



Vertebrate frugivory and seed dispersal of a Chihuahuan Desert cactus

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Abstract

Vertebrate frugivory of fleshy-fruited plants may be very important for the recruitment of sexually derived seedlings if it represents the main mechanism of primary seed-dispersal. *Opuntia rastrera* produces fleshy fruits rich in water and sugars that are attractive to vertebrate frugivores. However, there is a very low rate of seedling recruitment in natural conditions. One of the causes that can influence this low recruitment is an insufficient seed dispersal due to a low fruit removal even under different resource (fruits) availability. To test this prediction, we studied the production and consumption of fruits in two consecutive years in two vegetation types: nopaleras (dense *Opuntia*-dominated scrublands) and grasslands with sparse populations of *O. rastrera*. Plant cover, fruit production and removal, and frugivore identity were recorded within each vegetation type in four randomly selected circular plots (7854 m²). Fruit production per area was higher in nopaleras in both years whereas per cladode production did not differ between vegetation types but differed between years in response to variation in precipitation. Fruit consumption by vertebrates was high (100%) and independent of spatial and temporal fruit availability. The intensity of fruit removal was inversely related to resource availability: it was faster in the less dense community (grassland) and in the driest year. Contrary to other studies with similar cacti, fruit removal by small mammals was insignificant whereas main consumers were birds and large mammals. Vertebrate frugivory represents the only mechanism of primary dispersal of seeds as all fruits are removed in about one month. Despite the high quantity of viable seeds (more than one million per ha in nopaleras and a tenth of that in grasslands) that are dispersed by frugivores after the consumption of about 300 kg of fruit per ha in nopaleras and a tenth of that in grasslands, the rare establishment of seedlings (about one seedling per three million of seeds produced) reported in the literature indicates that the interaction between *O. rastrera* and the disperser guild is indeed very asymmetrical. We speculate that the harsh conditions for cactus establishment found in this ecosystem demand a high investment in disperser rewards (fleshy fruits) to allow a very modest rate of sexually-derived seedling establishment.

Introduction

Vertebrate frugivory represents the start of the primary dispersal for propagules of many plants (phase I of dispersal *sensu* Chambers & MacMahon 1994). The subsequent spatio-temporal patterns of seed movements may importantly influence the reproductive success of the species (Willson 1986, 1993; Fleming 1991; Jordano 1992; Fleming & Sosa 1994) by determining the conditions that seeds and seedlings will find for germination and establishment before they can be re-

cruited as new genets (seed-derived individuals) in the population (Shupp 1995; Shupp & Fuentes 1995).

Frugivory and subsequent dispersal of viable seeds offer three basic advantages to the potential new recruit: (1) reduced density-dependent competition between seedlings or between them and established adults (Janzen 1970; Connell 1971; Howe & Smallwood 1982; Venable & Brown 1988); (2) increased availability of safe sites for germination, allowing a more complete occupation of available sites and the colonization of new sites suitable for germination and establishment (Dirzo & Domínguez 1986;

Shupp 1993; Chambers & MacMahon 1994); and (3) increased local genetic variability through recruitment of genets coming from distant populations, thus contributing to reduced potential endogamy and local extinctions (Mandujano et al. 1997).

Many cacti of semiarid zones produce fruits rich in water and sugars (Bravo-Hollis 1978; Pimienta-Barrios 1997) that are consumed by birds, mammals and ants, which can act as effective seed dispersers (Quintana-Ascencio 1985; González-Espinosa & Quintana-Ascencio 1986; Janzen 1986; Trujillo-Argueta & González-Espinosa 1991; Vargas-Mendoza & González-Espinosa 1992; Mandujano et al. 1997). However, the impact of frugivory and seed dispersal on the population dynamics of semiarid plants is poorly known due to the scarcity of quantitative studies on the spatio-temporal variability of frugivory in these ecosystems (Pulliam & Brand 1975; Reichman 1979; Inouye et al. 1980; González-Espinosa 1982; Buckley 1982; Quintana-Ascencio 1985; González-Espinosa & Quintana-Ascencio 1986; Trujillo-Argueta & González-Espinosa 1991; Chambers & MacMahon 1994).

The recruitment of sexually derived cactus seedlings has been reported to be a very rare event (Turner et al. 1966; Nobel 1988; Mandujano et al. 1996). In most of the species studied, seeds can only germinate in safe sites under nurse plants (Turner et al. 1966; Nobel 1988; Mandujano et al. 1996). Seed predation in these ecosystems (Reichman 1979, 1984; Brown et al. 1979; Davidson et al. 1985; González-Espinosa & Quintana-Ascencio 1986; Kemp 1989) can reduce the success of dispersal. This will be more critical when dispersers are not adequate (due to small numbers or to low dispersal effectiveness; Janzen 1986; Nobel 1988) and do not deposit a sufficient number of seeds in microsites appropriate for germination and establishment. Under a scenario of high fruit production and a very low rate of recruitment, the plant-frugivore interaction appears to be asymmetric (cf. Dirzo & Domínguez 1986; Shupp 1993); dispersers receive a disproportionate reward compared to the benefit received by the plant.

Opuntia rastrera Weber is a Chihuahuan Desert species that produces fleshy fruits rich in water and sugars that are attractive to vertebrate frugivores. However, there is a very low rate of seedling recruitment in communities where this species is present (about one seedling per three million seeds produced; Mandujano et al. 1997). One of the causes that can influence this low recruitment is an insufficient seed

dispersal due to a low fruit removal even under different resource (fruits) availability. To test this prediction, we studied the production and consumption of fruits in two vegetation types with contrasting *O. rastrera* densities and in two consecutive years.

Methods

Study area

Field work was done in the Mapimí Biosphere Reserve in the southern Chihuahuan Desert (26°40' N, 103°40' W; 1100 m altitude; 264 mm of mostly summer rains with 80.2% falling between June and October; average temperature = 20.8°C; Montaña 1990). *O. rastrera* is found in two vegetation types: grasslands and *Opuntia*-dominated scrublands locally called nopaleras. Nopaleras at the study site are dominated by *O. rastrera* and *Larrea tridentata* on gently sloping bajadas (slope = 2–4%) with gravelly sandy loam to clay loam soils. Other common species in this habitat include *Jatropha dioica*, *Prosopis glandulosa* var. *torreyana*, *Castela texana*, *Opuntia microdasys* and *Fouquieria splendens* (Montaña 1990). In this vegetation type *O. rastrera* propagates profusely by vegetative means whereas the establishment of seed-derived individuals is almost nil (Mandujano et al. 1998). Grasslands are on clay loam to clay soils in periodically flooded playas with slopes <1%. They are dominated by the grass *Hilaria mutica* with scattered individuals of *O. rastrera*, *Opuntia violacea* and *P. glandulosa* var. *torreyana* (Montaña 1990). In this vegetation type, *O. rastrera* reproduces only by seeds (Mandujano et al. 1998).

Study plant

O. rastrera (Cactaceae, subfamily Opuntioideae) is a cactus of prostrate to erect habit that sometimes grows in dense associations, in plains and slopes of semiarid central and northern Mexico (Bravo-Hollis 1978). Most plants have long (up to two meters or more) and prostrate suites of 10–20 cm diameter pads which gives the name to the species. Pads bear regularly distributed spines. Flowering begins in April, and the diurnal and insect-pollinated flowers with yellow to pink corollas last only one day. Red to purple fleshy fruits are available from June until August. Each fruit bears 208 seeds (± 0.13 SE) (Mandujano et al. 1996) and weighs 39.94 g (± 1.46 SE, $n = 143$).

Plant cover and fruit production

Field work was done in the summers of 1996 and 1997. Four permanent circular sampling plots (50 m radius, 7854 m² in area) were established inside each vegetation type, by randomly selecting coordinates from a vegetation map (Montaña 1988). In June 1996 all cladodes of each *O. rastrera* plant were counted in the eight plots and plant cover was calculated using a regression (cover in cm² = 672.8 + 99.3 × number of cladodes) provided by Briones et al. (1996). In early July of each year (i.e. when the flowering period was over and all fruits were initiated) the number of fruits in the grassland plots was counted. In the nopalera plots this was estimated by counting the number of fruits per pad in five randomly selected plants of each plot. Then, the number of pads bearing fruits was determined for each plant and the number of fruits per plot was obtained by multiplying the number of fruit-bearing pads by the average number of fruits per pad. In all cases, the number of seeds was also estimated using the number of seeds per fruit provided by Mandujano et al. (1996).

Vertebrate fauna visiting nopaleras and grasslands

Vertebrates visiting the plots were identified by systematic observations with 10 × 50 binoculars made from the center of each plot. Observations were made in July 1996 from 05:30 to 09:30 h and again from 1600 to 2000 h during eight consecutive days in each vegetation type. Forty-five-min observations were alternated between plots within each 4-h observation period. All visits of vertebrates and the number of fruits eaten per visit were recorded. Identification of birds was done using Peterson & Chalif (1989), and Grenot & Serrano (1981) and Brown & Harney (1993) in the case of rodents. Besides vertebrates, the presence of ants in *O. rastrera* fruits was also recorded and identities were determined based on Rojas-Fernández & Fragoso (1994).

Fruit consumption

In August 1996 and 1997 fruit consumption was recorded in all sampling plots. Due to differences in yearly fruit production, experimental plants in nopaleras were randomly selected from all plants bearing at least 25 ripe fruits in 1996 and 50 ripe fruits in 1997. In the less productive grasslands, plants bearing 10 and 20 fruits were randomly selected in each year. Five plants were selected in each case and in each plant

fruits were randomly selected (five in 1996 and 10 in 1997). Selected fruits were marked with permanent ink at their base and checked every four days, recording total or partial damage by frugivores. The identity of frugivores was determined on the basis of the traces left on the remaining fruit tissues or the tracks or scats left at the site. The categories used were: bird consumption (fruits showing holes caused by bird bills), rodent consumption (fruits showing scars of incisors in the external fruit tissue), ant consumption (pierced fruits in a few holes heavily visited by ants), and large mammal (*Odocoileus hemionus* and *Canis latrans*) consumption (fruits removed from the pad and traces of these animals left at the site). Although ants visit and consume fruits that have been attacked by vertebrates, ant consumption was recorded when the only discernible attack suffered by the fruit was made by ants. In the other cases the primary consumer (bird, rodent or large mammal) was recorded. Observations were made until all marked fruit were consumed.

Data analysis

O. rastrera cover was compared between vegetation types using a one-way analysis of deviance from a logit model with binomial error (Crawley 1993). Data on fruit production (numbers of fruits per pad, numbers of pads bearing fruits and numbers of fruits produced) were analysed with a repeated measures analysis of variance (ANOVAR; Zar 1996) with a between-subjects factor, vegetation type (two levels, nopalera and grassland), and a within-subjects factor, time (two levels, year 1996 and year 1997). Each treatment had four replicates (i.e., the four plots in each vegetation type). Following Crawley (1993), a linear model with normal error was used to analyse the average number of fruits per pad, and a log-linear model with Poisson error to analyse the numbers of pads bearing fruits and the numbers of fruits produced per plot. Shannon diversity index was calculated for bird visits to the experimental plots, and compared between vegetation types with Hutcheson's *t*-test (Zar 1996). Data on fruit consumption was analysed with an ANOVAR (Zar 1996) using vegetation type (two levels, nopalera and grassland) as the between-subjects factor, and year (two levels, year 1996 and year 1997) and time-step (eight levels determined by the eight consecutive dates on which data were recorded) as within-subjects factors. Because the response variable was the proportion of fruits damaged by frugivores, a logit model with

binomial error was used. Each treatment had four replicates.

To assess if vegetation type and year influenced the probabilities of fruit consumption by different frugivores, a multinomial logit model (Aitkin et al. 1989) was used. The response variable (proportion of fruits) had four levels (fruits damaged by birds, rodents, ants and large mammals), and there were two classification factors: vegetation type (with two levels, nopalera and grassland) and year (with two levels, year 1996 and year 1997). All linear models were fitted with GLIM (Generalized Linear Interactive Modelling; Francis et al. 1994).

Results

Plant cover and fruit production

O. rastrera cover was an order of magnitude greater ($\chi_1^2 = 1493$, $P < 0.001$) in nopaleras ($4.97\% \pm 0.43$ SE) than in grasslands ($0.38\% \pm 0.11$ SE). Fruit production per pad did not differ between vegetation types (1.98 ± 0.04 SE in nopaleras vs. 1.91 ± 0.19 SE in grasslands, $F_{1,3} = 1.77$, $P > 0.05$). However, there was a difference between years (1.65 ± 0.1 SE fruits per pad in 1996 vs. 2.24 ± 0.08 SE in 1997, $F_{1,6} = 40.66$, $P < 0.001$), and the interaction vegetation type by year was also significant ($F_{1,6} = 20.04$, $P < 0.005$) because the 1997 increase in fruit numbers per pad was larger in grasslands than in nopaleras (Table 1).

The number of pads bearing fruits was higher in nopaleras (2708.16 ± 328.72 SE pads per ha) than in grasslands (276.92 ± 97.19 SE, $\chi_1^2 = 14413$, $P < 0.001$). This variable also differed between years (1190.47 ± 478.41 SE pads per ha in 1996 vs. 1794.62 ± 533.63 SE in 1997, $\chi_1^2 = 774.7$, $P < 0.001$), and the interaction vegetation type by year was also significant ($\chi_1^2 = 586.3$, $P < 0.001$) because the increase of 1997 over 1996 production was higher in grasslands than in nopaleras (Table 1). Numbers of fruits and seeds produced per ha followed the same pattern as the number of pads bearing fruits, since they are a function of fruiting pads (Table 1). Indeed, number of fruit were higher in nopaleras (5394.06 ± 653.43 SE fruits per ha) than in grasslands (631.52 ± 255 SE, $\chi_1^2 = 26943$, $P < 0.001$), and in 1997 (3784.05 ± 1043.15 SE fruits per ha), as compared to 1996 (2241.53 ± 919.77 SE, $\chi_1^2 = 2477$, $P < 0.001$). A ten-fold increase in grasslands, as

compared to a 50% increase in nopaleras, resulted in a significant interaction between vegetation type and years ($\chi_1^2 = 1851$, $P < 0.001$; Table 1).

Vertebrate fauna visiting nopaleras and grasslands

Large mammals that visited the plots also consumed *O. rastrera* fruits, both in nopaleras and grasslands; these were *O. hemionus* (mule deer) and *C. latrans* (coyote). Only one lagomorph, *Lepus californicus* (jackrabbit), was present but was never observed eating fruits. Despite their low importance as fruit consumers, a wide array of rodents visited the plots: *Spermophilus spilosoma*, *Dipodomys merriami*, *Dipodomys nelsoni*, *Chaetodipus penicillatus*, *Perognathus flavus*, *Peromyscus eremicus* and *Neotoma albigula*. The desert tortoise (*Gopherus flavomarginatus*) also consumed some fruits, and ants of the genera *Myrmecocystus*, *Pogonomyrmex*, *Paratrechina*, *Solenopsis* and *Crematogaster* were observed visiting *O. rastrera* fruits.

The richest group of visitors was that of birds. This group had a higher diversity in nopaleras than in grasslands ($H' = 0.98$ vs. $H' = 0.78$, respectively; $t_{202(2)} = 4.06$, $P < 0.05$). Four out of the 15 species recorded in nopaleras (*Amphispiza bilineata*, *Lanius ludovicianus*, *Corvus corax* and *Mimus polyglottos*) were the most frequent visitors to the plots (Table 2). Twenty six percent of species recorded in nopaleras consume primarily fruits, and the same proportion are primarily granivores according to the feeding guilds reported by Thyollay (1981). Four out of the 12 species recorded in grasslands (*A. bilineata*, *Pipilo fuscus*, *L. ludovicianus* and *Zenaida macroura*) were the most frequent (Table 2); 67% of the species recorded in grasslands are primarily insectivores, and the remaining are frugivores and granivores (Thyollay 1981).

In both nopaleras and grasslands, *M. polyglottos*, *Toxostoma curvirostre* and *C. corax* were the birds most frequently observed consuming *O. rastrera* fruits. *C. corax* usually consume the fruit almost completely, but the first two species consume about 50% of the pulp leaving the remaining pulp tissue exposed to secondary visitors such as ants of the genera *Myrmecocystus* and *Solenopsis*. After feeding on fruits, birds flew to perches in surrounding shrubs such as *L. tridentata*, *C. texana*, *F. splendens* and *P. glandulosa* var. *torreyana*. Contrary to the other species, *C. corax* almost completely detached the fruit and carried it out to other sites where it was immediately consumed.

Table 1. Mean (\pm SE) of number of pads, plant cover, number of fruits and number of seeds produced per ha in two consecutive years by *O. rastrera* plants in two vegetation types from the southern Chihuahuan Desert.

	Nopaleras		Grasslands	
	1996	1997	1996	1997
Pads ($\times 1000$) ha ⁻¹	50.06 (4.35)	–	3.90 (1.14)	–
Plant cover (%)	4.97 (0.43)	–	0.38 (0.11)	–
Fruits per pad	1.90 (0.04)	2.06 (0.04)	1.40 (0.05)	2.43 (0.05)
Pads bearing fruits ($\times 1000$) ha ⁻¹	2.30 (0.49)	3.11 (0.38)	0.08 (0.03)	0.47 (0.13)
Fruits ($\times 1000$) ha ⁻¹	4.37 (0.09)	6.41 (0.12)	0.11 (0.003)	1.15 (0.02)
Seeds ($\times 1000$) ha ⁻¹	909.17 (19.06)	1334.75 (25.95)	23.30 (0.79)	239.40 (5.03)

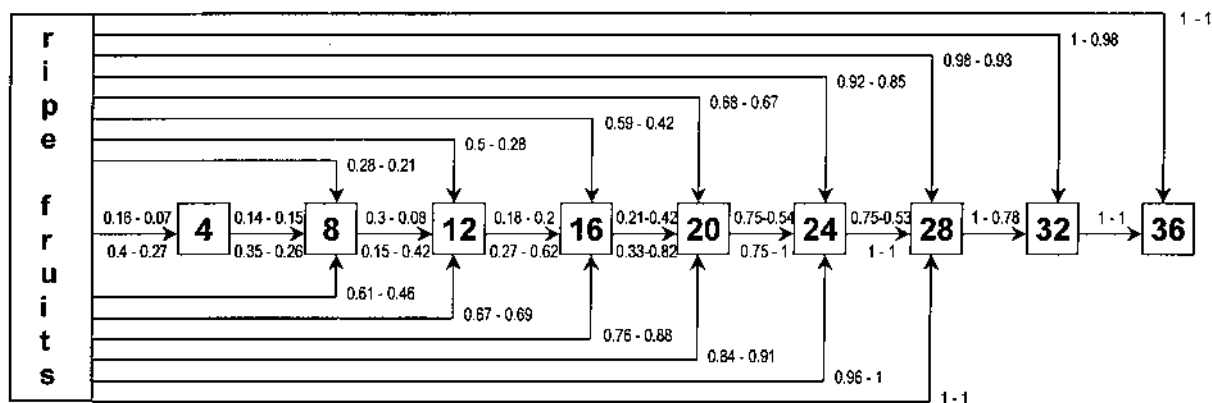


Figure 1. Vertebrate removal of *O. rastrera* fruits in nopaleras and grasslands from the southern Chihuahuan Desert in two consecutive years. Arrows originating from the ripe-fruit box and their associated values indicate the cumulative probability of removal from the start of the experiment, until the day indicated in each box (upper arrows are data for nopalera, and lower arrows for grassland). Arrows connecting adjacent boxes and their associated values (upper values for nopalera and lower values for grassland) indicate the probability of removal in the time step elapsed between both boxes. In all pairs of values, the first corresponds to 1996 data and the second to 1997 data.

Fruit consumption

Fruit consumption was faster in grasslands than in nopaleras. All marked fruit were consumed within 32 days in nopaleras in 1996 and within 36 days in 1997. In grasslands, frugivores consumed all marked fruit in 28 days in 1996 and in 24 days in 1997 (Figure 1). Fifty percent of the fruit were removed in the first 12 days in nopaleras in 1996 and in 20 days in 1997. In grasslands, consumption rates were faster (61% in the first eight days in 1996 and 46% in 1997). The ANOVAR revealed significant differences in the rate of fruit consumption between vegetation types (59.75% \pm 0.04 SE fruit per time step in nopaleras vs. 78.37% \pm 0.03 SE in grasslands; Table 3 and Figure 1), between years (71.12% \pm 0.03 SE in 1996 as compared to 67% \pm 0.04 SE in 1997) and between time steps (it was faster in the first time-steps; Figure 1).

Large mammals (mule deer and coyote) and birds were the most important frugivores because they consumed 90% and 88% of marked fruit in 1996 and 1997 (Figure 2). Rodents consumed a few fruit (less than 10% in both vegetation types and years). Ants were unimportant as consumers of fruits. Only in 1997 and in nopaleras were five percent of the fruit attacked by ants; this granivore was eliminated from subsequent analyses. Fitting of the multinomial logit model to the data showed that the pattern of fruit consumption did not differ between vegetation types ($\chi^2_2 = 1.1$, $P > 0.05$) or between years ($\chi^2_2 = 0.58$, $P > 0.05$).

Discussion

The between vegetation-types variability in fruit production is due to differences in the density of *O. rastrera*; per-pad production of fruits did not differ between habitats. The between years variability seems

Table 2. Feeding guild (according to Thyollay 1981), number of individuals (#), and relative frequency (rf) of bird species recorded at morning- and evening-visual censuses made in the summer of 1996 in nopaleras and grasslands from the southern Chihuahuan Desert.

Species	Guild*	Nopaleras # (rf)	Grasslands # (rf)	Total
<i>Amphispiza bilineata</i> (Black-throated Sparrow)	GR-IN	18 (20.4)	67 (38.2)	85
<i>Callipepla squamata</i> (Scaled Quail)	GR	8 (9.1)	–	8
<i>Cardinalis sinuatus</i> (Pyrrhuloxia)	GR	3 (3.4)	–	3
<i>Corvus corax</i> (Common Raven)	OM	14 (15.9)	8 (4.5)	22
<i>Chordeiles acutipennis</i> (Lesser Nighthawk)	IN	1 (1.1)	3 (1.7)	4
<i>Geococcyx californianus</i> (Greater Roadrunner)	IN-CA	5 (5.6)	–	5
<i>Icterus parisorum</i> (Scott's Oriole)	FR-IN	1 (1.1)	–	1
<i>Lanius ludovicianus</i> (Loggerhead Shrike)	IN-CA	15 (17)	25 (14.2)	40
<i>Myarchus cinerascens</i> (Ash-throated Flycatcher)	OM	–	1 (0.5)	1
<i>Mimus polyglottos</i> (Northern-common-Mockingbird)	FR	12 (13.6)	4 (2.2)	16
<i>Molothrus ater</i> (Brown-headed Cowbird)	FR-NE	1 (1.1)	–	1
<i>Parus gambeli</i> (Mountain Chickadee)	IN	3 (3.4)	–	3
<i>Polioptila melanura</i> (Black-tailed Gnatcatcher)	IN	1 (1.1)	2 (1.1)	3
<i>Pipilo fuscus</i> (Brown Towhee)	IN	–	36 (20.5)	36
<i>Sayornis saya</i> (Say's Phoebe)	IN	2 (2.2)	2 (1.1)	4
<i>Sayornis phoebe</i> (Eastern Phoebe)	IN	–	1 (0.5)	1
<i>Toxostoma curvirostre</i> (Curve-billed Trasher)	FR-IN	2 (2.2)	7 (4)	9
<i>Zenaida macroura</i> (Mourning Dove)	GR	2 (2.2)	19 (10.8)	21
Total		88	175	263

(*) FR=frugivore; GR=granivore; IN=insectivore; NE=nectarivore; CA=carnivore; OM=Omnivore. Species nomenclature follows Peterson & Chalif (1989).

Table 3. Analysis of deviance (logit model with binomial error) with repeated measures of the proportion of *O. rastrera* fruits removed by frugivores as a function of vegetation type, year and time step.

Source of variation	Deviance (χ^2)	df	P
Total	2713	127	
Between plots			
Vegetation type	230.6	1	< 0.00001
Plot [Vegetation type]	85.38	6	
Within plots			
Year	9.04	1	< 0.005
Year \times vegetation type	9.39	1	< 0.005
Year \times plot [vegetation type]	97.49	6	
Time step	2160	7	< 0.00001
Time step \times vegetation type	22.34	7	< 0.005
Time step \times plot [vegetation type]	54.22	42	
Time step \times year	14.14	7	< 0.05
Vegetation type \times year \times time step	9.84	7	> 0.05
Year \times time step \times plot [vegetation type]	20.51	42	

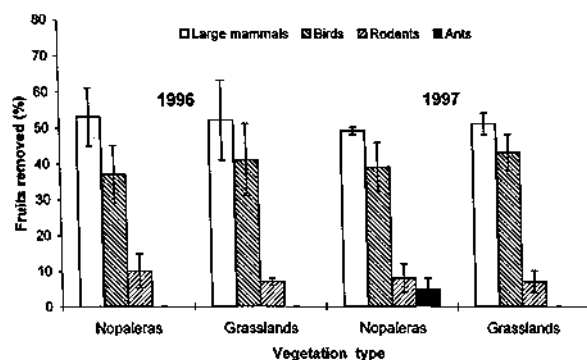


Figure 2. Percentage (mean \pm SE, $n = 4$ plots) of *O. rastrera* fruits removed by each frugivore group in nopaleras and grasslands from the southern Chihuahuan Desert in two consecutive years.

to be related to differences in the precipitation of the previous year. Two dry years (138.5 mm and 200.4 mm of rainfall) preceded the low fruit production recorded in 1996, whereas 234.7 mm fell during 1996 before the relatively high production of 1997 (data from the Mapimi Biosphere Reserve weather station). This temporal variability in fruit production, which has also been reported for other *Opuntia* species in North American deserts (González-Espinosa 1982; Quintana-Ascencio 1985), generates low predictability in resource availability to granivores at ground level, which may enhance escape from predation and thus survival opportunities for sexual propagules (Murphy 1968; Reichman 1979, 1984; Brown et al. 1979; Davidson et al. 1985; Quintana-Ascencio 1985; González-Espinosa & Quintana-Ascencio 1986; Kemp 1989; Vargas-Mendoza & González-Espinosa 1992).

Fruit consumption was high (100%) in both habitats and years. Only the rate of fruit consumption differed between vegetation types and years. In the vegetation type (nopalera) and year (1997) where there was higher fruit availability, fruits were consumed at a slower rate. This tendency of slower consumption rate when resources are abundant may reflect the adjustment time required by frugivores to totally consume the fruit production. When availability levels are high the consumption rate is limited by stomach volume, the time needed to process the food, or by the time necessary to obtain it (Holling 1965). When low levels of the resource are available (e.g., in grasslands and in 1996) these limitations are relaxed and a smaller time adjustment may be necessary to deplete the food resource (cf., Crawley 1983).

Nearly 90% of *O. rastrera* fruits were consumed by large mammals and birds in both vegetation types (nopaleras and grasslands) and years of study (1996 and 1997). These results differed from those reported by Quintana-Ascencio (1985) on the removal of fruits of two similar cacti, *Opuntia streptacantha* and *O. robusta* in nopaleras from central Mexico. In a one year study, he found that both groups of frugivores removed less than 30% of the fruits on the plants, whereas most of the fruits were removed by cricetid rodents such as *N. albigula*. According to Mandujano et al. (1997), this rodent is a predator (i.e., it consumes and totally destroys seeds) of *O. rastrera* seeds in the Mapimi Biosphere Reserve.

Both in nopaleras and grasslands *M. polyglottos*, *C. corax* and *T. curvirostre* were the most important frugivores among birds. The potential efficiency of these species as seed dispersers lies principally in their large home ranges (González-Espinosa & Quintana-Ascencio 1986), in the little damage they inflict upon seeds, and in the small quantity of seeds they deposit in their widely scattered faeces or pellets (Quintana-Ascencio 1985; Mandujano et al. 1997). All of these characteristics, together with their habit of perching in neighbouring shrubs (e.g., *L. tridentata*, *C. texana*, *F. splendens* and *P. glandulosa* var. *torreyana*) after feeding on *O. rastrera* fruits, may allow dispersed seeds to arrive at suitable sites for germination and seedling establishment under appropriate nurse plants. Under these plants the harsh desert conditions are mitigated (reduced evapotranspiration, temperature and solar radiation) and protection from seed predators and herbivores is greater than in open spaces (see Mandujano et al. 1998 and references therein).

Besides birds, *O. hemionus* and *C. latrans* were among the most important frugivores. Mandujano et al. (1997) found that mule deers are more efficient seed dispersers than coyotes because they do not affect seed viability and deposit a small number of seeds per scat. As in the case of birds, the sparse distribution of seed resources arising from the deposition of a small number of seeds in each scat or pellet may allow them to escape from predation by heteromyid rodents (González-Espinosa & Quintana-Ascencio 1986; Brown & Harney 1993) and seed harvester ants (González-Espinosa & Quintana-Ascencio 1986). The opposite can be expected in the case of coyote scats, which typically contain nearly 1,000 seeds (Mandujano et al. 1997).

Vertebrate frugivory determines phase I (*sensu* Chambers & MacMahon 1994) of *O. rastrera* seed

dispersal, and this endozoochorous process generates the input of seeds to the soil and consequently to the seed bank of nopaleras and grasslands. However, efficient fruit removal does not guarantee effective seed dispersal (Hugues & Westoby 1992) unless seeds are deposited with little or no damage in microsites suitable for germination and establishment (Willson 1986, 1993; Fleming & Sosa 1994; Shupp 1995; Shupp & Fuentes 1995). Mandujano et al. (1998) found that better microhabitat conditions (quantity and quality of safe sites) and lower granivore density favour *O. rastrera* seedling survival in grasslands, as compared to nopaleras. Despite these differences in conditions for establishment, the seedling recruitment recorded in both vegetation types is very low compared to the number of seeds produced.

As almost all fruits produced are removed by vertebrates, it can be concluded that the advantages expected from sexual reproduction (e.g., colonization of distant sites and generation of genetic variability in the population) greatly depend on seed dispersal by vertebrate frugivores. The high reproductive effort of producing a huge quantity of seeds (more than one million per ha in nopaleras and one tenth of that in the grasslands) contained in fleshy fruits rich in water and sugars (about of 300 kg of fruit per ha in nopaleras and a tenth of that in grasslands) seems to be the price that *O. rastrera* must pay, in a very asymmetric interaction with the frugivore guild, to cope with the strong ecological bottle neck that seedling establishment represents in the very harsh environmental conditions found in semiarid ecosystems.

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References

- Aitkin, M., Anderson, D., Francis, B. & Hinde, J. 1989. Statistical modelling in GLIM. Clarendon Press, Oxford.
- Bravo-Hollis, H. 1978. Las Cactáceas de México. Volumen I. Universidad Nacional Autónoma de México, México, D.F.
- Briónes, O., Montaña, C. & Ezcurra, E. 1996. Competition between three Chihuahuan Desert species: evidence from size-distance relations and root distribution. *J. Veg. Sci.* 7: 453–460.
- Brown, J. H., Reichman, O. J. & Davidson, D. W. 1979. Granivory in desert ecosystems. *Ann. Rev. Ecol. Syst.* 10: 201–227.
- Brown, J. H. & Harney, B. A. 1993. Population and community ecology of heteromyid rodents in temperate habitats. Pp. 618–651. In: Genoways, H. H. & Brown, J. H. (eds), *Biology of the Heteromyidae*. Special Publication No. 10. The American Society of Mammalogists.
- Buckley, R. C. 1982. Ant-Plant interactions: A world review. Pp. 111–142. In: Buckley, R. C. (ed.), *Ant-Plant Interactions in Australia*. Dr. W. Junk Publishers, The Hague.
- Chambers, J. C. & MacMahon, J. A. 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. *Ann. Rev. Ecol. Syst.* 25: 263–292.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298–312. In: Den Boer, P. J. & Gradwell, G. (eds), *Dynamics of Populations*. PUDOC, Wageningen.
- Crawley, M. J. 1983. *Herbivory. The dynamics of animal-plant interactions*. Blackwell Scientific Publications, Oxford, UK.
- Crawley, M. J. 1993. *GLIM for ecologists*. Blackwell Scientific Publications, Oxford, UK.
- Davison, D. W., Samson, D. A. & Inouye, R. S. 1985. Granivory in the Chihuahuan Desert: Interactions within and between trophic levels. *Ecology* 66: 486–502.
- Dirzo, R. & Domínguez, C. 1986. Seed shadows, seed predation and the advantages of dispersal. Pp. 237–249. In: Estrada, A. & Fleming, T. H. (eds), *Frugivores and Seed Dispersal*. Dr. W. Junk Publishers, Dordrecht.
- Fleming, T. H. 1991. Fruiting plant-frugivore mutualism: the evolutionary theater and the ecological play. Pp. 119–144. In: Price, P. W., Lewinsohn, T. M., Fernandes, D. W., Benson, W. W. (eds), *Plant-Animal Interactions*. Wiley, New York.
- Fleming, T. H. & Sosa, V. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *J. Mammalogy* 75(4): 845–851.
- Francis, B., Green, M. & Payne, C. 1994. *GLIM 4. The statistical system for generalized linear interactive modelling*. Royal Statistical Society, Oxford University Press Inc., New York.
- González-Espinosa, M. 1982. Seed predation by desert harvester ants and rodents in central Mexico. Ph. D. Thesis. University of Pennsylvania, Philadelphia. USA.
- González-Espinosa, M. & Quintana-Ascencio, P. F. 1986. Seed predation and dispersal in a dominant desert plant: *Opuntia*, ants, birds, and mammals. Pp. 274–284. In: Estrada, A. & Fleming, T. H. (eds), *Frugivores and Seed Dispersal*. Dr. W. Junk Publishers, Dordrecht.
- Grenot, C. & Serrano, V. 1981. Ecological organization of small mammal communities at the Bolsón de Mapimí (Mexico). Pp. 89–100. In: Barbault, R. & Halffter, G. (eds), *Ecology of the Chihuahuan Desert*. Instituto de Ecología, A.C. México, D.F.
- Holling, C. S. 1965. Functional response of predator to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Canada* 45: 1–60.

- Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201–228.
- Hugues, L. & Westoby, M. 1992. Effect of diaspore characteristics on removal of seeds adapted for dispersal by ants. *Ecology* 73(4): 1300–1312.
- Inouye, R. S., Byers, G. S. & Brown, J. H. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61: 1344–1351.
- Janzen, D. 1970. Herbivores and the number of tree species in tropical forest. *Am. Nat.* 104: 501–528.
- Janzen, D. 1986. Chihuahuan Desert nopaleras: defaunated big mammal vegetation. *Ann. Rev. Ecol. Syst.* 17: 595–636.
- Jordano, P. 1992. Fruits and frugivory. Pp. 105–156. In: Fenner, M. (ed), *Seeds: The ecology of regeneration in plant communities*. CAB, Wallingford, UK.
- Kemp, P. R. 1989. Seed banks and vegetation processes in deserts. Pp. 257–281. In: Leck, M. A., Parker, V. T. & Simpson, R. L. (eds), *Ecology of soil seed banks*. Academic Press, New York.
- Mandujano, M. C., Montaña, C. & Eguiarte, L. E. 1996. Reproductive ecology and inbreeding depression in *Opuntia rastrera* (Cactaceae) in the Chihuahuan Desert: Why are sexually derived recruitments so rare? *Am. J. Bot.* 83(1): 63–70.
- Mandujano, M. C., Golubov, J. & Montaña, C. 1997. Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the southern Chihuahuan Desert. *J. Arid Environ.* 36: 259–266.
- Mandujano, M. C., Montaña, C., Méndez, I. & Golubov, J. 1998. The relative contributions of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. *J. Ecol.* 86: 911–921.
- Montaña, C. 1988. Las formaciones vegetales. Pp. 167–197. In: Montaña, C. (ed), *Estudio integrado de los recursos vegetación, suelo y agua, en la Reserva de la Biósfera de Mapimí*. I Ambiente Natural y Humano, Instituto de Ecología, México, D. F.
- Montaña, C. 1990. A floristic-structural gradient related to land forms in the southern Chihuahuan Desert. *J. Veg. Sci.* 1: 669–674.
- Murphy, G. I. 1968. Pattern in life history and the environment. *Am. Nat.* 102: 391–403.
- Nobel, P. S. 1988. *Environmental biology of agaves and cacti*. Cambridge University Press, Cambridge.
- Peterson, J. & Chalif, M. 1989. *Las Aves de México. Guía de campo*. Editorial Diana, México, D.F.
- Pimienta-Barrios, E. 1997. Prickly pear (*Opuntia* spp.): a valuable fruit crop for the semi-arid lands of Mexico. *J. Arid Environ.* 28: 1–11.
- Pulliam, H. R. & Brand, M. R. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. *Ecology* 56: 1158–1166.
- Quintana-Ascencio, P. F. 1985. *Dispersión de las semillas de nopal (Opuntia spp.) por animales silvestres y domésticos en 'El Gran Tunal'*, San Luis Potosí. Tesis de Licenciatura. UNAM, México, D.F.
- Reichman, O. J. 1979. Desert granivore foraging and its impact on seed densities and distributions. *Ecology* 60: 1085–1092.
- Reichman, O. J. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. *J. Biog.* 11: 1–11.
- Rojas-Fernández, & Fragoso, C. 1994. The ant fauna (Hymenoptera: Formicidae) of the Mapimi Biosphere Reserve, Durango, Mexico. *Sociobiology* 24 (1): 47–75.
- Shupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Pp. 15–29. In: Fleming, T. H. & Estrada, A. (eds), *Frugivory and seed dispersal: ecological and evolutionary aspects*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Shupp, E. W. 1995. Seed-seedling conflicts, habitat choice and patterns of plant recruitment. *Am. J. Bot.* 82(3): 399–409.
- Shupp, E. W. & Fuentes, M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2(3): 267–275.
- Thyollay, J. M. 1981. Structure and seasonal changes of bird population in a desert scrub of northern Mexico. Pp. 143–167. In: Barbault, R. & Halffter, G. (eds), *Ecology of the Chihuahuan Desert*. Instituto de Ecología, A.C. México, D.F.
- Trujillo-Argueta, S. & González-Espinosa, M. 1991. Hibridación, aislamiento reproductivo y formas de reproducción en *Opuntia* spp. *Agrociencia. Serie Recursos Naturales Renovables* 1(1): 39–57.
- Turner, R. M., Alcorn, S. M. & Booth, J. A. 1966. The influence of shade, soil and water on saguaro seedling establishment. *Bot. Gazette* 127: 95–102.
- Vargas-Mendoza, M. C. & González-Espinosa, M. 1992. Habitat heterogeneity and seed dispersal of *Opuntia streptacantha* (Cactaceae) in nopaleras of central Mexico. *The Southwestern Naturalist* 37(4): 379–385.
- Venable, D. L. & Brown, J. S. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131: 361–384.
- Willson, M. F. 1986. Avian frugivory and seed dispersal in eastern North America. *Current Ornithology* 3: 223–229.
- Willson, M. F. 1993. Mammals as seed-dispersal mutualists in North America. *Oikos* 67: 159–176.
- Zar, J. H. 1996. *Biostatistical Analysis*. Third Edition. Prentice-Hall Inc., Englewood Cliffs, New Jersey.