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

Heather P. Griscom,1,4 Elisabeth K.V. Kalko,2,3, and Mark S. Ashton1

1PRORENA program, School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511, U.S.A.

2Department of Experimental Ecology, University of Ulm, Albert-Einstein Allee 11, 89069 Ulm, Germany

3Smithsonian Tropical Research Institute, Balboa, Panama

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.

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

Received 2 January 2006; revision accepted 2 March 2006.

4 Corresponding author; e-mail: hgriscom@aya.yale.edu

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; Martínez-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 Sturini distribute 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 (Sigmoidon 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; Martínez-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 fence). 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.
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) Taaffe 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 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 as trees propagated by farmers.

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 closest 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.

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 ($H_{5,5,5} = 47.97; P < 0.001$) and in species richness between habitats ($H_{5,5,5} = 48.40; P < 0.001$). 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

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Forested Riparian Zone</th>
<th>Live Fence</th>
<th>Open Pasture</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Birds</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>Observed</strong></td>
<td><strong>637</strong></td>
<td><strong>333</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Species</strong></td>
<td><strong>24</strong></td>
<td><strong>21</strong></td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td><strong>Observed</strong></td>
<td><strong>127 ± 26.4</strong></td>
<td><strong>66 ± 29.5</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Species</strong></td>
<td><strong>18 ± 2.7</strong></td>
<td><strong>14 ± 2.5</strong></td>
</tr>
<tr>
<td><strong>Bats</strong></td>
<td><strong>Captured</strong></td>
<td><strong>117</strong></td>
<td><strong>0</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Species</strong></td>
<td><strong>13</strong></td>
<td><strong>0</strong></td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td><strong>Captured</strong></td>
<td><strong>23 ± 6.8</strong></td>
<td><strong>0</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Species</strong></td>
<td><strong>6 ± 0.7</strong></td>
<td><strong>0</strong></td>
</tr>
<tr>
<td><strong>Rodents</strong></td>
<td><strong>Captured</strong></td>
<td><strong>—</strong></td>
<td><strong>41</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Species</strong></td>
<td><strong>—</strong></td>
<td><strong>3</strong></td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td><strong>Captured</strong></td>
<td><strong>—</strong></td>
<td><strong>14 ± 4.5</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Species</strong></td>
<td><strong>3. ± .6</strong></td>
<td></td>
</tr>
</tbody>
</table>
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 ochraceoferrugineum* (Dunal) Fernald (Solanaceae) 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. adpersus* 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...

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 (Fleming 1983a,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 adenpus have been reported to move seeds, such as E. cyclocarpum, S. mombin, Coccolobum vitifolium, and Guaunuma 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.

ACKNOWLEDGMENTS

We thank the Achorines Laboratory of the International Tropical Tuna Commission and manager Vernon Scholey for use of their research and lodging facilities and O. Batista and P. Batista for permission to conduct experimental research on their land. Logistic support was provided by PRORENA (Panama Native Species Reforestation Project), a joint program between the Smithsonian Tropical Research Institute, and the Yale School of Forestry and Environmental Studies. We thank M. DeAngelo for her help with rodent trapping and identification and the field assistants, D. Mancilla and L. Herrera, for their help with animal captures. Financial support was provided to HG by an USDA fellowship through the Yale School of Forestry and Environmental Studies and The New York Botanical Garden, the Graduate fellowship through the Yale Graduate School of Arts and Science, and Yale departments of International Area Studies and Ecology and Evolutionary Biology.

LITERATURE CITED


