Behavioural Processes 189 (2021) 104426

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Multimodal cues facilitate ripe-fruit localization and extraction in free-ranging pteropodid bats

Valliyappan Mahandran [a], Chinnaperamanoor Madhappan Murugan [b], Wang Gang [a], Chen Jin [a], Parthasarathy Thiruchenthil Nathan [b,*]

[a] *CAS-Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan, 666303, China*
[b] *Department of Zoology, School of Life Sciences, Periyar University, Salem, Tamil Nadu, 636011, India*

ARTICLE INFO

Keywords:
Bat fruits
Free-ranging bats
Haptic cues
Olfactory cues
Visual cues

ABSTRACT

Sensory cues play an important role in any plant–animal interaction. Yet, we know very little about the cues used by wild mammals during fruit selection. Existing evidence mainly comes from captive studies and suggests that the pteropodid bats rely on olfaction to find fruits. In this study, we avoided captivity-generated stressors and provide insights from natural selective forces by performing manipulative experiments on free-ranging fruit bats (*Cynopterus sphinx*) in a wild setting, in a tree species that exhibits a bat-fruit syndrome (*Madhuca longifolia* var. *latifolia*). We find that visual cues are necessary and sufficient to locate ripe fruits. Fruit experiments exhibiting visual cues alone received more bat visits than those exhibiting other combinations of visual and olfactory cues. Ripe fruit extractions were higher by bats that evaluated fruits by perching than hovering, indicating an additional cue, i.e., haptic cue. Visual cues appear to be informative over short distances, whereas olfactory and haptic cues facilitate the fruit evaluation for those bats that used hovering and perching strategies, respectively. This study also shows that adult bats were more skillful in extracting ripe fruits than the young bats, and there was a positive correlation between the weight of selected fruits and bat weight. This study suggests that the integration of multimodal cues (visual, olfactory and haptic) facilitate ripe-fruit localization and extraction in free-ranging pteropodid bats.

1. Introduction

Frugivory among bats has evolved independently in Asia/Africa and the Americas within the families Pteropodidae and Phyllostomidae, respectively (Fleming, 1986, 1993; Simmons et al., 2008; Hodgkison et al., 2013). Although the evolutionary histories of these two families differ, previous studies suggest that their foraging behaviour relies on olfactory cues for locating ripe fruits (pteropodid bats: Acharya et al., 1998; Raghuram et al., 2009; Zhang et al., 2014; phyllostomid bats: Rieger and Jakob, 1988; Kalko et al., 1996; Korine and Kalko, 2005). As most of the studies were conducted in captive conditions, the potential for stress-based biases in the behaviour of animals is significant (Fischer and Romero, 2019). The study of wild bats will help to interpret previous patterns and will provide new insights. Here, we ask the fundamental question about the behavioural ecology of bats, i.e., what are the prominent cues used by free-ranging fruit bats for finding fruits in the wild?

The recent phylogenetic studies divide the order Chiroptera into Yinpterochiroptera and Yangochiroptera. The pteropodid bats in Asia/Africa belong to the former and are morphologically distinctly different to the latter, i.e., the phyllostomid bats in the Americas (Teeling et al., 2005). Pteropodid bats often have a larger body size, bigger eyes but smaller ears without tragus, whereas phyllostomid has smaller body size, smaller eyes but larger ears with tragus (Bates and Harrison, 1997; Simmons et al., 2008). These morphological differences suggest the two bat types may rely on different sensory cues for finding their food resources; however, empirical studies testing this hypothesis are lacking. Nonetheless, there is evidence that fruit bats use odour cues for finding food sources in passive mode (Denzinger and Schnitzler, 2013; Gonzalez-Terrazas et al., 2016; Simões et al., 2019; Danilovich and Yovel, 2019). As identified in a previous study, bats not only approached the ripe fruits with the typical odour but also fruit models without odour when they were offered at the correct position (Kalko and Condon, 1998). Among the sensory modalities, olfaction has the function of

---

* Corresponding author.
E-mail address: nathan_pt@periyaruniversity.ac.in (P.T. Nathan).

https://doi.org/10.1016/j.beproc.2021.104426
Received 3 November 2020; Received in revised form 20 May 2021; Accepted 21 May 2021

long-distance information transfer (Hodgkison et al., 2007; Fleming et al., 2009; Valenta et al., 2017; Nevo et al., 2018), whereas vision has a multitude of functions, namely obstacle avoidance, homing and escape along with fruit detection (Boonman et al., 2013; Eklof et al., 2014); however, direct evidence for the use of visual cues by the fruit bats is limited.

Apart from the visual and olfactory cues, animals also use haptic cues that are informative to foraging mammals (Weber, 1973; Dominy, 2004; Melin et al., 2014; Valentia et al., 2016). In phyllostomid bats, a study showed that the echolocation of bats along with eco-acoustic properties of flowers provide detailed supporting information to bats during the process of finding potential flowers at closer ranges (Gonzalez-Terrazas et al., 2016). Similarly, haptic cues were shown to have a role in water detection for the free-ranging bats (Russo et al., 2012). However, no study has so far looked at the possibility of fruit bats making use of haptic cues to assess the fruit quality/ripeness. Assessing the ripeness of fruits by manual squeezing is usually found in primates with sensitive tactile pads in their fingertips (Dominy et al., 2016; Melin et al., 2019).

Studies on fruit characteristics suggest the existence of fruit syndromes, co-varying character complexes that have evolved in response to selection to favour feeding by particular groups of potential dispersers such as birds, fruit bats or primates (van der Pijl, 1957, 1982; Valenta and Nevo, 2020). These dispersal syndromes possibly reflect the ability of dispersers to perceive and process specific sensory information such as vision and/or olfaction (Willson and Whelan, 1990). Among the animal-mediated dispersal systems, so far about 549 species (in 191 genera of 62 families) are posited to have the bat-fruit syndrome (Geiselman et al., 2002; Lobova et al., 2009; Bat Conservation International, 2020). The bat-fruit syndrome includes characters such as drab greenish or whitish fruit colour, night-ripening fruit with dangling fruit display (Kalko and Condon, 1998). Some bat-dispersed vines in the Americas have relatively odourless fruits (e.g., family: Cucurbitaceae), and in this case, bats likely use different senses other than odour cues to find particular kinds of fruit. Those vines that produce odourless fruits have the adaptation of dangling at distance from leaves, hence this could make the fruits more conspicuous to the bats (Condon and Gilbert, 1988). Similarly, the fruits of *Solanum granuloso-leprosum* turn green-yellowish colour when ripe and produce fruits with faint odour, and are dispersed by bats (Jacomassa and Pizo, 2010).

Fruit size is another trait that provides a selective constraint for filtering different dispersers. Large fruit size limits ingestion by relatively small-sized seed dispersers, and the size of the ingested fruits, therefore, tend to be positively correlated with body size and/or gape size of frugivores (Jordano, 2000; Lord, 2004; Onstein et al., 2017). This is particularly true in the case of phyllostomid bats (Kalko et al., 1996), whereas the co-evolution and co-adaptation of bats and plants are considered to be much stronger than the Asian/African counterparts (Fleming, 1986). Fruit size, therefore, is not an issue for pteropodid bats although empirical studies testing this hypothesis is lacking.

Our aim in this study is to address the following questions by conducting field observations and experiments on the free-ranging fruits bats in the wild: (1) Among the visual, olfactory and haptic cues, which matters to the pteropodid bats while foraging in their natural habitat? (2) Are there any differences between the age groups (i.e., adult vs. young bats) in the effectiveness of ripe fruit removal? (3) Is there any relationship between the fruit size and the body size of bats? Based on the above questions, we tested the following predictions: (a) considering the morphological adaptions (large eyes), visual cues would be used by pteropodid bats, (b) adult bats would be more efficient in extracting ripe fruits, (c) there would be a positive relationship between the fruit weight and the body weight.

2. Material and methods

2.1. Study species

In this study, a ubiquitous free-ranging fruit bat species (*Cynopterus sphinx:* Pteropodidae) and a plant species that bear fruits exhibiting bat-fruit syndrome (*Madhuca longifolia* var. *latifolia:* Sapotaceae) were chosen to study how fruit bats locate, evaluate and extract fruits in a complex naturalistic environment.

2.1.1. Greater short-nosed fruit bats

The short-nosed fruit bats (*C. sphinx*) are non-echolocating medium-sized fruit bats, widely distributed across the Indo-Malayan biogeographic region constituting South Asia, Southeast Asia and Southern China including Taiwan (Neuweiler et al., 1984; Storz and Kunz, 1999). These bats are well adapted at roosting both in forest patches and also in the urban habitats where there are a lot of avenue trees such as *Polyalthia longifolia*, *Caryota urens* and also in curtain creeper plant *Vernonia scandens.* Adult bats weigh about 56.03 ± 5.01 g (forearm length, FL: 68.98 ± 4.18 mm; n = 31), and the young weigh about 34.66 ± 6.02 g (FL: 52.16 ± 2.72 mm; n = 36), respectively. The physical difference in body sizes enabled us to visually differentiate the adult and young bats while they perch on and/or hover near the fruits.

2.1.2. Butter tree (Mahua)

Fruits of butter tree exhibit a typical bat-fruit syndrome, i.e., the fruits are drab green in colour when ripe that matched the colour of the leaves, with no clear chromatic contrast to human vision. Fruits grow in bunches of about three to seven and have exposed positioning. Ripe fruits tend to be bigger in size, softer (without latex content) and weighed about 27.50 ± 1.92 g (length: 30.21 ± 2.82 mm; width: 19.13 ± 2.11 mm; stalk length: 68.10 ± 4.50 mm; n = 30), whereas the semi-ripe fruits comparatively smaller, harder (with latex content) and weighed 22.20 ± 2.32 g (length: 18.25 ± 1.02 mm; width: 16.03 ± 0.91 mm; stalk length: 43.25 ± 2.20 mm; n = 30) with one to two seeds (mostly two seeds) embedded within a pulpy mesocarp. These trees are completely dependent on fruit bats for both pollination and seed dispersal (Nathan et al., 2009; Mahandran et al., 2018).

2.2. Study site

This study was conducted in the suburban outskirts of Salem city, south India (11°43’ N, 78°04’ E; 287-m. asl) in 2019 and 2020 during two fruiting seasons (July–August) of *M. longifolia* var. *latifolia*. This region experienced dry weather from March to mid-May, followed by the southwest monsoon from June to July. The mean annual temperature was about 31.2 °C (range: 24.1–35.2 °C). About 70 % of annual precipitation (i.e., 690–825 mm/year) occurred during the rainy season. The study was carried out on three different trees (n = 5 nights per tree), that were located at least 1.5-km from each other, to facilitate the experiments with a different group of animals in the natural conditions. Each night, we dedicated the first three hours (19:00–22:00 h) for manipulative experiments and the next seven hours (23:00–05:00 h) for behavioural observations. This study had a total of 150 h of observations.

2.3. Cue tests (Behavioural assay)

The study was conducted in the natural population of short-nosed fruit bats (*Cynopterus sphinx*), in their natural habitat, to check which cues they used to locate and extract fruits. Following experimental conditions were facilitated enabling and/or disabling different cues. From a tree, eight ripe fruits were chosen from the lowermost fruit-bearing branch with a minimum distance between two adjacent fruits to be *c.* 30-cm. The ripeness was judged by the palpable softening of fruits in daylight conditions before bagging them (around 17:30 h) with four categories of zip-lock bags, namely (i) transparent bags with pores (both visual and olfactory cues present), (ii) transparent bags without pores (only visual cue present), (iii) opaque bags with pores (only olfactory cue present) and (iv) opaque bags without pores (neither visual nor olfactory cues present). By limiting the observation only to the lower branches, the number of visits each experimental fruit types received from the bats were quantified. Furthermore, the lower branches received visitations only from *C. sphinx* (and not from the larger bats *Pteropus giganteus* as they preferred foraging in the upper canopy layers).

2.4. *Observations on fruit localization and extraction*

In the present study site, the fruit maturation and ripening period coincided with the last quarter and new moon phases (i.e., with lesser light illumination period, 0–24 % visibility). The foraging activity of the bats started approximately 35–40 min after the sunset (*c.*18:32 h). The peak of the foraging activity occurred between 19:00 h and 22:00 h, and most of the ripe fruits available for that particular night were taken up during this period. Therefore, the manipulative experiments were limited to the peak foraging hours i.e., 19:00–22:00 h ($n = 15$ nights). Thereafter, all the experimental bags were removed and the focal observations on fruit removal strategies were carried out by limiting the observations to the proximate fruit-bearing branches located at the best visual position. Observations were conducted without obstructing the bat foraging using a professional red-filtered headlamp with diffused light (Tikka Plus 2; Petzl). Light intensity in the foraging ground was measured with a digital lux-meter with a detachable light sensor (Tondaj® LX1010B).

After the manipulative experiments, we made observations on fruit extraction strategies (i.e., hovering and perching). “Hovering” referred to the “stationary flight at zero net forward speed” (Hakansson et al., 2015) made by bats near a fruiting branch, whereas “perching” referred to the “act of landing on a fruit-bearing branch to remove a fruit of its choice”. Also, we recorded the type of fruits being removed by the bats, i.e., ripe (big-sized softer fruits without latex content) and semi-ripe (medium-sized harder fruits with latex content). The difference in the duration for the fruit removal by the two strategies (viz. hovering and perching) was recorded using a handheld stopwatch (HS-3V-1BRDT; Casio, India). Simultaneously, observations were made to identify the differences in the fruit extraction strategies by the two age groups (i.e., adult vs. young bats). Besides, we carried out mist-netting (2.6 × 6 m, Avinet, USA) sampling sessions at least one time in each site ($n = 3$ sites). Mist-nettings were carried out at irregular intervals in the vicinity of feeding roosts to maximize the chance of capturing bats while they returned with fruits. This was performed to check if the focal observation data, on fruit extraction based on age-group classification, conformed to the bats captured with fruits while they returned to the feeding roosts. This study was carried out following the Guidelines for the Use of Animals in Research (1991) and ethical clearance for the mist-netting and animal captures were obtained from the Animal Care and Use Committee of the Periyar University, Salem, India.

2.5. *Statistical analyses*

First, we tested the data for normality using Shapiro−Wilk test. For the data not normally distributed, we used non-parametric Kruskal–Wallis one-way ANOVA with Bonferroni’s multiple comparison corrections (Zar, 2007). Multiple comparison tests were performed to compare the behavioural response of free-ranging bats to cue tests with four conditions: (i) only visual cue present, (ii) both visual and olfactory cues present, (iii) only olfactory cue present and (iv) neither visual cue nor olfactory cue present. Similarly, the differences in the foraging strategies, i.e., perching vs. hovering and age-based (adult vs. young bats) differences in the fruit removal effectiveness were compared using multiple comparison tests. A Pearson’s correlation test was performed to check if there was any association between the bat size (body weight) and the fruit weight. All the statistical analyses were performed using the Origin Pro ver.2020b (OriginLab Corporation, Northampton, MA 01060, USA).

3. Results

3.1. *Bat foraging*

The average light intensity during the full moon nights with a clear sky was about 0.50–1 lx; however, in the last quarter, during the new moon, the nightlight intensity declined to <0.010 lx, and the fruit-ripening periods coincided with the dark moon phases (Fig. S1). In addition to the experimental species (*C. sphinx*), the Indian flying foxes (*Pteropus giganteus*) were also observed foraging on the same tree, but in the upper canopy layers. This vertical stratification enabled the smooth performance of the experiments, especially bagging of the fruits in the lower canopy, where smaller bats foraged (Fig. 1). The visitor bats included both male and females of all age groups including pregnant and lactating females, and none of them (*C. sphinx*) exhibited in-situ foraging. After extracting the fruits, these bats carried fruits to the feeding roosts (night roosts) for consumption, and consequently, facilitated seed dispersal.

3.2. *Role of visual and olfactory cues in fruit localization*

The behavioural experiments (cue tests) demonstrated that free-ranging bats primarily rely on visual cues to locate and extract ripe fruits (Fig. 2). There was a significant difference in the bat’s approach towards those bagged fruits with and without visual cues (i.e., transparent and opaque bags) (Kruskal-Wallis one-way ANOVA: $F_{3,\,56} = 304$, $p < 0.001$). Fruits that were bagged with “only visual cue present” (46 %, $n = 508$) and “both visual cue and olfactory cue present” (44 %, $n = 495$) received equally high visit rates. Comparatively, fruits that were bagged with “opaque” bags (with pores; only olfactory cue present) received very few visitations (8 %, $n = 88$), and those with neither of the cues, received only negligible visitations (2 %, $n = 23$).

3.3. *Role of haptic cues in fruit evaluation*

While extracting fruits, these bats exhibited two strategies, perching and hovering. Bats were observed to be quite successful in locating and extracting the bigger ripe fruits over medium-sized unripe fruits, provided they perched on the fruits (Fig. S2a), and a significant difference was observed between the two foraging strategies (Kruskal–Wallis one-way ANOVA: $F_{1,\,38} = 13.5$, $p < 0.001$). After perching on a bunch of fruits, bats adjusted their body close to the fruits and grabbed a single fruit using their mouth after spending a few seconds on different fruits in a bunch before making the choice. Mostly ripe fruits were extracted by the perching strategy (71 %). Many times, there were conflicts among conspecifics for the same fruits and this resulted in a quick fruit evaluation and removal of semi-ripe (medium-sized) fruits. At the same time, for the semi-ripe fruits, there was no significant difference between the two extraction strategies. The difference in the duration of fruit extraction by two foraging strategies was more or less equal (non-significant) i.e., *c.* 6–9 s was spent “on” (while perching) and “near” (while hovering) the fruit before extracting (Fig. S2b).

3.4. *Difference in fruit extraction by adult and young bats*

The field observations indicated that adult bats removed a significantly higher number of ripe fruits than the young bats (Fig. S3), and also a significant difference was observed between the adult and young bats on the extraction of ripe and semi-ripe fruits (Kruskal–Wallis ANOVA: $F_{3,\,76} = 29.14$, $p < 0.001$) (Fig. S4). Similarly, the mist-netting captures of bats in the foraging ground confirmed the same, that there was a significant difference between the adult and young bats in the

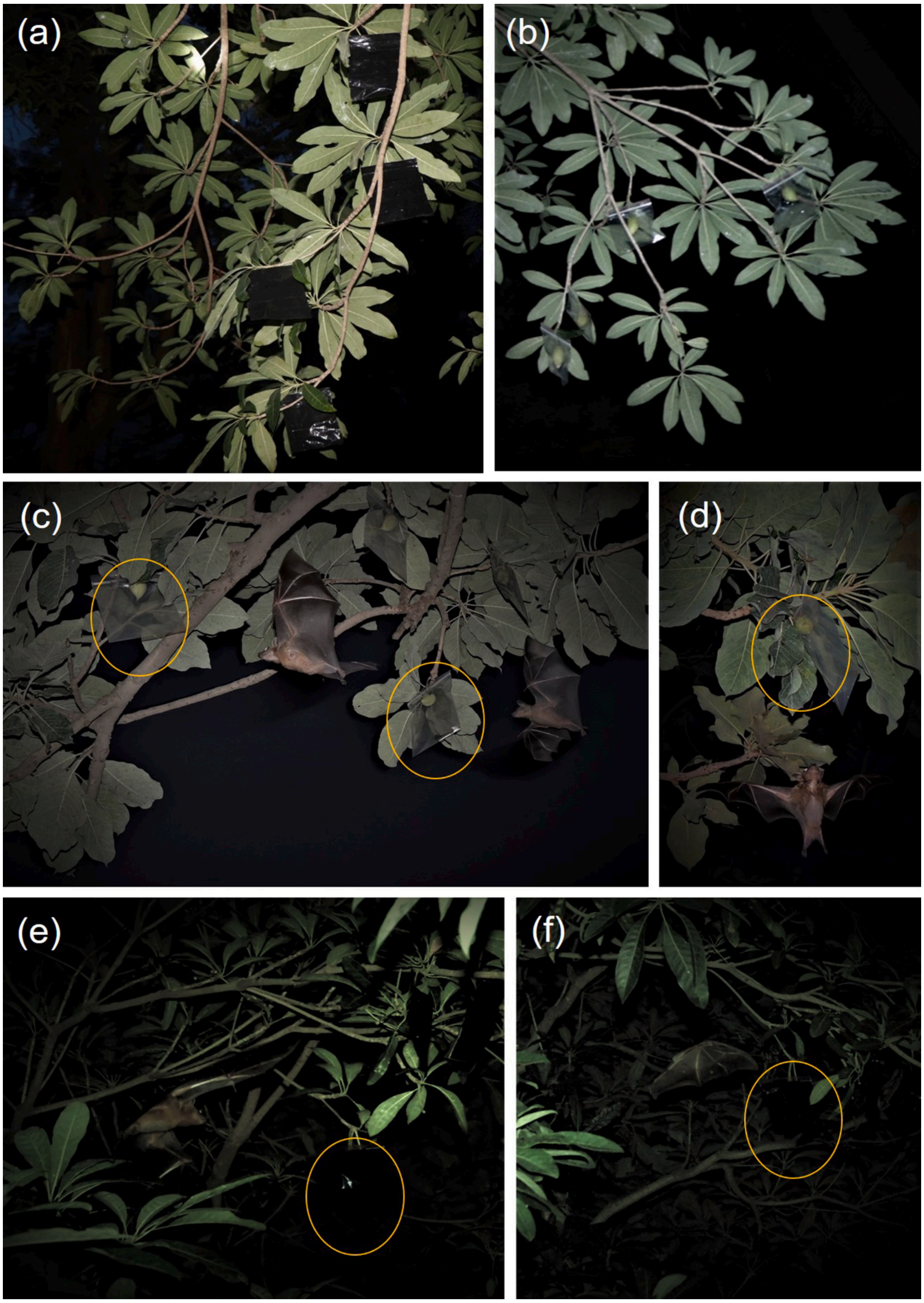

Fig. 1. Experimental set-up in the field site (bags were arranged in such a fashion that two adjacent bags were spaced about *c.* 30-cm apart from each other): (a) opaque bags (with and without pores) and (b) transparent bags (with and without pores). Free-ranging short-nosed fruit bats responding to different experimental conditions: (c) only visual cue present, (d) both visual and olfactory cues present, (e) only olfactory cue present and (f) neither visual nor olfactory cue present.

removal of ripe and semi-ripe fruits (Fig. 3; see also Fig. S5). A significant positive correlation was observed between the bat size (body mass) and the fruit size (Pearson's $r = 0.71$, $p = 0.001$).

4. Discussion

This study demonstrates that free-ranging pteropodid bats integrate multimodal cues in finding ripe fruits in a complex naturalistic environment, in which visual cues were found to be necessary and sufficient for fruit extraction. Pteropodid bats have evolved physical traits that help them roam in the dark more effectively (Neuweiler, 2000). They have evolved bigger eyes and wider pupils that help them collect more light to the reflective layer (tapetum lucidum) located behind retinas containing rod cells, enhancing the visual sensitivity of fruit bats to near-darkness (Olliver et al., 2004).

Earlier captive studies on pteropodid bats have demonstrated the role of olfaction in finding fruits (e.g., *Cynopterus sphinx*: Acharya et al., 1998; Zhang et al., 2014; *Pteropus jagori*, *Pteropus pumilus*: Luft et al.,

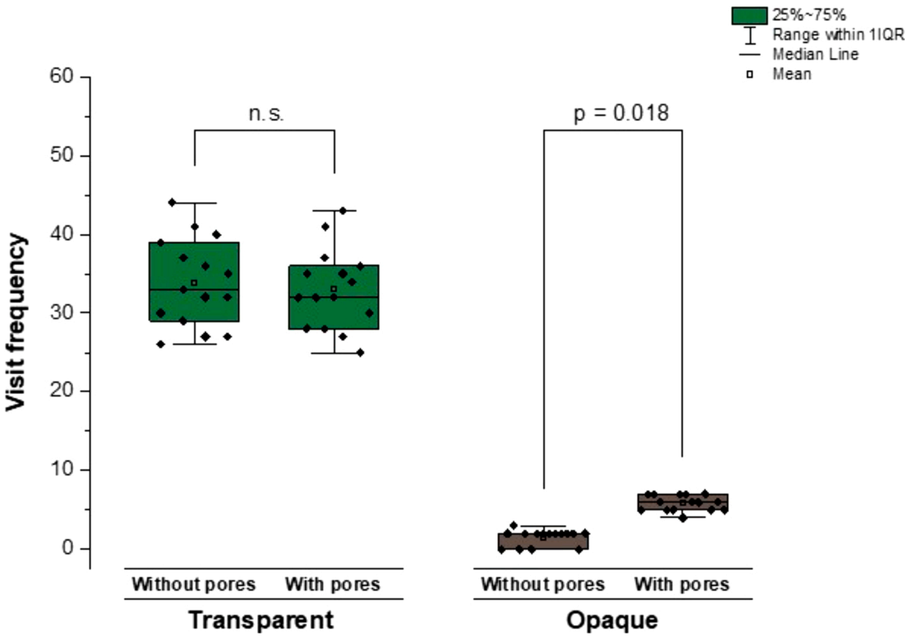

Fig. 2. Response of free-ranging short-nosed fruit bats to different conditions of cue tests, (i) transparent bags without pores (only visual cue present), (ii) transparent bags with pores (both visual cue and olfactory cue present), (iii) opaque bags without pores (neither visual nor olfactory cues present) and (iv) opaque bags with pores (only olfactory cues present).

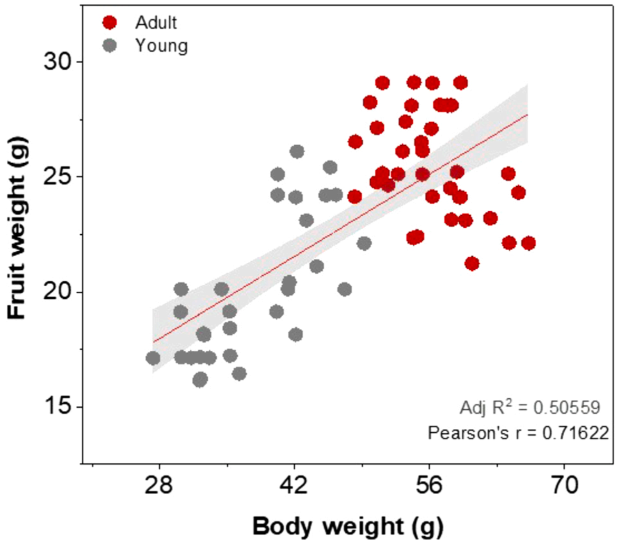

Fig. 3. Mist-net captures of bats with fruits showing the association between the fruit weight (g) and body weight (g) of the fruit bats.

2003; *Rousettus aegyptiacus*; Sánchez et al., 2006*; Rousettus leschenaultii*: Raghuram et al., 2009). Similarly, in this study, bats performed significantly better in the presence of olfactory cues bats as opposed to the total absence of visual and olfactory cues. However, the performance of bats in the presence of visual cues was even better, highlighting its importance. At the same time, olfactory cues were still found to influence behaviour, especially in the absence of visual cues.

Cue-manipulative experiments with transparent and opaque bags with and without pores demonstrated that pteropodid bats could find fruits in the wild with or without olfactory cues provided there were visual cues present. However, bats were not that successful in locating fruits with only the olfactory cue present and/or when neither of the cues (visual and olfactory) present. The reason for the avoidance of the opaque bags could also be because of their odd appearance, and bats could be neophobic. Further, bats that used the hovering strategy evaluated fruit ripeness with the help of visual and olfactory cues, whereas bats that used the perching strategy (mostly adult bats) distinguished ripe from unripe fruits possibly with help of an additional cue (i.e., haptic cue). Haptic cues might also be important, but not in the absence of other cues.

The major strength of this study is that this was performed in a wild setting without any stress to the forging animals. Although the physical needs of the animals are met in captivity, captive conditions can be a source of physiological stress. The potential stressors include abiotic factors such as artificial lighting, exposure to aversive sounds, foreign odours, and uncomfortable temperatures or substrates and confinement-specific stress such as restricted movement, reduced retreat space, forced proximity to humans, reduced feeding opportunities, maintenance in abnormal social groups and other restrictions of behavioural opportunity (Morgan and Tromborg, 2007; Fischer and Romero, 2019). Thereby the response of bats in captivity could be influenced by variables that are not of interest to the study questions. By observing bats in their natural environments, wild experimental set-ups offer opportunities to better understand the actual responses to foraging cues.

The fruits of the genus *Madhuca* (Sapotaceae) have a very faint scent (unlike its flowers with musky scent) and they have the adaptation of well-exposed fruit display, i.e., without obstruction from clutter, helping bats to locate them with visual cues alone. Similarly, vines of the genus *Gurania and Psiguria* (Cucurbitaceae) produce odourless fruits with the adaptation of dangling at distance from leaves (Condon and Gilbert, 1988), and also fruits of the genus *Solanum* exhibit similar bat-fruit syndrome with faint odour (Jacomassa and Pizo, 2010), which makes the fruits more conspicuous to the bats. It has also been shown that vision and echolocation are sufficient for nectar bats to locate exposed flowers, whereas olfaction is only necessary for those flowers in the clutter (Muchhala and Serrano, 2015). As short-nosed fruit bats do not have echolocation capability (Neuweiler et al., 1984), they must rely largely on vision to locate fruits. It has been noted in captive experiments that bats not only approached the ripe fruits with the typical odour but also approached fruit models without odour when they were offered at the correct position (Kalko and Condon, 1998), this strengthens our claims that visual cue is necessary and sufficient for fruit bats to find fruits in the wild.

Our study also highlights the fruit ripening and seed dispersal of these bat fruits coincided with the last quarter and new moon phases with lesser light illumination periods suggesting low-light could be the favourable light condition for pteropodid bat foraging. In the wild/natural conditions, these bats preferred foraging in low-light conditions (Elangovan and Marimuthu, 1999). Many bat species are shown to be lunar phobic and avoid bright moonlight both in the Americas and Asia/Africa (Fleming and Heithaus, 1986; Zeppelini et al., 2019). Likely, the adaptation for finding fruits in low-light conditions could also help them avoid predation from other nocturnal predators.

It is evident from a previous study that the consumption of semi-ripe fruits could be detrimental to bats (Mahandran et al., 2016). This study showed that these bats were quite successful in extracting ripe fruits using the perching strategy. The duration of the fruit extraction by perching and hovering strategies was not significant. Perching likely helps the fruit bats to establish close contact with the fruit and thereby assess the fruit quality by a reliable haptic cue (Valenta et al., 2016). The use of haptic cues by bats was not directly evaluated and this could be a limitation of this study. However, studies across the range of animal kingdom from insects to birds have shown animals using various haptic cues (e.g., in fig-wasp interactions, haptic cues from the surfaces of figs were shown to have a role in enabling physical matching to ensure host specificity among fig wasps (Wang et al., 2013). In hummingbirds, the haptic reflex helps them to adjust their position while feeding nectar from flowers (Goller et al., 2017). Among mammals, bats are shown to use innate recognition of the habitat cues (Greif and Siemers, 2010). Likewise, chimpanzees and capuchin monkeys integrate sensory information to select fruits in the wild (Valenta et al., 2015; Dominy et al., 2016; Melin et al., 2019). This behaviour was most commonly observed in adult bats than in young bats. Use of haptic sensation may require time to learn the foraging and gathering strategies for palatable and safe food sources from their parents (mostly mother bats), conspecifics, or for self-discovery through experimentation (Jones et al., 2013; O'Mara et al., 2014; Ganesh et al., 2016).

This study shows that adults bats were more skillful in evaluating and extracting ripe fruits to a greater extent when compared to the young bats. Data from mist-net captures of bats returning to feeding roosts support the focal observation data. We put forward five possibilities for the selection of semi-ripe fruits by young bats. First, conflicts among conspecifics (i.e., competition between young and adults) could be one of the reasons, because adult bats are larger, and presumably, stronger than younger bats. Second, the difficulty in accessing the ripeness of these fruits by young bats as these fruits could be a "novel" resource as they were available only once a year and for a short duration (*c.* for 14–18 days). Third, the lack of colour contrast (drab green colour) and faint scent could make foraging rather subtle and difficult to distinguish for the young bats. Fourth, the relatively smaller body size of young bats may force them to choose semi-ripe fruits that are comparatively smaller in size, and a positive correlation was observed between the body size of the bats and the choice of fruit size. Finally, the cognitive ability of bats likely improves with age, suggesting why adult bats were more successful in locating and extracting ripe fruits than the young bats. Similarly, an earlier study has shown that among "bat figs", fruit size is correlated with the body size of the bats that prefer them (Kalko et al., 1996).

In short, this study demonstrates that free-ranging pteropodid bats integrate visual and olfactory cues to find ripe fruits in a complex naturalistic environment. Also, the perching strategy plausibly enabled an additional cue (i.e., haptic cue) to evaluate the fruit ripeness by its softness. Fruit hardness is an important physical property that drives fruit selection by mammals (e.g., primates: Valenta et al., 2015; bats: Dumont and O'Neal, 2004). Many animals are known to integrate and/or modify senses to better interact with their environment (e.g., bees: Ostwald et al., 2019; chimpanzees: Dominy et al., 2016; bats: McGowan and Kloepper, 2020). This study shows visual cues are far more important than any other cues for the free-ranging pteropodid bats. A recent study has also shown that bats may actively prefer vision for orientation or object discrimination (Danilovich and Yovel, 2019). Further, olfactory and haptic cues help in the evaluation of fruit quality for bats that extract fruits by hovering and perching strategies, respectively. Most importantly, this is the first study on free-ranging bats that testifies their integration of multimodal cues to facilitate the ripe-fruit localization and extraction in the wild.

Author contribution statements

VM and PTN conceived the project ideas and provided logistics for the experiments; GW and JC conceptualized the methods and further improvised the project ideas; CMM and VM performed the field works; VM performed data analyses and led the writing of the manuscript and all the authors contributed substantially to the draft and gave consent for the publication.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgements

This study belongs to the project "Finding fruits in the darkness: on the cues that matter to the pteropodid bats". The financial supports from the National Natural Science Foundation of China (International Cooperation and Exchange Project No.: 31950410559) and XTBG postdoctoral fellowship to VM, financial support through a major research project (Project No. F.39/641) from University Grants Commission, New Delhi, India to PTN and additional financial support received from the Periyar University, Salem through a University Research Fund (Project No.: PU/AD-3/URF) to CMM are gratefully acknowledged. We extend our thanks to Dr. P. Pushparajasekaran (London, UK) for the language corrections, Dr. Tiziana A Gelmi Candusso (University of Toronto, Canada) and Dr. Manjari Jain (IISER Mohali) for additional valuable inputs. We thank Mr. K. R. Prenesh and Mr. K. R. Renish for field assistance and logistic assistance throughout the course of this study. We are grateful to the two anonymous reviewers for helpful suggestions on the manuscript. Finally, we express our profound gratitude to Dr. Amanda D. Melin for providing final edits to this manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2021.104426.

References

Acharya, K.K., Roy, A., Krishna, A., 1998. Relative role of olfactory cues and certain non-olfactory factors in foraging of fruit-eating bats. Behav. Process. 44, 59–64. https://doi.org/10.1016/s0376-6357(98)00028-x.

Bat Conservation International, 2020. On Fruits, Seeds and Bats. https://www.batcon.org/article/on-fruits-seeds-and-bats/.

Bates, P.J.J., Harrison, D.L., 1997. Bats of the Indian Subcontinent. Harrison Zoological Museum, Sevenoaks, Kent, United Kingdom.

Boonman, A., Bar-On, Y., Cvikel, N., Yovel, Y., 2013. It's not black or white – on the range of vision and echolocation in echolocating bats. Front. Physiol. 4, 248. https://doi.org/10.3389/fphys.2013.00248.

Condon, M.A., Gilbert, L.E., 1988. Sex expression of *Gurania* and *Psiguria* (Cucurbitaceae): neotropical vines that change sex. Am. J. Bot. 75, 875–884. https://doi.org/10.2307/2444007.

Danilovich, S., Yovel, Y., 2019. Integrating vision and echolocation for navigation and perception in bats. Science 5, eaaw6503. https://doi.org/10.1126/sciadv.aaw6503.

Denzinger, A., Schnitzler, H.U., 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Front. Physiol. 3, 164. https://doi.org/10.3389/fphys.2013.00164.

Dominy, N.J., 2004. Fruits, fingers, and fermentation: the sensory cues available to foraging primates. Integr. Comp. Biol. 44, 295–303. https://doi.org/10.1093/icb/44.4.295.

Dominy, N.J., Yeakel, J.D., Bhat, U., Ramsden, L., Wrangham, R.W., Lucas, P.W., 2016. How chimpanzees integrate sensory information to select figs. Interface Focus 6, 20160001. https://doi.org/10.1098/rsfs.2016.0001.

Dumont, E.R., O’Neal, R., 2004. Food hardness and feeding behaviour in Old World fruit bats (Pteropodidae). J. Mammal. 85, 8–14. https://doi.org/10.1644/BOS-107.

Eklof, J., Jurgis, S., Gunars, P., Rydell, J., 2014. Visual acuity and eye size in five European bat species in relation to foraging and migration strategies. Environ. Exp. Biol. 12, 1–6. https://doi.org/10.22364/EEB.

Elangovan, V., Marimuthu, G., 1999. Effect of moonlight on the foraging behaviour of a megachiropteran bat *Cynopterus sphinx*. J. Zool. 253, 347–350. https://doi.org/10.1017/S0952836901000310.

Fischer, C.P., Romero, M.L., 2019. Chronic captivity stress in wild animals is highly species-specific. Conserv. Physiol. 7, coz093 https://doi.org/10.1093/conphys/coz093.

Fleming, T.H., 1986. Opportunism vs. specialization: the evolution of feeding strategies in frugivorous bats. In: Estrada, A., Fleming, T.H. (Eds.), Frugivores and Seed Dispersal. W. Junk Publishers, Dordrecht, Netherlands, pp. 105–118.

Fleming, T.H., 1993. Plant-visiting bats. Am. Sci. 81, 460–467.

Fleming, T.H., Heithaus, E.R., 1986. Seasonal foraging behaviour of the frugivorous bat *Carollia perspicillata*. J. Mammal. 67, 660–671. https://doi.org/10.2307/1381127.

Fleming, T.H., Geiselman, C., Kress, W.J., 2009. The evolution of bat-pollination: a phylogenetic perspective. Ann. Bot. 104, 1017–1043. https://doi.org/10.1093/aob/mcp197.

Ganesh, A., Mukilan, M., Marimuthu, G., Rajan, K.E., 2016. A novel food preference in the greater short-nosed fruit bat, *Cynopterus sphinx*: mother–Pup interaction in a strategy of learning. Acta Chiropterol. 18, 193–198. https://doi.org/10.3161/15081109ACC2016.18.1.009.

Geiselman, C., Mori, S.A., Lobova, T.A., Blanchard, F., 2002. Database of Neotropical Bat/Plant Interactions. https://www.nybg.org/botany/tlobova/mori/batsplants/database/dbase_frameset.htm.

Goller, B., Segre, P.S., Middleton, K.M., Dickinson, M.H., Altshuler, D.L., 2017. Visual sensory signals dominate tactile cues during docked feeding in hummingbirds. Front. Neurosci. 11, 1–16. https://doi.org/10.3389/fnins.2017.00622.

Gonzalez-Terrazas, T.P., Martel, C., Milet-Pinheiro, P., Ayasse, M., Kalko, E.K.V., Tschapka, M., 2016. Finding flowers in the dark: nectar-feeding bats integrate olfaction and echolocation while foraging for nectar. Royal Soc. Open Sci. 3, 160199 https://doi.org/10.1098/rsos.160199.

Greif, S., Siemers, B.M., 2010. Innate recognition of water bodies in echolocating bats. Nat. Commun. 1, 107. https://doi.org/10.1038/ncomms1110.

Guidelines for the Use of Animals in Research, 1991. Anim. Behav. 41, 183–186.

Hakansson, J., Hedenstrom, A., Winter, Y., Johansson, L.C., 2015. The wake of hovering flight in bats. J. R. Soc. Interface 12, 20150357. https://doi.org/10.1098/rsif.2015.0357.

Hodgkison, R., Ayasse, M., Kalko, E.K.V., Häberlein, C., Schulz, S., Mustapha, W.A.W., Zubaid, A., Kunz, T.H., 2007. Chemical ecology of fruit bat foraging behaviour in relation to the fruit odors of two species of paleotropical bat-dispersed figs. J. Chem. Ecol. 33, 2097–2110. https://doi.org/10.1007/s10886-007-9367-1.

Hodgkison, R., Ayasse, M., Häberlein, C., Schulz, S., Zubaid, A., Mustapha, W.A.W., Kunz, T.H., Kalko, E.K.V., 2013. Fruit bats and bat fruits: the evolution of fruit scent in relation to the foraging behaviour of bats in the New and Old World tropics. Funct. Ecol. 27, 1075–1084. https://doi.org/10.1111/1365-2435.12101.

Jacomassa, F.A.F., Pizo, M.A., 2010. Birds and bats diverge in the qualitative and quantitative components of seed dispersal of a pioneer tree. Acta Oecol. 36, 493–496. https://doi.org/10.1016/j.actao.2010.07.001.

Jones, P.L., Ryan, M.J., Flores, V., Page, R.A., 2013. When to approach novel prey cues? Social learning strategies in frog-eating bats. Proc. Roy. Soc. B 280, 2013–2330. https://doi.org/10.1098/rspb.2013.2330.

Jordano, P., 2000. Fruits and frugivory. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. CABI Publishing, Wallingford, UK, pp. 125–165.

Kalko, E.K.V., Condon, M.A., 1998. Echolocation, olfaction and fruit display: how bats find fruits of flagellichorous cucurbits. Funct. Ecol. 12, 364–372. https://doi.org/10.1046/j.1365-2435.1998.00198.x.

Kalko, E.K.V., Herre, E.A., Handley, C.O., 1996. The relation of fig fruit syndromes to fruit eating bats in the New and Old World tropics. J. Biogeogr. 23, 565–576. https://doi.org/10.1111/j.1365-2699.1996.tb00018.x.

Korine, C., Kalko, E.K.V., 2005. Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. Behav. Ecol. Sociobiol. 59, 12–23. https://doi.org/10.1007/s00265-005-0003-1.

Lobova, T.A.C., Geiselman, C.K., Mori, S.A., 2009. Seed Dispersal by Bats in the Neotropics. New York Botanical Garden Press, New York, UK, p. 471.

Lord, J.M., 2004. Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. Austral Ecol. 29, 430–436. https://doi.org/10.1111/j.1442-9993.2004.01382.x.

Luft, S., Curio, E., Tacud, B., 2003. The use of olfaction in the foraging bahaviour of the golden-mantled flying fox, *Pteropus pumilus* and the greater musky fruit bat, *Ptenochirus jagori* (Megachiroptera: Pteropodidae). Naturwissenschaften 90, 84–87. https://doi.org/10.1007/s00114-002-0393-0.

Mahandran, V., Raghuram, H., Nathan, P.T., 2016. Geophagy by the short-nosed fruit bat, *Cynopterus sphinx* (Pteropodidae) while foraging on *Madhuca latifolia* (Sapotaceae) in Tamil Nadu, South India. Acta Ethol. 19, 95–99. https://doi.org/10.1007/s10211-015-0227-7.

Mahandran, V., Murugan, C.M., Marimuthu, G., Nathan, P.T., 2018. Seed dispersal of a tropical deciduous Mahua tree, *Madhuca latifolia* (Sapotaceae) exhibiting bat-fruit syndrome by pteropodid bats. Glob. Ecol. Conserv. 14, e00396 https://doi.org/10.1016/j.gecco.2018.e00396.

McGowan, K.A., Kloepper, L.N., 2020. Different as night and day: wild bats modify echolocation in complex environments when visual cues are present. Anim. Behav. 168, 1–6. https://doi.org/10.1016/j.anbehav.2020.07.025.

Melin, A.D., Young, H.C., Mosdossy, K.N., Fedigan, L.M., 2014. Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. J. Hum. Evol. 71, 77–86. https://doi.org/10.1016/j.jhevol.2014.02.009.

Melin, A.D., Nevo, O., Shirasu, M., Williamson, R.E., Garrett, E.C., Endo, M., Sakurai, K., Matsushita, Y., Touhara, K., Kawamura, S., 2019. Fruit scent and observer colour vision shape food-selection strategies in wild capuchin monkeys. Nat. Commun. 10, 2407. https://doi.org/10.1038/s41467-019-10250-9.

Morgan, K.N., Tromborg, C.T., 2007. Sources of stress in captivity. Appl. Anim. Behav. Sci. 102, 262–302. https://doi.org/10.1016/j.applanim.2006.05.032.

Muchhala, N., Serrano, D., 2015. The complexity of background clutter affects nectar bat use of flower odour and shape cues. PLoS One 10, e0136657. https://doi.org/10.1371/journal.pone.0136657.

Nathan, P.T., Karuppudurai, T., Raghuram, H., Marimuthu, G., 2009. Bat foraging strategies and pollination of *Madhuca latifolia* (Sapotaceae) in Southern India. Acta Chiropterol. 11, 435–441. https://doi.org/10.3161/150811009X485657.

Neuweiler, G., 2000. The Biology of Bats. Oxford University Press, New York, USA.

Neuweiler, G., Singh, S., Sripathi, K., 1984. Audiograms of a South Indian bat community. J. Comp. Physiol. A 154, 133–142. https://doi.org/10.1007/BF00605398.

Nevo, O., Razafimandimby, D., Jeffrey, J.A.J., Schulz, S., Ayasse, M., 2018. Fruit scent as an evolved signal to primate seed dispersal. Sci. Adv. 4, eaat4871 https://doi.org/10.1126/sciadv.aat4871.

O’Mara, M.T., Dechmann, D.K.N., Page, R.A., 2014. Frugivorous bats evaluate the quality of social information when choosing novel foods. Behav. Ecol. 25, 1233–1239. https://doi.org/10.1093/beheco/aru120.

Olliver, F.J., Samuelson, D.A., Brooks, D.E., Lewis, P.A., Kallberg, M.E., Komaromy, A. M., 2004. Comparative morphology of tapetum lucidum (among selected species). Vet. Ophthalmol. 7, 11–22. https://doi.org/10.1111/j.1463-5224.2004.00318.x.

Onstein, R.E., Baker, W.J., Couvreur, T.L.P., Faurby, S., Svenning, J.C., Kissling, W.D., 2017. Frugivory-related traits promote speciation of tropical palms. Nat. Ecol. Evol. 1, 1903–1911. https://doi.org/10.1038/s41559-017-0348-7.

Ostwald, M.M., Shaffer, Z., Pratt, S.C., Fewell, J.H., 2019. Multimodal cues facilitate nest recognition in carpenter bee aggregations. Anim. Behav. 155, 45–51. https://doi.org/10.1016/j.anbehav.2019.06.023.

Raghuram, H., Thangadurai, C., Gopukumar, N., Nathar, K., Sripathi, K., 2009. The role of olfaction and vision in the foraging behaviour of an echolocating megachiropteran fruit bat, *Rousettus leschenaulti* (Pteropodidae). Mamm. Biol. 74, 9–14. https://doi.org/10.1016/j.mambio.2008.02.008.

Rieger, J.M., Jakob, E.M., 1988. The use of olfaction in food location by frugivorous bats. Biotropica 20, 161–164. https://doi.org/10.2307/2388189.

Russo, D., Cistrone, L., Jones, G., 2012. Sensory ecology of water detection by bats: a field experiment. PLoS One 7, e48144. https://doi.org/10.1371/journal.pone.0048144.

Sánchez, F., Korine, C., Steeghs, M., Laarhoven, L.J., Cristescu, S.M., Harren, F.J.M., Dudley, R., Pinshow, B., 2006. Ethanol and methanol as possible odor cues for Egyptian fruit bats (*Rousettus aegyptiacus*). J. Chem. Ecol. 32, 1289–1300. https://doi.org/10.1007/s10886-006-9085-0.

Simmons, N.B., Seymour, K.L., Habersetzer, J., Gunnell, G.F., 2008. Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 452, 818–822. https://doi.org/10.1038/nature06549.

Simões, B.F., Foley, N.M., Hughes, G.M., Zhao, H., Zhang, H., Rossiter, S.J., Teeling, E.C., 2019. As blind as a bat? Opsin phylogenetics illuminates the evolution of colour vision in bats. Mol. Biol. Evol. 36, 54–68. https://doi.org/10.1093/molbev/msy192.

Storz, J.F., Kunz, T.H., 1999. *Cynopterus sphinx*. Mamm. Species 613, 1–8. https://doi.org/10.2307/3504423.

Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O’Brien, S.J., Murphy, W.J., 2005. A molecular phylogeny for bats illuminates biogeography and fossil record. Science 307, 580–584. https://doi.org/10.1126/science.1105113.

Valenta, K., Nevo, O., 2020. The dispersal syndrome hypothesis: how animals shaped fruit traits, and how they did not. Funct. Ecol. 34, 1158–1169. https://doi.org/10.1111/1365-2435.13564.

Valenta, K., Brown, K.A., Rafaliarison, R.R., Styler, S.A., Jackson, D.J., Lehman, S.M., Melin, A.D., 2015. Sensory integration during foraging: the importance of fruit hardness, colour, and odour to brown lemurs. Behav. Ecol. Sociobiol. 69, 1855–1865. https://doi.org/10.1007/s00265-015-1998-6.

Valenta, K., Miller, C.N., Monckton, S.K., Styler, S.A., Jackson, D.J., Melin, A.D., Lehman, S.M., Chapman, C.A., Lawes, M.J., 2016. Forest-wide fruit ripening signals: haptic cues more reliably signal fruit ripeness than visual cues to dichromatic dispersers in tropical dry forest in Madagascar. Evol. Biol. 43, 344–355. https://doi.org/10.1007/s11692-016-9374-7.

Valenta, K., Nevo, O., Martel, C., Chapman, C.A., 2017. Plant attractants: integrating insights from pollination and seed dispersal ecology. Evol. Ecol. 31, 249–267. https://doi.org/10.1007/s10682-016-9870-3.

van der Pijl, L., 1957. The dispersal of plants by bats (Chiropterophily). Acta Bot. Neerl. 6, 291–315. https://doi.org/10.1111/j.1438-8677.1957.tb00577.x.

van der Pijl, L., 1982. Principles of Dispersal in Higher Plants. Springer-Verlag, Berlin.

Wang, G., Compton, S.G., Chen, J., 2013. The mechanism of pollinator specificity between two sympatric fig varieties: a combination of olfactory signals and contact cues. Ann. Bot. 111, 173–181. https://doi.org/10.1093/aob/mcs250.

Weber, I., 1973. Tactile communication among free-ranging langurs. Am. J. Phys. Anthropol. 38, 481–486. https://doi.org/10.1002/ajpa.1330380251.

Willson, M.F., Whelan, D.J., 1990. The evolution of fruit colour in fleshy-fruited plants. Am. Nat. 136, 790–809. https://doi.org/10.1086/285132.

Zar, J.H., 2007. Biostatistical Analysis, fifth ed. Prentice-Hall Inc., Englewood, Cliffs, New Jersey.

Zeppelini, C.G., Azeredo, L.M.M., Lopez, L.C.S., 2019. Bats like dimmer lights: lunar phobia as a luminosity threshold phenomenon on Neotropical bats. Acta Ethol. 22, 125–128. https://doi.org/10.1007/s10211-019-00314-w.

Zhang, W., Zhu, G., Tan, L., Yang, J., Chen, Y., Liu, Q., Qiqi, S., Chen, J., Zhang, L., 2014. Role of olfaction in the foraging behavior and trial-and-error learning in short-nosed fruit bat, *Cynopterus sphinx*. Behav. Process. 103, 23–27. https://doi.org/10.1016/j.beproc.2013.10.004.