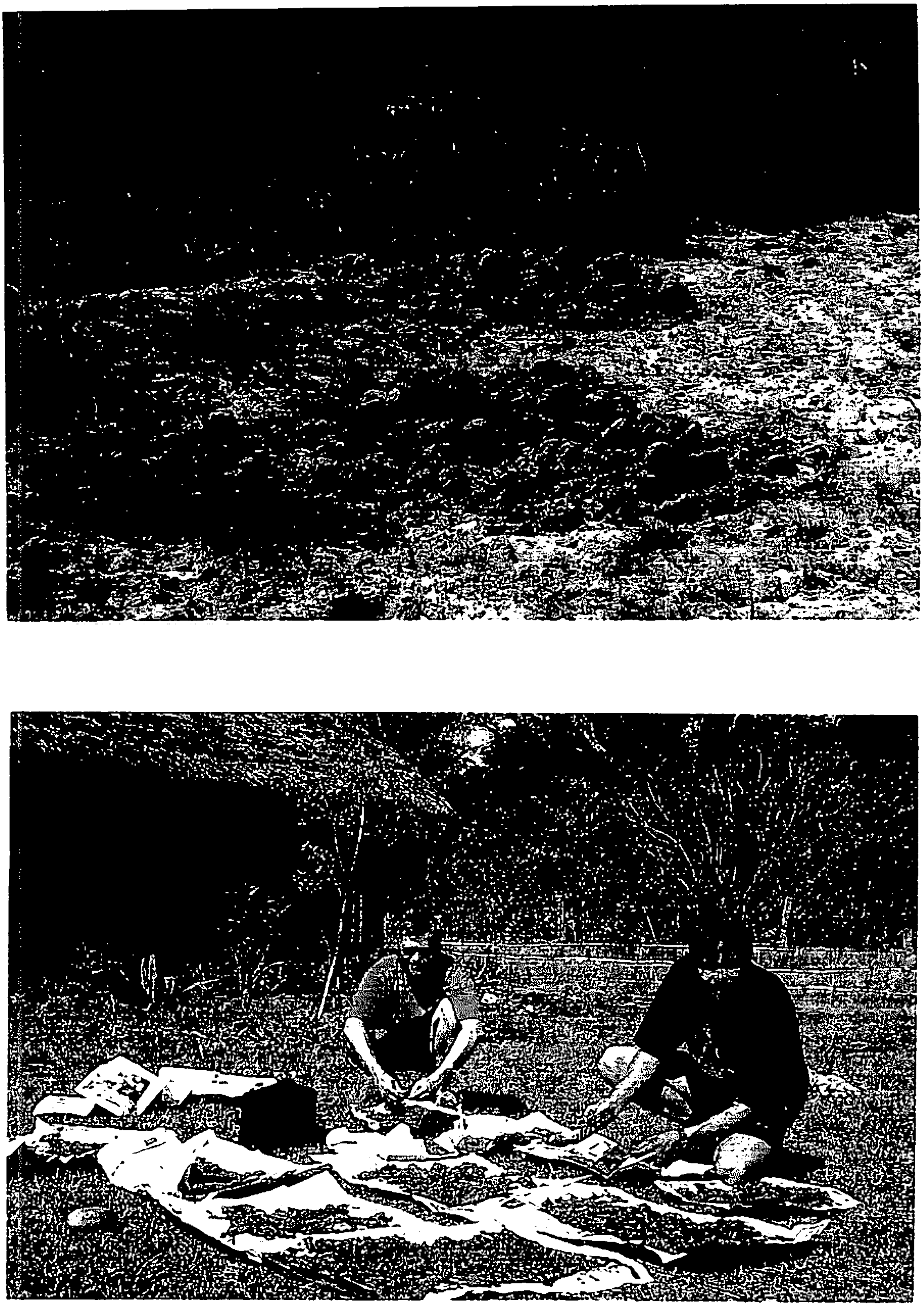

Plate 1: Top; a rhino latrine (*photo: J.I. Fjellstad*).
Bottom; faecal samples spread out to dry (*photo: N. Eide*)

tubes were heated in a boiling water bath for 4-6 minutes. The particles were allowed to settle before the supernatant dark fluid was removed. The treatment was repeated 3-7 times until relatively clear solution was produced, the material was then washed 4 times with warm distilled water, and dehydrated through a series of 25%, 50%, 75% and 100% alcohol treatments. The alcohol was removed through a series of xylene and alcohol mixtures (25%, 50%, 75% and 100% xylene). A small amount of material was dried between tissue paper, transferred to a slide and then evenly spread and mounted in Canada balsam under a 24 x 50 mm cover slip.

The plant reference collection was made following exactly the same procedure as for the faecal samples, except for using 10% NaOH solution. Detailed drawings were made of species-specific cell characteristics.

Slide interpretation

Before reading the slides of faecal samples, the observer went through a training and testing programme designed as recommended by Holechek and Gross (1982). The training continued until satisfactory accuracy was reached.

The faecal slides were read using a microscope, at 200x magnification, with a measuring scale in the ocular. Following transects across the slide, only non-overlapping fragments, identifiable at least to the categories "grass", "browse" or "herbs", and intercepted by the scale line, were recorded.

Fragments with good identifying features, but not to be found in the reference collection were classified as "other browse", "other grass" or "other herb". 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". A special category, "woody remnants", was made for fragments of bark and wood. Two grasses, *Phragmites karka* and *Arundo donax*, could not be distinguished from each other, and were grouped.

There is some controversy regarding the necessary number of identifications per sample to ensure satisfactory estimates of diet composition. Rogerson *et al.* (1976) recommended 200 identifications, while Sparks and Malechek (1968) considered 100 to be sufficient. However, to obtain best possible estimates, and since time needed for reading slides was small compared to that for preparing slides and learning to recognise the plant species in the reference collection, we continued reading until 400 fragments had been classified from each pooled sample.

Statistics

All statistical analyses were carried out by computer using SigmaStat statistical software (Jandel Corporation 1994).

A chi-square test was carried out to test the null hypothesis that the grass/browse/herbaceous proportions were the same for rhino and elephants. Paired chi-square tests were executed to determine the significance of any differences found within each category. We also performed a chi-square test to test the null hypothesis that the two species had the same diets in terms of the quantities of the individual food items.

Spearman's rank order correlation test was performed to test the null hypothesis that the ranked importance of food items for the two species were arrayed at random with each other. The test was carried out both for the overall diets and within the grass and browse categories.

A diet selection value (DSV) for each plant species was calculated by dividing the proportion of the plant species in the diet, by its availability. Time did not allow quantification of availability of individual plant species in our study area. Hence, a measure of availability was obtained by assuming that prominence values were the same as those calculated in the nearby and similar Karnali flood plain area (Jnawali 1995). The prominence value of a species in a particular vegetation type is calculated by

$$PV_x = M_x \times \sqrt{f_x}$$

where M_x is the percentage cover of species x, and f_x is the frequency of occurrence of species x in sample quadrates. A total prominence value for the entire study area was calculated for each plant species, by weighting the prominence values (PV_x) according to each vegetation types' percent contribution to the study area (see "Part 2: Habitat use - results" for the composition of the study area).

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

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

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 two frequencies.

Results

Of the total of 4000 fragments classified, 41% were "unidentified", and were classified only to category. Unless otherwise indicated, "unidentified" fragments are excluded from the following results. We did not find remnants of aquatic plants in either the elephant or rhino faecal samples.

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. 2), comprising 63.3%, followed by browse (28.8%) and herbaceous plants (7.9%). The results for the diet of elephants were strikingly different ($P < 0.0001$, $\chi^2 = 620.7$, $df = 2$); the browse plants dominated strongly with 65.6%, while grasses made up 25.1% and herbaceous plants 9.3% of the diet. Paired chi-square tests showed that

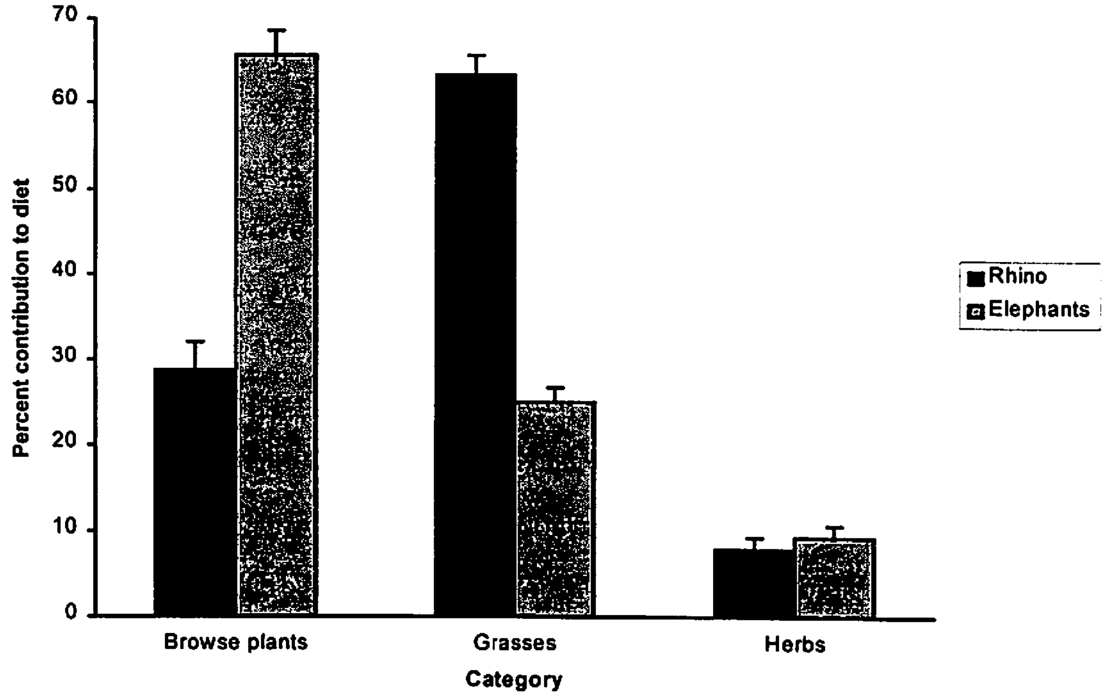

Figure 2: Proportions of browse, grass and herb in diets of rhino and elephants. Fragments identified only to category and not to species level are included. Error bars denote one standard deviation.

the differences between elephants and rhino were significant for the proportions of browse ($P < 0.0001$, $\chi^2 = 543.0$, $df = 1$) and grass ($P < 0.0001$, $\chi^2 = 591.4$, $df = 1$). We could not detect any difference for the herbaceous plant proportions ($P = 0.1266$, $\chi^2 = 2.330$, $df = 1$).

The elephants and rhino did not have the same diets in terms of quantity of individual food species ($P < 0.0001$, $\chi^2 = 1129.3$, $df = 20$). By far the most abundant plant species in rhino faecal samples was *Saccharum spontaneum* (Fig. 3). This grass species alone accounted for 35.0% of the diet. Other frequently found grasses were *Phragmites karka/Arundo donax* (8.0%), *Imperata cylindrica* (6.4%) and *Cynodon dactylon* (4.9%). The most abundant browse species was *Mallotus phillippinensis* with 7.6%, while *Dalbergia sissoo* and *Litsea monopetala* were represented with 5.7% and 5.0%, respectively. Woody remnants contributed 7.5%.

By contrast, in the elephant dung samples, "other browse" formed the largest single component of the diet with 40.3%. Woody remnants contributed 26.1%, and the thorny bush *Ziziphus mauritiana* 6.6%. As for the rhino diet, *Saccharum spontaneum* was the most common grass species, at 9.8%, followed by *Phragmites karka/Arundo donax* with 4.1%.

The diet selection values (DSV) of elephants and rhino for the different food species are given in Table 1. Although significant only at 90% level of confidence, Spearman's rank order correlation coefficient for the DSVs showed that the elephants' and rhino's ranking of food species was correlated to some extent ($R^2 = 0.48$, $P = 0.051$). Investigating further, we found that the two megaherbivores' ranking of grass species was significantly and closely correlated ($R^2 = 0.94$, $P = 0.0167$), whilst there was no significant relationship between their ranking of browse plants ($R^2 = 0.51$, $P = 0.138$).

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

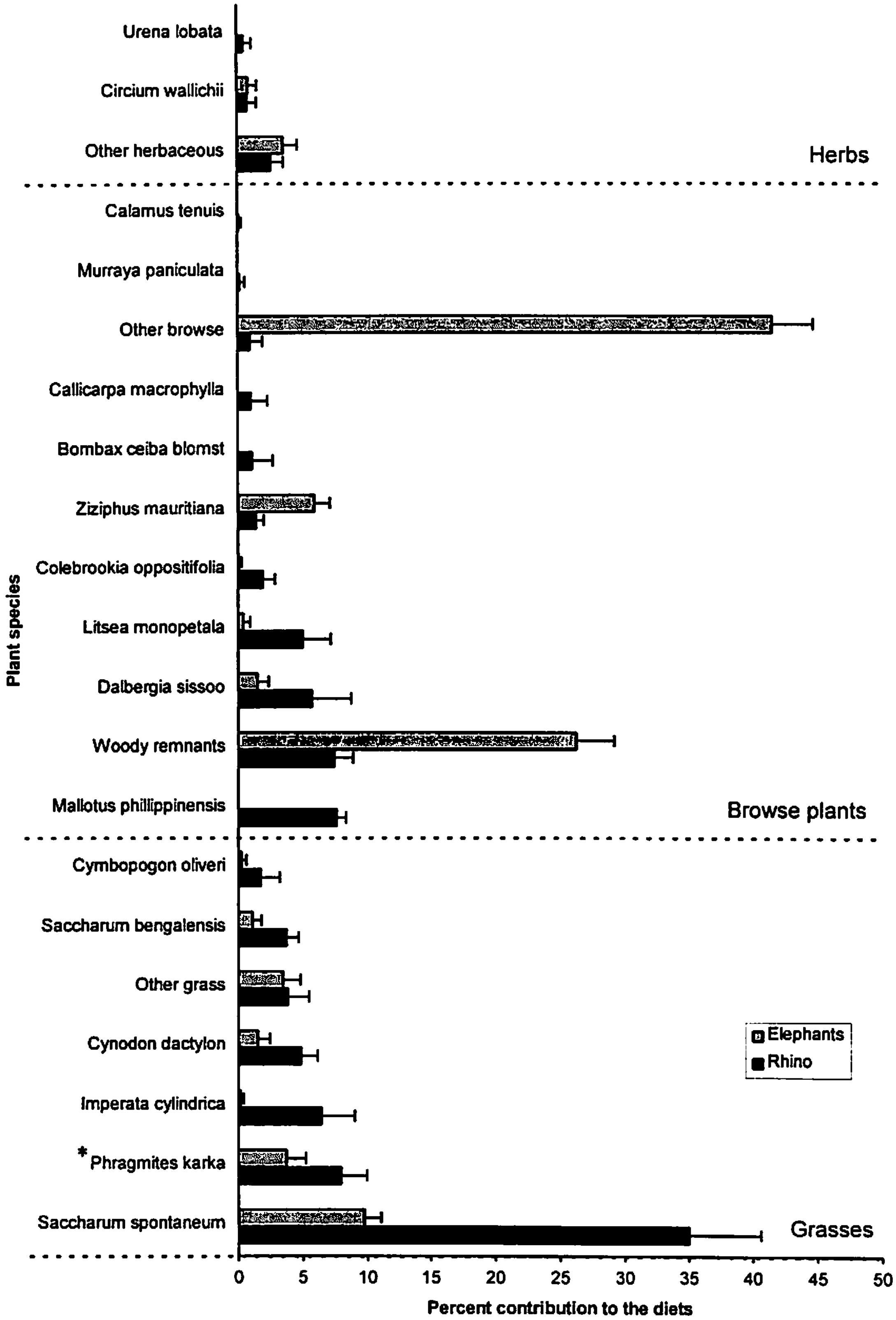

Figure 3: The contribution of different food items to rhino and elephant diet, divided into categories and ranked by importance to rhino. Fragments not identifiable to species level are omitted from the calculation. Error bars denote one standard deviation. * Includes *Arundo donax*, which could not be distinguished from *Phragmites karka* in the faecal analysis.

Table 1: Diet selection values (DSV) for rhino and elephants in our study area in Babai. See main text for explanation of DSV calculation.

Rhino		Elephants	
Plant species	DSV	Plant species	DSV
	Browse plants		
Litsea monopetala	8,295	*Ziziphus mauritiana*	1,642
Dalbergia sissoo	3,539	*Dalbergia sissoo*	0,938
Bombax ceiba	3,183	*Litsea monopetala*	0,695
Mallotus phillippinensis	1,005	*Colebrookia oppositifolia*	0,005
Ziziphus mauritiana	0,386	*Bombax ceiba*	-
Colebrookia oppositifolia	0,103	*Mallotus phillippinensis*	-
Callicarpa macrophylla	0,024	*Ficus glomerata*	-
Calamus tenuis	0,020	*Callicarpa macrophylla*	-
Ficus glomerata	-	*Calamus tenuis*	-
	Grasses		
Phragmites karka/Arundo donax	2,391	*Phragmites karka/Arundo donax*	1,112
Cynodon dactylon	0,550	*Cynodon dactylon*	0,172
Saccharum bengalensis	0,542	*Saccharum bengalensis*	0,159
Cymbopogon spp.	0,369	*Saccharum spontaneum*	0,090
Saccharum spontaneum	0,321	*Cymbopogon spp.*	0,054
Imperata cylindrica	0,047	*Imperata cylindrica*	0,001
	Herbs		
Cirsium wallichii	2,194	*Cirsium wallichii*	2,370
Urena lobata	0,760	*Urena lobata*	-

Discussion

In comparative studies of large sympatric herbivores (Cuartas and Garcia-Gonzalez 1992, Garcia-Gonzalez and Cuartas 1989), a 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 radically different grass and browse proportions between the two species' diets are striking. The results on grass/browse/herbaceous proportions in the diet of rhino, show a close similarity to the results obtained in the Karnali flood plain area by Jnawali (1995), while Laurie (1978) found rhino in RCNP to consume much more grass, a discrepancy probably explained by the poorer flood plains in RBNP. The grass/browse/herb proportions of the elephants' diet 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 significantly different in terms of the quantity of the different food items consumed, not only for the categories but also for individual food species. There was no significant correlation between the two species in terms of selection for browse plants (ranking of DSVs). Also, the DSVs for the elephants were generally lower than for rhino, reflecting the fact that the elephant diet consisted of a large proportion of "other browse".

This large proportion of "other browse" in the elephant diet is not a surprising result: the plant reference collection consisted of key food species for rhino, for which browse is of secondary importance, whereas for elephants browse made up two-thirds of the diet. We have some indications of the composition of "other browse". The game scouts in RBNP believed that several *Ficus* spp. were preferred by elephants (G. Singh, pers. comm.), moreover *Ficus* spp. are among the most important browse fodder for domestic elephants (Lemkuhl 1989, K. Thorsrud, pers. comm.). 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 in the faecal samples consisted only of naked leaf nerves, and neither species nor genus determination of adequate certainty could not 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 and G. Singh, pers. comm.).

Mallotus phillippinensis was the most important browse species for rhino in our study area. A. C. Williams (unpubl.) considers this species to be an important food item for elephants as well, based on preliminary results from a study in Corbett National Park in India, yet, interestingly, *Mallotus phillippinensis* did not occur in the diet of the Babai elephants.

As for the "woody remnants" category, the elephants ate considerable amounts (26.2%) of bark and wood, as is also the case in southern India (Sukumar 1989). Bark eating behaviour is likely to be common for the same reasons as are proposed for African elephants, namely to obtain minerals (Dougall and Drysdale 1978, Laws *et al.* 1975) and essential fatty acids (McCullagh 1973). African elephants have been shown to spend up to 80% of their foraging time feeding on bark, wood and roots during draughts (Owen-Smith 1988). We observed elephants in the study area feeding on wood and bark of *Acacia catechu* and bark from *Bombax ceiba*. This behaviour was also confirmed by large, easily identifiable remnants in the fresh elephant dung, and signs of debarking on a number of these trees (Plate 2, p. 24). It is interesting in this context that many of the elephants (at least six of the males, pers. obs.) in the study area had tusks, which are obviously valuable tools, together with the trunk, when stripping bark.

Compared with the elephants, the rhino ate small amounts of bark and wood. Our results show, however, that the rhino in our study area consumed more woody remnants (7.5%) than reported by other authors. Whilst Jnawali (1995) gives no information on bark and wood content in the diet of the Karnali rhino, Laurie (1978) found the rhino of RCNP to consume an unspecified amount of small branches of trees and shrubs which cannot have been great, since the entire browse proportion in his study was only 8.4%.

This far we have focused mainly on differences in the diets of rhino and elephants. However, the Spearman's rank order correlation test for the DSVs showed that the rhino's and elephants' ranking of food species was not arrayed completely at random with each other. The underlying cause of this was the close correlation in the ranked DSVs for grass species. Both showed strongest preference for *Arundo donax/Phragmites karka*, with *Cynodon dactylon* second and *Saccharum bengalensis* third.

Another similarity was that *Saccharum spontaneum* contributed most, quantitatively, to the grass proportions of both diets. This similarity is all the more important since *Saccharum spontaneum* was the plant species contributing most to the diet of the rhino. *Saccharum spontaneum* is the dominating species in the tall grass flood plain. Unlike most other grasses, this species is sprouting during the dry season, providing food of relatively good quality. Generally this sprouting is retarded in RBNP compared to RCNP, due to lower soil moisture (Jnawali 1995), but green areas of *Saccharum spontaneum* were still a striking feature in the flood plains of the study area (Plate 2, p.24).

Aquatic plants are considered to be important food for rhino by Laurie (1978) and Sinha (1991). We did not find such plants to occur in either rhino or elephant samples, a result probably due to biases in the microhistological method. Jnawali (1995) suggests that aquatic plants might be digested thoroughly due to their more delicate physical structure, and hence do not appear in the samples, and this would seem to be supported by our results.

Although the rhino is reported to be a generalist feeder, we found that only 8 species contributed over 75% of the diet. Whilst this may seem surprising, it is supported by work in RBNP (Jnawali 1995) and in RCNP (Jnawali 1995, Laurie 1978). It seems safe to assume that many species may be eaten in very small quantities. A similar pattern was reported for elephants in southern India by Sukumar (1989), who found that 25 of the 112 species consumed, contributed about 85% of the diet.

Plate 2: Top; the result of elephants stripping bark from *Bombax ceiba* (*photo: G. Steinheim*).
Bottom; sprouting *Saccharum spontaneum* on the flood plain (*photo: J.I. Fjellstad*).

PART 2: HABITAT USE

Methods

We had insufficient resources to carry out a radio telemetry study to monitor habitat use, and dense vegetation in most of the area precluded direct observation of animals as a mode of data collection. We therefore chose to determine the habitat use of elephants by counting dung piles along transects, a method recommended by Dawson and Dekker (1992) for surveying Asian elephants, after being widely used in African forests (Barnes and Barnes 1992, Barnes *et al.* 1995, Fay 1991, Jachmann and Bell 1979, Jachmann and Bell 1984). Dung count surveys are based on the assumption that defecation rates for 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 synchronisation in defecation (Ratnasooriya *et al.* 1994). Hence, dung count surveys give information on movements of elephants during the whole 24 hour cycle.

Rhino deposit their dung in fixed spots, rhino latrines (Plate 1, p. 15), shared by several animals (Laurie 1978, Penny 1988). In our study area, it was rare to find rhino dung outside latrines. Hence, counting dung is unsuitable for rhino habitat surveys. We assumed that the rhino in Babai valley have time-space patterns of habitat use similar to those detected in the Karnali flood plain area by Jnawali (1995), and used his radio telemetry data when comparing the habitat use patterns of rhino to those of elephants in Babai valley. It should be noted, however, that Jnawali only monitored the movements of rhino during daytime.

Elephant dung counts

A team of four observers (two experienced field observers and the authors) searched 20 metre wide transects for all elephant dung piles. Person A (one of the authors) had the responsibility for maintaining a straight line along fixed compass bearings. He also measured the distance walked by counting steps (aided by a Global Positioning Systems unit and an optical Rangefinder), and searched a narrow strip on both sides. Persons B and C (field observers) walked on either side of A, and were responsible for finding every dung pile in a 10 metre strip. Person D (the other author) assisted the searching in difficult places, and served as a control behind the other observers. In cases of doubt as to whether dung lay inside the 20 metre strip, a control measurement was done by observer D, using a tape measure. 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 tall grass flood plain (low visibility) than in sal forest (high visibility).

Distances walked in different vegetation types were recorded. For every dung pile encountered, vegetation type was recorded. Each dung pile was classified according to degradation stage, following the method of Dawson and Dekker (1992), where stage one is fresh dung and stage five is old, nearly completely degraded dung. We divided the dung into two age classes; "new" dung, comprising degradation stages 1 and 2; and "old" dung, comprising degradation stages 3-5. The division is done such that we feel confident that the vast majority of the "new" dung is from the hot period of the dry season. The bulk of the "old" dung is believed to originate from the cool period of the dry season. Little is believed to remain from the monsoon and the hot period of the last dry season, due to rapid degradation in humid conditions (Barnes and Barnes 1992).

Transects were designated in a systematic random manner: from a randomly placed starting point, all transects were laid perpendicular to the Babai river, and equidistant from one another (Fig. 4). On completion of these transects, time was available to walk additional transects to improve data quality. Four (short) transects were designated as follows: from 9 potential starting points, which were at the Babai river, midway between already completed transects, four were randomly chosen. We flipped a coin to decide whether to walk north or south from these starting points. The total length of the transects was 30 km.

Statistics

All statistical analyses were carried out by computer using SigmaStat statistical software (Jandel Corporation 1994).

The relative coverage of the different vegetation types present in the study area was estimated directly from the transect data, as the proportional distance walked in each vegetation type.

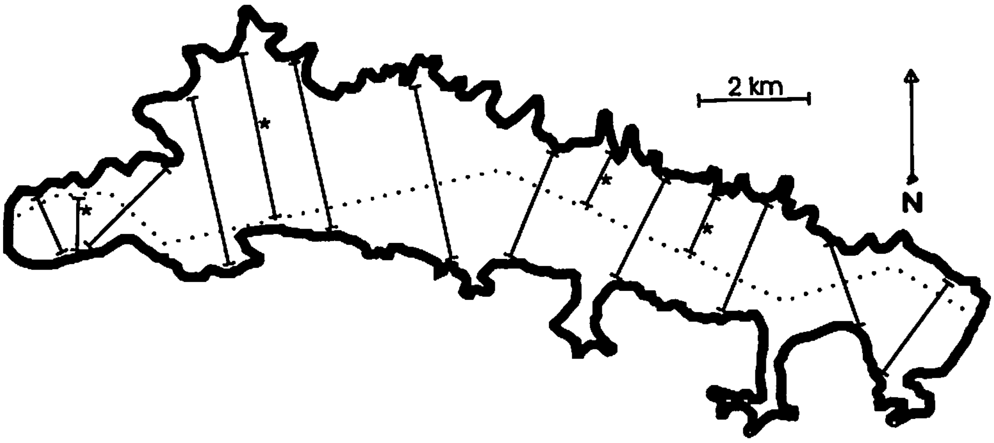

Figure 4: Map showing the design of transects. The dotted line indicates the Babai river. Stars (*) denote the additional four transects (see main text).

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 and Krausman 1984) were calculated for the usage proportions. The proportions of different vegetation types within the study area were taken to represent the expected proportions of elephant usage, to which the confidence intervals were compared.

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

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

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, zero 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, we also calculated IEI separately for the cool period (old dung) and the hot period (new dung) of the dry season.

Information on habitat use of rhino was adapted from Jnawali's (1995) study in the Karnali area. When males and females differed in their preferences, we used the data on females, this being more reliable, since only two males were radio collared. We calculated the strength of rhino preferences (IEIs) 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 two megaherbivores were habitat specific.

Results

Table 2 shows the proportions of the different vegetation types in the study area, the dominating types being sal forest, moist riverine forest and phanta. The corresponding figures for the Karnali area were taken from Jnawali (1995). Our study area differed from the Karnali flood plain area in that sal forest, moist riverine forest, phanta and wooded savannah contributed relatively more, whilst khair-sissoo forest and tall grass flood plain contributed less to our study area than to the Karnali area.

To gain an overview of elephant habitat use over the whole dry season, we used information from dung of both age categories, and, using a chi-square goodness-of-fit test, were able to reject the null hypothesis that the elephants occupy the vegetation types according to availability ($P < 0.0001$, $\chi^2 = 63.9$, $df = 7$). Looking at the strength of preferences (Fig. 5) we find that the vegetation type most preferred by elephants was wooded savannah (IEI = 0.32), closely followed by tall grass flood plain (IEI = 0.24) and khair-sissoo forest (IEI = 0.23). After rivers and riverbeds (IEI = -0.69), sal forest (IEI = -0.22) was the vegetation type most strongly avoided by elephants.

Table 2: Vegetation composition of our study area in the Babai valley, compared with the study area of Jnawali (1995) in the Karnali flood plain area.

	Tall grass flood plain	Khair-sissoo forest	Moist riverine forest	Phanta	Wooded savannah	Mixed hardwood forest	Sal forest	Rivers and river beds
Babai	7.8%	7.8%	16.1%	14.3%	7.1%	9.1%	26.6%	11.3%
Karnali[a]	11.9%	19.6%	9.9%	1.4%	4.5%	1.5%	11.2%	31.0%

[a] The numbers do not add up to 100%, as the Karnali area also contained some pasture and cultivated land.

An overview for rhino shows that moist riverine forest was the most strongly preferred vegetation type (IEI = 0.49), followed by khair-sissoo forest (IEI = 0.36) and tall grass flood plain (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 the hot periods of the dry season ($P = 0.0005$, $\chi^2 = 26.2$, $df = 7$). Comparison of expected use with Bonferroni confidence intervals for actual use (Table 3), shows whether preference/avoidance was significant for each vegetation type during the cool period and the hot periods of the dry season. Significance of rhino preferences was taken from Jnawali (1995).

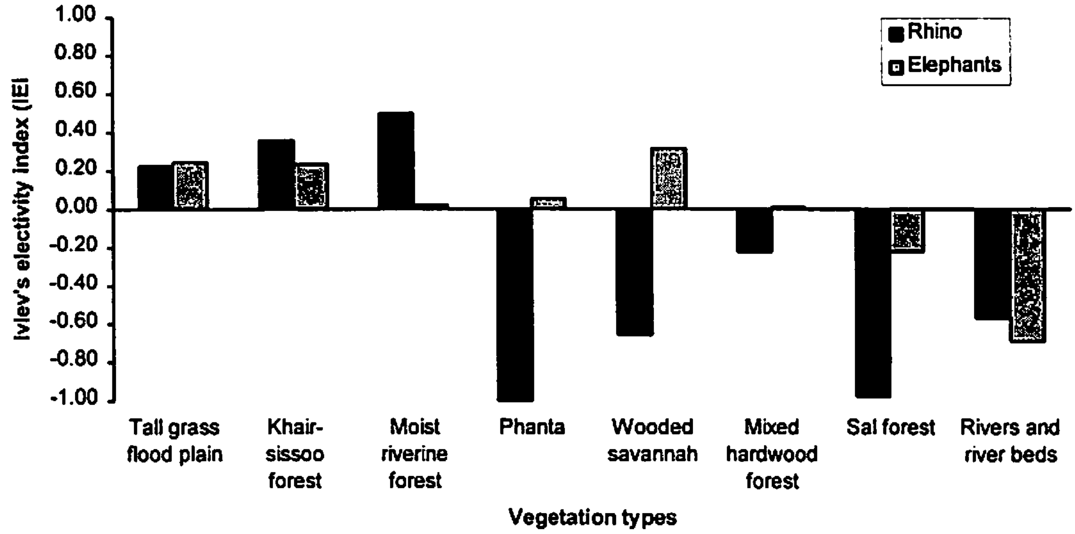

Figure 5: Histogram of Ivlev's electivity indices for rhino and elephants, showing the magnitude of preferences for the different vegetation types during the entire dry season

Table 3: Habitat preferences of elephants during the entire dry season. Results for the cool period are calculated from counts of "old" dung (stages 3-5), and results for the hot period are calculated from "new" dung (stages 1-2).

Vegetation types	Expected use[a]	Period	Actual use (p)	Bonferroni confidence intervals[b]	Significance for elephants[c]	Significance for rhino[d]
Tall grass flood plain	7.8%	Cool	12.0%	8.3% ≤p≤ 15.8%	++	ns
		Hot	15.6%	11.4% ≤p≤ 19.8%	++	+
Khair-sissoo forest	7.8%	Cool	11.1%	7.5% ≤p≤ 14.7%	+	+
		Hot	17.6%	13.2% ≤p≤ 22.0%	++	+
Moist riverine forest	16.1%	Cool	17.0%	12.6% ≤p≤ 21.3%	ns	+
		Hot	16.1%	11.8% ≤p≤ 20.3%	ns	+
Mixed hardwood forest	9.1%	Cool	9.4%	6.0% ≤p≤ 12.8%	ns	ns
		Hot	8.8%	5.5% ≤p≤ 12.1%	ns	ns
Wooded savannah	7.1%	Cool	12.2%	8.4% ≤p≤ 15.9%	++	-
		Hot	19.5%	14.9% ≤p≤ 24.1%	++	-
Phanta	14.3%	Cool	17.9%	13.5% ≤p≤ 22.3%	ns	0
		Hot	8.8%	5.5% ≤p≤ 12.1%	--	0
Sal forest	26.6%	Cool	18.0%	13.6% ≤p≤ 22.5%	--	0
		Hot	12.7%	8.8% ≤p≤ 16.5%	--	ns
Rivers and river beds	11.3%	Cool	2.4%	0.6% ≤p≤ 4.1%	--	-
		Hot	1.0%	-0.2% ≤p≤ 2.1%	--	-

[a] Proportions of vegetation types in the study area.

[b] Simultaneous confidence intervals using the Bonferroni approach (99% level of confidence)

[c] + +/- -, significant preference/avoidance at 99% level of confidence; +, significant preference at 95% level of confidence; ns, not significant.

[d] Radio telemetry data from Jnawali (1995). Where males and females had different preferences, we have used data for females, this being more reliable since only two males were radio collared. Preferences were tested at 95% level of confidence; +, significant preference; -, significant avoidance; 0, no telemetry locations.

Figures 6 and 7 show the strength of selectivity (IEI) for both rhino and elephants during the cool period and the hot period, respectively. This indicates that, for elephants, tall grass flood plain was more preferred during the hot period, khair-sissoo forest and wooded savannah were much more preferred during the hot period, and sal forest was selected less during the hot period than during the cool period of the dry season. Whilst selecting phanta to a small degree during the cool period of the dry season, the elephants switched to avoidance during the hot period.

For rhino, the main differences between cool and hot periods were the increased preference for tall grass flood plain in the hot period and an increased use of mixed hardwood forest, although this vegetation type was still not significantly preferred.

As for differences between rhino and elephants, during the cool period, rhino seem to have had stronger selection of khair-sissoo forest and moist riverine forest than elephants, they used tall grass flood plain slightly less than elephants and they strongly avoided all other vegetation types. During the hot period the differences between the two species were less pronounced. Tall grass flood plain and khair-sissoo forest were almost equally preferred by both. In addition, rhino preferred moist riverine forest, which was used only according to availability by elephants. Conversely, wooded savannahs were preferred only by elephants while being avoided by rhino.

Average absolute values of IEI for elephants were 0.21 in the cool period and 0.33 in the hot period of the dry season. For rhino the values were 0.65 during the cool period and 0.55 during the hot period (Jnawali 1995).

The preferred vegetation types for elephants comprised 23% of the study area, while the vegetation types preferred by rhino made up 31%. By comparison, the study area of Jnawali (1995) contained more, 41%, of the vegetation types preferred by rhino.

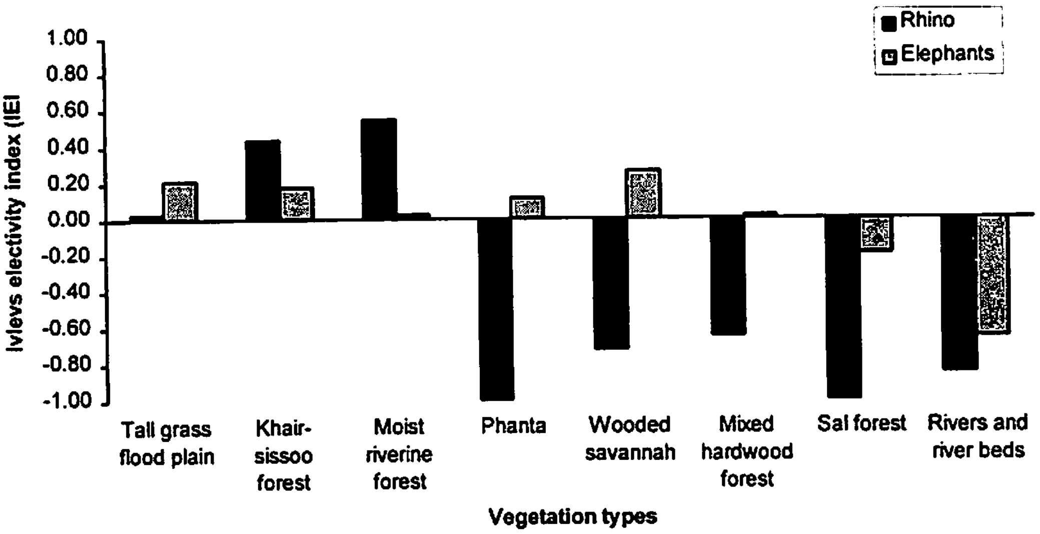

Figure 6: Histogram of Ivlev's electivity indices for rhino and elephants (calculated from "old" dung for elephants), showing the magnitude of preferences for the different vegetation types during the cool period of the dry season.

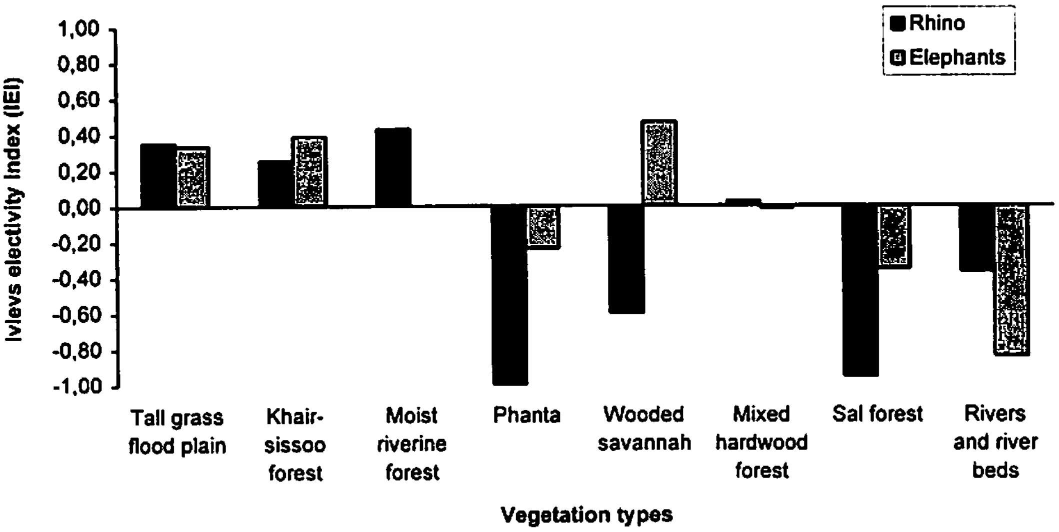

Figure 7: Histogram of Ivlev's electivity indices for rhino and elephants (calculated from "new" dung for elephants), showing the magnitude of preferences for the different vegetation types during the hot period of the dry season.

Discussion

Tall grass flood plain was preferred by elephants throughout the entire dry season, whilst rhino preferred this vegetation type only during the hot period (Jnawali 1995). The IEI indicates that both had stronger preferences for tall grass flood plain during the hot period of the dry season than during the cool period, probably because other habitat types offer negligible amounts of fresh grass during the hot period. Tall grass flood plain contains the important grass *Saccharum spontaneum* and the preferred grasses *Phragmites karka* and *Arundo donax* (as previously and later discussed). It is also possible that both species were foraging on aquatic plants in submerged areas adjacent to flood plains, but as mentioned earlier, the microhistological method probably is biased against recording these plants in faecal samples (Jnawali 1995).

Khair-sissoo forest was preferred by elephants and rhino in both the cool and the hot periods of the dry season. *Ziziphus mauritiana* and bark from *Acacia catechu* were important in the diet of elephants, explaining their preference for khair-sissoo forest, while the preference displayed by rhino most likely results from the large proportion of *Dalbergia sissoo* in their diet.

Elephants in our study area used moist riverine forest in proportion to its availability. Interestingly, Jnawali (1995) found moist riverine forest to be heavily used and preferred by rhino during the entire dry season. A possible explanation for this difference between the species is that *Mallotus phillippinensis*, a dominant tree species of the moist riverine forest, has been shown to be an important part of the rhino diet, both by Jnawali (1995) and in the present study. In contrast, the elephants in our study area did not eat *Mallotus phillippinensis* at all.

The strong preference of elephants for wooded savannah, throughout the dry season and especially during the hot period, may be due to the elephants feeding extensively on bark of *Bombax ceiba* and *Acacia catechu*. Woody remnants made up a large part of the diet of elephants, and inspections of fresh dung piles showed that *Bombax ceiba* and *Acacia catechu* bark contributed considerably to this diet category. Rhino, contrary to elephants, strongly avoided wooded savannahs (Jnawali 1995). This vegetation type offers little of the important rhino food plants and, compared with elephants, the rhinos ate only small amounts of bark and wood.

Phanta was avoided by elephants during the hot period of the dry season, whilst it was slightly preferred (not significantly) during the cool period. Use of phanta in the cool period of the dry season is possibly due to presence of *Saccharum spontaneum* during at least the beginning of this period, whilst the phanta is too dry to support sprouting during the hot period. Also, the phanta offers little shade from the intense sunlight during the hot period, and elephants are known to suffer from prolonged periods exposed to direct sun (Sikes 1971). Jnawali (1995) suggested lack of shelter as an explanation of rhino avoiding phanta throughout the dry season, moreover, lack of food plants was probably a factor behind the avoidance.

Sal forest was avoided by both rhino and elephants, throughout the dry season. The strongly negative IEI for rhino is the result of an almost total lack of radio locations from this vegetation type (Appendix 2). The negative IEI for elephants (indicating "strong avoidance") has however, a somewhat different explanation. In cases 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 most used vegetation type during the cool period. Sal forest probably provides some foraging opportunities during the cool period. In the hot period, however, sal forest moves down in ranked importance from first to fifth (Appendix 2). This can be explained by the fact that sal forest has only a sparse grass and shrub layer in the hot period (Dinerstein 1979a).

Having considered the trends and strengths of preference and avoidance in each of the vegetation types, it is interesting to note that the overall strength of habitat selection, both for rhino and elephant, differed between the cool and hot periods of the dry season. Rhino preferred two vegetation types in the cool period, khair-sissoo forest and moist riverine forest, and were found scarcely at all in the majority of other vegetation types. During the hot period of the dry season, food is of poorer quality in these preferred areas so the tall grasslands, where *Saccharum spontaneum* is sprouting, become important. Habitat use was thus spread over three vegetation types rather than two, resulting in a lower overall preference strength for the hot period.

For elephants, the situation was the reverse, with stronger habitat selection in the hot period. This is most easily explained if use of vegetation types is evaluated simply in terms of time expenditure (Appendix 2), rather than through preferences based on availability. It is then clear that elephants used a wide range of vegetation types which became more restricted during the hot period as the habitat got drier and food quality declined, hence, the elephants were forced to spend more time in high quality areas. Habitat use contraction during the driest periods and widening during the rest of the year have been observed also for African elephants by Leuthold (1977), who suggested that they, by this behaviour, avoid unnecessary depletion of food reserves which could prove critical during the driest period.

It appears then, that rhino have a rather confined choice of vegetation types which they are forced to expand in the hot period in order to obtain food of adequate quality. Elephants, on the other hand, use a variety of habitat types in the cool period but are forced to 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, is 140% higher for rhino (0.54) than elephants (0.22) 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 (tall grass flood plain, moist riverine forest and khair-sissoo forest) (Jnawali 1995), whilst elephants utilised none of the vegetation types more than 19.5% of the time (Appendix 3). To reach 85% habitat occupancy for elephants, we had to include six vegetation types in the calculation. The rhino can therefore be said to have a narrower niche in the habitat dimension than the elephants.

PART 3: GENERAL DISCUSSION AND CONCLUSIONS

Whilst both elephants and rhino are mixed feeders and generalists, they have, however, somewhat different feeding strategies. The diet of rhino was strongly dominated by grasses, whilst the elephants relied mostly on browse. Bearing in mind the two species' gut anatomy and digestive physiology, 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. However, this long retention time results in a fairly effective fermentation of cellulose, and rhino depend 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 an inherent digestive throughput rate which is comparatively rapid. Feeding on browse is favourable due to the woody plants' suitable mix of easily digestible carbohydrates and completely indigestible fibres, 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 seems to be, largely, an adaptation for browsing, giving opportunities for browsing from a higher layer than accessible for any other ground dwelling Asian herbivores. Data on African elephants show that this species browse 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, Ishwaran 1983), thus gaining access to otherwise inaccessible browse, although Asian elephants are less inclined to this behaviour than the African elephants (Ishwaran 1983).

The two megaherbivores showed relatively similar habitat preferences in terms of which vegetation types were preferred or avoided. The exceptions were wooded savannahs, which were avoided by rhino and preferred by elephants, and moist riverine forests which were preferred by rhino, and used according to abundance by elephants. Both species seemed to prefer vegetation types of relatively early seral stages, as is also indicated in the literature (Ishwaran 1983, Laurie 1982, Mueller-Dombois 1972). However, the two species differed in their degrees of preference; the IEI revealed that rhino have a stronger tendency to avoid several vegetation types than elephants do, and the complex of tall grass flood plain/moist riverine forest/khair-sissoo forest seemed to be a critical habitat feature for rhino.

As for the overall strength of habitat selection, the elephants in the study area displayed less pronounced avoidance of vegetation types, and used more vegetation types according to availability than rhino did. The much lower average absolute value of IEI for the elephants compared with that of rhino confirmed this picture. In fact, the rhino can be considered a habitat specific species, as also suggested by Sinha and Sawarkar (1991), the results on time expenditure strongly reinforcing this suggestion.

Yet another difference between rhino and elephants is the scale of their spatial strategies. Elephants occupy annual home ranges far larger than those of rhino. Sukumar (1989) indicates a minimum size of annual home ranges of 100-300 km^2 for elephant family groups. We observed extensive movements of elephants in the study area, with individuals walking up to 18 km, straight line distance, in less than 20 hours. Rhino on the other hand, although reported to make extensive movements in a period before home ranges are established (Jnawali 1995), do not seem to move widely after stabilisation of ranging behaviour, unless forced to flee their area due to catastrophic events such as flooding (Goswami 1993). The rhino in Royal Chitwan National Park have annual home ranges of around 3 km^2 while rhino in Karnali occupy larger areas, averaging about 30 km^2, probably due to low animal density in this area (Jnawali 1995).

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

Although the diets and habitat preferences of elephants and rhino were found to be quite different in our study area, there were some important similarities which may lead to competition. Both megaherbivores ate considerable amounts of *Saccharum 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 *Saccharum spontaneum*. Two other grass species, *Phragmites karka/Arundo donax*, were highly preferred by both elephants and rhino, but were only present in small amounts in the diets, which may indicate scarcity of these species in the area during the hot period of the dry season. All three grasses are more abundant in flood plains than in any other habitat type, thus making the flood plain the critical habitat, in which competition between the two megaherbivores is most likely to occur.

As we have shown, the hot period is the period of the dry season in which elephants and rhino had largest overlap in habitat use, as indicated by both magnitudes of preferences (IEIs) and time expenditure results: elephants contracted their habitat use and used flood plains more than in the rest of the dry season. At the same time rhino expanded their habitat use to include flood plains to a larger extent. Interestingly, the diet analysis pointed at flood plains as an important habitat type for both rhino and elephants, in which the potential for competition is largest.

If competition should occur, then the different spatial strategies of rhino and elephants will influence the outcome. Since rhino are restricted to relatively small home ranges throughout the dry season, whilst elephants have the possibility to roam to new areas in times when food is plentiful, it would seem that rhino would be the weaker part. An important question in this context is if interference or exploitation is the mode of competition between the two megaherbivores, however no literature exists on the subject.

Competition is of course dependent on the densities of the species concerned. The density of rhino in the study area is still low. A rough maximum estimate of 0.5 individuals/km^2 is comparable to that in the Karnali flood plain area and much lower than in RCNP (Jnawali 1995). For elephants, Sukumar (1989) estimated a density in his study area of 0.7 elephants per km^2 during the dry season, while a rough maximum estimate of density in the Babai study area is lower, approximately 0.6 elephants/km^2. Sukumar's results from his 1130 km^2 study area are, however, not necessarily comparable with our results, which are from an area too small to contain an elephant family group's entire home range. Neither does Sukumar indicate the level of habitat saturation of elephants in his study area.

From tracks and direct sightings it was clear that both the elephant and rhino populations included several juveniles, indicating good recruitment and populations under the carrying capacity. However, the long generation time-spans of these megaherbivores (Jnawali 1995, Owen-Smith 1988, Sukumar 1989) result in time-lags in the species' responses to resource scarcity. Consequently, one should be cautious in inferring competition status from breeding status. Still, appreciable competition between the elephants and rhino in Babai valley seems unlikely at present, as population densities were relatively low, and the overlaps in diet and habitat use were not extensive.

Habitat specific animals, such as rhino, depend upon protection of sufficient areas containing their preferred habitat types. At present, the Babai valley is relatively undisturbed by man, except for the presence of park's staff and a low level of poaching, mainly of sambar and wild boar (G. Singh, pers. comm.). Poaching of rhino or elephants has not been reported during the last 3 years, due to a relatively large army force patrolling the valley, aided by the Park's personnel (Martin and Vigne 1995, RBNP staff, pers. comm.) On the international black market rhino horn is in high demand, and horn of the greater Indian one-horned rhinoceros obtains prices ten times those of the African species (Martin and Vigne 1995). Thus, maintaining the efficient anti poaching efforts is important to secure the Babai rhino population (Martin and Vigne 1995). Local protection of habitat and the population itself then, seems the key to future survival of the Babai rhino.

The number of rhino in Babai is low at present and since this population is isolated from others, except possibly the Karnali rhino, future translocations of animals might seem desirable, considering genetic factors. However, Dinerstein and McCracken (1990) showed that the rhino in RCNP carry high levels of genetic variation, even after a bottleneck comparable to that experienced by the rhino in our study area. A rapid increase in numbers through translocations would, of course, reduce the chance of extinction caused by adverse stochastic events.

Considering the mobility and high area demands of elephants it is clear that conservation of this species is dependent on protection measures outside RBNP. Since a family group of elephants will commonly demand a home range area at least four times as large as the study area, a conservation strategy will have to include at least the whole district of Bardia. In order to ensure a viable population in the future, the corridors through which elephants move from Babai to Karnali and further to Sukla Phanta and India (Sinha and Sawarkar 1991, Smith and Mishra 1992) should be protected, or even improved by afforestation. A dialogue with Indian authorities concerning elephant management should be established. Elephants are reported to have remained more permanently in the Bardia area in recent years (RBNP staff, pers. comm.). We can only speculate whether this is a sign of an Indian-Nepalese elephant population expanding, or whether habitat or corridor destruction have forced the animals into more sedentary behaviour.

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LIST OF FIGURES AND TABLES

APPENDIX 1: SPECIES IN THE PLANT REFERENCE COLLECTION

The table shows the plant species included in our reference collection, with prominence values (see main text for explanation of the calculation) and contribution to the diets of rhino and elephants.

Scientific name	Local name	Availability (prominence values)	Proportion in the rhino diet	Proportion in the elephant diet
Bombax ceiba[a]	Simal	0.35 %	1.13 %	-
Calamus tenuis		4.25 %	0.09 %	-
Callicapra macrophylla	Dohikamala	42.58 %	1.04 %	-
Circium wallichii	Gaidakaro	0.36 %	0.78 %	0.84 %
Colebrookia oppositifolia	Dhusrel	18.53 %	1.91 %	0.08 %
Cynodon dactylon	Dubo	8.83 %	4.86 %	1.52 %
Cymbopogon oliveri	Pire gans	4.69 %	1.73 %	0.25 %
Dalbergia sissoo	Sissoo	1.62 %	5.72 %	1.52 %
Hydrilla spp.[b]		-	-	-
Imperata cylindrica	Siru	137.33 %	6.42 %	0.17 %
Litsea monopetala	Kutmiro	0.61 %	5.03 %	0.42 %
Mallotus philippinensis	Rohini	7.59 %	7.63 %	-
Murraya paniculata[c]	Lattikath	-	0.17 %	-
Paspallum spp.[b]	Panigaus	-	-	-
Phragmites karka[d]	Narkat	3.34 %	7.98 %	3.71 %
Saccharum bengalensis	Baruwa	6.88 %	3.73 %	1.10 %
Saccharum sponteum	Kans	109.07 %	35.04 %	9.78 %
Urena lobata	Sanubalu	0.68 %	0.52 %	-
Ziziphus mauritiana	Bayar	3.59 %	1.39 %	5.90 %

[a] Only flowers were found in the diet

[b] For the aquatic plants, no prominence values were available

[c] No prominence value available, since it was not present in the Karnali area

[d] Includes *Arundo donax*, which was not possible to separate from *Phragmites karka* in the diet analysis

APPENDIX 2: HABITAT USE OF ELEPHANTS AND RHINO

The table shows the proportional time spent by elephants and rhino in the different vegetation types, in the Babai study area and the Karnali study area, respectively. The results are divided into the cool and the hot period of the dry season.

	Cool period		Hot period	
Vegetation types	Elephants (%)[a]	Rhino (%)[b]	Elephants (%)[c]	Rhino (%)[b]
Tall grass flood plain	12,03	12,68	15,61	24,96
Khair-sissoo forest	11,11	49,96	17,56	33,08
Moist riverine forest	16,99	33,84	16,10	24,70
Phanta	17,91	-	8,78	-
Wooded savannah	12,16	0,72	19,51	1,12
Mixed hardwood forest	9,41	0,32	8,78	1,58
Sal forest	18,04	-	12,68	0,24
Rivers and river beds	2,35	2,48	0,98	14,32

[a] From counts of "old" dung

[b] From radio telemetry data (Jnawali 1995)

[c] From counts of "new" dung

APPENDIX 3: OVERALL DRY SEASON HABITAT PREFERENCES OF ELEPHANTS

The table shows habitat preferences for elephants throughout both the dry periods, calculated from all the dung (stages 1-5).

Vegetation types	Expected proportion of usage[a]	Actual proportion of usage (p)	Bonferroni confidence intervals[b] for p	Ivlev's Electivity Index (IEI)
Tall grass flood plain	7.8%	12.8%	8.9% $\leq p \leq$ 16.6%**	0.24
Khair-sissoo forest	7.8%	12.5%	8.7% $\leq p \leq$ 16.3%**	0.23
Moist riverine forest	16.1%	16.8%	12.5 $\leq p \leq$ 21.1%	0.02
Mixed hardwood forest	9.1%	9.3%	5.9% $\leq p \leq$ 12.6%	0.01
Wooded savannah	7.1%	13.7%	9.7% $\leq p \leq$ 17.7%**	0.32
Phanta	14.3%	16.0%	11.7% $\leq p \leq$ 20.2%**	0.06
Sal forest	26.6%	16.9%	12.6% $\leq p \leq$ 21.2%	-0.22
Rivers and river beds	11.3%	2.1%	0.4% $\leq p \leq$ 3.7%**	-0.69

[a] Proportion of study area.

[b] Simultaneous confidence intervals using the Bonferroni approach (99% level of confidence).

[c] **, significant at 99% level of confidence; *, significant at 95% level of confidence; ns, not significant.