

Constant-frequency and frequency-modulated components in the echolocation calls of three species of small bats (Emballonuridae, Thyropteridae, and Vespertilionidae)

M.B. Fenton, J. Rydell, M.J. Vonhof, J. Eklöf, and W.C. Lancaster

Abstract: The echolocation calls of *Rhynchonycteris naso* (Emballonuridae), *Thyroptera tricolor* (Thyropteridae), and *Myotis riparius* (Vespertilionidae) were recorded at the Cãno Palma Field Station in Costa Rica in February 1998. All three species produced echolocation calls at low duty cycle (signal on ~10% of the time). While *T. tricolor* produced low-intensity echolocation calls that were barely detectable when the bats were <0.5 m from the microphone, the other two species produced high-intensity calls, readily detectable at distances >5 m. *Myotis riparius* produced calls that swept from about 120 kHz to just over 50 kHz in about 2 ms. We found no evidence of harmonics in these calls. *Rhynchonycteris naso* and *T. tricolor* produced multiharmonic echolocation calls. In *R. naso* the calls included narrowband and broadband components and varied in bandwidth, sweeping from just under 100 kHz to around 75 kHz in over 5 ms. Most calls were dominated by the higher harmonic (ca. 100 kHz), but some also included a lower one (ca. 50 kHz). The calls of *T. tricolor* were 5–10 ms long and dominated by a single frequency (ca. 45 kHz), sometimes with a ca. 25 kHz component. The echolocation calls of all three species included frequency-modulated and constant-frequency components. While these terms describe the components of the echolocation calls, they do not necessarily describe the bats' echolocation behaviour.

Résumé : Les cris d'écholocation de *Rhynchonycteris naso* (Emballonuridae), *Thyroptera tricolor* (Thyropteridae) et *Myotis riparius* (Vespertilionidae) ont été enregistrés à la station de recherche de Cãno Palma, Costa Rica, en février 1998. Les trois espèces produisent des cris d'écholocation à coefficient d'utilisation faible (signal fonctionnel ~10% du temps). Alors que *T. tricolor* produit des cris de faible intensité à peine perceptibles plus loin que 0,5 m du microphone, les deux autres espèces produisent des cris très forts, facilement audibles au-delà de 5 m. Les cris de *M. riparius* vont de 120 kHz à un peu plus de 50 kHz en 2 ms environ et ne semblent pas comporter d'harmoniques. *Rhynchonycteris naso* et *T. tricolor* produisent des cris d'écholocation à plusieurs harmoniques. Chez *R. naso*, les cris comportent des composantes à bandes étroites et à bandes larges et la largeur des bandes est variable, passant d'un peu moins de 100 kHz à 75 kHz en plus de 5 ms. La plupart des cris sont dominés par l'harmonique la plus aiguë (c. 100 kHz), mais certaines contiennent aussi une harmonique plus grave (c. 50 kHz). Les cris de *T. tricolor* durent de 5 à 10 ms et sont dominés par une seule fréquence (c. 45 kHz) et comportent parfois une autre composante de c. 25 kHz. Les cris d'écholocation de ces trois chauves-souris ont des composantes de fréquence modulée et des composantes de fréquence constante. Ces termes définissent les composantes des cris d'écholocation, mais ne décrivent pas le comportement d'écholocation des chauves-souris.

[Traduit par la Rédaction]

Introduction

What influences echolocation-call design in bats? Statistically, body size is one of the best predictors of the frequencies dominating the echolocation calls of a wide range of microchiropteran bats, but superimposed on this is variation

among families and among bats that use different approaches to foraging (e.g., Barclay and Brigham 1991; Jones 1996; Bogdanowicz et al. 1999). At the same time, the patterns of frequency change over time (bandwidth, call duration, sonagram shape) appear to reflect the general setting in which aerial-feeding bats hunt (Simmons and Stein 1980). Features such as pulse-repetition rate, however, are also influenced by body size, with smaller species producing calls at higher rates than larger ones (Jones 1993, 1994; Kalko 1995a; Fenton et al. 1998a).

In recent years a dichotomy has emerged from the study of echolocation by microchiropteran bats. On one hand, many species of aerial-feeding bats in different zoogeographic areas produce distinctive echolocation calls (e.g., Ahlén 1981; Fenton and Bell 1981), albeit with considerable intraspecific variability (e.g., Rydell 1990; Obrist 1995; Betts 1998). A spectacular example of species recognition

Received May 3, 1999. Accepted August 10, 1999.

M.B. Fenton¹ and M.J. Vonhof. Department of Biology, York University, North York, ON M3J 1P3, Canada.
J. Rydell, J. Eklöf, and W.C. Lancaster.² Department of Zoomorphology, University of Goteborg, SE 405, 30 Goteborg, Sweden.

¹Author to whom all correspondence should be addressed (e-mail: bfenton@circus.yorku.ca).

²Present address: School of Osteopathic Medicine, Pikeville College, Pikeville, KY 41501, U.S.A.

by means of echolocation calls is the discovery, through its echolocation calls, of a "cryptic" form of *Pipistrellus pipistrellus* (Barratt et al. 1997). On the other hand, several data sets suggest convergence in echolocation-call design among aerial-feeding bats that hunt in similar settings or situations. This includes, for example, the short, low-intensity, high-frequency calls of gleaners, or the long, narrowband search-phase calls of some rhinopomatids, emballonurids, vespertilionids, and molossids (e.g., Neuweiler 1989; Fenton et al. 1995). A striking example of convergence involves *Craseonycteris thonglongyai* and *Myotis siligorensis*, two small (<5 g) bats from Thailand representing the superfamilies Emballonuroidea and Vespertilionoidea, respectively (Surlykke et al. 1993). Both species search for airborne insects using 3–5 ms long narrowband signals of high intensity, and this is interpreted as reflecting their common hunting setting (Surlykke et al. 1993).

The possibility of convergence in echolocation-call design means, as noted by others (e.g., Neuweiler and Fenton 1988), that the shorthand used to describe the echolocation calls of bats (e.g., constant frequency (CF) and frequency modulated (FM)) may be appropriate for calls and their components but not for describing the echolocation behaviour of the bats themselves. Take, for example, the common use of CF to describe some bats (e.g., Schnitzler 1973; Schnitzler et al. 1976). Some microchiropteran bats (Rhinolophidae, Hipposideridae, and the mormoopid *Pteronotus parnellii*) produce echolocation calls at high duty cycle that rely on Doppler-shifted echoes to separate pulse and echo in frequency and allow them to broadcast and receive at the same time (Fenton et al. 1995). CF calls of long duration would mask echoes returning from nearby objects, limiting the minimum effective range that bats with echolocation calls at low duty cycle could achieve with calls of this design. These bats produce echolocation calls dominated by CF components, so they have been known as CF bats for over 25 years (Sales and Pye 1974). Most echolocating bats, however, produce calls at low duty cycle, separating pulse and echo in time, which makes them unable to broadcast and receive at the same time (Fenton et al. 1995). Some of these species also produce CF echolocation signals, but their echolocation behaviour (low duty cycle) is quite different. Thus, CF describes only the calls (or some components) themselves (zero change in frequency over some period of time), not the echolocation behaviour.

The purpose of this study was to examine the utility of using CF and FM to describe the echolocation calls of three smaller (<5 g adult body mass) insectivorous species of microchiropteran bats representing two superfamilies: *Rhynchonycteris naso* (Emballonuroidea) and *Thyroptera tricolor* and *Myotis riparius* (Vespertilionoidea). We compared these data with those previously published (e.g., Surlykke et al. 1993) for other small bats from different phylogenetic lineages as described by Simmons and Geisler (1998), with a view to considering the extent of convergence in echolocation-call design among bats. The echolocation calls of *R. naso* have been described (Kalko 1995b; O'Farrell and Miller 1997), but we know of no published data on the calls of either of the other two species we studied. Our fieldwork was conducted at the Cãno Palma Field Station (10°32'N,

83°35'W) near Tortuguero in Costa Rica between 14 and 22 February 1998.

Materials and methods

Thyroptera tricolor (2 individuals) and *M. riparius* (2 individuals) were recorded as they flew freely in a permanent greenhouse made of mesh at the Cãno Palma station. The greenhouse was 7 × 5 × 2.2 m, with the upper half of the space almost free of the low-growing herbaceous plants. *Rhynchonycteris naso* (8 individuals) were recorded as they flew about and left a roost on beams supporting the roof of a boathouse of over the water nearby. Two *T. tricolor* were recorded as they emerged from a roost in an unfurled leaf.

Most recordings were made through the time-expansion unit (10×; 8 bits) of a hand-held Pettersson D-960 bat detector (Pettersson Elektronik AB, Uppsala, Sweden), and the signals were stored on one channel and spoken comments on the other using a Sony TC-D5 M cassette tape recorder. Other recordings were made using an Ultrasound Advice S200 bat detector and a Racal Instrumentation tape recorder operated at 76 cm·s⁻¹. We also recorded the echolocation calls of *R. naso* by means of an Anabat II detector with Anabat 5 software and an Anabat ZCR module operated with a DOS laptop computer.

The time-expanded signals were analyzed on Pettersson bat sound analysis software. Pulse durations were read from sonagrams and frequencies from power spectra. The sampling rate was 44 100 Hz (12 bits). The Racal recordings were analyzed with Canary 1.2 software by slowing down the tape appropriately to bring the frequency range of the signals into the range of Canary analysis. Anabat recordings were analyzed with the Anabat 5 software.

Results

The echolocation calls of *T. tricolor* differed strikingly in intensity from those of the other two species, being detectable only when the bats flew within 1 m (usually 20–30 cm) of the microphone (compared with 5–10 m for the other two species). *Thyroptera tricolor* produced narrowband echolocation calls dominated by one frequency (Figs. 1a and 1c, Table 1), with some calls consisting of both the fundamental (ca. 23 kHz) and second harmonic (ca. 46 kHz; Figs. 1a and 1c) and others of just the second harmonic. In one sequence of 17 calls from the same bat, for example, 9 included both fundamental and harmonic but in no obvious pattern. In two other sequences of 8 and 7 calls, there was no evidence of the fundamental. In contrast to this lack of obvious pattern, the echolocation calls of *T. tricolor* showed a bimodal distribution in the frequency with the most energy. The prevalent pattern (26 of 29 adjacent calls) was an alternation of frequencies between adjacent calls, usually changing between 45 and 47 kHz (Fig. 2). When emerging from leaf roosts, the bats produced much shorter calls, which often included a fourth harmonic (Fig. 1b).

The search-phase echolocation calls of *R. naso* (Fig. 3) also varied in harmonic structure. The most common pattern consisted of calls showing only the fourth harmonic, as proposed by Kalko (1995b), ca. 100 kHz (Figs. 3c and 3d; 29 of 58); 4 of 58 calls consisted of just the second harmonic (ca. 48 kHz). The fourth- and second-harmonic components differed in that the fourth was longer and terminated in a longer FM sweep (Fig. 2a) than the second (Fig. 2b). Some fourth-

Table 1. Features of echolocation calls recorded and analyzed using the Pettersson system.

	Sequence 1	Sequence 2	Sequence 3	Sequence 4	Sequence 5
<i>Thyroptera tricolor</i>					
<i>n</i> (harmonic)	29	16	9	7	9
Narrowband (kHz)	46.8±0.96	45.43±1.38	45.32±1.07	45.61±0.92	22.61±0.89
Minimum frequency (kHz)	44.8±1.17	40.45±1.38	40.41±1.19	40.77±1.15	20.75±0.86
Duration (ms)	7.3±1.64	7.09±1.18	9.4±0.53	10.13±0.88	5.95±0.94
Interval (ms)	102±40				
Duty cycle (%)	7.1				
<i>Rhynchonycteris naso</i>					
<i>n</i>	5	3	3	10	5
Highest frequency (kHz)	95.2±0.6	98±2.9	99±0.5	97.5±1.1	99.6±0.7
Lowest frequency (kHz)	88.1±3.8	79.8±2.9	96.2±1.1	81.2±4.7	82.2±2.8
Second harmonic (kHz)	Absent	49.2±0.5	Absent	49.3±0.4	Absent
Duration (ms)	6±0.4	5.9±0.7	5.2±0.2	5.4±0.4	5.2±0.2
Interval (ms)	96±4.5	na	198±8.5	34.7±2.1	n/a
Duty cycle (%)	6.25	na	2.8	15.6	n/a
<i>Myotis riparius</i>					
<i>n</i>	4	7	13	5	4
Highest frequency (kHz)	121.9±3.1	111.1±13.3	113.9±12.3	122.3±8.3	107.8±11
Lowest frequency (kHz)	56.9±2	54.8±1.7	55.6±2.3	53.9±3.5	58±0.75
Maximum amplitude (kHz)	96.7±1.8	67.5±3.1	65.2±4	63.8±3.8	64.6±3.6
Duration (ms)	1.4±0.05	1.8±1.2	2.1±0.4	2.7±0.5	2.4±0.5
Interval (ms)	20.3±4.8	40.8±16.1	43.9±13.1	46.2±17.1	68.3±5.1
Duty cycle (%)	6.9	4.4	4.8	5.8	3.5

Note: Values are given as the mean ± SD; *n* is the number of calls analyzed and sequences are calls from single bats detected as they flew through the airspace sampled by the microphone (= a bat pass).

harmonic echolocation calls made by *R. naso* had shorter rather than longer terminal FM sweeps (compare Figs. 3a and 3b). Differences in harmonics and FM sweep corresponded to differences in call bandwidth (see below).

The Anabat system portrayed the echolocation calls of *R. naso* by the information in the fourth harmonic. In one sequence of 12 consecutive calls, 10 included the long FM sweep and 2 the shorter one. In another sequence of 15 consecutive calls, 5 included the long sweep and 10 the shorter one. The first sequence was dominated by 100 kHz and the second by 98 kHz, and the average durations were 2.79 ± 0.46 and 2.87 ± 1.11 ms (mean ± SD), with average intercall intervals of 25.18 ± 5.59 and 33.9 ± 4.06 ms, respectively. These durations were consistently shorter than those obtained with the other system (see Table 1), and the intervals were typically much shorter, apparently reflecting the recording situation, namely the bats flying around in the open boathouse where they roosted, rather than over the water.

Unlike those of the other two species, the search-phase echolocation calls of *M. riparius* (Fig. 4c) showed no variation in the pattern of harmonics. The calls were FM calls of varying bandwidth (Table 1), often consisting of both steep FM (broadband) and narrowband components (Fig. 4c).

The echolocation calls we analyzed from all three species were produced at low duty cycle (Table 1) and fell into two broad categories, broadband and narrowband; the differences are immediately obvious in the power spectra of calls (Fig. 5) and the sonagrams (Figs. 1–3). In narrowband signals the energy is concentrated in a particular frequency or frequencies (Figs. 5b and 5d), while broadband calls cover a

broader range of frequencies (Figs. 5a and 5c). The spectra show the striking differences in bandwidth between two kinds of *R. naso* calls, as well as the impact of the second harmonic on the spectra (Figs. 5a and 5b). The broad bandwidth of the *M. riparius* call (Fig. 5c) compared with the *T. tricolor* call (Fig. 5d) is evident, and is comparable to the bandwidth of *R. naso* calls (Fig. 5a). The difference is that the call energy is skewed to the left in *M. riparius* calls (Fig. 5c) and to the right in *R. naso* calls (Fig. 5a), corresponding to a terminal or an initial narrowband component, respectively. The narrowband calls of *T. tricolor* and *R. naso* are comparable in bandwidth to those of a high duty cycle echolocator such as *Rhinolophus megaphyllus*, (Fig. 5e).

In a sample of 23 species of bats with forearms <45 mm long (Fig. 6), forearm size was not found to be a good predictor of lowest frequency in the echolocation call (linear regression, $r^2 = 0.03$, $F = 0.66$, $p = 0.43$). The variable presence of harmonics in the echolocation calls complicates the relationship. This is clear for *R. naso* and *T. tricolor* (Fig. 6), since, depending upon the choice of call(s), the lowest frequency or the frequency dominating the call changes by a factor of 2. Another conspicuous outlier is *Furipterus horrens*, whose calls are much higher in frequency than predicted from their size (Fig. 6).

Discussion

The echolocation calls of *R. naso* and *M. riparius* appear to be well suited for aerial foraging, and it is clear that *R. naso* uses this approach to hunting (Kalko 1995b). The

Fig. 1. Sonagrams of echolocation calls of *Thyroptera tricolor*, recorded from free-flying bats (*a* and *b*) and from a bat emerging from a roost (*c*), obtained from Pettersson recordings and sound-analysis software. Note that the horizontal scale is the same in *a* and *b* but different in *c*.

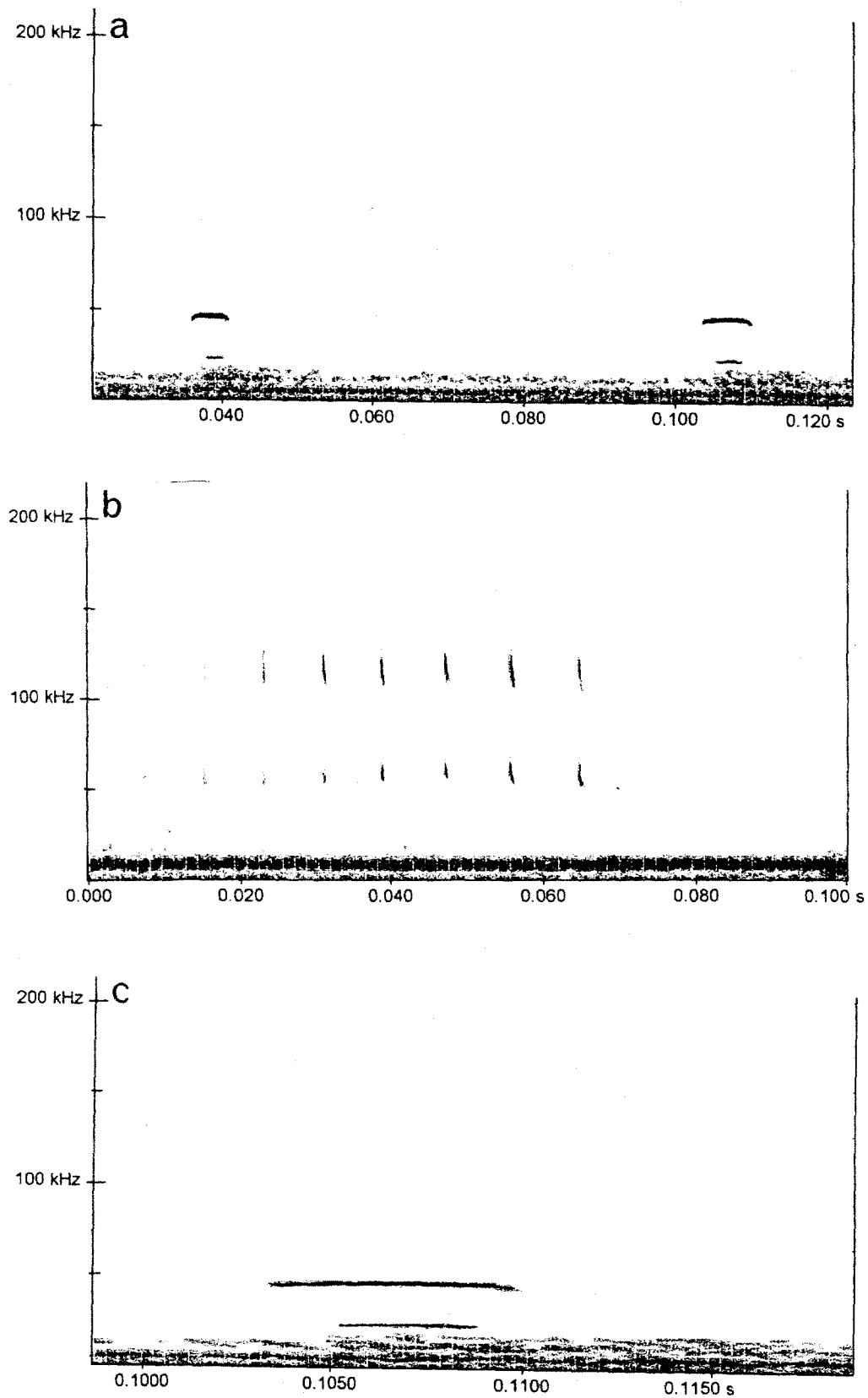
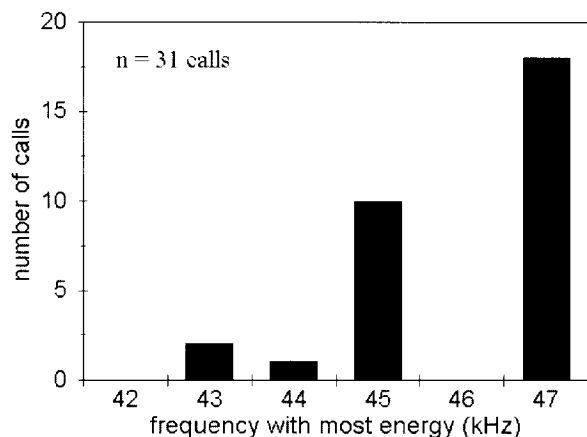


Fig. 2. Bimodal distribution of echolocation calls of *Thyroptera* with respect to dominant frequency, the bats typically switching between 45 and 47 kHz.



combination of high-intensity signals with narrowband and broadband components presumably increases the effective range of operation (intensity, narrowband), while providing details about the prey (broadband), following the proposals of Simmons and Stein (1980). Neither bat produces search-phase echolocation signals as narrow in bandwidth as those of *M. siligorensis* or *C. thonglongyai* (Surlykke et al. 1993), which suggests that *M. riparius* and *R. naso* can hunt in areas with more clutter. The combination of narrowband and broadband components is a prevalent theme among bats, from small species (FA < 40 mm) such as *Myotis californicus*, *Myotis ciliolabrum* (Fenton and Bell 1979), *Pipistrellus* spp. (Kalko 1995a), and *Rhogeessa anaetus* (Audet et al. 1993) to larger ones (FA > 40 mm) such as *Lasiurus* spp., *Eptesicus fuscus* (Obrist 1995), and *Nyctalus leisleri* (Waters et al. 1995). As noted above, the pattern of frequency change over time differs markedly between the emballonurids and vespertilionids (compare Figs. 3 and 4).

The low-intensity echolocation calls of *T. tricolor* should result in a very short effective range. In intensity, these echolocation calls resemble those of gleaners, i.e., bats that take prey from surfaces. But gleaners studied to date produce echolocation calls that are very short in duration (\leq ms compared with >5 ms) and broad in bandwidth (e.g., megadermatids, nycterids, phyllostomids, and vespertilionids; Fenton et al. 1995) compared with those of *T. tricolor*. The narrowband component of *T. tricolor* echolocation calls is reminiscent of the CF element in the echolocation calls of high duty cycle bats (compare Figs. 3d and 3e), but a rhinolophid or hipposiderid bat the size of *T. tricolor* would produce echolocation calls dominated by a much higher CF, over 100 kHz (Jones 1996; Bogdanowicz et al. 1999). Furthermore, as noted above, the long duration of these calls imposes a relatively large minimal distance of detection of a low duty cycle echolocator. Until we know more about the foraging behaviour of *T. tricolor*, the significance of the design of its echolocation calls will remain unclear. If *T. tricolor* is an aerial feeder, the long narrowband signals could encode flutter, a benefit of high duty cycle echolocation (Schnitzler 1987), while imposing a relatively large minimum range reflecting the duration of the calls.

Alternation of frequencies between pulses in the order of 2–5 kHz has been reported for a number of species of aerial-feeding bats (Pye 1973), including emballonurids (Barclay 1983), rhinopomatids (Habersetzer 1981), vespertilionids (Ahlén 1981; Heller 1989; Obrist 1995), and molossid (Fenton et al. 1998a). Explanations for the function of this alternation range from distinguishing between the echoes from prey and those from the ground (Pye 1973), to social influences such as jamming avoidance (Habersetzer 1981; Obrist 1995) and range enhancement (Heller 1989; Fenton et al. 1998a). The low intensity of their echolocation calls means that none of these explanations appears to apply directly to *T. tricolor*, which we recorded as they flew alone.

Our results reinforce the view that while terms like CF and FM and narrowband and broadband can reasonably describe the components of bats' echolocation calls, often they are not good descriptors of bats' echolocation behaviour (Neuweiler and Fenton 1988). Although its echolocation calls are dominated by CF components, the echolocation behaviour of *T. tricolor* appears to be quite different from that of rhinolophids, hipposiderids, or *P. parnellii*, the traditional CF bats. Furthermore, its echolocation calls differ markedly from those of other gleaners. Although CF calls have been associated with flutter detection (e.g., Schnitzler 1987), bats can use broadband FM calls to detect flutter (Summe and Menne 1993). Furthermore, in some cases (e.g., *Noctilio albiventris*), narrowband components in calls trigger windows of analysis in the brain, whatever other role they play in data collection (Roverud 1987). Narrowband components may also increase the effective range of echolocation because the higher energy at one or a few frequencies can reduce the impact of atmospheric attenuation (Lawrence and Simmons 1982). In any case, introducing the term quasi constant frequency (Kalko and Schnitzler 1993) does not resolve the discrepancy associated with using CF to describe bats. There remains the issue of how much of the information available through echolocation is actually used by foraging bats (Barclay and Brigham 1994).

Convergence in call design can bedevil the identification of bats by their echolocation calls. Broad convergences can be distinguished using local information, and knowledge of location would preclude, for example, confusing the echolocation calls of the Nearctic *Myotis lucifugus* with those of the Palaearctic *Myotis daubentoni*. Intraspecific variation in call features (Rydell 1990; Obrist 1995; Betts 1998; Barclay 1999) complicates the process of using echolocation calls to identify species of bats, and for some species, recognition by means of call features may be impossible with current technology. Variation in harmonic composition is a further difficulty, and the calls of *R. naso* make it obvious that a bat-detection system like Anabat (e.g., O'Farrell et al. 1999a), which does not display information about harmonics, may not be reliable for identifying some species (Barclay 1999; O'Farrell et al. 1999b) such as *R. naso*. In our study, the Anabat representation of *R. naso* calls showed signals dominated by frequencies of 98 or 100 kHz, while O'Farrell and Miller (1997), using an Anabat system, reported signals of similar design dominated by 47 kHz. Kalko's (1995a) and our data from a different bat-detection system demonstrate that *R. naso* varies the harmonic structure of its echolocation calls. The low intensity of its echolocation calls would make

Fig. 3. Sonograms of echolocation calls of *Rhynchonycteris naso* recorded from free-flying bats and showing the variation in harmonic composition and degree of frequency-modulated sweeps. The calls may be dominated by two harmonics (*a* and *b*) or one (*c* and *d*) and there are differences in the magnitude of the terminal frequency-modulated sweep (compare *a* with *b*, *c*, and *d*). These sonograms were obtained from Pettersson recordings and sound-analysis software. Note that the horizontal scale in *a* is different from that in *b-d*.

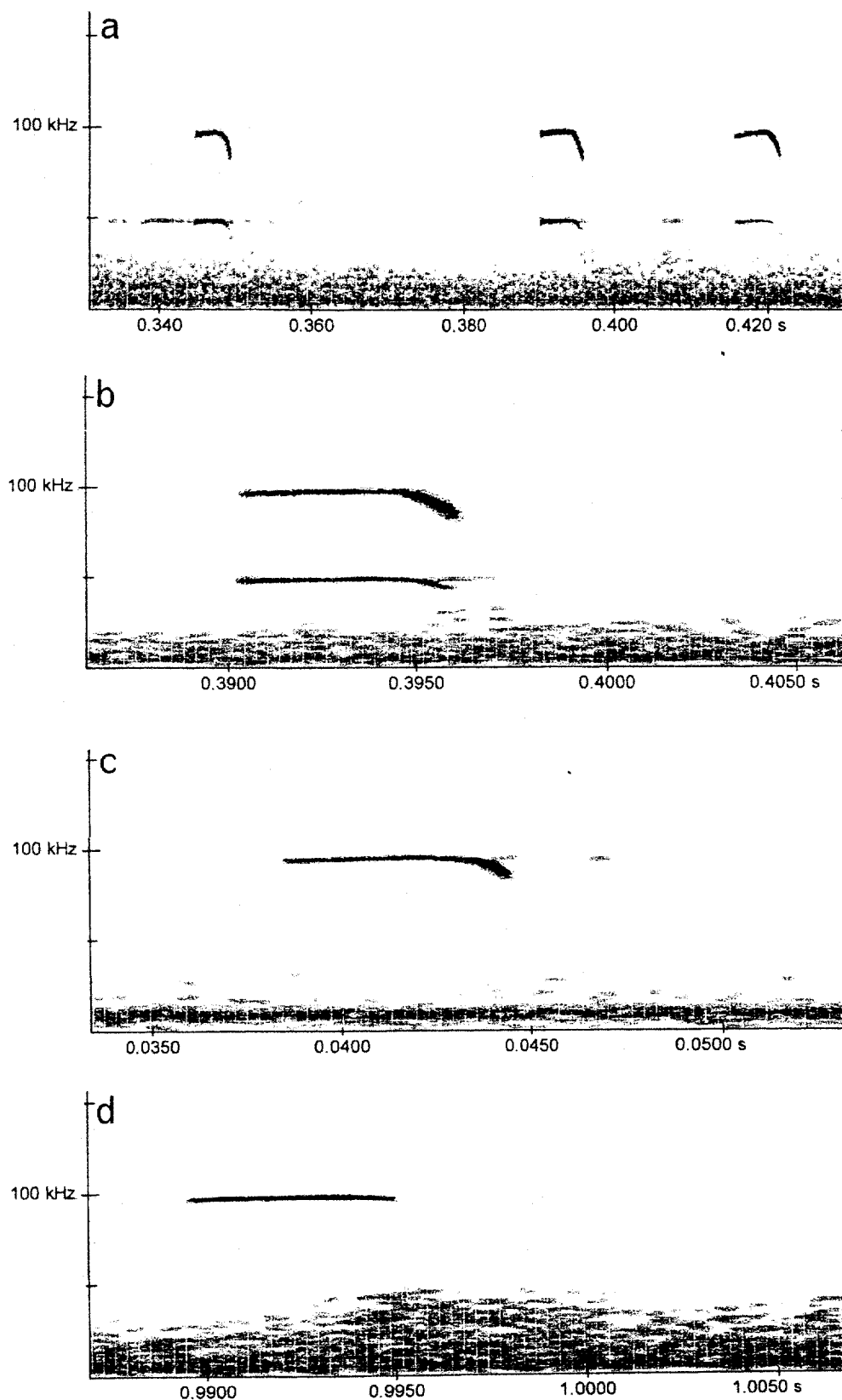


Fig. 4. Sonagrams of echolocation calls of *Myotis riparius* recorded from free-flying bats, showing the variation in call pattern. These sonagrams were obtained from Pettersson recordings and sound-analysis software. The difference in horizontal scale (compare *c* with *a* and *b*) accounts for the apparent difference in call design.

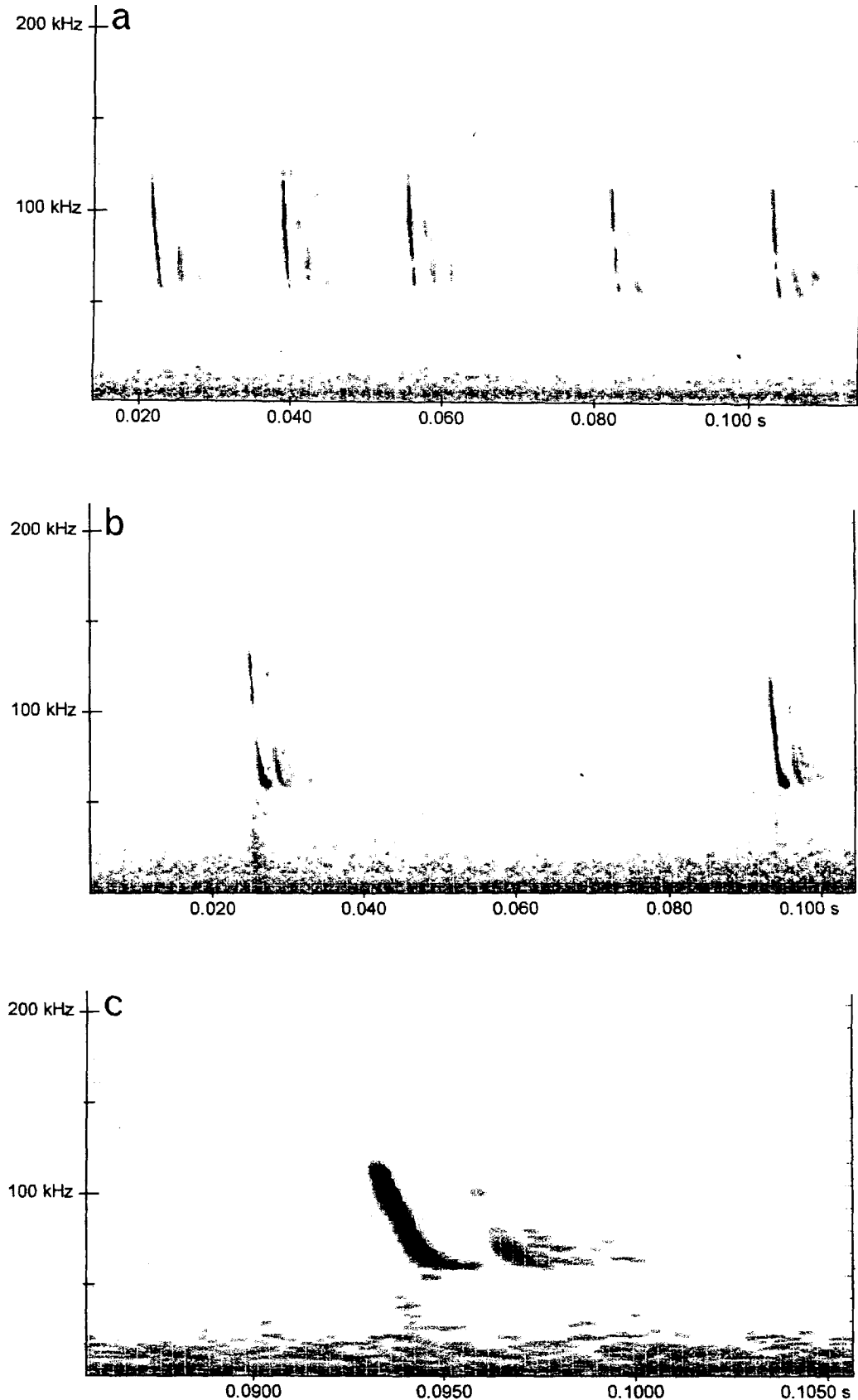


Fig. 5. Power spectra of echolocation calls. (a) *Rhynchonycteris naso*, both harmonics, full sweep. (b) *Rhinolophus naso*, fourth harmonic, limited sweep. (c) *Myotis riparius*. (d) *Thyroptera tricolor*. (e) *Rhinolophus megaphyllus*; these calls were recorded in northern Queensland by J.R. All spectra were obtained from Pettersson recordings and sound-analysis software.

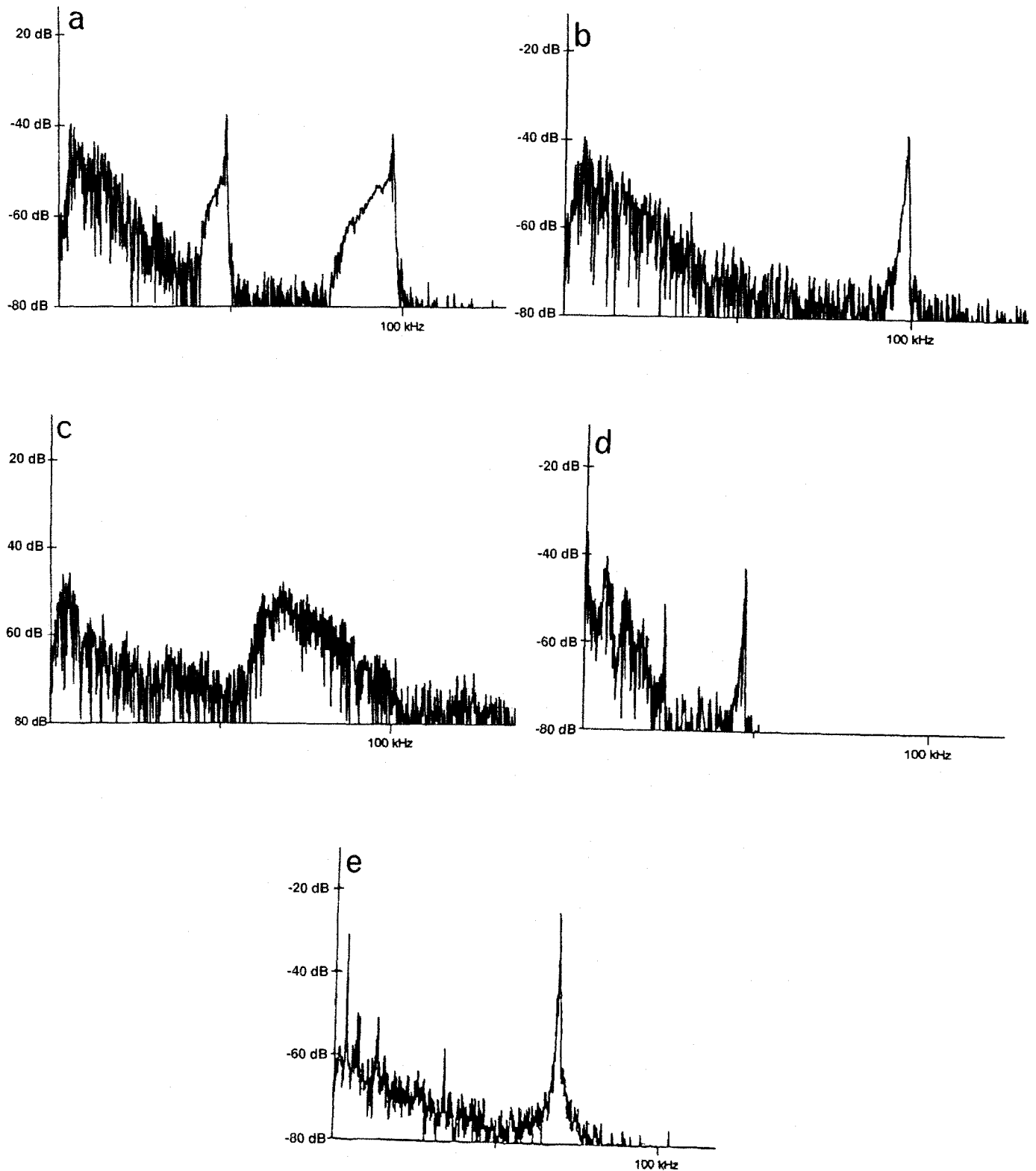
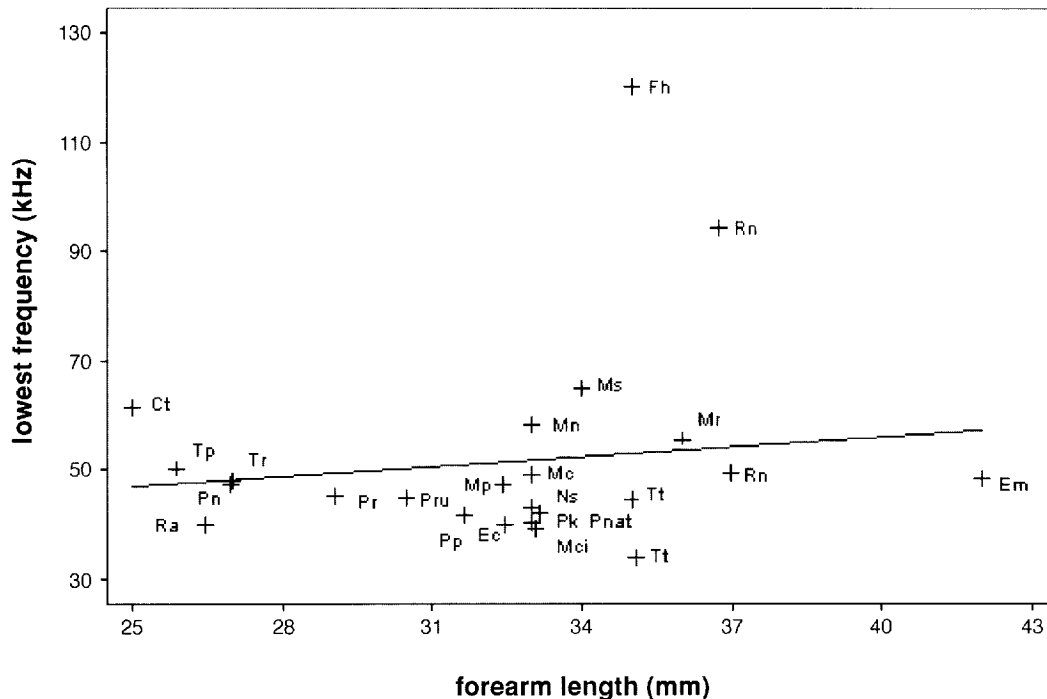


Fig. 6. Results of a linear regression analysis of bat size (forearm length (mm)) against the lowest frequencies (kHz) in the echolocation calls. Here the lowest frequency = $21.548 + 0.9393$ (forearm size). Of special note are the calls of *Furipterus horrens* (Fh), *Thyroptera tricolor* (Tt), and *Rhynchonycteris naso* (Rn), the latter two because of the variation in harmonic composition of echolocation calls, which influences the lowest frequencies in the calls. Included here are data for *Craseonycteris thonglongyai* (Ct), *Myotis siligorensis* (Ms; Surlykke et al. 1993), *Furipterus horrens* (Fh; M.B. Fenton, unpublished observations), *Myotis californicus* (Mc), *Myotis ciliolabrum* (Mci; Fenton and Bell 1979), *Myotis leibii* (Mlei; M.B. Fenton, unpublished observations), *Myotis nigricans* (Mn), *Nycticeius schlieffeni* (Ns), *Pipistrellus rueppellii* (Pru), *Pipistrellus rusticus* (Pr), *Pipistrellus nanus* (Pn), *Eptesicus capensis* (Ec; Fenton et al. 1998b), *Pipistrellus kuhlii* (Pk), *Pipistrellus pipistrellus* (Pp), *Pipistrellus nathusii* (Pnat; Kalko 1995a), *Emballonura monitcola* (Em), *Tylonycteris pachypus* (Tp), *Tylonycteris robustula* (Tr; Heller 1989), *Rhogeessa anaeus* (Ra; Audet et al. 1993), and *Mormopterus planiceps* (Mp; Fullard et al. 1991).



T. tricolor flying more than 1 m away "invisible" to even the most sensitive of bat detectors.

Acknowledgements

We thank the Canadian Organization for Tropical Education and Rainforest Conservation for permission to work at Cãno Palma, Sylvie Bouchard, Jenna Dunlop, Brenna Forster, Dave Johnston, Monica Svensson, and Jason Taylor, who assisted with the fieldwork, and Joanna Zigouris for her contributions to the Canary analysis. We thank Robert M.R. Barclay, and R. Mark Brigham for reading and criticizing earlier versions of the manuscript. The research was supported by The Royal Swedish Academy of Sciences (J.R. and J.E.), The Swedish Foundation for International Cooperation in Research and Higher Education (W.C.L.), and the Natural Sciences and Engineering Research Council of Canada (M.B.F. and M.J.V.).

References

- Ahlén, I. 1981. Identification of Scandinavian bats by their sounds. Rep. No. 6, Department of Wildlife Ecology, Swedish University of Agricultural Science, Uppsala.
- Audet, D., Engstrom, M.D., and Fenton, M.B. 1993. Morphology, karyology, and echolocation calls of *Rhogeessa* (Chiroptera: Vespertilionidae) from the Yucatan Peninsula. *J. Mammal.* **74**: 498–502.
- Barclay, R.M.R. 1983. Echolocation calls of emballonurid bats from Panama. *J. Comp. Physiol. A*, **151**: 515–520.
- Barclay, R.M.R. 1999. Bats are not birds—a cautionary note on using echolocation calls to identify bats: a comment. *J. Mammal.* **80**: 290–296.
- Barclay, R.M.R., and Brigham, R.M. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *Am. Nat.* **137**: 693–703.
- Barclay, R.M.R., and Brigham, R.M. 1994. Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. *Anim. Behav.* **48**: 1013–1021.
- Barratt, E.M., Deaville, R., Burland, T.M., Bruford, W.M., Jones, G., Racey, P.A., and Wayne, R.K. 1997. DNA answers the call of pipistrelle bat species. *Nature (Lond.)*, **387**: 138–139.
- Betts, B.J. 1998. Effects of interindividual variation in echolocation calls on identification of big brown and silver-haired bats. *J. Wildl. Manage.* **62**: 1003–1010.
- Bogdanowicz, W., Fenton, M.B., and Daleszyk, K. 1999. The dietary consequences of what bats say and what moths hear. *J. Zool. (Lond.)*, **247**: 381–393.
- Fenton, M.B., and Bell, G.P. 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). *Can. J. Zool.* **57**: 1271–1277.
- Fenton, M.B., and Bell, G.P. 1981. Recognition of species of insectivorous bats by their echolocation calls. *J. Mammal.* **62**: 233–243.

- Fenton, M.B., Portfors, C.V., Rautenbach, I.L., and Waterman, J.M. 1998a. Compromises: sound frequencies used in echolocation by aerial feeding bats. *Can. J. Zool.* **76**: 1174–1182.
- Fenton, M.B., Cumming, D.H.M., Rautenbach, I.L., Cumming, G.S., Cumming, M.S., Ford, A.G., Taylor, R.D., Dunlop, J.M., Hovorka, M.D., Johnston, D.S., Portfors, C.V., Kalcounis, M.C., and Mahlanga, Z. 1998b. Bats and the loss of tree canopy in African woodlands. *Conserv. Biol.* **12**: 399–407.
- Fenton, M.B., Audet, D., Obrist, M.K., and Rydell, J. 1995. Signal strength, timing and self-deafening: the evolution of echolocation in bats. *Paleobiology*, **21**: 229–242.
- Fullard, J.H., Koehler, K.C., Surlykke, A., and McKenzie, N.L. 1991. Echolocation, ecology and flight morphology of insectivorous bats (Chiroptera) in south-western Australia. *Aust. J. Zool.* **39**: 427–438.
- Habersetzer, J. 1981. Adaptive echolocation sounds in the bat *Rhinopoma hardwickei*. *J. Comp. Physiol. A*, **144**: 559–566.
- Heller, K-G. 1989. Echolocation calls of Malaysian bats. *Z. Säugetierkd.* **54**: 1–8.
- Jones, G. 1993. Flight and echolocation in bats: coupling, and constraints on optimal design. *Comp. Biochem. Physiol. B*, **1**: 603–606.
- Jones, G. 1994. Scaling of wingbeat and echolocation pulse emission rates in bats: why are aerial insectivorous bats so small? *Funct. Ecol.* **8**: 450–457.
- Jones, G. 1996. Does echolocation constrain the evolution of body size in bats. *Symp. Zool. Soc. Lond. No. 69*, pp. 111–128.
- Kalko, E.K.V. 1995a. Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). *Anim. Behav.* **50**: 861–880.
- Kalko, E.K.V. 1995b. Echolocation signal design, foraging habits and guild structure in six Neotropical sheath-tailed bats, Emballonuridae. *Symp. Zool. Soc. Lond. No. 69*, pp. 259–273.
- Kalko, E.K.V., and Schnitzler, H.-U. 1993. Plasticity in the echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. *Behav. Ecol. Sociobiol.* **33**: 415–428.
- Lawrence, B.D., and Simmons, J.A. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.* **71**: 585–590.
- Neuweiler, G. 1989. Foraging ecology and audition in echolocating bats. *Trends Ecol. Evol.* **4**: 160–166.
- Neuweiler, G., and Fenton, M.B. 1988. Behaviour and foraging ecology of echolocating bats. *NATO ASI (Adv. Sci. Inst.) Ser. A Life Sci.* **156**: 535–549.
- Obrist, M.K. 1995. Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav. Ecol. Sociobiol.* **36**: 207–219.
- O'Farrell, M.J., and Miller, B.W. 1997. A new examination of echolocation calls of some Neotropical bats (Emballonuridae and Mormoopidae). *J. Mammal.* **78**: 954–963.
- O'Farrell, M.J., Miller, B.W., and Gannon, W.L. 1999a. Qualitative identification of free-flying bats using the Anabat detector. *J. Mammal.* **80**: 11–23.
- O'Farrell, M.J., Corben, C., Gannon, W.L., and Miller, B.W. 1999b. Confronting the dogma: a reply. *J. Mammal.* **80**: 297–302.
- Pye, J.D. 1973. Echolocation by constant frequency bats. *Period. Biol.* **75**: 21–26.
- Roverud, R.C. 1987. The processing of echolocation sound elements in bats: a behavioural approach. *In Recent advances in the study of bats. Edited by M.B. Fenton, P.A. Racey, and J.M.V. Rayner.* Cambridge University Press, Cambridge. pp. 152–170.
- Rydell, J. 1990. Behavioural variation in echolocation pulses of the northern bat, *Eptesicus nilssonii*. *Ethology*, **85**: 103–113.
- Sales, G., and Pye, D. 1974. Ultrasonic communication by animals. Chapman and Hall, London.
- Schnitzler, H.-U. 1973. Control of Doppler shift compensation in the greater horseshoe bat, *Rhinolophus ferrumequinum*. *J. Comp. Physiol. A*, **82**: 79–92.
- Schnitzler, H.-U. 1987. Echoes of fluttering insects: information for echolocating bats. *In Recent advances in the study of bats. Edited by M.B. Fenton, P.A. Racey, and J.M.V. Rayner.* Cambridge University Press, Cambridge. pp. 226–243.
- Schnitzler, H.-U., Suga, N., and Simmons, J.A. 1976. Peripheral auditory tuning for fine frequency analysis by the CF-FM bat, *Rhinolophus ferrumequinum*. III. Cochlear microphonics and auditory nerve responses. *J. Comp. Physiol. A*, **77**: 306–331.
- Simmons, J.A., and Stein, R.A. 1980. Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. *J. Comp. Physiol. A*, **135**: 61–84.
- Simmons, N.B., and Geisler, J.H. 1998. Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaechiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. *Bull. Am. Mus. Nat. Hist.* **235**: 1–182.
- Summe, Y.W., and Menne, D. 1993. Discrimination of fluttering targets by the FM bat *Pipistrellus stenopterus*. *J. Comp. Physiol. A*, **163**: 349–354.
- Surlykke, A.-M., Miller, L.A., Möhl, B., Andersen, B.B., Christensen-Dalsgaard, J., and Jørgensen, M.B. 1993. Echolocation in two very small bats from Thailand: *Craseonycteris thonglongyai* and *Myotis siligorensis*. *Behav. Ecol. Sociobiol.* **33**: 1–12.
- Waters, D.A., Rydell, J., and Jones, G. 1995. Echolocation call design and limits on prey size: a case study using the aerial-hawking bat, *Nyctalus leisleri*. *Behav. Ecol. Sociobiol.* **37**: 321–328.