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Rousettus madagascariensis (Chiroptera: Pteropodidae) shows a preference for native and commercially unimportant fruits

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ABSTRACT: Flight cage choice experiments carried out over 4 mo demonstrated that a Malagasy fruit bat, *Rousettus madagascariensis* G. Grandidier, 1928, prefers native or introduced fruit of no commercial value (*Ficus polita*, *Syzygium jambos* and *S. malaccense*) to commercially important fruits (*Litchi chinensis* and *Diospyros kaki*). We presented 10 fruit species to the bats: one native (*F. polita*) and the remainder introduced, 3 of which are commercially important. Most bats responded to fruit presented in a flight cage. Bats swallowed fruit juice and pulp and spat out the fibre of all fruit species provided except *L. chinensis* and *Eugenia jambolana*, the flesh of which was swallowed. Chemical composition was the most important determinant of selection by bats. Feeding preference was evidenced by large amounts of chewed pulp, repeated visits to the same fruits and more intensive feeding on lipid- and calcium-rich fruit species. Although commercially important fruit such as *L. chinensis* and *D. kaki* tended to have higher fructose content than other species, our results indicate that lipid and calcium content were more important in fruit selection. We suggest that maintaining natural food availability in humid forests and providing alternative sources of fruit (e.g. *Syzygium* spp.) may contribute to limiting the damage caused by *R. madagascariensis* to commercially important crops.

KEY WORDS: Flight cage · Choice experiment · Preference · Fruit bat · Madagascar

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INTRODUCTION

Feeding preferences of fruit bats are greatly influenced by the nutritional quality of fruit (Bonnaccorso & Gush 1987) and its hardness (Dumont 1999, Dumont & O'Neal 2004). Although fruits are generally considered soft foods, they exhibit a wide range of textures (Strait & Overdorff 1996). Their relative hardness imposes selection pressures on bats to evolve solutions to the mechanical challenge of feed-

ing on them. Some bat species have evolved unique cranio-dental morphological specializations, while others have developed behavioural adaptations (Dumont 2003). Nutritional value is also important in food choice. Wendeln & Runkle (2000) found that small bats in Panama preferred *Ficus bullenei*, which had high levels of lipid and carbohydrates and low levels of lignin and tannin. Two possible reasons for eating a variety of fruit species are: (1) a preferred species, which could alone fulfil the bat's nutritional

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needs, may not always be available; or (2) no one fruit species is sufficient to meet the bat's nutritional needs. In addition to the fructose content and fruit mass influencing fruit choice, Fleming (1986) suggested that bats are also influenced by extrinsic factors, such as ambient light levels (related to the risk involved in flesh removal) and spatio-temporal abundance of the fruits, and intrinsic factors, such as the size of the animal, its reproductive status and social position. Moreover, the structure of the cones in the eye of *Rousettus madagascariensis* indicates that this species does not have colour vision (Müller et al. 2007, Zhao et al. 2009); hence, fruit colour would not be among the factors that influence this species while foraging.

Bats that feed on native forest plants are affected by the loss, degradation and fragmentation of native forest habitat (Ochoa 2000, Pacheco et al. 2006, Jenkins et al. 2007). In response to the loss of native fruit species, fruit bats are likely to be attracted by introduced fruit species, some of which are of commercial value. Charles-Dominique (1986) noticed that 90% of introduced pioneer plants in some tropical areas produce fruits eaten by bats and birds. Plants dispersed by bats produce green fruits externally located on the plant to favour their removal by flying animals (Charles-Dominique 1991). In this study, we investigated the feeding preferences of a small endemic Malagasy fruit bat, *Rousettus madagascariensis* G. Grandidier, 1928, in an experimental situation. We investigated intra-specific differences in the bats' feeding behaviour with different fruit species and determined whether they show a preference for commercially important fruit. We also measured the chemical composition of the fruits. Some Malagasy farmers consider *R. madagascariensis* a pest because it eats cultivated fruits, and we aimed to investigate whether it prefers these to native and commercially less important introduced fruits.

MATERIALS AND METHODS

Study site, bat capture and marking techniques

We conducted our study from January to April 2007, near the town of Anosibe An'Ala, Alaotra Mangoro Region (eastern Madagascar, 19° 27' S, 48° 12' E, 800 m above sea level). The remaining forest vegetation surrounding the town consists of eastern Malagasy moist montane forest (Moat & Smith 2007), equivalent to the *Weinmannia* and *Tambourissa* series (Humbert & Cours-Darne 1965). The climate in the study area has

distinct wet and dry seasons, and rainfall varies from a monthly peak of 500 mm in March to a minimum of 100 mm in October (Donque 1972).

Bats were captured with mist nets in February and April in banana (introduced *Musa paradisiaca*, Musaceae) and in January in litchi (introduced *Litchi chinensis*, Sapindaceae) plantations, and in March at a fig tree (native *Ficus polita* Moraceae). Bats were kept in a dark room with a dish of sugar water available during the remainder of the night of capture. Animals were then kept for about 24 h, used in the experiment the following night and then immediately released at the site of capture.

The bats were weighed, measured and marked dorsally with different coloured reflective tape (red, white, red-white, none) to allow individual recognition. Depending on the number of bats captured, 2, 3 or 4 individuals were introduced into a flight cage (ca. 4 × 2 × 2 m) constructed from dark polythene sheets, which prevented external light from penetrating. The bats flew freely and hung from the top of the flight cage. We followed the techniques of several authors who have studied bats in temporary captivity to allow close-range observation and better control of the experimental setting (Hernández-Conrique et al. 1997, Kalko & Condon 1998, Thies et al. 1998, Dumont 1999).

Before their release after the experiments, the bats' head fur was dyed (Balsam & Sagarin 1972) so that they could be recognised if recaptured during subsequent trapping sessions. *Rousettus* were abundant at the site, and it was possible to introduce different individuals into the flight cage on successive nights.

Fruit species used

Each fruit species used during the experiments was classified as being either of relatively high commercial importance or of no commercial importance, and as being native to Madagascar or not.

Ten fruit species were offered to the bats from January to April, according to the availability of fruits. Fruits of 1 native species (*Ficus polita*, Moraceae) were used in March and 3 commercially important species in January (*Litchi chinensis* and *Prunus cerasus*, Rosaceae) and March to April (*Diospyros kaki*, Ebenaceae). Other species of no commercial importance were used in January (*Syzygium jambos*, Myrtaceae and *Chrysophyllum imperiale*, Sapotaceae), February and March (*Eugenia jambolana* and *Psidium cattleianum*, Myrtaceae), March and April (*P. guajava*, Myrtaceae) and April (*S. malaccense*). These

10 species were selected for the experiments because they were available at the study site, and *Rousettus madagascariensis* was reported by local people to feed on *L. chinensis*, *D. kaki*, *E. jambolana*, *S. malaccense* and *P. guajava*. *Rousettus* also feed on ripe banana fruit in south-east Madagascar (Goodman 1999), but this was not offered to the bats because local growers gather the fruits before they ripen. The native fig species *F. polita* is found in the town of Anosibe An'Ala and grows near the river and sometimes in the adjacent villages. The 3 commercially important fruits are harvested for local and larger distant markets (e.g. Moramanga and Antananarivo) and provide important seasonal income for growers and transporters. However, other fruits such as *E. jambolana*, *P. guajava*, *P. cattleianum*, *S. jambos* and *S. malaccense* were occasionally eaten by the villagers in the Anosibe An'Ala market. Some fruit species were present and used during 2 consecutive months, such as *E. jambolana* and *P. cattleianum* (February and March), *D. kaki* and *P. guajava* (March and April; Table 1).

Experimental protocol

The experimental protocol involved presenting up to 25 fruits of each species, depending on the number of bats in the cage; so that the number of fruits of each species for 4 bats was approximately double

that for 2 bats. We used 2 to 4 bats in the flight cage during 27 sessions over 4 consecutive months. Bats were offered 2 to 5 ripe fruit species each month depending on fruiting phenology. Four fruit species were offered at the same time in January, 2 in February, 5 in March and 3 in April. Fruits were impaled on toothpicks or spikes and hung from the roof of the cage, 15 cm apart, from 5 to 7 horizontal nylon ropes (Fig. 1). The bats were over-supplied with fruits, so that they would exercise choice and not be solely motivated by hunger.



Fig. 1. *Rousettus madagascariensis*. Flight cage with a fruit bat feeding on a *Ficus polita* fruit. (Photo by Radosoa A. Andrianaivoarivelo)

Table 1. Feeding behaviour of *Rousettus madagascariensis* in a flight cage with a variety of fruits. Each fruit species is classed as being either of commercial importance or not. Values are means \pm SD (range). No. of bats: total number of bats feeding on the respective fruit species. See 'Materials and methods' for detailed descriptions of the response variables

Commercial importance Fruiting months	Species (no. of bats)	Mean reaction time (min)	Feeding duration (min)	Flesh removal efficiency (g fruit g ⁻¹ bat)	No. fruits chewed per bat (range)	No. contacts per ind. bat
Important						
January	<i>Litchi chinensis</i> (9)	17.2 \pm 15.0	7.2 \pm 4.6	0.1 \pm 0.1	0.9 \pm 1.5 (0–4)	2.4 \pm 2.1
January	<i>Prunus cerasus</i> (0)	Not eaten	0	0	0	0
March	<i>Diospyros kaki</i>	39.7 \pm 41	4.2 \pm 5.0	0.06 \pm 0.19	1.0 \pm 1.0 (0–2)	2.0 \pm 1.7
April	(3: March; 3: April)	53.0 \pm 43.8	7.4 \pm 1.3	0.02 \pm 0.07	1.0 \pm 1.0 (0–1)	1.5 \pm 0.7
Not important						
January	<i>Chrysophyllum imperiale</i> (0)	Not eaten	0	0	0	0
March	<i>Ficus polita</i> ^a (23)	17.1 \pm 13.0	25.1 \pm 16.5	0.4 \pm 0.4	2.4 \pm 2.3 (1–6)	3.9 \pm 2.2
February	<i>Eugenia jambolana</i>	34.2 \pm 16.4	10.3 \pm 4.0	0.1 \pm 0.1	3.4 \pm 0.5 (3–4)	4.0 \pm 0.9
March	(9: February; 6: March)	36.3 \pm 32.3	18.0 \pm 14.4	0.05 \pm 0.05	2.9 \pm 1.7 (1–5)	3.1 \pm 2.1
February	<i>Psidium cattleianum</i>	12.0 \pm 8.7	3.8 \pm 2.8	0.04 \pm 0.04	2.3 \pm 1.0 (1–4)	2.5 \pm 1.0
March	(8: February; 7: March)	20.7 \pm 14.5	6.7 \pm 5.7	0.02 \pm 0.06	2.0 \pm 2.0 (1–6)	2.1 \pm 2.0
March	<i>Psidium guajava</i>	69.0 \pm 31.2	4.0 \pm 1.0	0.1 \pm 0.4	1.5 \pm 0.7 (0–2)	1.5 \pm 0.7
April	(3: March; 7: April)	31.6 \pm 45.7	4.9 \pm 6.0	0.2 \pm 0.4	1.1 \pm 0.3 (0–2)	2.1 \pm 2.0
January	<i>Syzygium jambos</i> (22)	14.9 \pm 14.0	22.7 \pm 23.90	0.5 \pm 0.6	2.3 \pm 1.4 (1–5)	4.3 \pm 2.5
April	<i>Syzygium malaccense</i> (20)	10.5 \pm 7.6	17.2 \pm 10.5	1.2 \pm 0.9	2.2 \pm 1.6 (1–5)	4.3 \pm 2.5

^aNative species

All fruits were collected from trees and none was bought in the market. No fruits were collected from the ground. Only ripe fruits were presented to the bats, as judged by size, colour, softness and, in the case of figs, absence of latex and exit holes made by wasps.

We observed bats for 90 min per experimental session. The flight cage was illuminated with low lights (2×5 W) and 2 observers watched and recorded the data from holes (3 cm diameter) in the cage fabric.

We assessed the following 5 response variables to investigate the feeding preference of *Rousettus madagascariensis* for native, commercially important or commercially unimportant fruits: (1) the reaction time (in minutes) from the introduction of a bat into the flight cage to its first contact with a fruit; (2) the feeding duration (in minutes) of each individual on each fruit species (1 or more fruits) within 1 experimental session (in minutes); (3) the fruit flesh removal efficiency, or the mass of chewed fruit per species per g of bat body mass (g fruit g^{-1} bat). This required an estimate of the volume of fruit removed by the bats. Removed flesh was assessed visually and rated as a percentage of the total volume of the fruit after the bat's visit. The percentage volume (percent of the fruit volume removed after the bat visit) was then converted into grams using the mean mass of the fruit. This was divided by the mass of the individual bat to give the flesh removal efficiency; (4) the number of contacts with the same fruit species by the same individual bat; (5) the number of chewed fruits per plant species per bat within 1 experimental session.

Analysis of fruit

The fruit mass and fructose concentration of the pulp juice of 20 to 53 ripe fruits of each species were measured. The fruit pulp was squeezed to extract the juice, and the fructose content was measured in degrees brix ($^{\circ}\text{Bx}$) using a 0–32% refractometer (Trading Company, Jiang Su) (Frost & Frost 1981). Each degree Brix is equivalent to 1 g of fructose per 100 g of fruit juice (Roger et al. 1996). The fruits were weighed using an electronic balance with an accuracy of 0.05 g. Fruits were collected on the same day as the flight cage experiment, and fruit mass and fructose content were measured prior to the flight cage experiment.

Additionally, 10 to 20 fruits per species were brought soon after harvesting to the Centre National de Recherche pour l'Environnement laboratory,

Antananarivo, Madagascar, and the following components were analysed: acid ($\text{mg H}_2\text{SO}_4$ 100 g^{-1}), protein ($\text{g } 100 \text{ g}^{-1}$), lipid ($\text{g } 100 \text{ g}^{-1}$), calcium ($\text{mg } 100 \text{ g}^{-1}$), ash (%), moisture ($\text{g } 100 \text{ g}^{-1}$) and fruit mass.

Statistical analysis

Because of the significant and positive correlation between the number of contacts with the same fruit species and the number of chewed fruits ($R = 0.89$, $p < 0.001$), we analysed only the former. The resulting 4 response variables were log transformed before we tested for the influence of fruit species and fruit categories (native or not, commercially important or not) upon them by means of linear models and F -tests. In addition to these explanatory variables, we considered covariates that could have influenced bat preference such as month, number of bats, total number of fruits used and the total number of fruits of the species chosen by the bat in the flight cage during the experiment. For each response variable, we built models that considered all variables (and their interactions) that had a significant effect on the response variable when taken individually (potentially including fruit species and all covariates). We also started with all variables and used Akaike's information criterion (AIC) to remove variables that did not improve model fit. The 2 procedures led to the same results. We then added to the final model the fruit categories as a nested variable for fruit species. Because all fruit species were not available during all months (Table 1), we made these comparisons between fruit categories only for the months where 2 fruit categories were actually available. All models were finally visually checked by looking at residual distributions and quantile-quantile (QQ) plots to assess the distribution normality of the samples and estimate whether the sample could be considered as part of the whole group.

Fruit components such as acid, protein, lipid, calcium, ash, moisture, fructose and fruit mass were not incorporated into the modelling procedures because there was only a single measure per chemical component for each fruit species (the flesh of 20 fruits per species was mixed in the laboratory and the concentrations of the chemical components were measured). These data were used simply for the interpretation of the tendency we observed for each of the 4 response variables. All statistical analyses followed Crawley (2007).

RESULTS

Feeding observations and behaviours

The bats fed on 8 fruit species (*Litchi chinensis*, *Eugenia jambolana*, *Psidium cattleianum*, *P. guajava*, *Syzygium jambos*, *S. malaccense*, *Ficus polita* and *Diospyros kaki*) and refused 2 of them (*Chrysophyllum imperiale* and *Prunus cerasus*). The total duration of the observations was 42 h, and involved 27 different experimental sessions. Seventy-nine of the 88 bats used in the feeding trials made contact with suspended fruits. In total, 992 fruits were offered to the bats, and 298 of these were consumed. A maximum of 23% of a given fruit species was eaten by a bat during a single experiment (Fig. 2).

When released into the flight cage, all bats flew to a perch. The mean interval between the introduction of the bat to the cage and first contact to a fruit was 23 ± 22 min ($n = 120$). Subsequently, they approached a fruit in direct flight, sometimes rotating in the air to land head-down next to it. They fed on that fruit for 4.7 to 25.1 min (Table 1), then rested beside it or flew off. The bats ate part or all of the fruit and on some occasions returned repeatedly to the same fruit (4.7 ± 2.40 contacts), depending on the species. Bats visited and chewed up to 9 fruits within 1 experimental period. They held the fruit between the 2 forearms and patagia and the thorax and sometimes with the foot, then started to chew it. The fibres were spat out and the juice was swallowed in the case of most fruit species, but the flesh of *Litchi chinensis* and *Eugenia jambolana* was swallowed. The bats peeled the litchi pericarp before starting to feed on the white flesh.

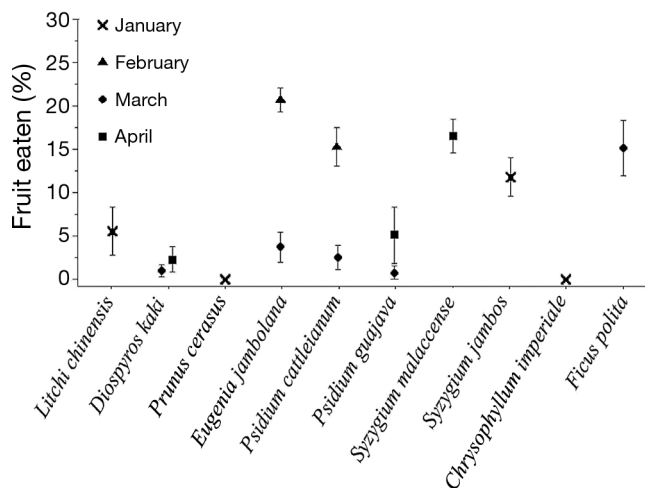


Fig. 2. Mean percentages of fruits eaten in each experiment by individual *Rousettus madagascariensis* in the flight cage. Bars represent SE

The feeding marks on the litchi pericarp were distinctive, and were caused by the incisors.

A small piece of fruit that may otherwise have dropped to the ground was held between the patagia and thorax and eaten first before larger pieces. The fruit was eaten from its distal end or from 1 side, and the proximal part occasionally remained fixed to the cage. The bats approached fruits of *Chrysophyllum imperiale* but not *Prunus cerasus*. There were occasional attempts to feed on *C. imperiale*, but it was avoided after the first bite without removal of flesh. Bats sometimes fed on consecutive fruit of the same or other species (1 to 6 fruits, Table 1). Occasionally, some individuals hovered and tried unsuccessfully to carry the fruit away.

Response variables affecting the feeding preference among the bats

Reaction time varied between fruit species (analysis of variance, ANOVA, $df = 7$, $F = 4.4457$, $p < 0.001$) to the exclusion of all other variables. The reaction times were similar for the commercially important species (*Litchi chinensis*) and the species of no commercial value (*Syzygium jambos*) available in January (ANOVA, $df = 1$, $F = 0.7036$, $p = 0.4090$). In contrast, the reaction time for the commercially important *Diospyros kaki* was higher when compared to species with no commercial value, *Eugenia jambolana*, *Psidium cattleianum* and *P. guajava* in March (Table 1, ANOVA, $df = 1$, $F = 5.5360$, $p = 0.03$). During April, few data were obtained on bats feeding on commercially important species (*D. kaki*) because of few visits to the fruits ($n = 3$) and could not be analysed with ANOVA. There was no difference in reaction times between native and non-native species (ANOVA, $df = 1$, $F = 0.51$, $p = 0.48$) in March when native species were available (Fig. S1 in the supplement at www.int-res.com/articles/suppl/n019p019_supp.pdf).

Feeding duration was affected only by fruit species (ANOVA, $df = 7$, $F = 7.84$, $p < 0.001$) and was higher for *Syzygium jambos*, *Ficus polita* and *S. malaccense* than for other species (Fig. S1). However, feeding duration was significantly different between commercially important fruits in January and March (January: *Litchi chinensis*, March: *Diospyros kaki*) and species of no commercial value (January: *S. jambos*, March: *Eugenia jambolana*, *Psidium cattleianum* and *P. guajava*, *F. polita*) (ANOVA, January, $df = 1$, $F = 13.10$, $p = 0.0011$; ANOVA, March, $df = 1$, $F = 5.13$, $p = 0.030$). In contrast, the feeding duration of these fruit categories was not significantly differ-

ent in April (ANOVA, $df = 1$, $F = 0.029$, $p = 0.87$). The feeding duration for native species (*F. polita*) was significantly higher compared to that for non-native species (March, ANOVA, $df = 1$, $F = 18.27$, $p < 0.001$).

Flesh removal efficiency was affected only by the fruit species (ANOVA, $df = 7$, $F = 20.97$, $p < 0.001$; Fig. S1 in the supplement). The flesh removal efficiency in January and March did not differ between commercially important and unimportant species (ANOVA, January, $df = 1$, $F = 3.42$, $p = 0.075$; ANOVA, March, $df = 1$, $F = 0.81$, $p = 0.04$). Although the flesh removal efficiencies for commercially important (*Diospyros kaki*) and unimportant species (*Syzygium malaccense*) were significantly different in April (ANOVA, $df = 1$, $F = 7.61$, $p = 0.01$), there was no difference in flesh removal between native and non-native species (ANOVA, $df = 1$, $F = 3.63$, $p = 0.07$), i.e. the amount of flesh removed for *Ficus polita* was similar to that for non-native species (*Eugenia jambolana*, *Psidium cattleianum* and *P. guyajava* and *D. kaki*) in March.

Models built using the number of contacts with the same fruit species led to residuals that were not normally distributed and whose variance increased with their value (Fig. S2 in the supplement at www.int-res.com/articles/suppl/n019p019_supp.pdf). We thus decided not to show the results of these analyses (which did not contradict the results shown for the other variables).

For every month, the proportion of economically unimportant fruit species taken by bats was always higher than that for economically important ones.

Fruit characteristics and bat preferences

When compared with the 5 chemical component data (Table 2), the results for the 4 response variables (Table 3) suggested that the bats sought fruits according to their chemical composition. They preferred fruits with high lipid and calcium content (Table 3), properties found in fruit of no commercial

Table 2. Chemical component values and 3 fruit factors (moisture, fructose, fruit mass) of the 10 fruit species used during the flight cage experiments with *Rousettus madagascariensis*. Values (mean \pm SD) for protein, lipid, ash and moisture are in g per 100 g of fruit. Preferred fruits are in **bold**. n: no. of samples

Species	Acid (mg H ₂ SO ₄ 100 g ⁻¹)	Protein	Lipid	Calcium (mg 100 g ⁻¹)	Ash	Moisture	Fructose, % (n)	Fruit mass, g (n)
<i>Litchi chinensis</i>	30.00	2.50	0.17	3.22	0.54	82.62	18.9 \pm 2.5 (201)	15.8 \pm 4.7 (106)
<i>Syzygium jambos</i>	26.20	1.90	2.17	22.60	0.43	81.07	13.4 \pm 1.2 (26)	22.1 \pm 5.88 (27)
<i>Chrysophyllum imperiale</i>	31.60	2.00	0.08	14.47	0.56	80.15	17.7 \pm 1.1 (21)	20.3 \pm 2.5 (21)
<i>Prunus cerasus</i>	29.40	2.20	0.20	42.11	0.47	85.65	13.7 \pm 1.5 (23)	4.7 \pm 0.9 (23)
<i>Eugenia jambolana</i>	1.71	8.05	0.17	13.30	0.43	83.67	13.3 \pm 2.3 (32)	3.0 \pm 1.0 (51)
<i>Psidium cattleianum</i>	1.53	1.75	0.74	51.19	0.80	80.10	12.7 \pm 1.5 (30)	6.6 \pm 3.0 (30)
<i>Psidium guajava</i>	2.10	1.31	0.52	11.46	0.52	81.65	7.2 \pm 1.8 (12)	72.1 \pm 25.7 (12)
<i>Ficus polita</i>	1.82	1.40	0.90	85.00	0.99	83.51	8.6 \pm 1.3 (34)	15.1 \pm 4.4 (34)
<i>Syzygium malaccense</i>	1.64	0.90	0.99	14.30	0.36	89.43	8.6 \pm 1.5 (51)	71.6 \pm 33.0 (51)
<i>Diospyros kaki</i>	1.72	1.40	0.22	16.46	0.50	92.68	16.6 \pm 2.2 (21)	72.0 \pm 18.0 (21)

Table 3. Summary of the fruit species most preferred by *Rousettus madagascariensis*, showing the respective chemical components for which we measured the highest values out of all fruit species investigated. Calcium values are in mg per 100 g of fruit; lipid values are in %

Response variable	Preferred species	Fruit category	Highest-value chemical component
Reaction time	<i>Ficus polita</i>	Native	Calcium (85), Lipid (0.90)
	<i>Syzygium jambos</i>	Commercially unimportant	Lipid (2.17)
Feeding duration	<i>S. malaccense</i>	Commercially unimportant	Lipid (0.99)
	<i>F. polita</i>	Native	Calcium (85), Lipid (0.90)
Flesh removal efficiency	<i>S. malaccense</i>	Commercially unimportant	Lipid (0.99)
	<i>F. polita</i>	Native	Calcium (85), Lipid (0.90)
No. contacts per bat	<i>S. jambos</i>	Commercially unimportant	Calcium (22.60), Lipid (2.17)
	<i>S. malaccense</i>	Commercially unimportant	Lipid (0.99)
	<i>S. jambos</i>	Commercially unimportant	Calcium (22.60), Lipid (2.17)
	<i>S. malaccense</i>	Commercially unimportant	Lipid (0.99)

importance during the study. The relevance of the other chemical components in fruit selection (acid, fructose, protein) by *Rousettus madagascariensis* was equivocal. Fruits with higher fructose content received a similar number of contacts as those with lower fructose content.

DISCUSSION

Feeding preference

This is the first attempt at a systematic analysis of the food preferences of *Rousettus madagascariensis* in experiments using native and introduced species, some of which are commercially important. We investigated the foraging decisions made by *R. madagascariensis* among fruits of different species, and showed that this bat does not prefer commercially important fruit when other fruit species (native or not commercially important) are available.

In addition to the importance of chemical composition in fruit choice, we also found that *Rousettus madagascariensis* prefers species with heavy fruits (Table 2). Frugivores select fruits based on size, phenology and nutritional quality (Howe & Estabrook 1977, Thomas 1984). A bat fares better energetically by taking a few large fruits (*Syzygium malaccense*, *S. jambos* and *Ficus polita*) than by selecting more small fruits, which would involve more commuting and approach flights for a similar nutritional reward (Kalko et al. 1996). Apart from the fruit choice criterion of size, Sánchez et al. (2006) found that frugivorous bats from the Old and New World use odour cues to locate and assess fruit condition. They hypothesized that *R. aegyptiacus* used volatile compounds as odour cues, and that their emission rate increased as fruit ripened.

The commercially important species contained higher fructose concentrations compared to other fruit categories (Table 2), suggesting that the choice of fruit species by the bats was not driven by this variable. However, Baker et al. (1998) and Ogunbiyi & Okon (1976) demonstrated that the enzyme sucrase was present in sufficient concentration in the gut of fruit bats to suggest that nectar and fruit juices containing fructose could be digested easily by these bats.

Mattson (1980) described fruits as either 'nutrient-poor' (those providing energy from carbohydrates but with relatively few lipids and less than 0.5% protein) or 'nutrient-rich' (those with higher protein, i.e. ca. 6 to 7% fresh weight, and lipid content). Obligate

frugivores should feed on high-protein fruits, whereas facultative frugivores can eat poor-quality fruits, which they supplement with insects, seeds and leaves (Kunz & Diaz 1995). Our laboratory analyses of fruit components (Table 2) showed that the fruit species preferred by the bats were also rich in lipids. There seemed to be a preference for calcium-rich fruits in January (*Syzygium jambos* compared to *Litchi chinensis*) and March (*Ficus polita* compared to *Diospyros kaki*).

Because many fruits consumed by bats are high in carbohydrates and low in protein, Thomas (1984) suggested that plant-visiting bats over-ingest fruits to meet their protein requirements and dump carbohydrates. Conversely, if plant-visiting bats supplement their fruit diet with protein-rich food (Zortea & Mendes 1993), they do not need to over-ingest carbohydrate-rich fruits, which may explain the high preference of *Rousettus madagascariensis* for *Ficus polita* in March. *Diospyros kaki* has a similar amount of protein as *F. polita*, but the bats fed more on the latter fruit, possibly to avoid over-ingesting carbohydrates from *D. kaki*. However, Korine et al. (1996) determined the digestible nitrogen requirements for free-ranging *R. aegyptiacus* (134 mg N kg⁻¹ d⁻¹), and concluded that energy rather than nitrogen was the limiting factor in this species. Subsequently, Delorme & Thomas (1999) evaluated the nitrogen and energy requirements of captive *R. aegyptiacus* and concluded that this species may be specialized for the retention of nitrogen, especially when accessible foods have low nitrogen availability. The maintenance nitrogen requirement of *R. aegyptiacus* is much lower than that reported for other fruit bat species (Korine et al. 1996), and the bats may be constrained by the low-protein fruit diet which makes a long lactation period necessary, similar to observations made for large mammals (Korine et al. 2004).

According to O'Brien et al. (1998), given the high concentration of calcium in *Ficus* fruits, it is not surprising that they are preferred as food by many plant-visiting bats (Morrison 1978), including *Cynopterus sphinx* and *C. brachyotis* in Asia (Bhat 1994). Fourteen of 17 fig species found on Barro Colorado Island in Panama are eaten regularly by bats (Kalko et al. 1996). Wendeln & Runkle (2000) found that figs might be able to sustain some frugivores without additional food. The lipid concentration of figs is higher than for some other tropical fruits (Wendeln & Runkle 2000), and Morrison (1980) found that protein made up 4.8% (dry weight) of the fig juice. Figs are a source of calcium, which is critical for successful reproduction in both wild and domesticated mam-

mals (Sadlier 1969), and is a limiting nutrient for milk production (Kunz et al. 1995). The availability of *F. polita* and the preference for this species coincided with captures of lactating female *Rousettus madagascariensis* in our study area during March.

Extraction efficiency varies depending on the nutrient concerned, ranging from 50.0 to 63.8% for organic nutrients and from 0 to 35.7% for macrominerals (Ruby et al. 2000). Fruit bats in the wild appear to meet their nutrient needs by consuming large quantities of a mixture of native fruits, with some consumption of flower parts, pollen, leaves and insects (Zortea & Mendes 1993, Courts 1997, Ange et al. 2001, Long & Racey 2007).

Conservation management of bats

Recently, Singaravelan et al. (2009) called for the majority of fruit bats in India to be removed from national vermin lists because they are forest dwellers and there is no evidence that they feed on commercially important fruits. Although the fruit bats of Madagascar do feed on such fruits, the present study provides evidence that their preferences lie elsewhere. The damage caused by *Pteropus niger* to litchis in Mauritius (Jenkins & Tatayah 2009) is likely the result of a decrease in native vegetation and the poor reproductive success of native plant species (Lorence & Sussman 1986) on which the bats feed.

Conserving and managing plants used as food by frugivorous bats is important in maintaining populations of frugivorous bats and ensuring plant species dispersal. We found that, in addition to feeding on native species (*Ficus polita*), the bats consumed several introduced plant species (*Syzygium jambos*, *S. malaccense* and *Psidium cattleianum*) and fed less on commercially important crop species. In the Neotropics, some bat species are favoured by increases in secondary forest areas (Lopez & Vaughan 2007), where native and/or introduced plant species coexist. Our results suggest that maintaining natural food supplies in humid forests and providing alternative sources of fruit (e.g. *Syzygium* spp.) may contribute to limiting the damage that *Rousettus madagascariensis* causes to commercially important crops.

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