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Observations on the role of frugivorous bats as seed dispersers in Costa Rican secondary humid forests

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The role of frugivorous bats as seed dispersers in humid neotropical tropical forests was evaluated between January and August 1995. Thirty germination trials were set up using seeds defecated by six bat species. Seeds of *Piper multiplinervium* and *Ficus insipida*, defecated by *Carollia brevicauda* and *Artibeus jamaicensis*, respectively, showed significantly higher germination percentages than seeds not ingested by bats. Of seven seed species regurgitated by bats, only *Markea neurantha* showed significant increases in percent germination compared to seeds not ingested by bats. Of 19 tents and three active feeding roosts found, 12 tents and three feeding roosts were in primary forest, while six tents were in abandoned plantations. For tent construction, four bat species used six plant species. Fifty-two percent of seeds found under tents and feeding roosts were from secondary forest species. Twenty-two percent of seed species in fecal samples from netted bats in three secondary forest types were primary forest species. Bats in our study dispersed seeds between different habitat types.

Key words: Costa Rica, frugivorous bats, germination, La Selva Biological Station, seed dispersal

INTRODUCTION

A mutualistic relationship exists between plants and their seed dispersers (Howe and Smallwood, 1982). Seed dispersers receive nutrients from seeds and plants obtain seed mobility. From the viewpoint of plant-animal relationships, frugivory is a mechanism that maintains high plant diversity in the tropical forests (Janzen, 1970). In a rain forest, such as in La Selva Biological Station (LSBS), Costa Rica, over 90% of shrub and tree species produce fruits dispersed by animals (Frankie *et al.*, 1974; Opler *et al.*, 1980). Among Neotropical bats, the Carolliinae and Stenodermatinae subfamilies are primarily frugivorous and abundant (Howell and Burch, 1974; Gardner, 1977; Levey *et al.*, 1994) and have evolved a mutualistic system with their host plants.

Ecological factors favoring seed dispersal could include: a) escaping greater seed mortality close to the mother plant, b) colonizing regeneration sites, and c) dispersing plant species to adequate sites for seedling establishment (Howe and Smallwood, 1982). McKey (1975) proposed four criteria to evaluate a successful dispersal by a frugivore. These include changes in: a) probability that a seed germinates after digestion, b) seed size ingested or transported, c) probability that seeds are deposited in sites favorable for germination and subsequent establishment, and d) visitation consistency towards a plant with mature fruits.

In Central America, seed dispersal by bats has been studied in forests with marked seasonality (Heithaus *et al*., 1975; Morrison, 1978; Bonaccorso, 1979; Fleming *et al*., 1985; Fleming, 1988). At LSBS, bats are an important group of frugivores; however, the literature on their role in seed dispersal is scarce (Levey *et al*., 1994). The objective of the present study was to evaluate the role frugivorous bats play in seed dispersal between habitat types in the tropical rain forest at LSBS. Specifically, we wanted to know the viability of seeds passed by bats, regurgitated or dropped while feeding.

MATERIALS AND METHODS

Study Site

La Selva Biological Station (LSBS), administered by the Organization for Tropical Studies (OTS), is located at the base of the Central Volcanic Mountain Range, approximately 2 km east of the town of Puerto Viejo de Sarapiqui, Heredia Province, Costa Rica (10°26'N; 83°59'W). LSBS encompasses 1,536 ha and varies in elevation from 35 to 137 m a.s.l. (McDade and Hartshorn, 1994). LSBS has tropical humid forest and premontane rain forest life zones; a mosaic of forest types exist in different successional states (Hartshorn and Hammel, 1994). Annual precipitation is 3,962 mm with over 400 mm/month falling between June–July and November–December. Rainfall is lowest between February and April. Average monthly temperature is 25.8°C with little monthly variation (Sanford *et al*. 1994).

Sample Sites

Bats were captured in different habitats to determine which seed species they were transporting. Using aerial photographs, topographical maps and field site visits, we selected three sites with different vegetation cover types (Fig. 1). Vegetation types we sampled were: a) young secondary forest in LSBR success ional plots. It consisted of five 0.5 ha adjacent plots felled every five years. Vegetation in the youngest plots was dominated by herbaceous plants such as *Erichtites hieracifolia* and *Phytolacca rivinoides*. In the oldest plots, the following plants dominate: *Piper* spp., *Acalypha* spp., *Hamelia patens*, *Solanum rugosum* and pioneer trees such as *Cecropia obtusifolia*, *Heliocarpus appendiculatus* and *Ochroma lagopus* (Hartshorn and Hammel, 1994); b) plantations dominated by cacao (*Theobroma cacao*) that had been abandoned 13 years earlier. The upper canopy consisted of native species and the understory had regenerating shrubs; and c) cattle pastures abandoned 17 years ago that were undergoing succession. Dominant tree species included: *Cecropia insignis*, *C. obtusifolia*, *Psidium guajava*, *Goethalsia meiantha*, *Laetia procera*, and *Rollinia microsepala* (Hartshorn and Hammel, 1994).

Captures

Between January and August 1995, each site was sampled monthly for bat species and their numbers. Each sampling event consisted of four consecutive capture nights (17:30 to 24:00 h) using four to six mistnets, each measuring 18.6 m × 2.7 m and with a 4 cm^2 mesh (Avinet Inc., Dryden, New York 13053-1103, USA). Each captured bat specimen was identified, measured, weighed, sexed, and reproductive condition and age class were determined. Fruits found in mouths of captured individuals were collected, labeled by capture site, date and bat species and stored. Fruits and seeds were identified by comparison with a reference collection made for this study or an existing one at LSBR. When necessary, plant taxonomists identified fruits and seeds.

Fecal Collection from Mist Netted Individuals

Individuals captured in mistnets frequently defecated while being handled. Captured bats not defecating were placed in a clean cloth bag for up to two hours to obtain fecal samples and then released. Each fecal sample was stored in an individual waxed paper envelope and information taken on: identity number, species, capture site and date. Some samples were collected in glass vials and later used in germination experiments.

Fecal Collection and Fruit Parts Left under Bat Tents and Feeding Roosts

Bat feeding roosts were found above piles of pulp and seed parts regurgitated or defecated during bat feeding (Handley *et al*., 1991). Resting or sleeping roosts were found in hollow trees, underneath foliage and in leaf-tents used by the Stenodermatinae (Timm, 1987). Tents and feeding roosts were found during weekly walks along 9 km of the six trails at LSBS. Data we recorded for each roost included location, plant species, bat species using them (when active) and number of bat individuals. Tents and feeding roosts were considered active if: a) they were occupied by bats; b) showed recent signs of use; and/or c) had seeds or fruits underneath. Fruit and seed samples were collected on a daily basis under each active site by suspending a plastic screen with four stakes above ground level in the afternoon and checking it the following morning. Food traps were replaced daily while tents or roosts remained active. All fruit and seed samples were weighed and placed in waxed paper envelopes, and data taken on date, roost location, roost type and bat species (whenever possible). For each bat species, masses of only regurgitated samples were compared to defecated samples using a Mann-Whitney test (Sokal and Rohlf, 1981).

Seed Germination Experiments

Effects of fruit manipulation by bats were evaluated by germination experiments, separating seeds in experiments into the following treatments: a) seeds passing through the digestive tract, and b) seeds regurgitated by frugivorous bats. For these experiments, seeds were obtained from bats that defecated when captured and from seed traps located under tents and feeding roosts. The control was mature seeds from fruits taken directly from plants of the same species.

For each seed sample, seeds from defecated, regurgitated and control treatments were placed in petri dishes (9 cm diameter) with moistened humid filter paper (Lieberman *et al*., 1979; Fleming *et al*., 1985; Palmeirim *et al*., 1989). Seeds weighing more than 2 g were placed in plastic pans (30 × 20 cm) with sterilized earth the day following its collection, with a similar number of seeds in treatments and controls. Petri dishes and plastic pans were put in the environmental control laboratory at LSBR, with constant environment temperature and low indirect light

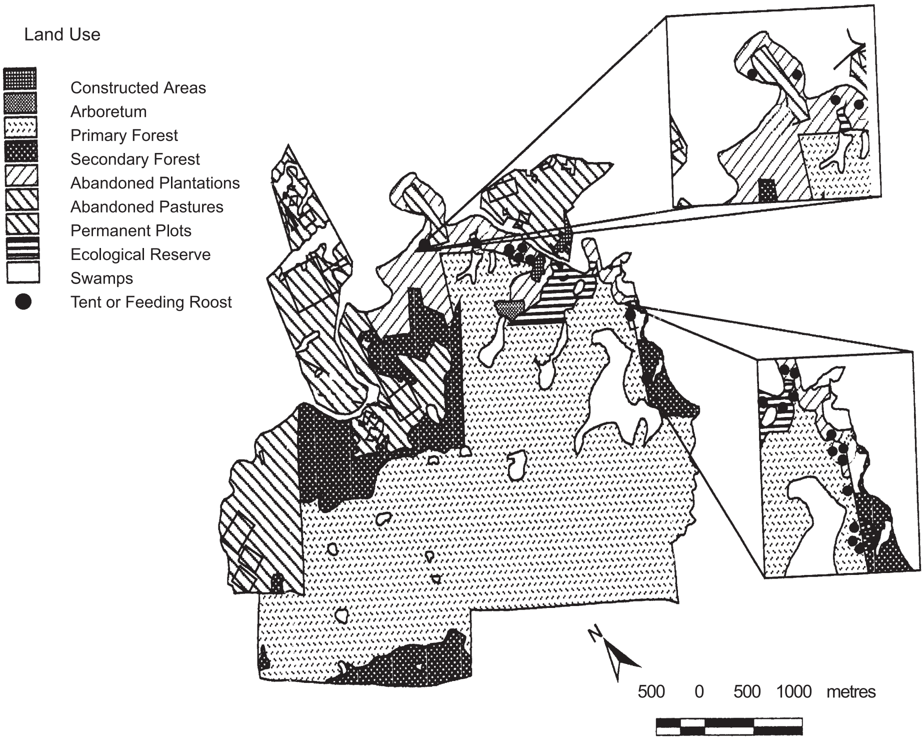

FIG. 1. Location of the tents and feeding stations in La Selva Biological Station, Costa Rica

(Fleming *et al*., 1985; Palmeirim *et al*., 1989). Treatments were moistened with distilled water when necessary. The number of seeds germinating in each treatment was counted on a daily basis for up to 60 days (Quijada and Salinas, 1981; Orozco-Segovia *et al*., 1985).

Percent germination of seeds in both treated petri dishes or plastic pans (defecated or regurgitated) and in control petri dishes and pans were calculated and compared with a *G*-test for independence with Yates' correction (Sokal and Rohlf, 1981). For these calculations, the Biomstat program was applied (Rohlf, 1985).

RESULTS

Captures

Between January and August 1995, 854 fecal samples were collected from 1,316 individuals captured in mist nets. Of 47 plant species identified in the feces, 22% were from primary forest tree species.

Seed Germination Experiments

Seed germination after passing through digestive tracts of six bat species was studied (Table 1). Seeds belonged to 12 plant species frequently eaten by frugivorous bats at LSBS. Seeds from *Piper multiplinervium* defecated by *Carollia brevicauda* germinated significantly more than the control group ($G = 10.11$, *d.f.* = 1, $P < 0.005$). Seeds from *Ficus insipida* defecated by *Artibeus jamaicensis* also germinated significantly more then the control group ($G = 12.88$, *d.f.* = 1, $P < 0.001$). All other seeds studied showed no significant germination effect comparing experimental and control groups. Twelve

TABLE 1. Germination responses of defecated seeds by bats compared with seeds taken from fruits. Percentages were compared with a *G*-test with Yates' correction. Significant results in bold

Seeds (mass in mg)	No. trials	% germination (*n*)		*G*-value	*P*-level
		defecated	not defecated		
		Carollia brevicauda			
Piper auritum (0.15)	3	56.4 (415)	60.5 (345)	0.21	> 0.1
P. multiplinervium (0.11)	1	75.0 (40)	52.5 (40)	10.11	**< 0.01**
P. sancti-felicis (0.11)	1	62.5 (40)	70.0 (40)	0.95	> 0.1
		C. castanea			
P. friedricsthalii (0.10)	1	68.0 (50)	74.0 (50)	0.61	> 0.5
P. multiplinervium (0.11)	1	77.1 (35)	74.3 (35)	0.95	> 0.1
P. sancti-felicis (0.11)	1	65.6 (125)	70.4 (125)	3.14	> 0.05
		C. perspicillata			
P. auritum (0.15)	1	82.9 (105)	88.6 (105)	0.91	> 0.5
Senna fructicosa (24.5)	4	95.9 (98)	96.9 (98)	0.00	
Vismia panamensis (0.48)	1	50.0 (20)	60.0 (20)	1.63	> 0.5
		Artibeus jamaicensis			
Cecropia obtusifolia (1.21)	3	73.7 (255)	75.1 (184)	0.00	> 0.9
Ficus cahuitensis (0.72)	6	55.1 (276)	42.7 (363)	2.65	> 0.1
F. insipida (1.95)	1	70.0 (10)	58.3 (12)	12.88	**< 0.001**
		Dermanura spp.			
C. obtusifolia (1.21)	2	68.0 (50)	76.0 (50)	1.22	> 0.5
P. auritum (0.15)	1	70.0 (50)	57.6 (52)	3.11	> 0.1
P. colonense (0.55)	1	100.0 (78)	100.0 (78)	0.00	
		Glossophaga commissarisi			
C. insignis (0.55)	1	81.3 (16)	75.0 (16)	0.82	> 0.5
P. auritum (0.15)	1	75.0 (4)	70.0 (10)	0.40	> 0.5

samples were taken to compare seed germination from seeds regurgitated by bats to a control group (Table 2). The experiment involved four bats species and eight plant species. Seeds from *Markea neurantha* regurgitated by *Dermanura* spp. were the only seeds germinating significantly more than the control group ($G = 17.33$, $d.f. = 1$, $P < 0.001$).

Location and Duration of Tents and Feeding Stations

Nineteen tents and three feeding stations were found. Four genera of bats used seven plant species for tents (Table 3). Feeding stations were used less than a week each on average. Some tents constructed in *Calyptrogyne sarapiquensis* by *Dermanura* spp. were active the entire study period. About 71% of tents and feeding stations were found in primary forest (Table 4). Of 21 plant species with fruit or seeds deposited under tents or at feeding stations, 12 (51%) were from secondary forest species. Weight of fruit under tents or feeding stations ranged from 1.0–25.2 g. Five fruit species found under bat tents and feeding stations were not found in feces of individuals captured in the mistnets. These plant species were: *Dipteryx panamensis*, *Hernandia stenura*, *Quararibea parvifolia*, *Simphonia globulifera*, and *Spondias radlkoferi*. These fruits were significantly heavier than feces from bats caught in mistnets (Mann-Whitney, $n_1 = 5$, $n_2 = 8$, $Z = -2.68$, $P < 0.01$).

DISCUSSION

Seeds are not randomly transported by bats; instead bats handle, consume and digest fruits in predetermined tents and feeding sites and deposit more seeds there than elsewhere (Fleming and Heithaus, 1981). Over 71% of tents and feeding sites were found in primary or mature forest, with 29% in abandoned plantations. About 52% of seeds and fruits found under tents and feeding sites were from secondary forest, but deposited mostly in primary forest areas where they can participate in light gap regeneration. Twenty-two percent of seed species defecated by bats captured in secondary forests were from primary forest species. Thus, it appears that bats move and exchange seeds between different habitat types; this promotes natural regeneration of different forest types.

TABLE 2. Germination responses of seeds regurgitated from bats compared to seeds taken from fruits off plant by the researcher. Percentages were compared with a *G*-test, using Yates' correction. Significant results in bold

Seeds (mass in mg)	No. trials	% germination (*n*)		*G*-value	*P*-level
		regurgitated	not regurgitated		
		A. jamaicensis			
Cecropia obtusifolia (1.21)	2	54.5 (110)	45.5 (110)	1.30	> 0.1
Ficus insipida (1.95)	1	66.6 (30)	73.3 (30)	3.30	> 0.1
		Dermanura spp.			
C. obtusifolia (1.21)	1	73.0 (30)	66.0 (30)	3.42	> 0.1
Markea neurantha (1.45)	1	78.9 (19)	50.0 (20)	17.33	**< 0.001**
Piper reticulatum (2.41)	1	100.0 (32)	95.0 (42)	3.76	> 0.1
Quararibea parvifolia	1	25.0 (8)	30.0 (10)	0.40	> 0.5
Spondias radlkoferi	1	10.0 (10)	18.2 (11)	2.16	> 0.1
		U. bilobatum			
C. obtusifolia (1.21)	1	27.9 (74)	27.0 (74)	0.00	
F. cahuitensis (0.72)	1	28.1 (89)	32.0 (100)	0.29	> 0.1
		V. nymphaea			
C. obtusifolia (1.21)	2	95.8 (97)	88.7 (124)	2.66	> 0.05

TABLE 3. Plants used by frugivorous bats as feeding stations ([1]) and tents, and time active and habitat type where they were found, La Selva Biological Station, Costa Rica, January–August, 1995. Abbreviations: A — less than a week; B — one to three weeks; C — more than three weeks; Bp — primary forest; Pa — abandoned plantations

Taxon	*n*	Time active	Habitat type
Artibeus spp.			
Arecaceae[1]	3	A	Bp
Potalia amara	1	B	Bp
Dermanura spp.			
Calyptrogyne sarapiquensis	6	C	Bp
Pentagonia sp	2	C	Bp
Pentagonia sp.	4	C	Pa
U. bilobatum			
Cocos nucifera	1	C	
Musa × *paradisiaca*	2	B	Pa
Pouteria calistophylla	1	B	Bp
V. nymphaea			
Anthurium sp.	2	B	Bp

Based on germination experiments using seeds from 12 plant species, only *P. multiplinervium* defecated by *Carollia brevicauda* and *F. insipida* defecated by *A. jamaicensis* had significantly higher germination rates when seeds passed through bat digestive tracts as compared to the control group. *Piper* and *Ficus* are the principal taxon (sensu Fleming, 1986) in diets of *Carollia* and *Artibeus*, respectively (Lopez, 1996). According to Janzen (1983), these genera have evolved strong plant-disperser interactions. Results of this study support Janzen's (1983) conclusion.

Germination of *Piper* seeds varied between 53% and 89% of their seeds in this study; Fleming (1988) and Palmeirim *et al.* (1989) reported less germination from seeds defecated by *Carollia* bats. The reason for this difference is unknown. Germination of seeds of *C. obtusifolia* defecated by spider monkeys (*Ateles geoffroyi*) and howler monkeys (*Alouatta palliata*) was significantly lower than undefecated seeds (Estrada and Coates-Estada, 1984; Vásquez-Yanes and Orozco-Segovia, 1986). Likewise, Howe and Vandekerckhove (1981) found *Virola surinamensis* seeds defecated by spider monkeys less viable than undefecated seeds. However, our study found *C. obtusifolia* seeds defecated by *A. jamaicensis* and *Dermanura* spp. similar in percent germination to *C. obtusifolia* seeds not ingested by bats.

Of nine species of regurgitated seeds, only *M. neurantha* showed significant increases in percent germination after regurgitation by *Dermanura* spp. (50–73%). *S. radlkoferi* and *Q. parvifolia* showed very low germination for both regurgitated (10%) and for harvested seeds (18%). Most plant species used in these germination trials were from secondary forest species; their germination might have required special temperature and light regimes nonexistent in this experiment (Vasquez-Yanes and Smith, 1982).

In summary, germination of 10 of 13 plant species was not affected significantly after defecation or regurgitation by eight bat species. Perhaps passage through a bat's digestive tract has no impact on germination rate of most defecated seeds. Howe and Vanderkerckhove (1981) found many tropical fruits with seeds remaining in the pulp until attacked by fungi. Therefore, bats may directly benefit host plants by removing seeds from fruits and defecating them without pulp, thus reducing seed numbers destroyed by fungi (Fleming, 1988).

Reviewing the criteria proposed by McKey (1975) for evaluating consequences of dispersal, we found: a) There was increased probability of germination. Germination experiments in this study showed that six bat species enhanced, but not significantly, seed dispersal for 10 plant species because none was negatively affected by contact with the bat; b) Seed dispersers and seed sizes are correlated for

TABLE 4. Seed and fruit remains under feeding stations and tents of bats: *A. jamaicensis* (body mass 55.4 g), *Dermanura* spp. (12.9), *U. bilobatum* (18.4), *V. nymphaea* (12.0). Quantities represent the number of samples with a determined fruit or seed type, La Selva Biological Station, Costa Rica. January–August 1995. Habitats used by bats: (m) — mature forest, (s) — secondary forest, (a) — in both forest types

Plant species	Fruit mass (g)	*A. jamaicensis*	*Dermanura*	*U. bilobatum*	*V. nymphaea*
Hepiphytes					
Markea neurantha (s)	1.0		13		
Ficus cahuitensis (m)	5.2	2	2	6	3
F. nymphaeifolia (m)	3.1		1		
F. pertusa (s)	1.2		7	1	
Bushes/shrubs					
Piper auritum (s)			11		2
P. glabratum (s)	2.0		2		
P. multiplinervum (s)	1.5		2		
P. reticulatum (s)	2.6		1		
P. sancti-felicis (s)	1.6		3		1
Senna fructicosa (s)			1		
Solanum arboreum (s)	2.5		1		
S. rugosum (s)	1.7		4		
Vismia panamensis (s)	1.8		5		
Trees					
Cecropia obtusifolia (a)		2	8	3	
Dipteryx panamensis (a)	25.2	7			
Ficus popenoei (m)	3.5		3		
F. insipida (a)	23.5	5			
Hernandia stenura (a)	10.2		4		
Quararibea parviflora (m)	3.0		9		
Simphonia globulifera (m)	2.5		2		
Spondias radlkoferi (m)	8.5		11		

maximum ingestion and transport efficiency. The maximum fruit size a bat can transport is correlated with body size (Bonaccorso, 1979; Fleming, 1986). Regurgitated seeds were significantly larger than defecated seeds, thus seed size determined ingestion, not dispersal by bats. Larger bat species, such as *A. jamaicensis* (body mass 55.4 g) should be one of few bat species able to disperse heavier fruit plants, such as *F. insipida* (23.5 g) and *Dipteryx panamensis* (25.7 g). Smaller bat species, such as *Dermanura* spp. (12.9 g), *U. bilobatum* (18.4 g) and *V. nymphaea* (12.0 g) would be likely dispersers of smaller fruit plants (< 10 g), including *Piper* spp., *M. neurantha*, *Solanum rugosum*, and *Vismia panamesis*; and c) Seeds should be left in a favorable site for germination and subsequent establishment. The bats we studied provided low quality seed dispersal. Many seeds were deposited under feeding roosts, forming potentially easily preyed upon mounds of seeds and seedlings by seed predators (Fleming, 1988). In these sites, Janzen (1978) observed high seed and seedling mortality and Vasquez-Yanes (1977, 1981) concluded that germination conditions for pioneer species at such sites were unfavorable. In the LSBS, pioneer species make up about half (52%) of seeds transported to feeding roosts, thus a high probability for seed mortality exists. However, seeds defecated or regurgitated in open areas or incorporated into the seed bank may produce a new generation of plants (Fleming, 1988; Levey *et al*., 1994). We did not evaluate fates of seeds dispersed into open areas or seeds incorporated into the seed bank. Nevertheless, 22% of primary forest plant species were transported by bats into secondary forested areas. Also certain seeds (*P. multiplinervium* and *F. insipida*) had better germination rates if they were defecated by bats rather than harvested and planted. Our research showed that frugivorous bats disperse seeds between different habitats, but much research remains on their fate once deposited.

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