

Size-based fruit selection of *Calophyllum brasiliense* (Clusiaceae) by bats of the genus *Artibeus* (Phyllostomidae) in a Restinga area, southeastern Brazil

MARCO AURELIO RIBEIRO MELLO¹, NATÁLIA OLIVEIRA LEINER¹,
PAULO ROBERTO GUIMARÃES JR.^{1,2}, and PEDRO JORDANO²

¹Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, CEP 13083-970, Cidade Universitária, Campinas, SP, Brazil; E-mail of MARM: marmello@gmail.com

²Integrative Ecology Group, Estación Biológica de Doñana (CSIC), Avda. M^a Luisa s/n, Sevilla 41013, Spain

Key words: frugivory, seed dispersal, seed size, optimal foraging, Atlantic Forest

INTRODUCTION

When feeding on fruits, frugivores face foraging decisions at least on three levels: choice among fruits of different species, among individual crops of a single species, and among fruits borne on the same plant (Sallabanks, 1993; Wheelwright, 1993). Specifically, selection based upon fruit size, or related otherwise to size constraints (e.g., seed size), has been repeatedly documented (Jordano, 1995b). However, we found little information about the details of this kind of fruit selection by bats, particularly in the case of individual fruits within the crop of an individual parental tree. In this study we investigated the influence of fruit size of *Calophyllum brasiliense* on fruit choice by large Neotropical bats of the genus *Artibeus* Leach, 1821 (family Phyllostomidae, subfamily Stenodermatinae). Specifically we evaluated the roles of overall fruit size and amount of pulp in determining fruit choice in the wild.

MATERIALS AND METHODS

Our study site was a 'Restinga' area (coastal sandy forest) at the 'Parque Estadual da Ilha do Cardoso' (PEIC), municipality of Cananéia, state of São Paulo, southeastern Brazil. *Calophyllum brasiliense* Camb. (Clusiaceae) is a large-seeded, canopy tree widely distributed over Neotropical America. Bats have been reported to be one of its seed dispersers (e.g., Fischer and Santos, 2001). In PEIC we observed bats from larger species of the genus *Artibeus*, probably *A. lituratus* (considering the species list given

by Fazollari-Corrêa [1995]), removing *C. brasiliense* fruits.

In order to investigate the influence of parental tree and seed mass on pulp mass/fruit, we measured the seed mass and total fruit mass of 79 intact fruits randomly sampled from the canopy of five individual *C. brasiliense* trees. Total fresh fruit mass was recorded with a precision balance (± 0.01 g) for each individual fruit and divided into seed mass and mass of other fruit matter; we assumed that the latter to be equal to pulp mass but also included the fruit's pericarp.

Our analysis was based on the comparison of morphological variation among bat-handled fruits sampled beneath fruiting *C. brasiliense* trees and intact fruits sampled from tree canopies before removal by frugivores. We assumed fruits to have been handled by bats, only when they presented clear marks of bat teeth. All handled fruits were partially eaten, and fruits with single bite marks were not included. Thus we could assume that bats selected and ate these fruits, and that they were not accidentally dropped by a bat. We must consider the possibility that some of the fruits collected beneath trees might have come from other trees of the same species, but this does not invalidate our analyses. Furthermore, we considered only ripe fruits, which could be recognized by their relative softness (when compared to unripe fruits), because *C. brasiliense* fruits do not change their color when they ripen. It is also important to consider that, sometimes, when visiting particular plant species, bats may eat fruits inside the canopy of the parent tree, especially when fruits are above a certain size or if they are difficult to remove, although they use to carry fruits away from the parent tree in many circumstances (Heithaus *et al.*, 1975; Handley *et al.*, 1991; Bizerril and Raw, 1998).

First, we characterized the morphological patterns of *C. brasiliense* fruits in order to assess the correlates of pulp mass variation for individual fruits. The influence of seed mass and parental tree on fleshy pulp mass was estimated by ANCOVA (Zar, 1999).

We estimated variation in pulp mass/fruit independent of seed mass and individual tree by using the residuals of this ANCOVA. To test for allometric variation of fleshy pulp mass and fruit mass, we correlated fruit mass with residuals of the previous analysis. This would reveal variation in the amount of fruit pulp/fruit with overall fruit size after controlling for the effects of seed mass and of individual differences among trees. Thus, if there is a relationship between residual pulp mass and fruit mass, there is variation in the proportion of fleshy pulp related to fruit mass. Furthermore, we can expect bats could use overall fruit size as a cue to select more pulpy fruits, as visual clues may also play a role in fruit selection by phyllostomids (Kalko and Condon, 1998). The relationship between residual pulp mass and fruit mass was assessed by the least-square linear regression (Zar, 1999).

In order to investigate if bats select fruits based on overall fruit size, we compared seed mass of intact fruits ($n = 79$) with those from 65 fruits with evidence of bat removal. We used seed mass rather than fruit mass, because fruits removed by bats were partially eaten and did not have their pulp mass complete (intact). Both traits show a strong relationship ($r^2 = 0.73$, $d.f. = 77$, $P < 0.001$, $n = 79$ intact fruits), and we can use seed mass as a good estimator of overall fruit size for fruits handled and partially consumed by the bats. Fruits with teeth marks or any other evidence of handling by bats were sampled on the forest floor, under the canopy of five fruiting trees, and we assumed them to be produced by those trees. It is important to note that almost all fruits included in the analyses were clearly eaten, because they did not present only a few teeth marks, but lacked some pieces (proportional to an *Artibeus* mouth), what made it possible for us to assume that they were really selected for consumption. We performed a nested ANOVA, in order to test the percent of variation in fruit size and pulp mass that is accounted for by among-tree variation and within-tree variation. A two-way ANOVA was also performed to test if mean seed mass varies among fruits (removed by bats or intact) and among crops of fruiting trees (Zar, 1999). Seed mass was log-transformed prior to analysis.

RESULTS

Seed mass for 79 intact fruits was 1.96 ± 0.89 g ($\bar{x} \pm SD$), varying from 0.20 to 4.30 g, while seed mass for the 65 removed fruits was 2.30 ± 0.79 g, varying from 0.6 to 4.20 g. Mass for all 213 seeds (including totally clean seeds) was 2.20 ± 0.86 g, varying from 0.20 to 5.30 g. Mean seed mass varied

significantly among five parent trees ($F = 61.60$, $d.f. = 4$, $P < 0.001$), ranging between 3.20 ± 0.80 g (tree 1) to 1.60 ± 0.55 g (tree 3). The mass of fleshy pulp/fruit was positively correlated with seed mass ($F = 17.09$, $d.f. = 4$, $P < 0.001$), and significantly affected by parental tree ($F = 7.62$, $d.f. = 1$, $P < 0.001$), and the interaction of both factors ($F = 11.37$, $d.f. = 4$, $P < 0.001$). The residual pulp mass was positively related with fruit mass in intact fruits ($F = 10.93$, $d.f. = 78$, $P < 0.001$), indicating that the proportion of fleshy pulp increases with fruit mass, despite the relatively low r^2 (0.113) that might be related to between-tree variation in other fruit traits (e.g., shape) influencing the amount of pulp/fruit. The nested ANOVA results ($F = 25.32$, $d.f. = 4$, $P < 0.001$) suggest that 44.3% of the total variation in fruit mass can be accounted for by variation between crops of the individual trees, although there is also substantial variation in fruit mass among the fruits within a given crop (residual = 55.7%). This suggests that bats might select among crops of individual trees based on fruit size, but also selection can operate between individual fruits within a single crop. After controlling for the effect of parental tree, fruits removed by bats are significantly larger than the available, intact fruits ($F = 3.94$, $d.f. = 1$, $P < 0.05$; Fig. 1). It is interesting to note that the only tree that did not follow the general trend (removed fruits larger than intact ones) was the one with highest mean seed mass. It is possible that the reward obtained by bats when feeding on fruits from this individual tree is so high on average that bats do not have to select among fruits. There was also another individual tree, whose difference between mean seed mass of intact and removed fruits was small, but followed the general trend.

DISCUSSION

Our results suggest that bats consistently select and handle the larger fruits of

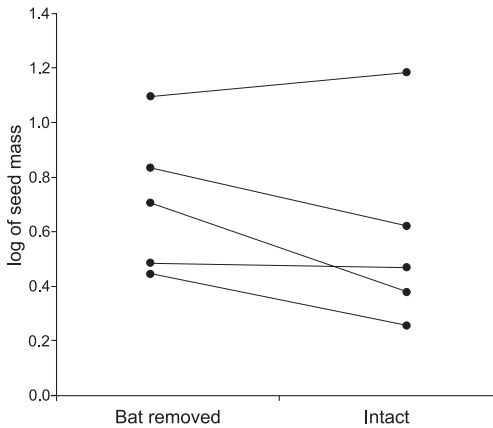


FIG. 1. Contrast between the mean seed mass of fruits removed by bats and of intact fruits collected from the canopies of five adult trees of *C. brasiliense* (Clusiaceae). Each line corresponds to the contrast for an individual tree

C. brasiliense, although this might not result in successful removal of larger seeds due to loading constraints imposed by fruit size or shape. This pattern is expected for foragers that maximize the difference between energy expenditure and intake while searching and handling food (Jordano, 1995a) according to the optimal foraging theory (originally proposed by MacArthur and Pianka, 1966). Foster (1990) suggested that fruit mass and size are key characteristics for frugivore foraging, because they influence reward and costs of handling for the frugivore. Nevertheless, Wheelwright (1993) pointed out that the selection pattern might differ among individual trees.

Some bat species have been reported to handle and successfully disperse extremely large fruits (Meehan *et al.*, 2002), and some studies suggest a positive relationship between the size of the bat species and of its preferred fruit (Fleming, 1991). Our results agree with the feeding preferences proposed for the larger *Artibeus* species (Bonaccorso and Gush, 1987). Most authors report that these bats tend to feed on species with relatively large fruits (when compared to other bat species), many of them with

large seeds, frequently involving long handling times (Marques, 1994).

By selecting larger fruits, *Artibeus* bats consume a large overall quantity of pulp per fruit. Moreover, as larger *C. brasiliense* fruits have a disproportionately higher amount of pulp than smaller fruits, our data suggest that bats select them on the basis of higher pulp-seed ratio, i.e., maximizing the pulp or juice ingested per unit fruit mass handled. Hence, as proposed by Howe and Vande Kerckhove (1981) for frugivorous birds, pulp-seed ratio can be a more important determinant on fruit choice by bats than fruit size, although overall fruit size is probably a proximate cue for more pulpy fruits, especially for drupaceous species.

Artibeus bats remove fruits and consume only the pulp, acting as legitimate seed dispersers. However, it is important to remember that *Artibeus* spp. do not ingest the whole pulp mass of the *Calophyllum* fruits they chew. They acquire nutrients by ingesting the fruit's juice, composed of water and many non-fibrous substances; after the chewing behaviour, they just expel fibrous pellets. See Nogueira and Peracchi (2003) for a detailed description of this kind of feeding behaviour in other Stenodermatinae bats of the genus *Chiroderma*.

Marques (1994) observed that even partial pulp removal by bats, may accelerate germination of *C. brasiliense* seeds. Moreover, Fischer and Santos (2001) observed that larger seeds of *C. brasiliense* germinated faster. In addition, large seeds are usually more resistant to seed predators (Mack, 1998) and have more nutritional reserves for the embryo (Westoby *et al.*, 1992). Although many fruits were dropped below the canopy of *Calophyllum* parent trees, some of them were away and were found below other tree species (a few per site). Hence, we suggest that *Artibeus* bats feeding on fruits of *C. brasiliense* may also increase the reproductive success of these trees by

contributing to selective removal of the largest seeds.

ACKNOWLEDGEMENTS

We would like to thank Mauro Galetti, Wesley Silva, and Marco A. Pizo for useful advice and help during the 'Curso Latino-Americano de Frugivoria e Dispersão de Sementes — 2003' (organized by UNICAMP and IBC), where this work took place. Environmental monitors at Parque Estadual da Ilha do Cardoso, especially Romeu, Carlinhos and Ari Caiçara, who helped to identify guanandi trees (*C. brasiliense*) in the forest and collect their fruits (even on tree canopies). Three anonymous referees and the editor for their detailed reviews of our manuscript. And especially our colleagues, who were very kind, making the course a very pleasant experience. MARM was supported by grants from CAPES and FAPESP; NOL and PRG were supported by grants FMB and FAPESP; PJ had funds from the Spanish MCyT (REN2003-00273) and a CSIC-CNPq agreement during the preparation of the manuscript.

LITERATURE CITED

- BIZERRIL, M. X. A., and A. RAW. 1998. Feeding behaviour of bats and the dispersal of *Piper arboreum* seeds in Brazil. *Journal of Tropical Ecology*, 14: 109–114.
- BONACCORSO, F. J., and T. J. GUSH. 1987. Feeding behaviour and foraging strategies of captive phyllostomid fruit bats: an experimental study. *Journal of Animal Ecology*, 56: 907–920.
- FAZZOLARI-CORRÊA, S. 1995. Aspectos sistemáticos, ecológicos e reprodutivos de morcegos na Mata Atlântica. Ph.D. Thesis (Zoology), Universidade de São Paulo, Brazil, 168 pp.
- FISCHER, E., and F. A. M. SANTOS. 2001. Demography, phenology and sex of *Calophyllum brasiliense* (Clusiaceae) trees in the Atlantic forest. *Journal of Tropical Ecology*, 17: 903–909.
- FLEMING, T. H. 1991. The relationship between body size, diet, and habitat use in frugivorous bats, genus *Carollia* (Phyllostomidae). *Journal of Mammalogy*, 72: 493–501.
- FOSTER, M. S. 1990. Factors influencing bird foraging preferences among conspecific fruit trees. *The Condor*, 92: 844–854.
- HANDLEY, C. O., JR., D. E. WILSON, and A. L. GARDNER. 1991. Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panamá. *Smithsonian Contributions to Zoology*, 511 pp.
- HEITHAUS, E. R., T. H. FLEMING, and P. A. OPLER. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology*, 56: 841–854.
- HOWE, H. F., and G. A. VANDE KERCKHOVE. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology*, 62: 1093–1106.
- JORDANO, P. 1995a. Angiosperm fleshy fruits and seed disperser: a comparative analysis of adaptation and constraints in plant-animal interactions. *The American Naturalist*, 145: 163–191.
- JORDANO, P. 1995b. Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology*, 76: 2627–2639.
- KALKO, E. K. V., and M. CONDON. 1998. Echolocation, olfaction, and fruit display: how bats find fruit of flagellichorous cucurbits. *Functional Ecology*, 12: 364–372.
- MACARTHUR, R. H., and E. R. PIANKA. 1966. On optimal use of a patchy environment. *The American Naturalist*, 100: 603–609.
- MACK, A. L. 1998. An advantage of large seed size: tolerating rather than succumbing to seed predators. *Biotropica*, 30: 604–608.
- MARQUES, M. C. M. 1994. Estudos auto-ecológicos do guanandi (*Calophyllum brasiliense* Camb. Clusiaceae) em uma mata ciliar do município de Brotas, SP. M.Sc. Thesis, Universidade Estadual de Campinas, Brazil, 105 pp.
- MEEHAN, H. J., K. R. MCCONKEY, and D. R. DRAKE. 2002. Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *Journal of Biogeography*, 29: 695–712.
- NOGUEIRA, M. R., and A. L. PERACCHI. 2003. Fig-seed predation by 2 species of Chiroderma: discovery of a new feeding strategy in bats. *Journal of Mammalogy*, 84: 225–233.
- SALLABANKS, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology*, 74: 1326–1336.
- WESTOBY, M., E. JURADO, and M. LEISHMAN. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution*, 7: 368–372.
- WHEELWRIGHT, N. T. 1993. Fruit size in a tropical tree species: variation, preference by birds, and heritability. Pp. 163–174, in *Frugivory and seed dispersal: ecological and evolutionary aspects* (T. H. FLEMING and A. ESTRADA, eds.). Kluwer Academic Press, Nordrecht, 392 pp.
- ZAR, J. H. 1999. *Biostatistical analysis*. Prentice-Hall, New Jersey, 693 pp.