

Per Wegge · Anil K. Shrestha · Stein R. Moe

Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands

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Abstract Based on microhistological analyses of faecal material, we compared the early dry season diets of greater one-horned rhinoceros *Rhinoceros unicornis*, swamp deer *Cervus duvauceli* and hog deer *Axis porcinus*, which inhabit the same alluvial grassland habitat complex in lowland Nepal. Their diets were quite similar, both at the forage category level and within sub-categories of graminoids and woody plants. Early successional tall grasses, especially *Saccharum spontaneum*, were the dominant food of all three species, underlining the key role of the threatened alluvial floodplains in large mammal conservation in South Asia. The two deer species ate significantly more graminoids (>66.5%) than did rhino (45.5%), and although they did not differ in proportions of graminoids, swamp deer ate significantly more late successional tall grasses (*Narenga porphyrocoma* and *Themeda* spp.) and short grasses (mainly *Imperata cylindrica*) than hog deer. The two deer consumed almost equal proportions of woody browse (ca. 10%), significantly less than that of rhino (33.0%). The prediction of the Jarman–Bell hypothesis, that large-bodied herbivores are less selective and subsist on lower quality graminoids than smaller ruminants, was not supported by the data. Based on this and previous studies in the same area we propose a conceptual model where the larger megaherbivores (rhino and elephant *Elephas maximus*) facilitate the smaller swamp deer and hog deer during the monsoonal growing season, while the smaller and more selective deer species outcompete the larger during the dry season when food is more limited. Owing to the all-year sprouting ability of *S. spontaneum*, facilitation may occur also in the dry season with low numbers of megaherbivores, thus accentuating competitive exclusion at higher deer densities.

Keywords Hog deer · Swamp deer · Rhinoceros · Elephant · *Axis porcinus* · *Cervus duvauceli* · *Rhinoceros unicornis* · *Elephas maximus* · Diet · Food competition · Resource partitioning

Introduction

Interspecific interactions among sympatric ungulates, such as food competition and resource partitioning, are much debated issues in theoretical ecology and practical wildlife management (White 1978; Caughley and Sinclair 1994; Putman 1996; Abrams 1998; Murray and Illius 2000; Arsenault and Owen-Smith 2002). Because resource use overlap in terms of habitat and diet is a useful approach to understanding such interactions (Schoener 1974; Jones and Barmuta 1998; Mysterud 2000), dietary patterns can provide insight into potential competition, although the relationship between diet overlap and interspecific competition is not clear (Abrams 1980).

Generally, high diet similarity between ungulate pairs indicates competitive interaction at high density and limited food resources. However, because species differ in morphological (Gordon and Illius 1988) and physiological (Hofmann 1989) characteristics, which lead to different feeding styles (Hofmann and Stewart 1972), they may also benefit from coexistence through feeding and/or habitat facilitation (Vesey-Fitzgerald 1960; Bell 1971; McNaughton 1976, 1979; Prins and Olf 1998; Arsenault and Owen-Smith 2002).

Among sympatric herbivores, niche differentiation is to a large extent related to differences in body size (Bell 1971; Jarman 1974; Demment and Van Soest 1985). According to the Jarman–Bell principle, smaller ungulates are more selective in their food uptake than larger species (Bell 1971; Jarman 1974; Gordon and Illius 1996). Because they require much food, large-bodied ungulates have less time to be selective; instead, they ingest larger quantities of lower quality forage (Owen-Smith 1988). In general, graminoids, especially when

P. Wegge (✉) · A. K. Shrestha · S. R. Moe
Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences, PO Box 5003, 1432 Ås,
Norway
E-mail: per.wegge@umb.no

matured and senescent, have lower nutritive quality than browse (Gwynne and Bell 1968; Robbins 1983).

Greater one-horned rhinoceros *Rhinoceros unicornis* (hereafter referred to as rhino), swamp deer *Cervus duvauceli* and hog deer *Axis porcinus* live sympatrically in the Karnali floodplain of Royal Bardia National Park (RBNP). Floodplain grasslands with interspersed woody seral stages are a preferred habitat of these ungulates (rhino—Laurie 1978; Dinerstein and Price 1991; Jnawali 1995; swamp deer—Schaaf 1978; Moe 1994; Pokharel 1996; and hog deer—Dinerstein 1980; Dhungel and O’Gara 1991; Biswas 1999; Odden et al. 2005).

Rhino is a nonruminant megaherbivore (1,500–2,000 kg) and swamp deer (230–250 kg) and hog deer (31–34 kg) are intermediate- and small-sized ruminants, respectively. Given their differences in body size and morphophysiological characteristics, a comparison of resource use, specifically diet overlap, also provides a test of the body mass hypothesis: as a large, nonruminant megaherbivore, rhino is expected to eat proportionally more grasses than the smaller sized deer. Moreover in the case of RBNP, information on food habits provides a basis for assessing the potential impact of rhino reintroduction on the present populations of the two sympatric ungulate species.

Many studies on food interactions among sympatric ungulates have already been carried out in temperate and Afro-tropical large mammal assemblages (Vesey-Fitzgerald 1960; Gwynne and Bell 1968; Bell 1970; McNaughton 1979; Jarman and Sinclair 1979; Jenkins and Wright 1988; Gordon and Illius 1989; Putman 1996; Johnson et al. 2000; Voeten and Prins 1999; Mysterud 2000; Woolnough and du Toit 2001; Stewart et al. 2003; du Toit 2003; Gayot et al. 2004). However, few studies have compared the diets of wild sympatric herbivores in the Asian subtropics (Dinerstein 1980; Martin 1982; Johnsingh and Sankar 1991; Bagchi et al. 2003; Steinheim et al. 2005). As a step in unravelling the complex interactions among sympatric ungulates in this region, in this study we describe the diets of rhino, swamp deer and hog deer at broader (forage category) and finer scale (within each forage category), and based on the results we discuss the potential for forage competition and

facilitation between them. Generally, food is most limiting for herbivores in the dry season, when it is of poor quality (Arsenault and Owen-Smith 2002). Along the alluvial floodplains in lowland Nepal, most plants begin to sprout in the late hot season before the rains (Dinerstein 1979a; Lehmkuhl 1989). We therefore compared the diets in the first (cool) part of the dry season, when plant biomass is high but of poorest quality.

Methods

Study area

Royal Bardia National Park covers 968 km² in the lowland of Nepal. The present study was conducted in a 50-km² area in the southwestern part, consisting of alluvial floodplains along the large Karnali River. Many small rivulets from the Karnali River intersect the floodplain, creating a mosaic of habitats. The climate is subtropical, monsoon type with three distinct seasons: cold dry season (November–February), hot dry season (March–June) and monsoon (July–October). Temperature ranges from a minimum of 10 °C in January to a maximum of 45 °C in June. Most of the rain (1,560–2,230 mm) falls in the monsoon between June and September.

The vegetation ranges from early successional tall-grass floodplain to climax stage sal (*Shorea robusta*) forest. Dinerstein (1979a) identified and described the vegetation types, which were later modified by Jnawali and Wegge (1993) (Table 1).

The mosaic of habitats inside and surrounding the floodplain harbours a large biomass of different herbivores (Dinerstein 1979b). In addition to the three target species of this study, some 70–80 Asian elephants *Elephas maximus* have recently become all-year residents (Steinheim et al. 2005). Other coexisting ungulates are spotted deer *Axis axis*, barking deer *Muntiacus muntjak*, nilgai antelope *Boselaphus tragocamelus* and wild boar *Sus scrofa*. Tiger *Panthera tigris* and leopard *Panthera pardus* are common predators, supplemented by fewer

Table 1 Vegetation types within the 50-km² Karnali study area in the Royal Bardia National Park, Nepal (after Jnawali and Wegge 1993)

Type	Appr. area (%)	Characteristic species
Tall grassland	50	Tall grasses, mainly <i>Saccharum spontaneum</i> . Others: <i>Saccharum bengalensis</i> , <i>Phragmites karka</i> , <i>Arundo donax</i> , <i>Themeda</i> spp.
Khair-sissoo forest	15	First seral stage on alluvial soils. Trees: <i>Dalbergia sissoo</i> , <i>Acacia catechu</i> , Shrubs: <i>Callicarpa macrophylla</i> , <i>Colebrookia oppositifolia</i>
Riverine forest	10	Later stage on waterlogged soils along rivers. Mostly evergreen trees: <i>Mallotus philippinensis</i> , <i>Syzigium cumini</i> , <i>Ficus</i> sp.
Mixed hardwood forest	5	Mostly deciduous trees: <i>Terminalia tomentosa</i> , <i>Schleicheria trijuga</i> , <i>Adina cordifolia</i> . Main shrub: <i>C. oppositifolia</i>
Wooded savanna	10	Man-modified. Sparse tree cover: <i>Bombax ceiba</i> , <i>A. cordifolia</i> . Dense short grassland: <i>Vetiveria zizanioides</i> , <i>Imperata cylindrica</i> , <i>Cynodon dactylon</i>
Phanta	5	Previously cultivated. Short grasses: mainly <i>I. cylindrica</i> , <i>V. zizanioides</i>
Sal forest	5	Climax on upland soils: <i>Shorea robusta</i>

numbers of wild dogs *Canis alpinus* and striped hyena *Hyaena hyaena*.

The rhino population has been reintroduced over the last two decades with the aim of establishing a second viable population in Nepal. Presently, there are about 73 animals in the park (DNPWC 2003), of which an estimated 20–30 individuals inhabit the study area (P.B. Shrestha, personal communication). In 1996, the population of swamp deer numbered about 75 animals (Ghimire 1996). In the floodplain, the density of hog deer was recently estimated at 77 animals/km² (Odden et al. 2005).

Microhistological analysis of faeces

Microhistological analysis of faeces has been widely used to study the diet of a range of wild and domestic animals from herbivores to carnivores (Holeček et al. 1982; Alipayo et al. 1992). The basic principle of this technique is that the cuticle of the plant epidermis survives digestion, and that the undigested epidermal parts in the faeces can be identified by comparing with known plant reference material (Sparks and Maleček 1968; Dawson and Ellis 1979; Jnawali 1995; Steinheim et al. 2005). We applied this technique because it is reliable and particularly useful in comparative studies (Butet 1985). It does not require sacrificing animals and is thus especially useful when studying endangered wild animals such as rhino, swamp deer and hog deer. Some researchers have pointed out the necessity of applying correction factors to accurately estimate diets by this method (Dearden et al. 1975; Westoby et al. 1976; Vavra and Holeček 1980); however, Alipayo et al. (1992) advocated the accuracy of the technique. In Asia, this method has successfully been applied to diet studies of rhino (Jnawali 1995), swamp deer (Pokharel 1996), takin *Budorcas taxicolor* (Wangchuk 1999), Asian elephant (Steinheim et al. 2005) and mountain ungulates (Harris and Miller 1995; Shrestha et al. 2005).

Faecal sample collection

Fresh faecal samples (< 2 days old) of rhino, swamp deer and hog deer were collected from mid-October through November 2004. Rhino defecate in latrines (Laurie 1978); we collected 32 samples from 18 defecation places distributed throughout the study area. Each sample consisted of about 400 g (wet weight) of mixed dung material. For swamp deer and hog deer, we first located a feeding herd or individuals from a distance and then collected 10–15 fresh pellets from each pellet group after the animals had moved away. We sampled a total of 32 pellet groups from swamp deer and 37 from hog deer.

Preparation of composite samples and slides

From the different pellet groups, we prepared composite samples for each species. First, 5–7 pellet groups were

randomly selected from each species collection. Five pellets were then picked from each group and pooled to make a composite sample. A similar procedure was followed for the preparation of the rhino composite. Here we took about 5 g of dung from each randomly selected dung sample. Each composite sample/species was ground through a 1-mm screen-fitted electric mill. The ground material was then sieved through Endecott sieves of 70 and 30 µm/cm² to ensure homogeneity in size of the plant fragments and to get rid of dust and large unidentifiable particles. We thoroughly cleaned the grinding machine after each grinding session to avoid mixing of samples.

Slide preparation

Three to five spatulas of the composite sample were placed into a test tube, which then underwent a series of treatments. First it was washed with 5% warm NaOH for 5 min. The particles were allowed to settle down in cold water for 3 min. We then removed the supernatant dark fluid from the test tube using a pipette. This treatment was repeated several times, 5–7 times for deer samples and four times for rhino samples. We then treated the material five times with warm distilled water, before it was dehydrated through a series of 25% (two times), 50% (two times), 75% (three times) and 100% (three times) alcohol treatments. Finally, it was treated with a series of xylene treatments as mentioned above. The material was dried using tissue paper. A small amount (quarter of a spatula) of dried material was placed on a warm slide with Canada balsam, which was then evenly spread using a needle and mounted under a 24 mm × 50 mm cover slip. We made four slides from the composite sample of each animal species.

Reference plant material

A total of 71 potential forage species were collected based on previous studies of rhino (Jnawali 1995), swamp deer (Schaaf 1978; Pokharel 1996) and hog deer (Dhungel and O'Gara 1991) and from plants that we observed to be grazed during fieldwork. Plant parts such as leaves, twigs, flowers and fruit were collected. Slides were prepared following the same procedure as above, except that we used 10% NaOH solution for the washing treatment.

Slide interpretation

The specific features of the epidermis (cell wall structure, shape and size of cells, hairs and trichomes, shape and size of stomata) of the fragments of the plant reference material were first photographed through a 100–400× microscope. The digital photographs ($N = 1,250$) were managed and stored in Picasa software, a free software for digital photos (<http://www.picasa.com>). We used a

compound microscope (200× and 400× magnification) with an ocular measuring scale to read the faecal samples. On each slide, two transects were randomly chosen and examined. We then identified the first 25 nonoverlapping fragments intercepted per transect/scale line by matching the fragments with the reference photographs. A total of 200 fragments for each animal species were read from eight transects on four slides (two transects per slide). The fragments, which could not be identified to species or genera level, only to category, were classified into “unidentified graminoids”, “unidentified woody plants” or “unidentified others”. Two closely related grass species, *Phragmites karka* and *Arundo donax*, were grouped due to difficulty in separating them. Fragments which we could not identify even to the forage category, were classified as “unknown”.

Data analyses

All species of monocots were included in “graminoids”. All woody dicot species (trees, shrubs and climbers) were included in the “woody plants” forage category. Herbs and fruits were included in the “others” category.

To determine diet composition, the relative frequency of each forage category and each plant species was calculated: the total number of fragments identified for a given forage category or species was divided by the total number of all counts made in the sample, multiplied by 100.

We used the chi-square statistic to test whether the proportions of forage categories were similar in the rhino, swamp deer and hog deer samples. One-way ANOVA was performed to determine if the proportions of “graminoids” were similar in the three species. Because of non-normality, we used a Kruskal–Wallis one-way ANOVA on ranks to test whether the proportions of the category “woody plants” were similar among the three species. To perform these analyses, we first adjusted the proportion of forage categories in the swamp deer material to the same basis as those of the other two animal species, because the “unknown” fractions differed between them: rhino 18.5%, swamp deer 8% and hog deer 18.5% (see Table 1). Hence, to avoid systematic bias in the analysis, the forage categories in swamp deer were reduced by 10%, thus increasing the unknown fraction to the same level as that of rhino and hog deer. When there were significant differences among the three species, pairwise multiple comparisons using Bonferroni simultaneous confidence intervals with adjusted critical *P*-value (Byers et al. 1984), or Dunn’s method in the case of Kruskal–Wallis ANOVA, were carried out.

To investigate dietary patterns at a finer scale, we classified the food plants into subcategories as follows, based on their successional affinity, dominance and height (Peet et al. 1999).

Graminoids:

- (a) “Early succession tall grasses” included *Saccharum spontaneum*, *A. donax*/*P. karka* and *Saccharum bengalensis*,

- (b) “Late succession tall grasses” included *Themeda* spp. and *Narenga porphyrocoma*, and
 (c) “Short grasses” consisted of *Imperata cylindrica*, *Cynodon dactylon*, *Vetiveria zizanioides*, *Cymbopogon* spp., *Desmostachya bipinnata*, *Aplauda mutica* and *Cyperus* spp.

Woody plants:

- (a) “Trees” included *Dalbergia sissoo*, *Bombax ceiba*, *Mallotus philippinensis*, *Ehretia laevis*, *Trewia nudiflora* and *Ficus glomerata*, and
 (b) “Other woody plants” included *Callicarpa macrophylla*, *Colebrookia oppositifolia*, *Acacia concinna*, *Calamus tenuis* and *Ziziphus mauritiana*.

The “Others” forage category was divided into herbs and fruits.

We examined if there were differences in proportions of these subcategories among the three ungulates, using the same statistical tests as above.

Niche breadth was calculated at plant species level using the Shannon–Wiener measure (Krebs 1999):

$$H' = -\sum P_j \log P_j$$

where H' is the Shannon–Wiener measure of niche breadth, P_j is the proportion of individuals found in or using resource j ($j = 1, 2, 3, \dots, n$), and n is the total number of resource states.

Since this equation gives results ranging from 0 to ∞ , the evenness measure, J' , provides a standardized scale of it, ranging from 0 to 1:

$$J' = \frac{H'}{\log n}$$

where J' is the evenness measure of the Shannon–Wiener function and n is the total number of possible resource states.

Diet similarity at broader (forage categories) and finer (within forage category) scales between ungulate pairs was calculated using the percentage similarity index (Gauch 1973). This index ranges from 0 (no similarity) to 100% (complete similarity).

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

where x and y are the frequencies of each plant species recorded in the diet of ungulate pair 1 and 2, respectively, and $\min(x, y)$ is the minimum frequency of each plant species recorded between ungulate pair 1 and 2.

Results

Diet composition

Rhino

The rhino diet was dominated by graminoids (45.5%) followed by woody plants (33%) and others (3%)

(Table 2). Ten species of graminoids, 11 species of woody plants and one herb were recorded. *S. spontaneum* (18.5%) was the main forage plant. Other common grasses were *Themeda* spp. (7%), *A. donax*/*P. karka* (3%), *Cynodon dactylon* (2.5%) and *Cymbopogon* spp. (2.5%). *Mallotus philippinensis* was the most important woody plant (8%), followed by *D. sissoo*, *C. macrophylla*, *C. oppositifolia* and *B. ceiba* (Table 2). *Circium wallichii* (3%) was the only herb recorded in the rhino diet.

Swamp deer

The swamp deer diet had the highest proportion of graminoids (74.5%), followed by woody plants (12.5%) and others (5%) (Table 2). Thirteen species of graminoids, three species of woody plants and two herbs including “aquatic plants” were recorded. Like in rhino, *S. spontaneum* was the most important forage plant (24%). Other important grasses were *Themeda* spp., *I. cylindrica*, *N. porphyrocoma*, *Cymbopogon* spp., *A. donax*/*P. karka* and *Vetiveria zizanioides*. Woody plants

consisted of *Z. mauritiana* (4%), *D. sissoo* (3%) and *C. oppositifolia* (2.5%). Herbs such as *Phoenix humilis* and “Pani leu” were also recorded (Table 2).

Hog deer

Hog deer also subsisted mainly on graminoids (66.5%). Nine grass species, five species of woody plants and fruits of one shrub were recorded (Table 2). Nearly one third of the diet consisted of *S. spontaneum*. Woody plants contributed comparatively less (8.5%) and consisted mainly of *D. sissoo* (3.0%), *B. ceiba* (1.0%) and *Z. mauritiana* (1.0%). Interestingly, 6.5% of the fragments in the hog deer samples consisted of fruits of *Z. mauritiana*.

Diet similarity and comparison

High similarities in diet at the forage category level (>70%) between all the ungulate pairs indicated that

Table 2 Proportion (% ± SD^a) of plant species in the diets of rhino, swamp deer and hog deer in the dry season in the Royal Bardia National Park, Nepal

Plant species	Rhino		Swamp deer		Hog deer	
	%	SD	%	SD	%	SD
Graminoids						
<i>Saccharum spontaneum</i>	18.5	7.4	24.0	7.1	30.5	4.2
<i>Saccharum bengalensis</i>	2.5	3.7	1.0	1.9	3.0	3.5
<i>Arundo</i> / <i>Phragmites karka</i>	3.0	2.8	3.0	4.1	1.0	1.9
<i>Themeda</i> spp.	7.0	5.6	7.5	5.8	3.0	3.5
<i>Narenga porphyrocoma</i>	1.5	2.1	6.0	3.7	1.5	2.1
<i>Cynodon dactylon</i>	2.5	2.1	1.5	2.1	3.0	3.5
<i>Imperata cylindrica</i>	0.0	0.0	6.0	5.7	2.5	3.7
<i>Cymbopogon</i> spp.	2.5	3.7	4.0	4.3	2.0	3.0
<i>Vetiveria zizanioides</i>	0.5	1.4	3.0	4.1	2.0	2.1
<i>Desmostachya bipinnata</i>	0.5	1.4	0.0	0.0	0.0	0.0
<i>Chrysopogon aciculatus</i>	0.5	1.4	0.5	1.4	0.0	0.0
<i>Cyperus</i> spp.	0.0	0.0	1.0	1.9	0.0	0.0
<i>Aplauda mutica</i>	0.0	0.0	1.5	2.1	0.0	0.0
“Ghode dubo”	0.0	0.0	0.5	1.4	0.0	0.0
Unidentified graminoids	6.5	5.2	15.0	6.0	18.0	8.6
Total graminoids	45.5	15.4	74.5	10.0	66.5	9.1
Woody plants						
<i>Callicarpa macrophylla</i>	4.0	0.0	0.0	0.0	0.0	0.0
<i>Colebrookia oppositifolia</i>	2.5	2.1	2.5	3.7	1.0	1.9
<i>Dalbergia sissoo</i>	5.5	3.0	3.0	3.5	3.0	4.1
<i>Bombax ceiba</i>	2.0	3.0	0.0	0.0	1.0	1.9
<i>Mallotus philippinensis</i>	8.0	4.3	0.0	0.0	0.0	0.0
<i>Ehretia laevis</i>	1.5	2.1	0.0	0.0	0.0	0.0
<i>Trewia nudiflora</i>	1.0	2.8	0.0	0.0	0.5	1.4
<i>Ficus glomarata</i>	1.0	1.9	0.0	0.0	0.0	0.0
<i>Acacia concinna</i>	0.5	1.4	0.0	0.0	0.0	0.0
<i>Ziziphus mauritiana</i>	1.0	1.9	4.0	4.3	1.0	1.9
<i>Calamus tenuis</i>	1.5	4.2	0.0	0.0	0.0	0.0
Unidentified woody plants	4.5	2.6	3.0	4.1	2.0	3.7
Total woody plants	33.0	10.2	12.5	5.0	8.5	5.8
Others						
<i>Circium wallichii</i>	3.0	2.8	0.0	0.0	0.0	0.0
<i>Phoenix humilis</i>	0.0	0.0	4.0	7.1	0.0	0.0
“Pani leu”	0.0	0.0	1.0	2.8	0.0	0.0
<i>Z. mauritiana</i> (fruit)	0.0	0.0	0.0	0.0	6.5	3.7
Total others	3.0	2.8	5.0	7.0	6.5	3.7
Unknown	18.5	12.8	8.0	6.0	18.5	5.6
Total	100.0		100.0		100.0	

^aStandard deviation in composite sample (from eight transects, *N* = 25 fragments per transect)

their diets were quite similar (Table 3). The two deer species had the highest overlap (92.2%), followed by nearly equal similarities between rhino and swamp deer and rhino and hog deer (Table 3).

However, the proportions of forage categories were significantly different among the three species ($\chi^2 = 65.2$, $df=6$, $P < 0.001$). They consumed significantly different proportions of graminoids ($F=7.68$, $P=0.003$) and woody plants ($H = 15.6$, $P < 0.001$). Pairwise Bonferroni comparisons revealed significant differences between rhino and swamp deer, and between rhino and hog deer for both categories ($P < 0.05$), with rhino consuming less graminoids and more woody plants than the two deer species. Swamp deer and hog deer did not differ in their proportions of graminoids or of woody plants (Bonferroni, $P > 0.05$, both). All species pairs were quite similar in their consumption of different subcategories of graminoids (Table 3), but proportions were significantly different ($\chi^2 = 16.1$, $P = 0.003$, $df = 4$).

“Early succession tall grasses” were the most important food plants for all three animals (Fig. 1), and they did not differ in their relative consumption of this subcategory ($F = 2.98$, $P = 0.074$). Hog deer consumed the highest proportion of the early succession tall grasses, especially *S. spontaneum*, followed by swamp deer and rhino (Fig. 1; Table 2).

The three herbivores consumed significantly different amounts of “late succession tall grasses” ($F=4.89$, $P=0.018$); swamp deer consumed significantly more of these than hog deer (Bonferroni, $P < 0.05$), whereas there were no differences between rhino and swamp deer or between rhino and hog deer (Bonferroni, $P > 0.05$, both). The highest proportion of late succession grasses was recorded in swamp deer, followed by rhino and hog deer (Fig. 1).

Rhino, swamp deer and hog deer also differed in their consumption of “short grasses” ($F=7.15$, $P=0.004$). Swamp deer ate proportionally more of these than both rhino and hog deer (Bonferroni, $P < 0.05$, both), whereas rhino and hog deer did not differ in their consumption of short grasses (Bonferroni, $P > 0.05$; Fig. 1).

Within the “woody plants” category, diet similarities among species pairs were comparatively less than within the graminoids. Highest similarity was recorded for swamp deer and hog deer (62%) and lowest for the rhino

and hog deer pair (37%) (Table 3). The proportions of the two subcategories of woody plants also differed ($\chi^2 = 7.9$, $df = 2$, $P = 0.019$). The relative proportions of “trees” were significantly different ($F = 16.4$, $P < 0.0001$). Pairwise Bonferroni tests showed that rhino and swamp deer and rhino and hog deer differed in their use of “trees” ($P < 0.05$, both), whereas the relative proportions among swamp and hog deer were not different ($P > 0.05$). “Trees” contributed more to the diet of rhino than to the two deer species (Fig. 2).

The three species also differed in their consumption of “other woody plants” ($H = 10.4$, $P = 0.006$). Again, rhino and hog deer were significantly different ($P < 0.05$), whereas rhino and swamp deer and swamp deer and hog deer were not different ($P > 0.05$, both).

Out of the 28 identified forage species, 11 were eaten by all three ungulates. *S. spontaneum*, *Themeda* spp., *N. porphyrocoma* and *D. sissoo* were important food plants of all three herbivores. *S. spontaneum* was by far the most important food plant, as it comprised 30.5, 24.0 and 18.5% of the hog deer, swamp deer and rhino diets, respectively. All other plant species contributed $< 10\%$ to the diets of the ungulates (Table 2). There were significant differences among the three species in their consumption of *S. spontaneum* ($F = 7.05$, $P = 0.004$). Pairwise Bonferroni comparisons showed that hog deer ate more *Saccharum* than rhino ($P < 0.05$), whereas proportions among rhino and swamp deer and among swamp and hog deer were not different ($P > 0.05$).

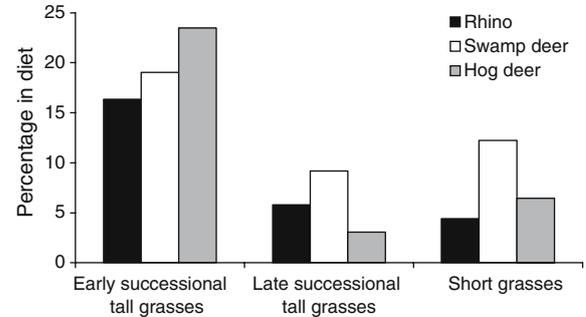


Fig. 1 Proportions of subcategories of graminoids in the diets of rhino, swamp deer and hog deer

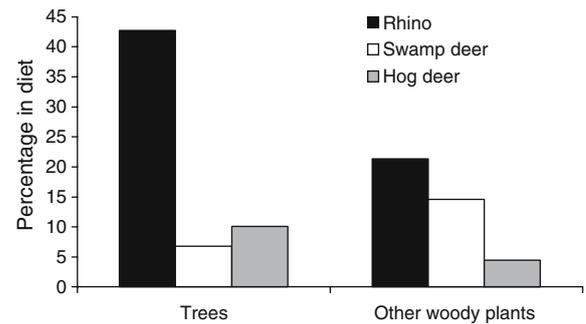


Fig. 2 Proportions of subcategories of woody plants in the diets of rhino, swamp deer and hog deer

Table 3 Percentage similarity indices (adapted by Gauch 1973) of diets among rhino, swamp deer and hog deer at different forage category levels

Species	Rhino	Swamp deer
Swamp deer		
All categories	70.3	
Graminoids	79.0	
Woody plants	50.0	
Hog deer		
All categories	69.9	92.2
Graminoids	80.0	77.0
Woody plants	37.0	62.0

Swamp deer consumed the highest number of grass species ($N=13$), while rhino consumed the highest number of woody plants ($N=11$) (Table 2). Niche breadth, expressed by the evenness measure, was higher in swamp deer (0.69) and rhino (0.67) compared to hog deer (0.55).

Discussion

The sympatric rhino, swamp deer and hog deer overlapped extensively in their dry season food habits. All three species consumed a high proportion of grass; the most pronounced interspecific difference was that rhinos ate more browse than the two deer. In addition to more total browse, the rhino also consumed more trees compared to other woody browse than the two deer species. The results did not support the Jarman–Bell hypothesis of a higher graminoid proportion among the larger species. The most likely explanation for the discrepancy is that this species of rhino, with its prehensile lip and rather narrow mouth, has adapted a more selective feeding style like that of the black rhino (*Diceros bicornis*) and can therefore exploit more nutritious browse when such is available. Also, the tall grass *S. spontaneum* has the unique ability of basal sprouting during the dry season (Lehmkuhl 1989). Hence it represents a food resource for the smaller deer species during the resource-limited dry season; the new sprouts are probably too small and spatially dispersed for rhino to exploit effectively.

This study documents the importance of tall floodplain grasslands for the conservation of endangered herbivores in south Asia. The early successional tall grass *S. spontaneum* was by far the most important food plant species for all three ungulates, comprising more than one third of the total hog deer diet. The results agree well with other diet studies conducted on these herbivores (hog deer—Dhungel and O’Gara 1991; swamp deer—Pokharel 1996; rhino—Jnawali 1995). This species of tall grass is also an important part of the diet of elephants (Steinheim et al. 2005).

Saccharum-dominated floodplains are extremely productive (Lehmkuhl 1989; Peet et al. 1997), and as such they can sustain dense populations of large mammals. However, due to conversion for human needs, tallgrass floodplains are becoming increasingly scarce on the Indian subcontinent (Dinerstein 2003). In the RBNP, like elsewhere, they are limited in size (< 30 km²). Hence, the growing numbers of reintroduced rhino and new elephants resident all-year round raise questions of resource partitioning among the coexisting herbivores. Studies on the African continent have shown that by removing coarser vegetation through feeding and trampling, large herbivores stimulate new and more nutritious vegetative growth, which thereby facilitates the smaller and more selective ungulates (e.g., Bell 1971; McNaughton 1976). However, recently Woolnough and du Toit (2001) showed that smaller browsers may competitively displace larger

browsers from the same feeding sites. Similarly, in another study in Africa, Murray and Illius (2000) found that the more selective smaller animals removed high-quality plant parts and thus displaced the larger and less selective grazers. Information collected in the Royal Chitwan National Park (Nepal) provides indirect evidence of such a process: With no swamp deer and a much lower density of hog deer (Seidensticker 1976; Dhungel and O’Gara 1991) compared to Bardia (Odden et al. 2005), the much denser population of rhinos there (Dinerstein and Price 1991) consumes proportionally far more grasses during the dry season than rhinos do in the Karnali floodplain of Bardia (Jnawali 1995).

Our studies in Nepal show that there is a high degree of resource overlap among rhino, elephant, swamp deer and hog deer. While hog deer remain in the floodplain throughout the year (Odden et al. 2005), the rhino (Jnawali 1995) and the elephant (Steinheim et al. 2005) and to a lesser extent the swamp deer (Schaaf 1978; Moe 1994; Ghimire 1996) also use other habitat types during the resource-limited dry season. While spatial and food plant overlap (particularly the *S. spontaneum*) is at its maximum in the monsoonal growing season, there is a higher degree of resource partitioning during the resource-limited dry season. Such seasonal segregation indicates competition (Rosenzweig 1981). While the smaller hog deer are able to efficiently utilize the *S. spontaneum* grasses throughout the year, the overall quality of the senescent plants may become too low in the dry season for the bulk-feeding rhinos and elephants. Hence, when available, they switch and consume more browse during that part of the year (Jnawali 1995; Williams 2002; Pradhan et al., unpublished data).

During the monsoon, both rhino and elephant consume large quantities of floodplain grasses. Their feeding and trampling probably stimulate high-quality grass regrowth, making this more accessible for the smaller swamp deer and hog deer. In tall grasslands in the Royal Chitwan National Park, Dinerstein and Wemmer (1988) reported that rhinos created “grazing lawns” for deer. A similar facilitation process has been described for the floodplains of the Rukwa Valley in Tanzania, where the African savanna elephants (*Loxodonta africana*) exposed medium-height grasses to buffalo (*Syncerus caffer*), while the buffalo impact subsequently provided short grasses for the smaller topi (*Damaliscus lunatus*) (Vesey-Fitzgerald 1960).

Based on this and previous studies of the Karnali floodplain herbivores, we propose a conceptual model that can be tested in future studies (Fig. 3). The model assumes food facilitation by the megaherbivores to the smaller hog deer and swamp deer during the monsoonal growing season. At low numbers of megaherbivores, such facilitation also occurs in the dry season, owing to the sprouting characteristic of *S. spontaneum*. At higher numbers of deer and megaherbivores, food competition by the smaller and more selective deer against the larger bulk feeders intensifies during the dry season. Assuming that the dry season is limiting population growth, hog

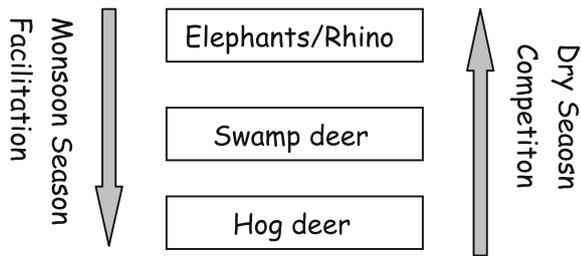


Fig. 3 A conceptual model illustrating the facilitation of swamp deer (*Cervus duvauceli*) and hog deer (*Axis porcinus*) by rhino (*Rhinoceros unicornis*) and elephant (*Elephas maximus*), stimulating regrowth of floodplain tall grasses during the monsoon season. During the resource-limited dry season, the more selective hog deer and swamp deer competitively displace the larger mega-herbivores

deer and swamp deer numbers may ultimately limit the populations of rhino and elephants. The two deer species may coexist with less food competition owing to their different usage of the available grass species.

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References

- Abrams PA (1980) Some comments on measuring niche overlap. *Ecology* 61:44–49
- Abrams PA (1998) High competition with low similarity and low competition with high similarity: exploitative and apparent competition in consumer–resource systems. *Am Nat* 152:114–128
- Alipayo D, Valdez R, Holechek JL, Cardenas M (1992) Evaluation of microhistological analysis for determining ruminant diet botanical composition. *J Range Manage* 45:148–152
- Arsenault R, Owen-Smith N (2002) Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97:313–318
- Bagchi S, Gopal SP, Sankar K (2003) Niche relationships of an ungulate assemblage in a dry tropical forest. *J Mammal* 84:981–988
- Bell RHV (1970) The use of the herb layer by grazing ungulates in the Serengeti. In: Watson A (ed) *Animal populations in relation to their food resources*. Blackwell, Oxford, pp 111–124
- Bell RHV (1971) A grazing ecosystem in the Serengeti. *Sci Am* 225:86–93
- Biswas T (1999) Habitat utilization by hog deer (*Axis porcinus*) in relation to other sympatric species at Jaldapara Wildlife Sanctuary, West Bengal, India. *Wildlife Institute of India, Dehra Dun*
- Butet A (1985) Methode d'étude du regime alimentaire d'un rongeur polyphage (*Apodemus sylvaticus* L., 1758) par l'analyse microscopique des feces. *Mammalia* 49:455–483
- Byers CR, Steinhorst RK, Krausman PR (1984) Clarification of a technique for analysis of utilization–availability data. *J Wildlife Manage* 48:1050–1053
- Caughley G, Sinclair ARE (1994) *Wildlife ecology and management*. Blackwell, Oxford
- Dawson TJ, Ellis BA (1979) Comparison of the diets of yellow-footed rock wallabies and sympatric herbivores in Western New South Wales. *Aust Wildlife Res* 6:245–254
- Dearden BL, Pegau RE, Hansen RM (1975) Precision of microhistological estimate of ruminant food habits. *J Wildlife Manage* 39:402–407
- Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *Am Nat* 125:641–672
- Dhungel SK, O'Gara BD (1991) Ecology of the hog deer in Royal Chitwan National Park, Nepal. *Wildlife Monogr* 119:1–40
- Dinerstein E (1979a) An ecological survey of the Royal Karnali–Bardia Wildlife Reserve, Nepal. Part I: vegetation, modifying factors, and successional relationships. *Biol Conserv* 15:127–150
- Dinerstein E (1979b) An ecological survey of the Royal Karnali–Bardia Wildlife Reserve, Nepal. Part II: habitat/animal interactions. *Biol Conserv* 16:265–300
- Dinerstein E (1980) An ecological survey of the Royal Karnali–Bardia Wildlife Reserve, Nepal. Part III: ungulate populations. *Biol Conserv* 18:5–38
- Dinerstein E (2003) *The return of the unicorns: the natural history and conservation of the greater one-horned rhinoceros*. Columbia University Press, New York
- Dinerstein E, Price L (1991) Demography and habitat use by a greater one horned rhinoceros in Nepal. *J Wildlife Manage* 55:401–411
- Dinerstein E, Wemmer CM (1988) Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. *Ecology* 69:1768–1774
- DNPWC (2003) *Royal Bardia National Park Management Plan 2001–2005*. Department of National Park and Wildlife Conservation, Babar Mahal, Nepal
- Gauch HG (1973) The relationship between sample similarity and ecological distances. *Ecology* 54:618–622
- Gayot M, Henry O, Dubost G, Sabatier D (2004) Comparative diets of two forest cervids of the genus *Mazama* in French Guiana. *J Trop Ecol* 20:31–43
- Ghimire JN (1996) Status of swamp deer (*Cervus duvauceli*) in Royal Bardia National Park, Nepal. *Tiger Paper* 24:13–16
- Gordon IJ, Illius AW (1988) Incisor arcade structure and diet selection in ruminants. *Funct Ecol* 2:15–22
- Gordon IJ, Illius AW (1989) Resource partitioning by ungulates in the Isle of Rhum. *Oecologia* 79:383–389
- Gordon IJ, Illius AW (1996) The nutritional ecology of African ruminants: a reinterpretation. *J Anim Ecol* 65:18–28
- Gwynne MO, Bell RNV (1968) Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* 220:390–393
- Harris RB, Miller DJ (1995) Overlap in summer habitats and diets of Tibetan Plateau ungulates. *Mammalia* 59:197–212
- Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443–457
- Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia* 36:226–240
- Holechek JL, Vavra M, Pieper RD (1982) Botanical composition determination of range herbivore diets: a review. *J Range Manage* 35:309–313
- Jarman PJ (1974) The social organization of antelopes in relation to their ecology. *Behaviour* 48:215–266
- Jarman PJ, Sinclair ARE (1979) Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair ARE, Norton-Griffiths M (eds) *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago, IL, pp 130–163
- Jenkins KJ, Wright RG (1988) Resource partitioning and competition among cervids in Northern Rocky Mountains. *J Appl Ecol* 25:11–24
- Jnawali SR (1995) Population ecology of greater one-horned rhinoceros (*Rhinoceros unicornis*) with particular emphasis on habitat preference, food ecology and ranging behavior of a

- reintroduced population in Royal Bardia National Park in lowland Nepal. PhD Thesis, Agricultural University of Norway
- Jnawali SR, Wegge P (1993) Space and habitat use by a small reintroduced population of greater one-horned rhinoceros (*Rhinoceros unicornis*) in Royal Bardia National Park in Nepal—a preliminary report. In: Ryder AO (ed) Rhinoceros biology and conservation. Proceedings of an international conference. Zoological Society of San Diego, San Diego, CA, pp 208–217
- Johnsingh AJT, Sankar K (1991) Food plants of chital, sambar and cattle on Mundanthurai plateau, South India. *Mammalia* 55:57–66
- Johnson BK, Kern JW, Wisdom ML, Findholt SL, Kie JG (2000) Resource selection and spatial separation of mule deer and elk during spring. *J Wildlife Manage* 64:685–697
- Jones ME, Barmuta LA (1998) Diet overlap and relative abundance of sympatric dasyurid carnivores: a hypothesis of competition. *J Anim Ecol* 67:410–421
- Krebs CJ (1999) Ecological methodology, 2nd edn. Benjamin/Cummings, Menlo Park, CA
- Laurie WA (1978) The ecology and behavior of the greater one-horned rhinoceros. PhD Thesis, University of Cambridge
- Lehmkuhl JF (1989) The ecology of a south Asian tall grass community. PhD Thesis, University of Washington
- Martin C (1982) Interspecific relationship between barasingha and axis deer in Kanha MP, India and relevance to management. In: Wemmer CW (ed) Biology and management of the Cervidae. Smithsonian Institution Press, Washington, DC, pp 299–306
- McNaughton SJ (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* 191:92–94
- McNaughton SJ (1979) Grazing as an optimization process: grass–ungulate relationships in the Serengeti. *Am Nat* 113:691–703
- Moe SR (1994) The importance of aquatic vegetation for the management of the barasingha *Cervus duvauceli* in Nepal. *Biol Conserv* 70:33–37
- Murray MG, Illius AW (2000) Vegetation modification and resource competition in ungulates. *Oikos* 89:501–508
- Mysterud A (2000) Diet overlap among ruminants in Fennoscandia. *Oecologia* 124:130–137
- Odden M, Wegge P, Storaas T (2005) Hog deer (*Axis porcinus*) need threatened tallgrass floodplains: a study of habitat selection in lowland Nepal. *Anim Conserv* 8:99–104
- Owen-Smith RN (1988) Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge
- Peet NB, Watkinson AR, Bell DJ, Sharma UR (1997) The management of tall grasslands for the conservation of biodiversity and sustainable utilization. A scientific and management report prepared for Department of National Parks and Wildlife Conservation, HMG, Nepal
- Peet NB, Watkinson AR, Bell DJ, Kattel BJ (1999) Plant diversity in the threatened sub-tropical grasslands of Nepal. *Biol Conserv* 88:193–206
- Pokharel CP (1996) Food habit and habitat utilization of swamp deer (*Cervus duvauceli*) in the Royal Bardia National Park, Nepal. MSc thesis, Tribhuvan University
- Prins HHT, Olf H (1998) Species richness of African grazer assemblages: towards a functional explanation. In: Newbury DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. Blackwell, Oxford, pp 449–490
- Putman RJ (1996) Competition and resource partitioning in temperate ungulate assemblies. Chapman & Hall, London
- Robbins CT (1983) Wildlife feeding and nutrition. Academic, New York
- Rosenzweig ML (1981) A theory of habitat selection. *Ecology* 62:327–335
- Schaaf CD (1978) Population size and structure and habitat relations of the Barasingha (*Cervus D. duvauceli*) in Sukla Phanta Wildlife Reserve, Nepal. PhD Thesis, Michigan State University
- Schoener TJ (1974) Resource partitioning in ecological communities. *Science* 185:27–39
- Seidensticker JC (1976) Ungulate populations in Chitwan Valley, Nepal. *Biol Conserv* 10:183–210
- Shrestha R, Wegge P, Koirala RA (2005) Summer diets of wild and domestic ungulates in Nepal Himalaya. *J Zool Lond* 266:111–119
- Sparks DR, Malechek JC (1968) Estimating percentage dry weight in diets using a microscopic technique. *J Range Manage* 21:264–265
- Steinheim G, Wegge P, Fjellstad JI, Jnawali SR, Weladji RB (2005) Dry season diets and habitat use of sympatric Asian elephants (*Elephas maximus*) and greater one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal. *J Zool Lond* 265:377–385
- Stewart KM, Bowyer RT, Kie JG, Dick BL, Ben-David M (2003) Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? *Ecoscience* 10:297–302
- du Toit JT (2003) Large herbivores and savanna heterogeneity. In: du Toit JT, Rogers KH, Biggs HC (eds) The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, DC, pp 291–309
- Vavra M, Holechek JL (1980) Factors influencing microhistological analyses of herbivore diets. *J Wildlife Manage* 33:371–374
- Vesey-Fitzgerald DF (1960) Grazing succession among East African game animals. *J Mammal* 41:161–172
- Voeten MM, Prins HHT (1999) Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120:287–294
- Wangchuk TR (1999) Diet selection by Bhutan Takin *Budorcas taxicolor whitei* on summer range in Jigme Dorji National Park, Bhutan. MSc Thesis, Agricultural University of Norway
- Westoby M, Rost GR, Weis JA (1976) Problems with estimating herbivore diets by microscopically identifying plant fragments from stomachs. *J Mammal* 57:167–172
- White T (1978) The importance of a relative shortage of food in animal ecology. *Oecologia* 33:71–86
- Williams AC (2002) Elephants (*Elephas maximus*), their habitats in Rajaji-Corbett National Parks. PhD Thesis, Saurashtra University, India
- Woolnough AP, du Toit JT (2001) Vertical zonation of browse quality in tree canopies exposed to size-structured guild of African browsing ungulates. *Oecologia* 129:585–590