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The roles of echolocation and olfaction in two Neotropical fruit-eating bats, *Carollia perspicillata* and *C. castanea*, feeding on *Piper*

Abstract We studied the echolocation and foraging behavior of two Neotropical frugivorous leaf-nosed bats (*Carollia perspicillata*, *C. castanea*: Phyllostomidae) in a flight cage. To test which cues *Carollia* uses to detect, identify, and localize ripe *Piper* fruit, their preferred natural food, we conducted experiments under semi-natural conditions with ripe, unripe, and artifical fruits. We first offered the bats ripe fruits and documented their foraging behavior using multiflash stereophotography combined with simultaneous sound recordings. Both species showed a similar, stereotyped foraging pattern. In *search flight*, the bats circled through the flight cage in search of a branch with ripe fruit. After finding such a branch, the bats switched to *approach behavior*, consisting of multiple *exploration flights* and the *final approach* when the bats picked up the fruit at its tip and tore it off in flight. Our behavioral experiments revealed that odor plays an important role in enabling *Carollia* to find ripe fruit. While foraging, *Carollia* always echolocated and produced multiharmonic, frequency-modulated (FM) signals of broad bandwidth, high frequency, short duration, and low intensity. We discriminated an *orientation phase* (mostly a single pulse per wingbeat) and an *approach phase* (groups of two to six pulses per wing beat). We conclude from the bats' behavioral reaction to real and artificial fruit as well as from characteristic patterns in their echolocation behavior that during exploration flights, *Carollia* changes from primarily odor-oriented detection and initial localization of ripe fruit to a primarily echo-oriented final localization of the position of the fruit.

Key words Bats · Phyllostomidae · Echolocation · Foraging behavior

Introduction

The Neotropical family of leaf-nosed bats (Phyllostomidae), with about 140 species (Koopman 1993) is one of the most diverse families of bats, not only in terms of species numbers, but also in their diet, which ranges from small vertebrates and invertebrates to fruits, pollen, nectar, leaves, and blood (see Findley 1993). Although phyllostomids use a wide variety of foods they live in remarkably similar habitats, mostly forests.

The perceptual difficulties all phyllostomids face when foraging in and around vegetation and searching for food in the darkness are similar: orientation in space, obstacle avoidance, and detection and acquisition of food. Since leaf-nosed bats echolocate (e.g., Barclay et al. 1981; Belwood 1988; Howell 1974) and produce short, multiharmonic, downward frequency-modulated (FM) signals of low sound pressure level (SPL), they could possibly use echolocation to perform those tasks. Short, broadband FM signals are well suited for exact localization and spectral characterization of targets (e.g., Schnitzler and Henson 1980; Simmons et al. 1995). However, because these bats glean mostly stationary food from vegetation or the ground (e.g., insects or fruits), the returning echoes of the food are often buried in a multitude of clutter-echoes from leaves, branches, and surfaces on which the food rests (highly cluttered space). In this situation, echolocation may provide only limited information (e.g., Schnitzler and Kalko 1998). There is evidence that foraging phyllostomids also use other sensory cues to find food. These include acoustic cues such as the mating calls of frogs and katydids (e.g.,

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Belwood 1988; Tuttle et al. 1985), olfactory cues of fruits and flowers (e.g., Dobat and Peikert-Holle 1985; Laska 1990b; van der Pijl 1957, 1982) or, under favorable circumstances, even visual cues (Bell 1985; Bell and Fenton 1986; Chase 1981; Chase and Suthers 1969; Hessel and Schmidt 1994; Joermann et al. 1988). Because most of the behavioral studies to date have been conducted under laboratory conditions with trained bats and artificial targets, and only few studies have been performed under natural or semi-natural conditions (e.g., Barclay et al. 1981; Bell 1985; Tuttle and Ryan 1981), for many phyllostomids, the significance of echolocation and other sensory cues in the context of foraging behavior is still unknown (Fenton 1995).

As a step toward filling this gap, we studied echolocation and foraging behavior of two frugivorous phyllostomids, *Carollia perspicillata* and *C. castanea*, as they feed on pepper plants (Piperaceae), their preferred natural food (e.g., Bonaccorso 1979; Fleming 1988). *Piper*, a shrub or small tree, is a pioneer plant in forest regeneration and grows in the forest understory, at forest edges, and in gaps. Its fruits are characterized by a suite of characters that are associated with dispersal by bats (Dobat and Peikert-Holle 1985; van der Pijl 1957, 1982). They ripen and become soft in late afternoon, remain greenish when ripe, and produce a typical "peppery" scent. Characteristically, *Piper* fruits have an erect, spike-like form and they stand out somewhat from the surrounding foliage. The bats could percieve characteristics of *Piper* fruits by means of echolocation (shape, surface structure), olfaction (scent) and, under favorable conditions, by vision.

To clarify which roles these cues play for a foraging *Carollia*, and to determine the relative role of echolocation for orientation in space and possibly also for detection and localization of *Piper* fruit, we first offered a branch with ripe and unripe *Piper* in a semi-natural setting in a flight cage to newly caught, untrained bats and simultaneously recorded their echolocation and foraging behavior. We then exposed the bats to a number of behavioral experiments in which we altered the properties of natural and artificial *Piper* fruits by manipulating their odor, shape, and surface structure. We wanted to answer the following questions. What characterizes the echolocation and foraging behavior of *Carollia* feeding on *Piper* fruits? What roles do echolocation and other sensory cues play in their foraging behavior?

Methods

Study site and animals

The study was conducted from December 1992 to March 1993 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 semi-deciduous, tropical lowland forest in several successional stages. Annual rainfall of about 2,600 mm is seasonal, with a dry period between mid-December and mid-April (Leigh

and Wright 1990). The two frugivorous phyllostomids, *C. perspicillata* and *C. castanea*, are common on BCI (Handley et al. 1991; Kalko et al. 1996a). We captured bats with mist nets over streams and trails close to fruiting *Piper* plants. Nets were open between 6:30 p.m. (onset of darkness) and 10:00 p.m. We studied 19 *Carollia*: 9 *C. perspicillata* (6 females, 3 males) and 10 *C. castanea* (3 females, 6 males, 1 unsexed). Species identification was based on morphological characteristics including body size, color, banding pattern of the fur, and shape of the 4th lower premolar (C.O. Handley, personal communication).

Sound recordings and analysis

Echolocation signals were picked up with an ultrasound microphone of a custom-made bat detector and recorder (delay line; University of Tübingen). The ultrasound signals were amplified, digitized, stored in a buffer (memory set at 3.3 s) and transferred at reduced speed (1/15 and 1/16) to a Sony-Walkman Professional recorder. The frequency response of the recording system was flat within less than 5 dB in the frequency range of the echolocation signals. We analyzed sound sequences with a SONA PC color spectrogram frequency analyzer (B. Waldmann, University of Tübingen), using a Fast Fourier Transformation (FFT). Signals were displayed as color sonagrams (400 lines) in 12 ms segments using a Hanning Window 256 at a frequency range of 160 kHz. This setting gave a frequency resolution of 345 Hz, and a time resolution of 37.5 μs (interpolated). The measurement points were set −40 dB below maximum.

We analyzed the harmonics with the highest energy content for each species. The harmonically structured signals of phyllostomids are filtered while passing through the vocal apparatus, so that only parts of the signal produced by the larynx are emitted (Fig. 1) (H.-U. Schnitzler, unpublished data). In both species, we classified the highest and lowest frequency of the harmonic signal measured in the sonagrams at −40 dB below maximum SPL as upper boundary (ub), and lower boundary (lb). Within these boundaries, the signals contain mostly parts of the 2nd and 3rd harmonic in *C. perspicillata* and mostly parts of the 3rd and 4th harmonic in *C. castanea*. Then we measured in *C. perspicillata* the terminal frequency (TF) of the 3rd harmonic (4th in *C. castanea*) and the starting frequency (SF) of the 2nd harmonic (3rd in *C. castanea*). To describe and compare signals unambiguously by their harmonic structure and their upper and lower boundaries, we reconstructed the lower harmonic (2nd harmonic in *C. perspicillata*, 3rd in *C. castanea*) by calculating its terminal frequency TF_{calc}
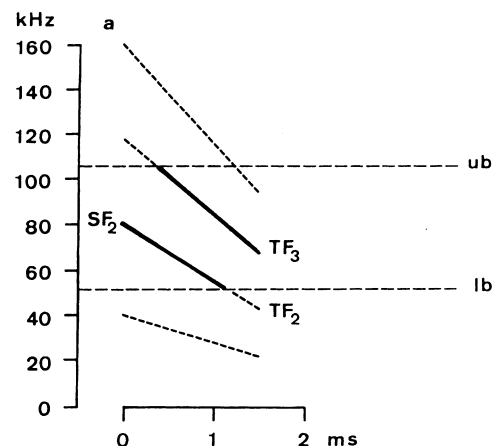

Fig. 1 Schematic representation of the structure of an orientation phase signal of *Carollia perspicillata*. The emitted parts of the signal are illustrated as *solid lines* in the sonagram, the reconstructed parts are depicted as *dotted lines* (*ub* upper boundary, *lb* lower boundary, *SF* starting frequency, *TF* terminal frequency)

$(TF_{2calc} = TF_3/3 \times 2$ in *C. perspicillata* and $TF_{3calc} = TF_4/4 \times 3$ in *C. castanea*).

We analyzed characteristic sound parameters, including upper- and lower-boundary frequency, starting and terminal frequencies of the harmonics, bandwidth (measured between upper- and lower-boundary frequency), sound duration, pulse interval (measured from the beginning of a signal to the beginning of the next signal), duration of signal groups (interval between the first pulse of a signal group and the first pulse of the following signal group), duty cycle (proportion of time filled with sound), sweep rate of the lower harmonic (SF_2–TF_{2calc}/sound duration in *C. perspicillata* and SF_3–TF_{3calc}/sound duration in *C. castanea*), and frequency overlap between the 2nd and 3rd harmonic in *C. perspicillata* and between the 3rd and 4th harmonic in *C. castanea* (SF–TF). All data on sound analyses are given as mean values of sample size $\pm$ 1 standard deviation. A general *t*-test was applied for comparisons. We chose a level of significance of $P < 0.001$.

Photography of foraging behavior

We monitored the foraging behavior of the bats in the flight cage with a night vision scope (Type Wild), two 35-mm cameras (Nikon F301; Nikon Nikkor 2.0/35), and 12 electronic flashes (Metz Mecablitz 45 CT3). The cameras were mounted 0.98 m apart on a bar, with the 12 flashes spaced between them, on top of a tripod. This allowed a three-dimensional reconstruction of photographed sequences. The bats were observed with the night vision scope. When a bat flew into the observation area, the multiflash array was triggered manually. The shutters of the cameras opened ($F = 5.6$ or 8) and remained open while the flashes automatically released in succession (flash duration approximately 1/1,000 s, flash interval 45 or 50 ms). With each flash, an electronic synchronization pulse registered on the simultaneous sound recordings, thus allowing the correlation of foraging and echolocation behavior. We used Kodak TMax 400 film (black and white, 400 ASA).

For analysis, we projected the photographic negatives on a magnetic tablet (Bitpad, Summagraphics) and digitized the data points. Custom-made computer programs were used to reconstruct and analyze the three-dimensional flight path of the bat and the position of the *Piper* fruit. To relate signal emission to the bat's flight behavior, we correlated both behaviors and calculated for each echolocation pulse the bat's position in three-dimensional space. For more details see Kalko (1995) and Schnitzler et al. (1994).

Setup in the flight cage

To document foraging and echolocation behavior, we released one or two wild, untrained *Carollia* into a flight cage (4.4 × 4.5 × 2.1 m) and exposed them to various setups. We mounted an ultrasound microphone on a stand together with a branch of *Piper* with several unripe fruits and one ripe or artificial fruit about 0.9 m above the ground. Ripe fruits were collected each afternoon and offered the same night to the bats. First, a ripe *Piper* fruit (*P. aequale*, *P. dilatatum*, *P. grande*, or *P. marginatum*) was fixed with tape directly in front of the microphone. The setup was positioned in a corner of the flight cage, about 0.5 m from the walls. The multiflash array and the delay line for sound recordings were 2.8 m from the microphone. A 25 W red light bulb (not infrared), additionally darkened with a red plastic cover, dimly illuminated the flight cage, just enough to make it possible to observe the behavior of the bats with a night vision scope (Wild). Some experiments were conducted in total darkness without any artificial light.

We started observations at 6:00 p.m. and ended them at 11:00 p.m., or when there were no more *Piper* fruits. We fed *C. perspicillata* between recording nights with bananas or papayas. *C. castanea* would not feed on these fruits and had to be released after a study session on the night it was captured. To minimize learning effects, individual *C. perspicillata* were kept no more than 4 nights in the flight cage.

To determine the sensory cues used by *Carollia* to detect, identify, and localize ripe fruits, we conducted experiments with artificial fruits whose odor, surface structure, and/or form were manipulated. Each bat was subjected only once to each experiment. On consecutive nights, one or two experiments were conducted with each bat. For each trial, we fixed one imitation fruit with tape onto a branch with unripe, natural fruits and offered it to a bat. We noted whether the bat approached or ignored the experimental setup and counted the number and types of approaches. Each experiment continued as long as the bat reacted towards the experimental setup. An experiment was scored as negative when the bat did not show a clear reaction towards the setup within its first 20 min in the flight cage. During an experimental session, we changed the location of the setup several times to avoid spatial learning by the bats.

Database

The study included 234 h of observation on 42 nights (15 nights with *C. castanea* and 27 nights with *C. perspicillata*) between December 1992 and March 1993. On 13 of these nights, we conducted experiments with imitation fruits. We took a total of 431 photographs and recorded 495 min of slowed-down echolocation sequences. We made a catalogue of all recordings and photographs and selected for analysis 65 echolocation sequences of *C. perspicillata* totaling 368 signals (22 orienting sequences with 111 signals and 43 approach sequences with 257 signals) together with 64 echolocation sequences of *C. castanea* totaling 690 signals (19 orienting sequences with 80 signals and 46 approach sequences with 610 signals). To compare the echolocation behavior of bats approaching imitation fruits, we took five approach sequences from *C. perspicillata* and three from *C. castanea* with good signal-to-noise ratio. To illustrate typical behaviors (foraging on real ripe *Piper* and experimental trials) we selected six stereophotographs of *C. perspicillata* and eight stereophotographs of *C. castanea* which were synchronized with good sound recordings and were suited for three-dimensional reconstruction. In our descriptions, we also included all relevant information from the remaining photographs which were either not suited for three-dimensional reconstruction or lacked good sound recordings.

Results

Inspection behavior

Before beginning to forage, *Carollia* released in the flight cage for the first time immediately began to inspect the cage. They flew 0.5–1.0 m above the ground along the walls or hovered up and down the walls without crossing the free space in the center of the cage. The bats did not show any obvious reaction to the experimental setup of branches with ripe *Piper* fruits. Flight speed ranged between 2 and 3 m/s. We observed this inspection of the flight cage only during each bat's first night in the flight cage. Later, the bats used every part of the flight cage, and flights were always conducted to find food.

Foraging behavior

To document their foraging and echolocation behavior, all 19 *Carollia* were first exposed to a branch with one

ripe and several unripe fruits. Without exception, all bats released in the flight cage foraged. Foraging behavior was similar in both *Carollia*. It began with search behavior and ended with approach behavior.

Search behavior

Bats that were familiar with the flight cage began foraging by circling through the cage about 0.2–1 m above the ground at a flight speed of 2–3 m/s. This behavior ended when the bats directed their attention towards the branch with the ripe fruit.

Approach behavior

This stage began with exploration flights, in which *Carollia* flew in narrow circles below the branch at heights of 0.2–0.5 m at a speed of 2 to 3 m/s. Circling below the ripe fruit was always the first stage of approach behavior. This stage was followed by passing close to the food (Fig. 2a). At a distance of about 1 m from the branch, the bats started to ascend until they were at the level of the fruit. They then passed within a few centimeters of the fruit (Fig. 2a) and frequently hovered in front of it (Fig. 3a). At this point, *Carollia* reduced flight speed, so that for several hundred milliseconds it came almost to a standstill (Fig. 3a). In the *final approach*, the bats grasped the tip of the fruit by mouth (Fig. 4a), tore the whole fruit-spike off, and carried it away to a dining roost where they ate it. The bats always attacked the fruit at its tip or highest point, whether the fruit was erect or U-shaped as in *P. marginatum*. Taken together, all stages of approach behavior lasted between a few seconds and 5 min.

We observed the behavioral stages of passing close to the fruit and hovering in front of it in any order and frequency. After multiple close passes, the bats often started again with large circles through the flight cage and small circles below the branch with the ripe fruit. In some cases, when the ripe fruit could not be dislodged at first, the bats tried several times to tear it off. These attempts were often preceded by repeated exploration flights.
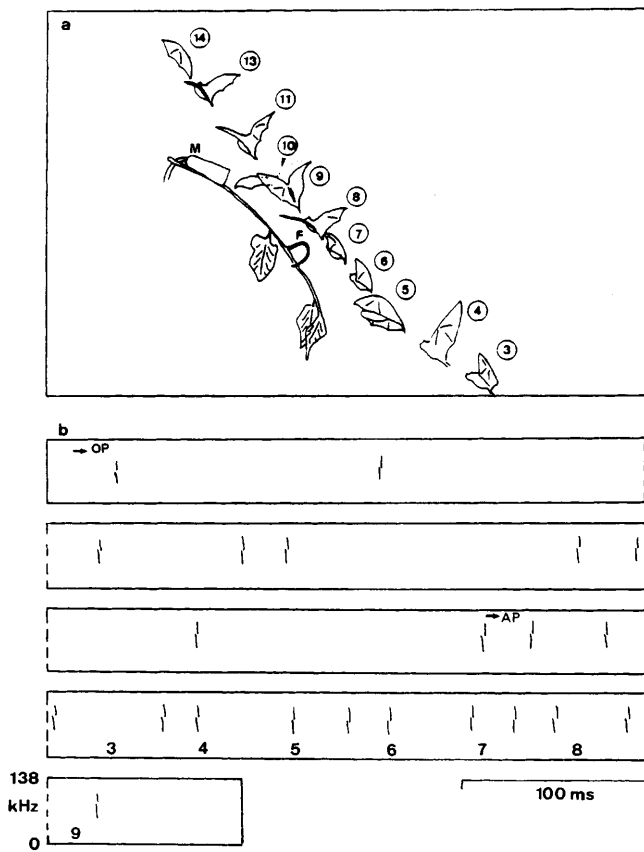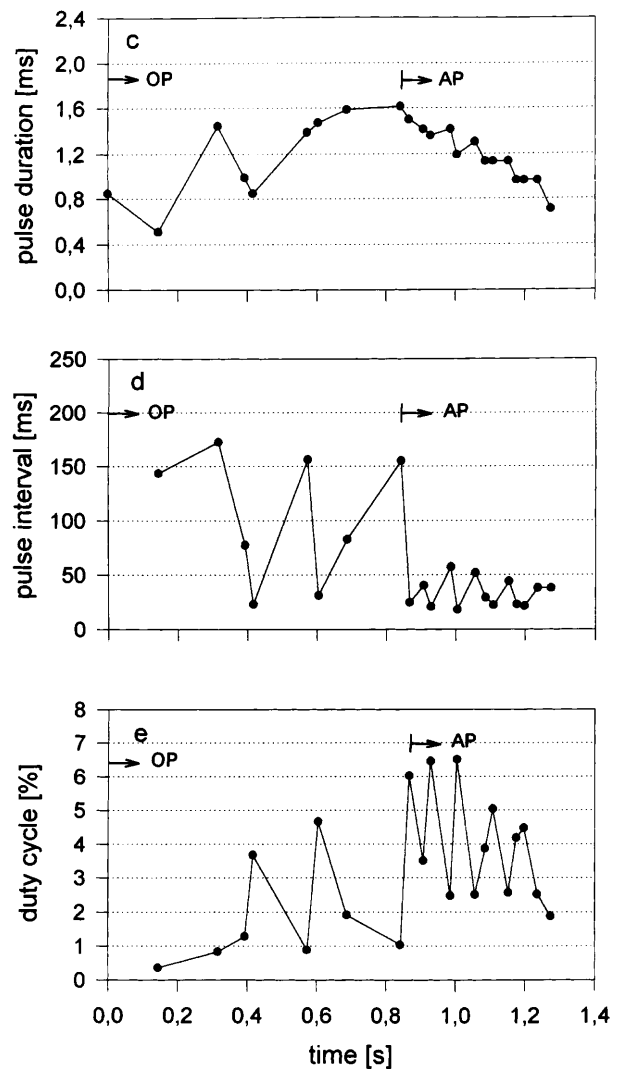

Fig. 2a–e Flight and echolocation behavior of *C. perspicillata* passing close to a branch with a ripe fruit (*F*) during an exploration flight (*OP* orientation phase, *AP* approach phase). **a** Eleven images of the same bat (numbered *3–14*) (*M* microphone). **b** Schematic drawings of sonagrams of the echolocation signals emitted by the bat during the passing flight. *Numbers* correspond to the photographic images. **c** Plots of signal duration. **d** Plots of the pulse intervals. **e** Plots of the duty cycle of the sound sequence emitted by the passing bat
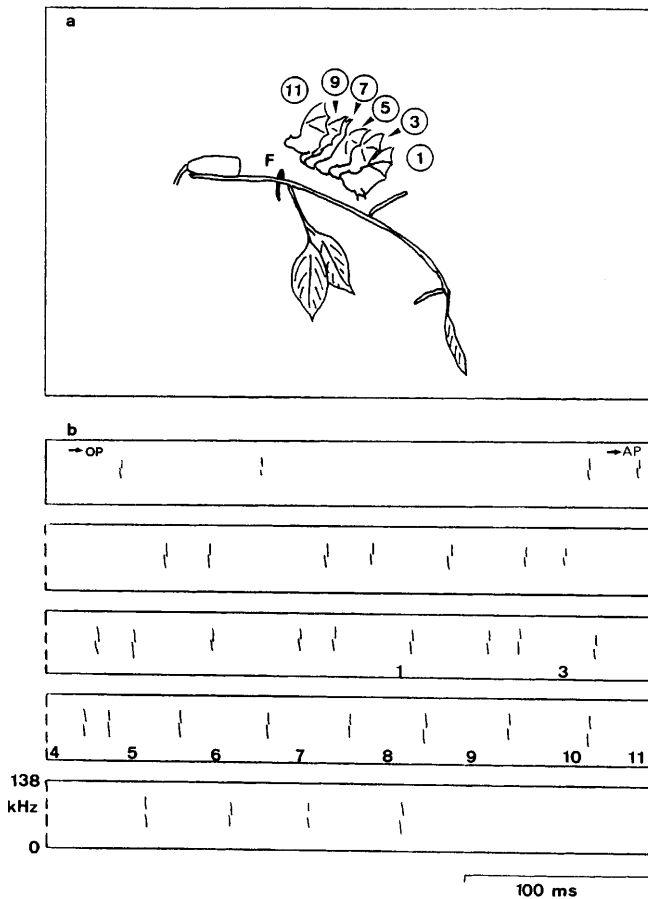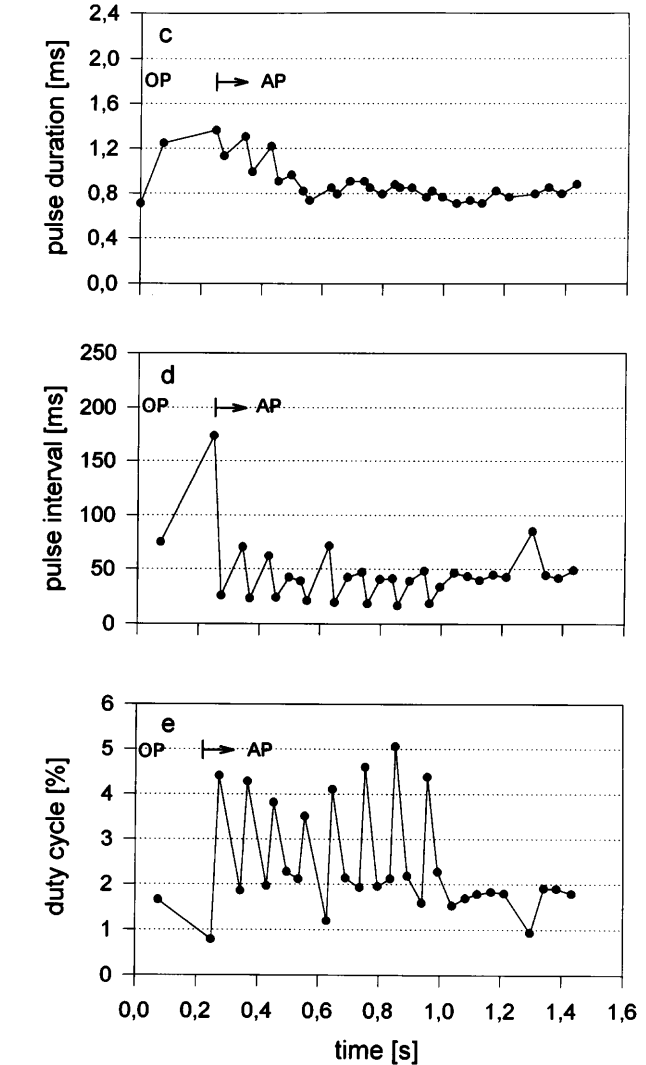
Fig. 3a–e Flight and echolocation behavior of *C. perspicillata* hovering in front of a ripe fruit during an exploration flight. See legend to Fig. 2 for definitions

The full-length exploration flight was shown only during the first 2 nights an individual bat spent in the flight cage. After this, the bats shortened the approach behavior, especially when the branch with the ripe fruit was offered more than twice in the same place. In this case, circling was not observed, and passing and hovering were drastically reduced. After 4 nights, approach behavior was observed only on the first fruit pickup. Thereafter, the bats often headed straight from their roost to the fruit.

To test whether the dim light in the cage influenced the behavior of the bats, individual *Carollia* were released into the flight cage on four occasions in complete darkness. Their behavior was followed by listening with headphones to the heterodyned echolocation signals of the bat detector. The bats searched for and picked up ripe fruits successfully and at similar speeds in the darkness and under dim light conditions.

Echolocation behavior

When flying, both *Carollia* species continuously emitted multiharmonic FM signals of short duration and wide bandwidth (Figs. 5a,b,6a,b). Their echolocation behav-

ior was characterized by two distinct phases: orientation and approach.

Orientation phase

We define as orientation phase, the part where the bats did not show a distinct reaction in their echolocation behavior (Figs. 2b, 3b, 4b) towards a target and emitted multiharmonic FM signals (Figs. 5a, 6a). They produced short signals (<2 ms) in a fairly regular pattern, mostly with one signal but rarely with two signals per wingbeat (Figs. 2d, 3d, 4d). The duty cycle was low (Table 1) and oscillated from $<1\%$ between signal groups to about 5–6% within signal groups (Figs. 2e, 3e, 4e).

Comparison of the orientation phase in the two species revealed significant differences in sound duration, duty cycle, harmonic structure, frequency range, and sweep rate (Table 2). Sound duration was shorter and the duty cycle lower in *C. castanea*. In *C. perspicillata*, most energy was concentrated in the 2nd
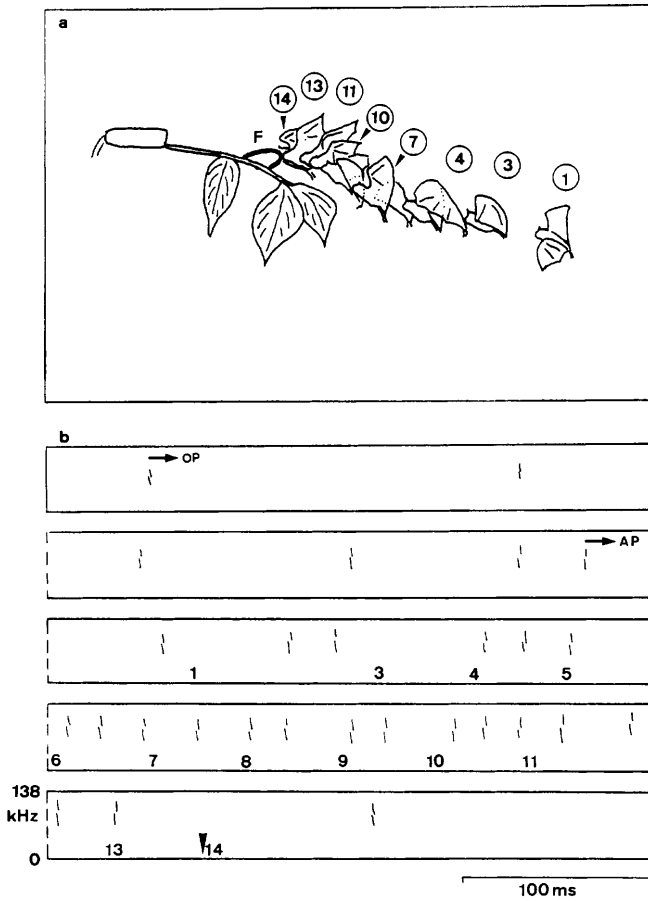
Fig. 4a–e Flight and echolocation behavior of *C. perspicillata* during the final approach, tearing a ripe fruit off. The *arrowhead* in **b** marks the removal of the fruit. See legend to Fig. 2 for definitions

and 3rd harmonic and in *C. castanea* in the 3rd and 4th harmonic (Figs. 5a, 6a). Occasionally, a lower harmonic was visible (Fig. 6a). The frequency range (characterized by the upper and lower boundary) of the multiharmonic signals emitted by *C. castanea* was higher (115–72 kHz) than in *C. perspicillata* (102–59 kHz) (Tables 1, 2). The sweep rate was 24 kHz/ms at the 2nd harmonic in *C. perspicillata* and 30 kHz/ms at the 3rd harmonic in *C. castanea*. Pulse interval, bandwidth, and overlap of the two strongest harmonics did not differ significantly between the species. Bandwidths of the multiharmonic signals were high and averaged 43.9 kHz in *C. perspicillata* and 42.4 kHz in *C. castanea*. The two strongest harmonics in both *Carollia* overlapped in frequency for 10–12 kHz.

Approach phase

We define as approach phase, the part of the echolocation behavior in *Carollia* in which the bats indicate their reaction to a target by changing pulse duration, pulse interval, and pulse structure. The approach phase begins with the first distinct reduction of pulse duration and
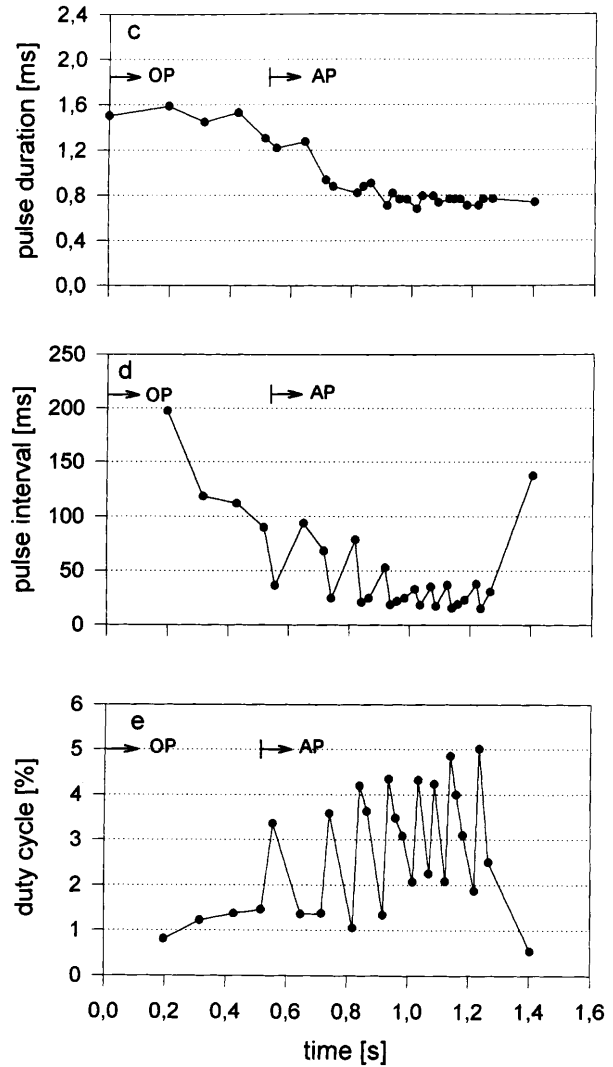
pulse interval, i.e., when the bats continuously emit groups of signals (Figs. 2b–e, 3b–e, 4b–e). Hence, in both *Carollia*, the approach phase differed from the orientation phase in having significantly shorter sound durations and pulse intervals (Table 1). With the beginning of the approach phase, *C. perspicillata* and *C. castanea* produced signal groups of two to six pulses (Figs. 2d, 3d, 4d). Almost simultanously with the beginning of the reduction in pulse interval, pulse duration was reduced to 0.8 ms (Figs. 3c, 4c). This value was reached after two to four signal groups and stayed constant until the end of the approach phase. The duty cycle did not increase markedly compared with the orientation phase. The frequency overlap between the two strongest harmonics was significantly reduced in both species from 10–12 kHz in the orienting phase to 5–7.5 kHz (Table 1). Bandwidth differed little between orienting and approach but, due to the shorter signals, the sweep rate increased from 24 to 39 kHz/ms in *C. perspicillata* and from 30 to 39 kHz/ms in *C. castanea*. In our study, even under optimal conditions, good recordings of orienting signals could only be obtained
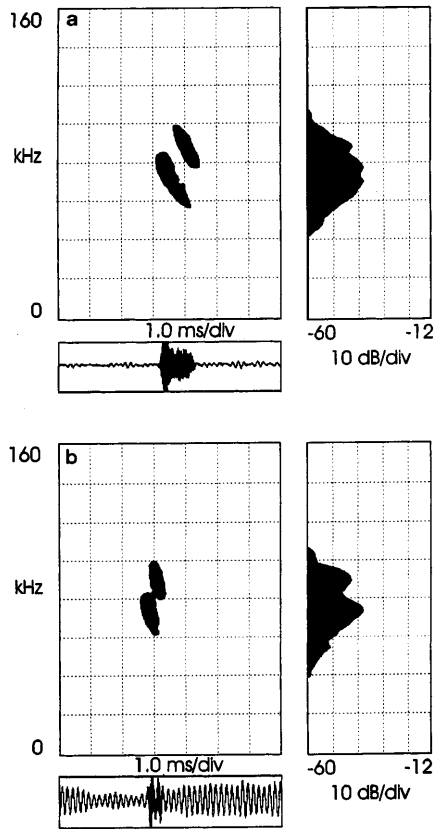
Fig. 5 Typical multiharmonic (frequency-modulated) FM signal of *C. perspicillata* with sonagram (frequency versus time), oscillogram, and averaged spectrum in the orienting phase (**a**) and approach phase (**b**)

Fig. 6 Typical multiharmonic FM signal of *C. castanea* with sonagram (frequency versus time), oscillogram, and averaged spectrum in the orienting phase (**a**) and approach phase (**b**)

when the bat was 2 m or less from the microphone, due to low signal SPL. Signals during the approach phase were even fainter.

Comparing their approach phases, the two *Carollia* species revealed, as in the orienting phase, significant differences in frequency structure, frequency range, and sound duration (Table 2). *C. castanea* produced significantly shorter signals of higher frequency than *C. perspicillata*. Pulse interval, bandwidth, and overlap of the two strongest harmonics were similar for both species.

Correlation of foraging and echolocation behavior

The transition from orientation phase to approach phase in echolocation behavior did not coincide with the transition from search to approach stages in foraging behavior. During search behavior and in the first part of exploration flights when the bats were 0.6–1.1 m away from the branch with the fruit, they emitted orientation signals. When the exploration flight brought the bats closer to the branch (< 1 m), the echolocation behavior switched into the approach phase.

In approach phases, differences in the number of pulses per signal group and duration of pulse intervals
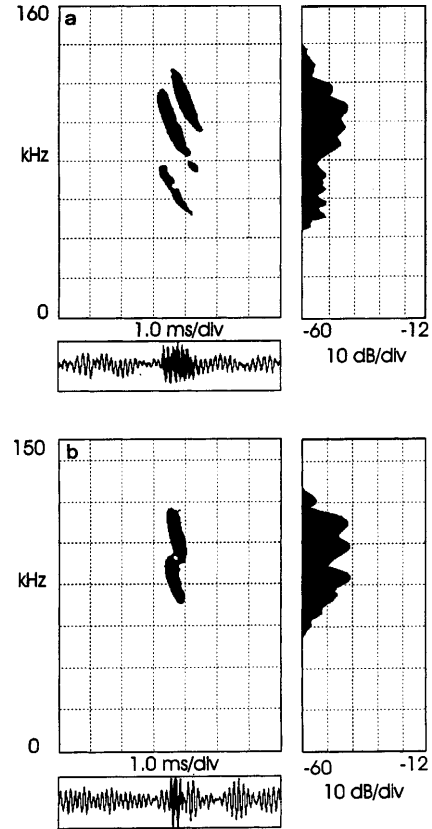
were related to passing, hovering, and final approach. Because none of the photographs for *C. castanea* in those behavioral situations were suitable for three-dimensional reconstruction of the flight path, we refer only to the results with *C. perspicillata*. However, in view of the overall similarities in the echolocation and foraging behaviors of the two species, the results for *C. perspicillata* should be applicable to *C. castanea* as well.

When passing close to a fruit, *C. perspicillata* emitted signal groups of no more than two to three pulses, with a minimal pulse interval of 20–25 ms (Fig. 2d). When hovering in front of the fruit, the echolocation behavior of *C. perspicillata* began with signal groups of two to three pulses, then changed to individual signals with regular pulse intervals of 43–45 ms (Fig 3d). When tearing off the fruit, *C. perspicillata* emitted signal groups with two to four, sometimes up to six pulses (Fig 4d). The pulse intervals reached a minimum of 13–15 ms.

Correlation of wingbeat and sound emission

The photographic sequences show that *C. castanea* and *C. perspicillata* usually emitted one signal or one signal group per wingbeat during orientation phase and approach phase (Figs. 2a, 3a, 4a). When emitting signal

Table 1 Comparison of orienting versus approach phase in *Carollia perspicillata* and *C. castanea*. Values in parentheses are the number of signals. (*ub* upper boundary, *SF* starting frequency, *TF* terminal frequency, *lb* lower boundary)

	Orienting phase	Approach phase	t	P	df
C. perspicillata					
Pulse interval (ms)	82.2 ± 51.0 (90)	42.2 ± 25.8 (194)	−8.784	0.000	282
Pulse duration (ms)	1.5 ± 0.4 (111)	0.8 ± 0.2 (257)	−22.410	0.000	366
Duty cycle (%)	2.3 ± 1.2 (90)	2.4 ± 1.1 (194)	0.284	0.804	282
ub_3 (measured) (kHz)	102.0 ± 4.2 (111)	104.1 ± 5.2 (257)	3.115	0.002	366
TF_3 (measured) (kHz)	75.0 ± 3.5 (111)	78.0 ± 3.5 (257)	7.337	0.000	366
SF_2 (measured) (kHz)	84.9 ± 4.0 (111)	82.9 ± 4.3 (257)	−4.272	0.000	366
lb_2 (measured) (kHz)	58.5 ± 6.0 (111)	59.1 ± 6.0 (257)	0.967	0.334	366
TF_2 (calculated) (kHz)	50.0 ± 2.3 (111)	52.0 ± 2.4 (257)	7.337	0.000	366
Bandwidth (kHz)	43.9 ± 7.8 (111)	45.0 ± 8.4 (257)	1.151	0.250	366
$Sweep_2$ (kHz/ms)	24.0 ± 5.1 (111)	39.3 ± 7.0 (257)	20.600	0.000	366
$Overlap_{2 \text{ and } 3}$ (kHz)	9.9 ± 3.9 (111)	4.9 ± 4.0 (257)	−11.059	0.000	366
C. castanea					
Pulse interval (ms)	76.9 ± 26.7 (61)	38.2 ± 15.5 (545)	−16.943	0.000	604
Pulse duration (ms)	1.2 ± 0.4 (80)	0.8 ± 0.1 (610)	−20.001	0.000	688
Duty cycle (%)	1.6 ± 0.6 (61)	2.3 ± 1.1 (545)	5.083	0.000	604
ub_4 (measured) (kHz)	114.8 ± 3.9 (80)	114.4 ± 4.0 (610)	−0.836	0.403	688
TF_4 (measured) (kHz)	86.9 ± 4.4 (80)	87.2 ± 3.9 (610)	0.552	0.580	688
SF_3 (measured) (kHz)	98.4 ± 7.0 (80)	94.7 ± 4.3 (610)	−6.631	0.000	688
lb_3 (measured) (kHz)	72.4 ± 6.6 (80)	69.6 ± 4.9 (610)	−4.667	0.000	688
TF_3 [calculated] (kHz)	65.2 ± 3.3 (80)	65.4 ± 2.9 (610)	0.553	0.581	688
Bandwidth (kHz)	42.4 ± 6.2 (80)	44.8 ± 5.9 (610)	3.458	0.000	688
$Sweep_3$ (kHz/ms)	29.6 ± 7.1 (80)	39.1 ± 5.9 (610)	13.134	0.000	688
$Overlap_{3 \text{ and } 4}$ (kHz)	11.4 ± 6.9 (80)	7.5 ± 5.3 (610)	−6.068	0.000	688

Table 2 Statistical comparison of orienting phase and approach phase in *C. perspicillata* versus *C. castanea* foraging for ripe *Piper* fruit in the flight cage (for abbreviations, see legend to Table 1)

	Orienting phase			Approach phase		
	t	P	df	t	P	df
Pulse interval (ms)	0.748	0.455	149	2.566	0.010	737
Pulse duration (ms)	5.869	0.000	189	−4.739	0.000	865
Duty cycle (%)	4.675	0.000	149	0.491	0.623	737
$ub_{3/4}$ (measured) (kHz)	−20.826	0.000	189	31.213	0.000	865
$TF_{3/4}$ (measured) (kHz)	−20.958	0.000	189	32.696	0.000	865
$SF_{2/3}$ (measured) (kHz)	−16.732	0.000	189	36.844	0.000	865
$lb_{2/3}$ (measured) (kHz)	−15.326	0.000	189	26.672	0.000	865
$TF_{2/3}$ (calculated) (kHz)	−37.532	0.000	189	65.179	0.000	865
Bandwidth (kHz)	1.457	0.147	189	−0.292	0.77	865
$Sweep_{2/3}$ (kHz/ms)	−6.311	0.000	189	−0.526	0.599	865
Overlap (kHz)	−1.982	0.049	189	2.345	0.019	865

groups, the bats produced the first one to two pulses during the upstroke of the wingbeat. The last pulses of the group were produced at the beginning of the downstroke (powerstroke). Hovering in front of the fruit presents a special case. The bats emitted signals with regular pulse intervals of 43–45 ms, which corresponds to two pulses per wingbeat. Thus, one pulse was emitted during the forward stroke of the wingbeat and another during the backward stroke.

Echo overlap

The simultaneous recording of the foraging and echolocation behaviors of *C. perspicillata* allowed us to demonstrate the relationship between pulse duration and distance from the fruit during the final approach. At the beginning of the approach phase, the pulse duration in *C. perspicillata* decreased continuously from approximately 1.3 ms to about 0.8 ms (see Figs. 2c, 4c) at which point the bat was 20–40 cm from the fruit. At this minimum value, overlap between emitted signal and echo from the target was avoided as long as the bat was at least 13.6 cm from the fruit. Sound recordings revealed that *C. perspicillata* stopped signal emission 30.2 ± 24.2 ms (min. 3.7 ms, max. 95.9 ms, $n = 22$) and *C. castanea* 22.4 ± 20 ms (min. 0.9 ms, max. 76 ms, $n = 14$) before tearing off the fruit. This translates at a flight speed of 1 m/s, estimated from the photographs, to mean distances of 22–30 cm with a minimum of 1–4 cm between bat and fruit. Consequently, signals at the end of the final approach frequently overlapped with echoes from the fruit (Fig. 7).

Experiments with manipulated and artificial fruits

To test the importance of odor, shape, and surface structure, and the role of echolocation in detection, classification, and localization of ripe *Piper* fruits by *C. perspicillata* and *C. castanea*, we conducted experiments with manipulated and artificial fruits (Table 3). Ten of the 19 bats (7 *C. perspicillata*, 3 *C. castanea*) were subjected to these experimental trials.

Unripe fruits of Piper

Here the shape, position, and presumably surface texture were similar to a ripe fruit, but the typical odor was lacking. If shape and/or surface texture of a *Piper* fruit were sufficient to elicit approach behavior, the bats should approach unripe fruit. However, none of the 19 *Carollia* ever approached unripe fruits even though unripe fruits were always present on the branch in the flight cage, either alone, with a ripe *Piper* fruit, or with imitation fruit (Table 3).

Artificial fruit with shape and odor of a real Piper *fruit*

We formed artificial fruits of foam rubber with approximately the same dimensions as real *Piper* fruit. We
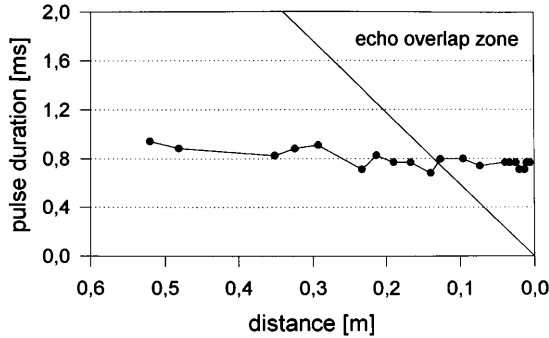

Fig. 7 Relationship between pulse duration (*y*-axis) and distance to the fruit (*x*-axis) of *C. perspicillata*. The fruit is torn off by the bat at 0 m depicted on the *x*-axis. The *solid line* marks the beginning of the zone of overlap between emitted signal and returning echo. All signals to the right of this line are within the overlap-zone

impregnated them with the sap of a ripe *P. marginatum* fruit and offered them to the bats on the branch in the typical erect *Piper* position. In this experiment, the artificial fruit resembled a real fruit except in surface texture. If shape and/or odor were sufficient for the bats to find and localize a fruit, *Carollia* should react to this artificial fruit. If surface structure is an important cue for the bats to recognize a ripe fruit, the bats should not approach the artificial fruit. The six *Carollia* tested approached the artificial fruit as they would have a real fruit. They circled below the branch, passed close to the imitation fruit, hovered in front of it, bit into it, and then flew off without taking it (Table 3).

Artificial fruit with shape of Piper *but without its odor*

As a control for the previous experiment, we offered a foam rubber fruit in the typical shape and position of a *Piper* fruit, but did not impregnate it with sap of ripe *Piper*. Thus it lacked the typical odor and surface texture of real *Piper*. If shape alone is a sufficient cue to recognize a ripe fruit, the bats should approach this artificial fruit. However, none of the five *Carollia* showed interest in the imitation (Table 3).

Artificial fruit without the shape of Piper *but with its odor*

We formed models of foam rubber in the shape of circles or triangles within the size range of real *Piper* fruits, impregnated them with the sap of ripe *P. marginatum* fruit and fixed them on the branch. Thus, while the typical odor of a real fruit was kept, shape, and surface structure were altered. If odor alone is a sufficient cue for the bats to find and localize a ripe fruit, the bats should approach this artificial fruit. The six *Carollia* exposed to this setup approached the artificial fruit (Table 3). However, although all bats tested with this model were in their first night in the flight cage and approached real ripe fruits in the standard way (circling, passing, hovering, and tearing the fruit off), they showed a reduced approach behavior towards this artificial fruit, with only a few circles below the branch,

Table 3 Behavioral reaction of *Carollia* towards artificial fruit. Data are given for *C. perspicillata*/*C. castanea*. Each bat was subjected once to each behavioral trial. A response of the bat to the experimental setup within the first 20 min was scored as reaction. In reacting bats, the number of exploration flights and final approaches were counted

Type of model	Number of bats tested	Number of bats reacting	Number of exploration flights		Number of final approaches	
			Passing	Hovering	Tearing off	Landing
Unripe *Piper*	9/10	0/0				
Piper shape, no odor	4/2	0/0				
Odor, no *Piper* shape	4/1	4/1	4/1	3/0	0/0	No/no
Piper shape, odor	4/2	4/2	10/3	7/5	7/2	No/no
No *Piper* shape, no odor	2/0	0/0				
Ripe *Piper* in gauze	3/1	3/1	5/3	7/2	38/4	Yes/yes

Table 4 Comparison of approach phase in *C. perspicillata* and *C. castanea* foraging for real ripe *Piper* fruit (for data see Table 1) versus artificial fruit in the flight cage

	Approach to artificial fruit	t	P	df
C. perspicillata				
Pulse interval (ms)	41.8 ± 23.4 (17)	0.066	0.947	209
Pulse duration (ms)	0.8 ± 0.1 (20)	−0.971	0.332	275
Bandwidth (kHz)	40.2 ± 6.2 (20)	2.479	0.014	275
Overlap$_{2 \text{ and } 3}$ (kHz)	5.7 ± 2.7 (20)	−0.870	0.380	275
C. castanea				
Pulse interval (ms)	46.0 ± 2.1 (7)	−1.328	0.185	550
Pulse duration (ms)	0.8 ± 0.1 (12)	−2.004	0.046	620
Bandwidth (kHz)	45.6 ± 5.3 (12)	−0.473	0.636	620
Overlap$_{3 \text{ and } 4}$ (kHz)	5.1 ± 3.9 (12)	1.568	0.117	620

few passes and hovering, and without attempts to bite into it (Table 3).

Artificial fruit without the shape and odor of a Piper fruit

Finally we offered artificial fruits made of foam rubber in the shape of a circle or triangle not impregnated with the sap of a ripe *Piper* fruit. The two bats tested did not react towards this model (Table 3).

Manipulated real ripe fruit, without Piper shape

This experiment was conducted to test whether the odor of a real fruit without *Piper* shape has the same effect on the bats' behavior as the artificial fruit without the shape of a real ripe fruit but prepared with its sap. In this experiment, ripe *Piper* fruit was wrapped loosely in gauze so that it formed an oval ball. If odor is a sufficient cue for detection, the bats should readily approach this model. The four bats tested showed the normal approach behavior with circling, passing, hovering, and finally landed on or near it (Table 3). However, while the bats approaching a foam rubber model in the shape of a fruit and impregnated with the odor of *Piper* gave up after they had bitten once or twice into it, they continued their attempts to tear off the wrapped fruit.

To summarize, both *Carollia* approached imitation fruits prepared with the typical odor of real ripe *Piper* fruit. They ignored unripe *Piper* fruits and imitation fruits that did not smell of ripe *Piper*. In addition to odor, the shape of the fruits was also important to the bats. A *Piper*-shaped artificial fruit with *Piper* odor evoked a strong response and an attempt to tear it off, while a non-*Piper*-shaped artificial fruit with *Piper* odor evoked only a weak response and no attempt to tear it off. A real ripe *Piper* fruit whose shape was masked with gauze elicited a strong reaction. However, presumably due to the larger size of the wrapped fruit and the lack of a pronounced tip that would allow a bat to grab it in flight, *Carollia* landed on the wrapped fruit in the attempt to tear it off.

We recorded echolocation signals in each of the experiments. The bats always emitted signals while they were flying. Generally, in the approach phase to imitation fruits, the structure and pattern of echolocation signals, including pulse interval, pulse duration, bandwidth and overlap of the strongest harmonics of *Carollia* did not differ significantly from the echolocation behavior during approaches to real fruits (Table 4). Further, we could not detect differences in echolocation behavior between the various experimental setups.

Discussion

Sensory cues used by foraging Carollia

Role of odor

Our experiments revealed that both *Carollia* species reacted towards potential food (artificial fruit and real ripe *Piper*) only when it had the typical odor of a ripe fruit. Unripe fruits which are very similar to ripe fruit in their shape, surface structure, and position, and any artificial fruit that did not smell like ripe *Piper* were ignored. We conclude that both species use odor as a primary cue for detecting ripe fruit.

The importance of odor in the foraging behavior of *Carollia* is corroborated by previous laboratory studies (Hessel and Schmidt 1994; Laska 1990a,b) and field observations (Rieger and Jakob 1988). Laska (1990a,b) used mashed banana or its odor components and demonstrated that *C. perspicillata* can recognize minute concentrations of particular odor components. Furthermore, *Carollia* can be attracted to food by its odor even in the absence of other cues (Hessel and Schmidt 1994; Laska 1990a). Similar results were obtained in the field by Rieger and Jakob (1988) with *C. perspicillata* attracted to pieces of banana wrapped in gauze hanging from a branch. Histological examinations of nasal epithelia support the morphological basis for the well-developed olfactory sense in phyllostomids (Bhatnagar 1975; Bhatnagar and Kallen 1975).

Role of shape and position

Our experiments with manipulated *Piper* fruits and artificial fruits showed that both *Carollia* species reacted most strongly to smelly models that had the shape of *Piper* and were offered on a branch in the typical *Piper* position. Other models that smelled like *Piper* but did not have the shape and/or position of a *Piper* fruit (i.e., hanging, triangular foam rubber models and real *Piper* wrapped in gauze) evoked an incomplete approach behavior. Both *Carollia* species always grasped a ripe real *Piper* fruit at its highest point in the final approach, no matter whether the fruit was erect or U-shaped. These observations indicate that shape and position play an important role in the foraging behavior of *Carollia*.

The highest point of a fruit cannot be determined precisely by odor alone, since odor spreads in air and thus gives only a rather vague indication of the location of a ripe fruit. Theoretically, *Carollia* can perceive fruit by vision or by echolocation. In our experiments, we attempted to exclude the use of vision for finding fruits by allowing only a small amount of red light in the flight cage, just enough to use a night vision scope. Furthermore, since we documented successful removal of ripe fruits in complete darkness and since the light conditions in the forest are normally very low, we suppose that vision is not necessary for the precise localization of fruit. If the bats cannot use olfaction or vision to precisely locate *Piper* fruits they must rely on echolocation.

Role of surface structure

Potentially, surface structure can be perceived by a bat by means of echolocation. *Carollia* produces broadband and high-frequency FM signals which are well suited for this task. Hence, *Carollia* could potentially use differences in surface texture as a cue to distinguish ripe from unripe fruits and fruits from other objects by analyzing differences in the spectral or temporal signature of the returning echo (Bradbury 1970; Habersetzer and Vogler 1983; Mogdans and Schnitzler 1990; Ostwald et al. 1988; Schmidt 1988; Simmons and Vernon 1971; Simmons et al. 1974, 1995). However, our study with untrained bats in the flight cage showed that both species approached, and even bit into foam rubber models of *Piper* which clearly differed in surface structure from real fruits. We conclude that surface structure does not play a crucial role in enabling *Carollia* to recognize a fruit and to distinguish it from other objects.

In summary, we conclude that odor is the primary sensory cue that *Carollia* uses for detecting ripe fruit and determining its approximate position. However, olfactory cues are not useful for determining the fruit's exact position and shape. We suggest that by approaching the odor source several times during exploration flights, the bats transfer from rather imprecise olfactory localization (passive mode) to a final approach guided by echolocation to exactly locate the fruit (active mode). Approaching a food source several times before a final approach is typical of other frugivorous (e.g., Bonaccorso and Gush 1987; Kalko et al. 1996b) and nectarivorous (e.g., Heithaus 1974; Sazima 1976, Sazima and Sazima 1978) phyllostomids which have to cope with perceptual tasks similar to those of *Carollia* while foraging.

The role of echolocation for foraging *Carollia*

Both species continuously emitted echolocation signals which we separated into orientation and approach phases. In the *orientation phase*, pulse intervals are rather long, usually with one signal emitted per wingbeat. *Carollia* produces rather short, multiharmonic FM signals with the main energy in the 2nd and 3rd (*C. perspicillata*) or the 3rd and 4th (*C. castanea*) harmonics and with a distinct overlap between harmonics. Orientation signals are emitted when the bats circle in the flight cage searching for fruit or when they circle at least once before making another approach towards a detected odor source. In neither situation do the bats approach a specific target, so we conclude that they are using echolocation only for orientation in space. Due to their short duration, broad bandwidth, high frequency, and low SPL, the signals are well suited for orientation in confined spaces, such as the forest understory. These signals allow precise localization of obstacles and produce narrow clutter overlap zones (Schnitzler and Kalko, in press). The low SPL creates less clutter due to the shorter range of weaker signals.

The *approach phase* always occurs when the bats close in on a specific target, either the branch with the odor source during exploration flights or the localized fruit in the final approach. In the approach phase, both species switch to groups of signals with more and shorter calls. Although frequency structure stays the same, overlap between the harmonics is greatly reduced or eliminated at the end of the approach phase. Characteristically, the approach phase in *Carollia* lacks a distinct terminal phase such as is found in aerial insectivores where the bats emit very short signals (0.3–0.5 ms) at high repetition rates (150–200 Hz). The lack of a terminal phase has also been described for gleaning bats of other families with different diets such as insects and small vertebrates (e.g., Anderson and Racey 1991; Barclay et al. 1981; Bell 1982, 1985; Faure and Barclay 1992; Fenton and Bell 1979; Kalko and Schnitzler, in press; Marimuthu et al. 1995).

Due to the reduced overlap of the harmonics and reduced sound duration, the approach signals are even better suited for a precise localization of targets in a confined space than are the orientation signals. With reduced overlap in the harmonics, pulse and echo produce unambiguous time markers in the corresponding frequency channels which are necessary to precisely measure target range (Schnitzler and Kalko, in press). The reduction of signal duration to 0.8 ms during the

approach phase prevents overlap of the emitted signal and echo from the fruit or overlap between echoes from the fruit and from surrounding leaves and branches at distances greater than 13.6 cm, but there is an overlap when the bat is closer to the fruit or the surrounding vegetation. This contrasts with aerial insectivores which keep potential prey in an overlap-free window (Kalko and Schnitzler 1993). They avoid overlap of emitted signals with prey echoes and overlap of prey echoes with clutter echoes by drastically reducing pulse duration and pulse interval at close range (Kalko 1995). However, whereas aerial insectivorous bats need precise information about prey movements to react towards final instant changes in prey trajectory, *Carollia* approaches a non-moving, stationary target. Furthermore, the short, multiharmonic, broadband FM signals of *Carollia* that sweep rapidly through a broad range of frequencies may be less overlap sensitive than the longer, narrowband search signals of insectivorous bats (Schnitzler and Kalko, in press).

Since the approach to a specific target such as fruit or avoidance of obstacles at close range imposes the same perceptual problem to a bat, that is, the precise localization of objects in space, the general pattern and structure of echolocation signals should be similar in both cases. Statistical comparison of echolocation calls of *Carollia* approaching ripe *Piper* or imitation fruit did not reveal significant differences in sound duration, pulse interval, bandwidth, and overlap of the strongest harmonics (Table 4), supporting the assumption that similar perceptual tasks lead to similar echolocation behavior.

Comparison of echolocation behavior in *C. perspicillata* and *C. castanea*

The two *Carollia* species had similar overall patterns and structures of echolocation signals. However, statistical comparison revealed significant differences between *C. perspicillata* and *C. castanea* in sound duration, frequency structure, and frequency range of the two strongest harmonics. We attribute these differences mainly to the differences in body mass of the species, a relationship well documented for a number of bats (e.g., Barclay and Brigham 1991). The smaller *C. castanea* (11–15 g) produced shorter and higher-frequency calls than the larger *C. perspicillata* (18–21 g).

Comparison of sensory cues used by other frugivorous phyllostomids to find fruit

Like *Carollia*, other frugivorous phyllostomids also use both olfactory cues and echolocation in foraging. However, the degree to which odor and echolocation are used appears to depend on how a fruit is displayed to a bat. For instance, neotropical figs, which are preferably taken by the common fruit bat, *Artibeus jamaicensis*,

remain green(ish) when ripe and are nestled among leaves (Kalko et al. 1996b). Hence, echoes of ripe fruits are often masked by echoes of leaves and unripe fruit, making it unlikely that a bat can find ripe fruit by echolocation alone. Behavioral experiments show that *A. jamaicensis* detects, localizes, and classifies ripe fruits mostly by their characteristic scent (Kalko et al. 1996b). As in *Carollia*, echolocation information is used for orientation in space and for obstacle avoidance. Only at close range may echolocation play a role in the final localization of a fruit so that it can be taken in flight.

Another problem has to be solved by the omnivorous spear-nosed bat, *Phyllostomus hastatus*, when it feeds on fruits of *Gurania spinulosa* (Cucurbitaceae), a vine whose ripe fruits are presented on leafless branches dangling in open spaces in the forest canopy. Here, the echolocation task is easier because the echo of the exposed fruit is not usually buried in clutter. Experiments with artificial fruits have shown that *P. hastatus* uses echo information for detecting and localizing fruits, while odor may serve for distinguishing between ripe and unripe fruits at close range (Kalko and Condon, in press).

Foraging behavior of the two *Carollia* is intermediate between these two extremes. They use odor as the primary sensory cue indicating the general location of ripe fruit, but after sufficient exploration, echolocation can be used for precise fruit localization. This is facilitated by the exposed position and the elongated shape of a *Piper* fruit which promotes localization of the tip of the fruit, the easiest point for the bat to grab it by mouth in flight.

These three cases show clearly that the extent to which echolocation and other sensory cues are used in foraging behavior of frugivorous phyllostomids varies with the perceptual problems confronting the bats in their habitats.

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