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Fruit-feeding behaviour and use of olfactory cues by the fruit bat *Rousettus leschenaulti*: an experimental study

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This paper describes the feeding behaviour of *Rousettus leschenaulti* Desmarest, 1820 on lychees, the preferred cultivated food of this bat in captive conditions. We found that feeding comprised 25–30% of the total activity of these animals in a flight cage and that feeding durations were not significantly different between two sexes. To evaluate the role of odor and vision in foraging behaviour, we provided animals with artificial lychees, real lychees and artificial lychees soaked in the juice of real lychees and we recorded the number of feeding approaches to the different "fruit" types. The results indicated that bats approached real fruit significantly more than artificial fruit, and that the number of approaches to the soaked artificial fruit was also significantly higher than to the unsoaked artificial fruit. There were no significant differences between sexes in approach rates to any "fruit" type. We discuss the role of different sensory cues in the foraging behaviour of these bats and emphasize that the olfactory cue is important in detecting food resources and discriminating between different kinds of food items.

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Introduction

Rapid discrimination between fruits of different kinds should be highly beneficial for bats because of reduced search time and increased quality and quantity of food intake per time unit (Kalko and Condon 1998). Correct detection and location of fruit is one of the most important aspects of the foraging ecology of frugivores (Luft *et al*. 2003). Fruit bats in the neotropics and paleotropics feed mostly on fruits and nectar (Fleming 1993, Tan *et al*. 1998). These large bats share a long evolutionary history with many of their food plants and they are important seed dispersers and pollinators (Fleming 1979, Marshall 1983). The fruits of many tropical plant species thus share morphological features that

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make use of the sensory capabilities of bats, a phenomenon known as the "bat syndrome" (van der Pijl 1957). The mechanisms used by fruit bats to detect and locate fruit resources vary between neo- and paleotropical fruit bats. Neotropical fruit bats rely mainly on echolocation and, to a lesser degree, on vision and olfaction to detect and locate fruits (Thies *et al*. 1998, Korine and Kalko 2005), whereas most paleotropical fruit bats, represented by the family Pteropodidae, lack the ability to echolocate (except members of the genus *Rousettus*) and rely primarily on olfaction and vision to detect food (Luft *et al*. 2003). The fruits of plants visited by bats are strongly scented when ripe (van der Pijl 1957), suggesting that scent is important for attracting bats and can guide them to a food source (Vogel 1958, Rieger and Jakob 1988, Acharya *et al*. 1998, Thies *et al*. 1998, Von Helversen *et al*. 2000).

The importance of odor in foraging activities in other bat groups, such as the Phyllostomids, has been clearly demonstrated (van der Pijl 1957, Bhatnagar and Kallen 1975, Laska 1990, Rieger and Jakob 1988, Thies *et al*. 1998). Direct evidence of the importance of olfaction in paleotropical fruit bats is more limited (Möhres and Kulzer 1956, Kulzer 1958, Oldfield *et al*. 1993, Acharya *et al*. 1998, Luft *et al*. 2003, Elangovan *et al*. 2006, Stoddart 1980).

Rousettus leschenaulti Desmarest, 1820 occurs throughout southern China and most of southeastern Asia, and is common in Xishuangbanna. It lives in caves, deserted buildings, temples and unused tunnels (Chandrashekaran and Marimuthu 1994). Its body mass is 98.6 g (n = 121) and its wingspan is 46 cm (n = 122). This species produces echolocation calls consisting of impulsive clicks, which are short in duration and have a wide bandwidth (Pye and Pye 1988). Bats of this species feed on both wild and cultivated fruit including guava, longan, lychee, bananas and papaya (Tang *et al*. 2005). Lychees are planted widely in Xishuangbanna. The fruits appear to demonstrate "bat syndrome" by attracting bats through the use of a wine-red colour, strong odor when ripening, and an open presentation permitting detection and easy access to bats in flight. *R. leschenaulti* feeds heavily on lychee when the fruits are ripe. However, little is known about its foraging behaviour and the respective roles of olfaction and other sensory cues used when feeding on lychees.

The aim of this study was to investigate the feeding behaviour of *Rousettus leschenaulti* toward lychee under captive conditions, which included measuring the frequency of visits to ripe fruits, the duration of feeding and resting periods, and the manner of fruit manipulation. In addition, we investigated the relative role of olfactory and visual cues in the feeding behaviour and determined if bats uses primarily olfactory cues in detecting fruits represented by baited nylon string sets. Through greater understanding of the feeding behaviour and sensory cues used by the bats, new mechanisms for non-destructive crop protection may be developed.

Material and methods

This study took place between 10 May and 20 June 2005. Bats were trapped using mist-nets in their natural habitats in the valley rainforest of Xishuangbanna Tropical Botanical Garden (XTBG), Yunnan Province, China (21°56'N, 101°15'E), and in the lychee garden of XTBG Ecological Station. Captured bats were housed in ventilated cages made of wire (0.9 m long × 0.6 m wide × 0.6 m in height). Before the experiments were carried out, bats were housed in the cages for two days and provided with food (pieces of apple or banana) and water. We used a total of 62 non-reproductive individuals; no bat was used more than once in this study in order to minimize the effects of learning. Bats were released at the point of capture once the trials were completed. Experiments were carried out in a large flight cage (15 m long × 10 m wide × 3.5 m in height) made of wire, with a glass roof to prevent rain enetering. The cage was open to the outside air and ambient light, with perches provided on the ceiling. The flight cage was in the open. During our study period, the temperature in the cage averaged 26°C, and relative humidity was approximately 85%. Bats could not hear, see or smell each other while being tested. Echolocation calls of bats were not monitored during the trials.

Observation of foraging behaviour

We observed the feeding behaviour of *Rousettus leschenaulti* on lychees in the flight cage to obtain base-line data on forage behaviour. Three strings, each baited with 10 lychees, were fixed horizontally on poles in the middle of the flight cage parallel to each other, approximately 1 m apart and 1.9 m above the ground. We observed the bats inside the cage using moonlight or faint light aided by infrared night vision equipment (Eagles eyes-316B, SOVIC Ltd. China). We recorded the timing and frequency of visits to the fruit using a stopwatch. A visit was defined as the flight of a bat to a fruit in which the whole fruit or a portion of the fruit pulp was removed. We calculated the duration of feeding and resting periods and the duration of handling time of fruit. The duration of feeding and/or resting periods was determined based on the criteria used by Bonaccorso and Gush (1987) in which a feeding period consisted of a series of visits to fruits with the time elapsed between visits being < 10 min. An interval of > 10 min between visits was considered a resting period. We observed 12 female and 10 male bats in all, with each individual being observed for 180–300 min according to the activity period of bats. For each trial, the observations began at 19:00 (30 min before sunset).

Bat behaviour trials

In order to test whether the bats use olfactory cues in detecting and locating fruits, we exposed the bats to two experiments in which we supplied the bats with real and artificial lychees (experiment 1) and with artificial lychees soaked to saturation with juices of lychee and with artificial lychees without juices (experiment 2).

Experiment 1

Six strings, divided into two sets of three, were set in the experimental flight cage. The sets were 3 m apart from each other and the strings within each set were 1 m apart. Each string of the first set was equally baited with 10 lychees, and each string of the second set was equally baited with 10 artificial fruits. Artificial fruits were made of floriculture foam and were similar in shape and color to real fruits but did not appear to smell of fruit (based on subjective tests by the researchers). Thirty real fruits and 30 artificial fruits were presented to each individual bat, partly consumed strings were replaced for each subsequent test individual. We recorded the number of approaches to the real and artificial fruits. An approach was defined as the flight of a bat to a string in which the distance between the bat and the string was < 20 cm. Twenty individuals (10 females and 10 males) were used in this experiment, and each individual was observed for 90 min. The location of the strings was changed once during each observation period to avoid the effect of learning by a bat over the course of their test. We ventilated the flight cage for 0.5 h between tests of individuals to remove potential olfactory clues.

Experiment 2

In this experiment we used the same design as described above but substituted artificial fruits soaked to saturation with the juices of lychee for real fruits. The strings were not soaked with juice. We observed and recorded the behaviour of bats approaching both sets and recorded the number of approaches to each. Twenty bats (10 females and 10 males) were observed for 60 min/bat.

Statistics

We calculated approach rate as numbers of approach to food per hour. One-sample Kolmogorov-Smirnov tests were used to determine whether data were normally distributed and Levene's tests were used to confirm homogeneity of variances (Sokal and Rohlf 1995). Two independent-sample Kolmogorov-Smirnov tests were used to determine whether there were statistical differences in the duration of feeding and resting periods between the sexes. We used *t*-tests to determine if differences existed in the number of approaches to real fruits and artificial fruits, and to soaked and unsoaked artificial fruits. Differences were considered significant if the *p*-value was 0.05 or lower. Where mean values are given in the text, they are shown ± standard deviation (SD).

Results

Bat activity

Rousettus leschenaulti began to forage approximately 30 min after sunset (about 19:20) each night, and their feeding behaviour consisted of short feeding periods interspersed with longer resting periods (Table 1). Bats typically made circling flights around the cage before hovering (flapping its wings at a very high frequency) in front of the fruit and selecting it for consumption. A fruit was often selected or rejected after "nosing" the fruit while hovering, which most likely represents an olfactory evaluation by the bat. Bats usually removed the fruit from the string by mouth while hovering. Once picked, a fruit was taken to a favored perch on the ceiling of the cage where it was consumed, and seeds were discarded. Some individuals perched directly on the string beside a fruit, which was consumed while still attached to the string. During feeding, *R. leschenaulti* used their thumbs and one foot for suspension and another foot to manipulate the fruit. Duration of feeding periods was not significantly different between two sexes (K-S test: $z = 1.137$, $p = 0.151$). Feeding behaviour comprised *ca* 25–30% of their total time of feeding and resting (Table 1).

Resting bouts of 10–21 min duration followed feeding bouts. During rest periods, bats groomed themselves and slept. Duration of resting bouts was not significantly different between the sexes (K-S test: $z = 0.900$, $p = 0.393$). Each bat ate ap-

Table 1. Duration of feeding and resting periods (min) and proportion of time spent feeding in *R. leschenaulti* while feeding on lychee. Values are presented as mean ± SD.

Individual	*n*	Feeding period	Resting period	Time feeding (%)
Female	12	5.7 ± 2.3	15.7 ± 2.9	24.3 ± 9.6
Male	10	5.6 ± 2.2	16.1 ± 3.3	25.6 ± 8.6
K-S test		0.151	0.393	

Table 2. Average number of approaches by bats to different "fruit type", SD is included in parentheses.

	Period of observation (min/bat)	Fruit type	Number of approaches	Approach rate (number of approaches/h)	t-value	p
Experiment 1	90	Fruit	67.4 (14.2)	44.9 (9.4)	13.791	< 0.001
		Artificial Fruit	14.9 (9.4)	9.9 (6.3)		
Experiment 2	60	Soaked artificial fruit	23.5 (8.5)	23.5 (8.5)	11.170	< 0.001
		Unsoaked artificial fruit	2.0 (1.4)	2.0 (1.4)		

proximately 8 fruits (average 7.3 ± 1.3 for female and 7.5 ± 0.9 for male) during our observations.

Sensory cues used in foraging

Experiment 1

In this experiment, bats could only use olfaction cues to find edible fruits because the sight cues of the real and artificial fruits were the same. We found that individual bats, both female and male, typically made several circling flights around the real and artificial fruit sets, before they approached the strings. The number of approaches of females and males to real fruits were 71.3 ± 4.7 and 63.4 ± 4.1, respectively. The number of approaches of females and males to artificial fruits were 18.5 ± 3.2 and 11.2 ± 2.4, respectively. There was no significant difference between the sexes in the number of approaches to real and artificial fruits (t-test: t = 1.266, p = 0.222; t = 1.835, p = 0.083). Because the number of approaches did not differ between sexes, these data have been pooled for subsequent tests. Bats approached real fruits significantly more frequently than artificial fruit (t = 13.791, p < 0.001, Table 2).

Our observations showed that bats spent more time in association with the real fruit (3–5 s) compared with the artificial fruit (1 s). Bats often hovered in front of the real fruit during their approach. Additionally, bats classified as approaching the artificial fruit were often simply flying past it at a distance of less than 50 cm, a behaviour very different from bats approaching the fruit and hovering.

Experiment 2

The numbers of approaches of females and males to the soaked artificial fruit were 24.2 ± 2.5 and 22.7 ± 2.9 respectively, and the numbers of approaches to the unsoaked artificial fruit were 1.8 ± 0.3 and 2.1 ± 0.6 for females and males respectively. There was no significant difference in the number of approaches to the soaked artificial fruit and to the unsoaked artificial fruit between two sexes (t = 0.386, p = 0.704; t = –0.471, p = 0.643). We pooled the data of sexes and found that the number of approaches to the soaked artificial fruit was significantly higher than to the unsoaked artificial fruit (t = 11.170, p < 0.001, Table 2). When bats flew over the soaked artificial fruit set they hovered (3–10 times) prior to approaching it. Bats nosed the artificial fruit when approaching them, then left without attempting to pick them out. This behaviour was not observed near the unsoaked artificial fruit; bats flew swiftly past without hovering. It was interesting that approach rates to the same cue (unsoaked artificial fruit) were significantly higher in experiment 1 than in experiment 2 (t = 5.52, p < 0.001).

Discussion

Our study shows that the fruit bat *Rousettus leschenaulti* is active under captive conditions. Individuals begin foraging about 30 minutes after sunset. This behaviour is similar to that of the fruit bat *R. aegyptiacus*, which is also known to begin feeding shortly after sunset in captivity (Van-der-Westhuyzen 1976). During feeding, *R. leschenaulti* used their thumbs and one foot for suspension and another foot to help manipulate the fruit. This behaviour is different from that displayed by phyllostomid bats, which use both feet to suspend themselves and invariably manipulated their food with the wrists and thumbs of both wings (Vandoros and Dumont 2004).

We observed that *Rousettus leschenaulti* usually ingested only the liquid fraction of fruit and rejected the fibrous portion as an oral pellet. This feeding method has been observed in other species of Pteropodidae and Neotropical bats (Courts 1998, Handley *et al*. 1991). We also observed the bats resting (a behavioural category that includes grooming and sleeping) after consuming fruit, and the resting period lasted about 20 minutes. This behaviour was similar to *Carollia perspicillata* and *C. suburfa* (Phyllostomidae) (Bonaccorso and Gush 1987). Howell (1979) reported that the foraging pattern of *Leptonycteris curasoae* at *Agave palmeri* flowers included feeding and resting periods of 20 min each. The resting periods of these neotropical bats was similar to *R. leschenaulti*.

The present study also shows that olfaction plays an important role in the foraging behaviour of *Rousettus leschenaulti*. The results of experiment 1 indicated that *R. leschenaulti* relied heavily on the odor of food during foraging activity. Bats approached real fruits significantly more frequently than artificial fruit, even though there was no difference in the visual cues offered by the two fruit types. In experiment 2, we concluded that odors could guide bats to a food resource when visual cues were similar. The bats exhibited olfactory discrimination between odourless (ie no smell of lychee) and odoured artificial fruit in that they predominantly approached the odoured artificial fruit. This result is congruent with earlier reports on other species of fruit-eating bats. *R. aegyptiacus* can distinguish between empty boxes and boxes containing bananas (Möhres and Kulzer 1956) while Oldfield *et al*. (1993) found that *Pteropus poliocephalus* exhibits olfactory discrimination between fruit-derived odors and control odors at a decision distance of 125 mm. Luft *et al*. (2003) found that species of Pteropodidae not only detected fruit by odour, but can also distinguish whether the fruit is ripe. Additionally, preference tests conducted in the laboratory and in the field showed that bats are able to distinguish different stages of ripeness of a fruit (Laska 1990, Fleming *et al*. 1977). Odor is more important than form and texture for food location and choice in *Carollia* spp. (Thies *et al*. 1998).

Although vision may also play a role in detection, and probably localization, of the all types of fruits, our experiments revealed that visual cues are not as important as olfactory cues especially in locating the fruit and distinguishing real fruits from artificial fruits, or artificial fruits with or without juice. Moreover, it should be noted that *Rousettus leschenaulti* echolacates using a tongue click (Pye and Pye 1988). It has been assumed that *Rousettus* uses its visual sense when flying and searching for food, and echolocation system is reserved for orientation within dark cave roosting sites (Henson and Schnitzler 1980, Herbert 1985). However, Waters and Vollraih (2003) found that *Rousettus aegyptiacus* echolocates in both the dark and the light to avoid obstacle and that it can detect wires 1.3 mm in diameter. In our experiments, *R. leschenaulti* approached both the artificial fruit with and without juice indicating that vision or echolocation may be used for detecting potential food sources as suggested in other echolocating fruit bats (Thies *et al*. 1998, Korin and Kalko 2005). Once they were close enough to the objects, olfaction appears to plays an important role in discriminating the real from artificial fruits.

Higher approach rates to real fruits (45.0/h) in experiment 1 than to artificial soaked fruits (23.5/h) in experiment 2 indicated that visual cues or possibly echolocation were combined in detecting the food resources. That approach rates to the same cue (unsoaked artificial fruit) were significantly higher in experiment 1 than in experiment 2 may be due to the fact that bats combined vision, olfaction and echolocation to detect food resources. In experiment 1, unsoaked artificial fruits were present synchronously with real fruits. This might have resulted in a higher approach rate than to the same unsoaked artificial fruit in experiment 2, because the olfactory cues from real fruits can be detected well; positive activity around real fruits may have resulted in an increase in approach rates to artificial fruit sets.

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