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Seed dispersal by greater one-horned rhinoceros *(Rhinoceros unicornis)* and the flora of *Rhinoceros* latrines

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Summary. — *Rhinoceros unicornis* in Royal Chitwan National Park, Nepal ingested the fruits of at least 23 species of herbaceous and woody plants. Seeds manured into grassland latrines used by *Rhinoceros* yielded distinct floras of dicotyledonous plants in flood plain grassland associations. *Trewia nudiflora*, the most common riverine forest tree in Chitwan and *Cassia tora*, a weedy herb, accounted for most of the plant cover. A survey of the woody flora of Chitwan revealed that < 10 % of plants are dispersed by large mammals but large-mammal dispersed species represented the most common trees in flood plain forest and savannah associations.

Résumé. — Dans le Royal Chitwan National Park du Népal, le grand rhinocéros unicorne se nourrit des fruits d'au moins 21 espèces de plantes herbacées et ligneuses. Les graines, qui ont trouvé un engrais dans les latrines de savanes herbeuses des rhinocéros, y ont donné des ensembles de plantes dicotylédones distinctes des associations caractéristiques des savanes de plaine inondée. *Trewia nudiflora* est l'arbre le plus commun des forêts galeries à Chitwan, et *Cassia tora* une mauvaise herbe généralement considérée comme une plante de couverture. L'étude de la flore ligneuse de Chitwan révèle que moins de 10 % des plantes sont dispersées par des grands mammifères mais que celles-ci représentent les arbres les plus communs dans les associations de forêt de plaine inondée et de savane.

INTRODUCTION

Greater one-horned rhinoceros (hereafter referred to as *Rhinoceros*) are mostly grazers but also eat fruit in abundance (Dinerstein and Wemmer 1988). During a four-year field study (1984-1988) of *Rhinoceros unicornis* in Royal Chitwan National Park, Nepal, I observed that *Rhinoceros* frequently ingested the fruits of at least 23 species of plants. Many intact seeds, embedded in boluses of dung, were deposited on latrine sites. Seeds of most species germinated quickly and by the end of a single growing season (Feb-Oct), grassland latrines supported a conspicuous, *Rhinoceros*-generated flora. Studies in Nepal have revealed that latrines in flood plain grasslands served as important colonization sites for the most common riverine forest tree, *Trewia nudiflora* (Euphorbiaceae) (Dinerstein and Wemmer 1988), which produced a large hard berry sought out by *Rhinoceros*.

The purpose of this study was to quantify the flora of flood plain grassland latrines and to identify which fruiting species found on latrines were dispersed by *Rhinoceros* and which species merely colonized latrines via other dispersal modes (e.g. wind or defecation by perching birds). Janzen and Martin (1982) outlined a suite of plant traits associated with dispersal by large mammals, dubbed the megafaunal dispersal syndrome. Traits included : large fruit size, tough endocarps or husks, hard seeds or tough seed coats to survive the molar mill and lengthy gut passage, fruit fall soon after ripening or lack of removal by arboreal or volant frugivores after ripening, and occurrence of megafauna-dispersed plants on flood plains, where large herbivores tend to be most common. The consistency of these fruit traits and in some instances the importance and magnitude of the large mammal/« megafauna fruit » interaction has been questioned (Howe 1985). The best sites to determine the magnitude of interactions between large mammals and fleshy-fruited plants are reserves like Royal Chitwan National Park, where frugivory can be observed directly and where giant fruit-eaters are still common (Dinerstein 1989). To this end, I evaluate the fruit traits of plants disseminated by *Rhinoceros* and survey the woody flora of Chitwan to identify the role of megafaunal dispersal among other dispersal modes.

STUDY SITE AND METHODS

I measured plant cover at 37 grassland latrines using the line intercept method (Canfield 1941). Prior to sampling I selected a random compass bearing along which all intercepts (a total of 306 m) traversing latrines were sampled. Sampling was stratified vertically to distinguish between seedling, sapling, shrub, and tree cover. The sum of total plant cover at latrine sites exceeded 100 % because cover for each species over the line-intercept was calculated separately. I restricted sampling only to those latrines > 1 m in diameter, sites that contained relatively fresh dung, and to latrines > 3 km from the border with agriculture. The study area included the *Saccharum spontaneum* grasslands of Icharni Island and the *S. spontaneum* and *S. benghalensis*-dominated grasslands along the Rapti River near Sauraha. These areas supported the highest densities of *Rhinoceros* in the park : 10.5/km² during the peak grazing season (Dinerstein and McCracken, in press). Plant sampling was conducted on 28 August 1984, when annual growth was nearing its peak.

To determine the fruit characteristics of the Chitwan woody flora, I measured fruit specimens in the field or else referred to data from Kanjilal (1928). Frugivory by large mammals other than *Rhinoceros* was documented by direct observation of frugivory or examination of fecal material (Dinerstein 1989).

RESULTS AND DISCUSSION

Physical characteristics of latrines.

In two grasslands, 78 % (N = 18) and 83 % (N = 6) of all grassland latrines supported dense tussocks of *Saccharum benghalensis*. The distinct bluish color and robust foliage of this 5-7 meter tall grass enabled me to recognize active latrines at a distance from elephant-back. Tussocks of *S. benghalensis* > 3 m from latrines were more green in hue and shorter than conspecifics on dung piles. *Rhinoceros* do not ingest the infructescenses of *S. benghalensis* which produce tufted seeds dispersed by wind.

On closer inspection, *Rhinoceros* latrines in flood plain grasslands were easy to identify because of the large quantities of dung deposited at them. Ten latrines removed from the field for seedling growth experiments were weighed and all contained > 100 kg of fresh dung. Twenty-four hr activity watches on radio-collared animals revealed that *Rhinoceros* averaged 11.1 kg/defecation (sd = 6.7 range = 3.7-24.3 kg N = 9 for weight of observed defecations) and defecated 1-3 times/day (Dinerstein and Wemmer 1988). Latrines were usually elliptical in shape and averaged 8.1 m in length (sd = 3.3 N = 37) along the longest axis of the ellipse. The amount of dung found at any latrine varied, depending upon such factors as how actively the latrine was being visited by *Rhinoceros*, how many *Rhinoceros* used the area, and time of year (dung decomposed rapidly during the summer monsoon and more slowly in winter).

Laurie (1978) showed that latrines were distributed non-randomly, being most common along well-used trails in tall grasslands and along the edge of old and new river terraces. In the lower Icharni grassland, where *Rhinoceros* occur in high densities, I found 45 latrines in a 0.5 km² area. Overall, 33 % of all observed defecations from free-ranging animals during the monsoon occurred in grassland latrines and the remainder on forest latrines (Dinerstein and Wemmer 1988). In an adjacent patch of riverine forest, I found only 10 active latrines. The large size of these latrines indicated that *Rhinoceros* probably defecated more frequently at the same latrines in forested habitats that in grasslands. Laurie (1978) noticed that 85 % of all defecations occurred at existing latrine sites, regardless of habitat, and the remainder as single defecations.

During heavy monsoon floods, latrines within 100 m of riverbanks were sometimes swept away or buried in a 25 cm layer of silt. At five such latrines, *Rhinoceros* began defecating again on the pre-existing sites within 1 month, even when no visible sign of the old latrine remained. The rapid accumulation of dung at latrines and the predictability of the latrine locations may explain why latrines serve as habitat for flood plain rodents (*Mus* spp.), estivating amphibians *(Rana tigrina)*, and possibly as a site to deposit eggs for incubation for a turtle species (*Melanochelys trijuga*, Dinerstein *et al.* 1987).

Plant cover.

I recorded 38 species of plants on the flood plain latrines. These included saplings of 4 tree species, 16 species of woody shrubs, 6 forbs, 5 grasses and 7 species of herbaceous climbers (Table 1). If cover values for taxa are summed across growth forms, the seedlings, saplings, and small trees of *Trewia nudiflora* had the highest cover value for any species. If growth forms are treated separately, the most common species encountered was *Cassia tora*, a common weed of overgrazed pastures outside the park. More than 1 km from the park borders, where domestic grazing was absent, *Cassia* is found only on *Rhinoceros* latrines (Joshi 1986). Five agricultural weeds *(Amaranthus spinosus, Xantium strumarium, Chenopodium album, Solanum xanthocarpum, S. indicum)* also common in overgrazed areas, like *Cassia*, occured inside the park either on *Rhinoceros* latrines

TABLE 1. — Plant cover on *Rhinoceros unicornis* latrines in the Sauraha area of Royal Chitwan National Park and some characteristics of the latrine flora. Latrines were sampled on 28 August 1984 (N = 37 latrines sampled).

Species.	Family:	Growth Form:	Percent of Total	Dispersal Mode:	Habitat	Fruit Size.	Fruit Type	Fruit Color
Cassia tora	Caesalpinaceae	annual	32.4	rhinoceros	overgrazed scrub	14 cm. long	pod	brown
Imperata cylindrica	Poaceae	intermediate grass	30.9	wind	disturbed grassland	0.5 cm. long	grain	brown
Saccharum benghalensis	Poaceae	tall grass	25.3	wind, water	grassland	0.4 cm long	grain	brown
S. spontaneum	Poaceae	tall grass	25.2	wind, water	grassland	0.6 cm long	grain	brown
Trewia nudiflora seedlings	Euphorbiaceae	tree	24.1	rhinoceros	riverine forest, flood plain	2.5 cm diam.	berry	yellow-green
Pogostemon benghalensis	Lamiaceae	shrub	16.0	gravity?	riverine forest	0.1 cm. diam.	nutlet	grey
Aegeratum conyzoides	Asteraceae	annual	12.9	wind	edge of riverine forest	0.18 cm. length	achene	brown
Trewia nudiflora trees and saplings	Euphorbiaceae	tree	11.8	rhinoceros	riverine forest, flood plain	2.5 cm. diam.	berry	yellow-green
Callicarpa macrophylla	Verbenaceae	shrub	10.5	rhinoceros, bird	riverine forest, scrub	0.4 cm. diam.	drupe	white
Artemesia vulgaris	Asteraceae	shrub	8.9	wind	scrub, game trails	0.1 cm. long	achene	brown
Clerodendron viscosum	Verbenaceae	shrub	8.2	bird	riverine forest, scrub	1.0 cm. long	drupe	blue
Amaranthus spinosus	Amaranthaceae	annual	4.6	rhinoceros	scrub	0.3 cm. long	utricle	green
Eupatorium odoratum	Asteraceae	annual	3.6	wind	scrub	0.4 cm. long	achene	brown
Cucurbitaceae sp. 1		herbaceous climber	2.6	rhinoceros	grassland	2.0 cm long	berry	red
Cassia occidentalis	Caesalpinaceae	herbaceous shrub	2.0	rhinoceros	overgrazed scrub	10 cm. long	pod	brown
Cucurbitaceae sp. 2		herbaceous climber	2.0	mammal, bird	grassland	2.0 cm. long	berry	red/ yellow
Cymbopogon flexulosus	Poaceae	intermediate grass	1.9	gravity	grassland	0.5 cm. long	grain	brown
Colebrookea oppositifolia	Lamiaceae	shrub	1.7	gravity	riverine forest	0.1 cm. diam.	nutlet	grey
Solanum xanthocarpum	Solanaceae	shrub	1.3	rhinoceros, small mammals	grassland, scrub	2.0 cm. diam.	berry	yellow
Acacia catechu	Mimosaceae	tree	1.0	wind, mammal	riverine forest, floodplain	10 cm. long	pod	brown
Urena lobata	Malvaceae	shrub	0.8	rhinoceros, animal fur	scrub, animal trails	0.5 cm. long	capsule	brown
Solanaceae sp. 1		annual	0.7	mammal	scrub	1.0 cm. diam	berry	yellow

Species.	Family:	Growth Form:	Percent of Total	Dispersal Mode:	Habitat	Fruit Size:	Fruit Type:	Fruit Color:
Xantium strumarium	Asteraceae	shrub	0.7	rhinoceros, animal fur	overgrazed scrub	1-2.0 cm long	capsule	brown
Cucurbitaceae sp. 3		herbaceous climber	0.6	bird, mammal	grassland	2.0 cm. diam.	berry	green
Ehretia laevis	Ehretiaceae	tree	0.6	bird	riverine forest	0.3 cm. diam.	drupe	yellow
Litsea monopetala	Lauraceae	tree	0.6	bird	riverine forest	1.0 cm. long	drupe	green
Solanum indicum	Solanaceae	shrub	0.5	rhinoceros	grassland, scrub	2.0 cm. diam.	berry	yellow
Zyziphus mauritiana	Rhamnaceae	shrub	0.5	mammal, bird	scrub	2.0 cm. diam.	drupe	red
Floccosa sp.	Commellinaceae	annual	0.4	bird, mammal	river edge	0.5 cm. diam.	fleshy capsule	blue
Stephania japonica	Menispermaceae	herbaceous climber	0.4	rhinoceros, bird	riverine forest	0.7 cm. diam.	drupe	red
Oplismenus compositus	Poaceae	short grass	0.3	animal fur	riverine forest	0.2 cm long	grain	brown
Piper indicum	Piperaceae	herbaceous climber	0.3	rhinoceros, small mammal?	riverine forest	2.2 cm. x 6.0 cm. long	multiple fruit	green
Bombax ceiba seedlings	Bombacaceae	tree	0.3	wind	grassland, riverine forest	10 cm. long	capsule	brown
Bombax ceiba saplings	Bombacaceae		0.3					
Grewia sclerophylla	Tiliaceae	shrub	0.2	bird	grassland	1.0 cm. diam.	drupe	blue
unidentified sp. 1		herbaceous	0.2	-	grassland	–	–	–
Desmostachia bipinnata	Poaceae	intermediate grass	0.2	gravity	grassland	0.2 cm. long	grain	brown
Murraya koeniggii	Rutaceae	shrub	0.1	bird	riverine forest	1.0 cm. long	drupe	blue
Triumfetta rhomboidea	Tiliaceae	shrub	0.1	rhinoceros, animal fur	game trails, riverine forest edge	0.5 cm. 1 wide	capsule	brown
Ipomea quamoclit	Convolvulaceae	herbaceous climber	0.1	rhinoceros, bird	riverine forest edge, scrub	0.5 cm. long	capsule	brown

or in grasslands disturbed by floods (E. Dinerstein, pers. obs.). Twenty species accounted for less than 1 % each of the intercept covered.

Plant species richness on latrines > 3 km from the park border contained fewer species because *Rhinoceros* in these areas rarely strayed into croplands and thus, did not ingest agricultural weeds (Joshi 1986). Latrines under the riverine forest canopy were even more depauperate in plant species than in grasslands because most species which germinated in the dung on the forest floor, such as *Trewia*, were shade-intolerant (Dinerstein and Wemmer 1988).

Dispersal modes of plants found on latrines.

By direct observations of frugivory by *Rhinoceros*, I estimated that 21 of the 38 species encountered on grassland latrines were dispersed at least in part by *Rhinoceros* (Table 1). Because the seeds of these 21 species were found embedded so deeply in boluses of dung, it was unambiguous that *Rhinoceros* had to be the major vector for dispersal to the latrine site. The two most common grasses found on latrines, *Saccharum spontaneum* and *S. benghalensis*, exceeded 4 m in height and experiments have shown them to be dispersed by wind and water (Lehmkuhl 1988). *Rhinoceros* ingested the inflorescences of these tall grasses only prior to seed set. Three other grasses, three members of the Asteraceae, and two other woody species produced seeds with attachments associated with wind-dispersal. A grass and several shrubs formed burrs and sticktights indicating dispersal via animal fur and at least 10 species produced bright-colored fleshy fruits eaten by birds. Bulbuls (*Pycnonotus* spp.), tits (*Parus major*), and mynahs (*Acridotheres* spp.) perched on the shrubs growing from latrines, ate fruits from these plants, and probably defecated seeds from other species into the latrines. *Rhinoceros* also fed on the fruits of two species of *Solanum* and the leaves of *Amaranthus spinosus* found growing on latrines.

The Chitwan woody flora, characteristics of large mammal fruits, and the megafaunal syndrome.

The Chitwan woody flora includes 77 fleshy-fruited species dispersed by vertebrates, 28 species of dry-pod legumes probably dispersed by vertebrates or gravity, 19 species adapted for wind dispersal, 6 species adapted for dispersal on animal fur, 2-3 species dispersed presumably by gravity, and 8 species whose dispersal mode has not yet been determined (E. Dinerstein, pers. obs.). *Rhinoceros* ingested the fleshy fruits of at least 20 species (26 %) of the common woody trees and shrubs that grow on or near the flood plain. However, among the species ingested by *Rhinoceros*, only a small portion exhibited all of the traits predicted by the megafaunal dispersal syndrome. *Rhinoceros* ingested fleshy fruits ranging in size from the 4 mm *Callicarpa macrophylla* berries (which occur in a clumped fruiting display) to the apricot-sized *Trewia* ; most fruits ingested were less than 1 cm in diameter. Many fruits eaten by *Rhinoceros* also were eaten by smaller frugivores. Surprisingly, the dry-pod legumes were well-represented in the Chitwan woody flora (28 species), but *Rhinoceros* ate only the pods of the common climber *Acacia concinna*. Legumes are probably more common in the diets of wild elephants as they are in South India (R. Selvakumar pers. comm.) but free-ranging elephants are so few in Chitwan today that consumption and dispersal of legumes is difficult to evaluate. Large herds of elephants were common in Chitwan a century ago (Oldfield 1880).

The most common fruiting species ingested by *Rhinoceros* were grassland shrubs and forbs in areas close to croplands and disturbed sites. In areas far from agriculture, trees and woody climbers, as predicted by the megafaunal hypothesis, dominated the non-graminoid flora of latrine sites.

In contemporary Chitwan, the fruiting species known or thought to be dispersed by *Rhinoceros* or other large ungulates include *Trewia, Spondias pinnata, Terminalia belerica, Acacia concinna, Emblica officinalis, Xeromphis uliginosa* and *Aegle marmelos* (Table 2). The number of large mammal-dispersed plants

TABLE 2. — Characteristics of some common large fruits eaten by *Rhinoceros unicornis* or other large ungulates in Royal Chitwan National Park.

Species	Family	Growth Form	Habitat*	Fruit Size	Fruit Type	Fruit Color	Texture of Endocarp at Ripening	Fruit Fall just after Ripening	Seed number
Trewia nudiflora	Euphorbiaceae	tree	FPF flood plain grasslands	2.5 cm d	berry	yellow-green	hard throughout	yes	1-5
Spondias pinnata	Anacardiaceae	tree	FPF/UF	5.0 cm l	drupe	yellow	hard throughout	yes	often 2-5, 1 perfect
Terminalia belerica	Combretaceae	tree	UF	2.5 cm l	drupe	brown	hard throughout	yes	1
Acacia concinna	Mimosaceae	woody climber	FPF	6.0 cm l	legume	brown	woody with fleshy interior	yes	6-10
Emblica officinalis	Euphorbiaceae	small tree	UF	2.4 cm w	drupe	green	hard throughout	yes	1
Xeromphis uliginosa	Rubiaceae	small tree	FPF/UF/ grassland	5.4 cm l 4.4 cm d	berry	yellow	hard throughout	yes	<100
Aegle marmelos	Rutaceae	tree	FPF/UF	6.0 cm d	berry	yellow	[illegible] shell [illegible] interior	yes	50-100

*Habitat Key:
FPF = Flood plain forest
UF = Upland forest (i.e. above the river terraces)

in Chitwan yields a shorter species list and a smaller proportion (> 10 %) of the total woody flora in comparison with the Tai Forest, the Ivory Coast, where over 30 % of the trees are dispersed by elephants (Alexandre 1978).

All of the Chitwan species (Table 2) produce large, hard, dull-colored, indehiscent fruits, drop fruit prior to or just after fruit ripening, and occur on the flood plain. All, with the exception of *Aegle*, contained a single hard seed or seeds. *Aegle* fruits contained soft seeds but was one of the hardest fruits in Chitwan. The pressure required to crack the shell ($\bar{x}$ = 347.5 lbs. pressure) and large fruit size implied that only elephants and *Rhinoceros* among contemporary fruit-eaters possessed sufficient gape and jaw strength to crush fruits. The genus *Feronia* in South India and Sri Lanka produces fruits similar in type and size to *Aegle* and are dispersed by elephants (R. Selvakumar pers. comm.). The list of large mammal-dispersed fruits will probably increase as more data on dispersal of *Xeromphis spinosa, Terminalia chebula, Dillenia indica* and other trees becomes available.

Although large indehiscent fruits, such as the 7 species listed in Table 2, represent but a small proportion of the woody flora on the flood plain, interactions between these fruiting plants and the local megafauna are intense. Today, *Trewia*, dispersed mainly by *Rhinoceros*, sambar deer *(Cervus unicolor)*, axis deer *(Axis axis)*, and domestic cattle, is the most common tree in riverine forest (Dinerstein and Wemmer 1988). *Xeromphis*, dispersed mainly by hog deer *(Axis porcinus)*, axis deer, and possibly gaur *(Bos gaurus)*, is one of the most common tree species in grasslands and savannahs. The extent of dispersal interactions among large mammals and the other 5 species listed in Table 2 remains to be clarified. We found seeds of all species in the droppings of wild and domestic ungulates and *Spondias, Terminalia* and *Emblica* are also eaten by langur and rhesus monkeys in other reserves (Dinerstein 1980).

In addition to being abundant, both *Trewia* and *Xeromphis* produced heavy fruit crops (see Dinerstein and Wemmer, 1988) and their consumption is limited to large herbivores. Thus, it is highly likely that on the Chitwan flood plain, the amount of fleshy-fruit biomass ingested by large herbivores exceeds annually the amount of fruit biomass consumed by birds, bats, and rodents. The magnitude of the interactions observed between megafruits and megaherbivores in Chitwan also support the belief that in habitats now devoid of a large mammal fauna, seed shadows for fleshy-fruited species may be substantially different today than when large fruit-eaters were still abundant.

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The species-genus relationship in Antillean bat communities

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Summary. — The ratio of the number of species to the number of genera in an island community has long been recognised as a potential proxy indicator of competitive interaction. An analysis of this relationship in the bat fauna of the Antillean archipelago demonstrates that the observed species-genus ratios are significantly depressed below null-model expectations, and that the magnitude of this depression is inversely proportional to the log of the appropriate island area. These observations are consistent with the hypothesis that interspecific competition may play an important role in structuring Antillean bat communities.

Résumé. — La proportion du nombre d'espèces par rapport au nombre des genres dans une communauté insulaire a été reconnue comme un indicateur d'interactions compétitives. Une analyse de cette relation dans la faune des chauves-souris de l'archipel des Antilles montre que les proportions d'espèces/genres que l'on observe sont réduites de manière significative par rapport à l'hypothèse du modèle et que l'importance de cette réduction est inversement proportionnelle au log. de la surface de l'île. Ces observations concordent avec l'hypothèse que la compétition interspécifiques peut jouer un rôle important dans la structuration des communautés de chauves-souris antillaises.

INTRODUCTION

Several authors (Elton 1946 ; Grant 1966) have noted the apparent decrease in the average number of species per genus in island communities when compared with their mainland equivalents. According to Darwin (1878 : 59) : « As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera ». If this is the case, then as Harvey *et al.* (1983) have noted, competitive exclusion might be expected to distance congeneric taxa so that local communities should exhibit

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