ZOOLOGIA 35: e20583
ISSN 1984-4689 (online)
zoologia.pensoft.net

ZOOLOGIA
An International Journal for Zoology

RESEARCH ARTICLE

Does frugivory in *Citharexylum solanaceum* (Verbenaceae) drive nomadism in the Ipanema bat *Pygoderma bilabiatum* (Chiroptera: Phyllostomidae)?

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http://zoobank.org/825EB39E-C240-45CE-80EA-D6A13620F299

ABSTRACT. Neotropical bats are recognized as effective seed dispersers, especially of small-seeded pioneer plants during early stages of forest regeneration. There had been few reports on the ecology of the bat *Pygoderma bilabiatum* (Wagner, 1843), which appears to be mainly frugivorous and to undertake vertical migrations in Brazil. Our analyzes of fecal samples of *P. bilabiatum* specimens captured in mist nets and direct observations of their feeding behavior on *Citharexylum solanaceum* Cham. fruits in a mosaic of restored forests and forest fragments in southeastern Brazil constitute one of the few records of consumption of large-seeded fruits by *P. bilabiatum*, and indicate that it may be an important disperser for large-seeded plants. We found evidence that the temporal availability of those fruits may influence the movement ecology of those bats.

KEY WORDS. Movements, philopatry, fruit-bat interactions, seed dispersal.

INTRODUCTION

Fruit consumption by bats can improve the effectiveness of seed dispersal and germination because the bats can fly long distances to disperse seeds distant from the parental plants, thus avoiding distance- and density-dependent mortality as well as increasing germination by their consumption behavior and gut-passage effects (Lobova et al. 2009). The diets of fruit-eating bats show little overlap with other frugivorous vertebrates (Fleming and Kress 2011), highlighting their importance for diaspore dispersal, especially of small-seeded, early-successional plants in the Neotropics (Muscarella and Fleming 2007). Some small phyllostomid bats may also be able to disperse large-seeded plants and play wider roles as seed dispersers than previously thought (Melo et al. 2009).

The Ipanema bat, *Pygoderma bilabiatum* (Wagner, 1843), occurs in the Atlantic Forest and Cerrado biomes of northeastern, southeastern, and southern Brazil, as well as Paraguay, southern Bolivia, and northern Argentina (Gardner 2008). It is known as a frugivorous species (Lobova et al. 2009), although there are only few records of fruit species composing its diet (Peracchi and Albuquerque 1971, Webster and Owen 1984, Faria 1997, Passos et al. 2003).

The movement patterns of *P. bilabiatum* have been related to seasonal changes in climate and/or the availability of their preferred fruits (Esbérard et al. 2011). The most recent review of the species' distribution analyzed 26 studies in 21 localities at different elevations within the Brazilian Atlantic Forest and found evidence of vertical migration of *P. bilabiatum* populations from highlands to lowlands during the coldest and driest months of the year in southeastern and southern Brazil (Esbérard et al. 2011). Those authors also reported evidence of differing strategies among males and females, including vertical migration in different seasons, or preferences for different elevations. Their sex ratio varied with elevation, with males being largely encountered at lower elevations, while females were predominant at all altitudes (Esbérard et al. 2011). Cryan (2003) reported that the females of some bat species dislocate more than males, possibly because the females have higher nutritional requirements and most frequent environments with better breeding conditions.

Plant communities globally are negatively impacted by natural enemies, with reduced survival rates of conspecific seeds and seedlings located close to reproductive adults or in areas of high conspecific density (Comita et al. 2014). One strategy to avoid those limitations involves using animals as seed-dispersers, enabling seeds to be disbursed at longer distances from the parent plants – as seen with fruit-eating birds and mammals that have established mutualistic relationships with flowering plants as seed dispersers over at least 90 Ma (Fleming and Kress 2011). The strong relations between animal-plant pairs that have coevolved within those ecological interactions have shaped functional roles as well as distribution and movement patterns. The activities of animal pollinators and frugivores play key roles in determining the spatial patterns of gene flow in plant populations that rely on those dispersal vectors (Nathan and Muller-Landau 2000); the movement patterns of frugivorous bats are likewise highly affected by food availability (Bianconi et al. 2006, Mello 2009).

Additional knowledge concerning the biological and ecological interactions between *P. bilabiatum* and plants will aid our understanding of the movements and functional roles of that bat species. We report here and assess the interactions between *P. bilabiatum* and *Citharexylum solanaceum* Cham. (Verbenaceae) and evaluate whether those interactions are related to nomadism or migration in that bat species.

MATERIAL AND METHODS

Our study was carried out at the Intermontes Farm (337 ha), Ribeirão Grande, state of São Paulo, southeastern Brazil (24°19.51'S; 48°42.32'W). The area is located within the montane Atlantic Forest domain, with abandoned fields, second-growth forests, restored forests, and forest fragments forming a heterogeneous landscape. This report is part of a broader study seeking to characterize fruit diets and space-use by bats in a recently restored forest.

We randomly selected twenty sites in the study area (all between 822 and 900 m a.s.l.) from a grid of intersecting lines plotted every 200 m throughout the area on a satellite image. We sampled the points during 17 discontinuous months (because of the weather and logistic problems) from May 2011 to April 2013, with 80 sampling nights; 40 of those nights were in the dry season (April to September) and 40 in the rainy season (October to March). We opened two mist nets (Avinet 2.6 × 12 m, 38 mm mesh, 75 denier polyester) per site, and four sites sampled per night during five consecutive nights. The nets were always set up at sunset and remained opened for six hours, being checked at intervals of no more than 30 minutes. We followed established guidelines for the care and use of mammals in research, as suggested by the American Society of Mammalogists (Sikes et al. 2011); the fieldwork was carried out with legal research permits (ICMBio/SISBIO #25984-1, #25984-2).

We examined monthly variation in bat abundances, considering *P. bilabiatum*, other frugivores, and bats with other diets, using circular statistics in ORIANA 4 (Kovach 2011). We constructed circular histograms by pooling samples from different months during the entire study period (17 months between May 2011 and April 2013), with the monthly intervals corresponded to 30°.

RESULTS

Our total sampling effort was 134.784 m^2.h (*sensu* Straube and Bianconi 2002), resulting in the capture of 687 bats belonging to 15 species. Of those, we identified 38 individuals as *P. bilabiatum* (26 males and 12 females). Temperatures varied from 12 to 21 °C when *P. bilabiatum* bats were captured. Seventy-nine percent of our captures (n = 30) occurred at temperatures above 17 °C. We captured all of the specimens, except one, between January and March. Only one male was captured in September in an abandoned pasture near an artificial lake at one of the farm borders; it produced no fecal sample.

We encountered adult individuals of the tree *C. solanaceum* on the Intermontes farm that had been planted during a restoration project in 2001; they also occur naturally in the region. *Citharexylum solanaceum* trees were located in front of the nets at two sampling sites. Three other sampling sites had *C. solanaceum* trees located only a few meters from the nets. We followed the fruiting phenophase of seven trees: the five mentioned above and two others located on a trail used to access the study area. All of those individuals set fruit between January and March,

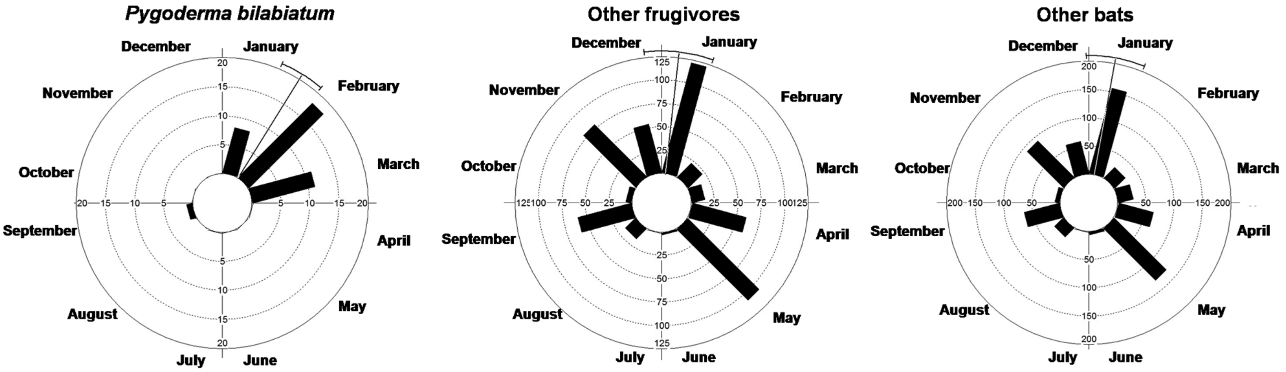

Figure 1. Circular histograms of the abundance variations of *Pygoderma bilabiatum*, other frugivorous bats, and all other bats captured at the Intermontes Farm, Ribeirão Grande, São Paulo, Brazil, throughout the year. The histograms were calculated by pooling samples from different years during the entire study (17 months between May/2011 and April/2013). Columns represent the numbers of captures per month, the radial lines represent the orientation of the median angle, and the perpendicular bars represent circular variance.

precisely during the same short period when *P. bilabiatum* bats were captured in the area (Fig. 1). Other *C. solanaceum* trees in the region set fruit in the same period (pers. obs.), and Lorenzi (2009) indicated the fruiting period as being in February and March.

We frequently observed Ipanema bats visiting *C. solanaceum* trees with ripe fruits. The tree crowns were 2 to 3 m tall and we identified the bats by the conspicuous white patches on their shoulders (clearly visible using binoculars, and absent from other bat species present in the study area). We observed several bats (four or more) feeding simultaneously on the same tree on most nights. A single bat was observed feeding on a tree during only one night. The bats picked the fruits (with their mouth) one fruit at a time; sometimes this made other ripe fruits fall from the same branch to the ground directly underneath the tree. On most occasions, the bats picked a fruit and flew out of sight (more than 100 m); some bats were also observed flying to feeding perches close by, where they ate the fruits and dropped their seeds. In those cases, we were able to fully confirm the bats as *P. bilabiatum* through direct observation (using binoculars). Clusters of seeds, apparently intact and almost or completely without any pulp were found on the ground. Two feeding perches (3 and 9 m away from the parent tree) were found at one of the sampling sites. Another feeding perch was found at 11 m away from the parent tree crown at another sampling site. Numerous ripe fruits were found on the ground at distances of up to 100 m from the parent trees (always with bite marks) during the fruiting season.

Ten of the individuals of *P. bilabiatum* we captured produced no fecal samples; only two of those specimens were captured near *C. solanaceum* trees. The other 28 bat specimens we captured had fruit pulp in their feces, whose color and odor corresponded to *C. solanaceum* (as compared by us, during visual and olfactory inspection, with ripe fruits collected directly from the trees). Of those fecal samples, 26 were obtained from bats captured in nets positioned directly in front of *C. solanaceum* trees with ripe fruits; two fecal samples were obtained from bats caught in nets placed a few meters away from the fruit trees.

We only recorded bat reproductive activities in February, with one lactating female being captured in February 2012, and one lactating and another pregnant female captured in February 2013. Those females all had *C. solanaceum* pulp in their feces, and were captured at two different sampling sites (with *C. solanaceum* trees bearing ripe fruits being located near the capture nets).

DISCUSSION

We report here for the first time interactions between the Ipanema bat *P. bilabiatum* and *C. solanaceum* fruits (a relatively large-seeded plant species for a small bat), with records of fruit consumption and descriptions of feeding behavior – highlighting the role of *P. bilabiatum* as a potential disperser of *C. solanaceum* seeds and the importance of that plant species for the presence of *P. bilabiatum* in the study area. Based on our observations, those interactions appeared to act as drivers of nomadism (or migration) in that bat species, although further studies will be needed.

There have been relatively few reports concerning the diet of *P. bilabiatum*, which includes a diverse array of fruits, such as those produced by *Pouteria caimito* (Ruiz & Pav.) Radlk (Sapotaceae), *Miconia brasiliensis* (Spreng.) (Melastomataceae), *Maclura tinctoria* (L.) Don ex Steud (Moraceae), *Ficus insipida* Willd, *F. enormis* (Mart. ex Miq.) (Moraceae), *Solanum sanctae-catharinae* and *S. granuloso-leprosum* Dunal (Solanaceae), and *Eugenia* sp. (Myrtaceae) (Peracchi and Albuquerque 1971, Webster and Owen 1984, Faria 1997, Passos et al. 2003). Our observations of *P. bilabiatum* indicated that it is maybe another small phyllostomid bat that disperses large-seeded plant species (Melo et al. 2009). The consumption of the pulp of *C. solanaceum* and the behavioral observations presented here (which include carrying the fruits to a perch), together with previous evidence of long-distance movements in search of preferred fruits (Faria 1997), help improve our knowledge of that bat's diet and its probable role in seed dispersal processes.

Although Neotropical frugivorous bats are usually considered irrelevant to the dispersal of large seeds (Muscarella and Fleming 2007), recent evidence suggests a few exceptions. The small tent-roosting bat *Dermanura watsoni* Thomas, 1901 appears to play an important role in the dispersal of large-seeded plants in Mexico (Melo et al. 2009); *Artibeus* bats are also known to disperse large-seeded plants, such as *Calophyllum brasiliense* Cambess. (Calophyllaceae), in Brazil (Mello et al. 2005). Our study demonstrated that *P. bilabiatum* is an example of a small bat that potentially acts as seed disperser for a relatively large-seeded tree.

Laboratory tests have shown that the germination rate of the congeneric species *Citharexylum myrianthum* Cham. (Verbenaceae) increased from 41 to 74% when the pulp was experimentally removed from its seeds (Pizo and Oliveira 2001). We found large numbers of *C. solanaceum* seeds under the trees and feeding perches (3, 9 and 11 m away from the parent trees) with bite marks, and with the pulp totally or partially removed. We also found seeds on the ground at distances of up to 100 m away from the parent tree with bite marks, some of them almost certainly dropped after manipulation by *P. bilabiatum* (*C. Scultori*, pers. obs.); other fruits appeared to have manipulation marks. Those observations suggest potentially increased seed germination rates after manipulation by *P. bilabiatum* through pulp consumption/removal, as observed in the congeneric *C. myrianthum* (Pizo and Oliveira 2001). Detailed studies of *C. solanaceum* germination after bat manipulation will be needed.

Distance from the parent plant is widely known as a crucial element of seed dispersal effectiveness (Schupp et al. 2010), as distance- and density-dependent mortality are well-established world-wide (Comita et al. 2014). We recorded many fruits dispersed by *P. bilabiatum* immediately under or near the parent tree, where seeds and seedlings will presumably demonstrate low survival rates. Despite this we also found ripe fruits (with the pulp partially removed and with bite marks) at distances of more than 100 m from the parent tree; most visiting bats flew for distances greater than 100 m while carrying the fruits, reinforcing the potential of these bats as seed dispersers of *C. solanaceum* (Faria 1997).

Our findings suggest that *P. bilabiatum* might acts upon both quantitative and qualitative components of seed dispersal (Schupp et al. 2010, 2017); quantitative in terms of the numbers of visits and number of fruits carried during flight, and qualitative in terms of apparently maintaining seed integrity while consuming the pulp and increasing the probability of seed germination and successful seedling recruitment by flying long distances and avoiding the negative effects of remaining near parental tree (Schupp et al. 2010, 2017, Comita et al. 2014). Further studies will be needed, however, to better explore the patterns observed and investigate whether this species truly acts as an effective disperser of *C. solanaceum*.

The absence of *P. bilabiatum* at the Intermontes farm during most of the year suggests a seasonal mobility pattern of migration or nomadism. We infer that those bats might possibly explore the well-preserved forests of the neighboring Intervales State Park (a protected area located only 5 km south of the Intermontes farm). Passos et al. (2003) captured 10 individuals of *P. bilabiatum* at the Intervales State Park during a one-year study, but obtained only a single fecal sample containing an unidentified pulp; Mello (2006) captured five individuals of *P. bilabiatum* in a three-year study in the same area. We were able to capture *P. bilabiatum* specimens only during the fruiting season of *C. solanaceum*, which suggests that the plant represents an important food resource for those animals. We presume that *P. bilabiatum* might moves to more distant areas in search for ripe fruits, as observed in a study that focused on *M. tinctoria* in another area in São Paulo State (Faria 1997). Other studies have indicated that temporal variations in phyllostomid assemblages are more strongly related to fruit abundance than to rainfall (Mello 2009).

A review by Esbérard et al. (2011) indicated that the sex ratios of *P. bilabiatum* vary with elevation, skewed towards males at lower elevations but with females predominating at all elevation bands in all of the areas in Brazil where it has been studied. Those authors noted that males and females appear to use different strategies (whether vertical migration in different seasons or preferences for different elevations); slightly less than half of the females of *P. bilabiatum* were recorded by us at 822–900 m a.s.l., reinforcing that observation. Among the bats found there are species in which the females dislocate more than males, possibly due to their high nutritional requirements and the need for environments with more optimal breeding conditions (Cryan 2003). The reproductive records of *P. bilabiatum* show that the species reproduces at different times during the year in different areas and regions (Esbérard et al. 2011). Reproductive activity was only observed in February in our study area, during the period of high resource availability. *Pygoderma bilabiatum* seems to frequently move to areas with abundant fruit resources, and can therefore reproduce throughout the entire year or at different times in different areas (Esbérard et al. 2011).

The existence of differential gender responses to forest disruption and degradation (Rocha et al. 2017) has been well-documented among some tropical phyllostomid species. The foraging behavior and seed dispersal behavior of the bat *Uroderma convexum* Lyon, 1902 varies according to gender: adult males generally restrict their movements to fruiting plants within 100 m of their tents and disperse a large proportion of the seeds they handle exclusively within disturbed areas associated with their tents; adult females move over greater distances, frequently dispersing seeds into multiple habitats (Villalobos-Chaves et al. 2016). Future investigation on *Pygoderma* bats may confirm if one or both behaviors apply to its species.

During the restoration project at the Intermontes Farm (in 2001) more than 80 native tree species occurring naturally in the region were planted between the forest fragments and the abandoned pastures. *Citharexylum solanaceum* was one of the trees planted, but we did not have any information available as to whether the individuals we observed had been planted by humans or occurred naturally in the study area. Independent of their origins, that species will be important to future restoration projects, in light of the ecological interactions observed between *P. bilabiatum* and *C. solanaceum*.

Our study constitutes one of the few records of pulp consumption of a relatively large-seeded fruit by *P. bilabiatum*. Additionally, observations on fruit-handling behavior during flight, and evidence that this bat species moves over long distances, all indicate that *P. bilabiatum* is a nomadic disperser of large-seeded plant species. *Pygoderma bilabiatum* may undertake seasonal vertical migration in the study area, probably driven by its interactions with *C. solanaceum*, so that its role as a disperser of both small- and large-seeded species may be greater than previously thought.

ACKNOWLEDGEMENTS

We thank G.S. Miranda, A. Degressi, A. Benaglia, C. Zaniratto, H.R. Vechi, D. Ramos, N. Novoselova, J.E. Brito, E. Sunter, as well as the local workers who helped with the field efforts; Marco A. Mello, Ivan Sazima and an anonymous reviewer who gave us essential suggestions for the manuscript; and Votorantim Cimentos for allowing us to carry out this study at Intermontes and partially funding it. Our study was supported by the Graduate Program in Ecology at UNICAMP. Carolina Scultori received a scholarship from the Brazilian Research Council (CNPq, 142784/2010-9).

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Submitted: September 18, 2017
Accepted: February 19, 2018
Available online: September 28, 2018
Editorial responsibility: Diego Astúa de Moraes

Author Contributions: CS designed the study, conducted the fieldwork and analyzed the data; CS and WRS wrote the paper.

Competing Interests: The authors have declared that no competing interests exist.