

The Foliage-as-Fruit Hypothesis and the Feeding Behavior of South Asian Ungulates¹

Eric Dinerstein²

Smithsonian/Nepal Terai Ecology Project (SI/NTEP), Conservation and Research Center, National Zoological Park, Front Royal, Virginia 22630, U.S.A.

ABSTRACT

The foliage-as-fruit hypothesis argues that some plants may actually promote herbivory by large ungulates at the time of seed set to achieve seed dispersal. I examined a minimum condition of this hypothesis, that large herbivores actually ingest and pass small seeds from non-fleshy-fruited plants, by screening the dung of large indigenous mammals at the time of seed set. In a lowland reserve in South Asia, I examined the dung of Greater One-Horned Rhinoceros, Indian bison, and four native cervids for seeds from plants not producing fleshy fruits but found no obvious examples supporting the foliage-as-fruit hypothesis. Frequent, predictable, and widespread disturbance of grasslands by annual flooding and periodic fires provides sufficient microsites for the propagation of annual plants. Under this disturbance regime, selection pressure for megafauna-mediated dispersal, as described by the foliage-as-fruit hypothesis, is not apparent in plants of South Asian flood plains.

JANZEN (1984) SUGGESTED THAT THE FOLIAGE of small-seeded plants may function ecologically as fruit, attracting large herbivores just as arils and fleshy berries attract and reward frugivores. In this intriguing evolutionary scenario, large ungulates, lured by a nutritious fodder "bait," ingested minute seeds and fruiting stalks cloaked in leaf tissues. Long coexistence with a herbivorous megafauna provided small-seeded plants with a unique dispersal guild of wide-roaming mammals that defecated seeds into favorable germination sites (e.g., edges of game trails, small forest openings, wallow edges, river and stream banks). Implicit in the foliage-as-fruit (FAF) hypothesis is the prediction that plants subjected to herbivory are compensated by effective dispersal and recruitment away from the parent. Selection for tough, digestion-resistant seeds would increase survival past the *Scylla* and *Charybdis* of megafaunal dispersal: massive, grinding molars and lengthy gut retention.

Most of the data supporting Janzen's hypothesis come from either fenced domestic livestock, free-ranging cattle, or fossilized ingesta of prehistoric large herbivores. Anecdotal accounts of seed dispersal by large mammals are common but most citations concern ingestion of small seeds concealed in fleshy fruits rather than consumption of seeds cloaked in foliage. Analyses of interactions between small-seeded plants and wild, large herbivores from different continents and habitats would lend more credence to the big mammal/small seed hypothesis, but data are few. A study conducted in an intensively-managed, North American grassland, reported that small-seeded plants are dispersed by wind and ballistic mechanisms rather than

by populations of buffalo, elk, deer, and longhorn cattle on the site (Collins & Uno 1985).

The hypothesis also lacks critical review because a direct test requires demonstrating that plants whose foliage and seeds are ingested by large mammals have higher fitness than do unbrowsed plants in the kinds of habitats in which the system evolved. The purpose of this paper is to evaluate a minimum condition for the FAF hypothesis to be valid: that indigenous megaherbivores ingest and pass a significant amount of seeds from "FAF-type" plants. My study site was the lush Gangetic flood plain of southern Nepal (known regionally as the Terai zone). The most conspicuous member of the megafauna is an extant, prehistoric herbivore, the Greater One-Horned Rhinoceros (*Rhinoceros unicornis*) (hereafter, referred to as rhinoceros). The large herbivore guild also includes 5 ruminants that are widespread over much of subtropical and tropical Asia: barking deer (*Muntiacus muntjac*), hog deer (*Axis porcinus*), axis deer (*Axis axis*), sambar (*Cervus unicolor*), and Indian bison or gaur (*Bos gaurus*).

Today, intact riverine grasslands of the Terai zone of India, Nepal, and Bhutan occur in a few reserves and parks, although five hundred years ago, the flood plain vegetation covered a huge belt of land along the Himalayan foothills. Wild herbivore biomass in these protected parks rivals figures estimated for some African game preserves, particularly in the tall grass/riverine forest mosaics (Seidensticker 1976, Dinerstein 1980). One would predict that FAF type interactions would most likely evolve in habitats supporting a diverse and dense megafauna. One such habitat is the grassland of South Asia.

More detailed information on Chitwan, habitat dynamics, rhinoceros, and other ungulates can be found elsewhere (Laurie 1978, Mishra 1982, Gyawali 1986, Joshi 1986, Dinerstein 1987, Dinerstein & Wemmer in press).

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² Present address: World Wildlife Fund, 1250 24th St. NW, Washington, D.C. 20037, U.S.A.

TABLE 1. Seed content of deer pellets during peak seed set for annual plants in a study area > 3 km from croplands.

Parameter	Deer species			
	Barking deer ¹	Hog deer ²	Axis deer ³	Sambar ⁴
Body weight (kg)	12-17	31	54	154-198
N pellet groups	22	300	300	300
N pellets examined	732	14,452	14,809	14,042
N seeds found	0	709	420	345
N seeds from fleshy-fruited herbs/shrubs	0	702 ⁵	26 ⁶	140 ⁷
N seeds from non-fleshy-fruited herbs/shrubs	0	3 ⁸	320 ⁹	165 ¹⁰
N seeds from grasses	0	4 ¹¹	74 ¹²	40 ¹¹

¹ *Muntiacus muntjak*.² *Axis porcinus*.³ *Axis axis*.⁴ *Cervus unicolor*.⁵ *Callicarpa macrophylla*—654; *Cucurbitaceae* sp.—3; *Solanum indicum*—22; *Piper indicum*—1; *Solanum* sp.—17.⁶ Unknown sp.—26.⁷ *Callicarpa macrophylla*—9; *Piper indicum*—3; unknown sp.—128.⁸ Legume sp.—2; unknown sp.—1.⁹ *Rabdosia coetsa*—240; *Rabdosia* sp. b—54; *Flemingia chappar*—10; other—16.¹⁰ *Rabdosia coetsa*—78; *Rabdosia* sp. b—80; Legume sp.—7.¹¹ Grass sp. 1—3; grass sp. 2—1.¹² From four spp.¹³ *Oplismenus compositus*—20; three other spp.—20.

METHODS

Janzen (1984) outlined a suite of traits exhibited by FAF-type plants assumed to promote large mammal dispersal (edibility before and during seed set; chemical changes in leaf palatability with seed set; nutritious foliage; synchrony of seed maturation; close contact between seeds and edible foliage; tough, minute, digestion-resistant seeds). One way to detect the presence of the FAF syndrome is to survey a local flora for the appearance of such traits among annuals (Collins & Uno 1985). I used this approach to examine the trait of close contact between seeds and edible foliage.

I tested the minimum condition of the FAF hypothesis by sampling and screening the dung of rhinoceros and other ungulates for the presence of small seeds during the annual peak in seed set for small-seeded plants. This approach preempts testing for increased fitness of FAF-type plants dispersed by megaherbivores vs individuals not dispersed via ingestion by large mammals. If native large grazers and browsers actually avoid or seldom ingest fruits of small-seeded plants at seed set, or pass few or no intact seeds over the range in time and space of the plant species in question, then the FAF interaction may not be prevalent in that system.

Rhinoceros dung was sampled from 100 latrines at least 3.5 km from the border with agriculture. For border-dwelling rhinoceros I also censused 20 natural latrines each month for the presence of FAF-type plants germinating from the latrines. All 20 latrines occurred adjacent to croplands so that seeds recovered from them provided a comparison with dung collected from rhinoceros that for-

age on natural vegetation. In addition, Gyawali (1986), using fecal analysis techniques, compared monthly diets of a population of border-dwelling rhinoceros with a population > 2.5 km from the border with agriculture.

I evaluated small seed/ruminant interactions by searching through 300 pellet groups/species for hog deer, axis deer, and sambar from several forest and grassland tracts during the peak period of seed set for annual plants (Table 1). Barking deer, a species most common in riverine forest, used latrines, and I searched through 22 latrines during the same interval. Indian bison droppings were searched during April. April is the beginning of the second peak in seed set for annuals which set seed in grasslands and it marks the time of year when bison are most common on the flood plain. Normally, bison spend most of the year in Chitwan's hilly tracts.

We fed fruits and foliage of small-seeded plants to a captive rhinoceros to estimate gut transit and seed survival (see Joshi 1986, Dinerstein & Wemmer 1988). All seeds recovered from wild ungulate dung were sown in soil and watered to test for germinability.

RESULTS AND DISCUSSION

Rhinoceros may exceed 2000 kg and fuel their massive bulk on a diet of flood plain grasses, tree saplings, shrubs, aquatic plants, herbs, and fruits (Laurie 1978, Gyawali 1986). The fruits and seeds of at least 30 species of plants are ingested by rhinoceros in a study area bordering croplands (E. Dinerstein pers. obs.). Of these, seeds of only

TABLE 2. Seed content from large herbivore dung during peak seed set for annual plants in a study area > 3 km from croplands.

Parameter	Indian bison (<i>Bos gaurus</i>)	Greater One-Horned Rhinoceros (<i>Rhinoceros unicornis</i>)
Body weight (kg)	702-880	1410-2000
N samples	54	100
Sample weight (kg)	117.7	891.4
N seeds	0	112
N seeds from fleshy fruit	0	10
N seeds from non-fleshy fruit	0	101 ¹
N seeds from grasses	0	1 ²

¹ *Flemingia chappar*—61; *Cassia tora*—10; legume sp. a—8, six unknown spp.—22.

² Rice—1.

13 non-fleshy-fruited forbs and grasses, out of a herbaceous flora exceeding 180 species, were recovered in minute quantities from rhinoceros latrines sampled > 3.5 km from the border with agriculture (Table 2).

The Chitwan graminoid flora contains a minimum of 30 species of short grasses, 22 species of intermediate grasses, 22 species of tall grasses, and 15 species in the Cyperaceae. Because the monthly diet of rhinoceros may contain up to 96 percent grass tissues (Gyawali 1986), the virtual absence of the FAF interaction among grasses and rhinoceros is puzzling. I suggest six factors that might reduce intake of small, foliage-wrapped (as opposed to berry-encased) seeds by large grazers. First, the prehensile upper lip of the rhinoceros permits highly selective foraging. Rhinoceros easily pluck small fruits from the ground and graze neatly around fruiting stalks of short grasses such as *Chrysopogon aciculatus* (a sticktight species) but graze its prostrate leaves and stems. Rhinoceros also avoid the short fruiting spikes of *Eleusine indica* and the sedge *Fimbristylis dichotoma* while cropping surrounding prostrate grasses.

Second, grazing lawns result where rhinoceros do graze short grasses (*sensu* McNaughton 1984); severe cropping reduces flowering and seed set. Moreover, the grasses that dominate on grazing lawns (*Imperata cylindrica*, *Cynodon dactylon*, and *Saccharum spontaneum*) spread predominantly by rhizomes, or stolons, or both. Of course, other extinct large herbivores might have grazed short grass swards differently than rhinoceros. However, domestic cows and buffalo maintain grazing lawns in the absence of rhinoceros and avoid fruiting parts of several of the same graminoids (J. Lehmkuhl, pers. comm.). In the Kaziranga Reserve in Assam, India, rhinoceros, wild buffalo, swamp deer, and hog deer crop grazing lawns in the same manner.

Third, the fruiting stalks of three small-seeded grasses

that contribute greatly to grass biomass in Chitwan (*Naranga porphyracorma*, *Themeda arundinacea*, and *Saccharum benghalensis*) are not eaten by rhinoceros at seed set. Two features of these three species make them unfavored food plants: 1) fruiting stalks reach 3-6 m at seed set, well above the reach of all the ungulates under consideration, and 2) mature foliage is low in crude protein but high in silicates, cellulose, and lignin during the dispersal phase. (*N. porphyracorma* 0.80% N in lvs, 0.12% N in fruiting stems; *T. arundinacea* 0.92% N in lvs, 0.13% N in fruiting stems; *S. benghalensis* 1.2% N in lvs, 0.29% N in fruiting stems. Figures represent mean values $N = 2$, E. Dinerstein, pers. obs.) Rhinoceros do graze the silky flowering plumes of *S. spontaneum* and *S. benghalensis* but only prior to seed set. These tall grasses are disseminated by wind and water (*S. spontaneum*, *S. benghalensis*), wind (*N. porphyracorma*), or on animal fur (*T. arundinacea* and *T. villosa*). During seed set in short grasses, foliage is brown and often withered and less attractive than the shoots and younger leaves of *S. spontaneum*, a staple of rhinoceros at this time. At least for short grasses, the fodder "bait" is passed by for more nutritious, and more abundant, seedless forage.

Fourth, a survey of short, intermediate, and tall grasses in Chitwan revealed that of 77 species identified to date, 97 percent display fruiting heads above the leaves rather than intermingle seeds with foliage (J. Lehmkuhl, pers. comm.). Only *Cynodon dactylon*, *Paspalidium flavidum*, and the sedge, *Kyllingia brevifolia* mix seeds and leaves. Fifth, if rhinoceros do occasionally ingest infructescences of small-seeded grasses such as *C. dactylon*, *Hemarthria compressa*, *P. flavidum*, *Digitaria setigera*, the sedge *K. brevifolia*, and perhaps a few other undetected species, few seeds appear to survive gut transit. The large seeds of rice do survive the molar mill and gut retention, and germinate in dung. This last observation must be qualified by the finding that during November (the month of rice harvest), paddy accounts for 43 percent of the diet in rhinoceros dwelling near the border with agriculture (Gyawali 1986). At such a high level of consumption, numerous rice kernels in dung would be expected.

Sixth, availability of quality germination sites within and at the edge of grasslands open after seasonal inundation and siltation during the mid-to-end of monsoon (July-September) and after the annual fires during the dry season (February-May). These two periods coincide with peaks in seed set by annual and perennial grasses. Colonization of exposed silt by wind, and water dispersal by grasses during the monsoon and post monsoon appears to be quite successful (J. Lehmkuhl, pers. comm.). During the dry season, the common grass *I. cylindrica* flowers and fruits immediately after the fires, and is dispersed by wind. After dispersal the grass send up new shoots at which time it is heavily grazed by rhinoceros and other ungulates, the direct opposite of the FAF strategy.

Grass seeds were absent in the dung of barking deer and bison and rare in the pellets of hog deer, axis deer, and sambar (Tables 1, 2). The combined total of 43,303 pellets from the latter three cervids yielded only 110 grass seeds. Most of these belonged to the two most common riverine forest grasses: *Oplismenus compositus*, and a panicoid species. The abundance of these two grasses in the forest understory and the low seed content in the pellets sampled indicate that Chitwan cervids do not play a large role in the dispersal of the graminoid flora via ingestion of seed stalks.

Ingestion of small-seeded herbaceous plants at seed set by rhinoceros in habitats far from agriculture is limited to about 8 of the 85 (9%) herbs identified to date. Of the 19 seeds from FAF-type herbs, none had germinated by the end of the pre-monsoon showers in May.

The most common FAF interaction between axis deer, sambar, and an annual herb is with the mint, *Rabdosia coetsa*. *R. coetsa* seeds accounted for 318 of the 765 total seeds found in axis deer and sambar pellets. It should be noted that 318 seeds constitute the seed load of about one plant and *Rabdosia* is common in the understory of the riverine forest.

In natural (*i.e.*, pristine) grasslands, Janzen's hypothesis predicts that FAF plants will often be those of ephemeral microsites, unpredictable in location. At least in South Asian flood plain grasslands, annual disturbance is cyclic, predictable, and widespread. Flooding and fire create openings for small-seeded annuals on a far grander scale than animal trails, scrapes, or wallows. Thus, animal-mediated dispersal may not have been selected for, in contrast with water and wind dispersal, when portions of flood plains are blanketed annually in silt, and tall and intermediate grasslands burn regularly. Under this disturbance regime, short herbaceous annuals could grow, flower, and set seed before the perennial grasses overwhelm them even in the tallest grasslands. A common fugitive species, *Cirsium wallachii* (known locally as "Gaidakara" or rhino thorn) is devoured by rhinoceros when young leaves are available in November and December. At seed set, rhinoceros avoid this wind-dispersed thistle, which spreads effectively into burned patches of grassland. Several other wind-dispersed composites set seed after the beginning of the fire season.

Janzen's resurrection of the evolutionary role of large herbivores in plant/animal interactions deserves widespread attention from biologists who study free-ranging large herbivores. But on Nepal's flat, ungulate-rich flood plain, the effects of "conventional" frugivory and seed dispersal by megaherbivores are far more visible in scope and importance than the FAF interaction. For example, each rainy season, rhinoceros and several other ungulates ingest the large fruits of the dominant riverine forest tree, *Trewia nudiflora*, and manure over 1.5 million seeds into the flood plain within a 10.5 km² study area (Dinerstein & Wemmer 1988). Frugivory by rhinoceros and other ungulates thus affects flood plain succession and supports the concept of megafaunal dispersal (Janzen & Martin 1982).

Perhaps in East African grasslands, with sequential removal of the short grass/herb layer by waves of migratory ungulates, the ingestion and dispersal of small seeds by big grazers will be more apparent. Perhaps among relic populations of European bison (*Bison bonasus*) surviving in herb-rich temperate forests, or among forest-dwelling bison (*B. bison*) in boreal forest, important FAF interactions await discovery. In the Chitwan flood plain, the foliage-as-fruit syndrome currently lacks a significant place among other modes of seed dispersal.

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