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Effectiveness of Dispersal of an Ornithocorous Cactus *Myrtillocactus geometrizans* (Cactaceae) in a Patchy Environment

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Abstract: Effectiveness of seed dispersal by different species that feed on the fruits of *Myrtillocactus geometrizans* was evaluated, considering both quantity and quality of dispersal, in a patch of tropical deciduous forest in Zapotitlán de las Salinas. Effectiveness was estimated to be strongly influenced by the post-foraging movements of the frugivores, leading us to suggest that the quality component of seed dispersal occupies a central role in the assessment of disperser effectiveness and to expect that dispersers that stay in the tropical deciduous forest patch after foraging would have highest effectiveness. Birds were the principal dispersers of *M. geometrizans*. This was particularly true of *Phainopepla nitens*, since this species showed a high fidelity within the tropical deciduous forest. These observations emphasize that it is important to determine the post-foraging habits of seed dispersers that may move across vegetation patches over the landscape in order to obtain a complete assessment of their role in Neotropical environments.

Keywords: Arid zone, birds, cactaceae, *Phainopepla nitens*, seed dispersal, Zapotitlan valley.

INTRODUCTION

One of the central aspects of reproductive biology of plants is the role of seed dispersal by frugivores on plant regeneration, distribution, and overall population biology. Seed dispersal has been considered a link in the demographic transition between the ripe fruit crop on the trees, delivery, and the subsequent life stages [1], leading up to a particular plant population dynamics.

Since the discussion of [2], it is clear that the assessment of effectiveness of frugivores as seed dispersal agents of their food plants depends not only on the quality component, or the probability that seeds are deposited unharmed in safe sites (*sensu* [3]), nor on the quantity component, or the amount of seeds dispersed, but on both components [4]. Disperser effectiveness therefore depends on their fruit-feeding behavior, fruit processing, and post-feeding movements.

The micro-environment in which seeds are deposited may sometimes be important influences. For example, in arid lands columnar cacti recruit themselves beneath perennial nurse plants [5], which modify the environment beneath their canopies and enhance seedling establishment [6, 7]. Nurse plants provide protection against direct solar radiation, decrease soil temperatures, and increase soil moisture for seed germination and early seedling survival [6-8]. Considering this micro-environmental pattern of seedling establishment and survival, reference [9] included the nurse plant effect in the quality component of disperser effectiveness in their study of the columnar cactus *Neobuxbaumia tetetzo* (F.A.C. Weber) Backeb, indicating that only the species that deliver seeds beneath nurse plants can be considered as true dispersers.

In arid environments, considerable local variation in the structure of plant populations over very small distances, often as little as few meters [10], has been largely associated with variation in soil characteristics [11], such as soil texture and the accumulation of calcium carbonate. These properties of soils in arid lands considerably affect soil moisture, leading to a mosaic of plant associations in which different species show a patchy distribution [12].

This paper attempts to link in a single study two stages of the dispersal cycle typically investigated separately. This study deals with the assessment of quantity and quality of seed dispersal effectiveness of both nocturnal and diurnal frugivores that feed on the fruits of the columnar cactus *Myrtillocactus geometrizans* (Martius) Console. This cactus produces non-dehiscent small fruits with a ornithochorous dispersal syndrome. This cactus shows successful recruitment in patches of deep soils, in contrast to the surrounding areas in which this cactus species is marginal and shows low recruitment rates. Because the nurse-plant effect is so strong in this environment, we propose that the natural variation in the distribution of this plant may be a reflection of the quality component of effectiveness, in which good dispersers may have high site fidelity within the patches where *M. geometrizans* is naturally distributed and where it recruits successfully.

At our study site on the summit of Cutá hill, tree canopies produce a plant cover close to 100%, and seedlings and juveniles of *M. geometrizans* are randomly distributed with respect to perennial plants except under parent plants or in the rare open spaces, where seedlings do not survive. Under this condition we have hypothesized that effective dispersers would be those which deposit seeds only away from the parent plant but within the same vegetation patch.

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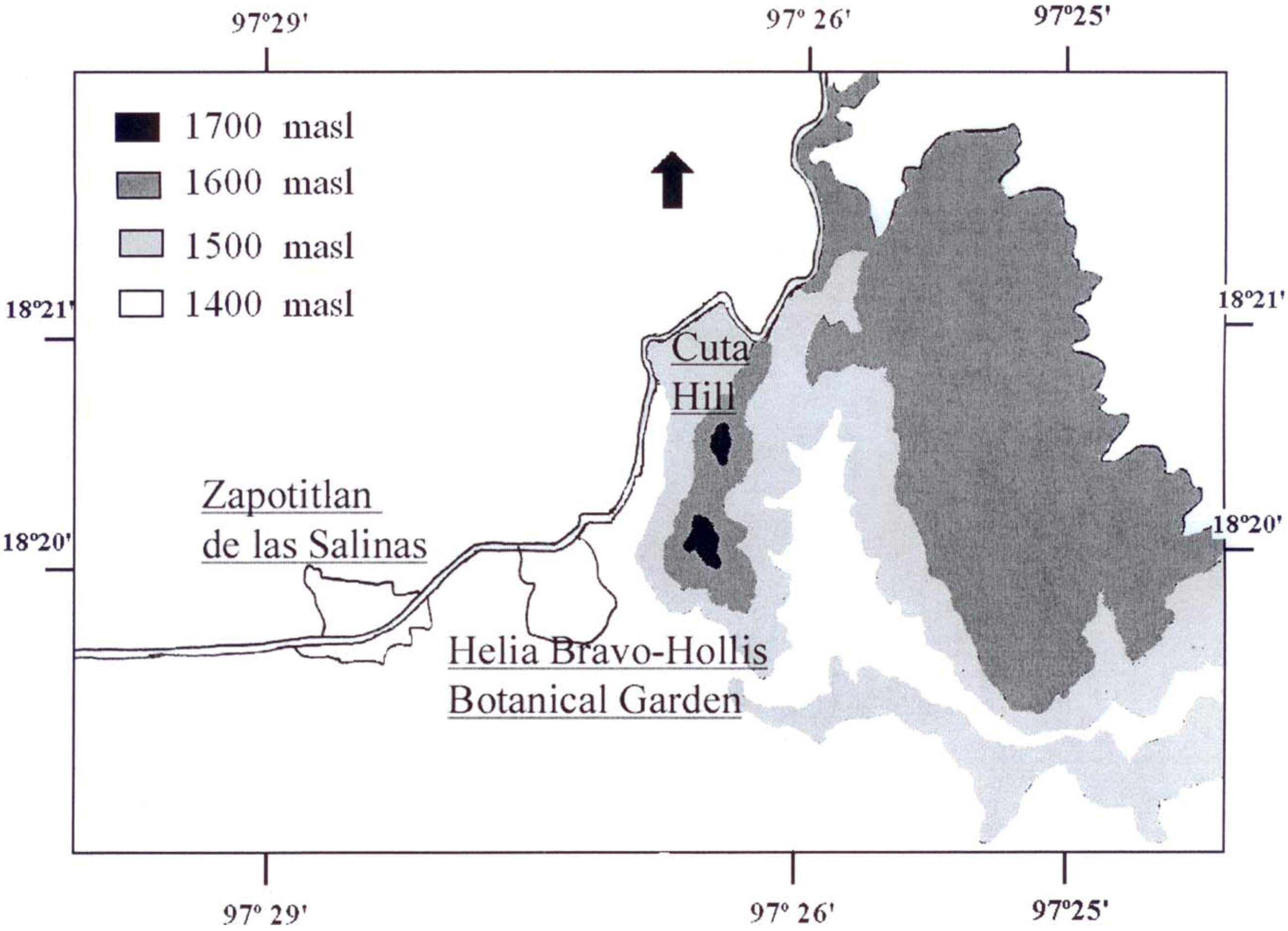

Fig. (1). Map showing the location of Cutá hill in Zapotitlán de las Salinas, México.

METHODS

Study Area

This study was conducted in the semiarid valley of Zapotitlán de las Salinas, a local basin of the Tehuacán-Cuicatlán Valley in the state of Puebla, Mexico. This region owes its aridity to the rain shadow produced by the Sierra Madre Oriental [13]. It has an annual mean rainfall of 380 mm, most of which falls during the summer months, and an annual mean temperature of 21°C with rare frosts [14].

The area is heterogeneous with hills and mountains dominating the landscape. Different lithologies are present in the study area including shale, limestone, and igneous materials [15]. The main plant associations, edaphically and lithologically controlled, are characterized by the dominance of columnar cacti which form a complex vegetation mosaic in which each patch is dominated by different columnar cacti [16]. *M. geometrizans* is distributed mostly in deep soils located at the summit of hills and in the bottom areas of the basin. Specifically, the study was conducted in the summit of Cutá hill (Fig. **1**), a mountain of Cretaceous age at 1700 m a.s.l. The vegetation on the summit is tropical deciduous forest, characterized by a predominance of *M. geometrizans*, *Pachycereus marginatus* (DC.) Britton and Rose, *Stenocereus pruinosus* (Otto) F.Buxb., *Ceiba parvifolia* (Rose), *Pereskiopsis oaxacana, Prosopis laevigata* (Humb. and Bonpl. ex Willd) M.C. Johnston, *Acacia sericea* (Mart. and Gal.) and the shrubs *Mimosa lacerata* (Rose), *Mimosa luisana* (Brandegee), *Opuntia pilifera* (F.A.C. Weber), and *Hechtia* sp. [16, 17].

Ornithochory Syndrome

The presence of ornithocory syndrome in *M. geometrizans* was determined using the characteristics of its fruits, such as size, color, location and the identity of its consumers. The importance of the fruits to its consumers was determined based on the fruiting season and the average number of fruits produced per plant, and was compared with the fruiting season of other cactus species in the region (Tehuacán valley, which includes Zapotitlán) using data from [18].

Fruit nutritional quality was assessed by determining their content of proteins (Kjeldahl's method), total carbohydrates (Antrona de Clegg's method) and lipids (Soxhlet's method) [19, 20].

Diurnal *vs*. Nocturnal Fruit Removal

To compare diurnal *vs*. nocturnal fruit removal, 154 mature *M. geometrizans* fruits from 5 adult plants were marked; the number of marked fruits was counted at 0600 and 1830 h over a 3-day period, and fruit traps were placed below each plant to account for the possibility of marked fruits having fallen rather than having been consumed. The number of fruits removed during day and night and those that fell below the parent were compared by using a X^2 test assuming an equal number of fruits during the three periods.

Dispersers and Effectiveness of Seed Dispersal

A species accumulation curve was made to estimate the total number of frugivores that feed on *M. geometrizans,* independently of whether all were actually recorded [21]. The species accumulation curve used an abundance-based coverage estimator [22] with 50 randomizations of sample order.

Effectiveness was estimated considering the quantity and quality components of seed dispersal, as proposed by [2]. The quantity component was estimated using data on the frequency of visits per hour by frugivores and mean number of fruits consumed per visit. The quality component was estimated using data on percent of germination after gut passage, probability that the seeds are deposited far from the parent plant, site fidelity (percent daily recapture rate, considered to be correlated with the probability that the seeds would stay within the summit of Cutá hill and therefore that they would be deposited in a suitable patch for germination) and probability of seeds being deposited under a shrub or tree.

Effectiveness of each potential frugivore species was calculated as the product of the following components: (Effectiveness= frequency of visits × mean of fruits consumed per visit × percent germination × probability of the seeds being deposited under a shrub × frequency of recapture × percent establishment).

Quantity Component

Frequency of Visits and Mean of Fruits Consumed per Visit

Frequency of visits was observed during the entire 1998 fruiting season of *M. geometrizans*, from March 9 to June 7. Observations were made on 3 individuals of *M. geometrizans* at each of four observation points as in [23]. In all, visit frequency was observed during 24 days from 0700 to 1200 and from 1500 to 1730 h, the peak hours of bird activity, embracing a total of 98 h of observation [24, 25].

Birds were recorded using 20 × 50 Super Zenith and 10 × 25 Samyang binoculars and identified using field guides [26, 27].

For each visit to a plant by a potential disperser the hours of arrival and departure were recorded, and when possible also the number of fruits consumed, the handling time in seconds from when the bird first touched a fruit until it swallowed the fruit, the foraging technique (following the classification of Moermond and Denslow [28]), whether the first perch after consuming fruits was a shrub (potential nurse-plant) or a cactus, and the distance to that first perch.

For mammals, the same observation points were used from 1900 to 2400 h, using a night-vision panoramic viewer (Night Voyager II Vision in Night 1 #50 N 3 I00520), embracing a total of 90 h of observation. Also, for mammals other than bats, droppings containing *M. geometrizans* seeds were collected for subsequent identification using [29]. Data recorded were whether the dropping was found under a tree, shrub or in an open area and the number of *M. geometrizans* fruits and seeds it contained.

Quality Component

Seed Germination

Captured birds and bats were placed in separate cloth bags during 10 min to collect their droppings. Droppings were placed in opaque paper bags. Mammal droppings found in the study area were also placed in paper bags.

The most frequent visitors that did not act as seed predators were placed in individual cages (90 × 60 × 40 cm) for up to 2 days. At least 3 replicates were obtained for each species placed in captivity. Following [30] and [31], birds were fed at 0800 h after their digestive tract had been emptied overnight. Bats were fed at night (2100 to 2400 h) following the same procedure (*cf.* [32]).

Ten fruits of *M. geometrizans* (each one weighing 1 g) were given to each individual and at approximately 1300 h, any fruit remaining was withdrawn and weighed (fresh weight). Droppings were placed in paper bags.

The following was recorded for each individual placed in captivity: foraging method, handling time and gut passage (time until the seeds were expelled) [30, 31, 33].

For each species of potential disperser, three replicas of 50 *M. geometrizans* seeds obtained from droppings were put to germinate in Petri dishes with filter paper and 4 mL of purified water (n=150 seeds for each potential disperser and 150 for the control). Three replicas of 50 control seeds obtained directly from fruits were treated in the same way as a control. Before being placed in the Petri dishes, seeds were washed with 10% sodium hypochlorite in order to avoid fungal contamination. Petri dishes were checked daily to count the number of germinated seeds and therefore to estimate daily germination rate. A seed was considered to have germinated once the radicle had emerged [34, 35]. Percent of germination measured after 24 days was arcsin transformed and both a one-way analysis of variance and Tukey's test (multiple comparison) were used to test for significant differences between species and to identify the species with significant differences in germination percentages [36]. The tests were conducted using SPSS For Windows [37].

Frequency of Recapture

Recapture frequency for each species was calculated as the number of times individuals of that species were recaptured divided by the total number of times that species was captured including recaptures.

Rate of Establishment

During the rainy season (June 2002), 450 *M. geometrizans* seeds extracted from frugivore droppings were planted on the summit of Cutá hill. Seeds were sowed under the dominant species *Prosopis laevigata*, with 50 seeds per experimental unit, taking care not to alter the proportion of stones and organic matter in the soil [38, 39]. Seeds were checked monthly from July to December to count the number of seedlings, in order to calculate percent germination on the summit of Cutá hill.

For the calculation of dispersal effectiveness, data was missing on the probability of seeds being deposited under a shrub for 5 of the 24 species, and data was missing on percent germination for 7 of the species. To fill in the gaps, data for the remaining species was used to perform linear regression between the variable with missing data and the other variables. Once the best linear regression (highest r^2) was found, the resulting formula was used to replace the missing data with realistic values. When the estimated value was negative (always close to zero), the arbitrary value 0.001 was used to fill in the missing value.

The regressions used to calculate these missing values were the following: the probability that a seed was deposited under a shrub was correlated with the frequency of recapture with an r^2 of 0.74, while the percentage of germination was correlated with the frequency of visits per day with an r^2 of 0.47.

RESULTS

The fruiting season for *M. geometrizans* (March to September) was long compared to other cactus species found in the region (Tehuacán valley) (Table **1**). Fruits are small, measuring 15.44 ± 3.04 by 10.20 ± 2.24 mm (mean ± standard deviation) and there was an average of 85 ± 33.34 seeds per fruit. Adult plants on average produced 7650 fruits. Mature fruits were purple and were composed mainly of water (63%), total carbohydrates (24%), lipids (3%) and protein (3%). Fruits were located on ribs along the branches (exposed). Fruit removal was significantly higher by diurnal seed dispersers (60%) than either nocturnal seed dispersers (33%) or fallen fruits (7%) ($X^2=42.15>X^2_{0.05(2)}5.99$).

Table 1. Fruiting Season of Different Species of Cacti in the Tehuacán Valley, Puebla. (+) Indicates the Species which occur in the Valley of Zapotitlán de las Salinas. Based on [18] and [40]

Fruiting Season of Some Cacti												
Species	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Myrtillocactus geometrizans (+)			■	■	■	■	■	■	■			
Cephalocereus columna-trajani (+)-					■	■	■	■				
Cephalocereus purpusii Britt. & Baker						■	■	■	■	■		
Escontria chiotilla (F.A.C. Weber) Rose								■	■			
Neobuxbaumia macrocephala (Weber) Dawson					■	■	■	■	■			
Neobuxbaumia mezcalensis (Bravo) Backeb.					■	■	■					
Neobuxbaumia tetetzo (+)				■	■	■						
Pachycereus fulviceps (Weber) Backeb.						■	■	■	■			
Pachycereus hollianus. (+)					■	■	■	■	■	■		
Pachycereus pecten-aboriginum Britt. & Rose	■	■	■	■	■	■						
Pachycereus weberi (Coutler) Backeb.		■	■	■	■	■						
Stenocereus chrysocarpus Sanchez-Mejorada					■	■						
Stenocereus dumortieri (Scheidw.) Buxb.					■	■						
Stenocereus fricii Sanchez-Mejorada				■	■	■	■	■				
Stenocereus marginatus (+)			■	■	■							
Stenocereus pruinosus (+)					■							
Stenocereus standleyi (Gonzalez-Ortega) F. Buxb.						■	■	■	■			
Stenocereus stellatus (Pfeiffer) Riccob. (+)						■	■	■	■	■		

Dispersers and Effectiveness of Seed Dispersal

Quantity

A total of 25 frugivorous bird species was recorded (Table **2**), of which 74% were considered seed dispersers rather than seed predators according to the literature, beak morphology and whether the seeds were expelled intact in faeces.

The species acumulation curve estimated that 91% of the frugivorous birds that feed on *M. geometrizans* were recorded (Fig. **2**).

Table 2. ^{1}**Species: Seed Dispersers° and Seed Predators**†
^{2}**Diet: G (Granivore), F (Frugivore); I (Insectivore), N (Nectarivore). Data on Diet are taken from [40, 41] and [42].**
^{3}**Habitat: MF (Mesquite Forest), C (*Cephalocereus columna-trajani* shrubland), T (*Neobuxbaumia tetetzo* shrubland).**
^{4}**Status: R (Resident), M (Long-distance migrant), ML (Local migrant).**

Birds Recorded Feeding on *Myrtillocactus geometrizans* Fruits in Zapotitlán de las Salinas, Puebla			
Order **Family** **Species^{1}**	**Diet^{2}**	**Habitat^{3}**	**Status^{4}**
Columbiformes			
Columbidae			
Zenaida asiatica † (Linnaeus)	GF	MF,C,T	R
Trogoniformes			
Trogonidae			
Trogon elegans$^{\circ}$	IF	MF	ML
Coraciiformes			
Momotidae			
Momotus mexicanus^{1} (Swainson)	IF	MF	R
Piciformes			
Picidae			
Melanerpes hypopolius$^{\circ}$	FIN	MF,C,T	R
Picoides scalaris$^{\circ}$ (Wagler)	IF	MF,C,T	R
Passeriformes			
Tyrannidae			
Myiarchus tuberculifer$^{\circ}$	IF	MF,T	R
Myiarchus cinerascens$^{\circ}$	IF	MF,T	M
Myiarchus nuttingi$^{\circ}$ (Ridgway)	IF	MF,T	R
Myiarchus sp.$^{\circ}$	IF	MF,T	
Tyrannus vociferans$^{\circ}$	IF	MF,T	R
Troglodytidae			
Campylorhynchus jocosus$^{\circ}$ (Sclater)	I	MF,T,C	R
Turdidae			
Catharus guttatus$^{\circ}$	IF	MF	M
Mimidae			
Mimus polyglottos$^{\circ}$	IF	MF,T,C	R
Toxostoma curvirostre$^{\circ}$ (Swainson)	IF	MF,T,C	R
Ptilogonatidae			
Phainopepla nitens$^{\circ}$	FI	MF	R
Emberizidae			
Aimophila mystacalis† (Hartlaub)	G	MF,C,T	R

(Table 2) Contd…..

Order **Family** **Species^1**	**Diet^2**	**Habitat^3**	**Status^4**
Cardinalidae			
Piranga sp.°	IF	MF,C	M
Pheucticus chrysopeplus† (Vigors)	IGF	MF	R
Pheucticus melanocephalus† (Swainson)	IGF	MF	R
Passerina versicolor†	IG	MF,C,T	R
Icteridae			
Icterus wagleri√	IFN	MF,T	ML
Icterus pustulatus√	IFN	MF,T	ML
Icterus parisorum√	IFN	MF,T	ML
Fringillidae			
Carpodacus mexicanus†	G	MF,T,C	R
Carduelis psaltria†	GI	MF,T,C	R

One frugivorous bat species (*Sturnira lilium* (Geoffroy) was recorded and 2 non-volant mammal species *Urocyon cinereoargenteus* (Schreber) and *Bassariscus astutus* (Lichtenstein) were identified from their droppings.

Tyrannidae, Cardinalidae and Icteridae were the bird families with the most species of potential dispersers of *M. geometrizans* (4-5,4 and 3 species, respectively). Five species of Tyrannidae were mainly insectivorous (*sensu* [42]), three species of Cardinalidae were mainly granivorous and all species of Icteridae were frugivorous-nectarivorous. Eight of the 25 bird species recorded can be found in all four habitats in the region, 16 are considered residents, 4 are local migrants and 3 are long-distance migrants (see Table **2**).

The majority (67%) of bird species plucked the fruits and swallowed them whole (e.g., *Phainopepla nitens* (Swainson), *Melanerpes hypopolius* (Wagler), *Mimus polyglottos* (Linnaeus) and *Tyrannus vociferans* (Swainson)).

Bird species such as *Carpodacus mexicanus* (Müller), *Passerina versicolor* (Bonaparte), *Carduelis psaltria* (Say), *Icterus pustulatus* (Wagler), *I. parisorum* (Bonaparte) and *I. wagleri* (Sclater) opened up fruits by pecking and then swallowed the pulp, a combination of foraging types II and

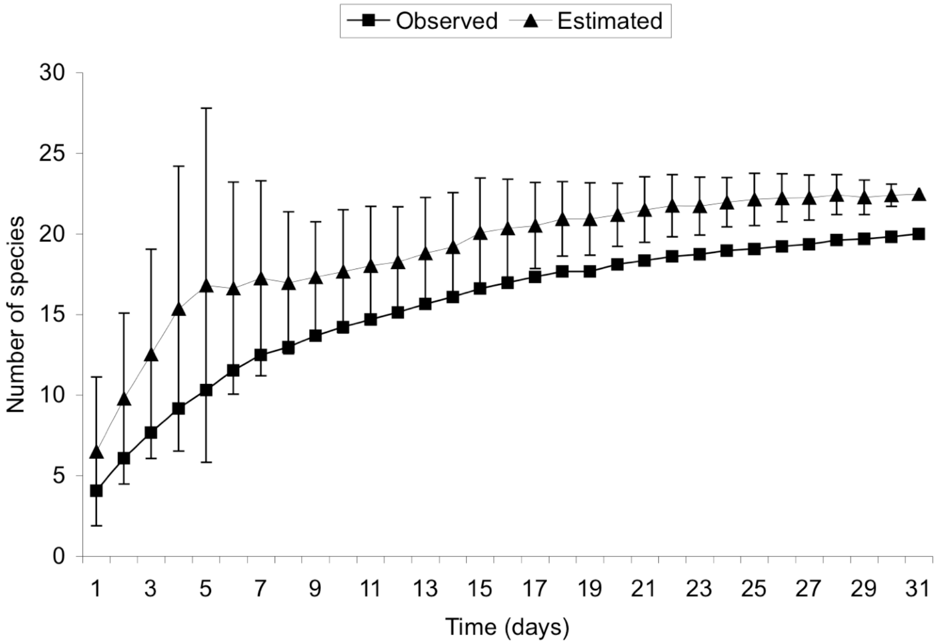

Fig. (2). Species acumulation curve for birds that were recorded feeding on the fruits of *Myrtillocactus geometrizans*_in Zapotitlán de las Salinas, Puebla (estimated values according to the Abundance-based Coverage Estimator, with standard deviation).

III described by [28], and in this way most seeds were destroyed.

Time spent foraging, foraging efficiency and social behaviour influenced the quantity of fruits that birds consumed, those birds that plucked fruits whole being the most efficient, taking only seconds to feed. For example, *P. nitens* visited individual *M. geometrizans* for short periods (average: 57 s) and in pairs, each individual consuming an average of 2 fruits per visit; *M. polyglottos* visited singly and consumed an average of one fruit per visit and *M. hypopolius* tended to forage in groups of three, with each consuming an average of 2 fruits per visit. These species consumed a larger number of fruits in a given time, and thereby removed a larger number of seeds per visit.

The bird species with the highest frequency of visits were *Melanerpes hypopolius, Phainopepla nitens* and *Carpodacus mexicanus*; however, *C. mexicanus* cannot be considered as a seed disperser because 99% of the seeds that pass through its digestive system were destroyed (Table **3**).

Because the same effort was made to observe diurnal and nocturnal frugivory in the field and yet no visits by mammals were observed, the visit frequency for *Sturnira lilium* and other mammals was not calculated, because our presence may have discouraged visits by those species during observation and according to Rojas-Martínez (pers. comm.), *S. lilium* is a rare species, both in the summit of Cutá and in the lower parts of the valley. Within its range, this species tends to be found in more humid areas close to permanent streams [43, 44].

Table 3. Probability of Seed Deposition and Estimated Number of Seeds Deposited Beneath Nurse Plants, [1]Calculated on the Basis of an Estimated 44753 Seeds Dispersed by Frugivores

Seed Deposition in the Zapotitlán Valley, Mexico							
Frugivore Species	**Frequency of Recapture**	**Estimated Number of Seeds Dispersed within the Patch**	**Number of Seeds Predated**	**Deposition Probability Beneath Nurse Plants**	**Number of Seeds Deposited Beneath Plants**	**Deposition Probability Beneath Columnar Cactus**	**Number of Seeds Deposited Beneath Cacti**
A. mystacalis	0.56	0	2550	0	0	0	0
C. jocosus	0	0	0	0	0	0	0
C. psaltria	0	0	170	0	0	0	0
C. mexicanus	0.33	0	17850	0	0	0	0
C. guttatus	0	0	0	0	0	0	0
I. parisorum	0	0	0	0	0	0	0
I. pustulatus	0	0	0	0	0	0	0
I. wagleri	0	0	0	0	0	0	0
M. hypopolius	0.04	1428.500	0	0.138	197.133	0.862	1230.881
M. polyglottos	0	0	0	0	0	0	0
M. mexicanus	0.4	14.570	0	0.857	12.486	0.143	2.081
M. cinerascens	0.33	100.180	0	0.001	0.100	0.999	100.080
M. nuttingi	0	0	0	0	0	0	0
M. tuberculifer	0.75	38	0	0.001	0.038	0.999	37.962
P. versicolor	0	0	85	0	0	0	0
P. nitens	0.5	18565	0	0.714	13255.410	0.286	5304.286
P. chrysopeplus	0	0	170	0	0	0	0
P. melanocephalus	0.15	0	1785	0	0	0	0
P. scalaris	0	0	0	0	0	0	0
Piranga sp	0	0	0	0	0	0	0
T. curvirostre	0	0	0	0	0	0	0
T. elegans	0.33	12.020	0	0.001	0.012	0.999	12.008
T. vociferans	0.5	1093	0	0	0	1	1093
Z. asiatica	0	0	1190	0	0	0	0
TOTAL		**21251.270**	**23800**		**13470.915**		**7780.298**
PERCENT[1]		**47.486**			**30.101**		**17.385**

Table 4. Average Handling Time and Gut Passage Time of Seeds of *Myrtillocactus geometrizans* of Species kept in Semi-Captivity. [1]± Standard Deviation. [2]min-max

Handling of Fruits				
Species	**Average Handling Time (s) [1]**	**Average Gut Passage Time (s)[1]**	**Handling Time[2] (s)**	**Sample Size**
Sturnira lilium	144.8 ± 84.3	4500	40-314.3	11
Icterus pustulatus	26.1 ± 35.4	2520	2.1-63.6	8
Phainopepla nitens	16.5 ± 14.3	1092 ± 7.7	1-52.77	8
Melanerpes hypopolius	13.7 ± 15.8	862.8 ± 8.4	3.2-36.38	17
Mimus polyglottos	4.7 ± 2.4	1005 ± 13	2.5-10.5	3
Tyrannus vociferans	4.2 ± 2.4	-	2-7	4

The frugivorous birds placed in captivity did not hold the fruits in their digestive tract for more than half an hour, whereas the bat *S. lilium* retained fruits for more than one hour (Table **4**).

Droppings of *Bassariscus astutus* contained 3 to 41 fruits and an average of 542.41 ± 436.29 seeds per dropping (n= 14). Droppings of *Urocyon cinereoargenteus* contained from 1 to 24 fruits and an average of 877 ± 483.9 seeds per dropping (n= 12). An estimated 94% and 99.25%, respectively, of the seeds in droppings of *B. astutus* and *U. cinereoargenteus* belonged to *M. geometrizans*, while most of the remainder were from *Stenocereus pruinosus*. All droppings of *U. cinereoargenteus* were found in open areas not suitable for seedling establishment (on trails or on top of boulders), while 96% of droppings of *B. astutus* were found in open areas (the remainder being beside rocks).

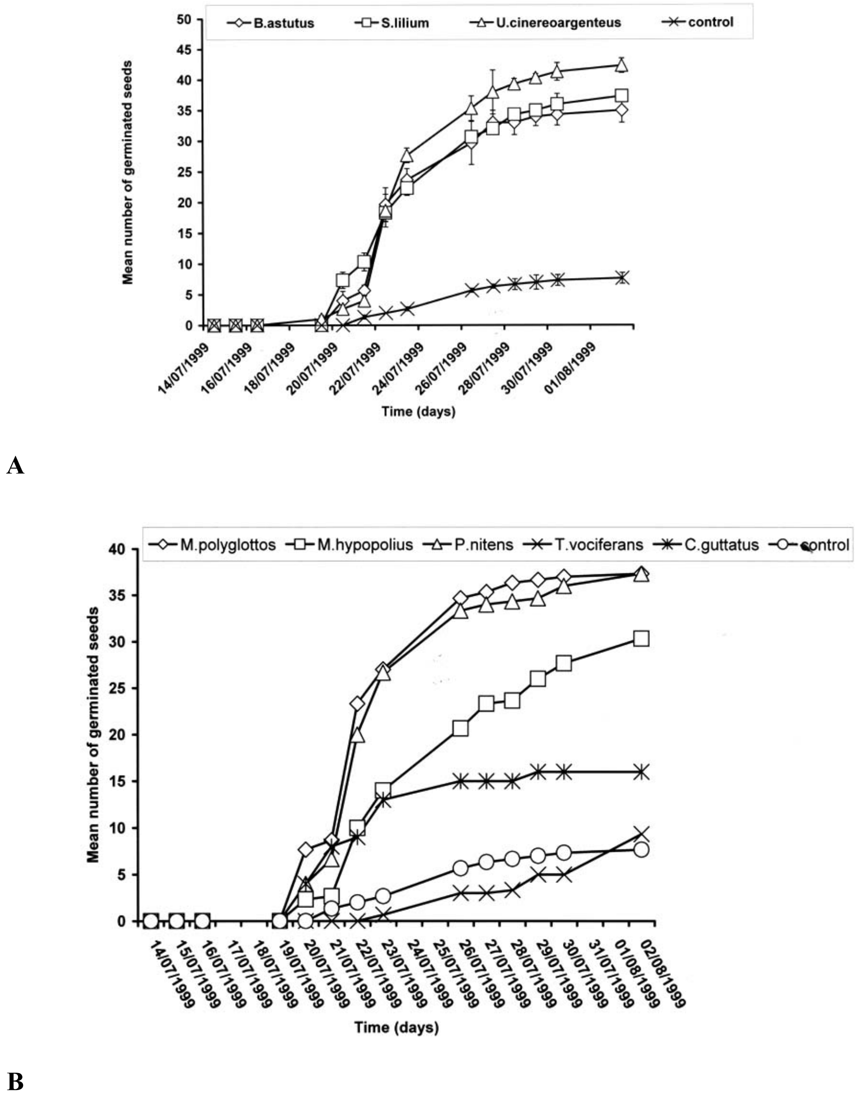

Fig. (3). Germination rate after passing through the digestive tract of mammals (**A**) and birds (**B**) in Zapotitlán de las Salinas, Puebla.

Quality

Percent Germination

Mean percent germination for mammal species in the laboratory were: *Urocyon cinereoargenteus* (85 ± 1.20), *Sturnira lilium* (75 ± 0.89) and *Bassariscus astutus* (70 ± 2). The bird species with the highest percent germination were *Mimus polyglottos* (75 ± 1.45), *Phainopepla nitens* (75 ± 2.2), *Melanerpes hypopolius* (61 ± 3.71), *Catharus guttatus* (Pallas) (34 ± 1.3) and *Tyrannus vociferans* (18.67 ± 1.45). Control seeds had the lowest percent germination (15 ± 0.89) (Figs. **3A** and **3B**), the difference being significant (F= 4.45, df= 9, P < 0.001). Tukey's test revealed significant differences between the percent germination of *U. cinereoargenteus* and *T. vociferans* (P<0.001), *U. cinereoargenteus* and control (P<0.003), *S. lilium* and *T. vociferans* (P<0.004), and between *S. lilium* and control (P<0.009). However, germination in the field was lower (2% for all disperser species). All species with high percent germination had high germination rates.

Site Fidelity

The post-feeding behavior of the most abundant bird species indicated that *Melanerpes hypopolius* left the patch (summit of Cutá hill) after feeding on *M. geometrizans* 82% of the time (n = 130), flying downhill to where *Cephalocereus columna-trajani* (Weber) Schuman, or *Neobuxbaumia tetetzo* were abundant. When the first perch after feeding was within the patch, the average distance from the plant on which the bird fed was 22 ± 18 m (n = 8). *Phainopepla nitens* remained within the patch 87% of the time (n = 163) and the average distance to the first perch was 20 ± 16 m (n = 30). Given this behavior, 47.486% of the fruits consumed were deposited within the patch (Table **3**).

The bird species that remained in the patch produced a higher probability that seeds were deposited below nurse plants, specially *P. nitens* (0.71) and *Momotus mexicanus* (0.85) (Table **5**).

Table 5. Effectiveness of Frugivores that Feed on *Myrtillocactus geometrizans* Fruits in the region of Zapotitlán, Puebla, Mexico. [1]Effectiveness was Calculated by Multiplying the Values in each Row of Table 5 **by 0.02, which was the Establishment Rate for *M. geometrizans* Seedlings in the Study Site**

Species	Mean of Fruits Consumed per Visit	Frequency of Visit/Day	Probability of Seeds Being Deposited Under Shrub	Frequency of Recap/Day	Germination (%)	Effectiveness[1]
Phainopepla nitens	1.620	6.292	0.714	0.500	74.667	5.4341
Melanerpes hypopolius	2.020	4.667	0.138	0.042	60.667	0.06629
Tyrannus vociferans	1.800	0.333	0.148	0.500	18.667	0.0165
Trogon elegans	1.000	0.010	0.0456	0.330	50.000	0.00015
Momotus mexicanus	1.000	0.010	0.857	0.400	0.13498	0.0000092
Myiarchus cinerascens	1.000	0.083	0.0456	0.330	0.1374	0.0000034
Myiarchus tuberculifer	1.000	0.042	0.001	0.250	0.136	2.86E-08
Aimophila mystacalis	3.000	0.417	1.000	0.560	0,000	0
Campylorhynchus jocosus	1.000	0.167	0.750	0.000	0.1402	0
Carduelis psaltria	1.000	0.083	0.001	0.000	0.000	0
Carpodacus mexicanus	2.800	3.125	0.507	0.330	0.000	0
Catharus guttatus	1.000	0.010	0.001	0.000	34.000	0
Icterus parisorum	1.000	0.042	0.286	0.000	30.000	0
Icterus pustulatus	1.000	0.250	0.286	0.000	30.000	0
Icterus wagleri	1.000	0.083	0.286	0.000	30.000	0
Mimus polyglottos	1.330	0.250	0.542	0.000	74.667	0
Myiarchus nuttingi	1.500	0.167	0.001	0.000	0.1402	0
Passerina versicolor	1.000	0.042	60.267	0.100	0.000	0
Pheucticus chrysopeplus	1.000	0.083	0.001	0.000	0.000	0
Pheucticus melanocephalus	3.000	0.292	90.478	0.150	0.000	0
Picoides scalaris	1.000	0.010	0.001	0.000	0.1349	0
Piranga sp	1.000	0.042	0.001	0.000	0.136	0
Toxostoma curvirostre	1.330	0.292	0.500	0.000	25.000	0
Zenaida asiatica	2.000	0.292	0.220	0.000	0.000	0

Recapture Frequency of the most Abundant Frugivores

Phainopepla nitens was sedentary in the summit of Cutá hill, at least during the fruiting season of *M. geometrizans*, with the highest daily recapture frequency (0.50/d), followed by *Myiarchus tuberculifer* d' Orbigny and Lafresnaye and *M. cinerascens.* Lawrence (0.25 and 0.33 respectively). *Melanerpes hypopolius* Gould had the lowest frequency of recapture (0.04) (Table **5**).

The rate of establishment in the field experiment was 0.02.

Phainopepla nitens (5.4341) was the species with the highest effectiveness, followed by *Melanerpes hypopolius* (0.06629) and *Tyrannus vociferans* (0.0165) (Table **5**).

Fig. (**4**) summarizes seed deposition by the two main dispersers, *P. nitens* remaining in the summit of Cutá hill while *M. hypopolius* carries out extensive movements into adjacent habitats, providing the possibility of carrying seeds to other vegetation associations such as those dominated by the columnar cacti *Stenocereus pruinosus*, *Neobuxbaumia tetetzo*, *Stenocereus stellatus*, and/or *Cephalocereus columna-trajani*.

DISCUSSION

Due to its large fruit crop and long fruiting season, fruits of *M. geometrizans* were an important resource to the bird and mammal populations of the Zapotitlán region, as revealed by the high proportion of *M. geometrizans* seeds in non-volant mammal droppings and the large number of bird species that fed on it. *M. geometrizans* produced fruit during the months of lowest fruit availability in the Zapotitlán region (see [18]), further indicating this plant's importance to the vertebrate community in the region. The observation that most of the consumers of *M. geometrizans* were bird species was consistent with its ornithocory syndrome revealed by the features of its fruits (numerous, small, succulent, colorful, with a large number of small seeds, and rich in carbohydrates), features typical of fruits dispersed by unspecialized dispersers [45-50]. The amount of carbohydrates and lipids fell within the range of values for ornithocorous fruits found in other studies (see [47, 51-54]).

The 24 species of frugivorous birds observed feeding on the fruits of *M. geometrizans* correspond to 27% of the avifaunal diversity recorded for the region [42] and 35% of the 68 bird species recorded in the summit of Cutá during the fieldwork. These bird species were either mainly frugi-

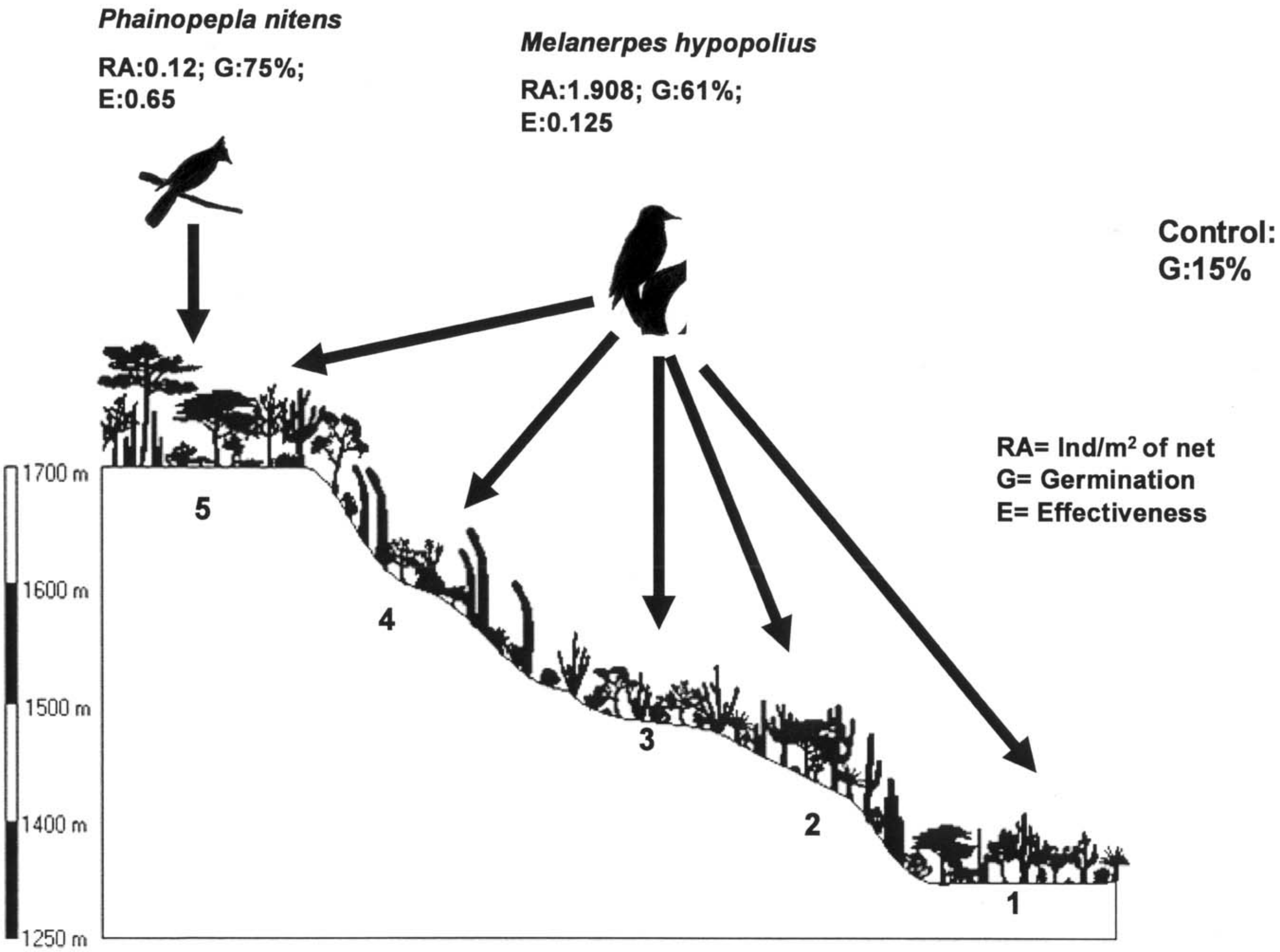

Fig. (4). Relative abundance (RA), germination after gut passage (G) and effectiveness in seed dispersal (E) of the most effective dispersers of the columnar cactus *Myrtillocactus geometrizans* in the Zapotitlán de las Salinas valley. Germination in control treatment considered seeds obtained directly from fruits. Numbers below the profile indicate plant associations dominated by the columnar cacti: (1) *Stenocereus pruinosus*; (2) *Neobuxbaumia tetetzo*; (3) *Stenocereus stellatus*; (4) *Cephalocereus columna-trajani*; and (5) *Myrtillocactus geometrizans* (modified from [13].

vorous, or mainly insectivorous but complement their diet with fruits mainly during the dry season when populations of insects diminish [55].

A high proportion of frugivorous birds in this study (67%) fed by plucking and swallowing fruits whole, being legitimate dispersers, in contrast to the species that mashed fruits such as *Carpodacus mexicanus,* which destroyed most of the seeds and deposited those that are not destroyed under the parent plant [4, 28, 31, 56]. The fallen seeds were probably destroyed by the harvester ant *Pogonomyrmex barbatus* F. Smith (M. Pérez-Villafaña, personal observation).

Most of the seeds of *M. geometrizans* were removed during the day by birds, whereas during the night the non-volant mammals, *U. cineroargenteus* and *B. astutus*, climbed the plants to get fruits [57]. Likewise, some seeds were obtained from the droppings of captured individuals of the bat *Sturnira lilium* but this species was not observed foraging in the field.

The non-volant mammals *U. cinereoargenteus* (877 seeds/dropping) and *B. astutus* (542 seeds/dropping), although they defecate a large number of viable seeds, placed their droppings in exposed sites that are not suitable for germination, placing them instead in sites where they function in intraspecific communication [57, 58]. On the other hand, birds deposited 2 to 4 seeds per dropping, thus increasing the probability of survival by reducing predation and competition [59], and tended to deposit their droppings while perched. In the Zapotitlán valley, the temperature in exposed sites has been found to reach up to 65°C, which causes death of the large majority of seeds or seedlings, whereas below nurse plants temperatures tend to be 10−20°C [9, 60].

Seed germination after passing through the gut of the majority of species tested was much higher than in seeds extracted directly from the fruit, highlighting the importance of these frugivores in seed germination, as occurs with *Pachycereus hollianus* (Weber) Buxb. and *Stenocereus gummosus* (Englem) [25]. Seed coats are exposed to grinding in a bird's gizzard, and the removal of the pulp sometimes is sufficient to increase germination by removing inhibitors found in the pulp [61, 62]. Also, various studies indicate that modification of the seed coat by substances in the ingested food can increase germination as a function of the time period during which the seed is retained in the digestive tract [63-66].

In the case of *M. geometrizans* it is possible that there is a specialized relationship with bird species which improve seed germination once the seeds have been passed through the digestive tract, whereas in other cacti such as *Neobuxbaumia tetetzo*, *N. macrocephala* (F.A.C. Weber) Dawson, *N. mezcalaensis* (H.Brav.-Holl) Backeb , *Stenocereus pruinosus* (Otto) F. Buxb., *Cephalocereus columna-trajani*, seed germination is not improved after seed passage through dispersers's digestive tracts [9].

Seed dispersal effectiveness values indicated that the birds *Phainopepla nitens* and *Melanerpes hypopolius* were the most important seed dispersers of *M. geometrizans* whereas the remaining 22 bird species had very low or even zero values because they destroyed seeds.

Likewise, when the seed dispersal process was analyzed considering post-foraging behavior of the species, the overall balance indicated that 31% of the seeds were dispersed within the vegetation patch in which *M. geometrizans* grows naturally, 35% were predated by birds and insects and only 34% of the seeds were dispersed out of the patch. Within the mesquite forest *Phainopepla nitens* showed a high fidelity to the vegetation type and after feeding spent most of the time perched on trees and shrubs, under which *M. geometrizans* successfully grows. This bird has been reported as an obligate inhabitant of honey mesquite forests in the lower Colorado Valley from Fall to Spring, feeding on fruits of the mistletoe (*Phoradendron californicum* Nutt.) which primarily parasites honey mesquite trees (*Prosopis velutina* Woot.). Mistletoe is used by Phainopeplas as nesting sites and as a main winter food, whereas wolfberry fruits (*Lycium pallidum* Miers.) are an important postnesting food [67].

In our study area, mesquite forests are dominated by the tree *Prosopis laevigata* which is parasitized also by the mistletoe *Phoradendron californicum* and Phainopeplas use it in the same way, both for nesting and for food. However, in Zapotitlán, an important nesting and postnesting food for Phainopeplas were *M. geometrizans* fruits.

M. hypopolius is in a high degree responsible for the long distance dispersion out of the patch. However, this species spent most of the time perched on the columnar cacti *Cephalocereus columna trajani* and *Neobuxbaumia tetetzo* after feeding, a behavior that is largely related to its nesting habits associated to columnar cacti [68]. By doing this, woodpeckers released the seeds beneath columnar cacti, where high solar radiation levels at soil level, and probably water competition with adult plants, made these microhabitats unsuitable for seedling establishment [7, 9, 69]. However, *Melanerpes hypopolius* indeed deposited part of the seeds, both within and out of the patch, beneath trees and shrubs and probably plays a significant role in the colonization of *M. geometrizans* to new habitats. This might explain the presence of scattered individuals of this cactus in the nearby communities. Consequently, an important part of the explanation for the contagious distribution of *M. geometrizans* over the landscape can be related to dispersal limitation, given that the highest proportion of seeds that are deposited beneath trees and shrubs are within the mesquite forests, in which *Phainopepla nitens* seems to maintain a tight interaction with this cactus, mistletoes and mesquite trees.

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