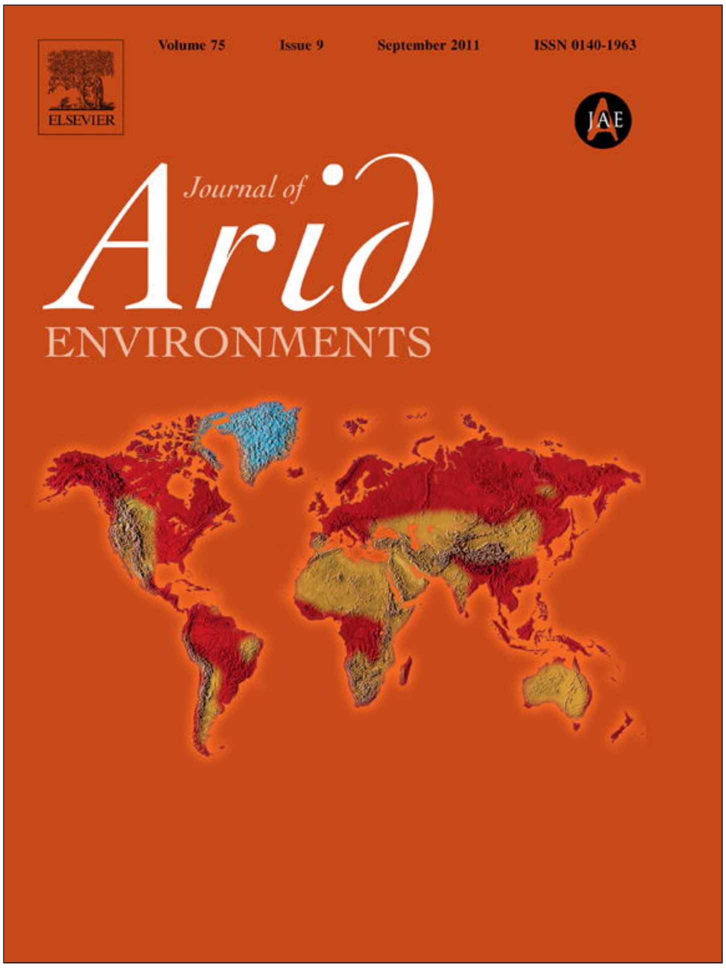
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Parthenocarpy, attractiveness and seed predation by birds in *Bursera morelensis*

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ABSTRACT

Parthenocarpy (production of seedless fruits) is a characteristic associated with a strategy to reduce seed predation by birds and to increase the attractiveness to frugivorous birds. Red cuajiote (*Bursera morelensis*) is an endemic tree species of Mexico that produces seeded and parthenocarpic fruits. The purpose of this work was to examine whether parthenocarpy is a factor that increases the number of bird visits to trees and if it is a strategy to diminish seeds predation by granivorous birds. We made field observations to determine the relation between the number of bird visits and fruit removal rate, to the total number of parthenocarpic fruits produced, and the number of birdpredated fruits to the number and proportion of parthenocarpic fruits in the trees. We found that in trees with a bigger amount of parthenocarpic fruits, both frugivoruos and granivorous birds made more visits; we then suggested that parthenocarpic fruits can act like a signal of attraction by means of a density and coloration effect. Also, we found that in trees with bigger proportions of parthenocarpic fruit, predation by granivorous birds is smaller. Parthenocarpy has an adaptative value for *B.morelensis* increasing bird visitation and reducing seed predation in the Tehuacan Valley.

1. Introduction

The production of fruits without seeds among flowering plants (parthenocarpy) can be triggered by several factors that promote ovary development and restrict ovule maturation (Gillaspy et al., 1993; Varoquaux et al., 2000). This process may be caused by pollen scarcity, damaged flower organs, environmental abnormalities, hormone disequilibrium, polyploidy and mistakes in gene expressions (Gay et al., 1987; Gillaspy et al., 1993; Jordano, 1988; Sato et al., 2001, 2002; Solomon, 1980; Varoquaux et al., 2000; Young et al., 2004). The ecological function of parthenocarpy is poorly known, with most research related to the production of seedless commercial fruits (Varoquaux et al., 2000).

Parthenocarpy can act as an adaptative trait to diminish the individual probability of fruit predation by birds and insects in the tree (Traveset, 1993; Verdú and García-Fayos, 2001). Coetzee and Giliomee (1987) and Traveset (1993) showed that insects laid eggs indistinctly in fruits with or without seeds allowing higher survival probabilities for seeded fruits. Zangerl et al. (1991) reported that lepidoterans preferred seedless fruits of *Pastinaca sativa* as these fruits contained less toxic materials than seeded ones. Ramos-Ordoñez et al. (2008) found that Cecidomids and Calcioideae only used parthenocarpic fruits of *B.morelensis* and suggested that this might be due to the absence of calcium oxalate crystals making seeded fruits more toxic and harder to penetrate.

Jordano (1990) described that *Carduelis chloris* (Aves: Fringillidae) can, on average, take five fruits per minute of *Pistacia lentiscus*, but only ingested three while discarding seedless fruits. Obeso (1996) studied *Ilex aquifolium* that had asynchronic fruiting period and produced very high numbers of fruits that included parthenocarpic fruits as a way to increase attractiveness to frugivorous birds. Fuentes and Schupp (1998) showed that trees of *Juniperus osteosperma* that had more parthenocarpic fruits had less predated seeds and suggested that *Parus inornatus* foraged selectively in trees with more fruits. Verdú and García-Fayos (2001) stated that seed predation by birds was reduced as the number of parthenocarpic fruits increased in *P. lentiscus*. However, in all studies, seedless fruits could not be assessed in trees and the reductions in seed predation probabilities were calculated as a correlation with total fruit crop.

B.morelensis produces parthenocarpic fruits that remain in trees for a long period until dispersion. In this case three different fruit types can be distinguished in trees according to dehiscence: mature seeded fruits, mature parthenocarpic fruits and immature fruits (Ramos-Ordoñez et al., 2008). The purpose of this work was to evaluate if (1) parthenocarpy can be considered as a factor that increases the attractiveness and so the number of frugivorous birds

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visits as suggested by Obeso (1996), and to (2) determine if parthenocarpy reduces seed predation by birds as proposed by Fuentes and Schupp (1998) and, Verdú and García-Fayos (2001).

2. Materials and methods

2.1. Study site

The study site was located in the alluvial fan covered by tropical deciduous forest in the Barranca de Muchil, San Rafael Coxcatlán, in the southeastern portion of the Tehuacán Valley, Puebla, México (18°12′ and 18°14′N; 97°07′ and 97°09′W), at 1000 m a.s.l. Mean annual temperature is 25 °C and annual precipitation 395 mm. Rains occur between June and October (Fernández, 1999). Soils on alluvial fans are very heterogeneous and determine four different vegetation zones: i) first one dominated by *Fouqueria formosa* Kunt denominated Fouquieral, ii) Cuajiotal dominated by *B.morelensis* Ramírez, iii) Chiotillal dominated by *Escontria chiotilla* (Weber) Rose and iv) Cardonal dominated by the columnar cacti *Pachycereus weberi* (Coulter) Buxb (Medina, 2000).

2.2. Studied species

B.morelensis is a diecious endemic tree that reaches between 3 and 10 m tall, and produces an aromatic resin. Locally it is known as copalillo, cuajiote rojo, palo mulato, palo colorado or xixiote (Rzedowski et al., 2004). It is a representative species of the tropical dry forests of Guerrero, Morelos, Puebla and Oaxaca where along with other burseras forms forests known locally as "Cuajiotales" (Becerra, 2005; Reyes et al., 2004). Flowering in the Tehuacan Valley is annual and happens between April and May (after the first rains). Two weeks later, immature fruits are completely formed and when fully grown, change from green to red while maturing. Fruits are trivalvated and measure 7.42 ± 0.47 cm long by 6.34 ± 0.8 cm wide, and weigh 0.48 ± 0.03 g. They have a complete orange pseudoarile. In parthenocarpic fruits orange pseudoarile is not complete. Seeds are gray dotted with black while in parthenocarpic fruits, seedcoat is not completely formed and remain white. Fruit maturation is asynchronic and occurs during the dry season (between November and May). During this season, fruits in trees can be separated into seeded fruits (presenting complete dehiscence), parthenocarpic fruits (with incomplete dehiscence) and immature (unripe) fruits. Most parthenocarpic fruits remain on the tree at least until the next stage of flowering. Prior to dispersion, fruits are predated by wasps of the superfamily Chalcidoidea, and flies of the family Cecidomyiidae (Ramos-Ordoñez et al., 2008).

2.3. Produced crop

To estimate total fruit crop we used 23 female trees of 40 individuals selected at random in the Cuajiotal and Fouquerial, in an approximate area of 2200 m^2;. In each tree we selected four branches (of similar diameter) at random and counted the number of fruits on each branch. Mean fruits per branch times the number of branches equaled total crop per tree. This procedure was repeated monthly from May 2006 to May 2007. To estimate size of trees and their ability to produce fruits, we measured the diameter at breast height (DBH) of each individual (Bullock and Solis-Magallanes, 1990; Chapman et al., 1994). To estimate the parthenocarpic crop we collected at random 50 fruits from each of the 23 trees ($n = 1150$ fruits) during January 2007 when most of the seeds were developing (Ramos-Ordoñez et al., 2008). Fruits were dissected and the proportion of parthenocarpic, seeded and insect-infested fruits was calculated. The total crop and parthenocarpic crop were correlated during the observation period.

2.4. Parthenocarpy and attractiveness

To determine the relation between total crop and bird visitation and seed removal we did focal observations from December 2006 to February 2007. We used the 23 female trees in which the crop size was calculated. We recorded the visits of birds during peak periods according to Foster (1990): from 07:00 to 13:00 h and from 16:00 to 18:00 h; we observed at the same time, groups of three randomly selected trees. We did not observe on windy or rainy days. We registered bird species, the number of visits, and the number of fruits consumed during each visit. One or two observers made observations and total observation time was 92 h (4 h/tree in 23 trees).

2.5. Seed predation

2.5.1. Field procedures

Of the 23 trees in which the crop size was calculated, we selected 13 trees at random, in order to know the fruit type removed by birds (mutualistic frugivorous or seed dispersers, and granivorous or seed predators), we counted and marked in the branches the number of fruits with seed and parthenocarpic, in at least an 80% of the tree (according to observed dehiscence; Ramos-Ordoñez et al., 2008), fruits were counted before observations; marking and counting of fruits was conducted in an average time of 2.5 h per tree, with the help of 5 persons and a scaffold; on the tip of each branch placed red and brown tape (red for seeded fruits and brown for parthenocarpic fruits) and put labels with the corresponding number of fruits. Focal observations were done from 07:00 to 13:00 h, from March to May 2007 for a total of 156 h (12 h per tree in 13 trees). We registered bird species, number of visits, number of fruits ingested and type of fruit consumed (with seed or parthenocarpic). During observations, a person registered the activity of the bird and once the bird went away from the tree, a second observer approached the tree to count the number of seeded and parthenocarpic fruits remaining in the branch, and confirming by subtraction how many fruits and what type were removed by the bird. Once the new count was done, the old labels were substituted with the new number for the next observation. A bird was considered as granivorous when in a captive field experiment done in the area, seeds that were ingested were found destroyed in droppings (Ramos-Ordoñez, 2009). With these data, we calculated number of fruits removed by each species and number of fruits with a predated seed.

2.5.2. Field captivity experiment

To determine if the different bird species preferred one fruit type (immature, parthenocarpic or seeded) we conducted a field experiment from March to May 2007. We captured 11 granivorous birds using 10 mist nets (12 m × 2.6 m, 9 m × 2.6 m and 6 m × 2.6 m) in sites around *B. morelensis* trees for a total of 28 days (14 d in March, 11 d in April and 3 d in May). Nets were opened for 10 h per day resulting in a total of 2220 net hours and 218.4 m^2;. Birds that showed signs of stress due to captivity (e.g. not eating, hitting against the walls of the cage, etc.) were not used. Captured birds were placed in individual cages (*Zenaida asiatica*, $n = 3$; *Aimophila mystacalis*, $n = 1$; *Pheucticus chrysopeplus*, $n = 3$; *Passerina versicolor*, $n = 1$; *Carpodacus mexicanus*, $n = 3$). We offered mature seeded fruits, parthenocarpic fruits, and immature fruits in different proportions resembling measured proportions in trees: (a) 33%:33%:33% ($n = 30$ fruits offered per trial per individual), (b) 40%:40%:20% ($n = 25$), (c) 40%:20%:40% ($n = 25$), (d) 20%:40%:40% ($n = 25$) and, (e) 0%:50%:50% ($n = 20$). Experiments were done during mornings and lasted 1 h. We registered fruit type selected by different birds, and whether it was ingested or rejected. After trials, birds were fed using commercial food (Trill) and soft fruit. For each bird species we did three trials; the data of species with 3 individuals (*Z. asiatica*, *P. chrysopeplus* and *C. mexicanus*) were averaged for analysis.

2.6. Data analysis

To evaluate fruit production, we correlated the crop size with tree size as a measurement of its ability to produce fruits (expressed by DBH), and then correlated the number and proportion of parthenocarpic fruits with the total crop size. To assess whether parthenocarpy increases the attractiveness of the tree, we evaluate whether the number of visits and the number of fruits removed were correlated with total crop size, and to parthenocarpic crop size. To determine with field data whether seed predation decreases with the presence of parthenocarpy, we correlated the number of seeded fruits with the total crop size, parthenocarpic crop and the proportion of parthenocarpic fruits. To determine if individual predation probability is reduced by having parthenocarpic fruits, we divided seeded crop by total crop, and results were correlated with parthenocarpic crop per individual. All correlations were made with the Spearman rank correlation (r_s) with a significance level of 0.05. With the data obtained in the captivity experiment, we evaluated by chi-square test, if the number of seeded and parthenocarpic fruits were eaten by birds in different proportions. Statistical analysis was done using Simfit V6.0.24 (Bardsley, 2009).

3. Results

3.1. Fruit production

Trees produced a mean of 8743 ± 6057 (mean values and standard deviation are presented) fruits between December 2006 and February 2007 (range 654–23,484, $n = 23$ trees). Bigger trees produced higher fruit numbers (Spearman rank correlation, $r_s = 0.666$, $n = 23$, $P = 0.0005$). Fruits dissected showed that all trees produced parthenocarpic fruits with percentage between 11.76% and 52.73% of the total crop. Mean parthenocarpic crop was 2876 ± 2457 fruits (range 249–10932). The number of parthenocarpic fruits increased as total crop increased (Spearman rank correlation, $r_s = 0.93$, $n = 23$, $P < 0.0001$), but no correlation was found when we compared the proportion of parthenocarpic fruits to total fruit crop (Fig. 1; Spearman rank correlation, $r_s = -0.132$, $n = 23$, $P = 0.54$).

3.2. Attractiveness

Parthenocarpy seems as an advantage for *B. morelensis* in terms of attraction, since the number of visits increased significantly when the proportion of parthenocarpic fruits increased (Spearman rank correlation, $r_s = 0.769$, $n = 23$, $P = 0.0001$). However the amount of fruit removed was not correlated with the proportion of parthenocarpic fruits (Spearman rank correlation, $r_s = -0.07$, $n = 23$, $P = 0.75$).

We registered 15 bird species visiting *B. morelensis* trees, but only 13 fed on fruits, with 61.5% of them being migratory, and 46.2% were seed predators (Table 1). In total, 503 fruits were removed in 643 visits. The relationship between the number of fruits removed and number of visits with respect to the total crop and parthenocarpic crop shown in Fig. 2. In trees with bigger crops more fruits were removed significantly (Spearman rank correlation, $r_s = 0.78$, $n = 23$, $P = 0.0005$). The number of visits was not related with total crop size (Spearman rank correlation, $r_s = 0.077$, $n = 23$, $P > 0.05$). Not all of the bird visits resulted in fruit consumption. Trees were also used as resting or preening sites. All bird species, both mutualistic frugivorous and seed predators, first visited a large number of fruits on different branches and then consumed. All bird species consumed mature and parthenocarpic fruits.

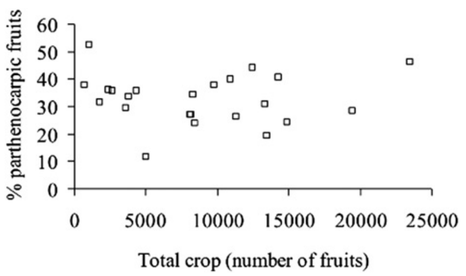

Fig. 1. Proportion of parthenocarpic fruits with respect to total crop in 23 trees of *B. morelensis* in the Tehuacan Valley.

3.3. Seed predation

3.3.1. Field tests

Mean number of fruits per observed tree was 10,976 ± 3693 (range 4992–19,441 fruits, $n = 13$). Mean number of parthenocarpic fruits per tree was 3428 ± 1585 fruits (range 587–5828 fruits, $n = 12$). The 13 species of birds feeding on *B. morelensis* removed 559 fruits in 356 visits. Mutualistic frugivores removed more fruits (427 fruits), with only 8.89% being parthenocarpic (38 fruits) and almost all of them were rejected and dropped (23 fruits). Six species of seed predators removed 132 fruits (23.61%) of all, 67.42% (89 fruits) containing seed and were predated, the rest were parthenocarpic (43 fruits). These birds selected a mean of 35.68 ± 14.31 parthenocarpic fruits, but not all of them were consumed (Table 2). *P. versicolor* selected a small amount of seedless fruits (18.18%) consuming all of them; *P. chrysopeplus* selected 55.56% of parthenocarpic fruits but rejected 20% of them, while *Z. asiatica* selected 32.43% of parthenocarpic fruits and rejected 83.33%. Bird species that consumed more seeds were *C. mexicanus* (33.7%), *Z. asiatica* (28.1%) and *A. mystacalis* (19.1%).

Seed predation was not correlated with total crop size (Spearman rank correlation, $r_s = 0.447$, $n = 13$, $P = 0.13$) or parthenocarpic crop size (Spearman rank correlation, $r_s = 0.047$, $n = 13$, $P = 0.877$). Number of seeded fruits removed by seed predators, was lower in trees with a higher proportion of parthenocarpic fruits but the relation was not significant (Spearman rank correlation, $r_s = -0.497$, $n = 13$, $P = 0.083$). The individual

Table 1
List of species, migratory status and effect of endozoochory in seed viability, of 13 birds registered feeding on *B. morelensis*, in the Tehuacán Valley.

Family	Species	Status	Effect of endozoochory
Columbidae	*Zenaida asiatica*	R	SP
	Columbina passerina	R	SP
Picidae	*Melanerpes hypopolius*	R	MF
	Picoides scalaris	R	MF
Tyrannidae	*Myiarchus tuberculifer*	ML	MF
	Myiarchus cinerascens	M	MF
	Myiarchus nuttingi	M	MF
	Myiarchus tyrannulus	ML	MF
Emberizidae	*Aimophila mystacalis*	M	SP
Cardinalidae	*Pheucticus chrysopeplus*	M	SP
	Passerina versicolor	M	SP
Icteridae	*Icterus pustulatus*	ML	MF
Fringillidae	*Carpodacus mexicanus*	R	SP

Status: R (resident), M (migrant), ML (local migrant) according to Arizmendi and Espinosa de los Monteros (1996).
Effect of endozoochory: SP (seed predator), MF (mutualist frugivorous) according to Ramos-Ordoñez (2009).

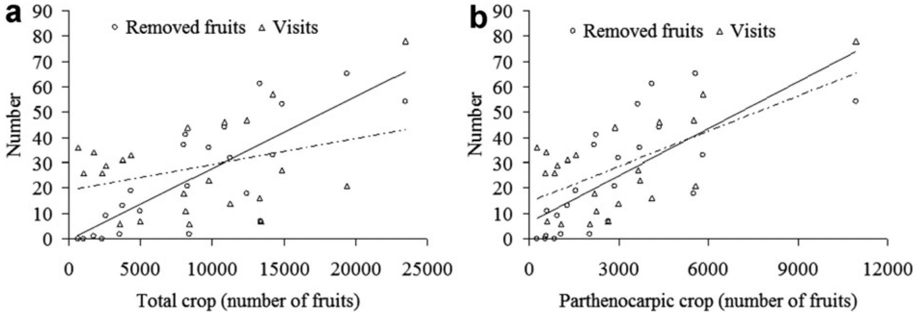

Fig. 2. Number of removed fruits and visits with respect to total crop (a) and to parthenocarpic crop (b) in 23 trees of *B. morelensis* in the Tehuacan Valley.

probability of predation decreased significantly when the number of parthenocarpic fruits increased (Fig. 3; Spearman rank correlation, $r_s = -0.802$, $n = 13$, $P = 0.001$).

3.3.2. Captivity experiments

Table 3 summarizes the results of experiments in captivity. We found that seed predators had no preference for the immature fruits, suggesting that exposed pseudoarile is an important factor in the fruit selection. We observed that the parthenocarpic fruits are a food resource for granivorous birds in the absence of seeded fruits, in trials that offered no seeded fruit (00% : 50% : 50%), the seed-eaters ate 14% of the total parthenocarpic fruit offered. When we offered the three types of fruit in different proportions no significant difference between observed and expected of the number of seeded or parthenocarpic fruits eaten was detected, however, when we offered the three fruits in the same proportion (33%: 33%: 33%) differences were detected.

4. Discussion

Number of removed fruits in trees of *B. morelensis* was positively related with total fruit crop size as predicted earlier (Howe and Estabrook, 1977; McKey, 1975; Snow, 1971). Moreover, we documented that bird visitation rates increased as parthenocarpic crop size increased as predicted by Obeso (1996).

Parthenocarpic fruits increased fruit crop size and increased bird visitation. This can be related to an increment in the attraction unit due to a greater display of color due to density as stated by others (Facelli, 1993; Fuentes, 1995; Willson and Hoppes, 1986; Willson and Melampy, 1983; Willson et al., 1990). Both parthenocarpic and seeded mature fruits have an orange pseudoarile that contrast with background coloration (Ramos-Ordoñez et al., 2008). Parthenocarpic fruits dehisce partially and contribute to attraction exposing pseudoarile by a density of color increment effect (Van der Pijl, 1982).

Birds inspected fruits on branches before removing them but also manipulated removed fruits rejecting and ingesting different amounts of fruit types. Jordano (1990) described this behavior in *C. chloris* which manipulated fruits detecting seeds and rejected parthenocarpic ones.

Frugivorous birds apparently were more selective than the granivorous birds, choosing more fruits with seeds. Most of them were migrants that needed a lot of lipids to cover their energetic needs (Bates, 1992; Greenberg et al., 1995; Janzen, 1977; McCarty et al., 2002). Pseudoariles are known as structures that contain high amounts of lipids (Foster and McDiarmid, 1983). Seeded fruits in *B. morelensis* showed a complete dehiscence exposing all the pseudoarile and probably increasing attractiveness to frugivorous birds.

According to Janzen (1971a,b), to consider parthenocarpy as an adaptation to avoid seed predation, two conditions must be met: i) first, it must occur early in the ontogenesis of fruit development to minimize the cost for the plant and ii) the number of predated seeds must not be correlated with fruit crop size. Both aspects are met in the case of *B. morelensis*. The development of parthenocarpic fruits begins during the first days after pollination and they lack calcium oxalate crystals which are present in the seeded fruits thus being less costly (Ramos-Ordoñez et al., 2008). Besides, as it was shown in the Section 3.3.1, the number of seeds predated was not correlated with total fruit crop size. This reinforces the idea of the ecological function of parthenocarpy as a mechanism to decrease seed predation probability as was reported for *P. lentiscus*, a plant from the Anacardiaceae family, closely related to Burseraceae (Verdú and García-Fayos, 2001).

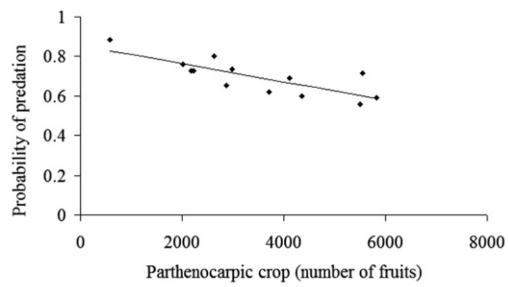

Fig. 3. Regression analysis and Spearman rank correlation between the probability of seed predation and the parthenocarpic crop produced by 13 trees of *B. morelensis* in the Tehuacán Valley ($Y = -5E-05x + 0.8551$).

Table 2
Seed predators detected consuming fruits in 13 trees of *B. morelensis*, and types of fruits consumed.

Species	Removed fruits	% Seeded fruits	% Parthenocarpic fruits	% Parthenocarpic fruits rejected	Number of visits
C. mexicanus	44	68.18	31.82	42.86	21
Z. asiatica	37	67.57	32.43	83.33	23
A. mystacalis	23	73.91	26.09	16.67	22
P. versicolor	11	81.82	18.18	0	19
P. chrysopeplus	9	44.44	55.56	20	14
C. passerina	8	50	50	25	18

Data were sorted by the number of fruits removed.

Table 3
Percentage and number of seeded, parthenocarpic and immature fruits of *B. morelensis* consumed by five granivorous birds in captive conditions according to different proportions of offered fruits (seeded : parthenocarpic : immature); total number of fruits offered per trials, and results of the chi-square test for seeded and parthenocarpic fruits eaten.

Proportion	Percentage of consumed fruits (n)			Total offered	χ^2	d.f.
	Seeded	Parthenocarpic	Immature			
00% : 50% : 50%	0	14 (42)	0	300		
20% : 40% : 40%	17.86 (67)	16 (60)	0	375	7.15	4
33% : 33% : 33%	29.11 (131)	13.77 (62)	0	450	14.9*	4
40% : 40% : 20%	36 (135)	18.93 (71)	0	375	7.87	4
40% : 20% : 40%	36.26 (136)	4 (15)	0	375	7.62	4

*$P = 0.01$.

Verdú and García-Fayos (2001) proposed that birds facing a plant with a high proportion of parthenocarpic fruits can fly away and search for another plant with more seeded fruits but the cost of this can be high if i) the density of female plants is low and ii) the proportion of parthenocarpic fruits present in trees in the population is similar among them. In our study, of the 40 trees chosen 23 were female. The proportion of parthenocarpic fruits in 23 trees varied between 11 and 52%, but was independent of the total crop size as shown in Fig. 1, making the decision of flying away and searching for another tree a non-profitable choice as stated by Verdú and García-Fayos (2001).

Parthenocarpy decreases seed predation as proposed by Fuentes and Schupp (1998) and Verdú and García-Fayos (2001). This is the first attempt to evaluate the number of parthenocarpic and seeded fruits removed in relation to fruit crop size.

The information presented here can be important to better understand the role of parthenocarpy in the breeding success of animal dispersed plants specially in stressful systems. For example in Mediterranean systems, where many plants have been reported as having parthenocarpic fruits as *Olea*, *Pistacia*, *Prunus*, *Rubus* and *Juniperus* (Ramos-Ordoñez, 2009), and where animal dispersed species can be prevalent (between 32 and 64% according to Herrera, 1995), and where dispersal is made by migrant species (between 25 and 50% species Herrera, 2001), the presence of parthenocarpic fruits can be the way to diminish seed predation and to allow plant dispersal and so plant conservation, and in the other hand to produce a huge and cheaper standing crop to maximize bird attraction as soon as they arrive from their migratory trips. In both Mediterranean and Mexican arid lands, as well as in other unstudied places, this mechanism may represent a successful strategy to maximize bird visitation reducing predation risks that needs to receive more attention and research.

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References

Arizmendi, M.C, Espinosa de los Monteros, A., 1996. Avifauna de los bosques de cactáceas columnares del Valle de Tehuacán, Puebla. Acta Zoológica Mexicana (n.s.) 67, 25–46.
Bardsley, W.G., 2009. Simfit version 6.0.24. http://simfit.man.sc.uk/. (accessed 22.09.09.).
Bates, J.M., 1992. Frugivory on *Bursera microphylla* (Burseraceae) by wintering Gray Vireos (*Vireo vicinior*, Vireonidae) in the coastal deserts of Sonora, Mexico. Southwestern Naturalist 37, 252–258.
Becerra, J.X., 2005. Timing the origin and expansion of the Mexican tropical dry forest. Proceedings of the National Academy of Sciences 102, 10919–10923.
Bullock, S.H., Solis-Magallanes, J.A., 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 22, 22–35.
Chapman, C.A., Wrangham, R., Chapman, L.J., 1994. Indices of habitat-wide fruit abundance in tropical forests. Biotropica 26, 160–171.
Coetzee, J.H., Giliomee, J.H., 1987. Seed predation and survival in the infructescences of *Protea repens* (Proteaceae). The South African Journal of Botany 53, 61–64.
Facelli, J.M., 1993. Experimental evaluation of the foliar flag hypothesis using fruits of *Rhus glabra* (L.). Oecologia 93, 70–72.
Fernández, N., 1999. Análisis de la dinámica de comunidades vegetales con relación a la evolución del paisaje en la zona semiárida de Coxcatlán, Puebla. Caso: Abanico aluvial de la Barranca del Muchil. Tesis de Maestria. Universidad Nacional Autónoma de México. México.
Foster, M.S., 1990. Factors influencing bird foraging preferences among conspecific fruit trees. Condor 92, 844–854.
Foster, M.S., McDiarmid, R.W., 1983. Nutritional value of the aril of *Trichilia cuneata*, a bird-dispersed fruit. Biotropica 15, 26–31.
Fuentes, M., 1995. The effect of unripe fruits on ripe fruit removal by birds in *Pistacia terebinthus*: flag or handicap? Oecologia 101, 55–58.
Fuentes, M., Schupp, E., 1998. Empty seeds reduce seed predation by birds in *Juniperus osteosperma*. Evolutionary Ecology 12, 823–827.
Gay, G., Kerhoas, C., Dumas, C., 1987. Quality of a stress-sensitive *Cucurbita pepo* L. pollen. Planta 171, 82–87.
Gillaspy, G., Ben-David, H., Gruissem, W., 1993. Fruits: a developmental perspective. Plant Cell 5, 1439–1451.
Greenberg, R., Foster, M.S., Marquez-Valdelamar, L., 1995. The role of the white-eyed vireo in the dispersal of *Bursera* fruit on the Yucatan Peninsula. Journal of Tropical Ecology 11, 619–639.
Herrera, C.M., 1995. Plant-vertebrate seed dispersal systems in the mediterranean: ecological, evolutionary, and historical determinants. Annual Review of Ecology and Systematics 26, 705–727.
Herrera, C.M., 2001. Dispersión de semillas en el Mediterráneo: ecología y evolución. In: Zamora, R., Pugnaire, F.I. (Eds.), Aspectos funcionales de los ecosistemas Mediterráneos. CSIC, Madrid, pp. 125–152.
Howe, H., Estabrook, G.F., 1977. On intraspecific competition for avian dispersers in tropical trees. American Naturalist 111, 817–832.
Janzen, D.H., 1971a. Seed predation by animals. Annual Review of Ecology and Systematics 2, 465–492.
Janzen, D.H., 1971b. Escape of *Cassia grandis* L. beans from predators in time and space. Ecology 52, 964–979.
Janzen, D.H., 1977. Why fruits rot, seeds mold, and meat spoils. American Naturalist 111, 691–713.
Jordano, P., 1988. Polinización y variabilidad de la producción de semillas en Pistacia lentiscus L. (Anacardiaceae). Anales del Jardín Botánico de Madrid 45, 213–231.
Jordano, P., 1990. Utilización de los frutos de Pistacia lentiscus (Anacardiaceae) por el verderón común (Carduelis chloris). In: Arias de Reyna, L., Recuerda, P., Redondo, T. (Eds.), Actas I Congreso Nacional de Etología, pp. 145–153. Cajasur, Córdoba, Spain.
McCarty, J.P., Levey, D.J., Greenberg, C.H., Sargent, S., 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. Forest Ecology and Management 164, 277–291.
McKey, D., 1975. The ecology of coevolved seed dispersal systems. In: Gilbert, L.E., Raven, P.H. (Eds.), Coevolution of Animals and Plants. University of Texas Press, Austin, pp. 159–191.
Medina, J.S., 2000. Determinación del vigor reproductivo de Stenocereus stellatus (Cactaceae) a lo largo de una cronosecuencia edáfica en un abanico aluvial en Coxcatlán, Valle de Tehuacán. Tesis de Licenciatura. Universidad Nacional Autónoma de México, México.
Obeso, J.R., 1996. Fruit and seed production in European holly, *Ilex aquifolium* L. (Aquifoliaceae). Anales del Jardin Botanico de Madrid 54, 533–539.
Ramos-Ordoñez, M.F., 2009. Dispersión biótica de semillas y caracterización de los frutos de *Bursera morelensis* en el Valle de Tehuacan, Puebla. PhD Thesis. Universidad Nacional Autonoma de México, México.
Ramos-Ordoñez, M.F., Márquez-Guzmán, J., Arizmendi, M.C., 2008. Parthenocarpy and seed predation by insects in *Bursera morelensis*. Annals of Botany 102, 713–722.
Reyes, S.J., Brachet, C., Pérez, J., Gutiérrez de la Rosa, A., 2004. Cactáceas y otras plantas nativas de la Cañada Cuicatlán, Oaxaca. Comisión Federal de Electricidad; Sociedad Mexicana de Cactología. Universidad Nacional Autónoma de México; CONABIO. Cuicatlán A. C. México.
Rzedowski, J., Medina, R., Calderón, G., 2004. Las especies de *Bursera* (Burseraceae) en la cuenca superior del Río Papaloapan (México). Acta Botánica Mexicana 66, 23–151.
Sato, S., Peet, M.M., Gardner, R.G., 2001. Formation of parthenocarpic fruit, undeveloped flowers and aborted flowers in tomato under moderately elevated temperatures. Scientia Horticulturae 90, 243–254.
Sato, S., Peet, M.M., Thomas, J.F., 2002. Determining critical pre- and post-anthesis periods and physiological processes in *Lycopersicon esculentum* mill. exposed to moderately elevated temperatures. Journal of Experimental Botany 53, 1187–1195.
Snow, D., 1971. Evolutionary aspects of fruit eating by birds. Ibis 113, 194–202.
Solomon, B.P., 1980. *Frumenta nundinella* (Lepidoptera: Gelechiidae): life history and induction of host parthenocarpy. Environmental Entomology 9, 821–825.

Traveset, A., 1993. Deceptive fruits reduce insect seed predation *in Pistacia terebinthus* L. Evolutionary Ecology 7, 357–361.

Van der Pijl, L., 1982. The Principles of Dispersal in Higher Plants, third ed. Springer-Verlag, Berlin.

Varoquaux, F., Blanvillain, R., Delseny, M., Gallois, P., 2000. Less is better: new approaches for seedless fruit production. Trends in Biotechnology 18, 233–242.

Verdú, M., García-Fayos, P., 2001. The effect of deceptive fruits on predispersal seed predation by birds in *Pistacia lentiscus*. Plant Ecology 156, 245–248.

Willson, M.F., Hoppes, W.G., 1986. Foliar "flags" for avian frugivores: signal or serendipity? In: Estrada, A., Fleming, T.H. (Eds.), Frugivores and Seed Dispersal. Junk, Dordrecht, pp. 55–69.

Willson, M.F., Melampy, M.N., 1983. The effect of bicolored fruit displays on fruit removal by avian frugivores. Oikos 41, 27–31.

Willson, M.F., Graff, D.A., Whelan, C.J., 1990. Color preferences of frugivorous birds in relation to the colors of fleshy fruits. Condor 92, 545–555.

Young, L.W., Wilen, R.W., Bonham-Smith, P.C., 2004. High temperature stress of *Brassica napus* during flowering reduces micro- and megagametophyte fertility, induces fruit abortion, and disrupts seed production. Journal of Experimental Botany 55, 485–495.

Zangerl, A.R., Berenbaum, M.R., Nitao, J.K., 1991. Parthenocarpic fruits in wild parsnip: decoy defense against a specialist herbivore. Evolutionary Ecology 5, 136–145.