

PRE-DISPERSAL SEED PREDATION OF THE COLUMNAR CACTUS (*NEOBUXBAUMIA TETETZO*, CACTACEAE) BY BIRDS IN CENTRAL MEXICO

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Resumen. – Depredación pre-dispersiva por aves del cacto columnar (*Neobuxbaumia tetetzo*, Cactaceae) en el centro de México. – La depredación de semillas es una fuerza ecológica que afecta a los individuos y poblaciones. Una disminución en la disponibilidad de semillas ocasionada por la depredación influenciará la tasa de reclutamiento, afectando el tamaño de la población y la composición de las comunidades. Evaluamos la importancia de las aves frugívoras como depredadoras de semillas del cactus columnar (*Neobuxbaumia tetetzo*) en el bosque tropical deciduo. Para esto, medimos la efectividad de las aves como dispersoras de semillas, utilizando los componentes de calidad y cantidad. Las aves removieron el 48,4% de las semillas, del cual 41,4% fue depredado, ya que las semillas fueron destruidas al pasar por el tracto digestivo de las Palomas ala blanca (*Zenaida asiatica*), Guacamayas verdes (*Ara militaris*) y Pinzones mexicanos (*Haemorhous mexicanus*). El desempeño de *N. tetetzo* hasta un año de sobrevivencia varió significativamente entre microhábitats, y solo seis microhábitats (*Cyrtocarpa procera*, *Ceiba aesculifolia* var. *parvifolia*, *Cnidosculus tehuacanensis*, *Euphorbia schlechtendalii*, *Amphyteriguim adstringens* y *Mimosa luisana*) tuvieron efectos positivos sobre la sobrevivencia del cacto. Los Carpinteros pecho gris (*Melanerpes hypopolius*) y los Carpinteros mexicanos (*Picoides scalaris*) no destruyeron las semillas al pasar por su tracto digestivo, pero después de alimentarse las aves visitaron con alta frecuencia otros individuos de *N. tetetzo*, lo que incrementaría la probabilidad de depositar las semillas bajo un conoespecífico. Este estudio mostró que desde la perspectiva de la dispersión, la depredación de semillas y la conducta de los carpinteros después de alimentarse afectaron negativamente a más de la mitad de las semillas producidas. Esto, puede afectar fuertemente el reclutamiento, uno de los estadios claves del ciclo de vida de este cacto.

Abstract. – Seed predation is an ecological and evolutionary force that affects individuals and populations. A decrease in seed availability caused by seed predation will influence recruitment rate, affecting population size and community structure. We evaluated the importance of fruit-eating birds as pre-dispersal seed predators on columnar cactus (*Neobuxbaumia tetetzo*) in tropical deciduous forest

by measuring their effectiveness as seed dispersers, which was calculated using the quantity and quality components of dispersal. The quality component included the quality of the microhabitat where seeds were deposited until one year after seed germination. Birds removed 48.4% of the seeds, of which 41.4% were predated by White-winged Doves (*Zenaida asiatica*), Military Macaws (*Ara militaris*), and House Finches (*Haemorhous mexicanus*), because the seeds that passed through its digestive tract were destroyed. The performance of *N. tetetzo* throughout one year of survival varied significantly between microhabitats, and only six yielded positive effects on the survival of this cactus (*Cyrtocarpa procera*, *Ceiba aesculifolia* var. *parvifolia*, *Cnidosculus tehuacanensis*, *Euphorbia schlechten-dalii*, *Amphyteriguim adstringens* and *Mimosa luisana*). Seeds consumed by Grey-breasted Woodpeckers (*Melanerpes hypopoliis*) and Ladder-backed Woodpeckers (*Picooides scalaris*) were not destroyed by passing through the gut-track, but after feeding, these woodpeckers had a high proportion of visits to *N. tetetzo* increasing the likelihood that seeds were deposited under conspecifics, which are inadequate sites for seedling establishment. Under the aspect of dispersal effectiveness, this study demonstrated that pre-dispersal seed predation by birds and the behavior of woodpeckers after foraging negatively affected the viability of almost half of the seeds produced by *N. tetetzo*. This may strongly affect seedling recruitment, one of the key steps in the life cycle of this cactus. Accepted 30 October 2014.

Key words: Military Macaw, *Ara militaris*, White-winged Dove, *Zenaida asiatica*, columnar cactus, *Neobuxbaumia tetetzo*, gut passage effect, Mexico, seed predation, tropical deciduous forest.

INTRODUCTION

Plant recruitment depends heavily on external factors that can positively or negatively affect plant demography (Harper 1977, Ibañez & Schupp 2002). Seed predation is an ecological and evolutionary force that has a negative effect on plant breeding ecology (Schupp 1998, Hulme 1998, Hulme & Benkman 2002, Silman *et al.* 2003). Seed predation plays an important role in plant demography and diversity in tropical environments, and imposes strong selection pressure on plants (Janzen 1970, Hulme & Benkman 2002). Seed predators decrease the probability of seed dispersal, and their impact depends on the intensity of seed predation and seed limitation (Janzen 1970, Calviño-Cancela 2007). Seed predation may also play a positive regulatory role in conserving the diversity of canopy trees in tropical forest by maintaining diversity in seed banks (Louda 1989, Renton 2001).

Pre-dispersal seed predation takes place when seeds are removed from the parent plant before they can be dispersed, and post-

dispersal seed predation occurs when seed consumers remove seeds after their dispersal (Hulme & Benkman 2002). Insects and mammals are the main seed dispersers (Peres 1991, Peres & Baidar 1997), whereas birds are primarily pre-dispersal seed predators (Janzen 1971). In the Neotropics, psittacids (parrots, parakeets, and macaws) have been identified as important pre-dispersal seed predators (Higgins 1979, Janzen 1981, Galetti & Rodrigues 1992, Galetti 1993; Renton 2001, 2006; Trivedi *et al.* 2004, Francisco *et al.* 2008, Haugaasen *et al.* 2008, Villaseñor-Sánchez *et al.* 2010, Ragusa-Netto 2011). Parrots represent a high proportion of the biomass of granivores in the tropical forest canopy (Villaseñor-Sánchez *et al.* 2010), since they have a high rate of seed consumption in canopy trees, assemble in large feeding flocks, and move quickly between food resources, which has an important impact on the plants they eat (Janzen 1972, Higgins 1979, Howe 1980, Janzen 1981, Coates-Estrada *et al.* 1993, Norconk *et al.* 1997, Kristosch & Marcodes-Machado 2001, Francisco *et al.* 2002, Bollen & Elsacker 2004, Villaseñor-Sánchez *et al.* 2010).

Some studies estimate that pre-dispersal seed predation by parrots represents between 6.4 and 10% of total seed predation (Howe 1980, Galetti & Rodrigues 1992, Trivedi *et al.* 2004), while other psittacid species have a high rate of fruit consumption (up to 99 or 100% of each piece of fruit; Francisco *et al.* 2008, Haugaasen 2008).

The availability of seeds and suitable sites (safe sites) for seedling establishment are key determinants for recruitment in plant populations (Harper *et al.* 1965, Crawley 1992, Ducan *et al.* 2009). In arid and semiarid zones, cacti require safe sites under perennial plant species (nurse plants) during the first steps of their life cycle, since these plants provide a suitable microhabitat for seed germination and seedling establishment and survival for cacti (Steenbergh & Lowe 1969, Valiente-Banuet & Ezcurra 1991, Callaway 1998, 2007). The availability of nurse plants in the environment, along with directed seed dispersal to these safe places, are decisive factors in cacti early survival (Harper *et al.* 1965, Callaway 1998, Ibañez & Schupp 2002, Schupp *et al.* 2010).

In this study, we evaluated the importance of fruit-eating birds as pre-dispersal seed predators on columnar cactus *Neobuxbaumia tetetzo* in tropical deciduous forest, by measuring their effectiveness as seed dispersers (Schupp 1993). This columnar cactus is endemic to Puebla and Oaxaca in central Mexico. It is highly ramified and grows up to 10 m tall (Bravo-Hollis 1978), and its fruits fit the chiropterochory syndrome (van der Pijl 1982, Valiente-Banuet *et al.* 1996). We estimated seed dispersal effectiveness by considering the quantity and quality components of seed dispersion, and considered the effect of the microhabitat where seeds were deposited, which is the last quality component for recruitment used to measure the effect that birds have on this cactus.

METHOD

Study area. The study was carried out in the southwestern area of the Tehuacán-Cuicatlán Biosphere Reserve in central Mexico, in Santa María Tecomavaca, Oaxaca, in Sabino Canyon (17°51'44.60"N, 97°2'43.89"W; Fig. 1). The site ranges from 610 to 885 m a.s.l. Its annual mean temperature is 32°C, with a mean total rainfall of 513.2 mm (García 1988). The rainy season occurs between June and October, and the dry season lasts up to eight months. The vegetation in the study area is tropical deciduous forest (TDF). The main tree species present are *Cyrtocarpa procerca* (Anacardiaceae), *Ceiba aesculifolia* var. *parvifolia* (Bombacaceae), *Neobuxbaumia tetetzo* (Cactaceae), *Parkinsonia praecox* (Caesalpiniaceae), *Amphipteringium adstringens* (Julianaceae) and several species of *Bursera* (Burseraceae), in addition to shrubs, such as *Euphorbia schlechtendalii* (Euphorbiaceae), *Cnidoscolus tehuacanensis* (Euphorbiaceae), and *Mimosa luisana* (Mimosaceae; Valiente-Banuet *et al.* 2009, Contreras-González 2007). Mean diameter at breast height (DBH) of the tree species in the study area was 2.93 ± 0.2 cm, and their mean height was 13.8 ± 2.42 m (Rivera-Ortiz *et al.* 2013). The study site was a small aggregation of columnar cactus *N. tetetzo* (such aggregations are known as 'tetcheras'), with densities of c. 315 individuals/ha (individuals > 1 m height).

Field work. The study was conducted during the fruiting season of *N. tetetzo* from the end of May until mid-June 2009, just before the rainy season. We calculated seed predation by fruit-eating birds on *N. tetetzo* by estimating seed dispersal failure, which was accomplished by measuring the effectiveness of the seed dispersal index, calculated as the product of the quantity and quality components of dispersal (Schupp 1993). The quantity component was estimated as the product of the

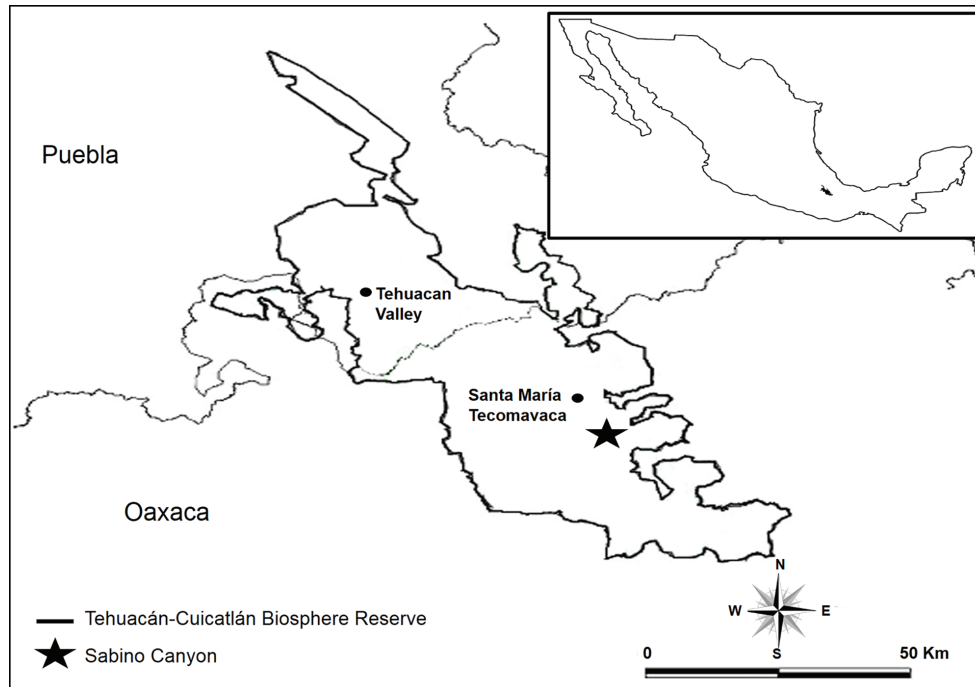


FIG. 1. Study site in Santa María Tecomavaca, Tehuacán-Cuicatlán Biosphere Reserve, central México, including the location of Sabino Canyon and columnar cactus shrubland in Tehuacán Valley.

number of seeds removed by each bird species, the frequency of visits to fruits, and the proportion of diurnal seed removal. The quality component was calculated as the product of the probability of seed germination after passing through the gut of each bird species, the probability that seeds were deposited under perennial plant species, and the quality of microhabitat, measured as probability of survival until up to one year after germination.

Diurnal and nocturnal seed removal. Since both diurnal and nocturnal animals consume *N. tetetzo* fruits, we conducted field seed removal experiments for both animal groups to estimate the mean number of seeds they removed. During seven days, ripe dehiscent fruits were tagged and assigned to one of the

following presentation methods under distinct removal events: (1) bird removal, where a total of 15 ripe dehiscent fruits, each from a different plant, were covered with a nylon mesh during the night to exclude nocturnal animals, and they were exposed to birds from 06:30 to 19:00 h, and (2) bat removal, where a total of 11 ripe dehiscent fruits, each from a different plant, were protected from birds during the day and exposed to nocturnal seed removers from 19:30 to 06:00 h (as proposed by Godínez-Álvarez *et al.* 2002). For each animal group (birds and bats), we recorded the percentage of seeds removed. The sample size of the ripe fruits was small when the study was conducted because the abundance of fruits produced by this cactus was low during 2009, as compared to 2006 (Contreras-González 2007), as we found only 11 fruits in

a parcel of 50 x 20 m, of which three were ripe. We estimated the proportion of pulp and seeds removed per fruit by determining the percentage of fruit that was consumed: 1) < 25%, 2) 25–50%, 3) 50–75%, or 4) > 75%), and then the number of consumed seeds was calculated as the product of the percentage of fruit consumed and the average number of seeds per fruit (Godínez-Álvarez *et al.* 2002); the latter was calculated by directly counting the seeds in ten randomly collected fruits.

Foraging observations. We conducted simultaneous observations of at least five *N. tetetzo* individuals with ripe fruits, using binoculars and/or a telescope. Observations were made during periods of high bird activity (from 06:30–10:30 h and 16:30–19:30 h) for a total of 170.37 h throughout the 2009 fruiting season (end of May until beginning of June). We recorded bird species, frequency of visits to each species, number of fruits/seeds consumed per visit, duration of each visit and number of feeding individuals. To calculate the number of seeds that were removed, we collected the fruits that birds had visited and estimated the number of seeds that were removed, as described above. The number of removed seeds per species was calculated as follows: (relative frequency of visits) x (number of seeds removed per visit) x [total number of removed seeds by guild (diurnal)].

Seed germination after gut passage. We determined the effect on seeds that passed through the gut by using seeds defecated by birds that were captured in mist nets. We captured birds with 11 mist nets (12 x 2.6 m, 9 x 2.6 m, and 6 x 2.6 m) placed near *N. tetetzo* individuals between 07:00 to 10:00 h and 17:00 to 19:30 h, for a total of 1617 net-hours. Captured frugivorous birds that eat *N. tetetzo* fruits were placed in individual 50 x 50 x 50 cm cages. These were 1 White-winged Dove (*Zenaida asiatica*), 3 Gray-breasted Woodpeckers

(*Melanerpes hypopolius*), 1 Ladder-backed Woodpecker (*Picoides scalaris*), 1 Curve-billed Thrasher (*Toxostoma curvirostre*), and 2 House Finches (*Haemorhous mexicanus*). After 30 minutes, the captured individuals were offered *N. tetetzo* fruits *ad libitum*. After defecating, birds were released and their feces were collected in paper bags for transportation to the lab. Ten captive Military Macaws from the African Safari Zoo were placed in individual 100 x 150 x 200 cm cages, and were left with no food overnight. The following morning, they were offered *N. tetetzo* fruits *ad libitum*, and their feces were collected in paper bags for transportation to the lab.

In the laboratory, we separated the seeds in bird feces and placed them in Petri dishes with filter paper (Whatman No. 1). In addition to the seeds obtained from birds, we established a control treatment of seeds obtained directly from *N. tetetzo* fruits. These seeds were germinated at room temperature under natural daylight conditions. Daily we tallied the number of seeds whose radicle emerged (Godínez-Álvarez *et al.* 2002, Castillo & Valiente-Banuet 2010). We calculated the probability of *N. tetetzo* seed germination after gut passage as follows: (mean number of defecated seeds/mean number of eaten seeds) x (mean number of germinated seeds/mean number of defecated seeds). *Icterus pustulatus* was not captured in the mist nets, and the probability of seed germination after consumption by it was obtained from Castillo (2011). However, the probability actually used was that of *N. mezcalaensis* seeds after consumption by *Icterus cucullatus* and *Icterus wagleri* (Castillo 2011). Bird species that destroyed seeds when they passed through their digestive tract were considered seed predators.

Probability of seed deposition. The terrain of the study area is rugged, which made it difficult to observe the particular plant species where

birds perched after feeding. Therefore, during our foraging observations we recorded the frequency with which birds perched in trees, shrubs, or columnar cacti after foraging (Godínez-Álvarez *et al.* 2002, Castillo 2011). In addition, we established six plots (50 x 20 m) in the area with aggregation of columnar cactus *N. tetetzo* where we quantified the percentage cover of each plant species and of bare ground. The coverage of each species was calculated under the assumption that its area is an ellipse, whose axis is the crown radius to the center of coverage and the crown radius perpendicular to that point (coverage = $\pi \times$ major radius \times minor radius; Gill *et al.* 2009). Bare ground was calculated as the difference between the total measured area and the percentage of coverage occupied by plant species (Castillo 2011). We then estimated the probability with which seeds are deposited in each microhabitat, according to the proportion of the number of times each bird species perched in trees, shrubs, and cacti, and the proportional coverage of each plant species in the area with aggregation of the *N. tetetzo* (Godínez-Álvarez *et al.* 2002, Castillo 2011).

Microhabitat quality. Data on microhabitat quality were obtained from Contreras-González *et al.* (in prep.). Microhabitat quality experiments were conducted on a southern slope of Sabino Canyon with an inclination between 6.9° and 28.4° in the area with aggregation of columnar *N. tetetzo*. A factorial experimental design with two factors was established: (1) microhabitat and (2) predation. The microhabitat factor had 14 levels, consisting of bare ground and underneath 13 perennial plant species (including *N. tetetzo*), whereas the predation factor had two levels, predator exclusion and non-exclusion treatments for *N. tetetzo* seeds. For the microhabitat, we selected the most abundant perennial plant, and species with a higher number of young

individuals of *N. tetetzo* (< 1 m high) growing beneath their crowns. These species were: *Cyrtocarpa procera*, *Plumeria rubra*, *Ceiba aesculifolia* var. *parvifolia*, *Bursera schlechtendalii*, *B. morelensis*, *N. tetetzo*, *Parkinsonia praecox*, *Senna wislizenii*, *Euphorbia schlechtendalii*, *Cnidiosculus tehuacanensis*, *Fouquieria formosa*, *Amphipteridium adstringens*, and *Mimosa luisana*.

Randomly selected seeds were collected from 15 ripe *N. tetetzo* fruits and sown beneath each perennial plant species and in bare ground. Five exclusion and five non-exclusion treatments were established for each microhabitat, with 20 seeds in each replicate. Seed predation by birds and rodents was prevented by wire net cages (15 x 10 x 7 cm) fixed to the ground. To avoid predation by invertebrates, we applied Tanglefoot and insecticide powder (Ant Stop Plus) around each cage after each monitoring session. Survival of seedlings was monitored every month for a year.

Data analysis. Diurnal and nocturnal seed removal was compared using a *t*-test. We compared the number of visits to fruits by different bird species by means of a Chi-square test. We also compared the number of seeds consumed per visit by each bird species, the time of each visit, and the number of feeding individuals by using an ANOVA, after testing for normality of data distributions. All analyses were performed using R software (R Development Core Team 2008).

RESULTS

Diurnal and nocturnal seed removal. During the 2009 fruiting season, diurnal and nocturnal seed removal was similar ($t = 2.01$, $P = 0.54$). Nocturnal removal of fruit pulp and seeds was 51.6%, and diurnal seed removal was 48.4%. As the mean number of seeds per fruit was 944.2 ± 209.7 (mean \pm SE; $N = 10$), seed removal was of 487 seeds per fruit during the

TABLE 1. Bird species observed feeding on fruits of *Neobuxbaumia tetetzo* in tropical deciduous forest in 2009: (part eaten, foraging time (min), number of seeds removed per visit, relative frequency of visits (visits/hour), total number of seeds removed by birds, and probability of germination of seeds of *Neobuxbaumia tetetzo* after gut passage in each bird species). ^aPart eaten/stage of development of the fruit: p – pulp, s – seed, unrp – unripe, rp – ripe. ^bTotal number of seeds removed per species was calculated by: (relative frequency of visits) x (number of seeds removed per visit) x (total number of seeds removed by guild). ^cProbability of seed germination of *N. tetetzo* seeds after gut passage was calculated by: [mean number of defecated seeds (NSD)/mean number of eaten seeds (NSC)] x [(mean number of germinated seeds (NSG)/mean number of defecated seeds (NSD))]. * Mean percentage of germination for columnar cactus *N. mezcalaensis* seeds after gut passage in *Icterus cucullatus* and *Icterus niger* (Castillo 2011).

Species	Part eaten/stage of ripeness ^a	Foraging time (min)	Mean number of seeds removed per visit ± SD	Frequency of visits (visits/hour) (percentage)	Total number of seeds removed ^b (%)	Percentage of seed germination of <i>N. tetetzo</i> after gut passage [(NSD/NSC) x (NSG/NSD)] x 100
White-winged Dove (<i>Zenaidura macroura</i>)	p, s/unrp, rp	3.5 ± 0.01	1618.8 ± 2.95	403 (57)	549,169 (50.6)	(0/10) x (0/0) = 0
Military Macaw (<i>Ara militaris</i>)	c/unrp, rp	8.9 ± 0.06	3022.5 ± 30.21	146 (21)	371,463 (34.2)	[(0/10) x (0/0)] x 100 = 0
Grey-breasted Woodpecker (<i>Melanerpes hypopolius</i>)	p, s/unrp, rp	1.4 ± 2.48	1341.1 ± 18.46	108 (15)	121,918 (11.2)	[(6/7.3) x (4.6/6)] x 100 = 54
Ladder-backed Woodpecker (<i>Picoides scalaris</i>)	p,s/unrp, rp	1.2 ± 0.02	1347.3 ± 33.47	20(3)	22,682 (2.08)	[(11/12) x (11/11)] x 100 = 0.91
Curve-billed Thrasher (<i>Toxostoma curvirostre</i>)	p, s/rp	2.7 ± 0.22	907.3 ± 44.53	13 (18)	9928 (0.91)	[(10/10) x (10/10)] x 100 = 100
Streak-backed Oriole (<i>Icterus pustulatus</i>)	p, s/rp	3.1 ± 0.71	748.5 ± 176.42	2 (0.3)	1260 (0.11)	87*
House Finch (<i>Haemorhous mexicanus</i>)	s/unrp, rp	2.7 ± 0.28	798.4 ± 25.76	14 (0.2)	9409 (0.86)	[(1/9) x (0/1)] x 100 = 0

night and 456.9 seeds per fruit during the day.

Foraging observations. We observed seven bird species feeding on *N. tetetzo* fruits (Table 1). Bird species fed on pulp and/or seeds. Most bird species consumed both immature and mature fruits, although Curve-billed Thrashers (*Toxostoma curvirostre*) and Streak-backed Orioles (*Icterus pustulatus*) fed only on ripe fruits (Table 1).

White-winged Doves and Military Macaws were the most frequent consumers of *N. tetetzo* fruits ($X^2 = 1050$, $df = 6$, $P < 0.0001$). White-winged Doves removed the highest percentage of seeds (50.6% of total number of seeds removed) because this species had a high frequency of visits to fruiting cacti. Military Macaws removed 34.2%, Grey-breasted Woodpeckers 11.2%, and other birds species removed less than 4% (Table 1). Military Macaws foraged in groups and had the highest number of individuals recorded feeding on *N. tetetzo* fruits (mean 1.79 ± 0.014 individuals, range 1–7 individuals; $F_{6,534} = 31.13$, $P < 0.0001$). This species consumed more seeds per foraging visit (3022.5 ± 30.2) than other bird species ($F_{6,504} = 89,225$ $P < 0.0001$). Furthermore, Military Macaws spent more time per visit feeding on the fruits of this cactus (8.9 ± 0.06 min) than any other bird species ($F_{6,737} = 996$, $P < 0.0001$).

Seed germination after gut passage. The number of seeds found in the feces of different bird species varied from 0 to 12. The control treatment had the highest probability of germination at $96 \pm 3.3\%$. Similarly, high probability of seed germination after gut passage was found for Grey-breasted Woodpeckers, Ladder-backed Woodpeckers, and Curve-billed Thrasher (80.5 ± 10 ; 100, 100, respectively). By contrast, all seeds consumed by White-winged Doves, Military Macaws

and House Finches were destroyed (Table 1), so these species acted as pre-dispersal seed predators.

Probability of seed deposition. *Mimosa luisana* provided the largest amount of plant cover in the study area (Table 2), while *B. morelensis*, *N. tetetzo*, and *F. formosa* had the lowest. After feeding, birds moved mostly to other *N. tetetzo* individuals. This was especially so for Streak-backed Oriole and Curve-billed Thrasher, which perched only on other *N. tetetzo* plants after feeding. Grey-breasted and Ladder-backed Woodpeckers perched in trees (0.41 and 0.27 of events, respectively). However, woodpeckers had a high frequency of visits to *N. tetetzo* (Table 3).

Microhabitat quality. After one year *N. tetetzo* seedlings survived only in the predation exclusion treatment, and only in six of the 14 microhabitats (*Cyrtocarpa procera*, *Ceiba aesculifolia* var. *parvifolia*, *Cnidosculus tehuacanensis*, *Euphorbia schlechtendalii*, *Amphypterigium adstringens*, and *Mimosa luisana*; Table 2). The best nursing plants with highest survival of *N. tetetzo* seedlings after one year were *C. procera* and *M. luisana*. Seedlings under *N. tetetzo* and in bare ground did not survive for more than 60 days.

Effectiveness of seed dispersal. Grey-breasted and Ladder-backed Woodpeckers had the highest effectiveness values as seed dispersers (0.00042 and 0.000065, respectively; Table 4). These species did not negatively affect seeds that passed through the digestive tract (germination = 54% and 91%, respectively). Grey-breasted Woodpeckers removed a large number of seeds and showed the highest frequency of perching in trees after feeding. The rest of the species had seed dispersal effectiveness values of zero as a result of the seeds being destroyed after passing through the gut, their low visitation frequency (Table 1), or

TABLE 2. Percentage of canopy cover of perennial plant species used in the survival experiments. Percentage of survival of *N. tetetzo* until one year after germination, either under the canopy of perennial plant species or in bare grounds in tropical deciduous forest. The latter data were obtained from Contreras-González *et al.* (in prep).

Microhabitat	Canopy cover (%)	Survival after one year (%)	
		Excluded	Non-excluded
Bare ground	2.5	0	0
<i>Cyrtocarpa procera</i>	4.3	7.6	0
<i>Plumeria rubra</i>	2.8	0	0
<i>Ceiba aesculifolia</i> var. <i>parvifolia</i>	9.8	6.6	0
<i>Bursera schlechtendalii</i>	6.2	0	0
<i>B. morelensis</i>	0.9	0	0
<i>Neobuxbaumia tetetzo</i>	0.1	0	0
<i>Parkinsonia praecox</i>	12.5	0	0
<i>Senna wislizenii</i>	1	0	0
<i>Cnidoculus tehuacanensis</i>	1.7	1.6	0
<i>Euphorbia schlechtendalii</i>	3	1.7	0
<i>Fouquieria formosa</i>	0.9	0	0
<i>Amphipterigium adstringens</i>	5.1	3.2	0
<i>Mimosa luisana</i>	26.7	6.6	0

because they perched in a *N. tetetzo* after foraging (Table 3).

DISCUSSION

The role of fruit eating animals as dispersers or seed predators can be determined by measuring quantity and quality components (Schupp 1993, Jordano & Schupp 2000, Schupp *et al.* 2010, Calviño-Cancela & Martín-Herrero 2009). The quantity component is related to the frequency of visitation and the number of seeds removed while the quality is related with germination parameters (treatment as passing through gut, germination micro-site, seedling survivorship; Schupp 1993, Jordano & Schupp 2000). In the study area, seed removal of *N. tetetzo* by birds was similar to nocturnal seed removal despite the fact that *N. tetetzo* produces fruits with chiropterochory syndrome. On the other hand, in shrubland in Tehuacan Valley, bats

removed a higher proportion of *N. tetetzo* pulp and seeds than birds (Godínez-Álvarez *et al.* 2002). Similarly, Castillo (2011) reported that bats removed a higher proportion of *N. mezcalaensis* seeds than birds in a shrubland in Tehuacan Valley. In the same area, in *N. macrocephala* which also exhibits fruits with a chiropterochory syndrome, bats played a secondary role to birds in seed removal (Rios 2009). The low nocturnal seed removal of *N. tetetzo* in TDF compared to shrubland could be associated with changes in fruit availability (Jordano 1999). In our study area, we observed that birds opened fruits during the day before these open naturally overnight, allowing more birds to remove seeds. This probably limited the nocturnal food resource for bats, which had been reported as effective seed dispersers of this cactus species in other area, lowering attractiveness of the resource and bat abundance (Godínez-Álvarez *et al.* 2002).

TABLE 3. Probability of seed deposition under perennial plant species used for survival experiments of *Neobuxbaumia tetetzo* in tropical deciduous forest. Bg – bare ground; Cp – *Cyrtocarpa procer*; Pr – *Plumeria rubra*; Ca – *Ceiba aesculifolia* var. *parvifolia*; Bs – *Bursera schlectendalii*; Bm – *B. moreletensis*; Pp – *Parkinsonia praecox*; Sw – *Senna wislizenii*; Ct – *Cnidocaulis tehuacanensis*; Es – *Euphorbia schlectendalii*; Ff – *Fouquieria formosa*; Aa – *Amphipterigium adstringens*; Ml – *Mimosa luisana*; Nt – *Neobuxbaumia tetetzo*.

Bird species	Perennial plant species													
	Bg	Cp	Pr	Ca	Bs	Bm	Pp	Sw	Ct	Es	Ff	Aa	Ml	Nt
<i>Zenaidura macroura</i>	0	0.012	0.01	0.028	0.001	0.002	0.03	0.002	0.0003	0.0006	0.002	0.015	0.005	0.69
<i>Ara militaris</i>	0	0.01	0.01	0.022	0	0.002	0.028	0.002	0	0	0.002	0.011	0	0.78
<i>Melanerpes hypopolius</i>	0	0.018	0.01	0.041	0	0.0037	0.052	0.0041	0	0	0.0037	0.021	0	0.59
<i>Picoides scalaris</i>	0	0.012	0.01	0.027	0	0.0025	0.034	0.0027	0	0	0.0025	0.014	0	0.73
<i>Taxostoma curvirostre</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Icterus pustulatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Haemorhous mexicanus</i>	0	0.01	0.01	0.023	0	0.0021	0.029	0.0023	0	0	0.0021	0.012	0	0.77

TABLE 4. Seed dispersal effectiveness of birds that feed on fruits in tropical deciduous forest in Sabino Canyon, measured as the contribution of frugivores to recruitment until one year after germination. The effectiveness values for each bird species were obtained from the sum of the products of removed seeds, probability of seed germination after gut passage, probability of deposition, and microhabitat quality for recruitment until one year after germination.

Bird species	Effectiveness
<i>Zenaida asiatica</i>	0
<i>Ara militaris</i>	0
<i>Melanerpes hypopolius</i>	0.00042
<i>Picoides scalaris</i>	0.000065
<i>Taxostoma curvirostre</i>	0
<i>Icterus pustulatus</i>	0
<i>Haemorhous mexicanus</i>	0

At our site, six bird species feed on the fruits of *N. tetetzo*, five of which have already been reported to consume the fruits of this cactus in shrubland: White-winged Dove, Grey-breasted Woodpecker, Ladder-backed Woodpecker, House Finch (Godínez-Álvarez *et al.* 2002), and Military Macaw in Sabino Canyon (Contreras-González *et al.* 2009). However, Streak-backed Oriole had not been reported to feed on *N. tetetzo* fruits before, although this species has been reported to feed on *N. mezcalaensis* fruits (Castillo 2011). Our analysis of the effectiveness of seed dispersal of *N. tetetzo* by birds in Sabino Canyon showed that only Grey-breasted and Ladder-backed Woodpeckers had values greater than zero on seed dispersal of *N. tetetzo*, as has been reported in shrubland (Godínez-Álvarez *et al.* 2002). This was due to the effects of gut passage on seed germination, since the percentage of seed germination of *N. tetetzo* passing through the digestive tract of these two woodpecker species were the highest measured; however, the majority of their visits after foraging were made to conspecifics of *N. tetetzo* (59% of visits by Grey-breasted

Woodpeckers and 73% of visits by Ladder-backed Woodpeckers). Similar post-feeding behavior has been reported for these birds visiting *N. tetetzo* (Godínez-Álvarez *et al.* 2002), *N. mezcalaensis* (Castillo 2011), and *N. macrocephala* (Rios 2009) in shrubland. This post-foraging behavior increased the probability of seed deposition under parent plant species, which is obviously inadequate for seedling establishment because seeds deposited under conspecifics experienced high mortality of seedlings during later growth phases (Contreras-González *et al.* in prep.).

Although Curve-billed Thrashers and Streak-backed Orioles were not considered seed predators, these species presented a low visitation frequency to *N. tetetzo* and all their visits after feeding were made to conspecific plants, resulting in a low seed dispersal effectiveness value. The low frequency of visits of these bird to this cactus species can be caused by the low fruit production of this cactus during the studied year, and by the influence of other cacti species producing fruits at the same time as *N. tetetzo* (Contreras-González 2007). In contrast, Godínez-Álvarez *et al.* (2002) reported that Curve-billed Thrashers had a high effectiveness value in shrubland because this species had a higher visitation frequency to *N. tetetzo* fruits, and it mostly visited shrubs after feeding.

Only some of the birds that feed on *N. tetetzo* fruits leave the seeds intact. This was the case for White-winged Doves, Military Macaws, and House Finches, which destroyed all seeds during gut passage. White-winged Doves and House Finches are also considered seed predators in shrubland (Godínez-Álvarez *et al.* 2002). Foraging by avian predators on *N. tetetzo* seeds could have negative effects on the recruitment of this cactus especially in non-mast years, since the density of available seeds has been reported as negatively related with predation probability (Hulme 1998, Hulme & Benkman 2002).

In shrubland, the values of seed dispersal effectiveness of birds visiting *N. tetetzo* were similar to our study (Godínez-Álvarez *et al.* 2002). However, for *N. mezcalaensis* the values of effectiveness in seed dispersal for bird species were higher than in our study (Castillo 2011), mainly due to the high frequency of visits and the deposition of seeds directly into safe sites for establishment of this cactus. We found that seed predation by birds represented 41.4% of total diurnal and nocturnal seed removal. In shrubland, Rios (2009) observed in columnar cactus *N. macrocephala* a high loss of seeds caused by birds. In shrubland, Godínez-Álvarez *et al.* (2002) also found that White-winged Doves had a high frequency of foraging visits to *N. tetetzo*, but the overall seed loss from predation was lower in shrubland, perhaps due to the absence of Military Macaws.

The consumption rate by Military Macaws was similar to that observed by Contreras-González *et al.* (2009) in the 2005 fruiting season in the same study area. This resembles the pattern of consistent seed predation found for Lilac-crowned Parrots (*Amazona finschi*) by Renton (2001). Previous studies have reported high rates of seed predation by parrots with potentially negative effects on plant demography (Galetti & Rodrigues 1992, Coates-Estrada *et al.* 1993, Haugaasen 2008, Francisco *et al.* 2008, Villaseñor-Sanchez *et al.* 2010, Ragusa-Netto 2011). The high pre-dispersal seed predation of *N. tetetzo* found in our study can be explained by the presence of White-winged Doves and Military Macaws in the area, since these species have the highest visitation frequency and the longest foraging time, and they removed the largest number of seeds.

The high level of fruit consumption by Military Macaws may also occur because the fruiting season coincides with the beginning of nesting and egg-laying, high fruit availability of *N. tetetzo* and low fruit availability from

other species in the study area (Rivera-Ortiz *et al.* 2008, Contreras-González *et al.* 2009). Fruits of *N. tetetzo* are rich in proteins and lipids (Contreras-González *et al.* 2009), which are required by birds during the breeding season (Vriends 1991, Koutsos *et al.* 2001).

Birds may deposit seeds of *N. tetetzo* at sites unfavorable for their establishment, as during the first year only seedlings established under six of the 13 nurse plant species studied will survive (Contreras-González *et al.* in prep). Such establishment is a critical stage for the effectiveness of seed dispersal, because not all sites where seeds are delivered provide favorable conditions for their survival (Callaway 1998, Callaway 2007, Calviño-Cancela & Martín-Herrero 2009, Castillo 2011).

Our results suggest that seed dispersal effectiveness could be affected negatively by i) delivering seeds into inappropriate sites for establishment, b) low fruit production, and c) pre-dispersal seed predation, which may decrease the availability of resources to effective dispersers (Godínez-Álvarez *et al.* 2002, Calviño-Cancela & Martín-Herrero 2009, Castillo 2011).

ACKNOWLEDGEMENTS

We appreciate the revision of this paper by Katherine Renton. Funding assistance for the project was provided by CONABIO DS005 and Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT) IN 217511 to MCA, and by a fellowship to AMC-G (Consejo Nacional de Ciencia y Tecnología: 164991). We thank the Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México for the financial and academic support extended to AMC-G. We also thank the authorities in Santa María Tecomavaca, Oaxaca, Mexico, for the facilities that were provided. Finally, we thank Ezel Galindo, Francisco Rivera, Emanuel Leal, Edson Espinoza, Gabriela de la

Cruz, Gabriel López, Karla Rodríguez, Ricardo Álvarez, Elisa Parra, Carlos Rosas, Angeles López, Jaqueline, Axel Sotomayor, Mauricio Pérez, Berenice Núñez, and Manuel Soberanes for field assistance.

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