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Frugivory by Small Vertebrates Within a Deforested, Dry Tropical Region of Central America

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ABSTRACT

Small vertebrates were inventoried within three habitat types in a degraded dry forest region of Panama. Animals were classified as frugivorous if they were observed foraging on fruit or if fecal samples contained mostly or exclusively seeds. Overall, we found that eight bat species and 21 bird species consumed fruit. The greatest numbers of birds were observed within live fences and bird species richness was greatest within riparian forests. Bat assemblages were not significantly different between habitats. The implication is that ecosystem services such as seed dispersal may still be functional in this landscape.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: dry forest; fragmented; frugivores; live fences; Panama; pastures; reforestation; riparian forest; seed dispersal.

In fragmented landscapes of Central America, small vertebrates play critical roles as seed dispersers in forest regeneration (Fleming & Heithaus 1981; Guevara *et al.* 1986, 2004; Janzen 1986a; Estrada *et al.* 2000; Galindo-Gonzalez *et al.* 2000; Barrantes & Pereira 2002; Martinez-Garza & Gonzalez-Montagut 2002). Large rodents and monkeys are often the first animals to be hunted out locally whereas smaller frugivorous birds, bats, and rodents are less frequently targeted. Furthermore, some frugivorous bats, rodents, and bird species are adaptable to habitat modifications and forage in undisturbed as well as in disturbed habitats (Silva *et al.* 1996, Estrada *et al.* 2000).

Birds and bats may be especially important seed dispersers in deforested ecosystems that have lost most of their flora and fauna. Bat species of the genera *Artibeus, Carollia*, and *Sturnira* disperse seeds of a wide range of plants including figs (Moraceae), *Piper* (Piperaceae), *Vismia* (Clusiaceae), *Solanum* (Solanaceae), and *Cecropia* (Cecropiaceae) underneath pasture trees (Fleming & Heithaus 1981, Guevara *et al.* 1986, Janzen 1986a, Nepstad *et al.* 1996, Estrada *et al.* 2000, Galindo-Gonzalez *et al.* 2000, Korine *et al.* 2000, Giannini & Kalko 2004). The majority of these seeds are small-seeded (Castilleja 1991) but occasionally, bats may disperse large-seeded species (*e.g.*, *Andira inermis*, Fabaceae) into pastures (Janzen *et al.* 1976). Rodents (*Sigmodon hispidus* and *Liomys* spp.) may also carry larger seeds into pastures (Janzen 1986b) or move seeds that have been previously dispersed by birds (Vander Wall *et al.* 2005).

While field studies have shown that small vertebrates play an important role in seed dispersal into open pastures in moist tropical forests (*e.g.*, Guevara *et al.*1986, 2004; Estrada *et al.* 1993, 2000; Nepstad *et al.* 1996; Galindo-Gonzalez *et al.* 2000; Barrantes & Pereira 2002; Graham *et al.* 2002; Martinez-Garza & Gonzalez-Montagut, 2002; Pizo 2004), their seed dispersal role within a pasture matrix of dry tropical regions is less known. Frugivorous bird assemblages within fragmented dry tropical forests were examined by Ortiz-Pulido *et al.* (2000) in Mexico. The most comparable bat inventories are from the dry tropical forest in Guanacaste, Costa Rica (Janzen 1983, Fleming 1988) and the most recent rodent inventory was conducted when most of the Azuero peninsula was still forested (Aldrich & Bole 1937). Thus, in this study, we conducted inventories of birds, bats, and rodents in three habitat types (forested riparian zones, open pasture, and within a live fences). Riparian zones are often the most common forested habitats remaining in a pasture matrix (Graham & Blake 2001). This was also observed in this study. In addition, we quantified animal foraging behavior by observation in the field (birds) and by examining fecal samples (bats) and cheek pockets (rodents). The goal was to identify potential frugivorous species that may still inhabit the fragmented, pastoral landscape.

Fieldwork was conducted in the Los Santos province on the Pacific side of Panama (7°15′30″ N, 80°00′15″ W), 1–2 km from the coast. Spaniards arrived to the Los Santos province in the 17th and 18th century and introduced cattle to the region. The last land to be cleared in the province was the hilly, relatively steep topography at the tip of the Azuero peninsula where our study took place. In the 1940s–1950s, clearance of the original dry tropical forest began for subsistence agriculture and cattle ranching. Currently, cattle farms are going up for sale and being purchased by landowners. Many of these new landowners are interested in reforesting the land, restoring biodiversity, and establishing connectivity between forest fragments.

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The study site falls into the dry tropical forest ecosystem classification of Holdridge (1967). The dry season is pronounced with 4 mo of the year receiving almost no rain (December through March). Rain begins in late April and ends in late November. During the course of this study (2002), the annual rainfall was 1300 mm. The undulating terrain, ranging in elevation from 10 to 100 m, is a mosaic of pastures planted with African grasses (*Hyparrhenia rufa* (Nees) Taphf and *Panicum maximum* L.), forested riparian zones, isolated trees, and live fences.

Animals were inventoried in at least two of the three main habitat types (forested riparian zone, open pasture, and live fences) within the cattle pasture matrix (Table 1). Live fences were classified as habitat because they were a combination of remnant trees as well as trees propagated by farmers. If animals were not inventoried in a particular habitat, it was due to constraints of the steep topography. Consistency in inventory design was achieved when possible. We do not attempt to make direct comparisons of relative abundance and completeness of samples between birds, bats, and rodents as methodology and intensity were different in each case.

Birds were observed during the dry season from a hilltop using binoculars from 0600 h (sunrise) to 0900 h (2.5 h total) in the three habitat types. The distance from hilltop observation position to the closet tree within each of these habitats was approximately the same (~20 m). Birds were recounted and identified every half hour from the same observational position for a total of five time periods (0630–0700, 0700–0730, 0730–0800, 0800–0830, 0830–0900 h). Birds were identified using Ridgely and Gwynne (1989). The same individual could have been counted twice within a different time period as individuals could not be easily distinguished. Observations were made for five consecutive mornings at each site for a total of 15 morning observations.

TABLE 1. *Total and mean values for number of captures/observations and species richness of birds, bats, and rodents within three habitat types: forested riparian zones, within live fences, and open pasture in a dry tropical forest region of Panama.*

	Forested Riparian Zone	Live Fence	Open Pasture
Birds			
Totals			
Observed	547	637	333
Species	30	24	21
Means			
Observed	109 ± 24.1	127 ± 26.4	66 ± 29.5
Species	20 ± 2.9	18 ± 2.7	14 ± 2.5
Bats			
Totals			
Captured	122	117	0
Species	10	13	0
Means			
Captured	24.4 ± 11.9	23 ± 6.8	0
Species	5 ± 0.5	6 ± 0.7	0
Rodents			
Totals			
Captured	14	—	41
Species	3	—	3
Means			
Captured	5 ± 4.5	—	14 ± 4.5
Species	2 ± 1	—	3. ± .6

During the rainy season, bats were captured in six 12 m long, 38 mm mesh polyester mist nets for five consecutive nights at each site for a total of ten nights starting at 1830 h and ending mist netting at 2230 h. Attempts were made to capture bats during the dry season but the high winds made the mist net setup and bat capture unsuccessful. Captured bats were placed in numbered cloth bags and identified to species using Reid (1997). Information was collected on sex, forearm length, and weight. Forearm length was measured with Plasti-cal® digital calipers (0.1 mm) and weight was determined using Pesola® Micro-line spring scales (0.1 g). Fecal samples were collected in glassine envelopes, and dried in the sun. Each fecal sample was carefully examined for seeds. Seeds were counted and identified with a reference collection of mature fruit collected at the study site.

Rodents were captured in two habitat types (riparian forest and open pasture) during the wet season. Fifteen Tomahawk® Collapsible Single Door traps (16 × 5 × 5") and ten small Sherman® Aluminum Folding Live Capture traps (2 × 2.5 × 6.5") were setup for three consecutive days in each habitat. Traps were spaced 15 m apart along a 750-m transect. Traps were baited with one-half teaspoon of peanut butter, whole oatmeal, and a slice of banana. Traps were opened at 1600 h and closed at 0900 h the following morning. The only rodent with cheek pockets (*Liomys adspersus*) was checked for seeds.

Significant differences in numbers of observations or captured individuals and in species richness between habitats were analyzed with nonparametric Mann–Whitney U and Kruskal–Wallis tests (H). Means and standard deviations were calculated by averaging the capture/observation days or nights within each habitat type.

A total of 1517 birds were counted and 34 bird species were identified (Table S1). There was a significant difference in bird counts ($H_{5,5,5} = 47.9$; $P < 0.001$) and in species richness between habitat types ($H_{5,5,5} = 48.40$; $P < 0.001$). Bird counts were greatest within the live fence and species counts were greatest within the riparian forest habitat (Table 1). Twenty-one of these species were observed foraging on *Bursera simaruba* (L.) Sarg. (Burseraceae) fruit (Table 1). This was the only tree species found with fleshy fruit at this time of year and has been cited in the literature as an important fruit resource for birds across Mexico and Central America (Trainer & Will 1984, Greenberg *et al.* 1995).

A total of 241 bats representing 16 species were captured in the riparian forest zone and along a live fence (Table S2). No bats were captured in the open pasture. Estrada *et al.* (1993) had similar results in pastures in Los Tuxlas, Mexico. The number of bats captured between habitats (forested riparian zone and live fence) was not significantly different ($U_{5,5} = 11.5$; $P > 0.05$) (Table 1). *Artibeus jamaicensis* and *Carollia perspicillata* were the two most frequently captured bat species (Table S2). Eight of the 16 captured species had seeds of three plant species in their feces. *Cecropia peltata L.* (Cecropiaceae) was the most frequent plant species represented in fecal samples (found in feces of eight species) in the riparian forest whereas *Piper marginatum* Jacq. (Piperaceae) was the most common plant species identified in bat feces within the live fence habitat (found in feces of two species) (Fig. 1). *Solanum ochraceo-ferrugineum* (Dunal) Fernald (Solanceae) seeds were found in a few samples.

A total of 55 rodents representing four species were captured (Table S2). The number of captured rodents was significantly different between riparian forest and pasture habitats ($U_{3,3} = 0.00$; $P < 0.05$) (Table 1). However, species richness did not differ significantly. Within the pasture site, *S. hispidus* was the most common species captured while *L. adspersus* was the most common species captured within the riparian habitat.

Bat assemblages were more similar between habitats than either bird or rodent assemblages. *Carollia perspicillata* and *A. jamaicensis* are often abundant in disturbed ecosystems because they specialize on secondary plant species, such as *Piper*, *Cecropia*, and *Ficus* (Moraceae) growing in these habitats (Goodwin & Greenhall

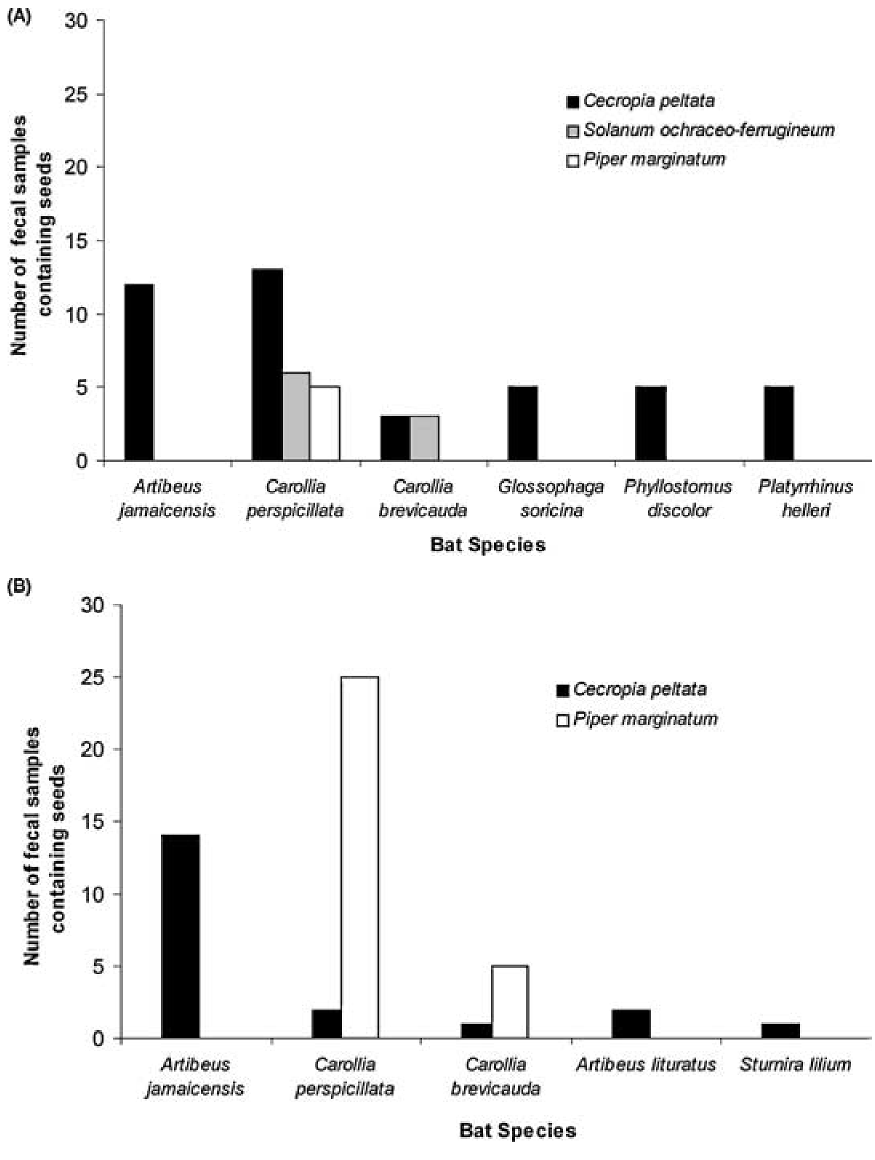

FIGURE 1. Number of captured bat species with seeds of *Cecropia peltata, Piper marginatum*, or *Solanum ochraceo-ferrugineum* identified in their feces. Bats were captured in a forested riparian zone (A) and along a live fence (B) in the dry tropical region of the Azuero peninsula, Panama.

1961, Fleming *et al.* 1972, Howell & Burch 1974, de Foresta *et al.* 1984, Charles-Dominique 1986, Fleming 1986, Peckham 2000, Lobova *et al.* 2003, Thies & Kalko 2004, Giannini & Kalko 2004). *Piper marginatum*, classified as a gap specialist (Thies & Kalko 2004), was frequently found regenerating in the experimental natural regeneration plots whereas *C. peltata* was rare after two years (Griscom 2004). The open structure of *P. marginatum* may facilitate the regrowth of tree species by ameliorating harsh microclimatic conditions of the open pasture.

Birds were most numerous within the live fence habitat. Many tree species with fleshy fruit were identified within these fences (*e.g.*, *Byrsonima crassifolia* [L.]. Kunth [Malpighiaceae], *Spondias mombin* L. [Anacardiaceae], *Eugenia coloradoensis* Standl. [Myrtaceae], *Sciadodendron excelsum* Griseb [Araliaceae]). However, only *B. simaruba* was in fruit at the time of the study. Birds foraged on the fruit in the parent tree and dropped the seeds below, a behavior observed in other studies (Pratt & Stiles 1983, Stiles & White 1986, Murray 1988, Thies & Kalko 2004). In addition to live fences, forested riparian zones are an important habitat for birds and bats (Estrada *et al.* 2000, Barrantes & Pereira 2002,Galindo-Gonzalez & Sosa 2003). The greatest bird diversity was observed in these areas. Unfortunately, trees along streams are often selectively removed by girdling; farmers view certain trees species as directly competing with cattle for water during the dry season.

The seed-dispersal role of rodents is less well defined because they function more as seed and seedling predators than as seed dispersers. *Sigmodon hispidus* and *Liomys* spp., the two most abundant species in the dry forest in Guanacaste, Costa Rica (Fleming1983a,b) were also the most abundant species within the pasture matrix at this study site. Rodents contributed to high mortality of planted tree seedlings (*Enterolobium cyclocarpum* [Jacq.] Griseb [Fabaceae]) in an experimental study conducted at the same location (Griscom *et al.* 2005). *Liomys adspersus* have been reported to move seeds, such as *E. cyclocarpum*, *S. mombin*, *Cochlospermum vitifolium*, and *Guazuma ulmifolia* in pastures (Fleming 1983a, Janzen 1983, Sanchez-Cordero & Fleming 1993). However, their infrequent captures in the open pasture imply that they are not common seed dispersers or predators outside of the forested riparian zone.

In conclusion, we identified small frugivorous vertebrates that persist within this dry tropical region and may serve as seed dispersers within the fragmented landscape. We suggest that rodents have a limited seed-dispersal role in this system and appear to have a more negative impact on forest succession, given the evidence of rodent predation on planted tree seedlings. On the other hand, birds and bats may be effectively dispersing seeds of pioneer shrubs and trees. Most species of frugivorous birds and bats were observed and/or captured in both open pastures as well as within forest fragments, suggesting mobility of the current fauna. Live fences, isolated trees, and forested riparian zones disrupt the homogeneity of open pasture and help maintain bird and bat diversity. In addition, we suggest that *B. simaruba* may be an especially important component of the landscape when food resources are limiting, as has been also found by Graham *et al.* (2002) in Mexico.

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