

Seed Dispersal of *Morus macroura* (Moraceae) by Two Frugivorous Bats in Xishuangbanna, SW China

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ABSTRACT

The dispersal of *Morus macroura* seeds by two species of frugivorous bats (*Rousettus leschenaulti* and *Cynopterus sphinx*) was studied in a forest at Xishuangbanna Tropical Botanical Garden in Southwest China from March to May 2005. Feeding roosts were identified within 500 m around parent trees and the types and number of seed loads under each roost were recorded. We found feeding roost density decreased with increasing distance from the parent, but found no correlation between distance and seed deposition. The effect of bat digestion on seed germination was investigated, and we found that germination percentage of all treatments involving ingestion by bats was significantly lower than control seeds and some germination parameters of seeds from different treatments changed.

Key words: *Cynopterus sphinx*; germination; *Rousettus leschenaulti*; seed shadow.

FRUGIVOROUS BATS HAVE BEEN IDENTIFIED AS IMPORTANT SEED DISPERSERS in both tropical and subtropical rain forests (Heithaus 1982; Thomas 1984, 1991; Fleming 1986, 1988; Charles-Dominique 1991; Medellín & Gaona 1999) and consequently play an important role in forest regeneration and maintaining forest diversity (Fleming & Sosa 1994, Galetti & Morellato 1994). Among the main behavioral characteristics of frugivorous bats that determine the deposition patterns of seeds are the foraging behavior and movement patterns, and the gut passage time of seeds (Godínez-Alvarez & Valiente-Banuet 2000).

Morus macroura (Moraceae) is widely distributed in Xishuangbanna, China. It is of low abundance in tropical seasonal rain forests, with a hectare of forest containing no more than one adult tree, and it is not uncommon to find isolated individuals. The fruits are suspended on long stems, ripen from April through May, and are yellowish green when ripening, with a noticeable pungent odor, which can be detected at least 100 m downwind from the parent trees by humans. Fruits are 40–100 mm long, 6–10 mm in diameter, have a fresh weight of 2–5 g, and contain 100–300 seeds. *Morus macroura* fruits are heavily consumed by the frugivorous bats *Rousettus leschenaulti* and *Cynopterus sphinx* in Xishuangbanna. Although bats are clearly the major consumers of *Morus* fruits, other small mammal species such as squirrels (*Callosciurus erythraeus*, *C. pygerythrus*, *Tamiops maccllellandi*), palm civets (*Paguma larvata*), and birds also eat the fruits (Wang *et al.* 2000).

Our knowledge regarding the specific role of frugivorous bats as dispersal agents of *M. macroura* is limited. In this study, we investigate the distribution of feeding roosts of frugivorous bats

around *M. macroura* parent trees and provide quantitative data of seeds dispersed by bats to different feeding roosts to document the spatial pattern of seed dispersal (seed shadow). We ask whether seed deposition decreases with distance from the parent tree and whether distribution of feeding roosts is related to distance from parent trees. Furthermore, we investigate germination and viability of seeds passed through their digestive tracts or spat out by bats as pellets (henceforth referred to as ‘ejecta’) while feeding on fleshy fruits.

The study was carried out in a protected area of forest (ca 30 ha, 21°55' N, 101°16' E, 550 m asl) in the Xishuangbanna Tropical Botanical Garden (XTBG), in Yunnan province, Southwest China. The vegetation of the research site is tropical seasonal rain forest dominated by *Pometia tomentosa* and *Terminalia myriocarpa* with an average canopy height of 30 m (Zhang & Cao 1995). Average annual rainfall is 1539 mm, of which 82 percent occurs in the rainy season (May–October) and another 18 percent occurs in the dry season (November–April). Average annual temperature is 21.4°C (Cao & Zhang 1997). In our study site, only two *M. macroura* trees were found, 200 m apart. Tree 2 fruited 2 wk after tree 1, permitting us to study seed dispersal separately.

We spent 45 h (5 h × 9 nights) observing the foraging behavior of the bats on *M. macroura* fruits, using moonlight or infrared binoculars after dark (ca 1900 h) around tree 1. We used infrared binoculars to focus on branches with abundant fruits and observe the bats’ feeding behavior. Bat species were identified by capturing the bats in mist nets near the tree when observing their foraging activity.

Active feeding roosts of bats were found by systematically searching the areas 500 m around parent trees every day from March 14 to May 13, 2005 and identified by fresh ejectas and feces under active feeding roosts. At these roosts, we suspended a horizontal

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plastic screen with four stakes, 1 m above ground to prevent the collected contents being preyed on by other vertebrates before sunset. Feces, ejecta, and dropped fruits were collected overnight and checked the following morning. Data on number of feces, ejecta, fruits, and roost type (tree species hung in while feeding on fruits) and position were recorded. We defined feces, ejecta, and fruits dropped by bats each as seed loads, because, besides feces, both ejecta and fruits dropped included seeds. The number of seed loads in feeding roosts was defined as seed deposition and was regarded as an indicator of frequency of roost utilization. We calculated the density of feeding roosts by separating the study area into a series of 10-m wide concentric strips spanning parent trees and then dividing roost numbers by the area of the corresponding circular strip.

The effects of fruit manipulation by bats on seed germination were evaluated with seed germination experiments. Three treatments were compared: (1) seeds from feces ($N = 308$ from *C. sphinx*, $N = 282$ from *R. leschenaulti*); (2) seeds from ejecta ($N = 362$ from *C. sphinx*, $N = 318$ from *R. leschenaulti*; obtained from feeding roosts); and (3) control seeds ($N = 586$). Seeds from feces were obtained from individuals of bats captured (7 fecal samples from 9 *R. leschenaulti* and 13 fecal samples from 22 *C. sphinx*). Seeds from ejecta were obtained from the plastic screens located under feeding roosts (ejecta spat out by *R. leschenaulti* or *C. sphinx* could be identified to species according to their shape: the ejecta manipulated by *C. sphinx* is elliptical/round in shape, while ejecta manipulated by *R. leschenaulti* has an elongated shape). The control seeds were obtained from ripe fruits taken directly from parent trees (20 fruits were collected). The pulp was removed using soft cloth and any pulp remains on the seed were washed off.

We placed at least 41 seeds (41–109 seeds for different treatments) in each of the six Petri dishes with moistened humid filter paper for each treatment. Each dish of each treatment was treated as a replicate. Petri dishes were placed in an Intelligent Man-made Climatic Incubator (MGC-35HP-2, Yiheng Science and Technology Limited Company, Shanghai, China), which maintained a constant temperature of 30°C, and 12 h under light in a 24-h cycle. Treatments were moistened with distilled water periodically. The numbers of seeds that germinated were counted daily until there was no further germination for over 1 mo. Germinated seeds were removed as they were counted to reduce their effect on the remaining ungerminated seeds. Germination was defined as the emergence of any seedling part from the seed (Izhaki *et al.* 1995). Quantitative evaluation of seed germination was based on the following three parameters: (1) Final germination percentage (GP), which refers to the percentage of seeds capable of germinating under experimental conditions; (2) Mean germination time (MGT), which was calculated according to the equation: $MGT = \sum n_i d_i / n$, where n is total number of seeds germinated during experimental period; n_i is number of seed germinated on day d_i ; d_i is day during germination period; (3) Beginning day of germination (BDG), which refers to the beginning of the germination process.

All statistical analyses were performed with SPSS 12.0 (Chicago, IL). The one-sample Kolmogorov–Smirnov test was used to determine whether data were normally distributed and the Levene's test was used to confirm homogeneity of variances. One-way

analysis of variance (ANOVA) was used to detect differences in germination percentage among treatments. We used post hoc Tukey tests to detect differences between treatments. Kruskal–Wallis test was used to detect the difference of seed germination distributions between different treatments because the data were not distributed normally. Germination proportions were arcsin-square-root transformed before analysis. Linear regression was employed to explore the relationship between density of feeding roosts and distance from parent trees. Correlations between the relative abundance of tree species selected by roosting bats and their relative abundance over the study area were tested by Spearman's rank correlation.

We found that night feeding activity began at a similar time for both bat species, around 2000 h, about 20–40 min after sunset. Individual bats flew to the canopy of the tree, and removed and carried fruits to feeding roosts (other trees) for consumption. Individuals seldom, if ever, remained in source trees to feed on fruits. Thirteen species of tree were used as feeding roosts by bats around tree 1 and five species around tree 2 (Table 1). An abandoned shed was also used by bats around tree 1. For both trees, feeding roost density was higher within 30 m of the parent tree than further away. Feeding roost density decreased with increasing distance from the parent tree (linear regression, $P < 0.05$; $R^2 = 0.56$, considering the distance range 10–140 m around parent tree 1; and $P < 0.05$; $R^2 = 0.268$, considering the distance range 10–200 m around parent tree 2; Fig. 1).

There was no correlation between the relative abundance of tree species selected by roosting bats and their relative abundance over the study area (Spearman's rank correlation; tree 1: $R = 0.403$, $P = 0.078$; tree 2: $R = 0.019$, $P = 0.937$). Thus, bats did not select feeding trees randomly, but probably according to particular features such as branch and foliage structure. *Mesua ferrea* was the most common tree used as a feeding roost by bats, receiving the majority of seed loads for both parent trees (Table 1). Correlations between distance of feeding roosts from the resource tree and proportion of seed loads was explored for tree 1 only, and we did not find significant correlation between them (Pearson's correlation analysis, feces distance: $r = 0.016$, $P = 0.936$; ejecta distance: $r = 0.098$, $P = 0.627$; fruit distance: $r = 0.223$, $P = 0.264$). The sample size for tree 2 was too small to explore correlations between them.

Significant differences among germination of seeds in the different treatments were observed (ANOVA, $F_{4,25} = 65.8$, $P < 0.05$). Germination distributions of seeds (Fig. 2; Table 2) differed significantly among the three treatments (feces, ejecta, control) for both bat species (Kruskal–Wallis, $P < 0.05$). The seeds from ejecta of the two bat species exhibited germination pattern roughly similar to the control seeds (Fig. 2). Compared to control seeds, the passage through *C. sphinx* digestive tracts resulted in a decrease in GP, an increase in MGT of 10 d, and an increase in BDG of 4 d. Similarly, passage through *R. leschenaulti* digestive tracts resulted in a decrease in GP, an increase in MGT of 3 d, and an increase in BDG of 1 d.

Our data show that the two bat species studied serve as seed carriers that transport seeds away from the parent tree to variable environments, and that feeding behavior of bats has different effects upon seed germination. Although the bats could carry seeds to a variety of feeding roosts available in the environment,

TABLE 1. *Frugivorous bat feeding roosts 2 M. macroura fruiting trees (1 and 2) from March 14 to May 13, 2005. Percentages are based on total feces, ejecta, and fruit samples collected. Sample sizes are included in brackets.*

Feeding roosts	Tree 1			
	Distance from parent tree (m)	Percentage of total feces samples (241)	Percentage of total ejecta samples (2265)	Percentage of total fruit samples (63)
Below parent tree 1	0		1.24	
Abandoned shed	48.2	43.57	18.90	14.29
<i>Mesua ferrea</i> -1	105	9.54	13.95	20.63
<i>Mesua ferrea</i> -2	110		0.22	
<i>Mesua ferrea</i> -3	113		5.47	7.94
<i>Mesua ferrea</i> -4	123	1.24	3.36	3.17
<i>Alstonia scholaris</i> -1	13.9			1.59
<i>Alstonia scholaris</i> -2	22.2	3.32	7.51	3.17
<i>Alstonia scholaris</i> -3	23.2		0.13	
<i>Alstonia scholaris</i> -4	23.6		0.04	
<i>Alstonia scholaris</i> -5	27.7		1.41	1.59
<i>Alstonia scholaris</i> -6	29.1	4.15	1.94	
<i>Alstonia scholaris</i> -7	31.8		0.13	
<i>Alstonia scholaris</i> -8	33.3		5.21	9.52
<i>Mayodendron igneum</i> -1	68.1		3.09	1.59
<i>Mayodendron igneum</i> -2	68.6	4.15	4.77	6.35
<i>Ficus curtipes</i> -1	59.4		0.09	
<i>Ficus curtipes</i> -2	72.2	0.41	3.84	4.76
<i>Baccaurea ramiflora</i>	37		9.85	6.35
<i>Caryodaphnopsis tonkinensis</i>	92.9	9.13	7.37	6.35
<i>Celtis tetrandra</i>	78.6	3.73	4.19	7.94
<i>Streblus asper</i>	80.3	5.39	3.13	
<i>Tetrameles nudiflora</i>	64		1.32	3.17
<i>Butea monosperma</i>	107		1.28	1.59
<i>Caryota urens</i>	78		0.57	
<i>Lagerstroemia villos</i>	68.3	13.70	0.49	
<i>Erythrina stricta</i>	114	0.41	0.49	
Near a small road		1.24		
Feeding roosts	Tree 2			
	Distance from parent tree (m)	Percentage of total feces samples (65)	Percentage of total ejecta samples (434)	Percentage of total fruit samples (3)
<i>Mesua ferrea</i> -1	105	21.54	14.28	
<i>Mesua ferrea</i> -2	119	1.54	2.53	33.33
<i>Mesua ferrea</i> -3	121	9.23	1.38	
<i>Mesua ferrea</i> -4	134	23.07	10.37	
<i>Barringtonia pendula</i>	17.9		26.04	
<i>Castanopsis indica</i>	33.3		23.04	
<i>Millettia leptobotrya</i>	20.9		19.35	33.33
<i>Bischofia javanica</i>	18.1		3.00	33.33
Near <i>Quisqualis caudata</i>	197	44.62		

including a manmade shed, they clearly preferred specific trees. Bats do not seem to select their feeding trees based on density because, although abundance of several tree species not used by bats in study area was relatively high, such as *Anthocephalus chinensis*

(1.33 individuals per hectare), *Albizia lucidior* (0.67), and *Syzygium szemaoense* (0.89), these species were not used as feeding roosts. Location of feeding roosts appears to depend more on roost type (tree species) than on distance. We suggest that tree architecture and

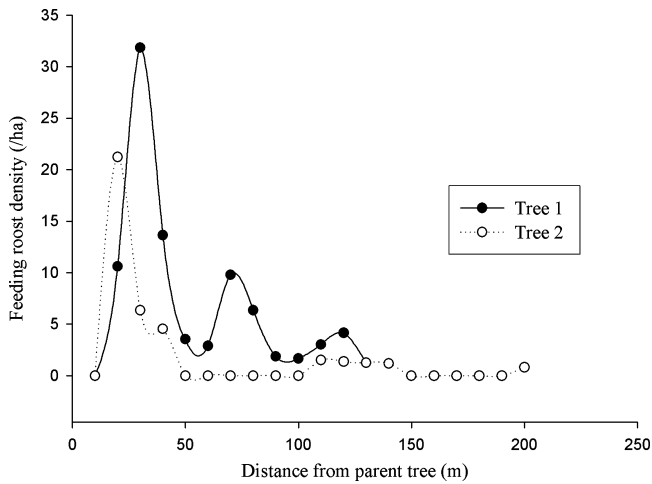


FIGURE 1. Feeding roost density in relation to distance from two parent trees of *Morus macroua* in XTBG, Yunnan province, South China.

microsite characteristics may be important factors affecting feeding roost selection. The tree species used most often, *M. ferrea*, *Alstonia scholaris*, and *Baccaurea ramiflora*, all have horizontal boughs with a dense drooping umbrella-like crown of leaves offering cover for roosting. Distance effect on roost density is counterbalanced by the absence of distance effect on the frequency of roost utilization. The frequency of roost utilization appears to depend on roost type rather than distance, which may promote evenness of seed shadow around parent tree.

Although the passage of seeds through the digestive tracts of bats did not improve germination percentage, seed ingestion by bats modified, to a large or small extent, the speed at which *M. macroua* seeds germinated, a result consistent with that reported by Naranjo *et al.* (2003), who tested germination of *Stenocereus griseus* and *Subpilocereus repandus* seeds when passing through the digestive tract of the Miller's long-tongued bat *Glossophaga longirostris*. Sosa (1997) also found that the ingestion of *Stenocereus thurberi* by bats does not improve germination and contributes only to dispersal by transportation of seeds. As pulp can act as a germination inhibitor and can also increase the probability of seed deterioration with fungi (Naranjo *et al.* 2003), it is possible that removal of the inhibiting factor present in the pulp resulted in higher germination of control seeds in our experiment. Most studies indicated that seed germination of many plant species improved after ingestion by bats (Fleming & Heithaus 1981, Lieberman & Lieberman 1986, Figueiredo & Perin 1995, Shilton *et al.* 1999). For example, seeds of *Cecropia peltata* and *Solanum bazenii* have higher germination percentages after gut passage through bats (Fleming & Heithaus 1981). Shilton *et al.* (1999) demonstrated improved germination probability in seeds ingested and retained (> 12 h in digestive tract) by *C. sphinx*, relative to control seeds (although different *Ficus* species responded differently).

An interesting result is that gut passage through *C. sphinx* resulted in a 10-d increase in MGT, but a 3-d increase for *R.*

leschenaulti, although retention time of seeds in the digestive tract was not significantly different between *C. sphinx* and *R. leschenaulti* (*C. sphinx*: 34.2 ± 5.5 [$N=5$] min; *R. leschenaulti*: 32.7 ± 3.0 [$N=11$] min, *t*-test, $t = 0.259$, $P > 0.05$). The mechanism by which it occurs remains unknown.

Seeds can be deposited by bats on different sites. Besides transporting seeds to feeding roosts, bats can also disperse seeds through fecal deposition on route to feeding roosts. The overall seed shadow is likely to be relatively extended and more homogeneous compared to those produced for large, uningested seeds (Hodgkison *et al.* 2003a). *Cynopterus sphinx* and *R. leschenaulti* are relatively wide-ranging frugivorous species, and are more likely to cover long distances and hence transport fruits/seeds further away than smaller-sized frugivores with relatively restricted ranges, such as *Balionycteris maculata* (Hodgkison *et al.* 2003b). Shilton *et al.* (1999) found that *Ficus septica* and *F. variegata* seeds can be retained in the digestive tract of *C. sphinx* for > 12 h and remain viable, which could result in dispersal distances of over 300 km from the parent plant. We did not test whether *M. macroua* seeds can be retained in the digestive tracts of *C. sphinx* and *R. leschenaulti* through the daytime resting phase, or whether seeds were viable after extended gut passage. However, observations of captured bats in free flight cages producing defecations after the cages were cleaned in the morning indicated that they could potentially retain *M. macroua* seeds in their digestive tracts for longer time periods and thus have the potential to be long-distance dispersers (Z. H. Tang, unpublished data).

The foraging habits of these bats produce a population of seeds with considerable variability in their germinability, and this will likely ensure that only part of the seed population will germinate at a given time, which can enhance the survival of seeds and spread germination relatively evenly over a long time period (Koller 1972, Gutterman 1985, Izhaki *et al.* 1995). This can be considered

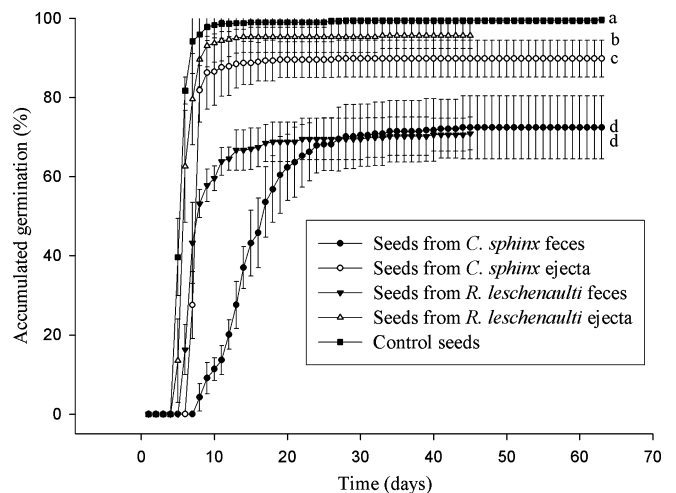


FIGURE 2. Accumulated seed germination (percentage) under different treatments. Significant differences among treatments ($P < 0.05$, using Kruskal–Wallis test and Tukey's test) are indicated by different letters: $a > b > c > d$.

TABLE 2. Seed germination trial results. The final germination percentage (GP), mean germination time (MGT) in days, and beginning day of germination (BDG) in days. Significant differences among the five treatments ($P < 0.05$, using one-way ANOVA, and Tukey's test) in GP are indicated by the superscript a–d: $a > b > c > d$.

	<i>Cynopterus sphinx</i>		<i>Rousettus leschenaulti</i>		Control
	Feces	Ejecta	Feces	Ejecta	
GP (%)	72.08 ^d	89.87 ^c	71.07 ^d	95.76 ^b	99.48 ^a
MGT (d)	15	7	8	6	5
BDG (d)	7	6	5	4	4

of key importance at the end of the dry season, when water is a limiting and unpredictable ecological factor during March to May in Xishuangbanna. The removal of the fruit pulp in seeds from feces by these two frugivorous bats may also increase seed survival by reducing the risk of seed predation and fungal attacks as suggested for some other bats (Janzen 1982). We found that seeds with fruit pulp (ejecta and fruit) suffered severely from ant predation, but seeds in feces were ignored; thus, pulp removal appears to provide an escape from ant predation. Flesh pulp is a potential source of infection by fungal or other pathogens (Traveset 1998, Liu *et al.* 2004), and our observations indicated that many ejecta and fruit were infected within 1 wk. Although seeds from ejecta germinated better, this advantage is negligible given the much lower probability of seed survival compared to seeds from feces. Seed germination experiments without removing pulp and seedling establishment under various habitats in field should be performed in future studies.

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LITERATURE CITED

- CAO, M., AND J. H. ZHANG. 1997. Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. *Biodivers. Conserv.* 6: 995–1006.
- CHARLES-DOMINIQUE, P. 1991. Feeding strategy and activity budget of the frugivorous bat *Carollia perspicillata* (Chiroptera: Phyllostomidae) in French Guiana. *J. Trop. Ecol.* 7: 243–256.
- FIGUEIREDO, R. A., AND E. PERIN. 1995. Germination ecology of *Ficus luschnathiana* drupelets after bird and bat ingestion. *Acta Oecol.* 16: 71–75.
- FLEMING, T. H. 1986. Opportunism versus specialization: The evolution of feeding strategies in frugivores and seed dispersal. In A. Estrada and T. H. Fleming (Eds.), *Frugivores and seed dispersal*, pp. 105–118. W. Junk Publishers, Dordrecht, The Netherlands.
- FLEMING, T. H. 1988. The short-tailed fruit bat: A study in plant-animal interactions. 359 p. The University of Chicago Press, Chicago, Illinois.
- FLEMING, T. H., AND E. R. HEITHAUS. 1981. Frugivorous bat, seed shadows, and the structure of tropical forests. *Biotropica* 13: 45–53.
- FLEMING, T. H., AND V. J. SOSA. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *J. Mammal.* 75: 845–851.
- GALETTI, M., AND L. P. C. MORELLATO. 1994. Diet of the large fruit-eating bat *Artibeus lituratus* in a forest fragment in Brazil. *Mammalia* 58: 661–665.
- GODÍNEZ-ALVAREZ, H., AND A. VALIENTE-BANUET. 2000. Fruit-feeding behavior of the bats *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: Consequences for dispersal of columnar cactus seeds. *Biotropica* 32: 552–556.
- GUTTERMAN, I. 1985. Flowering, seed development, and the influence during seed maturation on seed germination of annual weeds. In S. O. Duke (Ed.), *Weed physiology*, vol. 1. Reproduction and ecophysiology, pp. 1–25. CRC Press, Boca Raton, Florida.
- HEITHAUS, E. R. 1982. Coevolution between bats and plants. In T. H. Kunz (Ed.), *Ecology of bats*, pp. 327–367. Plenum Press, New York, New York.
- HODGKISON, R., S. T. BALDING, A. ZUBAID, AND T. H. KUNZ. 2003a. Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian Rainforest. *Biotropica* 35: 491–502.
- HODGKISON, R., S. T. BALDING, A. ZUBAID, AND T. H. KUNZ. 2003b. Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata* (Chiroptera: Pteropodidae), in a Malaysian lowland dipterocarp forest. *J. Trop. Ecol.* 19: 667–676.
- IZHAKI, I., C. KORINE, AND Z. ARAD. 1995. The effect of bat (*Rousettus aegyptiacus*) dispersal on seed germination in eastern Mediterranean habitats. *Oecologia* 101: 335–342.
- JANZEN, D. H. 1982. Simulation of *Andira* fruit pulp removal by bats reduces seed predation by *Cleogonus* weevils. *Brenesia* 19/20: 165–170.
- KOLLER, D. 1972. Environmental control of seed germination. In T. T. Kozlowski (Ed.), *Seed biology* 2, pp. 1–101. Academic Press, New York, New York.
- LIEBERMAN, M., AND D. LIEBERMAN. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *J. Trop. Ecol.* 2: 113–126.
- LIU, H., S. G. PLATT, AND C. K. BORG. 2004. Seed dispersal by the Florida box turtle (*Terrapene Carolina bauri*) in pine rockland forests of lower Florida Keys, United States. *Oecologia* 138: 539–546.
- MEDELLÍN, R. A., AND O. GAONA. 1999. Seed dispersal by bats and birds in forest and disturbed habits of Chiapas, México. *Biotropica* 31: 478–485.
- NARANJO, M. E., C. RENGIFO, AND P. J. SORIANO. 2003. Effect of ingestion by bats and birds on seed germination of *Stenocereus griseus* and *Subpilocereus repandus* (Cactaceae). *J. Trop. Ecol.* 19: 19–25.
- SOSA, V. J. 1997. Seed dispersal and recruitment ecology of columnar cacti in the lower Sonoran Desert. PhD dissertation, University of Miami, Coral Gables, Florida.
- SHILTON, L. A., J. D. ALTRINGHAM, S. G. COMPTON, AND R. J. WHITTAKER. 1999. Old world fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proc. R. Soc. Lond. B* 266: 219–223.
- THOMAS, D. W. 1984. Fruit and energy intake budgets of frugivorous bat. *Physiol. Zool.* 57: 457–467.
- THOMAS, D. W. 1991. On fruits, seeds and bats. *Bats* 9: 8–13.
- TRAVESSET, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: A review. *Perspect. Plant. Ecol. Evol. Syst.* 1: 151–190.
- WANG, Z. J., J. CHEN, X. B. DENG, Z. L. BAI, Q. YANG, AND Y. LIU. 2000. *Morus macroua* and the wildlife who eat their berry in different mountain regions, Xishuangbanna, Yunnan. *J. Mt. Sci.* 18: 267–271.
- ZHANG, J. H., AND M. CAO. 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biol. Conserv.* 73: 229–238.