# Dispersal of Small Seeds by Big Herbivores: Foliage is the Fruit

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# DISPERSAL OF SMALL SEEDS BY BIG HERBIVORES: FOLIAGE IS THE FRUIT

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I hypothesize that, for a number of species of small-seeded herbaceous plants, a normal and selected for mode of seed dispersal was through consumption of the seeds by large herbivores while they were eating the foliage of the parent plants. I also hypothesize that the big herbivores ate the plants, at least in part, because of plant traits selected for through the value to the plants of having their seeds thus dispersed. If the vegetative portions of a herbaceous parent function ecologically as an attractive fruit as well as photosynthetic machinery, numerous complications are introduced into the study of the function of secondary compounds and other aspects of the biology of herbaceous plants. Here I introduce the hypothesis and discuss how large mammals disperse small seeds.

It is commonplace to encounter herbaceous plant seeds in, and seedlings growing from, the dung of livestock (cows, horses, sheep) and the larger Old World herbivorous mammals in their native habitats (e.g., oryx, elephant, rhino, hippopotamus; Adams 1907; Brahmachary et al. 1974; Ridley 1930; Kurosaki and Iizumi 1960). Survival of weed seeds and pasture grass seeds during passage through livestock has been the subject of considerable experimentation and observation (Adams 1907; Wilson and Hennessy 1977; Courtney 1973; Milne 1915; Burton and Andrews 1948; Kurosaki and Iizumi 1960; Wicklow and Zak 1983; Ozer 1979; Sugawara and Iizumi 1960; Watkin and Clements 1978; Atkeson et al. 1934; Sarukhan 1974; Harmon and Keim 1934; Beach 1909; Yamada and Kawaguchi 1972; Yamada et al. 1972; Takabayashi et al. 1979; Piggin 1978; Korsmo 1911; Oswald 1908; Dore and Raymond 1942; Ridley 1930). These studies show unambiguously that: (1) the small seeds of both herbaceous dicots and grasses consumed as part of grazed or fed fodder can survive the trip through the animal gut and germinate directly in the dung or soil where the dung was deposited. Wicklow and Zak (1983) have shown that grass seeds can survive the trip through pronghorn antelope (*Antilocapra*) as well as through cows and germinate from dung as much as 30 mo old, cow parsnip seeds can survive the trip through grizzly bears (Applegate et al. 1979), and wheat seeds can survive passage through emus (Davies 1978).

2. While a few of the species are those with fleshy berries or other classical disperser rewards around the seeds (e.g., *Fragaria, Rubus, Solanum*), almost all

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the others are those with dry or otherwise inconspicuous fruits that are classically associated with no specific dispersal agent except "gravity," wind, surface water movement, and soil erosion; many constitute a major part of the soil seed bank in agricultural soils (e.g., *Agrostis, Poa, Capsella, Plantago, Trifolium, Medicago, Chenopodium, Rumex, Veronica, Carex, Juncus, Ranunculus, Stellaria, Potentilla, Geranium, Hordeum, Festuca, Echinochloa, Echium, Malva, Amaranthus, Lotus, Zoisia, Viola, Polygonum, Avena, Coronilla, Cirsium, Digitaria, Urtica, Hydrocotyle, Atriplex, Phleum, Stipa, Paspalum, Cynodon, Lespedeza,* etc.).

3. Survivorship of seeds varies with animal and plant species, and generally is in the range of 1%–50%.
4. The longer the seeds are in the animal (or buried in composted dung), the higher the seed mortality.
5. Seed dispersal by livestock occurs among pastures and crop fields, as well as within these habitats, and is of sufficient quantity to be of concern when managing plant species and variety composition (it has even been suggested as a means of planting pastures [Bulow-Olsen 1980; Wilson and Hennessy 1977]).

As Ridley (1930, p. 361) put it, speaking of a long list of herbaceous weed seeds germinated from the dung of Swedish cattle,

> If we take this as a typical list of plants eaten and disseminated by an ungulate, we can realize at once how very many small herbaceous plants with small dry fruits and seeds in capsules are so widely spread, and make their appearance so rapidly on bare ground, which otherwise would seem to have no method of dispersal except by a short-distance flight by wind and movement by rainwash. In past time the ungulates were vastly more abundant than at present. Wild cattle occurred, often in great numbers, all over the north temperate regions, and well into the tropics of the Old World. Browsing chiefly on low herbaceous plants, they ate the capsules and dry fruits with them, and passed the seeds uninjured, and are thus responsible largely for the spread of the small Scrophulariacae, Cruciferae, Leguminosae and Rubiaceae. In many parts of the world the wild cattle have been exterminated, and replaced by the domestic cattle, which now play their part as disseminators of herbaceous plants."

D. T. Wicklow, R. Kumar, and J. E. Lloyd (MS) approached my hypothesis even more closely when they observed that "although one typically thinks of grass seeds as being wind dispersed, we must now consider the possibility that blue gramma, and perhaps other short grass prairie plants as well, have adaptations which increase the chances that their seeds will be consumed and dispersed in the feces of cattle or other large herbivores."

## ECOLOGICAL CIRCUMSTANCES OF DISPERSAL OF SMALL SEEDS BY LARGE MAMMALS

Seed dispersal of herbaceous plants by large grazing mammals may be nothing more than the consequence of serendipitous contamination of the animal's forage with seed and subsequent fortuitous survival of the hazardous trip. To the degree that this is the case, there is no cause to puzzle over the possibility or form of a more directed evolutionary relationship between large herbivores and herbaceous plant seed dispersal. Further, the selection could operate only to make seeds more resistant to digestion, with the plant "making the best of a bad deal." Again, to the degree that this is the case, the interesting question is very narrow in scope though of importance in interpreting herbaceous plant and seed morphology, dormancy, hardness, etc. I hypothesize, however, that some of the plant species involved are users of a highly evolved dispersal mechanism that has been obscured by contemporary destruction of the relevant habitats and the large mammals that would have been the dispersers. If such a mechanism exists, the foliage is ecologically a fruit, as well as photosynthetic machinery, and may be expected to have some traits vis-à-vis the seeds and the mammal that are commonly encountered in more conventional fruit-seed-disperser relationships. Before examining such traits in detail, several relevant background facts and suppositions of plant biology need brief mention.

1. Vertebrate consumption of herbaceous plants and the infructescences they bear has been going on for many millions of years. There are even *Berriochloa* grass seeds from the fossilized gut contents of an extinct rhinoceros (*Teloceras major*) from the Miocene of Nebraska (Voorhies and Thomasson 1979). Moving closer to the present, as recently as the Pleistocene there was a large fauna of large grazing/browsing mammals in North America (Kurten and Anderson 1980; Janzen and Martin 1982), some of which were still here in 1492 (e.g., *Bison, Antilocapara, Ovibos, Ovis,* various Cervidae).

2. In preagricultural woody vegetation, the major habitats of the herbaceous plants found today in old fields, pastures, and roadsides were likely to have been highly discontinuous and ephemeral habitats such as tree falls, landslide scars, banks of water-courses, cliffs, talus slopes, etc. Such small or narrow habitats have the trait of being high quality, but ephemeral, for sun-loving herbs. They are used by the colonist, the colonist that has to move among them via wind, water, exploding capsules, or animal fur or guts. In herbaceous vegetation of long permanence (prairies), the highest quality sites for establishment of new individuals (perennials or annuals) were likewise not beneath the parent plant but rather at breaks in the sward (e.g., rodent burrow entrances and tumuli, arroyo edges, rock outcrops, water holes, game trails and resting sites, sites of drought or fire death) (Mack 1981; Mack and Thompson 1982; Formosov 1928; Grinnell 1923; Merriam and Merriam 1965; Greene and Murphy 1932; Platt 1976; Butynski and Mattingly 1979). In both forest and grassland, browsing large mammals would be ideal dispersers of herbaceous plant seeds to such new sites for establishment. Not only did these mammals frequent such sites, but they caused them or accentuated them as well. A forest bison, musk-ox, or mastodont would easily move seeds from tree fall to tree fall, or tree fall to riverbank (and back again), while maintaining both the tree fall and riparian vegetation in a state of arrested succession by browsing, grazing, and trampling.

3. In most contemporary anthropogenic ruderal-rich habitats, there is a large soil seed bank that has accumulated from many generations of herbaceous plants on repeatedly cleared soil. However, prior to this style of land use, in temporarily cleared habitats that quickly returned to the woody vegetation characteristic of long-term site occupation, the herbaceous plant that simply dumped its seeds below itself would often be as dead as the plant that never even made seeds. The chance of a second tree fall occurring where one has just occurred is very small. While some of the seeds of many species of forest and tree-fall herbs can survive dormant in the soil for tens of years, the fitness of such seeds will be substantially

lower through mortality and loss of generations while waiting for a tree fall to occur than will be the fitness of those seeds that move immediately to germination sites. In like manner, the probability that a grassland game trail or arroyo will drift in location so that it exposes the soil at the base of any particular large perennial grass plant is very low. The importance to a seed of moving out of an ephemerally disturbed site will depend on the longevity of seeds in soil and the probability of repeated disturbance (e.g., Keddy and Reznicek 1982); however, whether the plant evolves seed dormancy and specializes on such a life style or becomes quite mobile will also depend on the effectiveness of dispersal agents and their threat to the seed during transport.

4. Dispersal of seeds by birds among forest clearings, by ants within the forest, and by wind among breaks in grassland vegetation is well developed and involves many species of small- to medium-sized plants (e.g., Handel et al. 1981; Werner 1975; Smith 1975; Baird 1980; Thompson 1980, 1981; Thompson and Willson 1978). Since a number of aspects of these modes of dispersal are well known, and since a number of fruit traits are obviously and unambiguously associated with such dispersal, we do not hesitate to associate particular species of plants with these dispersal modes, irrespective of where we find the plants and irrespective of how badly their habitats have been decimated or rearranged by humans. However, dispersal of herbaceous plant seeds among highly particulate resources by large grazing mammals that eat the foliage of the plant and accidentally ingest the seeds does not easily lend itself to such categorization for a number of reasons.

*a*) The possibility that consumption of the above ground vegetative portion of a plant by a large mammal could be highly adaptive is counter to our training and intuition (however, nothing in the present essay should be viewed as explicit or implicit support of the philosophy that herbivory directly benefits the vegetative plant [Owen 1980; Owen and Wiegert 1981, 1982; see Silvertown 1982; Herrera 1982]).

*b*) Lacking any conventional "bait" for a dispersal agent, such seeds appear to be adapted to being dispersed by abiotic processes.

*c*) Detailed study of the animal-plant interaction with large wild mammals or free-ranging domesticates in quasi-natural habitats has been so unfashionable that we have no case studies that would produce information on the subject as spin-off.

*d*) The very traits that would have been important in dispersal by the guts of large herbivorous mammals (e.g., small and hard digestion-resistant seeds, large crops of small seeds per unit vegetative growth on insolated bare soil) are those that should be, quite serendipitously, of great value to the plant in fields, pastures, roadsides, and other repeatedly disturbed anthropogenic sites. Such plant species therefore persist following the removal of both their dispersers and the matrix in which their original microhabitats were imbedded.

*e*) Many of the herbaceous plant species that could have been dispersed by large mammals are recent introductions from Europe, and therefore seem so removed from their evolutionary origins as to be impossible to study as wild organisms. However, Europe has had much the same treatment by large herbivorous mammals as did North America, except that the extinctions of habitats and animals were more gradual; there is no reason to view the proposition that herbaceous plant seeds have evolved to be dispersed by large mammals as being unique to North America.

*f*) Many of the plant species involved have already had their geographic and ecological distributions so grossly altered by spread into anthropogenic habitats that we can no longer trust those somewhat natural habitats that contain them as really being where they evolved the majority of their traits. Ironically, large mammals probably caused part of this recent spread: "In former years the catalog of Maryland weeds did not include the large number of species that it does today . . . , the most common medium for transporting injurious seeds into a community is through the carloads of manure shipped from cities . . ." (Oswald 1908, p. 265). Likewise, when livestock were moved from one fattening or milking pasture to another they must have moved weed seeds in their guts. "The carriage of various plant seeds by grazing cattle into a place whose plant community was devastated as a result of the devouring of numbers of plant species would produce a great influence upon plant succession in a rangeland" (Kurosaki and Iizumi 1960, p. 59). "The flora of areas poor in species may be enriched by allowing cattle to dung there after they have grazed areas rich in species" (Bulow-Olsen 1980, p. 270).

## EXPECTED TRAITS OF SMALL-SEEDED PLANTS DISPERSED BY LARGE MAMMALS

Given that the large mammals were present and that seeds were dispersed among high quality habitats through the consumption of herbaceous fodder by large mammals, what plant traits were being selected for in such a dispersal interaction? (I caution that all plants selected to have small seeds dispersed by the guts of large herbivorous mammals are not expected to have all these traits.)

1. Herbaceous plant vegetation is edible to one or more species of large mammals, at least at the time the plant is bearing some mature seed.

2. The plant changes edibility as its seed crop matures, if it is not always edible. A suggestive example: "A *Datura* species (probably *D. stramonium,* locally known as 'stinkolieboom'), which is a weed in cultivated lands, is left untouched until the seed stage is reached, but then is completely eaten down by springbok and black wildebeest. It was also observed that ostrich fed on these plants at the same time as the antelope. These plants were never touched by domestic stock" (van Zyl 1965, pp. 67–68). It is particularly startling in this context that if dispersal by large herbivores was of great value to a toxic herb (annual or perennial), and a more edible mutant appeared in a habitat where large mammals were relatively scarce, the more edible mutant could be selected for even if substantial grazing of the mutant occurred in the growth season before the plant has set mature seeds.

3. Foliage is of sufficiently high nutrient value to be attractive to a large herbivore. That large herbivores voluntarily consume many herbs is undeniable, but this point is reinforced by the observation that wild weeds may have as much or more nutrient value (in vitro digestibility trials, mineral analyses) as do standard forage plants (e.g., Carlisle et al. 1980).

4. Seed maturation is synchronized such that the vegetative portion bitten off

is contaminated with mostly mature seed (though the expectation of this trait is complicated by the observation that immature reproductive parts, as well as sterile foliage, may be bait for the large herbivore).

5. Fruits are intermingled with foliage or in its immediate vicinity.
6. Mature seeds are retained by vegetative plant parts (R. N. Mack, N. T. Wheelwright, personal communication). D. T. Wicklow, R. Kumar, and J. E. Lloyd (MS) noted that "in early spring and summer, we have commonly observed erect blue grama spikes (2.5–5 cm long), with intact spikelets containing seeds. These fertile spikelets were produced during the previous growing season . . . Consumption of spikelets by cattle or other large herbivores and dissemination of seeds in feces can occur throughout most of the year." "Cattle grazing kikuyu [*Pennisetum clandestinum*] pasture . . . cannot avoid ingesting seed because the mature, short-stalked spikelets are mixed throughout the leafy material. Furthermore, kikuyu sets seed almost all the year. The seed is not readily shed and accumulates in the sward. Therefore, the quantity of seed ingested by cattle may be considerable" (Wilson and Hennessy 1977, p. 247). Such a trait is confounded by the opposing selective forces of seed predation by granivorous birds on retained seed-rich infructescences versus ant and rodent seed predation on fallen seeds.
7. Seeds are sufficiently small, tough, hard, and inconspicuous to escape the molar mill and spitting response of a large mammal (though such traits are also of evident value in escape from some small seed predators).
8. Seed coats have the ability to resist digestion during a transit period of days to months; this trait is also of evident value in, and selecting for, seed dormancy in the soil and litter.
9. Seeds are protected from conventional seed predators by toxins of insufficient severity to kill or debilitate a large mammal when eaten in small doses (e.g., fluroacetate would not be expected as a seed defense in a ruminant-dispersed variably digestible seed); however, such a restrictive trait may be of lesser importance for the large mammal that dilutes a toxin with a large meal of other material, dilutes a toxin with a large body mass, or attacks toxins with proficient rumination abilities.
10. Vegetative phenotypes do well in the particular kinds of disturbed habitats that large mammals frequent (and therefore defecate in).

## THE HYPOTHESIS

There are two ways to test the hypothesis that herbaceous plants with small seeds bear vegetative and seed traits that were selected for because they enhance seed dispersal by large mammals that consume their foliage or they increase the likelihood of foliage, and therefore seed, consumption by large herbivores. First, herbaceous plants can be examined for the relevant traits. However, we already know to some degree that herbaceous plants do have traits that appear to function in this manner. Second, large mammals foraging freely in relevant habitats can be observed to see if they are major dispersers of appropriate species of seeds, and if the vegetative traits are as mentioned earlier. This requires, however, more than simply observing that these animals have viable herb seeds in their dung. It requires study of the relative contribution to later generations of the plants from these seeds as compared to the contribution of the plants from seeds dispersed by other natural modes in natural habitats. Fields, pastures, roadsides, and woodlots are not relevant habitats unless very carefully placed in perspective. There are a number of other processes that render testing this hypothesis quite difficult.

In selection for a mechanism of dispersal, it is usual for a number of the relevant traits to be selected for through their value vis-à-vis many different aspects of the dispersal process. For example, the colors of fruits whose seeds are dispersed by birds and primates may be as much part of the bait (carotenoid vitamins) as they are a location signal. High concentrations of organic acids in ripe fruits may well be functional in protecting against microbes and the dispersal agents simply may be able to tolerate them. Seed density, weight, shape, and volume may be driven as much by consideration of food reserves for the seedling as by avoiding the molar mill or influencing rate of passage through the animal. Seed coat resistance to chemical degradation may be as important in seed survival in the soil after defecation as in seed survival in the intestine before defecation. Green fruit defensive chemistry is determined by both herbivore threats and by the chemical tolerances of the eventual seed dispersal agents. This class of complication certainly applies to the traits of herbaceous plant seeds dispersed by the guts of large mammals and to the relevant vegetative parts.

With any dispersal mechanism, the traits that yield high quality dispersal also increase susceptibility to some seed mortality processes. In the case under examination, seeds concentrated in large mammal dung may be easy prey for birds and mice (e.g., Janzen 1982*a,* 1982*b*; C. Herrera, T. Pratt, personal communication) and may be buried too deeply by dung beetles for the seedlings to survive (Wicklow et al. 1983; D. Janzen, unpubl.). If the seed germinates immediately in the dung, it may be killed by the community of dung-degrading organisms. Despite the survival of some seedlings in the intense peaks in the seed shadow generated by multiple defecations at favored resting sites, there is also likely to be severe mortality through inter- and intraspecific crowding. Seeds used as bait for large mammal dispersers cannot be as well defended chemically against smaller seed predators as can be seeds that are dispersed by agents that do not digest them. Likewise, the plant that uses herbaceous foliage as bait for dispersal agents has more limited options for purely defensive leaf chemistry than does the plant to which all herbivory is detrimental.

At least one complicated aspect of this large mammal dispersal mechanism may be elaborated on profitably even in the absence of information from the field. The vegetative parts of any specific individual plant will constitute only a very tiny fraction of the meal of a large herbivore, and therefore the chemistry of that individual's foliage is unlikely to have much influence on the passage rate and gut milieu of its seeds; this contrasts strongly with the case in which a vertebrate makes a meal of the conventional fruit crop of a large plant. In the latter case, the fruit traits may well have been evolutionarily molded by their value in influencing seed passage rate.

In a Pleistocene reconstruction of a vegetation in which large mammal dispersal of small-seeded herbaceous plants was commonplace, the species of plants involved should range from those entirely dependent on the mammal to move them from disturbed site to disturbed site to those in which many generations of the population persist at a long-term disturbance site (e.g., the margins of a cliff face) and the large mammal is of primary importance only on the rare occasion when a new example of this habitat type appears.

Seed mortalities of 50%–99% inflicted by the dispersal agent seem high for a highly evolved dispersal mechanism, and therefore seem to render this kind of dispersal mechanism improbable as something that would be selected for. However, such levels of seed mortality are in fact commonplace in dispersal. Wind is customarily lethal to most of the seeds it disperses, because it deposits them in the wrong place. The vast majority of seeds defecated by birds in natural habitats do not fall in suitable habitats or microhabitats for seed or seedlng survival. Squirrels and other rodents recover and kill most of the seeds they disperse. Assuming that large grazing mammals would have had dung shadows quite narrowly focused on the microhabitat portions that are rich in herbaceous plants, even with a high percent seed digestion such animals may have placed exceptionally high proportions of the viable seeds ingested in high quality germination sites.

With respect to the vegetative part of the plant, major herbivory may seem a large price to pay for seed dispersal. However, at least three processes weaken the impact. First, if the plant is a herbaceous annual at the end of its growing season, the vegetative structure has nearly outlived its function. Second, if the plant is a herbaceous perennial, it is likely to be losing only a portion of its vegetative structure. Third, plants commonly pay a large energetic price for conventional dispersal by vertebrates in the form of seeds preyed upon and fruit tissues eaten (as well as protected from a variety of herbivores). The cost of feeding a dispersal agent a bundle of stems and leaves in return for seed dispersal may be no greater than feeding it a bag of sugar, fats, proteins, and vitamins.

While it is traditional to view grazing herbivores as seeking the vegetative parts of plants, in fact they also selectively graze infructescences or infructescence-rich portions of herbaceous plant crowns. The animal's goal may not be, however, to eat a bait in the form of a classical fruit, but rather to obtain the nutrients gained from seed digestion. As Burton and Andrews (1948, p. 102) noted, ". . . the seeds of the forage plants considered here (*Lespedeza*) do . . . contribute to the nutrition of the cattle consuming them. . . . The proteins of ground Korean lespedeza seed were equal pound for pound to the proteins of a mixture of equal parts of cottonseed and soybean meals in the ration of lactating cows. Perhaps this helps to explain why cattle fatten well when grazing lespedeza in the late summer and fall." Oak trees and other masting tree species pay in offspring for the dispersal of other offspring by rodents and birds, and herbaceous plants may be paying the same class of cost.

## CONSEQUENCES

The small seed size of herbaceous annuals and perennials in forest and grassland has long been considered to be a direct consequence of the vagaries of their dispersal mode and the high environmental resource level available to the new seedling at the few sites where their seedlings have a chance of becoming adults (Harper et al. 1970). While not meaning to belittle the potential impact of both of these suites of selective pressures, if any of the plants were importantly dispersed by large mammals, there would have been additional selective pressures against increased seed size. If the seed is very large it runs the risk of being spit out (e.g., Janzen 1981*b*). However, much worse, the larger the seed, at least in the case of horses, the longer it stays in the animal (Janzen 1981*a*) and the greater the chance it will be found by seed predators searching in dung (D. Janzen, unpubl.). While long duration in the animal may result in dispersal to truly distant sites or seasons, it also greatly increases the chances of digestion through either killing of a germinating seed or chemically scarifying a seed coat, which in turn leads to death for the same reason. Smaller seeds mean more of them per unit reproductive effort, and the more of them there are, the more tries the parent plant makes; in the case of dispersal by large mammals, the large number of small seeds may be diluted in a large volume of dung rather than dumped in a high concentration around the base of the parent (where even herbs may suffer density-dependent seed predation; Platt 1976; O'Dowd and Hay 1980; Hay and Fuller 1981).

Sometimes passage through an animal increases the germination percentage or rate of the viable seeds that appear in the dung, and sometimes it does not. With respect to the large mammals and small seeds under discussion here, whether there is selection for a seed coat of a type that loses part of its resistance to germination cues in passing through the dispersal agent depends on whether it is best for the seed to germinate shortly after exit from the animal or best to wait until some seasonal or successional cue appears in the habitat. The results of classical germination tests are generally irrelevant to this question. It can be said with some certainty, however, that the more likely the trip is to scarify the seed, the more likely the plant is to be killed by the digestive system (unless the speed of passage through the animal is so fast that there is no risk).

Large mammals may be superior dispersal agents for herbs of disturbed sites for more than just the imroved distance and accuracy that they offer in generating seed shadows. For those species of herbaceous plants that germinate and grow rapidly shortly after dispersal, the animal dung may be a significant kind of site improvement. Some species of legume seeds coated with cattle dung show improved rhizobium nodulation as compared with seeds merely innoculated with rhizobium (Bhatnagar et al. 1981). Not only is the fitness of plants growing in dung-enriched soil greater (especially if dung beetles have buried part of the dung [Macqueen and Beirne 1975; Bornemissza and Williams 1970]), but the freshly fallen dung may kill or suppress a variety of herbaceous plants and thereby partly clear the arena for the seedlings from the dung. Dung beetle burial of seeds may result in placement in superior germination sites (Wicklow et al. 1983). Additionally, at least in pasture sites, there is the inexplicable behavior of livestock actually avoiding grazing on the vegetation immediately adjacent to fallen dung (e.g., Bornemissza 1960; Watkin and Clements 1978).

My discussion and scenarios have been restricted to forest and grassland habitats, but there is no reason why similar kinds of dispersal should not have occurred in other habitats such as arctic tundra, marshlands, and deserts. What better way to get masses of small seeds of aquatic herbs from one shallow seasonal marsh to another than through foraging movements of large mammals? At present, waterfowl have been left with the task, but they probably offer only a pale shadow of what once could have been massive seed flow by large herbivores. Ridley (1930) describes intact subarctic herb and grass seeds in frozen mammoth guts. It is well known that the large browsing and grazing mammals of the margins of the North African deserts customarily moved long distances between oases, stream-containing valley bottoms, and patches of desert annuals brought out by rare and local rains (e.g., Wilson 1978). Surely they moved the small seeds of the herbs they ate as well as the larger seeds of the shrubs and trees that have more classical mammal-dispersed seeds. There is every reason to assume that the same thing happened in North American arid lands when they still had their fauna of ground sloths, horses, glyptodonts, proboscideans, camelids, etc. While the system of desert annuals in North America appears to function quite normally at present, with seeds falling below the parent and dispersal by wind, rodents, and ants, the situation might have been very different when there were herds of thousands of small bovids, cervids, or antilocaprids moving into the flushes of annual herbs following a rain. Such large grazing animals may have been involved in moving herb seeds much longer distances than pollinators ever move gametes, and may have moved herb seeds repeatedly into habitats where the annuals were extinguished periodically through runs of dry years or intense activity of seed predators.

With respect to the dynamics of seed movement, much of what I have said above also applies to dispersal of burs and sticktights by large herbivorous mammals. "As range animals were taken from the Mediterranean region to Mexican and other parts of the world, weed seeds were carried along in the wool or hair and in mud on the hoofs. Wherever sheep walked or died weeds sprang up" (Benson and Walkington 1965, p. 262). To such a scenario, however, needs be added the observation that such animals probably had many more seeds inside than outside. It might appear that a seed firmly imbedded in hair would be carried for much longer than one in the digestive tract, but at least horses may carry viable seeds internally for more than 2 mo before defecating them (Janzen 1981*a*) and an elephant carried small hard objects in its "stomach" for 3 yr (Preston 1983).

What happened to the herbaceous plants between the Pleistocene extinctions and the recent invasions from Europe? Just as postulated for large-seeded perennials whose fruits were more unambiguously eaten by large mammals (Janzen and Martin 1982), I suspect that the herbaceous plants experienced rather drastic changes in population structure and local distributions (some of which again changed as some of the species became weeds in Indian fields and campsites). However, just as Thompson (1981) has noted that failure of birds to disperse the seeds of "bird fruits" may have led to the ecological or evolutionary change to seed dispersal by ants, removal of the large mammals should have resulted in relatively greater importance of seed dispersal by ants, wind, water, mice, and the remaining large mammals. Even seemingly trivial dispersal, such as the grass seeds in raptor-regurgitated pellets (Balgooyen and Moe 1973), would take on added importance. Burs and other sticktight seeds would have been subject to the same forces as the large mammals disappeared, but we tend not to doubt the cause of their morphology in view of its apparent function.

In a slightly different direction, it is clear that at present frugivorous birds and small mammals moving among forest clearings are major dispersers of bait-covered small seeds of perennials such as blackberries (e.g., Jordano 1982; Stiles 1980; Smith 1975; Brunner et al. 1976). However, the same large mammals that moved herb seeds would also have moved these seeds. Rust and Roth (1981) were forced to conclude that in a contemporary Delaware forest, eastern box turtles (*Terrapene carolina*) were a major dispersal agent for the mayapple (*Podophyllum peltatum*); I wonder how many fruits of this herb would have been gotten by turtles in the face of fruit harvest by forest bison and other large herbivores?

If there really has been the evolution of edibility of herbaceous plants to grazing mammals as a mechanism of seed dispersal, it will have a greatly confounding effect on the philosophical underpinnings of a variety of current areas of ecological research. Attempts to understand the relative amounts of various classes of potentially defensive chemicals in plant foliage (Rhoades and Cates 1976; Feeny 1976; Futuyma 1976) are all based on the concept that herbivory is indirectly as well as directly detrimental. The constraint of having to be edible to a large herbivore while being simultaneously inedible to other herbivores will place severe restrictions on the defense options feasible in herbaceous plants, restrictions that should by and large not apply to plants whose fitness is depressed by any kind of herbivory. Could the mustard oils of Cruciferae, for example, be attractants to large mammals as well as defenses against insects? The cattle rumination process effectively detoxifies glucosinolates (Lanzani and Jacini 1973). The strong odor and distinctive flavors of crucifers might have been selected for because they emphasize the olfactory and gustatorial distinctiveness of a herb to a large herbivore seeking particular plants among a mass of vegetation. Trying to understand the distribution of small herbivores (e.g., caterpillars, beetles) among the array of crucifers in a contemporary habitat free of large browsers (Rodman and Chew 1980) may be largely an ecological rather than evolutionary exercise.

In like manner, studies of competition among ruderals in natural disturbance sites (e.g., Hart 1980) are conducted in the absence of both major vertebrate herbivores and seed dispersers, animals with the potential to strongly influence the outcome of competition directly and indirectly through seed dispersal. Contemporary field and theoretical studies of predation on herbaceous plant seeds (e.g., Platt 1975; Thompson 1978; Thompson and Price 1977; Bullock 1976*a*, 1976*b*; Marshall and Jain 1970) may well be examining a highly evolved system from which one of the major selective pressures has been recently removed. Studies of seed dormancy vis-à-vis the seed coat (e.g., Baskin and Baskin 1980, 1981; Edwards 1968; Karssen 1981; Taylorson 1970; Marks and Prince 1982; Quinn 1977; Gutterman 1978, 1980; Quick and Patty 1975; Thurston 1960; Keya and van Eijnatten 1975) may be studying a trait whose original function in nature bore little or no relationship to the tests performed. Contemporary studies of the evolution of water-dispersed seeds (e.g., *Polygonum,* Staniforth and Cavers 1976), and geocarpy and anemochory (e.g., *Trifolium,* Katznelson and Zohary 1970) may be examinations of ecological processes quite distant from those that evolutionarily molded the seed. Even the seemingly unending variation in details of herb seed morphologies (e.g., the "germination flap" in panicoid grasses, Reeder 1977) may be less puzzling if viewed in the context of seed survival in a variety of large mammal guts over evolutionary eons. It is certain that the dispersal and destruction of grass seeds by large steppe grazing mammals should be added to the attempts at understanding the impact of cattle on native North American grasslands (Mack and Thompson 1982). In fact, this hypothesis offers at least one potential cause for why grasses are so edible to large grazers. However, viewing a prairie as an enormous planar chlorophyllous multispecies fruit may be premature, given the primitive state of knowledge of the facts that bear on the process that I propose here.

## SUMMARY

Many species of herbs (including grasses) have some of their seeds dispersed by the large grazing mammals that consume the seeds along with foliage. This is an interaction that has probably been occurring for many millions of years. It should result in a very effective kind of seed dispersal to sites newly open for colonization in a wide variety of habitat types. It should select not only for seeds with the traits that enhance survival percentage or amount during the trip though the animal (small size, large numbers, resistant seed coats), but for edibility of the plant's vegetation either at the time of ripening of seeds or throughout the vegetative life of the plant. Such a view of the vegetative structure of a herb as the functional fruit ("bait" for the dispersal agent) confounds attempts at understanding leaf defensive chemistry and seed coat traits solely in the context of fitness-depressing herbivory or seed dormancy.

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