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Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction

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Abstract We studied the role of echolocation and other sensory cues in two small frugivorous New World leaf-nosed bats (Phyllostomidae: *Artibeus watsoni* and *Vampyressa pusilla*) feeding on different types of fig fruit. To test which cues the bats need to find these fruit, we conducted behavioral experiments in a flight cage with ripe and similar-sized figs where we selectively excluded vision, olfaction, and echolocation cues from the bats. In another series of experiments, we tested the discrimination abilities of the bats and presented sets of fruits that differed in ripeness (ripe, unripe), size (small, large), and quality (intact/infested with caterpillars). We monitored the bats' foraging and echolocation behavior simultaneously. In flight, both bat species continuously emitted short (<2 ms), multi-harmonic, and steep frequency-modulated (FM) calls of high frequencies, large bandwidth, and very low amplitude. Foraging behavior of bats was composed of two distinct stages: search or orienting flight followed by approach behavior consisting of exploration flights, multiple approaches of a selected fruit, and final acquisition of ripe figs in flight or in a brief landing. Both bat species continuously emitted echolocation calls. Structure and pattern of signals changed predictably when the bats switched from search or orienting calls to approach calls. We did not record a terminal phase before final acquisition of a fruit, as it is typical for aerial insectivorous bats prior to capture. Both

bat species selected ripe over unripe fruit and non-infested over infested fruit. *Artibeus watsoni* preferred larger over smaller fruit. We conclude from our experiments, that the bats used a combination of odor-guided detection together with echolocation for localization in order to find ripe fruit and to discriminate among them.

Keywords *Artibeus* · *Vampyressa* · *Ficus* · Foraging · Sensory cues

Introduction

The species-rich family of New World leaf-nosed bats (Phyllostomidae) displays the highest dietary diversity worldwide among bats (Chiroptera) (e.g., Findley 1993; Kalko et al. 1996a). While foraging in the forest, leaf-nosed bats face several sensorial problems, namely orientation in space at night while avoiding collision with obstacles such as vines and branches, as well as detection, classification, and localization of food (e.g., Schnitzler and Kalko 1998, 2001). All phyllostomid bats echolocate and have well-developed visual and olfactory senses (for reviews see Bloss 1999; Altringham and Fenton 2003). Typically, they emit short multi-harmonic, downward frequency-modulated (FM) signals that are mostly of low intensity and high frequencies (e.g., Barclay et al. 1981; Kalko and Condon 1998; Thies et al. 1998; Kalko 2004). These signals are well suited to carry information about target range and position in three-dimensional space (e.g., Simmons 1973; Neuweiler 1990; Schnitzler and Kalko 1998, 2001). They are also potentially suited to deliver information on size, shape, and texture of objects (Simmons et al. 1974; Schnitzler and Henson 1980; Schmidt 1988; Schmidt et al. 2000). However, short, high-pitched signals operate only at short ranges since high frequencies are rapidly attenuated in air (Griffin et al. 1958; Lawrence and Simmons 1982). Furthermore, bats that forage very close to or within vegetation have to deal with interference of target echoes with clutter echoes (Schnitzler and Kalko 1998, 2001). This is particularly true for frugivorous phyllostomids that feed

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on fruits that are nestled among leaves. This makes detection by echolocation alone difficult or impossible, because echoes from leaves and branches frequently overlap with echoes from fruit(s). Due to masking effects, echolocation may provide only very limited information on the actual target (Schnitzler and Kalko 1998; Arlettaz et al. 2000; but see Schmidt et al. 2000; Siemers and Schnitzler 2000).

One way to overcome this problem is the use of multimodal cues. These include acoustical cues in animalivorous phyllostomids, such as advertisement calls of frogs and katydids or rustling noises of prey (e.g., Tuttle and Ryan 1981; Ryan and Tuttle 1983; Belwood 1988), olfactory cues in fruit- and nectar-drinking bats (Rieger and Jacob 1988; Laska 1990; Thies et al. 1998; Mikich et al. 2003), and to a limited degree also visual cues (Barclay et al. 1981; Bell and Fenton 1986; Joermann et al. 1988; Hessel and Schmidt 1994; Winter et al. 2003). In fruit-eating bats, there is increasing evidence that presentation of fruit determines to a large degree the respective roles of the various sensory cues. For instance, behavioral experiments of two understory frugivorous bats, *Carollia perspicillata* and *C. castanea* that feed on erect spikes of *Piper* infructescences have shown that bats change from a primarily odor-oriented detection of stands with ripe fruit to a mainly echolocation-guided, final localization of the position of individual fruit or a fruit's position (Hessel and Schmidt 1994; Thies et al. 1998). Furthermore, the omnivorous greater spear-nosed bat *Phyllostomus hastatus* uses echolocation rather than olfaction to detect the dangling fruits of the cucurbit *Gurania spinulosum* displayed on pendulous, leafless fruiting branches in the space between canopy and subcanopy (Kalko and Condon 1998). These findings also correspond well to a study on nectar-drinking bats that find flowers of *Mucuna holtonii* by echolocation because of the exposed position of the flower stand and the modified structure of a flower petal that acts as an acoustic nectar guide (Helvesen and Helvesen 1999).

However, to date, the respective roles of echolocation and other sensory cues have not been investigated in detail for any bat species feeding on fruit nestled among leaves, i.e. fruit within cluttered space sensu Schnitzler and Kalko (1998), where target echoes overlap with background echoes. Furthermore, the sensory basis upon which frugivorous bats select among fruit attributes such as ripeness, size, and quality is also still unknown (see Altringham and Fenton 2003). Rapid discrimination between fruit of different sizes and quality would be highly beneficial for bats because of reduction in search time and increase in quality and quantity of food intake per time unit. Previous studies point to such discrimination abilities. For instance, the size of bats feeding on figs (Moraceae) is positively correlated with the mass of ripe fruit taken (Bonaccorso 1979; Kalko et al. 1996b; Wendeln et al. 2000). Further, anecdotal observations of the common fruit-eating bat *Artibeus jamaicensis* (Phyllostomidae) suggest that the bats avoid fig fruits that are heavily infested with larvae other than the minute pollinator wasps (Handley et al. 1991). Engriser (1995) demonstrated that two phyllostomid bats, *Sturnira*

ludovici and *C. brevicauda*, reject insect-infested ripe fruit of *Acnistus arborescens* (Solanaceae).

To fill this gap we selected two little-studied, small fruit-eating bats, *Artibeus watsoni* and *Vampyressa pusilla* (Phyllostomidae), for detection and discrimination experiments. Both bats feed heavily on small fruits such as *Ficus citrifolia* (Moraceae) which is common in the study area. In detection experiments, we tested which cues are used by the bats to find ripe fruit nestled among leaves, i.e. in cluttered space. In discrimination experiments, we wanted to find out whether the bats differentiated between fruit of different sizes and between fruit with caterpillar infestation. We hypothesized that to overcome the clutter problem, olfaction should be the main sensory cue used by both bat species for detection and classification of ripe figs. We further postulated that echolocation plays a crucial role for orientation in space, as well as for final localization, and probably also for discrimination of size and type of fruit at closer range.

Methods

Study site and animals

The study was conducted from June to September 1997 on Barro Colorado Island (BCI), Panama (9°09'N, 79°51'W), a field station of the Smithsonian Tropical Research Institute. The island is covered with semideciduous tropical lowland forest. The climate is seasonal with a dry season from end of December until April and a rainy season from May to the middle of December when 90% of annual rainfall of 2600mm occurs (for further information see Leigh 1999). The two small frugivorous leaf-nosed bats (Phyllostomidae: *Artibeus watsoni*: 13g; *Vampyressa pusilla*: 7g) are common on BCI (Handley et al. 1991; Kalko et al. 1996a). They frequently feed on small-fruited figs such as *F. citrifolia* (Wendeln et al. 2000).

Depending on space, we set three or four mist nets (2.60 m × 12 m) around *F. citrifolia* trees with ripe fruit and captured bats between 6.30p.m. until 9p.m. We immediately brought the bats to a flight cage (4.4 m long × 4.5 m wide × 2.1 m high) on BCI for the behavioral experiments. Each bat was kept only for two nights in the flight cage to minimize possible learning effects. As the bats were caught at different localities, we minimized the chances of recaptures and we made sure that we did not use the same individual for our behavioral experiments by examining external features such as wing scars. As phyllostomid bats can see well, we conducted our experiments under very low light (a 25W red light bulb) conditions and as controls also in complete darkness. The flight cage on BCI was located under closed canopy at a distance from the lab buildings. We covered the meshed walls with black cloth to keep the interior of the cage as dark as possible. We did not conduct any experiments around full moon.

In the first night, behavioral experiments started after capture and lasted until midnight. During the second night, we performed experiments from 6.30–11p.m. and released

the bat afterwards at the respective capture site. We tested seven individuals of *A. watsoni* and six individuals of *V. pusilla*. Each individual was exposed at least once to each experimental set-up. We picked ripe fruits of *F. citrifolia* in the afternoon of the capture day and kept them in the fridge before the experiments. To avoid possible differences in fruit preferences, we collected all fruits from a single tree. Ripe fruits were soft, without latex, fragrant and with tiny exit holes of the fig wasps.

Experimental set-up

We conducted two types of experiments: detection and discrimination. In detection experiments, we tested which sensory cues the bats use to find fruit. In discrimination experiments, we tested whether the bats distinguish between ripe/unripe, small/large, and intact/infested fig fruit. Experimental design was similar for all trials. In each trial, we attached 10 fig fruits to a leafed branch (90–100 cm) of *F. citrifolia* with 20–30 alternate leaves. We attached five pairs (10 figs) on 2-cm long, rounded stainless-steel wires with a smooth tip onto a fig branch mimicking positions of natural fruit. As in the field, all fruits were close to or completely covered by leaves.

During the first night, we exposed the bats to three detection experiments. In the first experiment, we offered the bats five pairs of fruits to test each bat's motivation and to collect baseline data of its foraging and echolocation behavior. Each pair consisted of a ripe (with odor) and an unripe fruit (control, without odor). In the second experiment, we offered five pairs of ripe and freeze-dried figs to exclude possible scent cues. These freeze-dried fruits had the same shape and structure as ripe fruit but lacked their typical odor. In the third experiment, we placed ripe fruit in a cloth bag and hung it onto the branch to exclude the use of visual and echolocation cues but with odor cues penetrating the cloth.

On the second night, we exposed the bats to two discrimination experiments. As in the first night, we first presented the bats with ripe versus unripe fruit to test whether they were motivated. We then offered the bats five pairs of fruits where each pair consisted of a ripe and intact versus a ripe but infested fruit of similar fruit mass. The infested fruit were contaminated by caterpillars of a moth (Lepidoptera, species unknown, A. Herre, personal communication) that frequently lays eggs inside the cavity of the developing syconium of *F. citrifolia*. The caterpillars destroy part of the fig and fill it with frass. Infested figs differ from intact ripe fruit as they frequently show large exit holes in the fruit wall and appear to lack the typical fruity odor of intact ripe figs (Kalko et al. 1996b, personal observation). In the third experiment, we presented five pairs of ripe and intact fig fruit of two sizes, small (1.3 g) versus large (1.7 g). In earlier measurements, we had found that within fig species, fruit size and fruit mass were highly correlated ($n = 200$, $r^2 = 0.98$, $P < 0.001$; Korine et al. 2000). We followed the foraging behavior of the bats for each experiment with a night-vision scope (Type WILD, Switzerland) and recorded

the amount of time that each bat spent during its first approach to a branch with head and ears pointing toward the target suggesting that it was interested in it. In general, each experiment lasted between 45–60 min. If a bat did not react to our first experimental setting where we tested its motivation within the first 25 min, we stopped the experiment and released this individual. For each set of experiments and for each day we had a different branch. Between each set of experiments within each night, we randomly changed the position of the five pairs of fruits, and we randomly changed the location of the branch in the flight cage after each set of experiments, all to minimize spatial learning by the bats.

Recording set-up, sound recordings and analysis

We placed a custom-made ultrasound microphone next to the experimental set-up with a frequency response of ± 3 dB between 30 and 120 kHz and a drop in sensitivity of 0.2 dB/kHz at frequencies down to 15 kHz and up to 200 kHz. We attached it to a custom-made bat detector (Department of Animal Physiology, University of Tübingen, Germany), on a stand above the branch (5–10 cm) at about 0.9 m above ground. The ultrasound signals were picked up by a condenser microphone, amplified, digitized at a sampling rate of 312.5 kHz, stored in a memory array of 3.3 s real time, and then transferred at 15-times reduced speed to a WM-DC6 Sony-Walkman Professional recorder. The heterodyning system of the integrated bat detector was tuned to 90–100 kHz to make the sounds of the bats audible.

We analyzed the slowed-down sound sequences with a SONA PC color spectrogram frequency analyzer (B. Waldmann, University of Tübingen), using a Fast Fourier Transformation (FFT). The signals were digitized at a sampling rate of 25.6 kHz, and displayed on the monitor as color sonagrams (400 lines), using 256 points and a Hanning Window. Frequency range was set at 160 kHz for *A. watsoni* and at 320 kHz for *V. pusilla*. The settings gave a frequency resolution of 1.6 kHz and a time resolution of 0.6 ms for *A. watsoni* in real-time and 3.2 kHz and 0.3 ms for *V. pusilla*, respectively. The FFT's were calculated with 93.75% time overlap (240 points).

We analyzed the harmonics with the highest energy content for each species. Measurement points on the sonagrams were set at (40 dB below maximum SPL (−72 dB). To describe harmonics, we used the nomenclature of 1st harmonic, 2nd harmonic, 3rd harmonic and so on starting with the lowest element. In *A. watsoni* these were parts of the second (strongest) and third harmonic and in *V. pusilla* parts of the third (strongest) and fourth harmonic. We followed Thies et al. (1998) and classified the highest and lowest frequency of the signal as upper boundary (ub) and lower boundary (lb). Then we measured the terminal frequency (TF) of the third harmonic in *A. watsoni* (fourth harmonic in *V. pusilla*) and the starting frequency (SF) of the second harmonic in *A. watsoni* (third harmonic in *V. pusilla*). To reconstruct the complete structure of the lower harmonic for each species we calculated its terminal frequency, TF_{calc}

(see Thies et al. 1998). Additionally, we assessed bandwidth (ub–lb; kHz), duty cycle (dc; % of time filled with sound), pulse duration, pulse interval (from the beginning of one call until beginning of next call; ms), and sweep rate of the lower harmonic ($SF-TF_{calc}/\text{sound duration}$; kHz/ms). We divided the bats' echolocation behavior in relation to their foraging behavior into search or orienting calls and approach calls (see Schnitzler et al. 2003). Typically, phyllostomid bats emit search or orienting calls singly while approach calls are mostly emitted in groups (Kalko and Condon 1998; Thies et al. 1998). During recordings, we noted whether the bats explored the flight cage or flew close to the branch.

Database

We recorded 540 min of slowed-down echolocation sequences, approximately 270 min for each species corresponding to about 80 min real-time each. For each experiment, we only selected echolocation sequences with good signal-to-noise ratios where call energy was clearly above background noise. For comparison of echolocation behavior during different experiments, we only took sound sequences from bats approaching a branch because quality of the preceding search or orienting calls was often low because of the variable position of the bats toward the microphone.

To minimize possible effects of pseudoreplication inherent to many field studies of bat echolocation, we used averaged call parameters (mean) derived from one sequence per bat and experiment (Siemers et al. 2001). Comparisons between sound parameters of search or orienting calls and approach calls were tested with Wilcoxon Signed-Ranks nonparametric test and between species with Mann–Whitney U test. Comparisons of sound parameters within discrimination experiments were tested using a repeated-measures general linear model with Bonferroni correction. We used a Wilcoxon Signed-Ranks nonparametric test for the results of the fruit selection. We present results as means \pm S.D. A $P < 0.05$ was accepted as level of significance. All statistical analyses were done with Systat.

Results

Foraging behavior

In all experiments, where the bats reacted positively toward a target (i.e., ripe fig), we observed two distinct behaviors: orienting or search flight followed by approach behavior consisting of exploration flights, multiple approaches to a selected fruit and final acquisition of a fruit. During orienting or search flight, individuals of both bat species flew for several minutes (2–9 min) relatively high (mostly 1m) along the walls in the flight cage. As soon as a bat became interested in the stand with the fruit branch, it switched from a general circling flight pattern to short flights near the branch. At this stage, the bat performed exploration flights such as passing, circling up-front, below or above

the branch. Although we consistently changed the branch and its location between experiments, duration of exploration flights was always longest in the first trial when the bats were not yet familiar with the overall setting of the flight cage. In the first experiment, this stage lasted up to 6 min and was then subsequently reduced to 1–3 min. Exploration flights ended when the bat selected a fruit, then approached it closely several times and finally bit into it, tore it off and flew with it in its mouth into a corner of the flight cage where it immediately started to process it. In case the bat did not get the fruit at the first try, it returned and repeated either one or more approach flights. Usually, the bats took the fruit in flight. Bats rarely landed for a brief instant on the branch or hovered in front of it to pick it up.

Echolocation behavior

Both bat species continuously produced echolocation calls in flight. The calls emitted by *A. watsoni* and *V. pusilla* were multiharmonic, steep frequency-modulated (FM) calls of high frequency and large bandwidth, short duration (<2 ms), and low amplitude (Fig. 1a and b). During search or orienting flights, when both bat species had not yet become interested in the branch with fruits, duty cycle was low (around 1–1.4%) with comparatively long-pulse intervals (around 100 ms) and short-call durations (1.1–1.5 ms) (Table 1, Fig. 2a and b). Most of the calls were

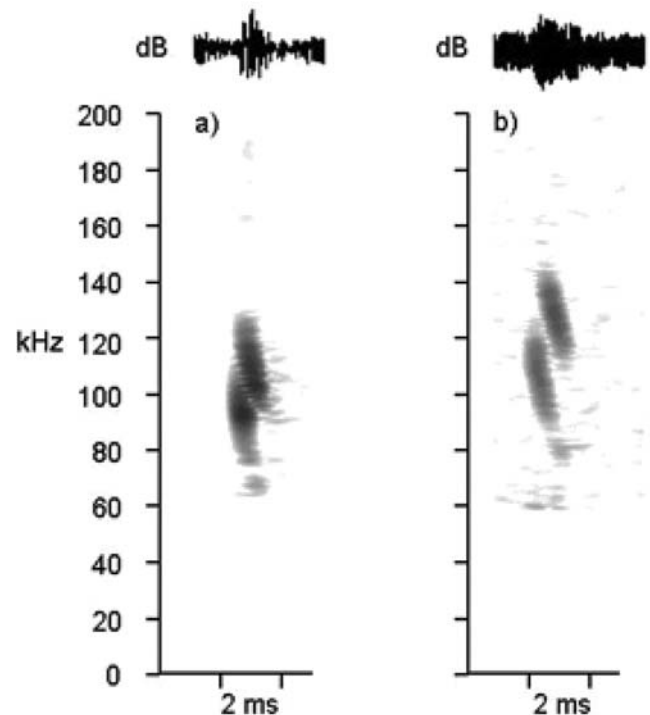


Fig. 1 Approach call of (a) *Artibeus watsoni* and (b) *Vampyressa pusilla* flying toward a branch with figs given as oscillogram (above) and sonagram (below). Sonagram parameters: FFT, Hanning window; 256 sampling points; 93,75% time overlap

Table 1 Comparison of acoustic parameters of search or orientation calls and approach calls to ripe and unripe fig fruits in *A. watsoni* and *V. pusilla*

	Search or orienting calls	Approach calls	<i>P</i>	<i>Z</i>
<i>A. watsoni</i> (<i>n</i> =7 individuals)				
Duty cycle (%)	1.0±0.2	2.2± 0.2	0.02	-2.36
Pulse interval (ms)	111.1±18.1	32.3±5.9	0.02	2.37
Pulse duration (ms)	1.1±0.3	0.6±0.1	0.02	2.37
Ub ₃ (measured) (kHz)	127.7±3.7	129.0±9.8	0.87	-0.17
TF ₃ (measured) (kHz)	87.3±4.6	90.8±4.8	0.06	-1.86
SF ₂ (measured) (kHz)	101.4±6.2	92.7±8.9	0.12	1.52
Lb ₂ (measured) (kHz)	67.7±6.4	65.3±7.7	0.74	0.34
TF ₂ (calculated) (kHz)	58.2±3.1	60.5±3.2	0.13	-1.52
Bandwidth (kHz)	59.9±5.4	63.6±8.9	0.18	-1.35
Sweep rate ₂ (kHz/ms)	40.5±9.4	53.7±10.4	0.04	-2.03
<i>V. pusilla</i> (<i>n</i> =6 individuals)				
Duty cycle (%)	1.4±0.1	1.5±0.2	0.03	-2.20
Pulse interval (ms)	87.2±13.7	31.9±7.9	0.03	-2.20
Pulse duration (ms)	1.2±0.1	0.4±0.01	0.03	-2.20
Ub ₄ (measured) (kHz)	152.7±3.0	152.3±2.7	0.75	0.31
TF ₄ (measured) (kHz)	118.9±5.4	121.3±4.8	0.92	-0.10
SF ₃ (measured) (kHz)	142.3±1.9	137.1±3.9	0.07	1.75
Lb ₃ (measured) (kHz)	101.6±5.2	101.7±2.8	0.34	-0.94
TF ₃ (calculated) (kHz)	89.3±4.6	91.0±3.6	0.92	-0.10
Bandwidth (kHz)	49.9±9.4	50.6±3.3	0.46	0.74
Sweep rate ₃ (kHz/ms)	45.9±8.8	115.3±14.2	0.03	-2.20

Results are presented as means ± SD: *P* – Probability; *Z* – Wilcoxon Signed-Ranks nonparametric test. Approach behavior includes exploration flights, multiple approaches, and final acquisition of fruit. Abbreviations: ub – upper boundary of the visible signal; TF – terminal frequency of the third or the fourth harmonic; SF – starting frequency of the second or third harmonic; lb – lower boundary of the visible signal; TF calculated – terminal frequency of the lower harmonic as it is visible in spectrogram

emitted singularly. As soon as a bat became interested in the fruit-bearing branch, it switched to approach behavior with exploration flights where patterns of sound emission changed significantly in both species until final acquisition of a fruit. The onset of approach behavior coincided in echolocation behavior with the point when a bat started to emit groups of calls instead of single calls. The most pronounced changes in both species were a significant decrease in pulse interval and sound duration, and a significant increase in duty cycle and sweep rate (Table 1, Fig. 3a and b). In contrast to aerial insectivorous bats which emit many short calls at very short pulse intervals prior to capture of an insect (terminal phase) in the air, we did not record such a distinct pattern prior to the acquisition of a fruit.

Overall, pattern of echolocation call emission was similar between both species. However, because of the fundamental differences in the strongest harmonics (2nd and 3rd harmonics in *A. watsoni* and 3rd and 4th harmonics in *V. pusilla*), all call parameters related to frequency differed significantly between the two bat species during search or orienting flight and approach behavior. Besides that, during search or orienting flight, duty cycle (Mann–Whitney *U* test = 42.0, *p* < 0.003) and pulse duration (Mann–Whitney *U* test = 42.0, *p* < 0.003) in *A. watsoni* were significantly lower and shorter than those of *V. pusilla*, while pulse interval (Mann–Whitney *U* test = 42.0, *p* < 0.003) was sig-

nificantly longer (Table 1). During exploration flights up to final acquisition of a fruit, duty cycle (Mann–Whitney *U* test = 42.0, *p* < 0.003) and pulse duration (Mann–Whitney *U* test = 35.0, *p* < 0.04) in *A. watsoni* were significantly longer than that of *V. pusilla*, while pulse interval was similar (Table 1).

Detection experiments: use of different sensory cues

The three detection experiments in which we manipulated the sensory cues available to the bats clearly indicated that both bat species only took figs when they broadcasted olfactory cues. Bats always took ripe fruit and ignored unripe fruit (Table 2). When freeze-dried fruits were present, for which the original shape was preserved but not the scent, the bats displayed a few passing flights but did not take any of the fruits. The bats either continued search flight for a while or stopped flying altogether and rested in the flight cage. When only odor cues were present as was the case with the bagged ripe fruit, the bats displayed extensive exploration flights and frequently hovered in front of the bag. Overall, the bats spent significantly less time around scentless fruits than around the bag containing ripe figs (Table 3). Furthermore, individuals of both species removed

Fig. 2 Echolocation sequence of (a) *A. watsoni* and (b) *V. pusilla* during search or orienting flight in the flight cage (A- pulse duration; B- pulse interval and C-duty cycle)

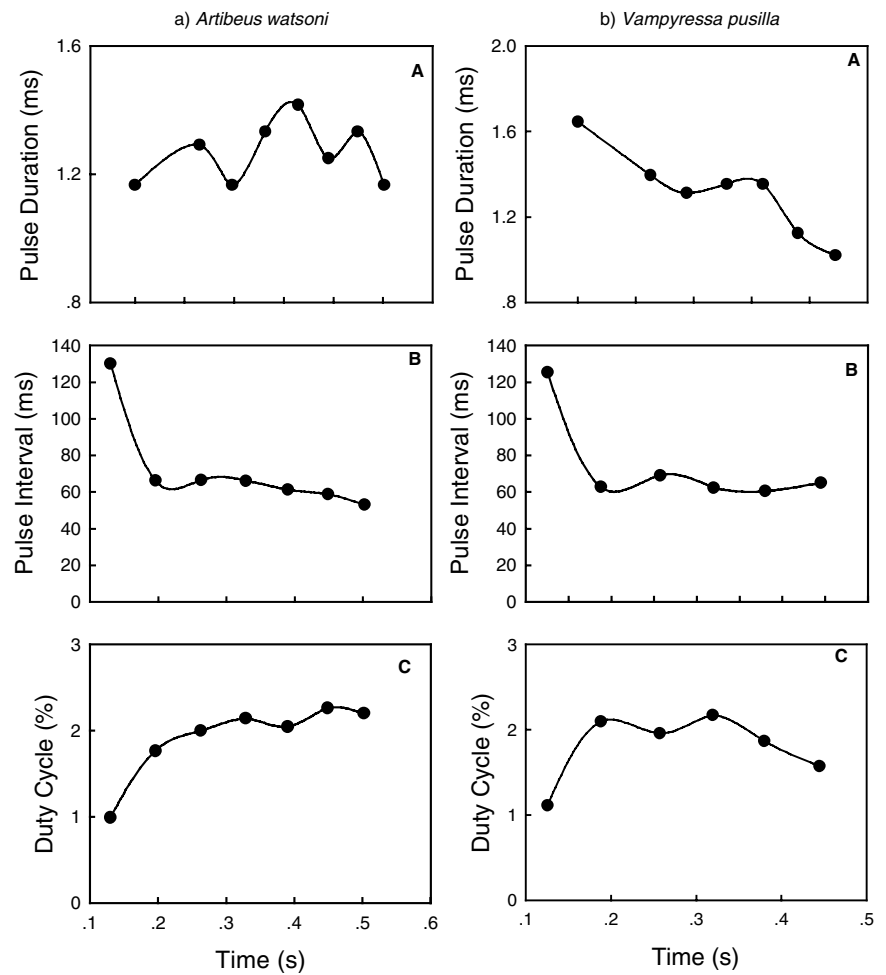
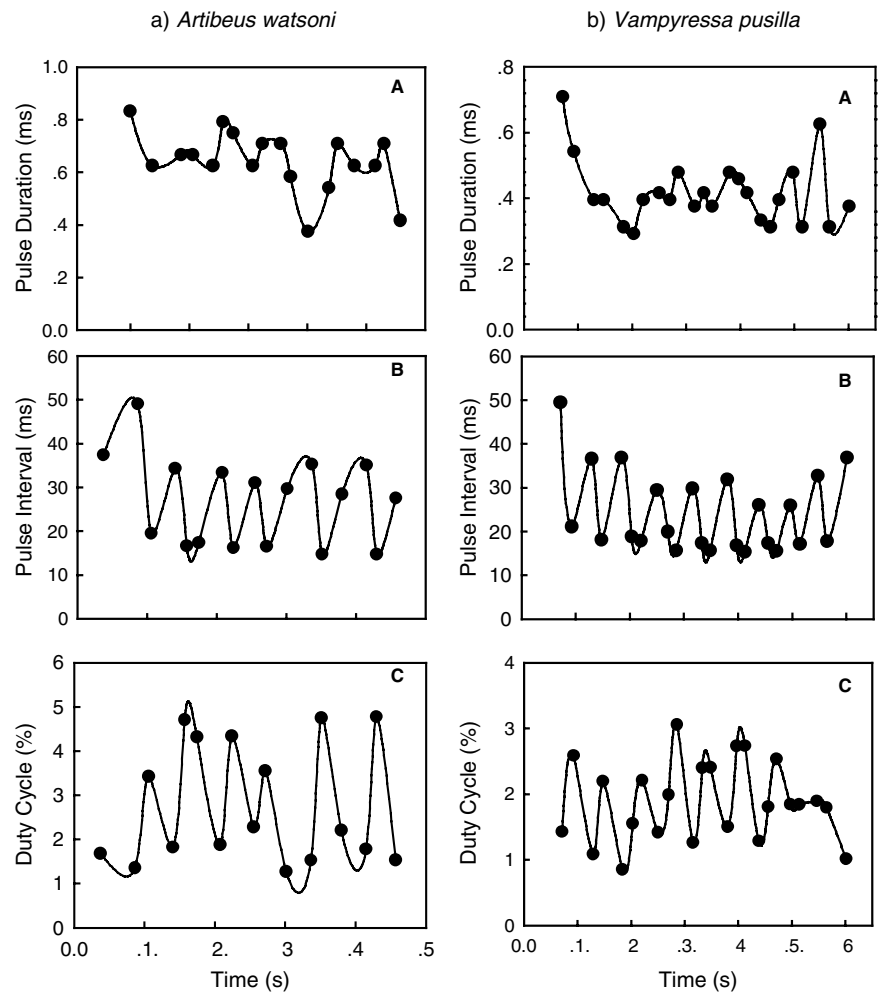


Table 2 Number and types of fig fruits consumed by *A. watsoni* and *V. pusilla*

Type of experiment	Control fruit		Infested fruit		<i>P</i>	Fruit size		<i>P</i>
	Ripe	Unripe	Ripe intact	Ripe infested		Big	Small	
<i>A. watsoni</i>								
Individual 1	3	0	3	0		2	1	
Individual 2	3	0	3	0		2	2	
Individual 3	3	0	3	0		3	0	
Individual 4	3	0	3	0		2	1	
Individual 5	3	0	3	0		3	0	
Individual 6	3	0	3	0		3	0	
Individual 7	3	0	3	0		2	1	
Mean						2.4±0.5	0.7±0.8	0.024
<i>V. pusilla</i>	Ripe	Unripe	Ripe intact	Ripe infested	<i>P</i>	Small	Big	<i>P</i>
Individual 1	3	0	2	1		2	1	
Individual 2	3	0	2	1		2	1	
Individual 3	3	0	2	1		1	2	
Individual 4	3	0	2	1		2	1	
Individual 5	3	0	2	1		1	2	
Individual 6	3	0	3	0		2	1	
Mean			2.2±0.4	0.8±0.4	0.02	1.7±0.5	1.5±0.6	0.41

Results are given for each individual and as mean ±SD for each species of bat. Note that both species consumed only ripe fruits and that *A. watsoni* consumed only ripe intact fruits. The results are based on the first trial of each experiment (for more details see methods). *P* – Probability; comparisons were done using the Wilcoxon Signed-Ranks nonparametric test

Fig. 3 Echolocation sequence of (a) *A. watsoni* and (b) *V. pusilla* approaching a ripe fruit of *Ficus citrifolia* in the flight cage (A-pulse duration; B-pulse interval and C-duty cycle)



ripe fruit in complete darkness with ease suggesting that visual cues were not necessary to find and to grasp ripe figs.

Echolocation behavior during detection experiments varied between both species. For *A. watsoni*, upper boundary and terminal frequency of the strongest (third) harmonic as well as starting frequency, lower boundary, calculated terminal frequency, and sweep rate of the lower harmonic (second) changed significantly while approaching fruits with different degree of ripeness, freeze-dried fruits, and bagged ripe fruits (Table 4). The mean values of different echolocation variables toward ripe fruits were lower than that of freeze-dried fruit or fruit in bags. The most obvious change was the decrease of sweep rate (Table 4). Echolocation behavior while approaching freeze-dried fruits and bagged ripe fruits remained similar in *V. pusilla* (Table 4).

Discrimination experiments: selection of fruit according to size and infestation

Both species significantly preferred undamaged and ripe fruit to infested fruit (Table 2). Furthermore, *A. watsoni* significantly preferred larger fruit of *F. citrifolia* to smaller fruit, while such a preference was not found in *V. pusilla*

(Table 2). For *A. watsoni*, as with the detection experiments (Table 4), starting frequency and sweep rate of the second harmonic in the approach calls to the ripe fruit were significantly lower than that of infested fruit and fruit of different size (Table 5). Duty cycle, lower boundary of the second harmonic and bandwidth in the approach to the branch with fruit of different size were significantly lower than that of ripe fruit and of infested fruit (Table 5). For *V. pusilla*, echolocation behavior while approaching infested fruit and fruit of different size remained similar to the approach of fruit with different degree of ripening with the exception of a decrease in sweep rate to infested fruit (Table 5).

Discussion

Foraging behavior and sensory cues

The basic foraging behavior pattern found in *A. watsoni* and *V. pusilla* through flight cage experiments consisted of two behaviors: search or orienting flight followed by approach behavior including exploration flights around the branch, multiple approaches and final acquisition of a fruit. The data on echolocation behavior revealed distinct changes at

Table 3 Time spent by *A. watsoni* and *V. pusilla* around scentless (freeze-dried) and bagged fig fruits

Experiment	Scent-less fruit	Scented fruit	<i>P</i>	Experiment	Scent-less fruit	Scented fruit	<i>P</i>
<i>A. watsoni</i>				<i>V. pusilla</i>			
	Time spent near fruit (s)				Time spent near fruit (s)		
Individual 1	10	70		1	20	90	
Individual 2	20	120		2	25	70	
Individual 3	30	140		3	25	60	
Individual 4	25	80		4	30	50	
Individual 5	30	45		5	40	50	
Individual 6	20	50		6	40	70	
Individual 7	45	100					
Mean	25.7±10.9	86.4±35.4	0.018	Mean	30.0±8.4	65.0±15.1	0.028

Results are presented for each individual bat and mean ±SD for each species. The results are based on the first trial of each experiment (for more details see methods). *P* – Probability; comparisons were done using the Wilcoxon Signed-Ranks nonparametric test

Table 4 Comparison of acoustic parameters of approach calls in the detection experiments (ripe fruit-control, freeze-dried fruit -scent-less, fruits in a bag -scent) in *A. watsoni* and *V. pusilla* (for abbreviations see Table 1)

	Ripe fruit (<i>n</i> =7)	Scent-less fruit (<i>n</i> =7)	Bagged fruit (<i>n</i> =7)	<i>P</i>	<i>F</i>
<i>A. watsoni</i>					
Duty cycle (%)	2.2±0.2	2.0±0.5	2.35±0.5	0.23	1.62
Pulse interval (ms)	32.3±5.9	30.2±7.5	27.44±4.7	0.36	1.08
Pulse duration (ms)	0.6±0.09	0.5±0.07	0.51±0.03	0.12	2.36
Ub ₃ (measured) (kHz)	129.0 ^b ±9.8	136.5 ^a ±9.8	134.0 ^{ab} ±3.3	0.006	6.82
TF ₃ (measured) (kHz)	90.8 ^a ±4.8	97.5 ^{ab} ±5.1	98.5 ^a ±6.3	0.05	3.67
SF ₂ (measured) (kHz)	92.7±8.9	106.7±10.4	108.5±5.8	0.06	3.22
Lb ₂ (measured) (kHz)	65.2 ^b ±7.7	77.8 ^a ±8.4	79.9 ^a ±4.8	0.007	6.44
TF ₂ (calculated) (kHz)	60.5 ^b ±3.2	65.0 ^{ab} ±4.8	65.7 ^a ±4.2	0.051	3.51
Bandwidth (kHz)	63.6±8.9	58.8±11.7	54.2±2.5	0.20	1.77
Sweep rate ₂ (kHz/ms)	53.7 ^b ±10.4	83.7 ^a ±15.2	84.1 ^a ±12.2	0.001	11.11
<i>V. pusilla</i>					
	Ripe fruit (<i>n</i> =6)	Scent-less fruit (<i>n</i> =6)	Bagged fruit (<i>n</i> =6)	<i>P</i>	<i>F</i>
Duty cycle (%)	1.5±0.2	1.6±0.2	1.58±0.2	0.86	0.15
Pulse interval (ms)	31.9±7.9	28.1±7.2	35.0±7.3	0.31	1.28
Pulse duration (ms)	0.4±0.06	0.4±0.05	0.4±0.07	0.28	1.39
Ub ₄ (measured) (kHz)	152.3±2.7	151.5±2.8	154.4±2.6	0.21	1.76
TF ₄ (measured) (kHz)	121.3±4.8	120.1±4.1	127.2±5.7	0.06	3.50
SF ₃ (measured) (kHz)	137.1±3.9	134.6±5.0	135.9±7.4	0.85	0.30
Lb ₃ (measured) (kHz)	101.7±2.8	97.9±4.3	100.4±3.2	0.19	1.87
TF ₃ (calculated) (kHz)	91.0±3.6	90.1±3.1	95.4±4.3	0.06	3.50
Bandwidth (kHz)	50.6±3.3	53.6±5.7	53.9±3.2	0.35	1.12
Sweep rate ₃ (kHz/ms)	115.3±14.2	111.9±10.7	101.4±9.0	0.15	4.33

Results are presented as means ±SD. Different letters within a row indicate significant differences (*P*<0.05) among experiments. *P* – Probability, *F*-repeated-measures general linear model

the transition from search or orienting flight to approach behavior, without a distinct terminal phase as it is typical for aerial insectivorous bats (Kalko and Schnitzler 1998; Schnitzler and Kalko 1998). Similar stages have been documented for other frugivorous phyllostomid bats searching for and approaching food (Kalko et al. 1996b; Kalko and Condon 1998; Thies et al. 1998). Both species, *A. watsoni* and *V. pusilla*, showed similar patterns in echolocation behavior. They differed, however, in the harmonics with highest energy content. This difference is probably mainly linked to size as it has been shown for a number of other species (e. g., Jones 1999) such as *Carollia* sp. (Thies et al. 1998) and *Pipistrellus* sp. (Kalko 1995) where smaller bats foraging in similar habitats emit higher-frequency calls than larger bats.

Our experiments with manipulated fruit clearly revealed that both species of bats need olfactory cues to find ripe

fig fruits nestled among leaves. These results are consistent with other studies on frugivorous phyllostomids (Laska 1990; Rieger and Jakob 1988; Hessel and Schmidt 1994; Thies et al. 1998; Mikich et al. 2003) where odor was also the main cue for bats in search of ripe fruits (but see Kalko and Condon 1998; Helversen and Helversen 1999). Although vision may also play a role in detection, and probably localization, of ripe figs (Altringham and Fenton 2003) our experiments revealed that visual cues are not necessary because both species of bats successfully removed ripe figs in complete darkness. Furthermore, fruits of fig species eaten by phyllostomid bats remain green(ish) when ripe (Kalko et al. 1996b; Korine et al. 2000) and thus do not provide good cues for visual discrimination, and light conditions inside the forest are often very poor. However, it would be interesting to measure the reflectance of figs as a study on nectar-drinking phyllostomid bats

Table 5 Comparison of acoustic parameters of approach calls during the discrimination experiments (ripe vs. unripe fruit, intact vs. infested fruit and large vs. small fruit) in *A. watsoni* and *V. pusilla* (for abbreviations see Table 1)

<i>A. watsoni</i>	Ripe versus unripe fruit (control)(<i>n</i> =7)	Intact versus infested fruit (<i>n</i> =7)	Large versus small fruit (<i>n</i> =7)	<i>P</i>	<i>F</i>
Duty cycle (%)	2.2 ^{ab} ±0.2	2.0 ^b ±0.3	1.6 ^c ±0.2	0.002	15.46
Pulse interval (ms)	32.3±5.9	33.1±5.3	37.1±5.9	0.26	1.46
Pulse duration (ms)	0.6±0.1	0.5±0.1	0.5±0.1	0.19	1.84
Ub ₃ (measured) (kHz)	129.0±9.8	130.0±3.1	131.1±6.6	0.86	0.16
TF ₃ (measured) (kHz)	90.8±4.8	91.4±4.2	89.7±5.8	0.96	0.04
SF ₂ (measured) (kHz)	92.7 ^b ±8.8	100.9 ^{ab} ±7.5	102.3 ^a ±6.3	0.006	6.80
Lb ₂ (measured) (kHz)	65.2 ^b ±7.7	65.9 ^b ±8.0	78.0 ^a ±10.4	0.04	4.04
TF ₂ (calculated) (kHz)	60.5±3.2	61.0±2.8	60.73±2.6	0.96	0.04
Bandwidth (kHz)	63.6 ^a ±8.9	64.1 ^a ±8.8	53.1 ^b ±6.2	0.03	4.69
Sweep rate ₂ (kHz/ms)	53.7 ^b ±10.4	79.9 ^{ab} ±18.8	83.5 ^a ±20.2	0.01	5.36
<i>V. pusilla</i>	Ripe versus unripe fruit (control) (<i>n</i> =6)	Intact versus infested fruit (<i>n</i> =6)	Large versus small fruit (<i>n</i> =6)	<i>P</i>	<i>F</i>
Duty cycle (%)	1.5±0.2	1.5±0.2	1.5±0.1	0.91	0.09
Pulse interval (ms)	31.9±7.9	37.2±8.8	34.4±9.7	0.59	0.54
Pulse duration (ms)	0.4±0.06	0.5±0.06	0.4±0.06	0.40	0.98
Ub ₄ (measured) (kHz)	152.4±2.7	153.2±1.7	153.1±1.4	1.37	0.28
TF ₄ (measured) (kHz)	121.3±4.8	124.1±2.9	127.2±3.3	0.26	2.30
SF ₃ (measured) (kHz)	137.1±3.9	135.9±2.7	138.7±1.9	0.28	1.37
Lb ₃ (measured) (kHz)	101.7 ^a ±2.8	96.6 ^b ±4.4	101.7 ^{ab} ±3.9	0.05	3.67
TF ₃ (calculated) (kHz)	91.0±3.6	93.1±2.1	95.4±2.5	0.13	2.29
Bandwidth (kHz)	50.6 ^b ±3.3	56.2 ^a ±3.5	51.4 ^{ab} ±4.7	0.05	3.67
Sweep rate ₃ (kHz/ms)	115.3 ^a ±14.2	85.6 ^b ±9.3	108.8 ^a ±16.8	0.01	8.57

Results are presented as means ±SD. Different letters within a row indicate significant differences ($P < 0.05$) among experiments. *P* – Probability, *F*–repeated-measures general linear model

revealed that those bats are sensitive to UV (Winter et al. 2003).

In neotropical figs, the role of odor cues for bats is enhanced because of their fruit characteristics. These trees produce huge fruit crops that ripen synchronously over a very short period. The simultaneous emission of a distinct aroma of a large fruit crop typically produces a distinct odor plume that is likely to facilitate detection of ripe fruits over long distances (Kalko et al. 1996b; Korine et al. 2000).

Echolocation behavior

What is the role of echolocation in both species while foraging? Both bat species continuously emitted echolocation calls during flight. The search for a branch with ripe figs was accompanied by steep, multi-harmonic FM signals with longer pulse durations and pulse intervals than the exploration flights followed by multiple approaches and final acquisition of a fruit. The bats showed this echolocation behavior only when they flew around the walls of the flight cage for several minutes without approaching a specific target. We conclude that this behavior may either correspond to a search for ripe figs as in the field or it may be used for orientation in a new environment as it was the case for the wild-caught bats when they were released for the first time in the flight cage.

Both bats changed their echolocation behavior once they approached a branch with figs by reducing sound duration and pulse interval. This led to a distinct increase in duty

cycle, which enhances the information flow between the bat and its surroundings. The distinct change in echolocation behavior clearly indicates to us that the calls deliver crucial information for foraging bats.

We propose that during search or orientation flight, both bat species emitted echolocation calls mainly to gain information about their immediate surrounding, i.e., monitoring obstacles. Detection and classification of figs by echolocation alone is unlikely as the calls of the bats were very faint. Further, the fruits were nestled among leaves and therefore largely within the echo-overlap zone where echoes from the figs overlap with echoes from the leaves. This overlap is likely to mask important information from the bat and makes detection by echolocation alone unlikely. For detection, and probably also for classification of the figs, the bats most likely used olfactory cues. Typically, species-specific odor bouquets characterize Neotropical figs taken by bats (Kalko et al. 1996b). However, precise localization of a fruit by olfactory cues is difficult to impossible because scent spreads quickly in air and is a rather imprecise marker. Therefore, we conclude that the bats must use information from echolocation calls when they are very near the chosen target. In this situation, the bat is close to the fruit and has reduced sound duration to a minimum (0.4–0.6 ms). Short sound duration combined with large bandwidth facilitates discrimination of individual fruit even with partial echo-overlap of the calls (see for an example the insectivorous gleaner in Siemers and Schnitzler 2000). The information obtained by echolocation is crucial for the bat to determine its own, as well as the fruit's, position in three-dimensional

space. The precision of final localization is further supported by the observation that the bats mostly took fruit in flight and not by landing on the branch. Overall, we propose that both bat species use a combination of odor-guided detection, classification, and rough localization of ripe figs with echolocation for orientation in space, and precise localization of selected fruit at close range.

The combined use of echolocation and odor in *A. watsoni* and *V. pusilla* foraging for ripe figs is in accordance with other studies. Short-tailed fruit bats of the genus *Carollia* (Phyllostomidae) use odor as a primary cue while searching for ripe *Piper* fruits. They then switch to an echolocation-guided final approach to grasp the erect, spike-like fruit stand at its tip (Thies et al. 1998). In contrast, *Phyllostomus hastatus* (Phyllostomidae) uses echolocation rather than olfaction to detect the fruits of *Gurania spinulosa* presented on pendulous leafless branches (Kalko and Condon 1998). Unlike the *Gurania* fruit, the figs we studied frequently occur in tight clusters that are interspersed by leaves, which often obscure the fruits (Kalko et al. 1996b; Korine et al. 2000). This configuration makes them difficult targets for echolocation. We suggest that echolocation is mainly used for localization of a fruit-bearing branch, and for final acquisition of a fruit. This is manifested by the significant changes in duty cycle, pulse duration, pulse interval, and sweep rate when the bats approached a branch in comparison to bats in search or orienting flight. Overall, the bats use a combination of exploration flights and orientation by odor to lead them to the target branch.

When freeze-dried figs or ripe figs in a bag were presented for both bat species, some changes in the structure of echolocation calls of *A. watsoni* were observed. Whereas pulse duration and pulse interval and therefore duty cycle did not change, other call variables varied significantly between experiments. The most pronounced change was a significant increase in sweep rate and the increase in lower boundary and upper boundary of the visible signal toward freeze-dried figs and ripe figs in the bag. The functional significance of those changes in call structure in relation to the sensorial tasks are difficult to explain. In case of freeze-dried figs it cannot be ruled out that the bats perceived the general shape of the figs with echolocation and changed call structure to enhance the resolution of their "acoustic image" even though no characteristic olfactory cues were present. In case of ripe figs in a bag, the bats clearly used olfaction for detection but then needed echolocation for exact localization of the fruits obscured by the bag. Furthermore, as the differences in call parameters in *A. watsoni* and *V. pusilla* were rather small, part of it may also been caused because of rounding and measurement errors as well as closeness to the maximum resolution of the sound analysis.

The role of echolocation in selection of different types of fruits

Both species of bats prefer ripe non-infested fruits to infested fruits. This is in accordance with previous experi-

ments with fruit bats (Handley et al. 1991; Engriser 1995). The two sets of experiments (large versus small fruit and intact versus infested fruit) presumably present a more difficult echolocation task to the bats than discrimination between ripe and unripe figs. For the infested fruit, it is highly possible that the odor bouquet has been altered or does not fully develop due to damage caused by caterpillar frass. This is likely to reduce the attractiveness of the fruit for the bats. Furthermore, because of the exit holes and other damage to the fruit shell, also caused by caterpillars, the drastically altered surface structure of the infested fruit may be perceived by echolocation at close range. *Artibeus watsoni* was emitting calls with higher sweep rate when approaching infested fruit while sweep rate decreased significantly toward infested fruit in *V. pusilla*. Other call variables did not change significantly between the two sets of experiments, which may indicate that odor is a more important cue for both species of bats when rejecting infested fruits.

The underlying sensory basis of the discrimination ability of *A. watsoni* in selecting larger over small fruit of the same fig species, *F. citrifolia*, is more difficult to explain. Perhaps echolocation at close range may deliver information to the bat about the size of the fig. *A. watsoni* changed its echolocation behavior by changing call variables such as bandwidth, and sweep rate compared to the control. In contrast to *A. watsoni*, *V. pusilla* did not show any preference for fruit size. Furthermore, in accordance with this observation, we did not find any clear differences in the echolocation behavior of *V. pusilla* when approaching fruit of different size.

Two other explanations may explain the different preference of both species of bats to fruit size. The first one is again related to smell. The bouquet of smaller fruits may be different or less intense than in large fruits and therefore, in case of *A. watsoni*, the bat preferred large fruits. Alternatively, the preference of *A. watsoni* to larger fruits may simply reflect the relationship between the size of the bat and the fruit (Kalko et al 1996b). *Vampyressa pusilla* may not benefit from picking a large fruit due to the trade-off between energy expenditure of transporting and handling larger fruits versus the energy contained in these fruits.

A central problem in sensory ecology is the extent to which FM calls can be used for distinguishing food objects from substrate, particularly for complex substrates that generate echo clutter, as is the case for figs nestled among leaves. Studies that directly address this question provide conflicting views (see for instance Neuweiler 1990; Schmidt 1988; Arlettaz et al. 2001; Schnitzler and Kalko 1998, 2001; Eklof et al. 2002). For example, studies on gleaning insectivorous/carnivorous bats (Schmidt et al. 2000; Siemers and Schnitzler 2000), gleaning frugivores (Kalko and Condon 1998; Thies et al. 1998), and nectarivores (Helvesen and Helvesen 1999) have shown that these bats can use FM-calls for detection of stationary food items. In contrast, Arlettaz et al. (2001) conclude that FM-calls are not adapted to detection of non-moving, silent prey in cluttered background. We argue that bats can use FM calls for detection of stationary food while they explore for instance a branch with fruits and that the extent which

information is transmitted by FM calls to the bat largely depends on the presentation and acoustic properties of the respective food and the complexity of the surrounding clutter, i.e. vegetation. In particular, we propose that FM calls can provide detailed information about the fine texture of an object if it is partially exposed and has a strongly reflective surface and a particular shape. This suggestion is based on observations that phyllostomid bats that feed on partially exposed fruits such as *Piper* use echolocation to localize individual fruits (Thies et al 1998), omnivorous bats use echolocation to detect and localize fruits of a climbing plant (Kalko and Condon 1998), and nectar eating bats use echolocation to detect and localize flowers (Helversen and Helversen 1999).

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