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Echolocation, olfaction and fruit display: how bats find fruit of flagellichorous cucurbits

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Summary

1. The relationship between plant morphology and the senses used by dispersal agents to find fruit was examined. 'Flagellichory' (fruit borne on pendulous structures), a costly morphology associated with dispersal by bats, is focused on.

2. Using *Gurania spinulosa*, a flagellichorous vine, and its major dispersal agent, *Phyllostomus hastatus*, the hypothesis was tested that flagellichory increases the conspicuousness of fruit to bats that use echolocation to find fruit.

3. The responses of wild-caught *P. hastatus* to various fruiting branch morphologies and fruit odour were recorded. *Phyllostomus hastatus* used echolocation rather than olfaction to detect fruit, and consistently chose fruit displayed on pendulous leafless branches, ignoring fruit held among leaves on horizontal branches.

4. By comparing echolocation signals with the distance between fruiting branches of *G. spinulosa* and surrounding vegetation, it was shown that pendulous fruiting branches present clear, clutter-free targets that can be detected by echolocating bats. This is the first demonstration of neotropical frugivorous bats using echolocation to find fruit.

Key-words: Dispersal syndrome, frugivore, *Gurania spinulosa*, Phyllostomidae, *Phyllostomus hastatus*

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Introduction

Frugivorous vertebrates play crucial roles in the dispersal of seeds of many plants, particularly in the tropics (see Estrada & Fleming 1993; Fleming 1993). Because seed dispersal can affect the reproductive success of plants, selection may act upon traits that affect the likelihood of dispersal. 'Dispersal syndromes' describe traits such as colour, shape, size, display, nutritional value and phenology that are associated with distinct groups of dispersers (e.g. Janson 1983; Knight & Siegfried 1983; Gautier-Hion *et al.* 1985; Moermond & Denslow 1985; Wheelwright & Janson 1985; Mack 1993). Although dispersal syndromes probably reflect dispersers' abilities to perceive and process specific sensory information such as visual and olfactory cues, few studies have used experiments to find out which senses dispersers use to find fruit (e.g. Willson & Whelan 1990).

The dispersal syndrome associated with frugivorous bats (van der Pijl 1982) includes characters such as whitish or greenish fruit colour, a strong odour of night-ripening fruit and 'flagellichory' (fruit dangling at a distance from leaves). Many bat-dispersed plants exhibit only a subset of these traits. For example, neotropical bat-dispersed figs produce a strong scent when ripe, but are nestled among leaves, not on leafless, pendulous branches (Kalko, Herre & Handley 1996). In contrast, some neotropical bat-dispersed vines (e.g. subtribe Guraniinae, Cucurbitaceae) have relatively odourless fruit and are flagellichorous (Condon & Gilbert 1988). These different modes of fruit display suggest that bats use different senses to find particular kinds of fruit.

Distinct modes of fruit display also impose quite different costs on plants. If measuring costs in terms of photosynthate, flagellichory is expensive. Long, leafless, pendulous branches, which lose the ability to climb and fall into shadier levels of the canopy, garner less photosynthate than leafy climbing branches that keep growing upwards (Condon 1984; Condon, Sasek & Strain 1992). Given the cost of hanging loose, what is the benefit to the plant?

Flagellichory could make fruit more conspicuous to dispersal agents such as echolocating bats. Frugivorous phyllostomids produce short, multiharmonic, downward frequency-modulated (FM) signals well suited for carrying information about size, shape, surface texture and position of objects as long as the object stands out from the surrounding clutter-producing background such as vegetation. Fruits borne at

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nodes of leafy branches are often 'hidden' from echolocating bats because echoes from the target overlap echoes from the clutter (Kalko & Schnitzler 1993; Schnitzler & Kalko 1998).

To test our hypothesis that flagellichory provides a clear target for an echolocating bat, we designed experiments to identify the senses used by wild *Phyllostomus hastatus* (Phyllostomidae) to find ripe fruit of *Gurania spinulosa.* The bats' foraging and echolocation behaviours were monitored simultaneously, and foraging bats' echolocation signals were compared with the positions of pendulous branches in the field.

Methods and materials

STUDY SITE

From 6 to 18 June 1993 we worked in Guatopo National Park, Venezuela, at a recreation area known as 'Agua Blanca' (10°03´N, 66°28´W, 400 m elevation), 70 km SE Caracas. Agua Blanca is in second growth forest (last cleared in the 1950s) surrounded by large tracts of undisturbed forest (Holdridge live zone: Very Humid Premontane Forest; Ewel, Madriz & Tosi 1976).

STUDY ORGANISMS

Plants

Common in Guatopo National Park, *Gurania spinulosa* (Cucurbitaceae) is a highly sexually dimorphic, functionally dioecious vine. Male branches are leafy and climb; female branches are leafless and pendulous (Condon & Gilbert 1988). Ripe fruits of *G. spinulosa* are green, relatively odourless cucumber-shaped berries (60–75 mm long x 16–20 mm wide, mass 10–20 g) that typically contain 50–75 flat seeds in a sweet juicy pulp. Unripe fruit are hard, crisp and bitter. Ripe fruits are soft, pliant and easily plucked from the vine. Each individual branch produces 7–20 fruits, with 1–3 ripening per night for about a week.

To document the spatial configuration of fruiting branches of *G. spinulosa* in the field, the lengths of the first 30 fruiting branches encountered were estimated, and their minimum horizontal and vertical distances from surrounding vegetation were also estimated (Fig. 1).

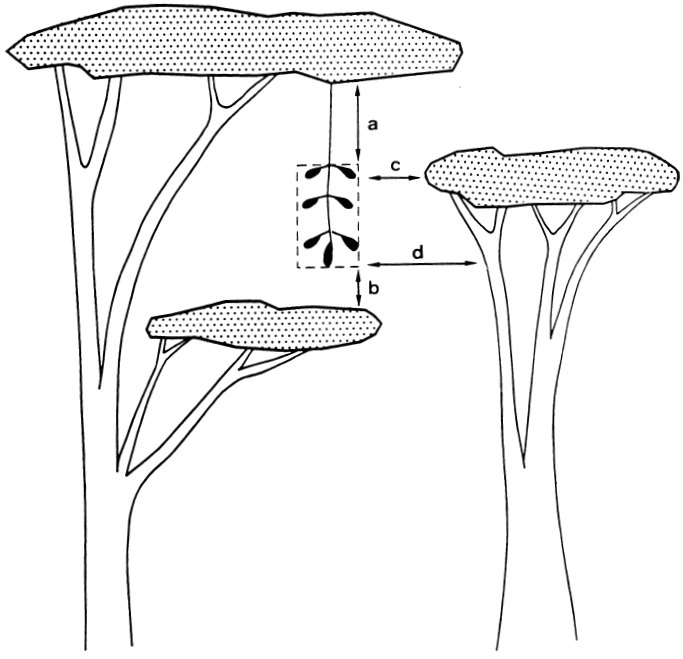

Fig. 1. Schematic drawing of a fruiting branch of *G. spinulosa* (not to scale). Distance to nearest vegetation was estimated conservatively as the (a, b) minimum vertical or (c, d) minimum horizontal distances to nearest vegetation from the top (a, c) or bottom (b, d) fruit.

Bats

Phyllostomus hastatus is a large omnivorous bat (forearm length 79–94 mm; adult mass 92–140 g) which is abundant and widespread throughout the neotropics (Emmons 1990). The fruit of *Gurania* is eaten by *P. hastatus* throughout its range (Peru, Gorchov *et al.* 1995; Trinidad, McCracken & Bradbury 1981; Venezuela, Condon & Gilbert 1990).

Wild *P. hastatus* were caught in mist nets set along flyways over streams at Agua Blanca and were kept in cloth bags until released to fly in a screen tent. Between trials, bats were housed in a wire cage and supplied with fresh water but no food. After the final trials (early the second or third evening after capture) the bats were released into the wild.

Two *P. hastatus* were radio-tagged with single stage transmitters (Custom Electronics of Urbana, Inc., Urbana, IL, USA) marked with reflective tape. The marked bats were observed foraging at *G. spinulosa* in the field.

EXPERIMENTAL ENCLOSURE AND SOUND RECORDINGS

Behavioural observations and experiments were conducted in a hexagonal screen tent (Fig. 2). For all trials, a female branch of *G. spinulosa* 1-m long was suspended from the highest point (2·5 m) in the centre of the tent. *P. hastatus* regularly removes fruit from equally low branches in the field (Condon 1984). A leafy horizontal branch was constructed by attaching fresh leafy branches of *G. spinulosa* to a string stretched taut across the widest point of the tent.

In the screen tent, bats were observed with night vision goggles (Type Wild) under low light (a headlight with dark-red plastic lens) to minimize visual cues and were photographed with a flash camera. Simultaneously, the echolocation signals of the bats were picked up by an ultrasound-sensitive microphone of a custom-made bat detector (University of Tübingen, Germany), amplified and recorded at 1/15

reduced speed on a Sony Walkman professional. From 225 min of sound recordings, 26 echolocation sequences with a total of 645 signals were selected for analysis with a custom-made program (B. Waldmann, University of Tübingen). Sequences were analysed using a Fast Fourier Transformation (FFT) with a Hanning Window 256 and a frequency range of 112 kHz. Signals were measured with cursors on the screen and displayed in 35 ms steps (vertical resolution 400 lines, horizontal 500 lines) which gave a frequency resolution of 281 Hz, and a time resolution of 0·069 ms (interpolated). The dynamic range of the frequency-analyser (– 72 dB) was restricted to – 60 dB and the measurement points were set – 40 dB below maximum. Values (sound duration, pulse interval, bandwidth) are given for the harmonic with the highest energy content (third). Data are presented as mean values of sample size ± 1 standard deviation. Student's *t*-test was used for comparisons.

BAT BEHAVIOUR TRIALS

In the screen tent, preliminary observational trials and three choice trials were conducted in which properties of 'fruit' placed on horizontal leafy branches *vs* vertical leafless branches were manipulated. During preliminary observational trials, foraging and echolocation behaviour was documented of 34 successful fruit removals by three *P. hastatus* approaching a vertical branch with ripe fruit of *G. spinulosa*.

For choice trials, one bat was worked with at a time, each being subjected to a predetermined series of trials. Five individuals were tested to determine which cues they used to find ripe fruit. The bat's behaviour and the time elapsed before the bat reacted to a fruit or a simulated fruit were recorded. If the bat did not react within an hour, its response was scored as a negative. The number of trials was limited by the difficulties in obtaining naive, wild-caught *P. hastatus* and enough fruit of *G. spinulosa* for the experimental set-up. To minimize learning effects each trial was conducted only once per bat.

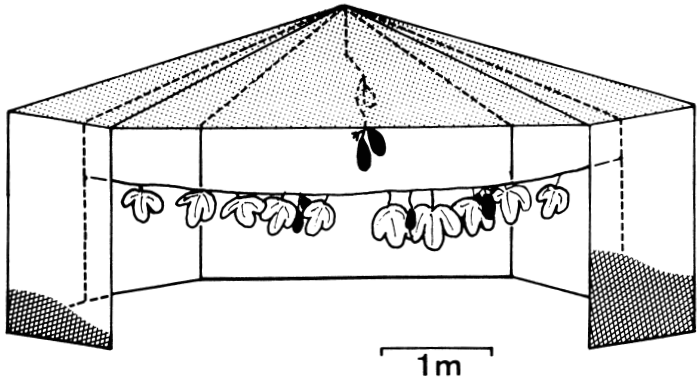

Fig. 2. Schematic drawing of the screen tent drawn to scale with one *Gurania spinulosa* branch attached horizontally and one *Gurania* branch dangling in the middle: open fruit, ripe; filled fruit, unripe.

In the first choice trial the effect of fruit display on foraging behaviour of *P. hastatus* was tested. Three fruits (one ripe and two unripe) were attached to nodes about 50 cm apart on a leafless pendulous (vertical) female branch (Fig. 2). Such spacing mimicked natural spacing of fruit on a branch at the end of a fruiting cycle. To simulate plants bearing fruit at nodes of leafy climbing branches, ripe and unripe fruits were arranged in three clusters at the bases of leaves on the horizontal branch: one cluster (two ripe fruit) was 1 m from one side of the tent; another cluster (two unripe, one ripe fruit) was 1 m from the other side of the tent; and a single unripe fruit was 30 cm from the cluster of three fruit.

In the second choice trial it was investigated whether *P. hastatus* responds to olfactory cues to find and approach *G. spinulosa* fruits. Using cotton saturated with juice from ripe fruit of *G. spinulosa*, flat, amorphous, cloud-shaped 'fruit' were made. These fruits had the aroma of *G. spinulosa* fruit but lacked their shape and surface structure. Both horizontal and vertical branches had the same arrangement of unripe fruit as in the first trial. One juice-soaked cotton 'fragrant fruit' was placed on the vertical branch and one on the horizontal branch near a cluster of unripe fruit of real *G. spinulosa*.

In the third choice trial artificial *G. spinulosa* fruit was made from melted candle wax to test whether wild *P. hastatus* will detect, locate and attempt to eat an object shaped like a *G. spinulosa* fruit, but without any *Gurania*-like olfactory cues. To protect against contamination, gloves were used and wax was kept away from any surfaces that had contacted *G. spinulosa* fruit or juice. Five artificial fruit were suspended from the vertical branch in arrangements similar to typical *G. spinulosa* branches. On the vertical branch no real *G. spinulosa* fruit was included, ripe or unripe. On the horizontal branch, wax fruit was placed along with unripe *G. spinulosa* fruit. Trials were conducted with artificial 'odourless' fruits on the final night before releasing each bat.

Results

FORAGING AND ECHOLOCATION BEHAVIOUR OF *P. HASTATUS* IN THE SCREEN TENT

When initially released in the pre-choice trials in the screen tent, the bats typically flew in for 10–15 min back and forth across the tent without aiming at a specific target. We name this behaviour *orientation flights*. *Phyllostomus hastatus* echolocated continuously. The *orientation phase* in echolocation is characterized by short, downward frequency-modulated, multiharmonic signals (Fig. 3a) which are emitted singularly or in groups of two, rarely three, calls with the main energy concentrated in the third harmonic, sweeping from 50–55 kHz to 32–36 kHz and to a lesser extent in the fourth harmonic, sweeping from

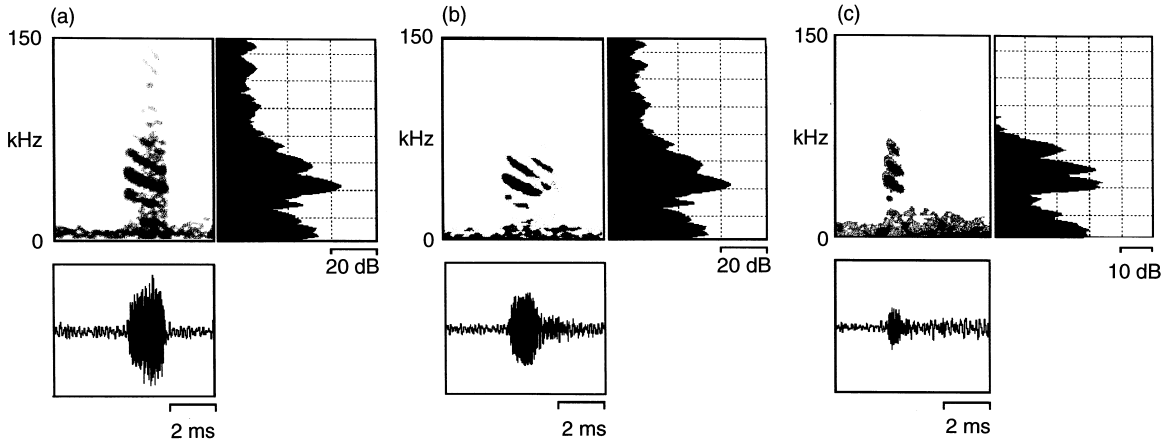

Fig. 3. Typical echolocation signal of *P. hastatus* depicted as sonagrams (frequency *vs* time), averaged spectra and oscillogram: (a) in orientation flight; (b) while resting and scanning; (c) during final approach.

65–72 kHz to 46–51 kHz. Parts of the second and fifth harmonic were also visible in the sonograms. The bandwidth of the third harmonic encompassed 15–20 kHz (Table 1). Sound duration ranged between 1·5 and 2·0 ms. With single signals and between groups, pulse interval was around 50–95 ms. With groups of signals, pulse interval was 25–40 ms. This gave a duty cycle (time filled with sound) of 3–5%.

Orientation flights were interspersed with *resting periods* where the bats landed on the screened sides of the tent. While hanging, the bats scanned their surroundings for up to 10 min by continuously moving their head and ears from one side to the other and emitted echolocation signals singularly or in groups of two to three. The call structure in this *resting phase* was similar to that of orientation flight (Fig. 3b). The bandwidth of the third harmonic did not differ significantly (t = 1·74; P > 0·05; df = 182) from orientation flight but sound duration (1·6–2·2 ms) was significantly longer (t = 5·21; P < 0·001; df = 182) reaching up to 2·7 ms (Table 1). Resting bats produced calls irregularly, so pulse intervals ranged from 37 ms to more than 430 ms, and the duty cycle oscillated between 0·5 and 4%.

After a series of orientation flights and resting periods *P. hastatus* began *exploration flights* oriented towards the dangling branch. Typically, a bat would circle several times around the fruiting branch and direct its approach closer and closer to a fruit cluster. With the exploration flights the bats changed their echolocation behaviour from orientation phase to *approach phase*. Sometimes the transition from orientation to approach phase at the beginning of the flights could not be clearly distinguished. However, during exploration flights the bats emitted signals almost exclusively in groups of two or more (Fig. 4a, b) instead of mostly regularly spaced individual signals in orientation flights. Sound duration (t = 3·89; P < 0·001; df = 249) and pulse interval (t = 4·82; P < 0·001; df = 234) were significantly reduced during exploration flights compared with orientation flights (Table 1). This reduction led to an increase in duty cycle from around 3·6% to about 4·1%. These distinct changes in echolocation behaviour indicate a reaction of the bat towards a target.

The exploration flights where a bat approached a branch with fruit multiple times (usually two to four times) ended in a *final approach* when the bat finally

Table 1. Sound parameters of *Phyllostomus hastatus* in various behavioural situations. The values refer to the harmonic with the highest intensity (third harmonic). They are given as mean ± SD, minimum, maximum and N

	Sound duration (ms)	Pulse interval (ms)	Duty cycle (%)	Bandwidth (kHz)
Orientation flight	1.7 ± 0.2	47.9 ± 13.5	3.6 ± 0.91	17.5 ± 2.1
	1.3; 2.5	25.5; 94.3	1.6; 6.1	13.5; 22.3
	N = 134	N = 126	N = 129	N = 134
Resting	1.9 ± 0.3	134.2 ± 108.4	2.1 ± 1.1	18.1 ± 2.0
	1.4; 2.7	37.1; 435.5	0.5; 4.0	11; 22.6
	N = 50	N = 46	N = 46	N = 50
Exploration flight	1.6 ± 0.2	40.2 ± 10.6	4.1 ± 1.0	18.2 ± 2.0
	1.1; 2.0	23.9; 76.7	2.4; 6.9	12.3; 22.3
	N = 117	N = 110	N = 110	N = 117
Final approach	1.1 ± 0.2	30.5 ± 17.7	4.2 ± 1.6	16.5 ± 2.4
	0.6; 1.5	16.6; 66.0	0.8; 11.0	10; 22.9
	N = 386	N = 371	N = 384	N = 382

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took a fruit. Occasionally, bats switched directly from orientation flight to final approach without exploration flights. Typically, during final approach, a bat would approach the vertical fruiting branch from below (Fig. 5a), swoop upwards to its upper end, make a tight turn, and while diving downwards along the fruiting branch, bite into and take a ripe fruit (Fig. 5b). Compared with the orientation phase, the signal structure was similar (Fig. 3c) in the final approach but the calls were significantly shorter (t = 29·9; P < 0·001; df = 518), had significantly shorter pulse intervals (t = 10·08; P < 0·001; df = 495), and a significantly smaller bandwidth (t = 4·28; P < 0·001; df = 514) (Table 1). The bat emitted signals mostly in groups of four or five or more (Fig. 4a, b). Sound duration decreased with decreasing distance to the fruit from 1 to 1·5 ms at the onset to 0·8 ms at the end of the phase (Fig. 4a, b). The pulse interval between groups was reduced from 40–50 ms to 30–40 ms and within groups from 20–30 ms to 10–20 ms (Fig. 4b). The bat echolocated until it reached the fruit, bit into it and removed it (Fig. 4a, b).

After successfully removing a fruit, the bat landed on the pendulous *G. spinulosa* branch and ate the fruit. *Phyllostomus hastatus* opened the fruit, licked its content, swallowed the seeds and then dropped the rind of the emptied fruit. Processing a fruit took 5–10 min (N = 25). While hanging, the bat continued to emit signals at irregular intervals.

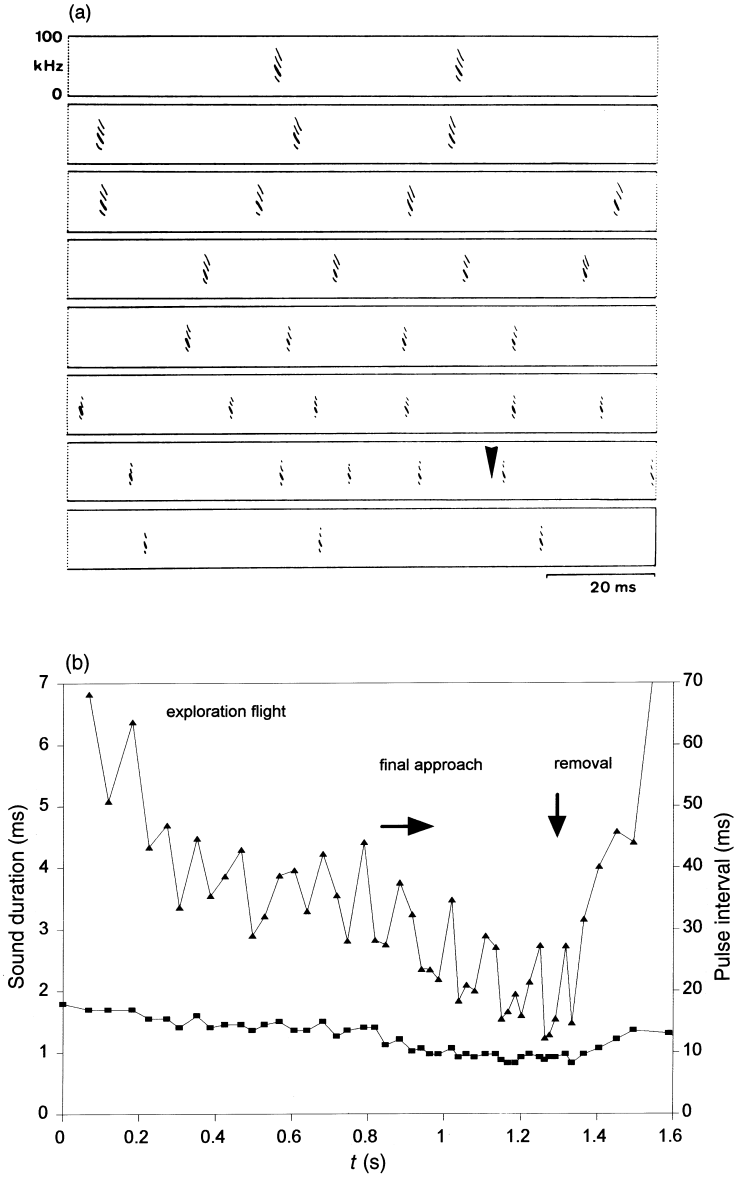

Fig. 4. Echolocation behaviour of *P. hastatus* during exploration flight, final approach and removal of fruit: (a) sonagrams of echolocation sequence; arrow indicates removal of fruit; (b) plots of sound duration (square) and pulse interval (triangle) derived from the echolocation sequence depicted in (a).

FORAGING BEHAVIOUR OF *P. HASTATUS* IN THE FIELD

On two consecutive nights one of the radio-tagged *P. hastatus* was observed feeding on ripe fruit of *G. spinulosa* in the field. On both nights, the bat came early in the evening, headed straight for the fruiting branch, approached the branch two or three times, and then took a fruit in flight. Overall, the sequence of fruit removal corresponded to our observations in the screen tent. However, in contrast to our observations in the screen tent, the bat did not process the fruit on the fruiting branch but carried it away from the plant, presumably to a nearby dining roost.

EXPERIMENTAL TRIALS IN THE SCREEN TENT

In the first choice trial (ripe *G. spinulosa* fruit on vertical and horizontal branches), all bats (N = 5) readily approached the vertically hanging branch in two to four exploration flights and removed and ate a ripe fruit within the first half hour of the trial (Table 2). The bats then approached the vertical branch a few more times in exploration flights but did not attempt to remove the remaining unripe fruit (Table 2). Only one bat found and took a ripe fruit from the horizontal branch within the first hour of the experiment. The bat landed on the horizontal branch and hung there for a few minutes before crawling along the branch, thereby finding and eating a ripe fruit.

In the second choice trial (aromatic juice-drenched amorphous cotton 'fruit'), four bats out of five approached the aromatic 'fruit' on the vertical branch within 45 min (Table 3). Three of those bats landed after two to four exploration flights close to the fruit and flew off again after they had sniffed at and bitten into the fruit. One bat continued to chew on the cotton 'fruit' for about 5 min. Another one of those four bats landed on the horizontal *G. spinulosa* branch near the aromatic 'fruit', started to groom, stopped grooming, crawled to the 'fruit' and sniffed at it briefly. The fifth bat in the experiment did not react towards any of the aromatic 'fruits' offered.

In the third choice trial ('odourless' wax *G. spinulosa* fruit), all bats (N = 5) approached the aromatic 'fruit' on the vertical branch in one or two exploration

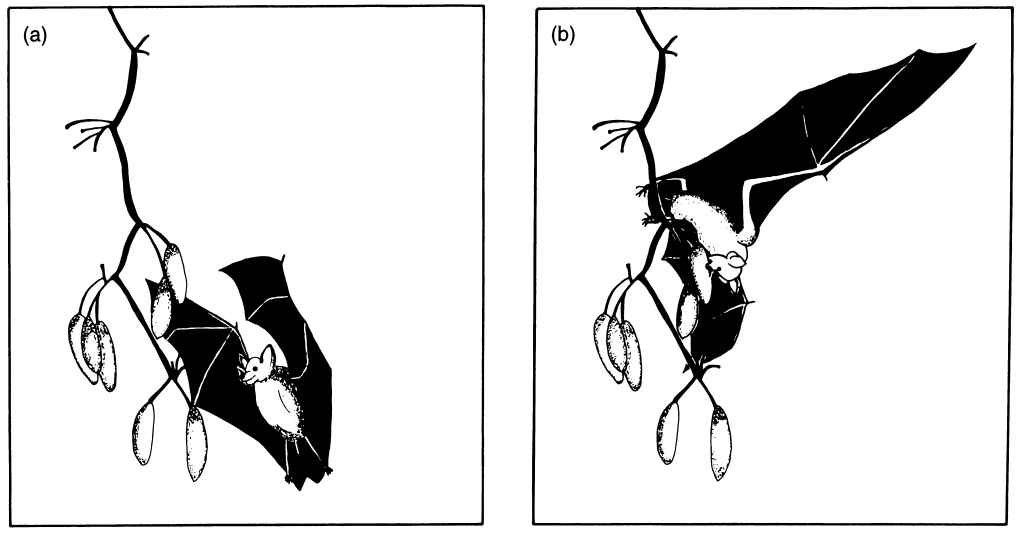

Fig. 5. (a) Approach of *P. hastatus* to a fruiting *G. spinulosa* branch in the screen tent (redrawn from a photograph). (b) Removal of ripe fruit of *G. spinulosa* by *P. hastatus* in the screen tent (redrawn from a photograph).

Table 2. Reaction of *Phyllostomus hastatus* to ripe fruits of *Gurania spinulosa* presented simultaneously on a vertical (one ripe fruit) and a horizontal branch (three ripe fruits) in the screen tent. Time elapsed since release of individual bats to experimental set-up in screen tent is given in parentheses

	Vertical	Horizontal
Bat A	+ (25 min)	–
Bat B	+ (17 min)	–
Bat C	+ (13 min)	–
Bat D	+ (20 min)	–
Bat E	+ (5 min)	+ (8 min)

Table 3. Reaction of *Phyllostomus hastatus* to cotton 'fruits' soaked in juice of ripe fruits of *Gurania spinulosa*. The 'cotton' fruits were presented simultaneously on a vertical and a horizontal branch in the screen tent. The reaction time of the bats is given in parentheses

	Vertical	Horizontal
Bat A	+ (41 min)	–
Bat B	+ (24 min)	–
Bat C	+ (2 min)	–
Bat D	–	–
Bat E	+ (2 min)	–

Table 4. Reaction of *Phyllostomus hastatus* to 'artificial' fruit made out of wax (Bats A–D) or corn flour (Bat E). The wax fruits were presented simultaneously on a vertical and a horizontal branch in the screen tent. The reaction time of the bats is given in parentheses

	Vertical	Horizontal
Bat A	+ (1 min)	–
Bat B	+ (5 min)	–
Bat C	+ (1 min)	–
Bat D	+ (1 min)	–
Bat E	+ (29 min)	–

flights within 1–5 min after release into the screen tent (Table 4). Two of the bats bit into a wax fruit. The other two landed briefly, sniffed at the artificial fruit and took off again. None of the bats approached wax fruit on the horizontal branch.

All bats echolocated throughout the trials while they were in flight and when they approached real fruit, pseudo-fruit or landing sites. The pattern and structure of echolocation signals during orienting flights, exploration flights and final approach were similar for all targets.

SPATIAL CONFIGURATION OF FRUITING *G. SPINULOSA* BRANCHES IN THE FIELD

Of the 30 female *G. spinulosa* that were measured in the field (Fig. 1), all but two dangled freely in unobstructed space (Table 5). The mean minimum horizontal distances of the top and bottom of the fruit-bearing section from the surrounding vegetation were 50 cm (top) and 70 cm (bottom). The mean minimum vertical distances were 30 cm (top) and 150 cm (bottom).

Discussion

THE ROLE OF ECHOLOCATION AND OLFACTION IN FORAGING *P. HASTATUS* AND FRUIT CHARACTERISTICS OF *G. SPINULOSA*

The basic pattern of foraging behaviour found in *P. hastatus* (orientation flights, multiple exploration flights and final approach) strongly resembles other frugivorous phyllostomids (Morrison 1978; Bonaccorso & Gush 1987; Handley, Wilson & Gardner 1991; Kalko, Herre & Handley 1996; Thies, Kalko & Schnitzler 1998). However, unlike other frugivorous phyllostomids known to use odour as a

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main cue for finding fruit (e.g. Laska & Schmidt 1986; Rieger & Jakob 1988; Laska 1990; Kalko, Herre & Handley 1996; Thies, Kalko & Schnitzler 1998), *P. hastatus* only responded to the odour of ripe fruit of *G. spinulosa* when fruits (or aromatic cotton fruits) were suspended on pendulous branches (Table 2). Despite the presence of olfactory cues, the bats did not readily approach real ripe fruit or aromatic cotton 'fruit' on the horizontal branch (Table 3) but readily approached pendulous branches bearing fruit models lacking food-specific olfactory cues (Table 4). These behaviours differ markedly from behaviours shown under similar experimental conditions by other frugivorous phyllostomid bats: *Artibeus jamaicensis* and *Carollia* spp. readily approached objects saturated with the scent of ripe fruits alone, without additional fruit-specific cues (Kalko, Herre & Handley 1996; Thies, Kalko & Schnitzler 1998). Unlike *P. hastatus*, *A. jamaicensis* and *Carollia* spp. ignored fruit and fruit-shaped objects without food-specific odour. Our experiments suggest that display of fruit on pendulous branches is an important cue used by *P. hastatus* to find fruit of *G. spinulosa*.

Phyllostomus hastatus does not appear to use fruit texture as a cue: bats readily approached cotton 'fruit' that clearly differed from real fruit in surface texture. Similarly, visual cues are probably not critical for detection and localization of fruit. In the forest understory (where most pendulous branches of *G. spinulosa* hang), light levels at night are extremely low, so visual cues would be minimal. Further, all our experiments were conducted under very low light conditions (at dark nights under the roof of a tent) in order to minimize visual cues, and bats were able to locate fruit. Ability to locate fruit in complete darkness has been documented for other frugivorous phyllostomids (Thies, Kalko & Schnitzler 1998).

Synchronous ultrasound recordings of *P. hastatus* in the screen tent showed that the bats echolocated continuously during orientation flight, exploration flight and final approach. In phyllostomids, echolocation is mostly used for orientation in space (e.g. Howell 1974; Schnitzler & Kalko 1998); however, our results suggest that *P. hastatus* uses echolocation not only for orientation and avoidance of obstacles but also to detect and locate pendulous fruit. The broadband, multiharmonic, FM echolocation signals of short duration and low intensity of *P. hastatus* are well suited to exact localization of targets (e.g. Simmons & Stein 1980; Schnitzler & Kalko 1998). Precise localization of the fruit's position by echolocation is probably facilitated by multiple approaches during exploration flights. At close range, *P. hastatus* may use olfactory cues to discriminate between ripe and unripe fruit.

Table 5. Distance in metres of fruiting *Gurania spinulosa* branches ($N = 30$) from the surrounding vegetation in the field (see Figure 2)

Branch no.	Vertical from top	Vertical from bottom	Horizontal from top	Horizontal from bottom
1	0.3	0.7	1.0	0
2	0.5	1.8	0.4	0.5
3	1.3	2	0.4	0.7
4	0.1	1.1	0.5	1.5
5	0.1	1.6	0.7	1.5
6	0	0.3	0.1	0.1
7	2.5	3	1.5	1
8	1.5	2	1.3	2
9	1	1.9	3	5
10	1.1	2	1	1.5
11	0.2	1	0.2	0.5
12*	0	0	0	0
13	0.2	2	0.5	0.7
14	0	1.2	0	0.7
15	0.8	3	5	3.5
16	0.1	0.8	0.1	0.1
17	0.1	1	0.1	0.3
18	0.1	1.1	0.1	0.1
19	1.2	2.1	1.5	2
20	0.2	1.2	3	4.5
21	3	3	2	2
22	1	1.5	0.2	0.2
23	1	3	0.7	2
24	2.5	3	2.5	2.5
25	0	0.9	0	0.7
26	0.6	1.2	0.4	0.2
27	0.8	1.2	0.5	0.5
28	0	0.7	0	1
29*	0	0	0	0
30	0	1.8	0	0

*Branch inside the vegetation.

ECHO-OVERLAP AND PLANT MORPHOLOGY

The ability of frugivorous leaf-nosed bats to detect food by echolocation depends largely on the position of a fruit relative to clutter-producing background such as surrounding vegetation. With the exception of species that produce constant-frequency (CF) signals, bats avoid situations that result in overlap of target echo with clutter echoes and mask important information (e.g. Kalko & Schnitzler 1993; Schnitzler & Kalko 1998). Most fruiting branches of *G. spinulosa* dangle freely far enough away from vegetation to be outside the 'echo-overlap zone'. For an echolocating *P. hastatus* with a signal duration of 2–2·5 ms, which is typical for this bat flying in the forest, fruits are in the echo-overlap zone when their distance from the surrounding vegetation is less than 34–42·5 cm. The mean minimum distance between *G. spinulosa* fruiting branches and surrounding vegetation in our sample was 50–70 cm, so the plant's morphology allows overlap-free detection. Further, like other echolocating bats, *P. hastatus* reduces sound duration during approach presumably to keep targets as long as possible in the overlap-free window.

The importance of overlap-free detection of targets may also explain why all bats tested in the screen tent approached fruits on the vertical leafless branch more readily than fruits on the horizontal leafy branch. Fruits on the leafless vertical branch were exposed

and offered better acoustical cues since they stood out from clutter (i.e. walls of the screen tent, no leaves). Fruits on the horizontal branch were difficult targets for echolocation because echoes from fruits were largely buried in echoes from adjacent leaves.

Conclusions

This is the first demonstration that neotropical frugivorous bats use echolocation to find fruit, and it suggests that echolocating dispersal agents could affect the evolution of plant morphology. Our study reveals at least one advantage of flagellichory: pendulous fruiting branches are clear, clutter-free targets for echolocating bats. By hanging in clutter-free space, fruiting branches may also provide more space for bats to manoeuvre at a distance from vegetation that might harbour bat predators. By being attractive to bats such as *P. hastatus*, plants profit in several ways. First, bats are the only animals we have observed that consistently remove and eat fruit without harming seeds (Condon 1984). Second, *P. hastatus* is a reliable dispersal agent. Our field observations revealed that the same radio-tagged bat returned on consecutive nights to remove fruit from a branch of *G. spinulosa*. Faeces at a night roost at Agua Blanca consistently contained rather large numbers of seeds of *G. spinulosa*. Finally, *G. spinulosa* also may benefit from long-distance dispersal by *P. hastatus*, which forages over areas as large as 80 ha and is known to fly up to several kilometres between day roosts and foraging areas (McCracken & Bradbury 1981).

Comparing our findings with other studies (e.g. van der Pijl 1982; Kalko, Herre & Handley 1996) we conclude that the characters included in the bat dispersal syndrome actually represent a composite picture of a suite of discrete strategies ranging from figs, which broadcast olfactory cues while nestled within clusters of leaves, to *G. spinulosa*, which advertises its availability by hanging loose.

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