BioOne COMPLETE

Differential Ingestion of Ficus Seeds by Frugivorous Bats: A First Experimental Test in Ptenochirus Jagori (Pteropodidae)

Author: Reiter, Jochen

Source: Acta Chiropterologica, 4(1) : 99-106

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/001.004.0110

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Acta-Chiropterologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Acta Chiropterologica, 4(1): 99–106, 2002
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS

SHORT NOTES

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

JOCHEN REITER

Conservation Biology Unit, Ruhr-Universität Bochum, Universitätsstrasse 150, 44780 Bochum, Germany
E-mail: jochen_reiter@yahoo.com

Key words: *Ptenochirus jagori*, germination, seed dispersal, *Ficus*, Philippines, differential ingestion

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

Downloaded From: https://complete.bioone.org/journals/Acta-Chiropterologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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, $P >> 0.05$ 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

Downloaded From: https://complete.bioone.org/journals/Acta-Chiropterologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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.

Acknowledgements

This paper is publication No. 42 of the Philippine Endemic Species Conservation Project (PESCP). The work of the PESCP is formalized under the aegis of a Memorandum of Agreement with the Department of Environment and Natural Resources (Quezon City, Philippines), and the help of the Protected Area and Wildlife Bureau (R. C. Bayabos, then W. S. Pollisco) is gratefully acknowledged. In the field, I enjoyed the untiring help of B. J. Tacud. The project is sponsored by the Frankfurt Zoological Society. Further support was rendered by the German Ornithologists' Society, The European Union, Andreas-Stihl-Foundation, Ministry of Science and Research of North Rhine Westfalia, the DaimlerChrysler AG, the Vitakraft-Werke, and by a generous donation from E. Mayr, Cambridge, Mass., USA, further by A. de Dios, H. Kessler and C. Sudhoff, Manila. My work has been made possible by a doctoral grant from the German Academic Exchange Service, DAAD, and the Wilhelm and Günter Esser Foundation. I want to thank E. Curio, Ruhr-University Bochum, Germany, for the manifold support throughout the study. Two anonymous referees made helpful suggestions to earlier versions of the manuscript.

Literature Cited

Anstett, M. C., M. Hossaert-McKey, and F. Kjellberg. 1997. Figs and fig pollinators: evolutionary conflicts in a coevolved mutualism. Trends in Ecology and Evolution, 12: 94–99.

Downloaded From: https://complete.bioone.org/journals/Acta-Chiropterologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

AUGUST, P. V. 1981. Fig consumption and seed dispersal by *Artibeus jamaicensis* in the Llanos of Venezuela. Biotropica, 13: 70–76.

BOON, P. P., and R. T. CORLETT. 1989. Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera). Malayan Nature Journal, 42: 251–256.

BRONSTEIN, J. L. 1988. Mutualism, antagonism, and the fig-pollinator interaction. Ecology, 69: 1298–1302.

HANDLEY, C. O., JR, D. O. WILSON, and A. L. GARDNER. 1991. Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panama. Smithsonian Contributions to Zoology, 511: 1–173.

HEIDEMAN, P. D., and L. R. HEANEY. 1989. Population biology and estimates of abundance of fruit bats (Pteropodidae) in Philippine submontane rainforest. Journal of Zoology (London), 218: 565–586.

JANZEN, D. H. 1978. A bat-generated fig seed shadow in rainforest. Biotropica, 10: 121.

JANZEN, D. H. 1979. How to be a fig. Annual Review of Ecology and Systematics, 10: 13–51.

KALKO, E. K. V., E. A. HERRE, and C. O. HANDLEY, JR. 1996. The relation of fig fruit syndromes to fruit-eating bats in the New and Old World tropics. Journal of Biogeography, 23: 565–576.

KAUFMANN, S., D. B. MCKEY, M. HOSSAERT-MCKEY, and C. C. HORVITZ. 1991. Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). American Journal of Botany, 78: 971–977.

LIN, TSAN-PIAO, CHIH-CHEN LIU, and SHU-WEN CHEN. 1989. Purification and characterization of pectinmethylesterase from *Ficus awkeotsang* Makino achenes. Plant Physiology, 91: 1445–1453.

LUFT, S. 1998. Feldökologische Untersuchungen an Flughunden (Megachiroptera: Pteropodidae) auf der Philippinen-Insel Panay. M. Sc. Thesis, Ruhr-University, Bochum, 122 pp.

MACHLIS, L., P. W. D. DODD, and J. C. FENTRESS. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Zeitschrift für Tierpsychologie, 68: 201–214.

MARSHALL, A. G. 1983. Bats, flowers and fruit: evolutionary relationships in the Old World. Biological Journal of the Linnean Society, 20: 115–135.

MARSHALL, A. G. 1985. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. Zoological Journal of the Linnean Society, 83: 351–369.

MURRAY, M. G. 1985. Figs and fig wasps: hypotheses for an ancient symbiosis. Biological Journal of the Linnean Society, 26: 69–81.

REITER, J., and E. CURIO. 2001. Home range, roost switching, and foraging area in a Philippine fruit bat (*Ptenochirus jagori*). Ecotropica, 7: 109–113.

RICHARDS, G. C. 1990. The spectacled flying-fox, *Pteropus conspicillatus* (Chiroptera: Pteropodidae), in North Queensland. 2. Diet, seed dispersal and feeding ecology. Australian Mammalogy, 13: 25–31.

SACHS, L. 1999. Angewandte Statistik: Anwendung statistischer Methoden. Springer-Verlag, Berlin, 884 pp.

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. Proceedings of the Royal Society of London, B 266: 219–223.

UTZURRUM, R. C. B. 1995. Feeding ecology of Philippine fruit bats: patterns of resource use and seed dispersal. Symposia of the Zoological Society of London, 67: 63–77.

UTZURRUM, R. C. B., and P. D. HEIDEMAN. 1991. Differential ingestion of viable vs nonviable *Ficus* seeds by fruit bats. Biotropica, 23: 311–312.

WHITTAKER, R. J., and S. H. JONES. 1994. The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. Journal of Biogeography, 21: 346–354.

Received 28 January 2002, accepted 26 May 2002

Downloaded From: https://complete.bioone.org/journals/Acta-Chiropterologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use