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SHORT NOTES

Differential ingestion of *Ficus* seeds by frugivorous bats: a first experimental test in *Ptenochirus jagori* (Pteropodidae)

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INTRODUCTION

Old World flying foxes and their Neotropical counterparts, the Phyllostomidae, feed mainly upon floral resources, fruits and leaves (Marshall, 1983, 1985; Handley *et al.*, 1991; Kalko *et al.*, 1996). Fruits are usually carried away from the parent plant to a distant feeding roost. The pericarp and other soft parts are ingested, the juice is extracted and swallowed, and the remaining solid matter is ejected. Especially in the case of *Ficus* species the tiny seeds may be either ejected or ingested passing through the gut and being expelled in feces (Janzen, 1978).

Frugivorous bats play a significant role as seed dispersal agents for many species of figs (Janzen, 1979; August, 1981; Utzurrum, 1995). Some species of fruit bats move over distances of at least 12 km in a single night (Heideman and Heaney, 1989) and thus act as potential long-distance dispersers (see also Shilton *et al.*, 1999; J. Reiter and S. Luft, unpubl. data). After the volcanic sterilization of the Krakatau islands in 1883 bats and birds probably introduced more than 100 plant species; the nearest source for the colonists are two islands 12 and 20 km from Krakatau, respectively (Whittaker and Jones, 1994).

Based on analyses of bat feces and ejecta, Utzurrum and Heideman (1991) suggested that the effectiveness of bats as seed dispersers may be enhanced by differential ingestion of viable seeds. The goal of the present study was to test this hypothesis through feeding trials using captive bats (*Ptenochirus jagori*). I predict that a markedly higher proportion of viable seeds is found in feces compared to ejecta. This may render long-distance dispersal, which mainly occurs through fecal deposition, much more effective.

MATERIALS AND METHODS

The study was conducted around Sibaliw station (11°49'N, 121°58'E), Province of Aklan, Philippines. The station is at 450 m a.s.l. and is surrounded by a mosaic of primary and secondary forest, a lowland rainforest. *Ptenochirus jagori* is the most abundant fruit bat species within the study site (Luft, 1998). Individuals were captured with mist nets during the early evening hours. Bats were housed individually (as per Memorandum of Agreement with the Department of Environment and Natural Resources) in cages measuring 90 × 80 × 120 cm. A plastic cover on the cage floor was installed facilitating the removal of food remains.

Ten bats of each sex were tested, all being adult. Males had a mean body mass (± SD) of 81.5 ± 5.84 g, whereas that of females was 83.9 ± 4.22 g. None of the females was pregnant. Bats were presented ripe fruits of a monoecious fig, Green Lonok (*Ficus* sp.; herbarium No. P400) which are naturally consumed by *P. jagori* (own data). Mean fruit wet mass was 17.2 ± 1.67 g, fruit length was 33.6 ± 1.35 mm and fruit width was 32.7 ± 1.34 mm (n = 10). Mean seed length was 2.2 ± 0.07 mm and seed width was 1.0 ± 0.10 mm (n = 10). Mean number of seeds per fruit was 758 (n = 3). Feeding trials were conducted in March 2000 (n = 8 bats) and in February 2001 (n = 12). Fruits generally were collected on the day of trial, although, in some cases, they were stored for 1 day at the station before being fed to the bats. Depending on availability, each bat was given 5–10 fruits in feeding bowls hung inside the cages at 18:00 h. On the next morning ejecta or feces were collected from the cage floor. A substantial portion of seeds within each fruit of Green Lonok is parasitized, i.e., damaged by fig wasps. Damaged seeds are no longer able to germinate. Those seeds were holed (and lacked the gelatinous coating of intact seeds) and could easily be distinguished from intact ones. The number of intact and damaged seeds for whole figs as well as for each collected sample of feces and ejecta was recorded by simply separating holed from unholed seeds using a magnifying glass (20×) and tweezers.

Since data were not normally distributed, percentages of parasitized seeds of ejecta and feces were arcsin-transformed und subsequently compared using Student's t-test (Sachs, 1999). Differences were deemed to be significant when $P \leq 0.05$. Single bats were treated as being the unit of replication. In cases where individual bats were subjected to more than 1 trial, data were averaged for single bats as not to commit the mistake of pseudoreplication (Machlis *et al.*, 1985).

Results

In ripe fruits, 78% of seeds (n = 6 syconia) is parasitized. A total of 3,082 seeds was recovered from feces and ejecta. Year-to-year differences among individuals in the proportions of unparasitized to parasitized seeds in ejecta and feces were not significant (Mann-Whitney U-test, $P \gg 0.05$ for both cases). Of the 1,239 seeds counted from ejecta, 89 ± 8.8% (range: 66–96%; n = 10 bats) of seeds were parasitized. By contrast, in feces, only 17 ± 9.0% (range: 5–34%) of 1,843 seeds were damaged (n = 10 bats). The difference is highly significant (2-tailed t-test, t = 15.3, n = 20, $P < 0.001$); therefore, the initial prediction that feces contain significantly more viable seeds compared to ejecta is clearly matched by the result.

The gelatinous cover of intact seeds appears to be largely resistant to digestive enzymes since the coating survived gut passage. On average, 22 ejecta (n = 10 bats) contained 56 ± 20.3 seeds each and had a mass of 0.5 ± 0.08 g. Fecal strands were highly variable in both length and consistency. Accordingly mean number of seeds per fecal sample could not be determined.

Discussion

Figs have a unique pollination system in which wasps of the family Agaonidae carry pollen to young syconia and also oviposit within certain ovaries. Additionally, minute wasps of the families Agaonidae and Torymidae parasitize fig wasps and/or fig seeds (Janzen, 1979; Murray, 1985; Bronstein, 1988; Anstett *et al.*, 1997). As a consequence a substantial portion of seeds of a single fruit will be killed by wasp larvae. In the *Ficus* species studied, Green Lonok, most of the seeds within each syconium are parasitized.

In at least some Asian fig species, individual seeds are covered in a lipid-rich exocarp (Lin *et al.*, 1989; Utzurrum and Heideman, 1991; present study). The gelatinous material seems to be associated solely with viable seeds (Utzurrum and Heideman, 1991). Kaufmann *et al.* (1991) reported that unparasitized seeds with such a jelly-like coating survive passage through a frugivorous birds' gut. This seems to be true for bats as well (Utzurrum and Heideman, 1991; present study). The cause for ingesting viable seeds appears to come from the figs rather than the dispersers. If the gelatinous coating causes intact seeds to slide out of the bolus and be swallowed, then bats (or any other disperser for that matter) are agents of selection acting on the figs to invest in the covering around intact seeds.

The low numbers of damaged seeds in feces in the present study could be due to differential digestion. However, the generally short gut passage times in frugivorous bats (Shilton *et al.*, 1999, and references therein) allow little time for digestion of hard seeds. Utzurrum and Heideman (1991), therefore, proposed the differential ingestion hypothesis which is strongly supported by the results of the present study. Significantly more intact seeds of *Ficus* sp. (Green Lonok) fruits were found in feces compared to ejecta. Following the reasoning of Utzurrum and Heideman (1991) the slippery gelatinous material on relatively small fig seeds (ca. 2 mm) would make it difficult for a bat to avoid swallowing intact seeds, while those seeds lacking the coating could be rejected more easily with the fiber as ejecta. The threshold size above which seeds are regularly dropped or spat out without passing through the entire gut is, besides for other vertebrates, in the 3–5 mm range for flying foxes (Boon and Corlett, 1989; Richards, 1990). Since seeds of *Ficus* species may generally lie below this threshold it is suggested that the phenomenon of differential ingestion will also be found in other *Ficus* species than those studied so far given that intact seeds are coated as described above.

The result of differential ingestion is that a higher proportion of intact, undamaged seeds will occur in feces. Since long-range dispersal is primarily through fecal deposition, dispersal is likely to be much more effective than it would be if damaged seeds were as frequent in feces as they are in ejecta and fig syconia. In *P. jagori*, seed dispersal may be mostly limited to areas representing home ranges of individual bats varying from 8.4 to 30.9 ha (Reiter and Curio, 2001). However, *P. jagori* as well as other Philippine frugivorous bats play a potential role in long-range seed dispersal (Shilton *et al.*, 1999; J. Reiter and S. Luft, unpubl. data). This would be the case if individuals and/or small groups of *P. jagori* displayed a nomadic or migratory behaviour which has not been described so far.

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