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EFFECTS OF RHINOCEROS UNICORNIS ON RIVERINE FOREST STRUCTURE IN LOWLAND NEPAL

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The effect of browsing by Asian megaherbivores (i.e., mammals > 1000 kg) on forest structure has received little attention from ecologists, even though several species feed extensively on foliage and stems (Laurie 1978, Olivier 1978) and can distort tree growth (Muller-Dombois 1972). The contemporary guild of large browsers includes Asiatic elephant (*Elephas maximus* L.), greater one-horned rhinoceros (*Rhinoceros unicornis* L.), and Javan rhinoceros (*Rhinoceros sondaicus* Desmarest). These mammals have coexisted with forest plants for millenia, and it is reasonable to assume that chronic herbivory has been an important selective force on certain Asian plant species as it has for plants in the Neotropics (Janzen 1986) and in Africa (Owen-Smith 1987).

The purpose of this study was to elucidate how large mammalian herbivores influence forest structure and canopy composition by inhibiting vertical growth of saplings that are frequently browsed and trampled. Specifically, I ask whether chronic browsing and bending of *Litsea monopetala* (Roxb.) (Lauraceae) by greater one-horned rhinoceros prevent most *Litsea* individuals from reaching the canopy. The participants in this interaction are common in the lowland riverine forests in the Royal Chitwan National Park (RCNP), Nepal (elevation ≈ 200 m). I present the results of a study conducted between 1985 and 1988 comparing growth response of *Litsea* saplings within and outside of protective exclosures from *Rhinoceros unicornis* (henceforth *Rhinoceros*). I suggest how size structure of woody

stems in riverine forest may be influenced by the feeding behavior of this large herbivore.

Methods

Study species. Between 350 and 380 *Rhinoceros* occur in RCNP (Dinerstein and McCracken 1990, Dinerstein and Price 1991). Adult *Rhinoceros* weigh ≈ 2000 kg and approach 4 m in head and body length; males may stand 1.72 m at the shoulder (Dinerstein 1991). *Rhinoceros* eat mainly herbaceous plants (Dinerstein and Wemmer 1988, Dinerstein 1989, *in press*), but during the winter months they frequently browse woody plants such as *Litsea* saplings. *Rhinoceros* walk over and trample to the ground *Litsea* stems < 15 cm dbh (diameter at breast height). When foraging on *Litsea*, adult *Rhinoceros* can either remove up to 100 g wet mass of leaves and stems with each bite or pluck individual leaves with the upper prehensile lip. *Litsea monopetala* is a canopy species reaching 25 m in riverine forest. In certain stands, *Litsea* saplings occur in high densities and can be the most common species of sapling encountered (E. Dinerstein, *personal observation*). Trees are evergreen with moderate leaf fall beginning in November (Dinerstein 1987). New leaves are produced in mid-February, coinciding with the period when new grass shoots emerge on the adjacent flood plain. *Rhinoceros* largely abandon browsing on *Litsea* and return to the grassland at this time.

Impact of Rhinoceros on vertical growth of Litsea. To determine if *Rhinoceros* inhibit *Litsea* saplings from reaching the canopy, I attempted to locate a control area where browse damage was not evident. I could find no such area within RCNP. Forested areas adjacent to RCNP could not be used because villagers use *Litsea* branches for cattle fodder. Thus, I used ex-

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TABLE 1. Nested one-way analysis of variance of sapling height of *Litsea monopetala* saplings protected by exclosures for 3 yr from browsing and trampling by *Rhinoceros unicornis* vs. saplings not protected over the same period in Royal Chitwan National Park, Nepal.

Source	ss	df	MS	F	P
Total	521.9	179	2.9		
Protection	211.7	1	211.7	105.9	.00001
Replicate	20.0	10	2.0	1.2	.3235
Error	290.3	168	1.7		

closures to assess the impact of *Rhinoceros* on vertical growth of stems. I employed a haphazard sampling regime to establish study plots in areas where a 10 × 10 m exclosure or control plot would contain at least 35 *Litsea* stems. A forest inventory revealed that such densities are typical in the riverine forest patches to the east of Icharni Island near Sauraha (E. Dinerstein, unpublished data). I randomly assigned six of the plots to be open to foraging *Rhinoceros* and six plots to be protected from *Rhinoceros* by 2 m high wooden fences. I located a control plot close to each exclosure. I initially marked and measured 180 *Litsea* saplings (15 per plot) in October 1985. At the time of exclosure, a nested one-way ANOVA (SAS 1989) indicated that sapling height did not differ significantly between pro-

tected (grand mean ± 1 SD for six plots = 2.49 ± 0.23 m, $N = 90$ saplings) vs. unprotected saplings (2.46 ± 0.23 m, $N = 90$ saplings in six plots) ($F_{1,179} = 0.11$, $P = .75$). At the end of 3 yr, I again used a nested one-way ANOVA (SAS 1989) to test for differences in sapling height.

To further evaluate the impact of browsing and trampling by *Rhinoceros*, I inventoried all woody stems in 10 0.5-ha plots located in five patches of riverine forest (two plots per patch). Stems were examined for characteristic browse marks and trampling left by *Rhinoceros*.

Distribution of leaves on browsed and protected plants. To determine if *Rhinoceros* browsing alters the amount of leaf tissue available below 2 m, I counted the number of branches supporting at least 10 whole leaves <2 m above the ground (henceforth leafy branches) on 337 saplings drawn from each of the 12 plots ($N = 172$ and 165 for protected and unprotected plots, respectively). I observed that *Rhinoceros* can readily browse leaves below 2 m height without trampling saplings. Stems were marked and followed during the 1st yr only. Many saplings marked to measure height were also used to measure distribution of leaves. I analyzed these data using a general linear model nested one-way ANOVA (SAS 1989) because of unequal replication of saplings within each plot.



FIG. 1. A *Litsea monopetala* sapling browsed and trampled by *Rhinoceros unicornis* in Royal Chitwan National Park, Nepal.

TABLE 2. Nested one-way analysis of variance of leafy branch production at heights < 2 m for *Litsea monopetala* saplings protected by exclosures for 3 yr from browsing and trampling by *Rhinoceros unicornis* vs. saplings not protected over the same period in Royal Chitwan National Park, Nepal.

Source	ss	df	MS	F	P
Total	12 195.9	11	1108.7		
Protection	7805.1	1	7805.1	64.47	.0001
Replicate	4390.9	10	439.1	3.63	.0001
Error	36 806.4	304	121.1		

Results

Impact of Rhinoceros on vertical growth of Litsea. About 60 *Rhinoceros* used the 7 km² study area in which I inventoried *Litsea* stems. Data from movements of radio-collared individuals and from population censuses revealed that from November until February 1–6 individuals per night fed on *Litsea* in the forest tract containing the exclosures (E. Dinerstein, *personal observation*). Exclosure studies revealed that browsing and trampling by *Rhinoceros* had a significant negative impact on sapling growth (Table 1). After 3 yr the grand mean \pm 1 SD for sapling height for all protected plots was 4.89 ± 0.28 m; 31 protected saplings were 6–7 m tall, 11 were 7–8 m, and 4 exceeded 8 m in height. In contrast, after 3 yr, the grand mean \pm 1 SD for unprotected saplings was 2.79 ± 0.13 m, the tallest plant was 5.5 m, and only six stems were > 4 m tall.

The inventory of forest plots included 2073 woody stems; 96% were saplings, treelets, and canopy individuals of six species. *Litsea* and another species browsed and trampled by *Rhinoceros*, *Mallotus philippinensis* Muell. Arg. (Euphorbiaceae), accounted for 33% of all stems. The size structure of *Litsea* was highly skewed towards trampled saplings; only 30 (< 5%) of the 574 *Litsea* stems measured were ≥ 3.5 m tall. All of the 544 understory stems showed signs of moderate to heavy browsing and trampling by *Rhinoceros*.

Distribution of leaves on browsed and protected plants. In response to chronic herbivory, saplings of *Litsea* sprout readily in February, producing new shoots along browsed and bent stems and from locations where old stems have been snapped. Partially broken and bent trunks often spread horizontally in several directions and may be > 3 m long (Fig. 1). Browsing and trampling stimulated production of new leaves and stems below 2 m. Saplings chewed and pruned by *Rhinoceros* produced significantly more leafy branches below the browse line than did unbrowsed saplings (Table 2). This is because most of the new growth on protected saplings was distributed at the

upper edge of the crown, thus above 2 m, instead of at the base of the tree. Increase in leaf abundance below 2 m on browsed saplings is related not to phenological changes induced by herbivory but rather to manipulation of branch height and growth.

Discussion

The wildlife literature is replete with exclosure studies addressing the impact of native and introduced herbivores on seedling survival and vegetation structure (Graf and Nichols 1967, Hanley and Taber 1980, Altverson et al. 1988). However, most studies focus on the effects of selective browsing by small ruminants < 100 kg or lagomorphs. The large mass, extended reach, and great strength of megaherbivores can intensify the potential impact foraging rhinoceroses and elephants can exert on tree growth and architecture. Anecdotal accounts and natural history observations of this impact are well known, but exclosure studies documenting these effects are lacking.

Exclosure studies in the riverine forest of RCNP clearly demonstrate that browsing and trampling by *Rhinoceros* inhibit vertical growth of *Litsea*. Because *Litsea* and *Mallotus* saplings occur in high densities in riverine forest, *Rhinoceros* browsing and trampling of their saplings affects forest structure. In forest patches where *Litsea* and *Mallotus philippinensis* are common, the first stratum of bent or prostrate saplings of these species forms a low canopy. Above this mat of saplings exists a gap occupied by a few adult *Litsea*, *Mallotus*, or *Bombax ceiba* Linn. (Bombacaceae). In the absence of *Rhinoceros*, this space undoubtedly would be occupied by a greater percentage of near mature or adult individuals of *Litsea* and *Mallotus*. Trampling of saplings of the pioneer tree species *Dalbergia sissoo* Roxb. (Fabaceae) is also common on the flood plains of RCNP (Laurie 1978; E. Dinerstein, *personal observation*).

The observed intensity of bending and browsing of saplings may seem characteristic of the impact of a large herbivore population that is beyond its carrying capacity. However, the RCNP *Rhinoceros* population was reduced by poaching to < 80 animals in 1962 and, although increasing steadily, is still considered to be below carrying capacity (Dinerstein and Price 1991). Although the entire Chitwan Valley probably supported > 1000 animals in the 1950s, its *Rhinoceros* population was < 400 individuals in 1988. Even at reduced population levels, the interactions described here between *Rhinoceros* and woody plants clearly suggest a significant evolutionary impact of selective browsing by large mammals with potential cumulative effects on forest structure and canopy composition. The impact of giant browsers may be particularly conspicuous on South Asian floodplains, where tree species

diversity is low and estimates of large browser biomass in riverine forest-grassland mosaics approach the highest values observed in protected reserves in East Africa (Eisenberg and Seidensticker 1976, Dinerstein 1980).

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FIELD EVIDENCE FOR A COST OF BEHAVIORAL ANTIPREDATOR RESPONSE IN A LARVAL AMPHIBIAN

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Trade-offs between the ability to garner resources and the risk of predation are central to a number of

recent theoretical considerations of animal behavior (e.g., Gilliam and Fraser 1987, Brown 1988, Ludwig and Rowe 1990). These models assume that when a forager behaves in a way that maximizes fitness, given a set of predation risk/foraging reward options, any reduction in predation risk is accompanied by a de-

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