# Chihuahuan Desert Nopaleras: Defaunated Big Mammal Vegetation

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# CHIHUAHUAN DESERT NOPALERAS: DEFAUNATED BIG MAMMAL VEGETATION

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## INTRODUCTION

The southern portion of the Chihuahuan Desert of subtropical north central Mexico (110, 186, 250, 254, 255, 262, 311) extends from the vicinity of Zacatecas and San Luis Potosi north to the area of Saltillo, Torreon, and Chihuahua (1100–2500 m elevation). It contains a number of vegetation types in which large perennial plants *(Opuntia, Yucca, Acacia,* and *Prosopis)* are a prominent part of the vegetation. Their names are often incorporated in the names for Chihuahuan Desert plant associations (202, 250–256, 270, 272, 311). A spectacular example is the nopalera (Figure 1), the stimulus for this eclectic review.

Nopaleras are dense stands of 1–4-m tall *Opuntia* cacti of several species, dotted with emergent *Yucca, Acacia,* and *Prosopis* (181, 254, 246). The name is local in origin and derives from the Mexican Indian (nahuatl) generic name of 'nopal' for the broad-stemmed species of *Opuntia* cacti. In a nopalera, the cacti are so abundant that the habitat resembles the monotypic forests of introduced *Opuntia* that grew in Australia [see figures in (69)] until the introduction of neotropical insects that decimated them. The area between the large plants in a nopalera contains numerous species and individuals of annuals and smaller perennials (e.g. *Agave, Larrea, Jatropha,* Gramineae, Leguminosae, Compositae, Cactaceae, Asclepiadaceae). The density and proportions of all of these plants vary with contour, soil type, rainfall, drainage, exposure, grazing regime, and recent historical events, but the large plants remain conspicuous.

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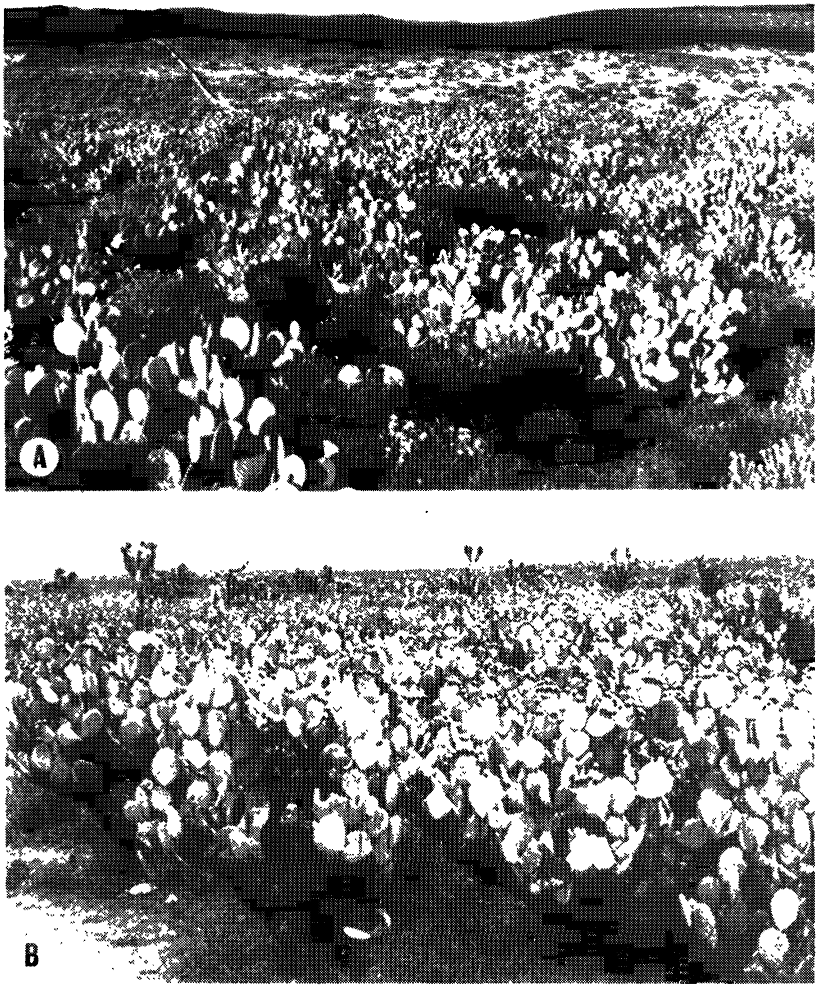

*Figure 1* A. Nopalera at Rancho El Carrizal near Río Grande, Zacatecas, México (2090 m elevation, 18 Oct 1981). The common cactus is *Opuntia leucotricha,* and the stone wall in the background is about 1.3 m tall. B. Nopalera at Rancho El Palmar, near Villa de Arriaga, San Luis Potosí, México (2150 m elevation, 19 Oct 1981). These *Opuntia streptacantha* (2–2.5 m tall) are in full brilliant red fruit and the emergent trees are *Yucca decipiens* in Figure 3.

Introduced livestock allow a striking and instructive habitat dichotomy in nopaleras. In livestock exclosures, the space between the large plants rapidly fills in with smaller and more herbaceous and shrubby plants, such as *Bouteloua* spp., *Sporobolus wrightii, Leptochloa dubia, Dalea* spp., *Brickelia veronicaefolia, Senecio longilosus,* other grasses and composites, etc

(101). The long-term effects of more than about five years livestock exclosure in a nopalera are unknown but are likely to be partial reduction in density of large perennials, because of their reduced seed dispersal and survival, and increased seedling competition with dense stands of small plants (and see 101, 110, 111, 245). Likewise, the large crops of fleshy fruits from woody plants in nopalera livestock exclosures are conspicuous and only slowly disappear from the ground. Surrounded by thorny plants and edible fruits, one cannot avoid visions of the herbivorous megafauna that recently occupied these habitats.

Nopaleras and other arid-land associations with numerous medium-sized to large perennials were the usual vegetation types in the southern portion of the Chihuahuan Desert at the time of Spanish conquest (252–254). The most spectacular nopaleras are (were) in the central parts of the state of Zacatecas and in adjacent parts of the states of Durango, Aguascalientes, Jalisco, Guanajuato, and San Luis Potosi; they experience annual rainfall of 300–600 mm and average annual temperatures of 16–20 C° (246, 254). Today, much of this vegetation type has been removed or severely altered for croplands and improved pasture. However, small areas remain that appear to have been altered only by grazing and browsing by livestock and by removal of wildlife by hunting. However, a contemporary nopalera with moderate numbers of livestock may be in many ways a habitat closer in its suite of selective pressures to the habitat in which its flora and fauna evolved than is a nopalera without livestock and containing only a small sample of the wild animals that the first Indians and Spaniards met.

My goal is to examine some of the vertebrate-related ecological and selective forces that were instrumental in the production of Chihuahuan nopaleras and the other large perennial plants of the Chihuahuan Desert. A nopal-rich vegetation cannot be understood solely through a consideration of contemporary cactus physiology, weather, and interactions with contemporary native animals. In North American arid lands, "the jackrabbit *(Lepus californicus)* is probably one of, if not the most, important native vertebrate grazers. In the Chihuahuan Desert, jackrabbits may annually process roughly 7 percent of the standing nitrogen crop" (100). This view (88, 100), while literally true, obscures the selective forces that generated the vegetation in which jackrabbits live; it considers neither the herbivorous megafauna and its carnivores that were present from 3,000,000 (and more) to 10,000 years ago (147a, 179, 191, 200, 218, 301) nor the remnant medium-sized faunas that have been very recently eliminated.

## OVERVIEW

There are many books and general treatises on the vegetation and vegetation types of the deserts of north central Mexico and the southwestern United

States (2, 10, 16, 17, 33, 35, 110, 193, 219, 250, 254, 271, 272, 296, 311). None give consideration to the role played by large herbivorous vertebrates in shaping individual plants or their arrays; even when contemporary large mammals are discussed, it is in the form of lament for their passing rather than a discussion of what they might have meant to nopaleras and other arid-land vegetation (e.g. 110). Likewise, Mexican ecologists attribute the peculiar vegetation of nopaleras to soil and climate interactions (181, 246, 254, 295). Bravo-Hollis' (31) thorough documentation of the incredible diversity of Mexican Cactaceae does not discuss the central role that the megafauna must have had in the evolution of the distinctive traits of this family. Papers on cactus ecology classically ignore the Pleistocene (and earlier) megafauna (e.g. 160), as do studies of spacing of desert plants (e.g. 311, 312). Likewise, general treatises on desert animal biology (10, 15, 35, 48, 67, 110, 134, 173, 201, 274, 286) do not consider the Pleistocene (and earlier) herbivorous megafauna; the megafauna must have had a major impact on the evolution of the extant flora and therefore on the animals that presently eat that flora. It is as though one were to discuss African arid-land vegetation and fauna while ignoring all large mammals except the human domesticates and one or two rare wild bovids.

In like manner, detailed discussions of the evolution of the biologies of the Pleistocene and pre-Pleistocene megafauna rarely consider that virtually the entire flora of large desert plants must have been continually under selection for defenses against these mammals. The camel has the largest gape of any extant ruminant and eats very thorny vegetation (94). The relationship of such a pair of traits is probably not evolutionarily fortuitous; and if it is, then it still needs consideration to understand ecological fitting of camels to deserts. On the one hand, arid-land mammals are collections of counteradaptations to arid-land plant defenses, and they probably always have been. On the other hand, the existence of a rich fauna of large herbivores nourished by African arid-land plants (some of which are introductions from the New World) within historical times argues strongly against the hypothesis that the Pleistocene megafaunal extinctions were brought about as a final winning evolutionary step by the plants (as suggested in 118). The substantial ability of nopaleras and other arid lands to support free-ranging livestock also argues against this hypothesis.

Central American lowland tropical forests contain many species of woody plants whose fruits were probably eaten and seeds dispersed by the extinct Pleistocene (and pre-Pleistocene) herbivorous megafauna—horses, ground sloths, gomphotheres, glyptodonts, camels, etc (147a, 301). Introduced livestock have to some extent replaced this lost megafauna. Neotropical lowland forest-grassland mixes with moderate livestock density are likely to be more similar to the habitats in which the plants evolved than were the highly defaunated vegetation types encountered by the invading Spaniards. The same applies to Mexican arid-land nopaleras and similar vegetation, though there was a high density of medium-sized bovids and antilocaprids as recently as the 1800s (110). It is not a coincidence that nearly all large perennial plants in nopaleras, and many other large Chihuahuan desert plants, have large fleshy fruits (Figure 2–4) that are readily eaten by livestock which defecate many of the seeds still alive. Likewise it is no coincidence that these same plants bear conspicuous spines (Figure 2) that function as partial deterrents to large browsing animals. Nopalera vegetation also has chemical traits that may function as deterrents to large herbivores. Just as the traits of African acacias are most appropriately viewed in the context of large herbivorous defoliators, seed predators, and seed dispersers (e.g. 309), the large fruits of *Opuntia* and other Mexican arid-land perennials cannot be understood without considering the extinct megafauna.

There has never been a study of nopaleras directed at the details of the interactions of large animals and large plants. There is only one on the response of the small native seed predators to the spectacular fluctuations in *Opuntia* fruit crops (101, 236), even though North American deserticolous small seed predators have been intensively examined (11a, 14, 26, 30, 36–38, 55, 60, 65, 88, 102, 110, 112, 113, 129, 130, 133, 152, 183, 184, 207, 213, 230–235, 238–242, 264, 274).

I do not review the paleobotany of the species of large perennials in nopaleras. However, these plants were present before the time of postulated or conspicuous human impact on the New World—e.g. *Opuntia* seed in a Mexican lacustrine deposit dated at 24,000 BP (188); *Opuntia* and other nopalera plants in fossil packrat nests, greater than 40,000 BP (302). It is not reasonable to suggest that *Opuntia* and other fleshy-fruited desert perennials were evolutionarily invented after the Pleistocene megafaunal extinctions. Cacti are widely believed to be of southern South American origin (A. Gentry, personal communication). If so, their original evolutionary interactions would have first been with the independently evolving South American megafauna, rich in large animals such as ground sloths, glyptodonts, and toxodonts (187, 275), and later with the North American Pleistocene and pre-Pleistocene megafauna as the cacti moved northwards (probably as seeds in the guts of megafauna).

Finally, the activities of the megafauna are of importance in the interpretation of paleobotanical evidence. Large mammals would have maintained herbaceous (and often wind-pollinated) plant arrays in the vicinity of the waterways that create the lacustrine deposits so important to palynology. Seeds would have been deposited directly in sedimentary materials by defecation of dung rich in herb seeds (145). The 215 *Opuntia* seeds at one site in a Mexican lacustrine deposit from 24,000 BP (188) could well have been the result of a single defecation by a Pleistocene horse drinking at the shore.

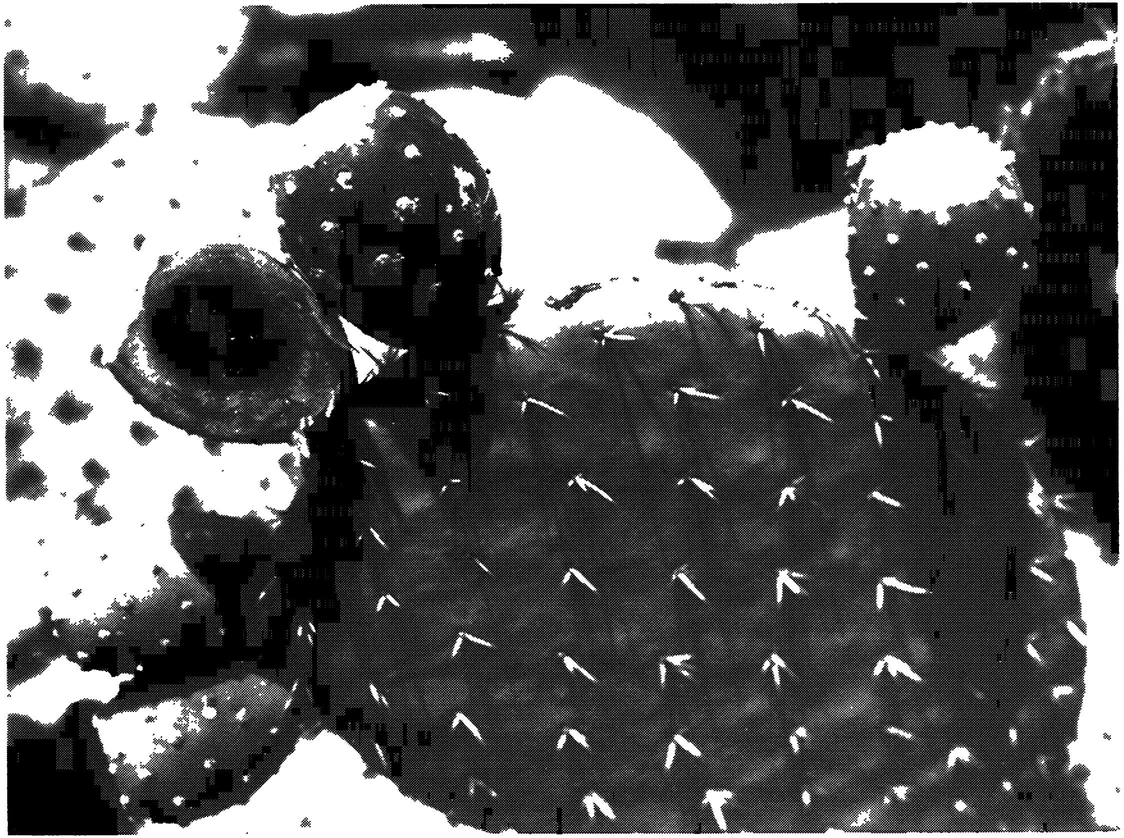

*Figure 2* Pad and fruits of *Opuntia* aff. *streptacantha* (site: Figure 1a). The fruits are brilliant red and 5–6 cm long; the bisected fruit shows the juicy and seed-rich central area. The bumps on the fruit surfaces are tight clusters of glochids (tiny spines).

*Figure 3* A. Pendant mature fruit cluster of *Yucca decipiens*. The lower end is 3 m above the ground. B. *Y. decipiens* 'datiles' or mature, sweet and pulpy date-like fruits in a cluster as in a. Site: Figure 1a.

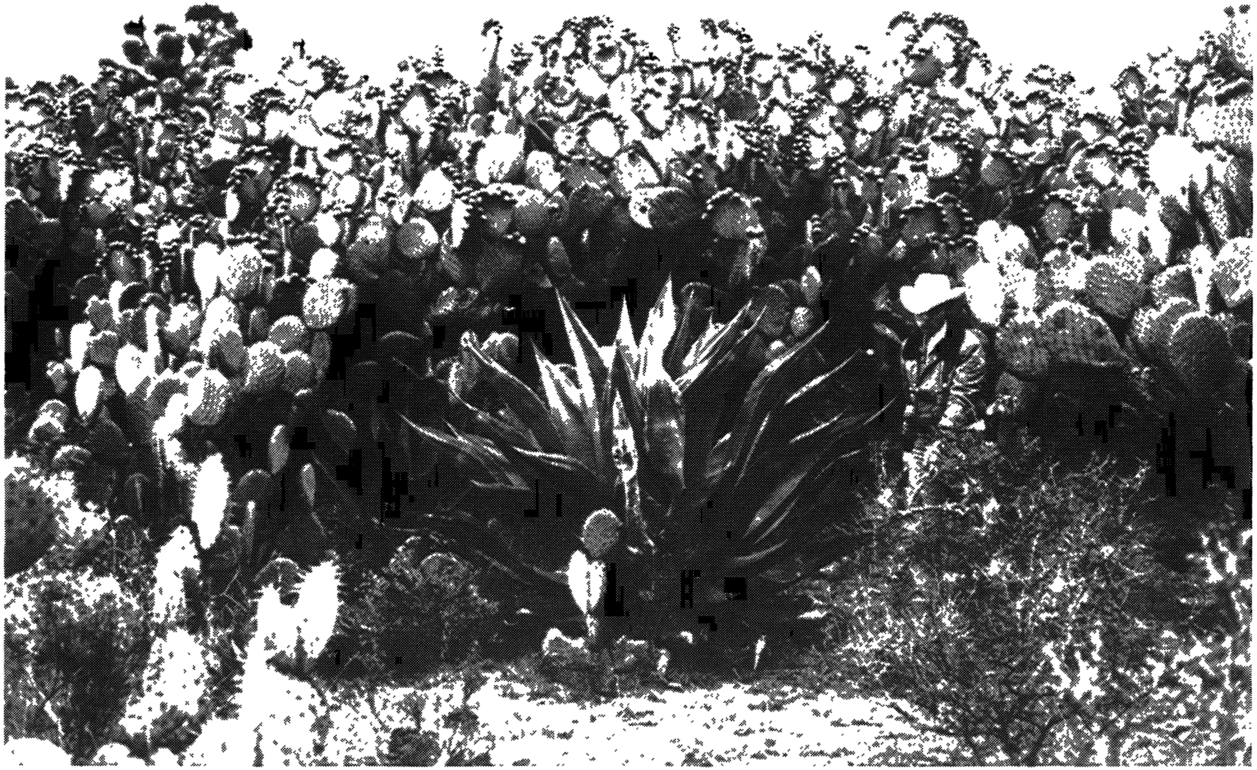

*Figure 4* Nearly mature *Agave salmiana* ssp. *crassispina* growing in a nopalera. The flower spike of a conspecific appears in the lower right corner of Figure 3a. Background plants are *O. streptacantha*. Site: Figure 1a.

## SEED DISPERSAL WITHIN NOPALERAS

### *Post-Pleistocene, Pre-Spaniard*

In post-Pleistocene nopaleras free of domestic animals (cattle, horses, mules, burros, goats, sheep, dogs) there are two nonhuman modes of dispersal of the seeds of the large plants (seed dispersal by humans is discussed later as a special case). In the first mode, the soft, sweet and fleshy (moist) fruits of *Opuntia* cacti and some yuccas (Figures 2, 3) and the dry and somewhat sweet pods of legumes are eaten by carnivores and several species of small to medium-sized browsing/grazing herbivores. These animals swallow the seeds as food contaminants. They kill some to many seeds through grinding and digestion and defecate the remainder alive. (However, these dispersed seeds are still subject to seed predation.) The fraction of the seeds that they kill and the potential fate of the seeds that they disperse are the subjects of an ongoing study (101, 236).

Jackrabbits (*Lepus* spp.) apparently kill many of the *Opuntia* seeds that they eat when consuming fruits, but enough seeds survive that their dung can be a source of *Opuntia* seedlings (11, 57, 291, 292). Ground squirrels *(Citellus)* and deer mice *(Peromyscus)* forage for viable seeds in the dung of jackrabbits (88, 244). Peccaries *(Tayassu tajacu)* readily eat cactus vegetative parts and fruits (80, 170, 172, 182, 279); their dung may be rich in viable *Opuntia* seeds in the right season and year (236). These defecated seeds are harvested by seed predators (236). Peccaries are also professional seed predators (158, 159, 147), and quantitative seed-feeding trials will probably show peccaries to be both predators and dispersers of cactus seeds (236). On the other hand, *Opuntia* seeds are small enough and hard enough to escape some peccary molar mills. Peccaries are also predators on the larger seeds in the fleshy indehiscent fruits of *Prosopis, Acacia, Yucca,* and *Pithecellobium.* White-tailed deer *(Odocoileus virginianus),* mule deer *(Odocoileus hemionus),* and pronghorn antelope *(Antilocapra)* are consumers of *Opuntia* fruits (5, 77, 78, 172, 236, 236a, 267, 281). Desert bighorn sheep *(Ovis)* and bison *(Bison)* probably responded in the same manner to *Opuntia* and other fruits, but no information is available. All of these medium-sized ruminants would probably defecate many intact seeds. But they also chew their food thoroughly enough so that they probably spit out some seeds and kill others by scarifying them sufficiently that they germinate in the gut (138, 139, 148). Tests must be conducted on a species-by-species basis (e.g. 236) to determine an animal's impact. For example, eland, impala, gazelles, and goats feeding on *Acacia* fruits grind up or digest many of the seeds (123, 150, 178, 203, 212, 266). However, they and other medium-sized to large African mammals also defecate many of these seeds intact (8, 41, 64, 70, 88, 121, 122, 124, 150, 168, 199, 212, 243, 280).

Coyotes *(Canis latrans)* and other small midlatitude to tropical canids do not grind up seeds and probablay do not retain them long enough to kill them by digestive processes. These animals are highly frugivorous (22, 28, 29, 39, 40, 98, 99, 103, 120, 135, 172, 185, 227, 282, 285), and a single dung may contain up to 700 apparently viable *Opuntia* seeds (101, 236) as well as some viable *Prosopis* and *Acacia* seeds (Daniel H. Janzen, unpublished). Defecation of viable seeds of *Opuntia* and other fleshy fruits by lizards and tortoises has been studied intensively only on the Galapagos Islands (237) and Tenerife (68), but the mainland desert vegetarian reptiles may be expected to be likewise effective seed dispersers—e.g. desert tortoises eat *Opuntia* fruits (182).

In sum, in Recent pre-Columbian nopaleras and other kinds of somewhat woody Chihuahuan desert vegetation, there were small to medium-sized wild mammals that would have eaten *Opuntia, Acacia,* etc, fruits and dispersed some of their seeds (101, 110, 111, 236). This native disperser array conspicuously lacks really large herbivores that would have obtained their fruits from the plant or quickly from the ground below, and swallowed and defecated large numbers of living seeds. However, these recent mammals did occasionally occur in large numbers (110, 172), and I do not wish to belittle their potential impact as dispersal agents operating in conjunction with the megafaunal dispersal agents. These contemporary animals were also undoubtedly very important in nopalera seed dispersal between the time of the extinction of the Pleistocene megafauna and the dates of their recent decimation (about 10,000 to about 1600–1900 BP). In fact, they were probably an important force in keeping some large desert perennials from becoming extinct when the megafauna was eliminated.

In the second mode of seed dispersal, the fruits of nopalera plants are opened and the seeds harvested as food (by a large array of small to medium-sized rodents such as *Dipodomys, Neotoma, Perognathus, Peromuscus*) or as contaminants on food (by harvester ants such as *Pogonomyrmex* and *Veromessor*). Galapagos finches consume (kill) *Opuntia* seeds regularly (104, 237), and I assume that arid-land continental birds do as well. At least seven species of Mexican birds consume *Opuntia* seeds and fruit (236), though it is not clear to what degree they kill rather than disperse the seeds. During the transport, storage, cleaning, and consumption of seeds, all of these vertebrate seed predators lose or discard some seeds and thereby disperse them to sites that are suitable for seedling survival. However, M. Gonzalez-Espinosa (personal communication) notes that *Pogonomyrmex* ants do not kill *Opuntia* seeds but rather clean them of their pulp and discard them. All the small seed predators also collect dispersed seeds of large plants (50, 88, 236) and may secondarily disperse them. While rodents and ants take other foods besides the seeds of the large perennials in nopaleras, when the seeds of perennials are available they are harvested in large quantities as preferred food (81, 101, 111, 185, 240). At the very least, *Opuntia* seeds appear to be rich in nutrients and undefended chemically (259).

In a pre-Columbian Recent nopalera relatively free of human influence, it is not clear what fraction of the large perennial plant seeds would have been harvested by fruit eaters (jackrabbits to bison) and what fraction by explicit seed predators taking them from the fruits. However, the density of the seed predators is certainly high enough to consume a major portion of the seed crop (and to consume nearly all of the seed in the severely defaunated nopaleras of the 1980s). It is the balance between dispersers and seed predators that would have been altered by a diverse megafauna in the Pleistocene and earlier.

In addition to the two groups of potential seed dispersers/predators mentioned above, a third group of seed predators influences the nopalera and would have been influenced by a Pleistocene megafauna. The large perennial legumes of the nopalera and other arid-land vegetation are preyed on by a coterie of bruchid beetles that oviposit on the full-sized immature fruits and develop in the seeds (e.g. 123, 161, 168, 278). Some of the bruchids also oviposit on the mature fruits in the tree and on the shed fruits on the ground until the time that the fruits are removed by vertebrates. How many seeds escape is directly related to how rapidly the vertebrates remove the fruits from below the parent plant (though some bruchids even oviposit on the seeds after dispersal, so dispersal does not guarantee escape).

Large animals may rapidly and thoroughly remove arid-land legume fruits; "the ostriches' favorite food was acacia pods, and they quickly consumed all the pods both on the ground and on trees. Apparently, the dorcas gazelles could not compete with them for acacia pods . . . When the ostriches retired to their sleeping grounds after sunset the gazelles would then spend hours under the trees in search of any pods overlooked by the birds" (7). In this situation, bruchids will not have access to the seeds in mature legume pods (and see 123). Indeed, in Argentina it is suspected that the severe spread of *Prosopis* as a weed (63, 204) is in part due to livestock eating the fruits before the bruchids can produce their usual 95% or better seed mortality (H. E. Erb, personal communication). Also, cattle that are feeding on *Acacia caven* in Chile have significantly contributed to the spread of this arid-land tree by dispersing seeds and barring a common seed predator bruchid from the seeds (119). Yucca fruits lose a substantial fraction of their seeds to predispersal seed predation by the larvae of the *Tegeticula* moths that pollinate the flowers (154, 228). While such predispersal seed predation may seem irrelevant to the interaction of fleshy-fruited yucca with fruit-eating vertebrates, it is part of the interaction. The moth larvae are often still in the ripe fruits after they have fallen to the ground (D. H. Janzen, personal observation). If the fruits are picked directly from the plant, the moth larvae have even less time to develop.

Their demise through fruit consumption may alter the density of adult moths as well as save some seeds. *Yucca* may therefore be favored by, for example, fruit harvest from the tall inflorescences (Figure 3) by camelids, and there will be selection for faster development of the moth larvae. This will in turn yield lower predispersal seed predation than if the larvae were to develop at leisure in the fruit. In the same context, if fruit eaters remove the *Opuntia* fruits before the rodent and ant seed predators can get at them to remove the seeds, this should have a strong salutory effect on the realized fecundity of *Opuntia*.

The usual pattern in a contemporary nopalera free of domestic animals is that much indehiscent fruit falls to the ground and then is gradually decimated by insects and small vertebrates. How much fruit rots (or mummifies) and how much is eaten or deseeded depends on the balance of the length of the warm summer season (e.g. harvester ant activity is strongly depressed by cold weather), fruit shedding rates (cacti, legumes, and yuccas all hold their ripe fruits for weeks and ripen crops gradually), animal density, relative abundance of plant species, and annual variation in fruit crop size. The aggregate cactus fruit crop at one site may vary tenfold among years, and there may be as much as 3000 kg of *Opuntia* fruit produced per ha (101, 236). In livestock exclosures, it is commonplace for large amounts of fruit to lie for weeks to months before all the seeds have been removed by small animals (M. Gonzalez-Espinosa, personal communication), but in areas where livestock have access, fallen fruits are very difficult to locate because they are eaten immediately after falling or before.

There is no explicit information on the impact of post-Pleistocene, pre-Columbian humans on the *Opuntia* fruit crop. However, without doubt humans intensely harvested the moisture- and nutrient-rich fruit (56, 126, 197, 259), just as they do today for home consumption and market sales (24, 31, 58, 127, 229, 251, 276, 277). In consuming fruits, pre-Columbians surely moved the seeds about and favored the establishment of preferred varieties around encampments and along trails. In addition, at least some humans were cactus seed predators (24, 93); "When available, quantities of fruit of a large cactus known as pitahaya dulce were eaten by the natives. During that harvest period, the Indians all defecated in one chosen location. Several weeks later, they collected their dried feces, ground them up, and winnowed out the undigested seeds. These were toasted, ground and eaten . . ." (172). It is well known that mesquite beans *(Prosopis)* and perhaps other legume fruits and seeds were eaten and preyed upon by humans (24, 63, 81, 93), and *Yucca* 'datiles' (dates) (Figure 3) were eaten as well (194). The devil's claw *(Proboscidea parviflora),* the fruits of which are dispersed by clinging around the lower legs of large ungulates, undoubtedly had its populations severely reduced by the loss of both its Pleistocene dispersers and habitat openers (Martyniaceae are usually large herbs of open and disturbed sites; 287);

however, the Indians not only kept it growing as a source of fibers for basketry but also bred a horticultural variety (20, 32). There is the strong possibility that some of the extensive nopaleras in the San Luis Potosi-Zacatecas region of the southern Chihuahuan desert are hardly more than the unkempt remnants of Indian orchards sustaining a large fauna of vertebrate pests.

In sum, barring humans and livestock, contemporary seed dispersal in Chihuahuan nopaleras and similar vegetation is largely by sloppy small seed predators, a few species of carnivorous/frugivorous gentle seed processors, and a few species of medium-sized browsers/grazers that disperse variable numbers of viable seeds.

### *Post-Spaniard*

The return of equids and several sizes of bovids to New World vegetation was the Spanish gift to paleoecology. Cattle, horses, sheep and goats readily eat the fruits of cacti, yuccas, mesquite and acacia (27, 42, 46, 62, 63, 73, 75, 79, 85, 115, 116, 119, 196, 223, 236, 243, 251). "Let me tell you how the mesquites got here. Got here through horses. There weren't any fences between here and the river, and the horses run back and forth. And they go down in the springtime where all the mesquites are, eat up on those mesquite beans and just carry them all over the country. . . . And those seeds are hard and they go right through the gut of the horse and start again" (217). When these animals are added to a nopalera, they have a major impact by consuming a large fraction of the ripe fruit crop before or after it falls and defecating many seeds in a viable state. The configuration and density of seed shadows generated by livestock are quite different from those generated by rotting fruit, rodent seed caches, carnivore dung, ant trash heaps, etc. Removal of the seeds and fruits from the vicinity of the parent lowers the probability that the seed will be found by pre-dispersal seed predators and increases the chance of seed dispersal. Furthermore, browsing, grazing, and trampling of herbaceous (and woody) vegetation should generally increase the probability of seedling survival by the perennial plants. However, we can never know how different are the seed shadows that are generated by livestock from those that were produced by bison, bighorn sheep, etc.

There has never been a study of nopalera seed shadows as generated by either native or introduced animals, but it is easy to predict some of the traits of these seed shadows.

1. Seed shadows generated by livestock will be concentrated in open areas along trails, near watercourses, and in heavily grazed herbaceous vegetation (e.g., 23, 41, 124). Unusually high concentrations of *Opuntia* seedlings occur on the dry shores of small artificial impoundments for watering livestock in the vicinity of Chihuahuan nopaleras (M. Gonzalez-Espinosa, personal com-

munication). Seedlings will come from seeds buried only to the depth that physical processes (or dung beetles) bury them, and they will experience maximum sunlight and desiccation, maximum exposure to trampling, competition from roots of grazed herbaceous plants, and minimal exposure to perennial plant competition (except where the large mammals defecated while resting in the shade of exceptionally large perennials). Where livestock are excluded, perennial plant seedlings are more likely to originate deeper in the soil (from rodent caches) (50, 240, 241), directly below the parent plant (where they rotted out of a fruit or were dropped by a seed predator dissecting fruits), and in much lower numbers (assuming that most of the seeds are harvested by seed predators). If defecated by a carnivore or a rabbit, etc, the seeds will be many fewer per site of defecation than is the case with livestock. Seedlings in ungrazed and untrampled herbaceous vegetation far from large perennial plants will be competing with a dense stand of herbs.

2. During dry weather, the seeds will be held in blocks of dry dung that will only gradually decompose and release the seeds into the soil; large animal dung may retain its form and contain seeds as long as 30 months in Colorado rangeland (306) and throughout a six-month dry season in Costa Rica (146). Elephant dung can average 8 kg per defecation (52), a substantial block of material in which seeds may be hidden or otherwise protected. Fogden (88) suspected that the seeds hidden in large dry cattle dung were significantly less likely to be found by rodents than were the seeds in jackrabbit pellets. During wet weather, the seeds will be exposed to the severe degradation forces in the dung (fungi, insects, fermentation) and for a short time will be flagged with an odoriferous cue as to their location. Small rodents have been recorded harvesting *Opuntia* and other seeds from jackrabbit dung (88, 244) and large seeds from horse and cattle dung (140, 141, 146). P. F. Quintana found that *Liomys irroratus* (a small heteromyid rodent) preferentially foraged for seeds in piles of dung in the Chihuahuan desert (M. Gonzalez-Espinosa, personal communication). Baboons forage for *Acacia* seeds in Namib Desert gemsbok dung and in very dry sites; ". . . antelope droppings are covered with sand quickly and dry hard so that baboons cannot rapidly process them for their acacia seed contents" (124). Wild pigs follow South African elephants to forage for seeds in their dung (224), and the Chihuahuan peccaries would surely have done the same to large herbivore dung.

3. Livestock will move seeds tens to thousands of meters from the parent tree, but they are still likely to defecate those seeds in habitats containing adult conspecifics. Jackrabbits may move *Opuntia* seeds at least several hundred meters (291), and coyotes may be expected to do so as well. However, these distances are much shorter than should occur when dormant seeds are retained for weeks inside cattle (142, 236), or months inside horses (139). With livestock as seed dispersers, a major portion of a plant's seed crop

may be spread widely through the population of conspecifics and deposited well-mixed with the seeds of other conspecifics and allospecifics. On the other hand, with rodents and ants as seed dispersers, a particular site of seed deposition is likely to contain representatives of a few seed crops, and most of a plant's seed crop is likely to end up in a few caches.

4. Since some seeds will remain inside livestock for weeks to months (139, 142, 236), they may be defecated in a quite different season from the one when they were swallowed. This yields both protection and distance. Such seeds may go on very long trips as animals change their seasonal ranges (Wyoming feral horses move tens of kilometers in such movements). In contrast, caches made by rodents or harvester ants largely occur at the time of fruit drop, though later recaching is possible (50). The transit time of seeds through carnivores and humans is at best a few days (e.g. 236).

5. Among free-ranging livestock, the type and thoroughness of fruit consumption will fluctuate strongly from year to year and site to site and depend on the timing of fruit ripening in relation to seasonal movements of animals, availability of herbaceous forage, proximity to water holes, etc. For example, as water holes progressively dried up during the Namib Desert winter, gemsbok had to move ever further from water to find fallen *Acacia* pods, until they were traveling daily as much as 14 km each way (124). Native small animal impact on seed crops in the nopalera should likewise fluctuate but in a manner influenced by such things as seed set by herbaceous plants, availability of prey or carrion for carnivores (137), and vegetative cover and other physical traits of the habitat that influence density of small predators on seeds (36, 38, 49, 125, 171, 214, 225, 240, 299).

When the 'livestock' referred to in the previous paragraphs are equids and cattle, the difference between livestock and native contemporary large animals is probably greatest. Sheep and goats, on the other hand, converge on deer and peccaries in that they are more brutal in their treatment of seeds in the molar mill and digestive tract. Small seeds may, however, survive the trip through pronghorn antelope and cattle (145, 306). In Zimbabwe "cattle, however, actively help spread certain species, especially Acacias, by eating the pods and passing the seeds through undigested . . . Most species of game, and goats, completely digest the seeds" (226). "The Departmental eland herd has at times been fed quantities of *Acacia* pods, the seeds of which are unusually hard . . . Scrutiny of the dung has never revealed a single intact seed" (178). There is variation on this point among the large wild bovids. As mentioned earlier, gemsbok *(Oryx gazella)* in South West Africa (Namib Desert) eat *Acacia* fruits and pass the seeds intact (124). Likewise, Israeli desert dorcas gazelles are major dispersers of *Acacia* seeds (7). Even within the large domestic livestock there is significant variation, in that I found cattle to neither spit out nor digest nearly as many of the large hard *Enterolobium* *cyclocarpum* seeds as did horses (138, 139, 142). In general, it appears that the larger the animal, the larger the seed that may be swallowed intact; elephants and cassowaries are at the upper end of the scale for extant herbivorous terrestrial vertebrates (e.g., 3, 284). From an evolutionist's viewpoint, studies showing that there are copious amounts of perennial plant seeds in livestock dung (e.g. 46, 75, 145, 236) are incomplete because they do not address the question of what percentage of the ingested seeds survived the trip through the animal.

When a nopalera contains both livestock and native potential seed dispersers/predators, the resulting overall seed shadow will be a complex mix of the two types of ecologically overlapping seed shadows sketched in the above four points. The livestock will get nearly all of the fruits that fall on open ground, while the native mammals will get theirs from those that fall where the livestock are excluded by spiny crowns (e.g. 143), steep slopes, distance from waterholes, etc. That native perennial herbs survive "only on steep, broken ravine banks, which afford considerable protection from grazing animals" (260) is an impression that applies to the accessibility of the fallen fruits of the larger perennials as well. The diffuse and abundant array of small wild foragers will also get fruits and seeds because these animals are thoroughly and finely spread over the habitat. On the other hand, the large mammals forage by day as well as by night (the seed-predator desert rodents are entirely nocturnal); this gives livestock about twice as long to forage for fruit. However, the hotter the weather, the more nocturnal are cattle in their foraging (151, 166, 215, 307); this could move them more directly into competition for fallen fruits during hot summer months.

### *Pleistocene and Earlier*

There was a substantial fauna of large browsing/grazing mammals foraging in and among Chihuahuan desert vegetation (wherever its microgeographic location) and its antecedents for at least 3 million years (179, 187, 200, 247) and for considerably longer if one considers only the mammals that evolved in North America. These animals have been absent for only about 10,000 years (165, 179, 191, 200). An "abundance of fossil remains of large herbivores has frequently been used as indirect evidence for the presence of grasslands in the geologic past" (253). It is tempting to think of desert, or at least what is commonly called desert in north central Mexico, as being too dry for very large mammals. However, African elephants occur (occurred) in habitats receiving as little as 300 mm of annual rainfall (174), and African arid-lands were rich in medium-sized to large herbivores.

In view of the small numbers of wild large herbivores that can be seen at present in Mexican and southwest US deserts, it is tempting to think that arid lands such as the Chihuahuan Desert would not have supported enough large herbivores to consume a significant fraction of nopalera fruit crops. However, in addition to animals that might occasionally move into fruit-rich sites, arid-lands can support a spectacular biomass of free-ranging large mammals. Coe et al (53) estimated a carrying capacity of from 2 to 16 300-kg herbivores per km$^2$ in the most arid portions of East Africa. The western Sahara grassland-acacia pastures can support as many as 250 camels per km$^2$ (94). In Sudan, arid acacia woodland supports 13 300-kg cattle per km$^2$ (1). A healthy nopalera in full fruit with a large crop bears about 7 million fruits per km$^2$ (101, 236). Assuming 100 cattle per km$^2$, this means that each cow would have 70,000 fruits, each weighing an average of 50 g. If each animal consumed 200 fruits per day for 6 months, it would consume roughly 50% of the fruit crop. Whatever the numbers of animals that can be sustained in an arid-land site, seasonal migration may also lead to megafaunal dispersal agents arriving in large numbers at ephemeral food sources (172, 308).

The livestock brought by the Spaniards certainly do not entirely make up for the extinct disperser coteries and vegetative browsers with which Chihuahuan plants or nopaleras evolved. A single large proboscidean, ground sloth, or glyptodont could conceivably swallow as much *Opuntia, Prosopis,* or *Acacia* fruit in one day as would a band of 5–10 horses. Furthermore, their molars are large (relative to the seeds) and would probably have ground the fruit (and seeds within) much less finely than would have those of the relatively smaller herbivores. If elephants can be used as model swallowers, they would have also swallowed large objects entire, since elephants will swallow entire fruits as large as oranges (e.g. 208). A cow dung pile from a single defecation (about 2 kg) can contain several thousand *Opuntia* seeds; thus, each 8-kg proboscidian dung pile (52) could be a very substantial peak in an *Opuntia* seed shadow (an African elephant dung pile from a single defecation may contain thousands of *Acacia* seeds (168)). While a 1000-kg glyptodont was probably sufficiently sedentary to generate only small seed shadows, the antilocaprids with antelope or gazelle life forms might well have moved hundreds of kilometers (with seeds in their guts) in response to arid-land local rainfall, as was the case with Sudanese oryx and antelope (308).

There were four genera of camelids in the western half of North America at the close of the Pleistocene (165, 179), and they probably treated the North American deserts just as the contemporary African camel does its deserts. Camels move long distances among local wet sites, eat fruits and defecate seeds, and range from Kenyan thorn forest to the driest deserts (94). Likewise, there is ample evidence that the large ground sloths inhabited arid-land vegetation (165, 189, 190). "The dung of the Shasta ground sloth *(Nothrotheriops shastensis)* contains fragments of roots, stems, seeds, flowers, and fruits of desert plants, including *Ephedra, Atriplex, Prosopis,* *Sphaeralcea, Agave, Yucca,* and *Opuntia* . . ." (165). A composite Pleistocene dung deposit in a Utah cave is rich in *Opuntia* spines and contains seeds as well (66); the spines were interpreted as being the results of packrat activity but could just as well have come directly from the dung. *Eremotherium* (one of the largest ground sloths) means "desert beast" (275). Yes, these animals were in Mexican arid-lands for perhaps only 3 million years [since the closure of the Central American landbridge, (187)], but there is no reason to argue that in their South American homeland they were ignoring arid-land plants such as cacti.

The heavily armored skin of a glyptodont or ground sloth probably evolved as protection against predators, but the armor would also have allowed these animals to plow through patches of *Opuntia* and get fallen fruits that are today accessible only to rodents and other small animals. In Argentina, *Prosopis* in heavily grazed pastures "now forms dense thickets that are impenetrable to cattle and men. Cattle eat the fruits from the edges of the thickets and deposit the seeds in their feces . . ." (63). I cannot conceive of a Chihuahuan thicket so dense that a proboscidean or glyptodont could not plow through it (but see the later discussion of spines). The tall animals could have reached the ripe fruits on the tallest of nopalera perennials, thereby giving the terrestrial small mammals no chance at the seeds unless they were willing to climb after the fruits or harvest the seeds from the dung. Such large fruit-picking mammals would also have selected for retention of ripe fruits. They also placed a selective premium on insect seed predators that got out of the fruit before it matured (e.g. bruchids in legume fruits, moth larvae in yucca fruits), and they prevented the second generation of bruchids in fallen legume fruits.

Even the large fauna of medium-sized to large carnivores and scavengers that fed on the Pleistocene (and earlier) herbivorous megafauna may well have eaten at least the more juicy fruits of *Opuntia* and generated an aspect of the seed shadow that is today represented only by coyotes and foxes (the frugivory of bears requires no elaboration).

It is puzzling that the ripe large juicy fruits of *Opuntia* (Figure 2) range in color from light yellow to pink through bright red to deep purple; the fruits of numerous other plants whose seeds are dispersed by being eaten by large mammals are much duller in color (though *Prosopis* fruits are a clear and conspicuous yellow-beige when ripe). Since red colors are often associated with fruits whose seeds are dispersed by birds or primates (e.g. 9, 243, 283, 294, 298), *Opuntia* fruits are sometimes vaguely referred to as 'bird fruits.' Apparently this is for want of a better suggestion, since there is neither a folklore of bird consumption of significant amounts of *Opuntia* fruits nor papers on the subject.

It is commonplace for a nopalera to produce millions of kilograms of red juicy ripe fruits for months without noticeable feeding damage to the fruits by birds. Indeed, Ridley's (243) comment was that "fruits destined to have their seeds disseminated by mammals are not brightly or conspicuously colored. Showy fruits are destined for the attraction of birds. . . . Conspicuously-coloured fruits are frequently eaten by mammals, when they come across them, but in all such cases the form and size of the fruit denote that it is for birds that they are destined." Ridley (243) had never encountered the large-fruited *Opuntia* in the wild and probably regarded the Old World reports of large mammals eating introduced *Opuntia* fruits as too artifactual to be relevant. There is no doubt that some species of cacti have fruits whose seeds are dispersed by birds that consume the very small fruits as units (e.g. *Mammillaria*) or that tear open large fruits to get at the moist pulp rich in tiny seeds (e.g. *Acanthocereus, Stenocereus*). However, while a seed-predator bird may on occasion tear open a large *Opuntia* fruit to get at the seeds, there is simply no circumstantial or observational evidence to suggest that the enormous crops of large *Opuntia* fruits with their relatively large seeds were ever consumed by flocks of some extinct (or extant) bird. Where it has been studied in the Chihuahuan desert, maximum "seed removal by birds rarely exceeds 1–5 percent of the crop" (M. Gonzalez-Espinosa, personal communication). Arid-land crows (*Corvus* spp.) do consume *Opuntia* fruits and regurgitate the seeds (236). It is possible that they were at one time more significant when they had large numbers of herbivore carcasses from which to scavenge.

Then why the bright colors of *Opuntia* fruits? The traditional view of mammal color vision is that it is restricted to primates, tree shrews, and ground squirrels. However, a series of color choice tests with wapiti *(Cervus canadensis)* show clearly that they can distinguish orange from a variety of other colors, and cones have been located in the retinas of white-tailed deer and wapiti (265). I view the brightly colored large fruits of *Opuntia* as circumstantial evidence that at least some of the large herbivorous megafauna used color vision in food location. Furthermore, it is even possible that conspicuous fruits were functional in signalling their presence and exact location in an otherwise inhospitable mass of spiny vegetation.

Large mammals feeding on arid-land fruits would have selected for fruit traits—juiciness, size, seediness, color (see above), nutrient kind and amount, resistance to rotting and desiccation, etc. There is no doubt that large mammals would have species-specific responses to a given fruit species. For example, east African giraffes were "never observed to eat the fruits of *Media volkensii,* which are commonly eaten by lesser kudu and eland" (176; see 177 for other examples). Dry but nutrient-rich fruits may well have affected the amount of movement between fruit trees and waterholes, thereby influencing the type of seed shadow generated. African elephants, when surface water is absent, make nearly daily treks of 2–10 km to waterholes (174). Very juicy fruits could well have influenced these distances by supplementing free water supplies. In like manner, the seasonal timing of very juicy fruits—e.g. *Opuntia* fruits appear during the dry time of year (246)—may well have been selected for in relation to other dry foods. *Opuntia* fruits are even more water-rich on wet years (61). Large arid-land mammals clearly have feeding patterns that are influenced by both local and overall water intake (51, 94, 149, 157, 162, 308). The geographic variation in *Prosopis* fruit sweetness (81) may well be the outcome of differential selection imposed by large mammals with different taste responses or with different background fruits against which *Prosopis* pods were gustatorially or nutritionally evaluated. *Opuntia* fruits have the high sugar and water content (167) of melons, and even have the flavors and odors normally associated with melons and cucumbers (86). Melons and cucumbers are Old World fruits whose seeds are presently dispersed by large herbivorous birds and mammals. Even the method of fruit presentation would have been under selection. Bews (23) noted that in African *Acacia arabica* "the long indehiscent pods hang down below the branches well away from the thorns." It is striking that succulent yucca fruits (datiles) (Figure 3) remain on the plant, 3–4 m above the ground, long after they are ripe and sweet; camels take note. It is also unlikely to be an accident that *Opuntia* fruits are borne along the upper rim of the pads (Figure 2–4), a location where they can be easily picked off by a large animal reaching over the spiny parts of the plant.

In a nopalera that is seasonally to permanently rich in large herbivores, there are several reasons why the density of ants and rodents would have been significantly different from the densities encountered in nopaleras lacking large animals. The density of small arid-land seed predators is affected by alteration of habitats by livestock (e.g. 101, 110, 111, 225, 239, 240, 242, 248, 264, 288, 305). There are numerous potential causes.

1. If much of the annual herbaceous vegetation is grazed to low levels (as is commonly the case in modern nopaleras), its seed production will be greatly lowered; seeds of annual plants are major foods of small arid-land seed predators. Whether the accompanying depression of species richness by heavy grazing (300) will be detrimental to seed predators as well depends on which species of plants are eliminated. Lowering the density of herbs may also influence the germination regime of the site (132, 133) and hence food stores for small rodents and ants. On the other hand, lowered herb density may increase survival of slow-growing (13) *Opuntia* seedlings, plants that are slow to rise above competing herbs.

2. The undigested seeds defecated by large mammals are a diffuse resource to harvest, compared with the concentration at the parent plant. In contemporary livestock-free nopaleras (within exclosures), small rodents and ants collect large amounts of *Opuntia* seeds merely by foraging in the abundant

fruits directly under large adult plants. However, rodents can also harvest some seeds from animal dung (101, 146, 236).

3. Not only do large mammals digest some seeds; by consuming the fruit pulp they deprive the smaller animals of this dietary item.

4. If the large animals are harvesting most of the fruit crops, the remaining crops (e.g. those on plants on cliff faces or in the center of impenetrable clumps) can only be reached by means of longer and therefore potentially more perilous treks by the small animals.

5. If the large mammals have severely cropped the herbaceous vegetation, there is less cover in which the small animals may hide from predators [though some like jackrabbits, coyotes and certain rodents (230–234) may prefer to forage in more exposed sites].

6. Arid-land large herbivores are highly selective in foliage choice (8, 45, 74, 82, 83, 206, 282, 289), thereby contributing to differential reproductive output by plant species. When the large mammals are removed, the consequences for small seed predators should be severe but often are unpredictable and dependent on the edibility of the seeds of the species that are newly released from herbivory.

7. By eating the herbaceous vegetation, the herbivores lower the chance of a severe fire. *Opuntia* cacti are especially susceptible to fire damage (18, 42). Grazing therefore minimizes the possibility of major destruction of seed (food) for the small seed predators.

8. When the herbaceous vegetation is grazed down, the seedlings and adults of the perennials are competitively favored, leading to more perennial plant seeds per unit area. Contemporary vegetation rich in other plants that often grow over low *Opuntia* [e.g. Wisconsin sand prairies (54) may turn into diminutive nopaleras if subjected to heavy grazing. *Opuntia compressa* is conspicuous and common in heavily grazed Tennessee cedar glades (13)]; in South Dakota pastures, the more heavily grazed the site, the greater the frequency of small *Opuntia* plants (19), just as thistles and other inedible pasture weeds take over 'overgrazed' pastures—e.g. (221, 260). Additionally, grazing selects for shorter strains of grasses (e.g. 156) which will be less of a threat when temporarily released from grazing.

9. With a fauna of large herbivores providing carcasses as starvation food for small carnivores and regular food for large carnivores, the biomass of carnivores ready to consume small mammals and nopalera fruits would have been significantly greater (see Ref. 137).

Whether the Pleistocene megafauna would have had a different impact on the above system than do modern livestock depends on the relative densities of the two groups of animals and on the kinds and diversity of life forms of fruit consumers among the two groups. Contemporary livestock faunas possess no members with the capacity for fruit consumption of an individual proboscidean, ground sloth, or glyptodont. Additionally, these large animals were probably much less seed predators than are the smaller large herbivores. On the other hand, an area with a high density of fenced-in livestock might do a faster and more thorough job of removing the ripening fruits than would an array of Pleistocene megafauna with freedom to range in response to the best food, water, etc. Whatever the details, it is clear that a livestock-enriched nopalera should have a fruit removal rate and aggregate multispecific seed shadow that is much closer to that of the Pleistocene than to that of a modern nopalera within a livestock exclosure.

## SPININESS IN NOPALERAS

In the absence of contemporary wild medium-sized to large herbivores, it has been fashionable to try to understand the spininess of arid-land plants largely in the context of their interactions with the physical environment (e.g. 43, 299). Spines on desert plants "were probably developed in the first place as a response to the dry atmosphere. . . . Furthermore, thorniness is most highly developed in the most arid deserts, exactly where large grazing animals are rarest" (43). Such a comment needs to be paired with the alternative view that the scarcer the perennial vegetation, the better protected it must be if it is to survive. The puzzle of why there are so many life forms among desert plants has likewise been answered with the hypothesis that it is due to the release of phylogenetically different lineages from inter-crown competition for light (271). The defensive chemistry of arid-land plants is frequently interpreted solely in the context of herbivorous insects. Just as it would be inappropriate to pursue such mammal-free explanations in those parts of arid Africa where the large mammals have been extinguished in just the past few years [see (89) for an example of giraffe's shaping their food plants by browsing them], it is also inappropriate to restrict explanations of thorniness and life form to weather, competition, and herbivorous insects in the New World. It is not hard to imagine how browsing megafauna could select for arborescent lilies (Figure 3) or botanical hedgehogs (Figure 4). However, it has recently become popular to consider mesic perennial plant defensive chemistry in the context of selection by megafauna. The hypothesis is being developed that defensive chemistry has evolutionarily developed to a level whereby plant inedibility has led to megafaunal extinctions (118). As mentioned earlier, I find this highly improbable in view of the obvious high capacity of subtropical and extra tropical New World vegetation to support livestock and other introduced Old World megafauna.

It is tempting to use the information that various large African animals can browse spiny plants [e.g. camels (94), giraffes (258), goats (212)] to conclude that spininess is not a defense. There are several natural history observations that suggest that such a conclusion would be in error.

1. When they are browsing spiny African plants, African large herbivores choose the least spiny branches first and stop browsing as they reach the spinier portions of the crown (212, and D. H. Janzen, unpublished observations). "*Salvadora persica* sometimes forms dense clumps which the giraffe are reluctant to enter. When they feed on this species, it is only at the edge of the clumps" (176). Tame East African buffaloes "experienced difficulty in holding spiny shoots with their tongue or lips . . . The leaves, but not the spiny stems of *Asparagus africanus* were eaten" (84).

2. Thorns slow down the browser (72). "It was clear that the giraffe could gather a mouthful of food much quicker from trees without thorns e.g. *Peltophorum africanum* (1.41 sec/bite) than from those with thorns e.g. *Ziziphus mucronata* (3.17 sec/bite). . . . The giraffe has a very flexible tongue which can be folded around a twig and all the leaves, petioles and bark stripped off with a single jerk of its head . . . (mean time 2 sec/bite). . . . Secondly, the animal may select the leaves from among the thorns. . . . This takes much longer. For example, with *Acacia erubescens* the mean time per bite was approximately 6 seconds" (258).

3. Numerous African arid-land plants have a facultative response of massive thorn production on the new branches produced following browsing (D. H. Janzen, unpublished observation); it is striking that at least the native *Acacia farnesiana* and *A. cochliacantha* in arid-land Mexico and Central America still display this behavior. African thorny plants are also intrinsically thornier below 3–5 m from the ground; "this suggests that the thorns have evolved mainly as a reaction to giraffe and perhaps some of the equally large extinct browsers" (90).

4. When Texas rangeland cattle, sheep, and goats browse *Opuntia* cacti from which the spines have not been singed, they sustain chronic mouth injuries (and see 42) and subsequent screwworm fly infestations. While starving livestock will browse cacti that have intact thorns, they preferentially feed on those from which the spines have been removed (62).

5. Large herbivores seem quite tough with respect to spines, but I have found Costa Rican range horses to be reluctant to harvest fruit from below spiny leaves (143); Baird's tapir *(Tapirus bairdii)* is strongly deterred by even slightly spiny foliage (144); and spines on acacia foliage being browsed by a brocket deer *(Mazama americana)* resulted in a slowing of browse rate and incomplete removal of leaves (136, and see 216). When elephants knock over large *Acacia tortilis* trees, the area where the thorny crown lies is a safe place for herbs, grasses, and tree seedlings to establish (59).

Beneath the spines of an *Opuntia* cactus lies an herbivore food that is not chemically well-protected against some large herbivores. Cactus pads (cladophylls) with their spines burned off are readily eaten by livestock (42, 115); if a diet of pure cactus pads is supplemented with "one or two pounds of cottonseed cake and old grass, or browsing plants are available for cattle, they will maintain strength and fair condition throughout the winter or an ordinary drought" (62). Gastrointestinal and ruminal microbes quickly adapt to high levels of oxalates in food (4) (oxalates are primary chemical defenses of *Opuntia* pads, but see last paragraph in this section). *Opuntia* are being introduced to North Africa as fodder plants (71). I have watched camels eagerly browse spiny *Opuntia* hedges in southern Morocco, and the photograph of a camel with a thorny acacia branch inside its mouth (94) supplements the message. Cattle and horses have to be fenced out of commercial plants of spineless varieties of *Opuntia* in Chile, Africa, and Mexico (D. H. Janzen, personal observation). It seems to be a safe conclusion that if the cacti of arid North America did not have spines, yet had their current level of chemical defenses, introduced livestock would have eliminated them just as thoroughly as they did many species of island plants that had never been exposed to browsing/grazing mammals.

The same applies to native animals. "Once the armature of an *Echinocactus* is penetrated, the rabbits eat it with avidity, often consuming it nearly to the ground surface" (299). Pronghorn antelope fed heavily on the pads of *Opuntia polycantha* when the spines were burned off by wild fires (281). The following animals have been reported as eating unaltered mainland *Opuntia* cactus pads: deer (5, 77–78, 236a, 279); jackrabbits (299); peccaries (170, 279); Shasta ground sloth (189, 190); cattle, goats, and sheep (62, 115, 116); and equids (D. H. Janzen, personal observation). Not only do packrats *(Neotoma)* eat *Opuntia* pads, they also make houses out of them (26), thereby underscoring the function of the spines. Foliage of yuccas may be browsed by desert deer or mountain sheep (201). In all these cases, the appropriate philosophy is, "It seems likely that thorns and spines while not preventing feeding, at least lower eating rates, and thus change the effective value of plants possessing these structures" (216).

Nearly all of the large perennial plants in nopaleras are spiny. Cacti (Figure 2) need no comment. However, some of the species noted for extreme physiological effects on mammals—e.g., peyote—are tiny and spineless. Likewise, "spineless cacti are rarely, if ever, found on the open ranges, but are restricted to well-protected sites on steep canyon walls where cattle cannot, and jack rabbits do not, ordinarily go . . ." (299). Agaves are just giant chlorophyllous hedgehogs (Figure 4); their long and stiff needle-tipped leaves protect both the leaves and succulent stem. Yuccas do not just only have needle-tipped leaves; the species that grow tall enough to be well above browsing range of all but the tallest herbivores also have much more flexible and less dangerous leaves (Figure 3) than do the smaller agave-like species. While the spines on mesquite and acacias do not seem spectacular, severe browsing of these plants is likely to bring out much more spininess.

While not the focus of this essay, the defenses of aromatic composite shrubs, resin-rich creosote bushes (*Larrea* tridentata)., cardiac glycoside-rich asclepiad shrubs, etc., that are found in overgrazed nopaleras clearly cannot be understood without at least considering contemporary and extinct large browsing mammals. The origin of jojoba *(Simmondsia sinensis)* "remains obscured in the past, perhaps . . . still maintaining or even expanding a wide distribution in the Sonoran Desert . . . The present day distribution may reflect the browsing pressure of herbivorous Pleistocene mammals" (34).

The classical and quite reasonable explanation for the evolution of the cactus life form is the ever-increasing ratio of volume to surface in a very dry habitat. However, a ratio of this sort can also be attained by succulent plants with considerably more branchy and even leafy life forms (e.g. Euphorbiaceae on the Canary Islands). A condensed crown also impedes browsing by a large mammal. Some species of African mammals are capable of chewing up quite spiny branches if those branches are small enough to place within the molar mill or are easily torn off the plant. The difference between browsed and unbrowsed African *Acacia* is essentially that of a flimsy diffuse crown and a severely pruned dense hedge (90, 164, 180) [see also (180) for an example of baboon impact on *Euphorbia*]. Heavy browsing selects for the presence of this life form from the beginning—a preformed hedge. The cactus may be viewed as the ultimate in preformed hedges. A number of small African antelopes make their living by carefully plucking very small leaves out from among the long thorns on *Acacia* and other shrubs. A plant that has the leaf surface condensed into a solid block (the cactus pad) covered with a dense grill of thorns may be relatively immune to such an animal. In like manner, a saguaro-like tree such as *Idria columnaris* (in Baja California) may be viewed as an independent evolution of the columnar cactus involving production of thorny and leafy branchlets during the season when herbaceous annuals are distracting the large herbivores.

The surface of a ripe *Opuntia* fruit bears numerous clumps of short and lightly barbed fine spines, or glochids (91) (Figure 2). While annoying to the human fruit harvester, these spines clearly do not deter large herbivores from eating the fruit. However, some animals may pay a price for this food. For example "in the winter months stock will graze on *Opuntia* that have not been singed [spines burned off] and will continue to eat the young buds, blooms and apples on into the summer. Stock that eat prickly pear [fruits] in this manner are affected by ulcers and sores in their mouths . . ." (62). Large cacti display a range of spininess: dense heavy spines to deter all classes of browsers on foliage, closely spaced clumps of small spines on small green fruits to make the green fruit less attractive to all classes of browsers, and widely spaced clumps of easily dislodged small spines on expanded sweet ripe fruits to deter the seed predators and wrong 'dispersal' agents. In other words, glochids are just another example of the many traits of fruits that may depress herbivory on green fruits and may reduce removal of ripe fruits by the wrong animal. However, until glochid-free *Opuntia* fruits are offered along with normal fruits in choice tests, we will not know which animals are deterred by them.

Spines are not the only vegetative traits of arid-land plants that are likely to have evolved in response to megafaunal browsing. Attempts at understanding cacti structure in the absence of consideration of their history with the same large animals that selected for the spines (e.g. 210) are doomed from the start. While the morphology of arid-land plants is under strong selection with respect to the physical environment (12, 209, 263, 268), plant shapes and heights, branching patterns and heights, bark thickness, petiole strength and length, branch brittleness, and firmness of rooting are all traits that megafauna would have selectively influenced. The cactus arborescent life forms that have been ecologically and evolutionarily generated by tortoises on the Galapagos Islands are a straightforward example. The tough and interwoven internal branch skeleton of *Opuntia* and other cacti (95, 96) may be designed to make the plant hard to tear apart. Might the tall inflorescences of agaves have been selected for by the same animals that selected for their needle-tipped leaves? Storage tuber depth and toughness would have been influenced by the megafauna; East African oryx and elephants dig up storage organs well below the surface (249). Cactus may even have glochids and spines on their roots (25). Even flowering times (155) may have been influenced as much by timing of browsing intensity and disperser selection for fruit ripening times as by rainfall.

Since cacti are well protected by spines yet can be readily consumed by many vertebrates if despined, it is tempting to view them as poorly defended chemically. However, they are also little fed on by herbivorous insects. The paucity of their insect herbivore load becomes even more impressive if one considers that they are evergreen and succulent. The frequent appearance of alkaloids in cactus phytochemical screening (11, 198, 220), the high oxalate content of *Opuntia* pads, the high mucilage content of cactus pads (153, 192, 205, 257, 293), the hypoglycemic effects of cactus pad diets on humans and rabbits (131), and a multitude of other miscellaneous secondary compounds in cacti (31) suggest a diverse set of chemical defenses against insects, defenses that are ineffective against at least some vertebrate herbivores. It makes one wonder if vertebrate herbivores were not a sort of mixed blessing, to be held at bay but not totally repulsed (in view of their value as seed dispersers and depressors of the herbaceous plants). Perhaps the *Opuntia* 'foliage' (pads) that are consumed should be viewed as part of the bait for large seed dispersers, along with the more traditional bait, the fruit pulp (145).

## DISCUSSION

What happened in nopaleras or their antecedents when the megafauna of the southwestern United States and Mexico was extinguished about 10,000 years ago? Almost all of the large perennials found in this habitat today display fruit and vegetative traits that were probably in part the evolutionary consequences of seed dispersal and browsing by large mammals during previous millenia. Such plants, freed from herbivory by large mammals and deprived of a major portion of their seed disperser coteries, should have ecologically fit together in quite a new manner. They should have become scarcer, flourished vegetatively, and withered sexually. In other words, once an individual plant was established, it had primarily the physical environment and competition from its neighbors to deal with vegetatively and was less frequently successful in the sexual production of new adults because (*a*) most of the seeds were killed in the dispersal process and (*b*) most of the habitat was already occupied by growing plants. This ecological process should be especially hard to study in habitats rich in slow-growing long-lived perennials such as those of the Chihuahuan desert. Just as perennial vegetation may not fully adjust to climate changes for hundreds to thousands of years (e.g. 297), changes in the disperser and browser regime may likewise take a very long time to produce what might be termed an ecological equilibrium. The situation may be even more unstable if during the 'adjustment period' the disperser and browser regime is continually changing due to increasing human populations and then (at the end) the variable introduction of surrogate Pleistocene megafauna.

In the extreme, megafaunal elimination may be expected to lead to monospecific or low species-richness stands that vary in dominant species among different habitats. The reverse case is provided by the consequences of introducing livestock to the grasslands of northern Mexico and the southwestern United States, whereupon mesquite, cacti, and other large perennials invaded many habitat types (thereby raising the species-richness of large perennials in them) from a few kinds of more local habitats (44, 63, 85, 92, 97, 310). In Chile, cattle have been directly implicated as the seed dispersers in the great expansion of *Acacia caven* over grasslands (119, and J. J. Armesto, personal communication) and have even been suggested as the tree's mode of transport from Argentina to Chile (P. H. Raven, personal communication). A mesquite forest standing where a grassland once grew may be the Texas analogue to a nopalera. "Old ranchers have told the writer that in the early days it was a common practice to carry a bag of mesquite pods to feed horses. . . . this could be expected to contribute to the dissemination along trail and wagon roads" (92) and to increase the small number of habitats occupied by mesquite. On the other hand, introduced livestock can selectively eliminate perennial plants, as has occurred frequently in Australia (e.g. 169), and can severely depress herb species richness (300).

Such a view of the nopalera suggests that with livestock and humans excluded, Chihuahuan nopaleras would lose their dense stands of *Opuntia* except in those peculiar habitats where they are the competitive dominants. In other words, with no large mammals one might find the yuccas, the large cacti, the agaves and the woody legumes each occupying a particular somewhat different habitat. Add back in the large mammals and all four might occupy the same habitat, albeit in proportions that change from habitat to habitat (as they do today where there are livestock). A nopalera with a moderate density of varied livestock might much more closely approximate the habitat in which the constituent plants evolved than would the area inside an exclosure. This simplified view can be profitably embellished by consideration of the specific natural histories of the animals and plants of the nopalera.

Even the largest adult plants of the nopalera habitat (as well as the smaller ones) appear to have a long evolutionary history of interaction with large mammals. This habitat is therefore quite different from the lowland neotropical forests on which the hypothesis was built that certain fruiting and vegetative traits were Pleistocene (and earlier) anachronisms (147a). In a neotropical forest, only a certain subset of the adults of the species of large plants is likely to have been strongly involved with large herbivores. When the large herbivores are removed, there is an extensive flora of large plants from which ecological processes will generate new associations of plants. If the herbivores were important dispersal agents, the animals' absence is likely to result in local extinction or severe population depression of the species of plants that were dependent on them.

By contrast, in a nopalera following megafaunal extinction, there may be strong shifts in relative density of species, but whatever woody perennial species finally come to occupy a site most heavily, the vegetation as a whole will be highly anachronistic. There is no set of wind-dispersed cacti standing in the wings to replace the vertebrate-dispersed cacti (though one could appear in evolutionary time). However, among the yuccas there are both wind-dispersed seeds and indehiscent fleshy fruits. "Yuccas with fleshy indehiscent fruit occur intermittently throughout the greater part of the southwest, only ceding to those with capsular fruit in regions of extreme aridity . . ." (194). Not only might one expect this result because large herbivores become scarcer with increasing aridity, but also because the relative proportions of species with either of these two fruit types should be drastically altered by Pleistocene and then Recent removal of the large herbivores. The same applies to the mammal- and wind-dispersed species of *Acacia*.

The loss of the New World megafauna makes life particularly difficult for those who would try to understand the selective pressures that generated desert plant traits. While there is no doubt that spininess and certain fruit types bear witness to natural selection by extinct megafauna, much more detailed traits may also have been influenced. For example, *Opuntia* seeds have tannins in their seed coats, and this is believed to increase seed hardness (87); if either the tannin or the seed hardness is interpreted solely in the context of extant desert animals, the explanation is guaranteed to come up short.

The removal of the herbivorous megafauna should have had quite different evolutionary consequences for the annuals and the perennials in the nopalera. While perennial plants freed from a major challenge may persist for a very long time (as well as evolve very slowly even when under very directional selection), the annual plant generation time should be changed by removal of the grazers. Not only do annuals have intrinsically faster evolutionary response times than do perennials, but freedom from grazing should greatly increase the size of the seed crop per established plant and produce evolutionary changes that are associated with this demographic shift. The possibilities for complex second- and third-order interactions abound. For example, M. Gonzalez-Espinosa (personal communication) found that the *Pogonomyrmex* ants in Chihuahuan nopalera cattle exclosures reach very high density when feeding on fallen *Opuntia* fruit crops, and then the high densities of ants commit severe seed predation on the annual plants in the autumn after the *Opuntia* fruits are gone.

The plant-megafaunal interactions within the nopalera cannot be viewed in isolation from other habitats. For example, it is well-appreciated that during the Pleistocene glaciations a much more forest-like vegetation covered what is presently desert and semidesert in northern Mexico and the southwestern United States (175, 222, 297, 298, 302–304). However, the herbivorous megafauna that occupied this vegetation (or at least its edges) probably contained in great part the same species as influenced nopaleras. It is easy to visualize a herd of gomphotheres ranging into nopaleras to eat *Opuntia* fruits in the summer, moving into the oak forest to eat acorns in the fall, and then back into the nopalera to eat *Opuntia* pads in the winter. If movements such as these occurred, then nopalera ecological construction and constituent evolution becomes even more complex, since the fate and activities of the participant animals depended on what was happening not only in the nopalera but in other habitats as well.

When megafauna are reintroduced to a nopalera, the edible herbaceous plant populations are decimated but not exterminated. Where do they persist? Numerous individuals survive among the clumps of very spiny or foul-tasting perennial plants (59, 195, 290). It is the offspring of these plants, attempting to grow to adult size on the soil between the perennials, that provide livestock with much of their food. In a grazed nopalera, a significant part of the growing population of annual herbaceous plants is nonreproductive and maintained by seed and pollen flow from a much smaller number of protected plants. Some species of herbs may also escape in time, by appearing in the vegetative phase only when there are very many other individuals; such vegetative predator satiation at the level of the population and the habitat should select strongly for synchronization of response to germination cues and termination of growth (conversion of resources to seeds). The effects of such a process will be virtually impossible to distinguish from synchronization brought on solely as a response to desert rainfall. Some herbs will also escape by growing in steep topography (260). Finally, some will escape by growing in portions of the desert that are so far from resident populations of large herbivores that the animals do not get to them even during annual migrations (but see 308). Chihuahuan nopaleras, as they presently appear, are probably too mesic for the latter process to work well, except when an exceptionally wet year follows a run of exceptionally dry years. In short, the megafauna selects for traits in annuals that will persist long after megafaunal extinctions. These traits may meet other challenges as well and are therefore very difficult to identify as having originated through selection by large herbivores (if indeed they did).

The interaction of the large herbivores with the herbaceous plants in a nopalera or other desert vegetation type is severely complicated by the fact that plant consumption may lead to an important kind of seed dispersal that was selected for rather than that appeared fortuitously. Many small herb seeds survive the trip through cattle and other livestock digestive systems (145). Some of the herbaceous plants of the nopaleras may well have depended on large mammals both for seed dispersal to certain kinds of high-quality germination sites (edges of game trails, nitrogen-rich soils below legume trees, heavily insolated sites, watercourse edges, etc) and for seed removal from the site of easy harvest by small predators that concentrate on harvesting seeds from maturing fruits near ground level (e.g. 213).

Arid habitats should be dramatically influenced by the removal of the megafauna for another reason than the great importance of these animals for normal seed dispersal. Deserts are characterized by periodic episodes of drought years (211, 308) so severe that plant populations can be locally extinguished. The guts of large mammals seeking new leafy browse in wet years are ideal transport systems for the recolonization of sites that are usually adequate for a population of plants (isolated oases, outwash fans, north-facing escarpments, etc). Not only will the animals cross as much as hundreds of kilometers of inhospitable habitat to visit locally mesic sites (308); their defecations may be very accurately placed in these sites (145). Additionally, large mammals regularly move about over large areas; for example "the majority of adult giraffes of both sexes were found to move over distances of 40 km. . . . The average home range was 82 km$^2$ for males and 68 km$^2$ for females" (21). Zebras have home ranges of 80 to 250 km$^2$ in area (163). Such movements will obviously generate seed shadows very different than those generated by rodents and small mammals.

The annual and supraannual variation in rainfall in desert habitats should influence the impact of large herbivores on species richness through herbivory. The greatest elevation of species richness through grazing appears to occur when intense grazing is followed by periods of light or no grazing (47, 128, 300). As large herbivores move in and out of the desert with 'good' and 'bad' years, these movements should generate exactly this kind of grazing pattern.

There is a general feeling among desert biologists that many genera of arid-land perennial plants have a few widespread species and more species with quite local distributions that could be either the remnants of once broader distributions or populations recently separated from the large ones (e.g. 269, 273). While repeated cycles of wet and dry years could generate such a pattern, this is also what would happen if a series of widespread species had their major dispersal agents eliminated and were therefore restricted to those few habitats where they can persist with essentially no dispersal [or remain widespread through vegetative propagation, as does jumping cholla *(Opuntia fulgida)* (17)]. It is likely that contemporary rare desert trees with very localized distributions and fleshy fruits [e.g. the desert palm *Washingtonia filifera,* which occurs in tiny groves in the Sonoran desert and has canid-dispersed seeds at present (40)] could become very common if once again serviced by a wide-ranging megafaunal dispersal agent (such as a camelid). Likewise, much of the difficulty in understanding pollination systems and interspecific hybridization in *Opuntia* (e.g. 105–109) may derive from relatively recent changes in population structure, habitats occupied, and selective pressures brought about by removal of the traditional dispersal agents for these cacti.

Burrs and sticktights are part of this story. Jumping cholla may well be the nastiest of the world's burrs. When cacti break up at the stem joints through rough (or not so rough) treatment by contemporary herbivores eating or trampling stems or fruits (5, 13), they are probably displaying a response selected for earlier by much more brutal treatment. It is easy to imagine the early evolutionary stages of jumping cholla as simply the spines on cactus pads lodged in thick skin on large feet.

It is likely that the past 10,000 years, relatively free of large herbivores, has been a most peculiar period in the evolutionary history of New World subtropical arid-land vegetation. Were the species in it allowed to continue to evolve without large herbivores, there might well appear an array of plant species of quite different life form and dispersal mode. These plants might put their resources elsewhere than in spines, chemicals defenses against large mammals, life forms and fleshy fruits of the sort that relate to large mammals, and seed and seed crop sizes appropriate for seed shadows generated by large mammals. Chew (47) and others have called for the experimental removal of entire faunas in order to determine their 'role' in the ecosystem. The experiment has been done for us, has been partly reversed, and is worth explicit study directed at understanding the outcome. The current species richness, demography, associations, etc, of large perennials in the Chihuahuan desert may represent certain kinds of partial ecological equilibria, but they certainly do not represent evolutionary equilibria.

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