Seed predation and dispersal in a dominant desert plant: Opuntia, ants, birds, and mammals

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Abstract. Several *Opuntia* spp. (Cactaceae) occur in large and dense stands in semiarid central Mexico. Their fruits and seeds are a major food source for rodents, and to a lesser extent, for harvester ants, birds, and other mammals. *O. robusta* and *O. streptacantha* differ in their timing of fruit production and presentation and in some fruit traits which may have different consequences for seed predation/dispersal interactions with the same group of animals. Multiple interactions suggesting a changing seed predation/seed dispersal facilitation among these plants and animals are reported. The fate of *Opuntia* seeds (either eaten or dispersed) after several possible seed predation/moving/dispersal interactions apparently depends on such characteristics of the habitat as the abundance of rodent populations and the availability of optional resources for these specialized granivores.

Introduction

Recent studies on granivory and seed dispersal in diverse habitats have suggested the potential role of ecological interactions in the evolution of morphological and phenological characteristics of fruits, seeds, individual plants, and the whole plant community (Snow, 1965, 1971, 1981; Janzen, 1969, 1971, 1983, 1984; McKey, 1975; Howe and Estabrook, 1977; Howe and De Steven, 1979; Beattie and Culver, 1981; Howe and Smallwood, 1982; Willson and Thompson, 1982; Herrera, 1982a,

1984; Janson, 1983; Beattie, 1983). Related studies conducted in arid and semiarid habitats have been mainly concerned with the interactions between plants and their major seed predators (see review by Brown *et al.*, 1979; Inouye *et al.*, 1980; González-Espinosa, 1982; Briese, 1982; Davidson *et al.*, 1985). Many studies which directly address the ecology of seed dispersal in desert habitats deal with the details of the interactions of one plant species with a small group of animals, finally identifying fruit and seed traits as seed dispersal adaptations (Racine and Downhower, 1974; Berg, 1975; Glyphis *et al.*, 1980; O'Dowd and Hay, 1980; McAdoo *et al.*, 1983; Davidson and Morton, 1984). However, a few studies conducted in these habitats have suggested the common occurrence of multiple direct and indirect interactions between several species of seed predators/seed dispersers with groups of similar plants (*e.g.* Pulliam and Brand, 1975; Reichman, 1979; Inouye *et al.*, 1980; González-Espinosa, 1982; Buckley, 1982; Davidson and Morton, 1984; Davidson *et al.*, 1985; Quintana-Ascenzio, 1985).

The available information on food items included in the diets of desert frugivores/granivores indicates that one plant many animals, and many plants one animal interactions may be fairly common (*e.g.* Tappe, 1941; Spencer and Spencer, 1941; McAtee, 1947; Reynolds, 1950, 1958; Glendening, 1952; Sowls, 1974; Zervanos and Handley, 1973; Whitford *et al.*, 1976; Fogden *et al.*, 1978; Berg and Chesness, 1978; Andrews and Bogess, 1978; Mac-

Adoo and Young, 1980; Davidson, 1982; and Bissonette, 1982). However, it can be stated that, from the seed dispersal interaction perspective, an information gap persists pertaining to the ecological and evolutionary interpretation of the diet composition of desert frugivores and granivores. In this context, and given the temporal and spatial heterogeneity of the abundance of fruit and seed resources typical of desert habitats, the following questions can be formulated: (1) How common is seed predation and dispersal specificity in desert systems? (2) Are these interactions qualitatively different in desert habitats as compared with those occurring in the more predictable temperate and tropical habitats?

In this paper we provide evidence on the shifting balance of the seed predation/dispersal interactions among a large group of animal taxa and two dominant species of *Opuntia* (Cactaceae; *O. robusta* and *O. streptacantha*) in a semiarid habitat in central Mexico. These interactions were studied in sites differing in plant community structure and level of perturbation. Finally, we interpret the effects of seed predators/dispersers as natural selective factors in the evolution of reproductive phenology, patterns of fruit presentation, and other fruit and seed traits of *Opuntia* species.

Study sites and methods

The study was conducted from June-November 1984 in three adjacent sites differing in the relative abundance of *Opuntia* species and in the intensity of past and current perturbation by domestic grazing animals (but see Janzen and Martin, 1982; Janzen, 1982c, 1985, for an alternative interpretation of domestic herbivores). The study sites represent contrasting conditions of the plant formations named 'nopaleras' (Miranda and Hernández-Xolocotzi, 1963), from the náhuatl generic name 'nopalli' = *Opuntia* (Bravo-Hollis, 1978). These plant formations are currently subjected to intense disturbance as a result of heavy land use in most of their geographic range. However, it is still possible to find some small and isolated remnants along the SW edge of the Chihuahuan Desert, in the north-

central plateau of Mexico, in the states of Durango, Guanajuato, San Luis Potosí and Zacatecas (Rzedowski, 1966, 1978; Rzedowski and McVaugh, 1966; Miranda and Hernández-Xolocotzi, 1963). These plant communities typically occur on plains and gentle slopes of bajadas on rather deep soils derived from volcanic rocks at 1800–2200 m of elevation; the climate here is semiarid with a summer rainfall regime (350–450 mm of annual rainfall, mostly from July-October). The dominant plant species in the sites are *Opuntia streptacantha* (trees up to 4 m high) and *O. robusta* (shrubs up to 1.5 m high), which together usually account for over 90% of the *Opuntia* individuals. Other characteristic tree and shrub species in the sites are *Yucca decipiens*, *Acacia schaffneri*, *Dalea bicolor*, *Mimosa biuncifera*, *Bouvardia ternifolia*, *Agave salmiana* spp. *crassispina*, *Jatropha spathulata*, and *Senecio douglassi* spp. *longilobus*, interspersed with variable cover dominated by perennial grasses such as *Bouteloua gracilis*, *Leptochloa dubia* and *Microchloa kunthii*. A detailed account of the flora and vegetation in the sites appears in Rodríguez-Zapata (1981) and Rivas-Manzano (1984). Some specific differences among the study sites follow:

Site 1. Dense nopalera on gentle slopes, with 1100–1200 *Opuntia* individuals per ha (*O. streptacantha* 80%, *O. robusta* 15%, other *Opuntia* spp. 5%; density estimates obtained with the point-quarter technique as described in Cox, 1980). Excluded from grazing since 1980 the area has a cover by herbaceous perennials that is over five-fold higher than in adjacent grazed areas (Rivas-Manzano, 1984).

Site 2. Open nopalera on gentle slopes with intense disturbance by grazing and browsing animals, with 200–300 *Opuntia* individuals per ha (*O. steptacantha* 57%, *O. robusta* 23%, *O. rastrera* 19%, and *O. leucotricha* 1%). The distribution of herbaceous perennials is restricted to protected areas below trees and shrubs and interspersed with large portions of bare ground and rocks.

Site 3. Very open nopalera on flat soils, with 150–250 *Opuntia* individuals per ha (*O. streptacantha* 32%, *O. robusta* 68%). The herbaceous perennials occur as a uniform and dense cover which is moderately grazed.

The coexisting dominant species of *Opuntia* in the nopaleras of central Mexico differ in the timing of initiation of their floral buds and fruit maturation, although considerable overlap of their phenological stages can be observed. In our study sites, *O. robusta* starts its reproductive events early in spring with a blooming peak in April, completing the abscission of fruits in the middle of the summer; *O. streptacantha* initiates floral bud production in April, attains a blooming peak in May-June, and completes fruit abscission at the end of the fall. Rodríquez-Zapata (1981) and García-Sánchez (1984) offer a more detailed description of the reproductive phenology of sympatric opuntias in the same study area. Some indicators of fruit maturity, such as the deep red-purple coloration of the fruit wall, size, and the flattening of the receptacle scar appear more slowly in *O. streptacantha* than in *O. robusta*, suggesting different patterns of fruit presentation to frugivores between these species.

The fruit and seed production, their availability, and their removal by birds and rodents from the parent plants was estimated by direct counts on 30 randomly selected individuals of *O. streptacantha,* and on 36 individuals of *O. robusta*. These estimates were obtained only at site 2; no fruits were produced at site 1 and only very few at site 3 during the period of study. We selected at random eight colony nests of the harvester ant *Pogonomyrmex barbatus* at site 2. This is the only ant which collects *Opuntia* seeds in the study area (González-Espinosa, 1982). On each nest we removed collected food items from the mandibles of workers entering and leaving the nest (collections were made in two 15 min. periods in the morning and the afternoon five days a month per colony). We used folding Sherman aluminum livetraps ($23 \times 9 \times 7.5$ cm) baited with rolled oats to obtain estimates of rodent population densities. We collected the cheek-pouch contents of heteromyids and took them to the laboratory for identification.

We used blue vegetable dye to color *Opuntia* seeds. The seeds were dyed so that we could relocate them easier. The seeds were exposed to nine ant colonies in 18 clumps (20 seeds each) covered with a fixed small cage ($5 \times 5 \times 5$ cm) of 0.63 cm galvanized steel mesh which allowed seed removal only by *P. barbatus* workers. We counted the number of seeds removed from the clumps and those ejected on the gravel disk of the nests during a period of four days. The coloring did not affect the removal rate of seeds.

The removal of seeds from dung was estimated from bovine dung piles of one-half liter mixed with 0, 25, 175, 350, and 700 *O. streptacantha* seeds (20 dung piles for each seed density). The dung piles with the seeds were set on the ground at 15 m intervals in random directions, and were exposed to animals for a period of 12 days. We also estimated the survivorship of 400 *O. streptacantha* isolated seeds randomly placed on a 1×1 m grid on bare ground (228), litter (133) and grass clumps (39) over periods of 10 and 47 days.

We offered ripe fruits of *O. streptacantha* and *O. robusta* to humans, cattle, horses, goats, deer, peccaries, coyotes, raccoons, doves, thrashers, passerine birds, jays, and ravens. The number of seeds in these fruits (Y) was estimated from regression equations relating this variable with fruit fresh weight (X) for each species ($Y = 8.9 X - 170.1$, $r = .93$, $N = 12$, for *O. robusta*; $Y = 2.8 X - 6.1$, $r = .84$, $N = 20$, for *O streptacantha*). Most observations were obtained with captive animals at the zoo in the city of Morelia. None of the individuals used were isolated from their groups; they were fed with their usual diet. None of these individuals had been fed *Opuntia* fruits and seeds for a minimum period of 30 days prior to testing. We collected their feces from one day before the consumption of the fruits up to five days for peccaries, cattle and goats, four days for horses and deers, three days for humans, coyotes, and raccoons, and one day for all bird species. We estimated the proportion of daily defecated seeds and made observations on their condition (apparently intact or damaged).

Results and discussion

Temporal presentation and consumption of Opuntia fruits

The fruits of *O. robusta* are usually available on the plant pads and on the soil at a time of the year
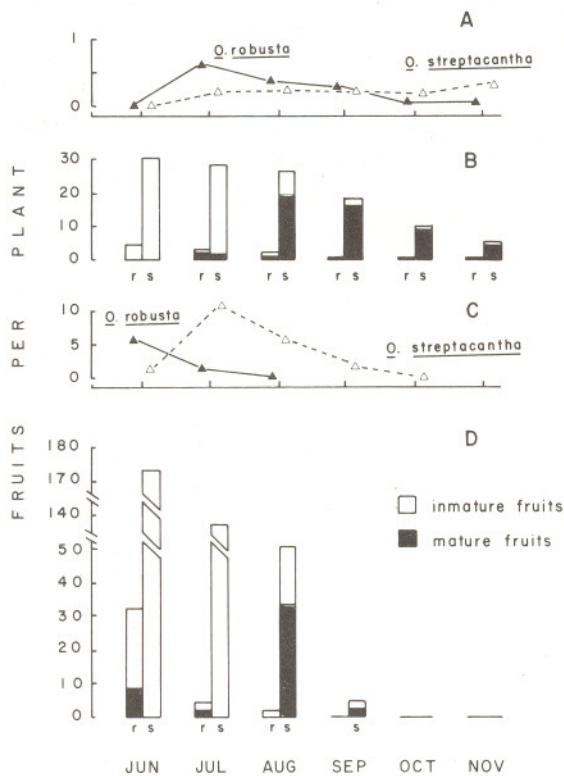
Fig. 1. Fruit availability and removal on plants of *Opuntia robusta* (r) and *O. streptacantha* (s) at El Palmar, Villa de Arriaga, San Luis Potosí, Mexico. A and C: Mean fruit removal at study site 1 during 1980, and at site 2 during 1984. B and D: Availability of immature and mature fruits in the same sites during 1980 and 1984, respectively. Data from the 1980 season after Rodríquez-Zapata (1981).

(June–July) when resource scarcity is at its highest and these fruits are virtually the only fresh material available (Fig. 1). The peak availability of ripe *O. streptacantha* fruits (August–September) usually coincides with the occurrence of the new growth by annuals and herbaceous perennials stimulated by the summer rainfall (Fig. 1; Rivas-Manzano, 1984). From 1980 through 1984 we have observed a very wide variation in the number of fruits produced by the same individuals.

The fruits can be consumed on the *Opuntia* plants by several birds, rodents (*Neotoma* spp.), carnivores, large herbivores, and humans (Table 1). The availability of these fruits to some animals depends on the size of the *O. streptacantha* plants. The shrubby growth habit of *O. robusta* allows the removal of its fruit crop by a larger group of ani-

mals, including some of relatively small size (*e.g.* carnivores, peccaries, and goats).

Heteromyid rodents only consume fallen fruits and their seeds available on the ground. Our observations indicate that *Pogonomyrmex* ants can remove seeds only from opened fruits on the ground. The fruits become attractive to these insects only when pulp or juice flows from the ripe abscissed fruit, or when the fruit has been previously left incompletely consumed by another animal (more frequently a bird or rodent species). We have observed in captivity and in the field that some seed-eating birds (doves, sparrows, finches) only remove seeds from previously opened fruits, either while they are still attached to the plant or are on the ground (Table 1).

Removal and consumption of Opuntia seeds

The seeds can be found by granivores after they have been removed from the fruits by frugivores. These seeds are available either clumped in feces, on the gravel disks surrounding *Pogonomyrmex* nests, or isolated in apparently non-specific places (Table 1). Dung beetles move some seeds within their fresh dung pellets, which enhances the chances of seeds escaping from granivores. Wicklow *et al.* (1984) have shown that seeds inside dung pellets can be exposed to more favorable conditions for germination.

Numerous colonies of *Pogonomyrmex barbatus* occur in the study sites (20 ± 4 colonies/ha; González-Espinosa, 1982). Fig. 2 shows the composition of all items carried by these ants at site 2 during the study period. These ants collected and carried into the nest a large number of *Opuntia* seeds (occasionally up to 400 seeds per nest per day) during late spring; numbers of seeds carried into nests declined during the summer and fall months (per. obs.). The ants do not kill the embryos and only remove the pulp adhering (seed funicle) to the seed coats. However, the workers occasionally moved seeds covered with feces or lacking pulp. Most of the seeds were ejected intact from the nest granaries and were deposited on the surrounding gravel disks where they could be eaten by granivorous birds and rodents (pers. obs.). Most (>80%) of the

dyed seeds that we offered to the ants were ejected within the first 24 h after they had been carried by the workers. The seeds of dominant grasses (*Bouteloua gracilis*, *Leptochloa dubia*, *Microchloa kunthii*, *Panicum* spp. and *Setaria* spp.) constituted the largest proportion of the ants' diet from August (15–82%) through November (53–88%). The seeds of composites (mostly *Heterosperma pinnatum*, *Parthenium bipinnatifidum* and *Zaluzania triloba*)

can be regarded as the second largest group of seeds included in the diet of these granivorous ants. We have observed a very wide variation in the seed species carried by different colonies; this variation apparently reflects the composition of vegetation surrounding the nest. The workers of *P. barbatus* rarely forage farther than 10–12 m from the nest (Santana-Sepúlveda, 1981).

We trapped rodents in different microsites, in-

Table 1. Animal species (non-exhaustive list) known to interact with *Opuntia robusta* and *O. streptacantha* fruits and seeds in nopaleras of central Mexico.

Species	Consumption of fruits	Mode of pulp and seed removal	Removal of seeds not in fruits	Interaction with seeds
Insects				
Dung beetles (Scarabaeidae)	–	–	F	3 m, 3 d
Harvester ants (*Pogonomyrmex barbatus*)	B, o	–	F, L	3 m, 1 d
Birds				
White-winged dove (*Zenaida asiatica*)	Or, Os, B, o	P	N, L	1 p?, 2 m, 3 d
Yellow-shafted flicker (*Colaptes auratus*)	Or, Os, i, o	P	–	1 m, 3 d
Curve-billed thrasher (*Toxostoma curvirostre*)	Or, Os, B, i, o	P	–	1 m, 3 d
Brown towhee (*Pipilo fuscus*)	Or, Os, B, i, o	P	F, N, L	1 m, 3 d
House finch (*Carpodacus mexicanus*)	Or, Os, o	P	–	1 m, 3 d
Gray-breasted jay (*Aphelocoma ultramarina*)	Or, Os, i, o	P	–	2 m, 3 d
White-necked raven (*Corvus cryptoleucus*)	Or, Os, i, o	P	–	2 m, 2 d
Rodents				
Nelson pocket mouse (*Perognathus nelsoni*)	B, i, o	G	F, N, L	3 p, 1 m, 1 d
Mexican spiny pocket mouse (*Liomys irroratus*)	B, i, o	G	F, N, L	3 p, 1 m, 1 d
Phillips' kangaroo rat (*Dipodomys phillipsii*)	B, i, o	G	N, L	3 p, 2 m, 1 d
Goldman's wood rat (*Neotoma goldmani*)	Or, Os, B, i, o	G	F, N, L	3 p, 1 m
White-throated wood rat (*Neotoma albigula*)	Or, Os, B, i, o	G	F, N, L	3 p, 1 m, 1 d
Carnivores				
Coyote (*Canis latrans*)	Or, B, i	S, C	–	3 m, 1 d
Gray fox (*Urocyon cinereoargenteus*)	Or, B, i	S, C	–	3 m, 1 d
Raccoon (*Procyon lotor*)	Or, Os?, B, i	U	–	3 m, 1 d
Badger (*Taxidea taxus*)	B, i	S	–	3 m, 1 d
Hooded skunk (*Mephitis macroura*)	B, i	S, C	–	3 m, 1 d
Other mammals				
Long-nosed bat (*Leptonycteris nivalis*)	Or, Os	G	–	1 p?, 1 m?, 3 d?
Desert cottontail (*Sylvilagus audubonii*)	B, i, o	G	F	2 p?, 1 m?, 1 p?
Horse (*Equus caballus*)	Or, Os, B, i	S	–	1 p, 3 m, 2 d
Collared peccari (*Tayassu tajacu*)	Or, B, i	S	–	2 p, 2 m, 1 d
White-tailed deer (*Dama virginiana*)	Or, Os, B, i	S	–	3 m, 1 d
Domesticated cattle (*Bos taurus*)	Or, Os, B, i	S	–	1 p, 3 m, 2 d
Goat (*Capra hircus*)	Or, B, i	S	–	1 p, 3 m, 2 d
Humans (*Homo sapiens*)	Or, Os	C	–	3 m, 1 d

Or = on *O. robusta*, Os = on *O. streptacantha*, B = below either *Opuntia* spp., i = intact fruits, o = previously opened fruits, P = pecking, G = gnawing, S = swallowing, C = crushing, F = from feces, N = from ant nests gravel disks, L = loose seeds, d = seed disperser, m = seed mover, p = seed predator. 1, 2 and 3 refer to low, moderate, and high frequency of interaction. Nomenclature follows Peterson and Chalif (1973), Hall and Kelson (1959), and Walker (1975).
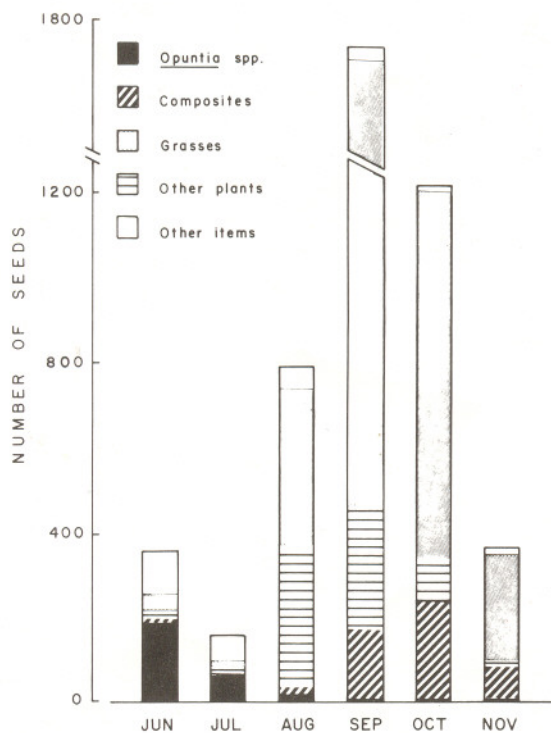
Fig. 2. Seeds and other items carried to nest granaries by *Pogonomyrmex barbatus* workers at site 2 during the period of study.

cluding on and below the *Opuntia* plants, on bovine feces, and on the gravel disks surrounding the *P. barbatus* nests (Table 2). There was a heterogeneous spatial distribution of rodent captures in all three study sites from July through November (site 1: $\chi^2_3 = 17.64$, P<.001; site 2: $\chi^2_{15} = 98.01$, P<.001; site 3: $\chi^2_{10} = 61.13$, P<.001). *Perognathus nelsoni* was equally abundant in captures on the ground (below opuntias, on feces, and on ant nests) at sites 1 and 2. This species was not trapped in the more open nopalera (site 3). Site 3 had similar *Opuntia* spp. densities to site 2 and had a scarcer cover by shrubs. Our results suggest that *P. nelsoni* is an opportunistic forager in sheltered areas, as has been found for other *Perognathus* species (Rosenzweig, 1973; Brown and Lieberman, 1973; Reichman and Oberstein, 1977; Hutto, 1978; Trombulak and Kenagy, 1980; M'Closkey, 1980; Price and Waser, 1985). On the other hand, *Dipodomys phillipssii* and *D. ordii* were more frequently caught on open areas (more frequently on ant nests than on bovine feces) than below the *Opuntia* plants. A lower number of kangaroo rats was trapped when we used bovine feces and *Opuntia* seeds as bait. The Mexican Spiny Pocket Mouse (*Liomys irro-*

Table 2. Number of captured rodents in different microsites (OS = on *Opuntia streptacantha*, BS = below *O. streptacantha*, OR = on *O. robusta*, BR = below *O. robusta*, GD = on gravel disks of *Pogonomyrmex barbatus* nests, and BF = on bovine feces. Pooled data obtained from July through November, 1984.

Rodent species	OS	BS	OR	BR	GD	BF	Total
Perognathus nelsoni							
Site 1	–	–	–	–	45	43	88
Site 2	0	22	0	22	25	20	89
Site 3	0	0	0	0	0	0	0
Dipodomys spp.							
Site 1	–	–	–	–	21	4	25
Site 2	0	15	0	15	21	26	77
Site 3	0	12	0	8	31	11*	62
Liomys irroratus							
Site 1	–	–	–	–	14	29	43
Site 2	0	31	0	28	12	22	93
Site 3	0	13	0	25	3	12*	53
Neotoma goldmani							
Site 1	–	–	–	–	32	27	59
Site 2	54	20	23	16	24	28	165
Site 3	64	23	19	26	19	17*	168

* Pooled data obtained from August through November.

ratus) was frequently caught in traps under *Opuntia* plants and occasionally in open areas (mostly at bovine feces), suggesting a preference for sheltered and fruit-rich microhabitats. The climbing cricetine species *Neotoma goldmani* and *N. albigula* were the only rodents trapped on the opuntias, although there is a considerable seasonal variation in the intensity of their activity on the trees and shrubs. González-Espinosa (1982) suggested a temporal vertical habitat partitioning between *N. goldmani* and *L. irroratus* at the time of peak availability of *Opuntia* fruits. Holbrook (1979) has suggested a similar partitioning as a mechanism contributing to the coexistence of a guild of cricetine rodents.

We have observed granivorous birds (*Pipilo fuscus* and doves; Table 1) removing seeds from feces and from ant nests gravel disks. We do not know if these birds damage the seeds. Racine and Downhower (1974), Grant and Grant (1981) and Millington and Grant (1983) have reported that other Fringillidae (*Geospiza* spp.) can kill the embryos by cracking the seed coats of *Opuntia* seeds in the Galápagos Islands.

Excretion of Opuntia seeds by birds and mammals

The seeds of *O. robusta* and *O. streptacantha* differ in their rates of passage through the digestive tracts of different animal species (Fig. 3). We found that two cows and a bull excreted about 40% of the total seeds of *O. robusta* and 80–90% of *O. streptacantha* seeds within five days following their ingestion. The pattern of seed passage of these opuntias is significantly different for cattle ($\chi_4^2 = 328.3$, P<.001; Siegel, 1956). However, the distribution of the number of seeds excreted in each defecation is relatively similar for both species, suggesting that the consumption of a higher number of seeds will result in a longer period of defecation. The fruits of *O. robusta* have more seeds than those of *O. streptacantha* (375.9 ± 191.4, N = 12, for *O. robusta*; 148.8 ± 37.8, N = 20, for *O. streptacantha*), suggesting that a cow eating a similar number of fruits of these *Opuntia* species would have a different efficiency as a seed mover/seed disperser. The seeds of *O. robusta* would travel for a relatively longer time in the bovine guts. We have observed
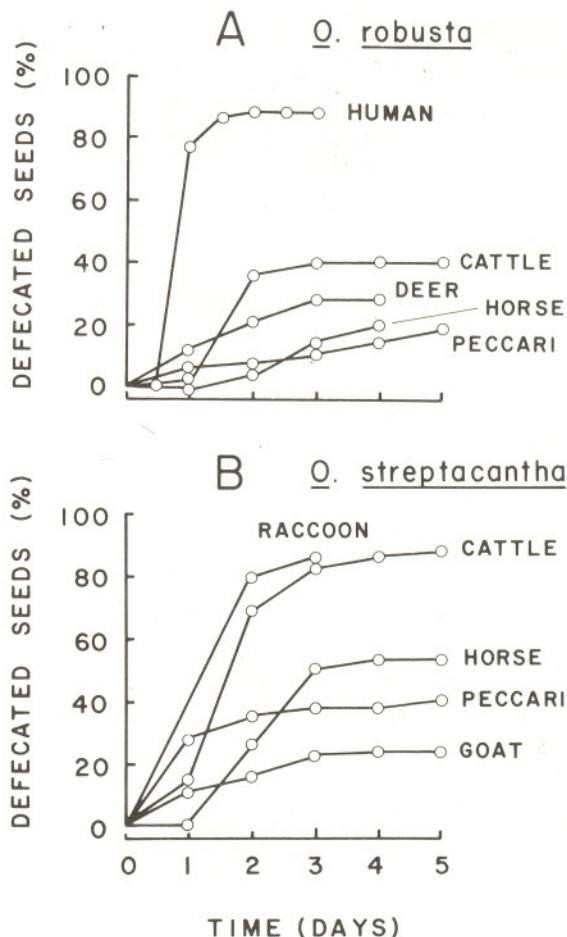

Fig. 3. Patterns of daily excretion of *Opuntia* seeds in feces. Sample sizes: 3 humans, 12 fruits each; 3 bovines, 25 fruits each; 2 horses, 10 fruits each; 2 peccaries, 15 fruits each; 2 deers, 5 fruits each; 2 goats, 5 fruits each; 2 raccoons, 5 fruits each. See text for details of seed number estimation from fruit weights.

that the *Opuntia* seeds are defecated by cattle intact and viable.

Similar results were obtained with two male horses and two mares ($\chi_3^2 = 91.1$, P<.001), and with two peccaries ($\chi_4^2 = 320.7$, P<.001), but the excretion of seeds by these animals occurs at a lower rate than in cattle (Fig. 3). The horses do not kill the *Opuntia* seeds, but the peccaries can destroy some of them (up to 25% for *O. robusta* and up to 7% for *O. streptacantha*). Our observations with goats and deer indicate that they do not kill the seeds and excrete them at a rather low rate (20–30% of total ingested seeds in a period of five days). The defecation of *Opuntia* seeds by carnivores and humans

occurred at a very high rate (up to 80%) within the first 24 h after ingestion.

Captive granivorous birds (*Carpodacus mexicanus*, *Passerculus sandwichensis*, *Ammodramus savannarum*, and *Cardinalis cardinalis*) fed *Opuntia* fruits pecked their edible portion, removed pulp from most of the seeds, and discarded many seeds around the eaten fruit. These bird species defecated one to five intact seeds in their fecal pellets. *Toxostoma curvirostre*, *Aphelocoma ultramarina*, and *Corvus cryptoleucus* behaved similarly with the fruits but excreted 10–48 intact *Opuntia* seeds in their one-day-old feces.

Predation on seeds in bovine feces

All rodent species present in the study sites visit fresh dung, and they probably eventually remove most of the defecated *Opuntia* seeds. We have observed that a few seeds are also collected from dung by *Pogonomyrmex* ants and dung beetles. Our data are insufficient to propose that the probability of seed predation by rodents varies with the number of seeds in the dung (see Janzen, 1982a, 1982b for a contrary result with a tropical rodent species). We found different intensities of seed predation by rodents at two of our study sites (50–70% of seed removal within a period of 12 days at site 3; 80–100% at site 1 during the same period). These differences are easily explained by the different rodent densities (the ranges of rodent numbers at site 3 was 39–87 and 68–118 in site 1), and by the absence of *Perognathus* spp., which are specialized granivores, at site 3. Also, the island-like spatial distribution of opuntias and other shrubs at site 3 probably prevented *Neotoma goldmani* and *Liomys irroratus* from foraging widely.

Removal of isolated Opuntia seeds

We do not know at this stage what fraction of the *Opuntia* seeds are moved by ants, birds and mammals to isolated sites. Removal of isolated seeds from apparently non-specific microsites in our m^2 grids indicated that the chances for seed predation escape are quite low after seven weeks of exposure (<2% at site 1; <20% at site 3; 20 seeds in each grid, 10 grids per site). The *Opuntia* seeds were equally at risk on bare ground or litter.

General interpretation

We have presented observations and results of field experiments indicating multiple direct and indirect interactions of *Opuntia* spp. with frugivores, granivores, and omnivores. It would seem that in habitats with high seed predation by rodents, as in dense nopaleras, even the most efficient *Opuntia* seed disperser might only function as a seed mover. In open habitats such as the adjacent grasslands and marginal nopaleras, where rodents can be less abundant, a highly efficient seed predator might act as a seed disperser. The shifting balance of the seed predator/mover/disperser role seems to depend more on where the interaction occurs, rather than on intrinsic traits of the animals themselves.

The sequential presentation of fruits and seeds by sympatric *Opuntia* species results in their differential mode and level of interaction with seed predators and dispersers. The peak of *Opuntia robusta* fruit availability coincides with the maximum scarcity of seeds and fresh tissues in the nopaleras of central Mexico (May and June). The seeds of *O. streptacantha* become more abundant at the time when green tissues of herbaceous plants are available. The pulp of *Opuntia* spp. fruits usually represents a rich source of water, sugars, and minerals (Lakshminarayana and Estrella, 1978; Delgado, 1985), making them particularly attractive to frugivorous animals. However, the fruits of *O. robusta* contain a higher proportion of pulp (up to 46% of fruit fresh weight) than those of *O. streptacantha* (33–35%, Delgado, 1985). Thus, fruits of *O. robusta* provide a larger reward (and the only one when they are available) to carnivores and large herbivores which will move and occasionally disperse their seeds. Herrera (1982b) has documented that fruits ripening during the driest season in Mediterranean habitats are the most watery, and has suggested this trait to be a result of coevolutionary interactions between plants and seed dispersers. In our study system, the ripe fruits of *O. streptacantha* would share seed dispersers/herbivores feeding on the highly nutritious new

growth of herbaceous plants, and it would be expected that a different set of fruit traits from that in *O. robusta* would be selected. Delgado (1985) has recently reported that *O. streptacantha* fruits have more soluble solids (12.44° *vs.* 10.82° Brix) and a larger proportion of reduced sugars (11.99 *vs.* 9.23%) than those of *O. robusta*. These phenological, morphological, and biochemical differences between *O. robusta* and *O. streptacantha* suggest that these species have evolved their fruit traits as a response to the seasonal needs and preferences of the same group of animals.

The pulp and seed contents of the *Opuntia* fruits can be extracted by different seed predators/dispersers, suggesting that some other fruit traits such as color, maximum size, fruit wall thickness, and the ease of its detachment from seeds and pulp can also be interpreted as the evolutionary result of interactions with other non-herbivore animals. We have observed that captive coyotes, gray foxes, and raccoons obtain most of the seeds and pulp of intact fruits by crushing them with their feet, leaving the empty fruit wall intact. Colunga-García-Marín (1984) found that the ease of peeling and retention of the shape of the *Opuntia* fruit contents are associated with other fruit traits resulting from interactions with humans during domestication. We did not observe frequent consumption of *Opuntia* fruits by birds on the plants. However, the deep-red and purple color of these fruits would be selected by birds, even if they only function as occasional seed dispersers.

Large herbivores (native and introduced) have been proposed as efficient seed dispersers for plants such as *Opuntia* spp. (Glendening, 1952; Janzen, 1981a, 1981b, 1981c, 1985). Our observations indicate that such contemporary large herbivores as cattle, horses, and donkeys do not damage the seeds. However, the deposition of these seeds in large clumps in their dung can hardly be interpreted as efficient seed dispersal when rodents are abundant. All rodent species in our study sites were frequently trapped at dung piles containing *Opuntia* seeds, and most of the seeds in this dung were eaten by granivores shortly after becoming available. We do not know if the abundance and diversity of rodent species mostly depends on the pattern of fruit and seed presentation and availability, or if it is mediated by the movement of the seeds once they have been ingested by all the other animal taxa that we have found to interact with them. Janzen (1985) has proposed that fruit traits in *Opuntia* spp., and the plant community structure of nopaleras might be interpreted as the evolutionary result of interactions with an extinct megafauna of herbivores. The frequent visitation to dung piles by rodents which we have documented suggests that their abundance and coexistence could be enhanced by the movement of seeds by such large herbivores. It rather seems that the currently observed traits in *Opuntia* fruits and seeds can be interpreted as the result of diffuse coevolutionary interactions among a dominant plant and a wide array of seed predators and dispersers.

Acknowledgements

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