



Queen palm fruit selection and foraging techniques of squirrels in the Atlantic Forest

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ABSTRACT

Queen palm seeds (*Syagrus romanzoffiana*) are a vital source of nutrients for Ingram’s squirrel (*Guerlinguetus ingrami*), a common inhabitant of the Atlantic forest biome of Brazil. *G. ingrami* acts as both a seed predator and disperser of this important palm; however, little is known about how *G. ingrami* selects or efficiently opens queen palm seeds. The objectives of this study were to: (1) investigate the squirrel’s capacity to determine the germinal orifice among the fruit’s three pores, which permits more efficient opening of the fruit; (2) assess whether the thickness and size of the fruit endocarp influence the squirrel’s palm selection during foraging; and (3) evaluate whether the rodents preferentially select fruits with invertebrate infestations. To answer these questions, we used a series of behavioral experiments measuring patterns of squirrel feeding behavior (fruit opening, fruit selection, and patch selection), controlling for environmental variables. We found that (1) squirrels identify the queen palm germinal pore by its greater relative depth to the other pores; (2) the average size and thickness of fruit does not influence the squirrel’s choice of palm for foraging; and (3) squirrels preferentially consume fruits infested by invertebrates. The development of methods for more efficient processing of queen palm fruit highlights the importance of this resource for *G. ingrami*. In addition, due to its preferential selection of infested fruits, *G. ingrami* may benefit palms by reducing parasite population loads.

Abstract in Portuguese is available with online material.

Key words: animal behavior; Atlantic forest; feeding strategy; germinal pore; *Guerlinguetus ingrami*; intraguild predation; *Syagrus romanzoffiana*.

ECOLOGICAL INTERACTIONS ARE ESSENTIAL FOR MAINTAINING COMMUNITY INTEGRITY (Jordano *et al.* 2006). Perturbations to the environment, particularly those that interfere with the reproductive success of plant species, can critically affect animal–plant interactions such as the dispersal and predation of seeds (Murcia 1996). Seed dispersal and predation are among the principal ecological processes that influence the structure and maintenance of diversity in tropical forests and the evolution of plants (Brewer & Rejmanek 1999). About 20 to 50 percent of bird and mammal species consume fruit during at least part of the year (Fleming *et al.* 1987), and the distribution of frugivores is particularly dependent on the availability of fruit in an area (Innis 1989). When seed predators reduce germination success, they limit the population growth of the plants they consume (Schupp 1993). Rodents are the mammalian group with the largest number of species that consume palm fruits in the tropics, and at least 38 rodent species are known to interact with 126 palm species (Andreazzi *et al.* 2009). In the Atlantic Forest of Brazil, squirrels are known to forage from at least 11 palm species (Bello *et al.* 2017). Palm trees may be particularly important for the maintenance of frugivores as an alternative food source in periods of otherwise low fruit availability (Genini *et al.* 2009).

The squirrel *Guerlinguetus ingrami* (Rodentia, Sciuridae) is a rodent likely to influence forest dynamics, partially because it buries seeds within its home range (Bordignon & Monteiro-Filho 2000). When the seeds are not retrieved, squirrels become effective seed dispersers, contributing to the maintenance and expansion of forested areas (Bordignon & Monteiro-Filho 2000). *Guerlinguetus ingrami* is one of seven species of the genus *Guerlinguetus* that occur in Brazil (Bonvicino *et al.* 2008). It prefers an arboreal habitat but moves occasionally on the ground, in leaps, and inhabits the low and intermediate strata of forest fragments of Atlantic Forest and Cerrado (Reis *et al.* 2011).

Most of *G. ingrami*’s diet consists of seeds from the palm *Syagrus romanzoffiana* (Arecaceae), also known as the queen palm (Galetti *et al.* 1992, Paschoal & Galetti 1995). Throughout the home range of the squirrel, the distribution of palms is patchy (personal observation by Mendes, C.P), and there is wide variation in palm phenotype (*e.g.*, fruit and stripe) likely related to local variations in climate, soil, and altitude (Barbosa-Rodrigues 1903). These rodents may therefore be selecting plants for foraging based on fruit phenotype.

The queen palm fruit is characterized by a thin exocarp and a fibrous and succulent mesocarp that forms a single seed, protected by a hard and thick endocarp (Ribeiro *et al.* 2009). The fruit has tri-radial symmetry, and there are three visually identical pores in the apex of the endocarp (Bordignon *et al.* 1996, Fig. 1).

Received 6 October 2016; revision accepted 24 October 2017.

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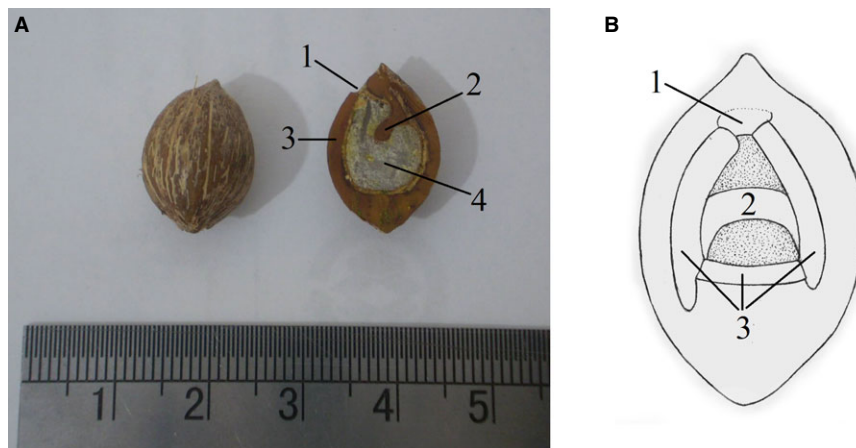


FIGURE 1. (A) Longitudinal cut of the *Syagrus romanzoffiana* fruit for better evidence of anatomical structures; (B) illustration of the most common form of opening of *S. romanzoffiana* fruits by *G. ingrami*, which consists in a triangular cut in the endocarp beginning at the germinal pore. 1- Germinal pore; 2- Internal gibbosity; 3- Endocarp; 4-Endosperm.

Two of these pores have dead ends (with 1-mm depth), and the third is the germinal pore, which is deeper but is closed by a soft and easily penetrable tissue, located on the side opposite the fruit's internal gibbosity. The internal gibbosity is a projection of the endocarp that inhibits the squirrel's access to the endosperm when the fruit is opened from the side containing the dead-end pores. The squirrel must determine the position of the internal gibbosity to avoid it and thus save energy and time in obtaining the endosperm. These rodents are known to identify the side without the internal gibbosity even before beginning to open the fruit, with >90 percent success (Bordignon *et al.* 1996, Mendes & Cândido-Jr 2014). However, how the squirrel identifies the side without the internal gibbosity remains unknown. As the gibbosity is always on the side opposite the germinal pore (Bordignon *et al.* 1996), this pore is an important access point that the squirrel can use to open the fruit efficiently. It is believed that the squirrel manipulates the fruit by pressing the three pores with its upper incisors, using the pore without a dead end for support so that the lower incisors can open the endocarp (Bordignon *et al.* 1996).

Efficiency is one of the main factors that determine the foraging strategy of Sciuridae. A laboratory study conducted with the squirrels *S. carolinensis* and *S. niger* found that individuals preferred various species of nuts with low energetic value that lacked an endocarp or shell over high energy nuts with an endocarp (Smith & Follmer 1972). These results suggest that there is a high cost in energy expenditure for processing seeds with endocarps for these species.

The fruit of *S. romanzoffiana* is also a host for some invertebrate species, which complete their larval instar by consuming the endosperm and embryo of its seed (Alves-Costa 2004). Beetles of the families Bruchidae and Curculionidae are examples of insects that lay eggs in the fruit so that their larvae can develop in this way (Delobel *et al.* 1995, Da Silva *et al.* 2007, Grenha *et al.* 2008). Vertebrate seed predators may intentionally prey on the larvae of these insects to increase available fruit for consumption,

a possible example of intraguild predation (Forget *et al.* 1994, Alves-Costa 2004). Rodents frequently manipulate the endocarps of palm fruits to feed on the larvae contained in their interior (Brancalion *et al.* 2011). Consuming the seeds containing larvae may be a more nutritious option for the squirrels (Cortinoz 2011), as the presence of the larvae increases the level of protein, lipids, and other nutrients in the fruit (Jordano 1987). Both the choice of food items and the strategy used to consume them are behavior patterns that affect individuals' foraging efficiency. These behaviors can affect both the fitness of the individuals in a population and, via intraspecific interactions, the structure of the ecosystem. Understanding the behavioral mechanisms underlying a squirrel's selection and manipulation of food such as palms is thus essential to a better understanding of its function within the ecosystem.

In this study, we investigated three questions related to *G. ingrami* and one of its main food items, the fruit of *Syagrus romanzoffiana*: (1) Does *G. ingrami* use the depth of the seed pores to identify the best side for opening the fruit?; (2) Does *G. ingrami* in the wild preferentially forage among trees that produce larger fruits or fruits with thinner endocarps?; and (3) Does *G. ingrami* possess a preference for preying on fruits with or without larvae?

METHODS

STUDY SITE.—We conducted experiments between August and November 2014, in a fragment of Atlantic Forest (22°15'20"S, 47°28'20"W, Datum SAD69) situated in Rio Claro, São Paulo. To develop the study, we selected a 47-ha fragment of secondary Atlantic Forest surrounded by sugar cane and corn fields. The climate of the site is subtropical (Cwa Köppen classification), with a dry winter and rainy summer. The mean annual precipitation is approximately 1,366 mm, and the mean annual temperature in the region is 21.6°C (Alvares *et al.* 2014).

FRUIT MANIPULATION.—We used a slingshot to collect 30 ripe fruits from 25 *Syagrus romanzoffiana* palms (750 fruits). As the home range of the squirrel is a not exclusive area of around 3.5 ha (Bordignon & Monteiro-Filho 2000), we sourced palms from across an area enough to include several squirrel individuals. With the help of a drill and a fine drill bit (1 mm), we perforated the fruit's three pores through the endocarp to the endosperm, making them equally deep. We left the perforated seeds in small open containers in the palms from which they were collected for seven days. After this period, we collected the fruits that were preyed upon by the squirrels and analyzed the openings that they made, recording the side through which the squirrel made the opening relative to the internal gibbosity.

We also sampled 10 fruits from each palm that had recently been preyed upon by squirrels under natural conditions ($N = 250$ fruits) as a control. We compared the orientation of the openings on the fruits in the control group to the openings on the fruits with perforated pores. As the germinative pore is naturally deeper than the dead-end pores (Bordignon *et al.* 1996), this difference in depth may be the clue that squirrels use to find the side opposite the internal gibbosity. We thus hypothesized that the squirrels would choose the dead-end pore sides with greater frequency when all the pores had the same depth due to perforations. To compare the frequency of the animals' accurate avoidance of the internal gibbosity, we used the Pearson's chi-squared test for count data.

PALM SELECTION BY SQUIRRELS.—We established four 50 m \times 50 m quadrats spaced 80 m apart in areas of the forest with high palm density. For all palms inside the quadrats, we estimated the following variables: productivity, mean size of the fruit, and mean thickness of the endocarp, and as the dependent variable, the proportion of seeds preyed by squirrels. The palms inside the quadrats were on average 6 m apart from each other, facilitating the visitation and selection by the resident squirrels.

To estimate the proportion of fruits preyed on by squirrels, we first established six 30 cm \times 30 cm plots around each palm, placed 1 m from the trunk in random directions. All the fruits within these plots were collected and scored based on evidence of squirrel predation. The fruits not preyed on by squirrels included both intact fruits and those obviously harvested by other animals. This differentiation was made based on characteristic marks left on the fruit when a squirrel opens the fruit to eat the seed (Bordignon *et al.* 1996).

We used the number of fruits inside the six plots as a productivity index of the palm, as the fruits decompose slowly over several flowering periods below the crown of the palm. We assumed that the seasonality did not interfere in our study, as the fruits from new flowering periods represented only a small portion of the collected endocarps under the crown of the palms. From each palm, we collected 10 ripe fruits and used calipers to measure their size. We measured endocarp thickness in the middle along the transverse axis of the fruit, on the opposite side of the internal gibbosity.

TABLE 1. Descriptions of the candidate models for squirrel selection of queen palm trees in the Atlantic forest.

Model name	Model description
GAM-Thickness	Predation of seeds by squirrels \sim Mean thickness of endocarps
GAM-Null	Predation of seeds by squirrels \sim Uniformly distributed random values
GAM-Size	Predation of seeds by squirrels \sim Mean size of fruits
GAM-Productivity	Predation of seeds by squirrels \sim Productivity of the palm
GAM-Size + Thickness	Predation of seeds by squirrels \sim Mean size of fruits + Mean thickness of endocarps
GAM-Size + Productivity	Predation of seeds by squirrels \sim Mean size of fruits + Productivity of the palm
GAM-Thickness + Productivity	Predation of seeds by squirrels \sim Mean thickness of endocarps + Productivity of the palm

To analyze the results, we first generated a series of biologically plausible models (Table 1) based on combinations of independent variables. Models were fit using generalized additive models (GAMs) as they work well with non-linear variables. We then compared the fitted models to each other using the corrected Akaike information criterion (AICc), which adaptively penalizes model complexity and allows for the selection of more parsimonious models. When the difference in AICc was less than 2, we considered the competing models equally plausible. To exclude the influence of plot on the proportion of preyed fruit, we created a generalized additive model of the proportion of preyed fruit as a function of the plot in which the palm was located. The residuals of the model, representing the corrected proportion of preyed fruit, were used as the dependent variable for model selection above. We used the same procedure to exclude the effect of the average size of the fruit on the thickness of the endocarp, as the two variables are highly correlated (*i.e.*, using the residuals of this model as the endocarp thickness predictor in models above). To assess the reliability of the analysis, we also used the π_i Frequency, a bootstrap method that evaluates the frequency of a given model being chosen as the best model from a set of candidate models (Burnham & Anderson 2010). For this process, we resampled the dataset and repeated analyses 10,000 times, recording the best model in each resampling. We calculated the Akaike weight (wAICc) and the Akaike difference (Δ AICc), which are the likelihood value and the relative difference between models, respectively. The Pearson correlation coefficient was used to double check the results of the model selection. We performed all analyses in R (R Core Team, 2013) using the packages 'bbml' (Ben Bolker and R Development Core Team, 2017). and 'gam' (Trevor Hastie 2017).

PREDATION OF LARVAE BY SQUIRRELS.—To assess whether the *G. ingrami* prefer the larvae or the endosperm of the seed, we first collected 30 fruits from 25 queen palms (750 fruits), which

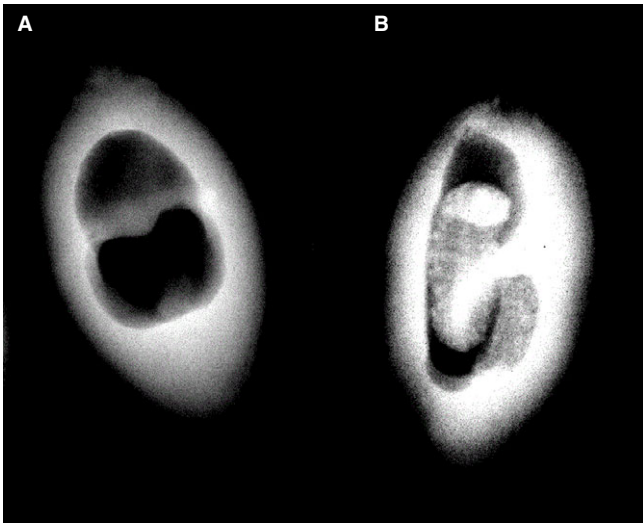


FIGURE 2. Radiograph of the queen palm fruits: (A) fruit with the cavity consisting only of endosperm; (B) fruit with the cavity containing developing larvae.

were then radiographed to determine infestation by beetle larvae (Fig. 2). We chose the radiographic method because it is fast and non-destructive (Brancalion *et al.* 2011). We took radiographs with digital X-ray equipment (Faxitron X-ray, model MX-20 DC12, Tucson, USA), exposing the seed to 26 kV radiation for 1.2 seconds.

After counting the number of larvae-infested fruits in the samples from each palm, we placed them in small, open containers in their palms of origin for one week (Fig. 3). We used camera traps to confirm that only squirrels were removing the fruit. After one week, we collected fruits that were not removed and broke them to check for the presence of larvae. Subtracting the remaining number of infested and healthy fruits from the number of fruits originally offered, we estimated the amount of larvae-infested fruits that were removed from each group. Using the

Pearson's chi-squared test for count data, we tested whether the probability of the removal of a fruit containing larvae was equal to the probability of removal of a fruit without larvae.

RESULTS

FRUIT MANIPULATION.—The percentage of fruits that were opened by squirrels using one of the dead-end pores (*i.e.*, the same side as the internal gibbosity) was only 2 percent in the control group, while in the treatment group, 39.2 percent were opened using one of the dead-end pores (Fig. 4). The proportion of fruits opened by each side was clearly different between the treatment and control groups (chi-squared = 81.65; $P \ll 0.001$). This confirmed our hypothesis that the squirrels use the depth of the germinal orifice to identify the optimal orientation for opening the fruit.

PALM SELECTION BY SQUIRRELS.—None of the models evaluated were superior to the others in explaining the proportion of palm seeds preyed by squirrels. The null model obtained a value of ΔAICc inferior to 2, indicating that none of the variables examined were helpful predictors of seed predation intensity by squirrels (Table 2). This result is corroborated by the overall low values of π_i Frequency and by the three models with higher values of ΔAICc also receiving the highest values of π_i Frequency. A good model would have received a low ΔAICc , commonly 0, and a high value of π_i Frequency. Low π_i Frequency values for all models are expected when the data contain no detectable pattern and the results are susceptible to be changed by any small variation in the values of the data (Burnham & Anderson 2010). These results indicate that mean fruit size (mean = 24.2 mm, SD = 2.5 mm), mean endocarp thickness (mean = 1.8 mm, SD = 0.3 mm), and palm productivity did not apparently affect the squirrels' selection of which palm to forage.

We observed no significant correlation between the proportion of preyed fruits from each palm and the mean size of the

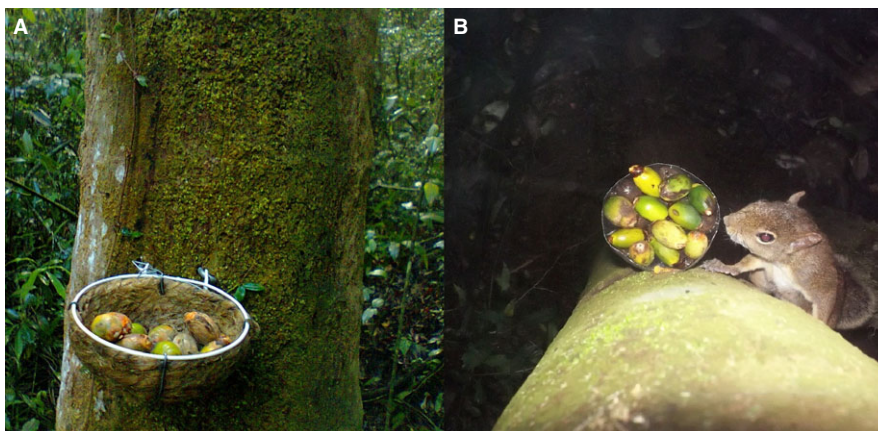


FIGURE 3. Photography of the open containers holding fruits in the field: (A) fruits affixed to a palm stem; (B) a squirrel, moments before remove a fruit.

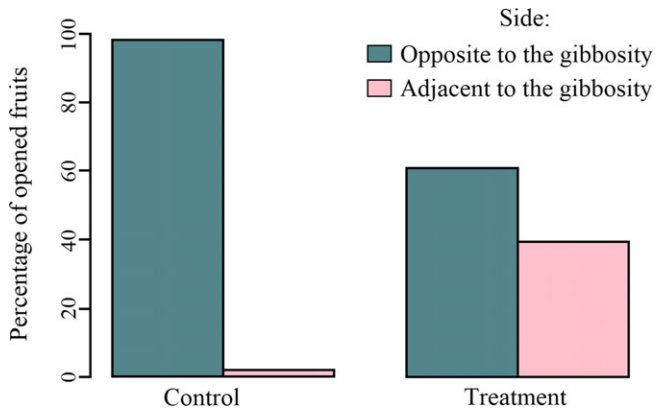


FIGURE 4. In the control group, the squirrels opened the fruits using mainly the germinal pore, which is located on the side opposite the internal gibbosity and allows complete access to the fruit's endosperm. In the control group, the squirrels opened nearly 40% of the fruits using the dead-end pores, which are located at the same side as the internal gibbosity.

fruits they produced (Pearson $r = 0.2$, $df = 31$, $P = 0.26$). The number of preyed fruits was also not correlated with either mean endocarp thickness (Pearson $r = -0.17$, $df = 31$, $P = 0.35$) or palm productivity (Pearson $r = 0.12$, $df = 31$, $P = 0.49$). However, despite not being one of our objectives, we found a positive correlation between the mean size of the fruits produced by the palm and the proportion of fruits infested by larvae (Pearson $r = 0.46$, $df = 20$, $P = 0.03$).

PREDATION OF LARVAE BY SQUIRRELS.—Infested fruits were removed more frequently (60.9%) than the healthy fruits (49.2%; Table 3; chi-squared = 7.0, $P = 0.008$). The proportion of fruits, both healthy and infested, removed from each palm was not correlated with the proportion of fruit infestation in that palm (Pearson $r = 0.22$, $df = 20$, $P = 0.32$), which indicates that the observed results are not caused by higher visitation in palms with more infested fruits.

TABLE 2. Results of model selection using the Akaike information criterion (AICc) for squirrel foraging preference in the Atlantic forest. Note that several models obtained low values (<2) of $\Delta AICc$ (difference in AICc between the model and the best fitted model); weight of AIC in favor of a model; π_i = frequency that a model was selected, given the list of competing models (based on 10,000 bootstrap samples).

Model	$\Delta AICc$	df	wAICc	π_i
GAM-Thickness	0.0	3.00	0.25	0.12
GAM-Null	0.5	3.31	0.20	0.03
GAM-Size	0.8	3.00	0.17	0.03
GAM-Productivity	1.0	3.66	0.16	0.04
GAM-Size + Thickness	1.2	3.99	0.14	0.34
GAM-Size + Productivity	2.7	4.51	0.07	0.21
GAM-Thickness + Productivity	5.6	9.28	0.02	0.23

TABLE 3. Frequency of healthy and infested fruits that were removed by squirrels in the Atlantic forest (chi-squared = 7.0, $P = 0.008$).

	Healthy	Infested	Row total
Removed	281	109	390
Not removed	290	70	360
Column total	571	179	750

DISCUSSION

FRUIT MANIPULATION.—Our results show that the squirrels' identification of the germinal pore for initiating the opening of the fruit is clearly dependent on the pore depth, as our hypothesis predicted. The queen palm fruits in the treatment group (perforated pores) were opened via dead-end pores 37.2% more frequently than the control group (unperforated). The opening of fruit in its most vulnerable region has also been observed in other studies of squirrels (Eibl-Eibesfeldt 1956, Bordignon *et al.* 1996). For example, when opening hazelnuts, *Sciurus vulgaris* uses its teeth on the fragile region of the fruit, applying pressure and opening a slit to expose the seed (Eibl-Eibesfeldt 1956).

As adult squirrels rarely fail to identify the side of the internal gibbosity, this identification likely provides a significant improvement in the efficiency of squirrels' foraging. Under natural conditions, identification failure rates of only 4.5 percent ($N = 534$) have been observed (Mendes & Cândido-Jr 2014). However, other studies have found rates as high as 37 percent ($N = 328$) (Bordignon *et al.* 1996). In this study, we observed very small failure rate of only 2 percent for the untreated fruits ($N = 250$).

It is well established that endocarps or lignified shells are common adaptations against predation by rodents (Zhang & Zhang 2008). We suggest that the internal gibbosity and the dead-end pores of *S. romanzoffiana* are also adaptations against rodents. As a protuberance in the endocarp, the internal gibbosity increases the mechanical resistance of the fruit to opening, requiring a greater time and energy commitment from a rodent. The two dead-end pores, in turn, are externally identical to the germinal pore and may have evolved as an adaptation that confounds the rodents' identification of the geminal pore.

PALM SELECTION BY SQUIRRELS.—In the present study, we found no significant relationship between the proportion of opened fruits at a palm and mean fruit size or thickness. By contrast, there are reports in the literature of squirrels giving preference to seeds with thinner endocarps (Smith & Follmer 1972). It is also possible that larger fruits are not preferred because of the higher relative costs (*e.g.*, opportunity cost and exposure to predators) of manipulating and consuming them (Lima *et al.* 1985).

Results of studies on the influence of a fruit's size on its predation by other rodents have been inconsistent. In some cases, rodents are reportedly capable of assessing the cost-benefits associated with the size of each fruit (Wang *et al.* 2013), such that the medium-sized fruits are often preferred due to optimal benefit vs. energetic cost (Wang & Yang 2014). Other studies found no

relationship between fruit size and a rodent's interest in manipulating it (Moles & Drake 1999). This apparent contradiction may result from the variety of fruit sizes used (Wang *et al.* 2013) as well as the variety of rodent and plant species considered. Moreover, such studies tend to necessarily ignore other relevant species traits, behaviors, and contextual information (Galetti *et al.* 2015). It is likely that other factors such as microhabitat, perception of predation risk (Lima *et al.* 1985), distance to the nest (Alvarenga & Talamoni 2005), or chemical signals in the composition of the fruit (*i.e.*, quantities of lipids, salts, and tannin) also influence a squirrel's choice of which palm to forage. Conversely, it is also possible that the squirrels predominantly select palms at random within their home range for foraging.

We found a positive relationship between the mean size of queen palm fruits and the proportion of fruits infested by beetle larvae. The preference of Bruchidae to oviposit on larger seeds has also been observed for the palm *Sabal palmetto*, in which larger fruits produced larger beetle offspring (Moegenburg, 1996). A similar interaction between *Revena rubiginosa* and *Syagrus romanzoffiana* would not be surprising considering that *R. rubiginosa* larval instars are synchronized with *S. romanzoffiana* fruit development (Alves & Knogge 2005). A high mortality of the larger seeds could act as a selective force on palm populations (Galetti *et al.* 2013). Combined with potential selection against small seeds due to lower germination probability or seedling quality, the heightened infestation of large seeds could create stabilizing selection (Moegenburg 1996). However, neither the heritability of seed size in *S. romanzoffiana* nor the relationship between seed size and fitness has been studied, to our knowledge.

PREDATION OF LARVAE BY SQUIRRELS.—We provide evidence that *G. ingrami* preferentially feed on palm fruits containing larvae. The presence of larvae in fruit often increases the rate of predation by vertebrates (Forget *et al.* 1994, Alves-Costa 2004, Visser *et al.* 2011). However, there are accounts of squirrels rejecting fruits containing larvae, even before the complete removal of the exocarp (Bordignon *et al.* 1996). The preference for fruits containing larvae may be advantageous, as larvae presence may increase the amount of some nutrients in the fruit (Jordano 1987). Moreover, the effort made to extract the larvae from the fruit—the squirrel makes a small opening in the form of a slit (Alves-Costa 2004)—appears to be lower than the effort made to extract the seed, which remains strongly fixed in the endocarp and requires a larger opening for its removal (Silvius 2002).

Although squirrels exhibited a preference for infested fruits and beetle larvae infestations were greater in palms with larger fruits on average, we did not detect any significant squirrel preference for foraging in palms with large fruits. Even if beetle larvae infestations of larger-fruited palms did lead squirrels to forage more in these palms, this indirect effect would be below the detection capabilities of the methods used. Other unobserved fruit characteristics such as chemistry, energetic content, and tannin amount could also have strong effects on palm selection by squirrels.

More studies are needed to investigate how *G. ingrami* identifies the presence of larvae in palm fruit. Potentially, the infested

fruit may undergo chemical changes or exude scents detected by the frugivores. Alternatively, the squirrels may hear noises produced by larvae as they feed on the endosperm or perforate the endocarp while emerging from the fruit.

New evidence suggests that in Neotropical forests, squirrels influence the population of beetles that prey on palm seeds, at least for the species *Attalea butyracea* (Visser *et al.* 2011) and the queen palm (Mendes *et al.* 2015). The present work suggests that squirrels have the ability to identify the fruits infested by larvae and prefer to consume them. Considering that these rodents also function as seed dispersers, their absence in the system would likely have an impact on palm population dynamics, leading to a significant increase in seeds on the soil (Price & Joyner 1997), which would remain exposed to attack from Bruchidae and Curculionidae longer (Visser *et al.* 2011).

In summary, we have determined that (1) squirrels use the depth of the germinal pore in *S. romanzoffiana* fruit to orient the endocarp for efficient opening; (2) the average size and thickness of the queen palm fruits do not appear to be important characteristics for squirrel choice of palms for foraging; and finally, (3) squirrels have a preference for consuming fruits containing larvae. We highlight that squirrels play important roles in tropical ecosystems, including (1) specialized seed predators for large and hard seeds such the queen and attalea palms (Visser *et al.* 2011); (2) primary and secondary seed dispersers, mainly due to their scatter hoarder behavior (Bordignon & Monteiro-Filho 2000), which affects the spatial distribution of plant species (Stoner *et al.* 2007); (3) regulators of beetle populations (Visser *et al.* 2011, Mendes *et al.* 2015) through the intentional predation of larvae; and (4) regulators of beetle populations through competition for palm fruits (Visser *et al.* 2011, Mendes *et al.* 2015), which are a necessary resource for the oviposition of these invertebrates.

ACKNOWLEDGMENTS

We are grateful to the Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP)—Processo 2013/ 50421-2 for the financial support that made fieldwork possible; Dr. Silvio Cícero for the use of the equipment in the Laboratório de Análise de Imagens da Universidade Estadual de São Paulo (USP)—Piracicaba; all those who helped with the field activities; and Megan F. King for proofreading the manuscript. MCR received a research grant from CNPq (312045/2013-1; 312292/2016-3).

DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.20h4h> (Alves *et al.* 2017).

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