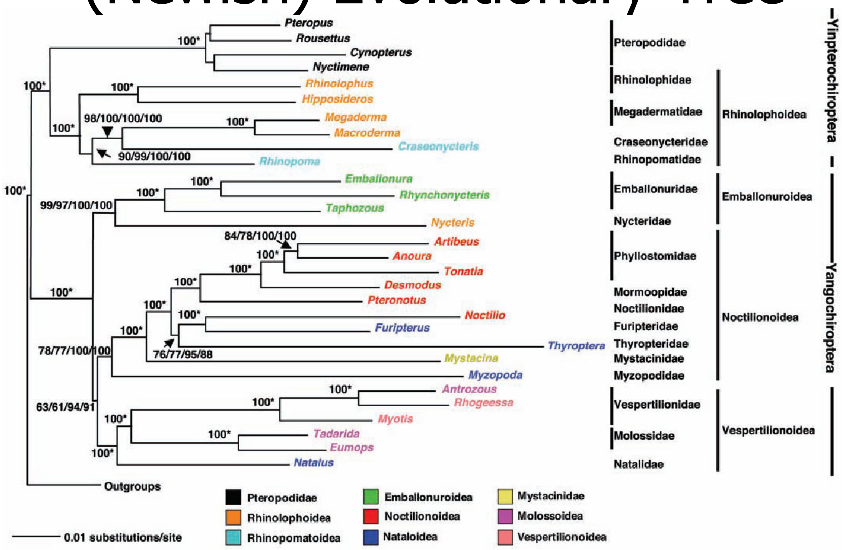


Echolocation calls as traits



(Newish) Evolutionary Tree



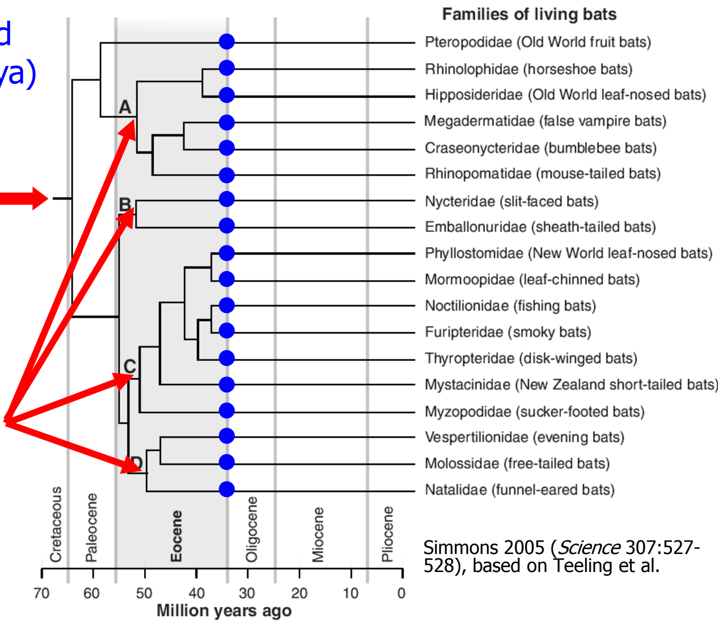
17 nuclear genes, all extant families, maximum likelihood tree: Teeling et al. 2005 (*Science* 307:580-584)

Eocene "Big Bang"

All 18 extant families by end Eocene (34 Mya)

Living bats: common ancestor at/just after K/T boundary: LAURASIAN

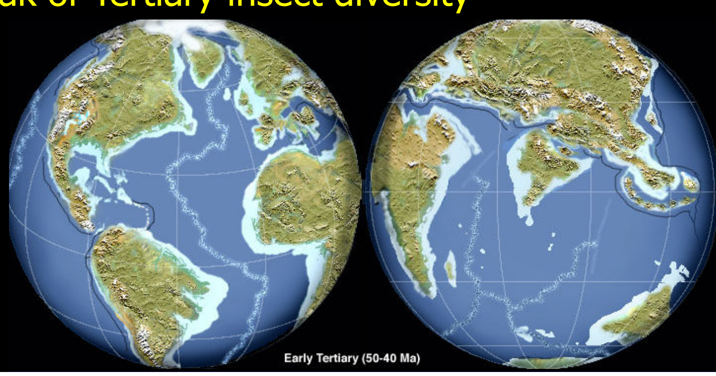
4 major lineages of living echolocating bats appeared early Eocene (52-50 Mya)



Simmons 2005 (*Science* 307:527-528), based on Teeling et al.

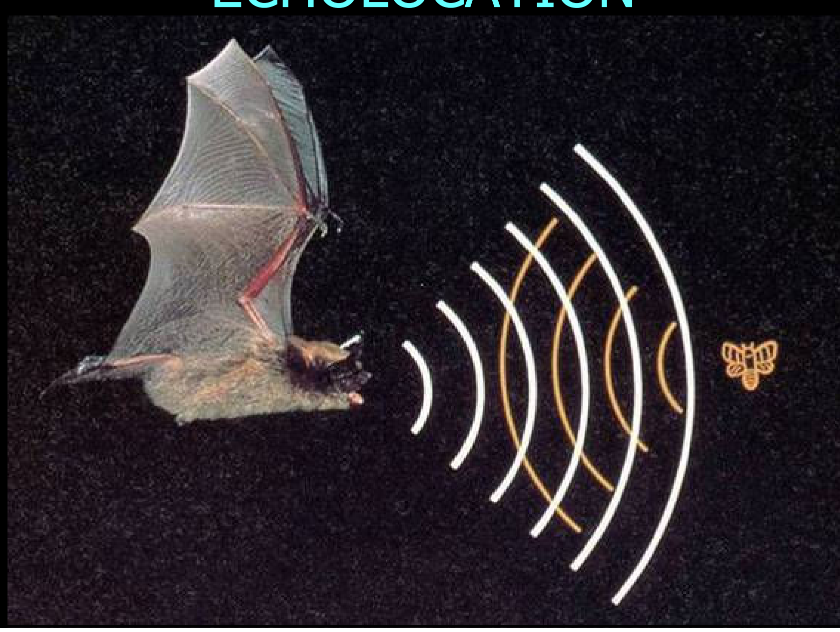
Eocene "Big Bang"

- Radiation unprecedented in mammalian history
- ↑ mean Tº
- ↑ plant diversity -- TRF to 30º latitude; sub-tropical and angiosperm dominate forests to 60º; broad-leaf deciduous (Ellesmere Island 75 º)
- Peak of Tertiary insect diversity



FLIGHT

ECHOLOCATION



ECHOLOCATION

- Echolocation – the analysis by an animal of the echoes of its own emitted sound

- Who ecolocates?
  - Oilbirds, cave swiflets
  - *Rousettus* spp tongue–clicking
  - All other non-Pteropodida

Sound production

- In the larynx, which is large.
- Air over vocal chords so that they vibrate; then muscles adjust the chord tension to change frequency.
- Sound emitted through
  - mouth e.g. vespertilionids
  - nose e.g. rhinolophids, hipposiderids,
- Ultrasonic > 20 kHz
- LOUD!!! 120 dB!

Echo detection

Large external pinnae; internal ear adaptations

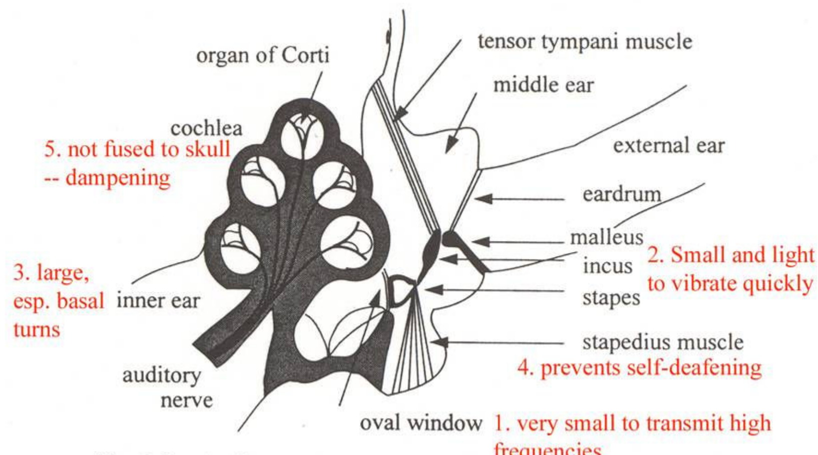
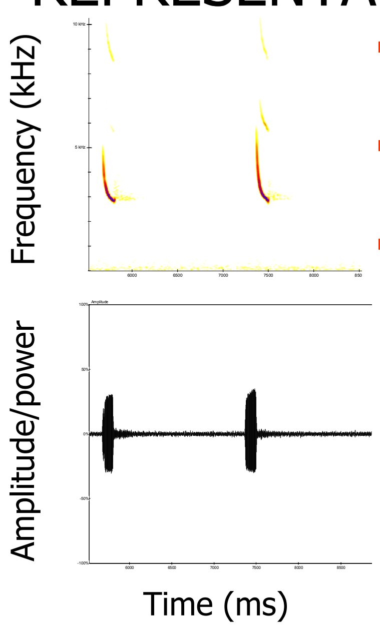
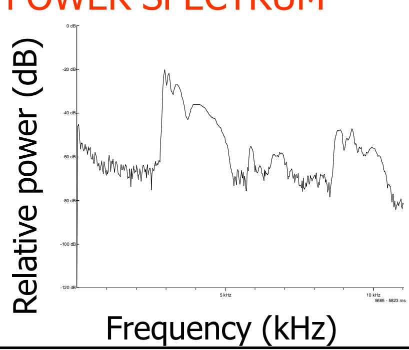


Fig. 3.3. Auditory apparatus (adapted from Hill and Smith, 1984).

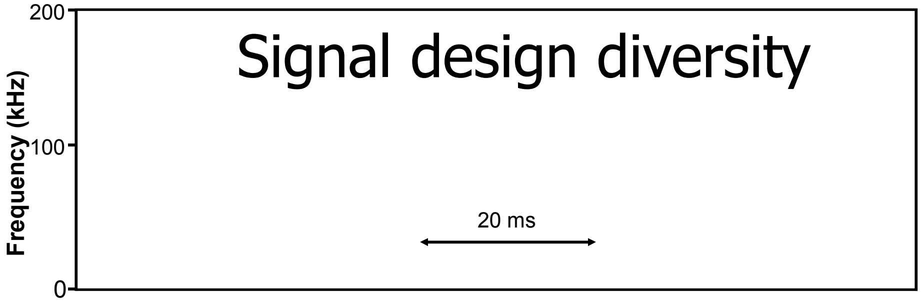
REPRESENTATIONS OF SOUND



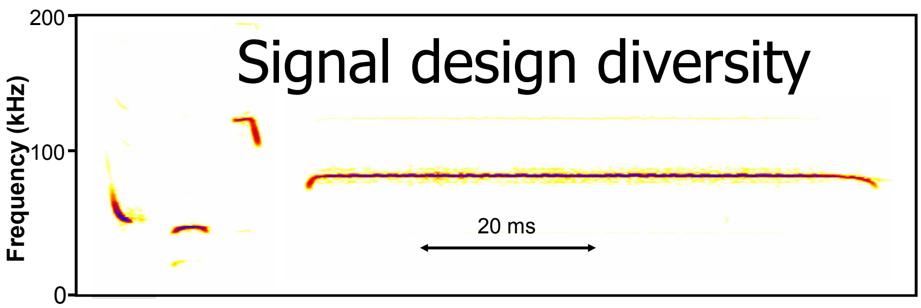
- Frequency v. time = SONAGRAM/SPECTOGRAM
- Amplitude v. time = OSCILLOGRAM
- Power v. frequency = POWER SPECTRUM

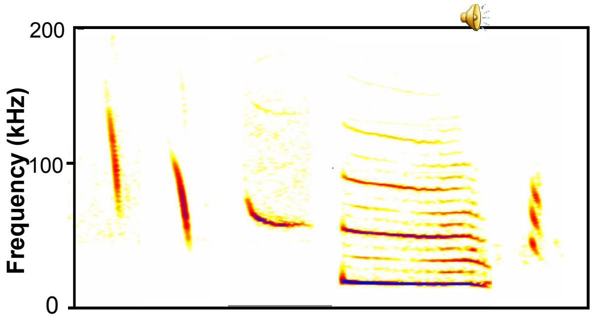


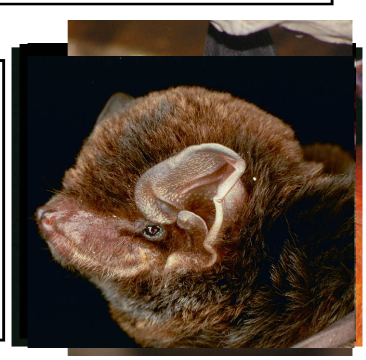
Signal design diversity



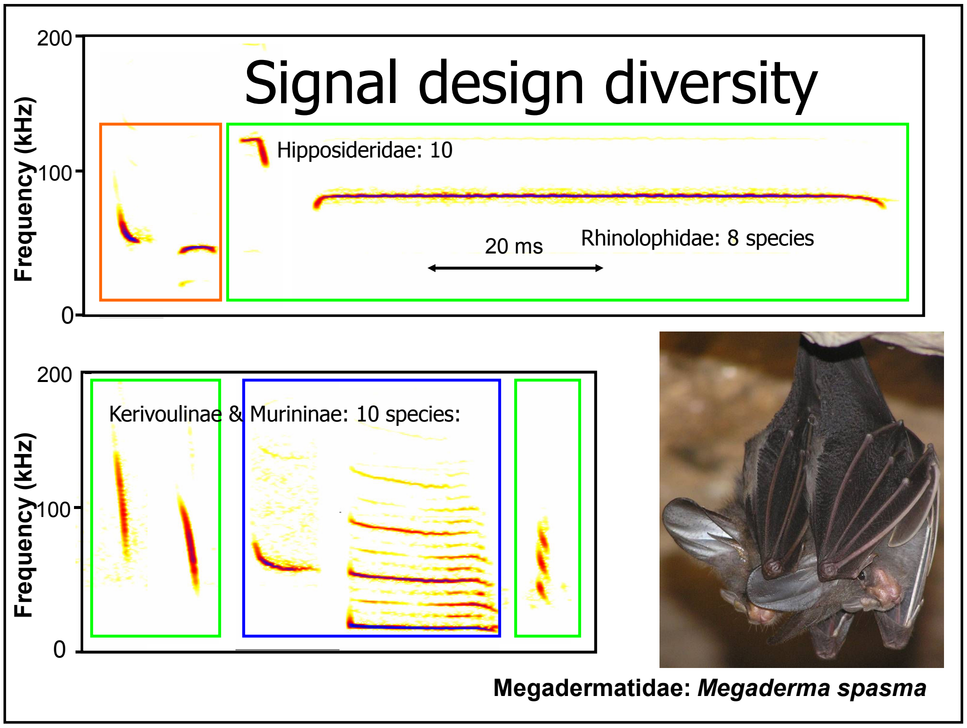
Signal design diversity



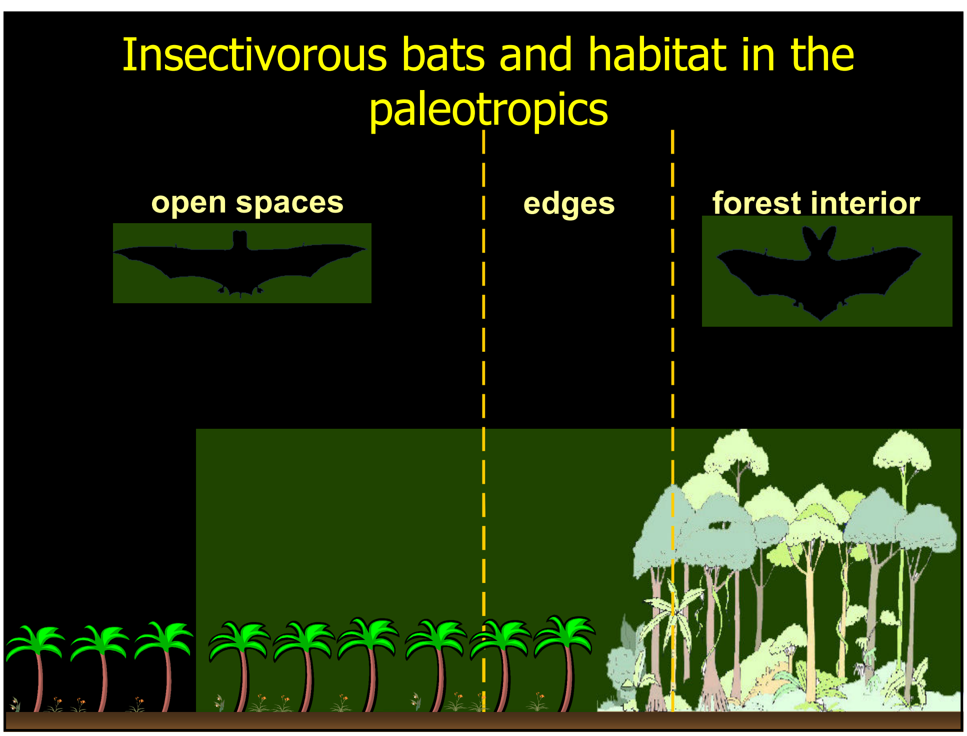




Kingston et al. 2003
(Proc R Soc 267:1381-1386)



Signal design diversity
Frequency (kHz)
200
100
0
Hipposideridae: 10
20 ms
Rhinolophidae: 8 species
Frequency (kHz)
200
100
0
Kerivoulinae & Murininae: 10 species:
Megadermatidae: *Megaderma spasma*



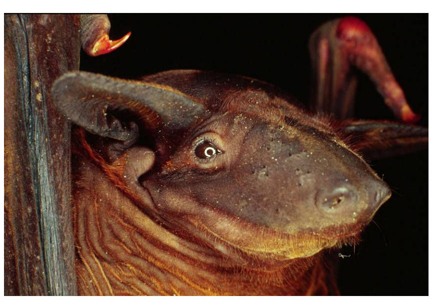
Insectivorous bats and habitat in the paleotropics
open spaces
edges
forest interior

SIGNAL DESIGN – THE TASKS

- Detect – presence of a prey item from echo of signal
- Classify – size, form, material, depth and angular extention, texture of target
  - Encoded in temporal spectral parameters
  - Amplitude and frequency modulations from wingbeats
  - Odour, noise
- Localize – position of target with respect to
  - Range – encoded in time delay between emitted signal and returning echo
  - Horizontal angle – from binaural echo cues
  - Vertical angle – from monaural echo cues

SIGNAL DESIGN – THE HABITAT AND FORAGING GUILDS

- Open-space bats –above forest, in large clearings, usually well clear of clutter.
  - No obstacles ☺
  - Prey items at low density ☹



SIGNAL DESIGN – THE HABITAT AND FORAGING GUILDS

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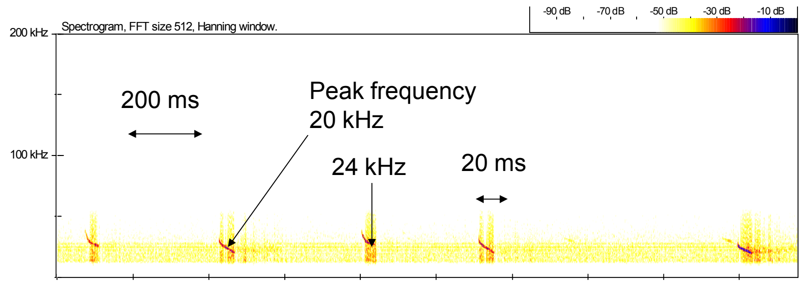
- Edge/gap bats –forest edge, small clearings and gaps, rivers and streams, around houses
  - Acoustic clutter in the background
  - Moderate prey density

SIGNAL DESIGN – THE HABITAT AND FORAGING GUILDS

- Open-space bats –above forest, in large clearings, usually well clear of clutter.
  - No obstacles ☺
  - Prey items at low density ☹
- Edge/gap bats –forest edge, small clearings and gaps, rivers and streams, around houses
  - Acoustic clutter in the background
  - Moderate prey density
- Narrow-space or forest interior bats – inside the densely cluttered environment of the forest interior.
  - Prey items at high density ☺
  - Acoustically cluttered environment ☹

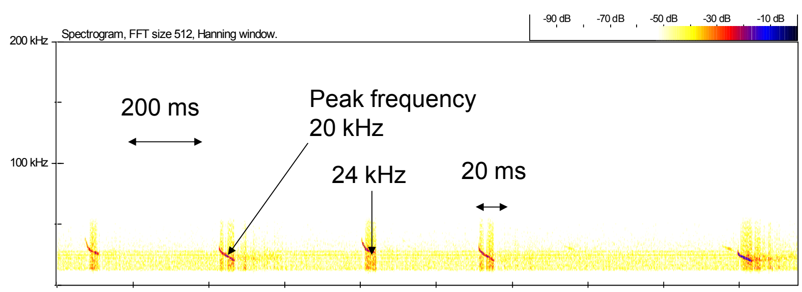
SIGNAL DESIGN & HABITAT: OPEN-SPACE BATS

- Problem: long range detection necessary because prey items at low density
- BUT: sound a poor medium for detection
  - Spreading losses
  - Sound attentuation



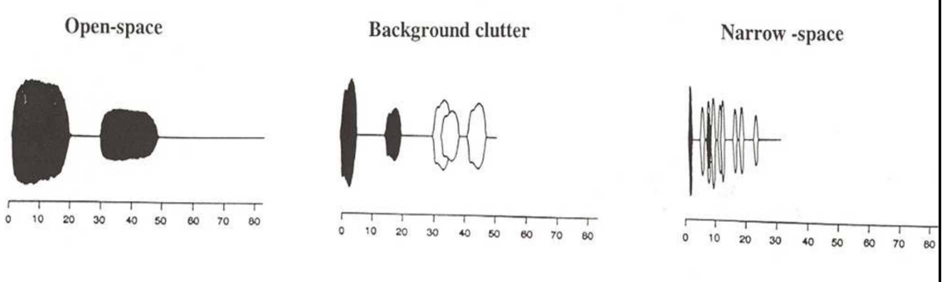
SIGNAL DESIGN & HABITAT: OPEN-SPACE BATS

- Signal design:
  - Low frequency to reduce attenuation
  - Narrow bandwidth (energy concentrated in a few frequencies)
  - Long duration to detect weak echoes and glints



SIGNAL DESIGN AND HABITAT: NARROW-SPACE BATS

- Problem : distinguish echoes from those reflecting from the vegetation
- Signal design:
  - Passive listening
  - Flutter detection
  - Accurate localization/spectral discrimination

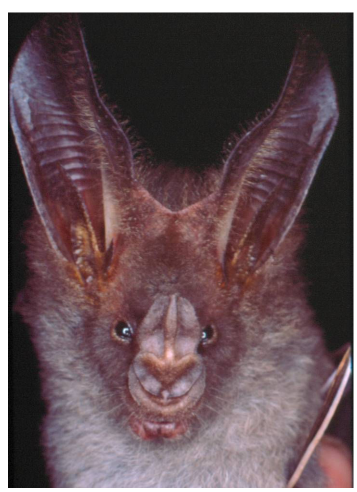


(Schnitzler & Kalko 1998).

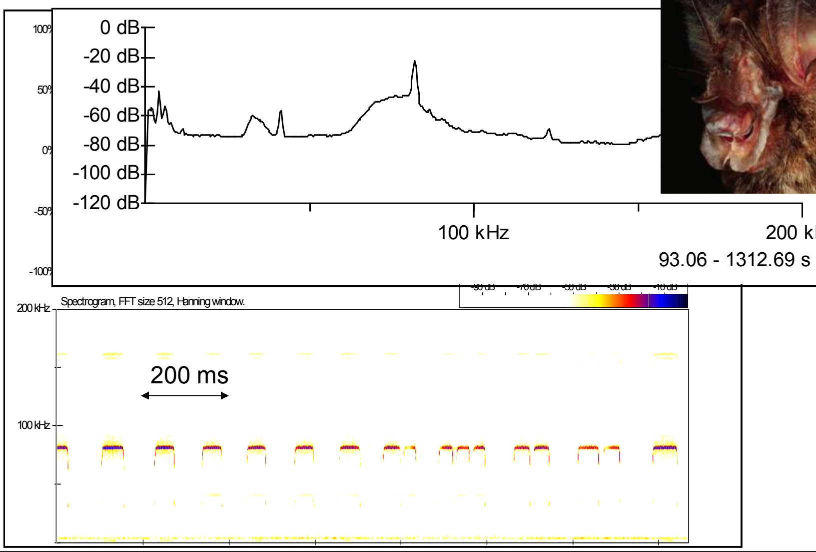
PASSIVE LISTENING

Megadermatidae, Nycteridae

- Echolocation used for orientation, but not prey detection
- Listen for rustling or use visual cues to detect prey; may use echolocation for final localization



FLUTTER DETECTION - RHINOLOPHIDAE



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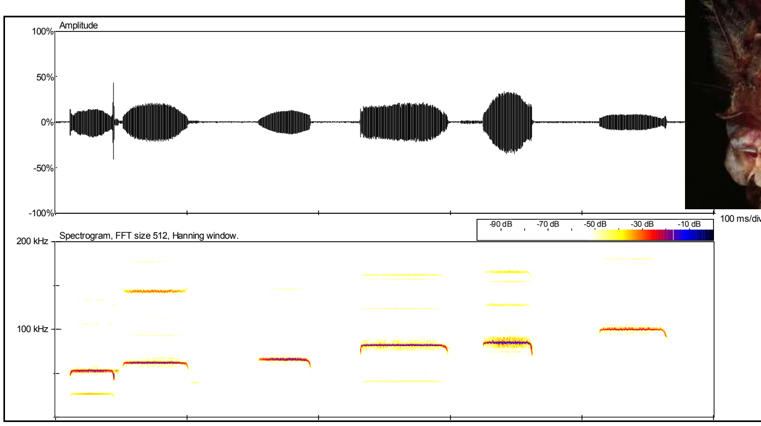
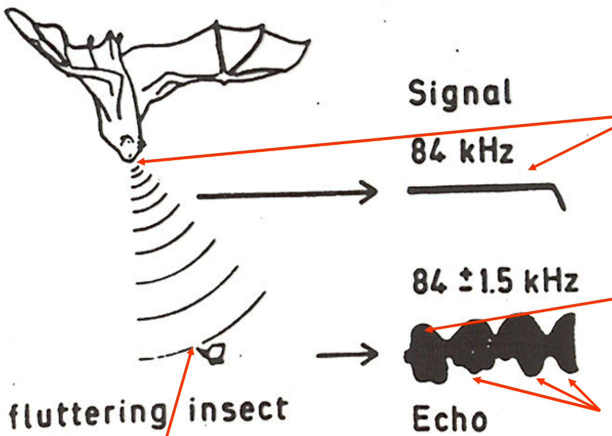


FLUTTER DETECTION



Echolocating bat emits CF signal at **84 kHz**

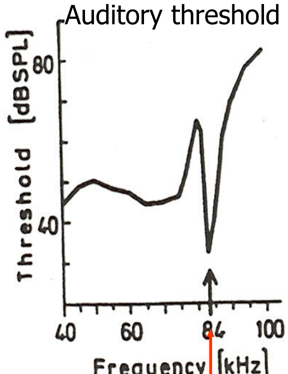
Creating a an amplitude peak and frequency shift in the echo (a glint).

Fluttering creates a series of glints

Signal hits wing of fluttering insect when it is perpendicular to incoming sound wave.

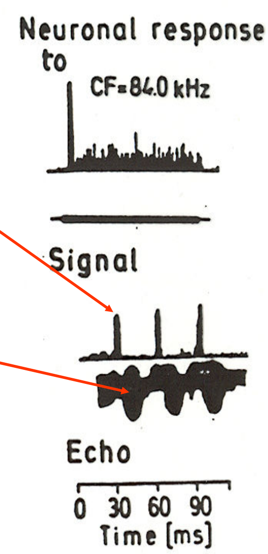
FLUTTER DETECTION

Auditory threshold



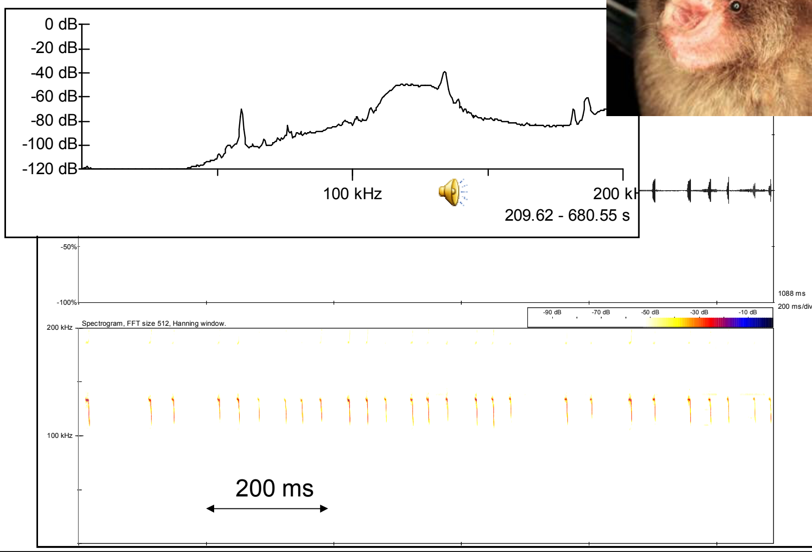
Sufficient to invoke a neuronal response.

Tiny amplitude & frequency changes in the echo caused by the fluttering insect wing

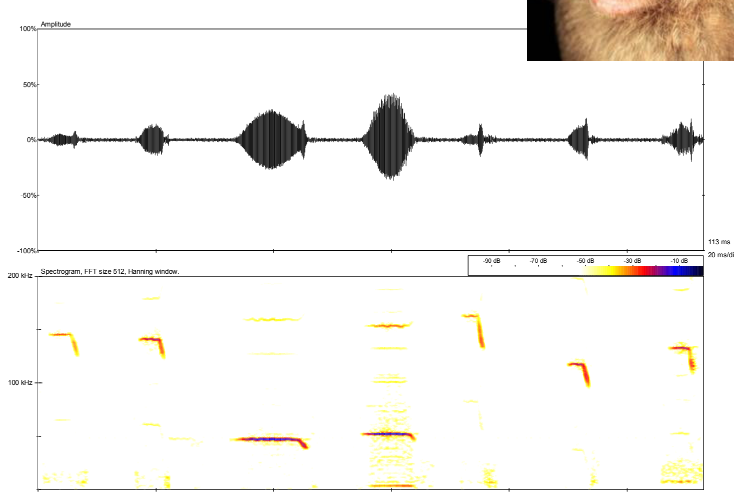


Bat hearing system ultra-sensitive at echo frequency (84 kHz); overrepresented in cochlea and inferior colliculus = **acoustic fovea**

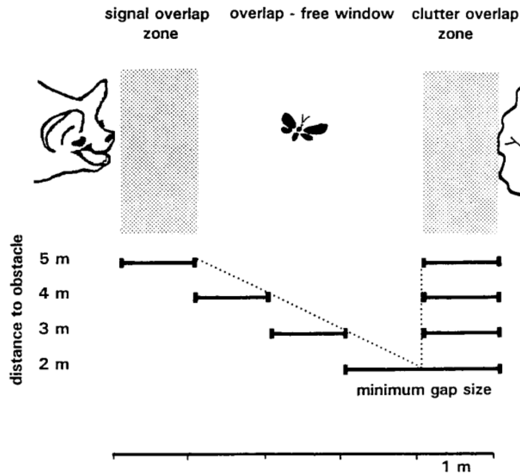
FLUTTER DETECTION - HIPPOSIDERIDAE



FLUTTER DETECTION - HIPPOSIDERIDAE



MASKING



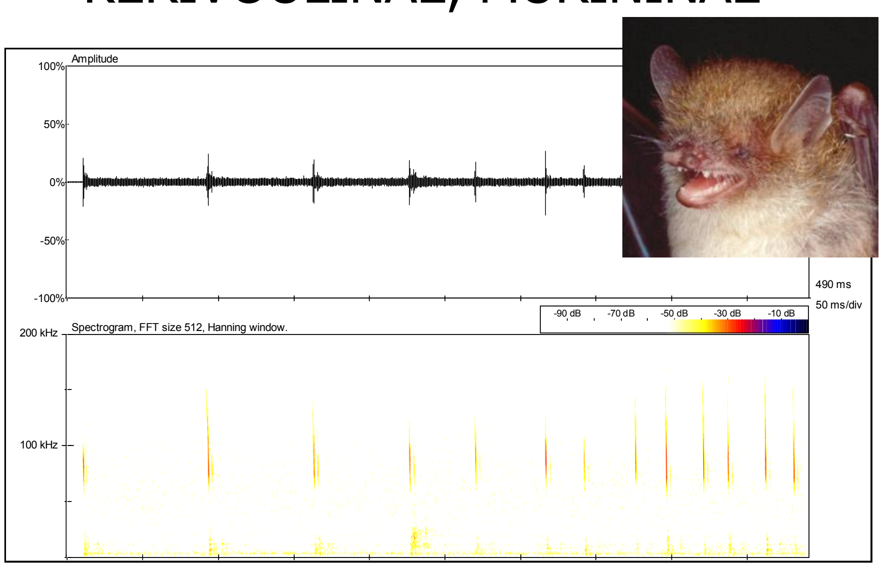
Forward masking – prey echo overlaps the emitted signal (interfering signals that precede the target echo)

Backward masking – prey echo overlaps with clutter echoes (interfering signals follow the target echo)

Width of overlap zone depends on signal design, especially duration

Not a problem for CF bats because separate in frequency domain

ACCURATE LOCALIZIATION – KERIVOULINAE, MURININAE



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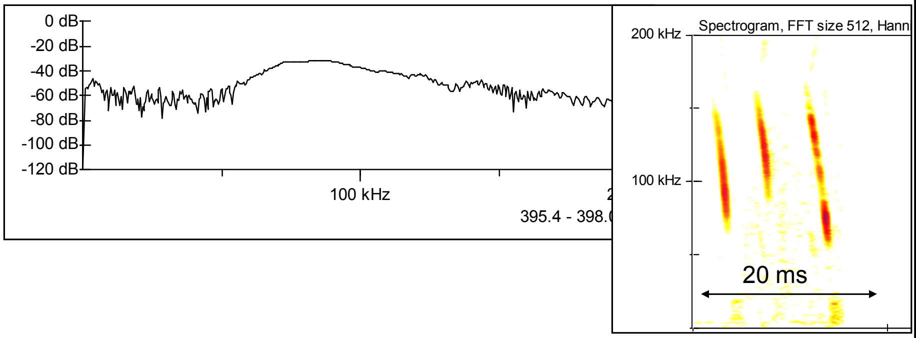
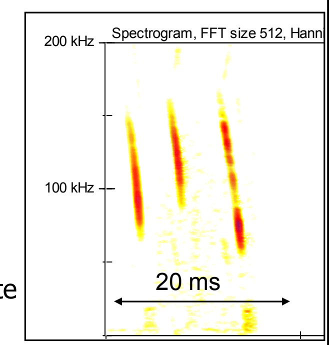
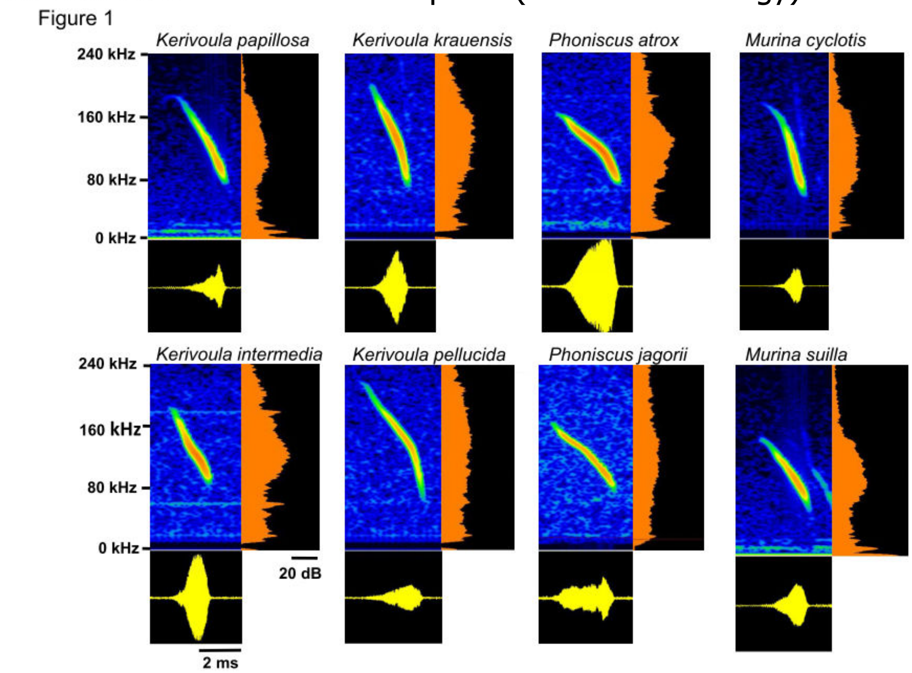


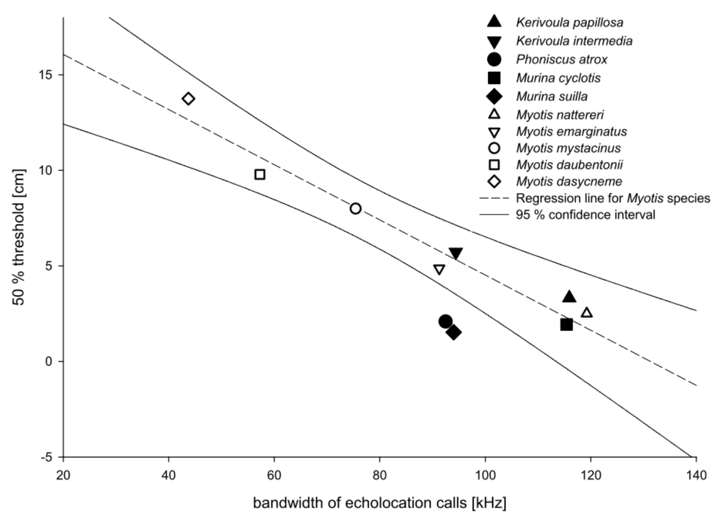
ACCURATE LOCALIZIATION – KERIVOULINAE, MURNINAE

- Short duration and very low intensity to reduce signal/echo overlap and auditory overloading
- Sound energy spread over bandwidth
- Broad bandwidth to provide accurate range measurements and horizontal and vertical angle.
- High frequency + broad bandwidth – possible spectral discrimination?? (Neuweiler idea), accurate time stamps for ranging (Schnitzler), ➔ forage v. close to background (Siemers)



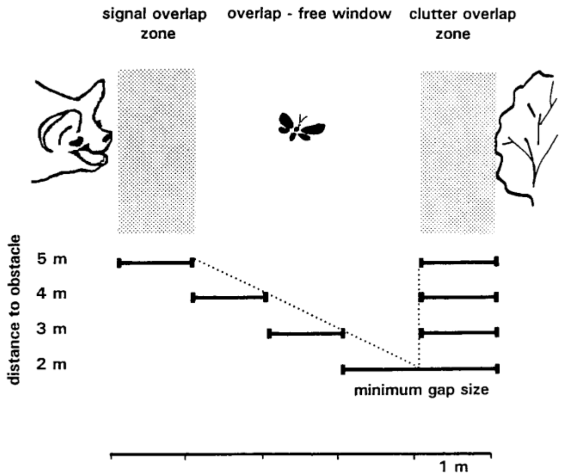
Schmieder et al. in press (Functional Ecology)





The relationship of prey detection performance (50% thresholds) in the clutter screen treatment and bandwidth of echolocation calls for all five tested Kerivoulinae and Murininae species (filled symbols) and additionally for five *Myotis* species (open symbols) tested by Siemers and Schnitzler (2004) is shown. Regression line and 95% confidence interval refer only to the *Myotis* species and were obtained from Siemers and Schnitzler 2004 (Distance [cm] =18.95 - 0.14 (bandwidth [kHz])]).

MASKING



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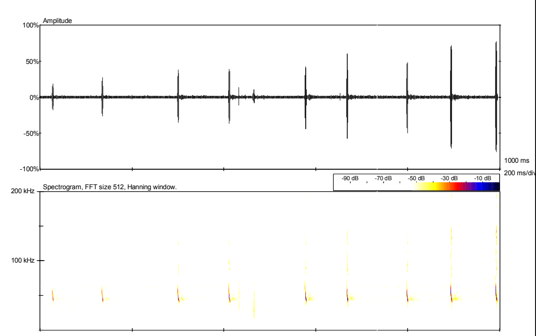
SIGNAL DESIGN AND HABITAT: EDGE/GAP BATS

Need:

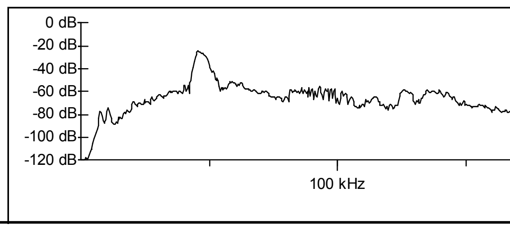
- long-distance detection
- good localization
- but must avoid pulse/echo overlap

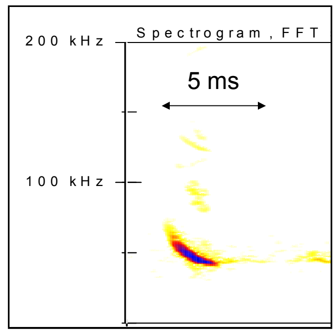


SIGNAL DESIGN AND HABITAT: EDGE/GAP BATS

Signal design

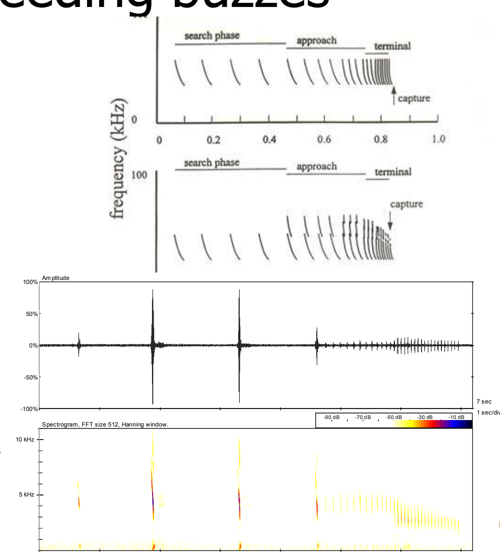
- Signal is a combination of FM & CF components
- Reduce CF component as get nearer clutter (reduce backward masking)

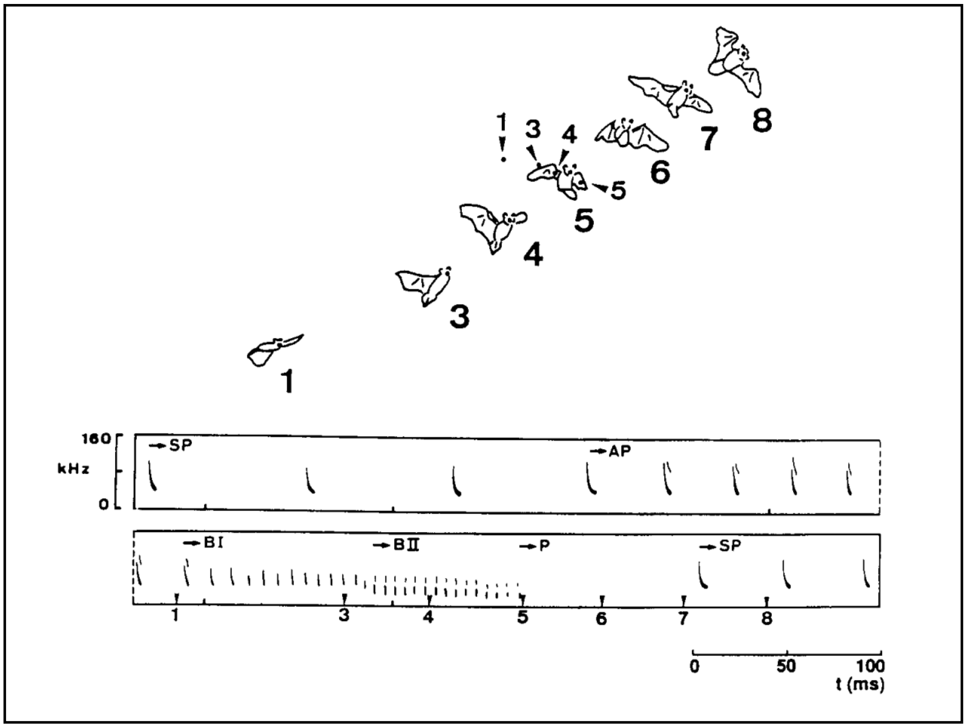


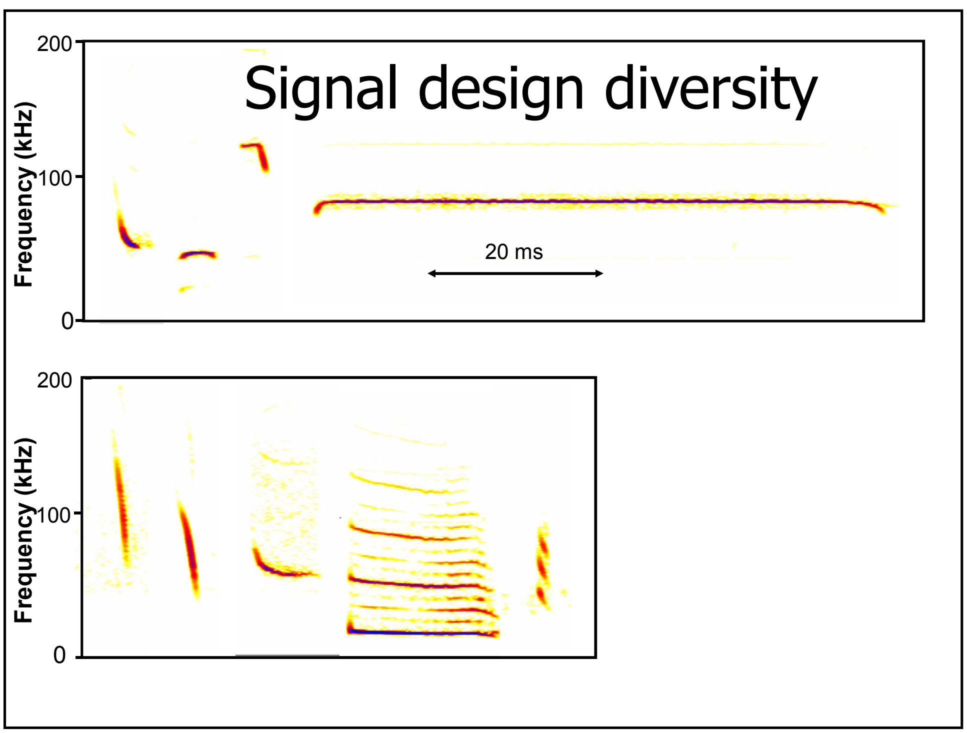


Signal structure during prey capture –feeding buzzes

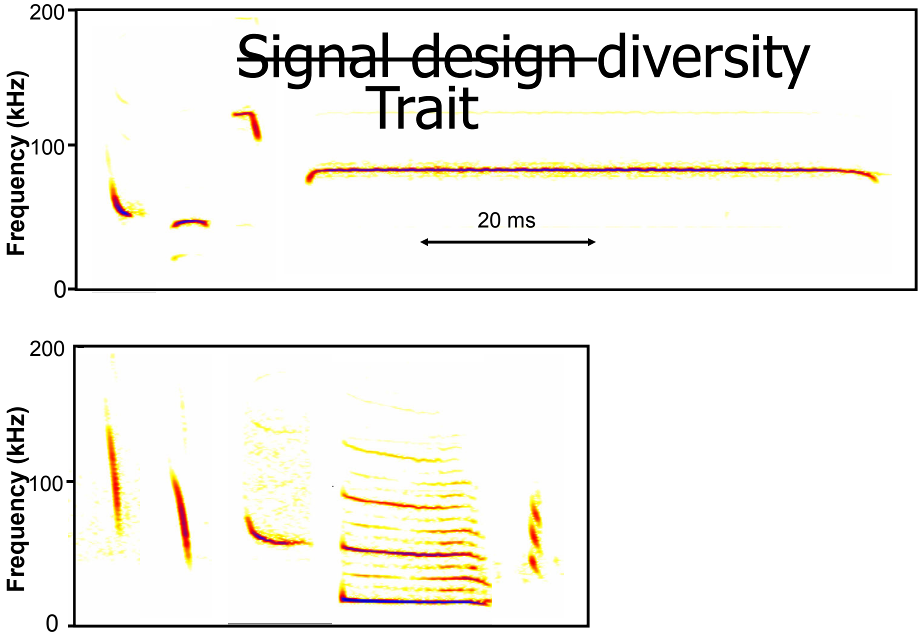
- Call structure changes as a bat approaches prey
- Needs to change from calls good at detecting prey, to those good at localizing it
- Call gets shorter, more FM, and the pulse repetition rate increases
- Ends in a 'terminal buzz'




1
3
4
5
6
7
8
160
kHz
0
SP
AP
BI
BII
P
SP
0
50
100
t (ms)


Signal design diversity
200
Frequency (kHz)
100
0
20 ms
200
Frequency (kHz)
100
0

~~Signal design~~ diversity
Trait



What makes a “good” trait for use in taxonomy and systematics?

Good trait characteristics (Tigga's version)

- Range of values don't overlap so ➔ can use it to distinguish/discriminate among species
- Can be measured, and measured consistently (repeated measurements ➔ same value (or close)
  - Measurement technique can be consistently applied (equipment issue)
  - Limited intra-individual variation (context issue)

Interspecific overlap?

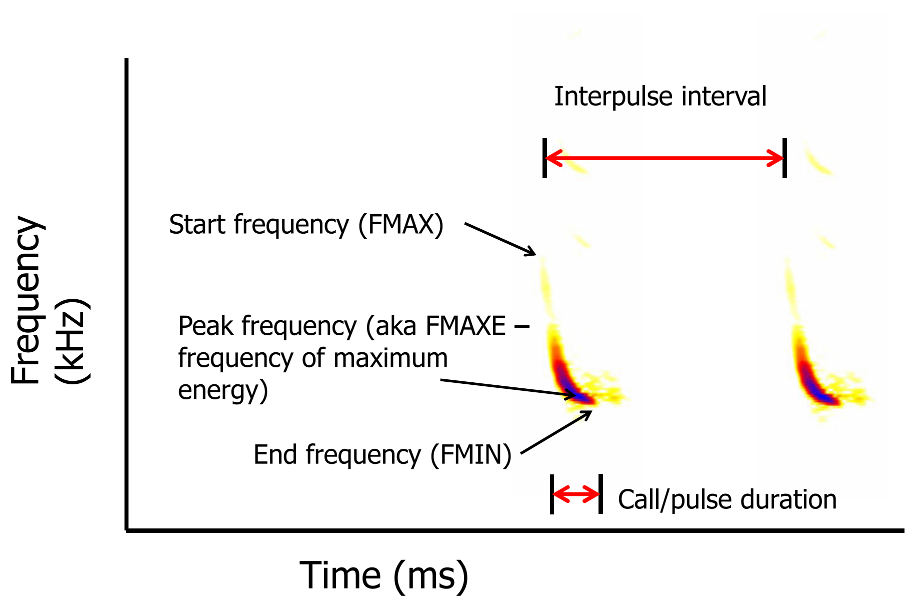
- Limited ☺ *Rhinolophus, Hipposideros* (i.e. CF bats)
- Overlap of some measurement variables (edge/gap bats (FM-CF bats))
- Substantial overlap of parameters (broadband FM bats – *Kerivoula, Phoniscus, Murina*)

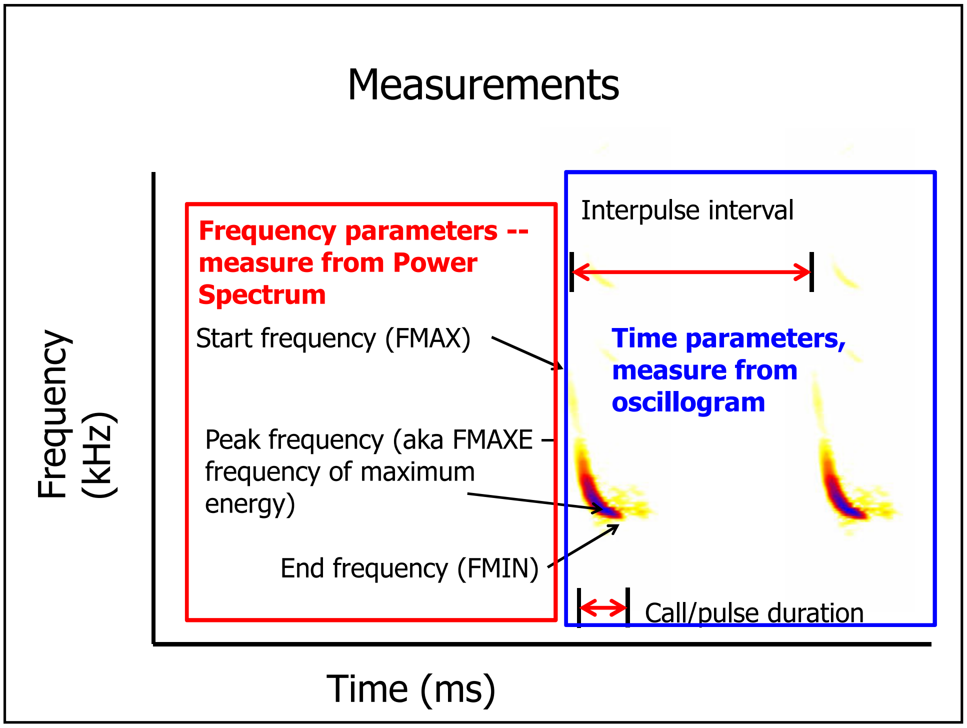
Measurements – what and how? (The classics)

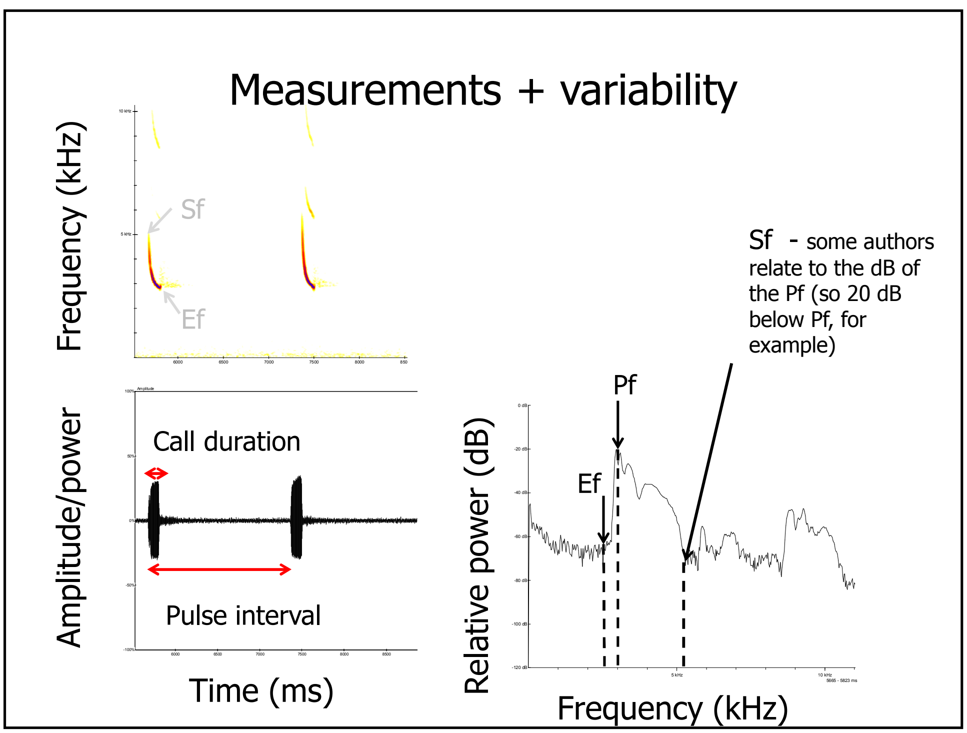
- Frequency parameters (kHz)
- Time parameters (ms)

- About the individual call
- About the sequence, or relationship among calls.

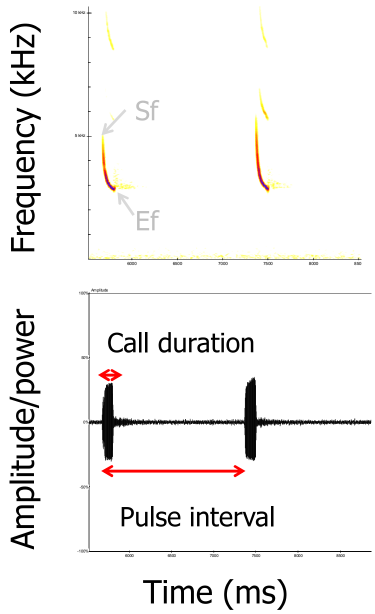
Measurements

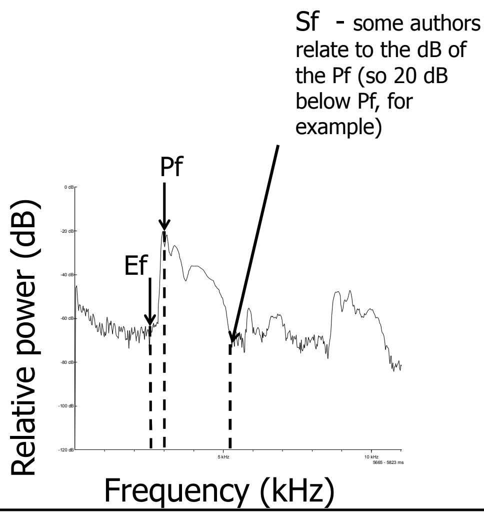



Measurements
Frequency (kHz)
Frequency parameters -- measure from Power Spectrum
Start frequency (FMAX)
Peak frequency (aka FMAXE – frequency of maximum energy)
End frequency (FMIN)
Interpulse interval
Time parameters, measure from oscillogram
Call/pulse duration
Time (ms)


Measurements + variability
Frequency (kHz)
Sf
Ef
Amplitude/power
Call duration
Pulse interval
Time (ms)
Sf - some authors relate to the dB of the Pf (so 20 dB below Pf, for example)
Pf
Ef
Relative power (dB)
Frequency (kHz)

Problems?

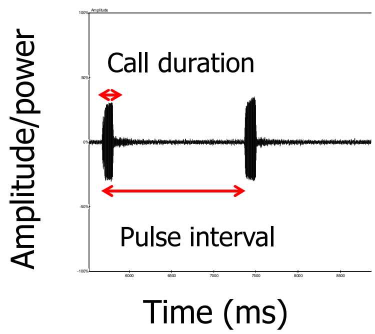




Problems?

Time parameters (especially pulse interval) can change a lot depending on what the individual is doing

- Calls are shorter closer to background and as prey are approached (to avoid masking)
- Pulse interval + calls shorter as they approach prey (Increase in Pulse Repetition Rate) to get more information on 3D location



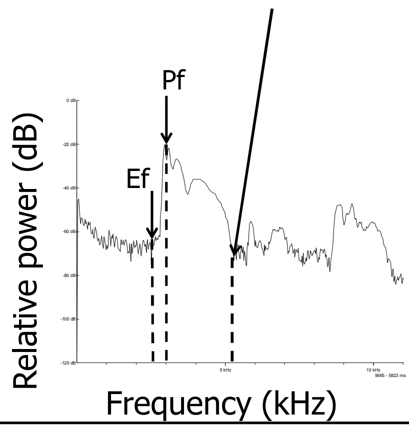
➔Most stereotypical during search phase

Problems?

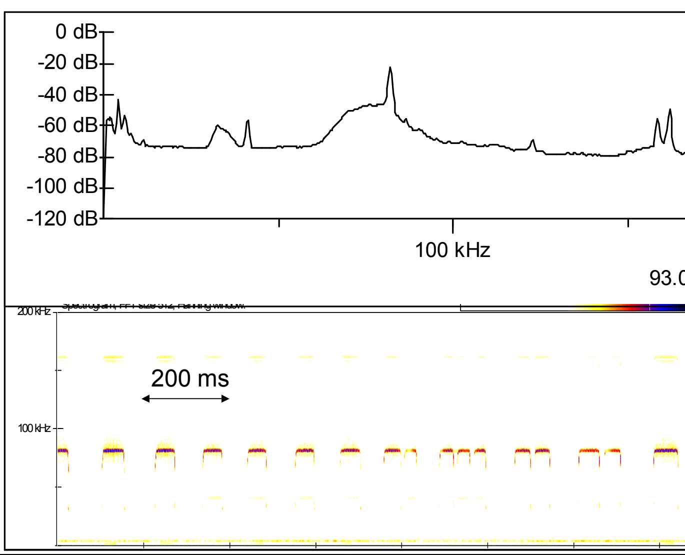
Sf: very hard to measure consistently (measurement error)
Attenuation at high frequencies → distance of bat to recording device will alter recording of this

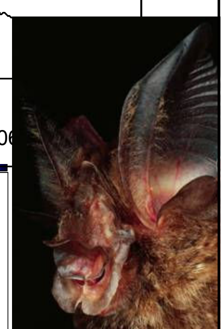
Ef: hard to measure but less attenuation (because lower frequency) than Sf

=>Peak frequency best trait

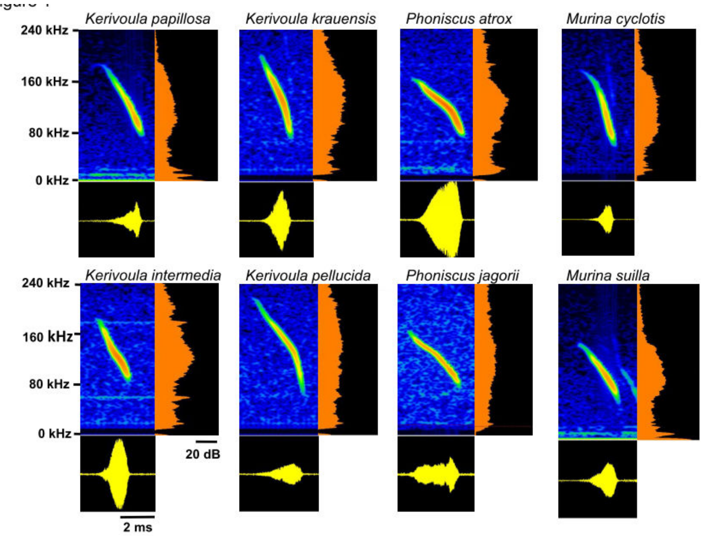


Pf especially good for rhinos/hippos because very stereotyped within an individual (because have to match to acoustic fovea)



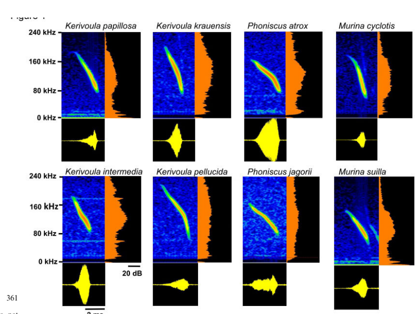


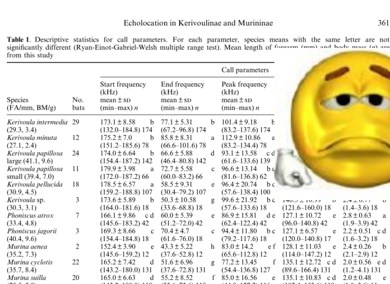
BUT…….Pf meaningless in broadband FM bats – sound energy spread out across frequencies.



BUT…….Pf meaningless in broadband FM bats – sound energy spread out across frequencies.

Also – calls overlap substantially – need nasty multivariate stats to tease species apart





Echolocation in Kerivoulinae and Murininae 361

Table 1. Descriptive statistics for call parameters. For each parameter, species means with the same letter are not significantly different (Ryan-Einot-Gabriel-Welsh multiple range test). Mean length of [illegible] from this study

Species (FA/mm, BM/g)	No. bats	Call parameters: Start frequency (kHz) mean ± SD (min–max) n	End frequency (kHz) mean ± SD (min–max) n	Peak frequency (kHz) mean ± SD (min–max) n	[illegible]	[illegible]
Kerivoula intermedia (29.3, 3.4)	29	173.1 ± 8.58 b (132.0–184.8) 174	77.1 ± 5.31 b (67.2–96.8) 174	101.4 ± 9.18 b (83.2–137.6) 174	[illegible]	[illegible]
Kerivoula minuta (27.1, 2.4)	12	175.2 ± 7.0 b (151.2–185.6) 78	85.8 ± 8.31 a (66.6–101.6) 78	112.9 ± 10.86 a (83.2–134.4) 78	[illegible]	[illegible]
Kerivoula papillosa large (41.1, 9.6)	24	174.0 ± 6.64 b (154.4–187.2) 142	66.6 ± 5.88 d (46.4–80.8) 142	93.1 ± 13.58 c d (61.6–133.6) 139	[illegible]	[illegible]
Kerivoula papillosa small (39.4, 7.0)	11	179.9 ± 3.98 a (172.0–187.2) 66	72.7 ± 5.58 c (60.0–83.2) 66	96.6 ± 13.14 b c (81.6–136.8) 62	[illegible]	[illegible]
Kerivoula pellucida (30.9, 4.5)	18	178.5 ± 6.57 a (159.2–188.8) 107	58.5 ± 9.31 e (30.4–79.2) 107	96.4 ± 20.74 b c (57.6–138.4) 100	[illegible]	[illegible]
Kerivoula sp. (30.3, 3.1)	3	173.6 ± 5.89 b (164.0–181.6) 18	50.3 ± 10.58 g (33.6–68.8) 18	99.6 ± 21.92 b c (57.6–133.6) 18	[illegible] (121.6–160.0) 18	[illegible] (1.4–3.6) 18
Phoniscus atrox (33.4, 4.8)	7	166.1 ± 9.86 c d (145.6–183.2) 42	60.0 ± 5.39 e (51.2–72.0) 42	86.9 ± 15.81 d e (62.4–122.4) 42	127.1 ± 10.72 e (96.0–140.8) 42	2.8 ± 0.63 a (1.9–3.9) 42
Phoniscus jagorii (40.4, 9.6)	3	169.3 ± 8.66 c (154.4–184.8) 18	70.4 ± 4.7 c (61.6–76.0) 18	94.4 ± 11.80 b c (79.2–117.6) 18	127.1 ± 6.57 e (120.0–140.8) 17	2.2 ± 0.51 c d (1.6–3.2) 18
Murina aenea (35.2, 7.3)	2	152.4 ± 3.90 e (145.6–159.2) 12	43.3 ± 5.22 h (37.6–52.8) 12	83.0 ± 14.2 e f (65.6–112.8) 12	128.1 ± 11.03 e (114.0–147.2) 12	2.4 ± 0.26 b (2.1–2.9) 12
Murina cyclotis (35.7, 8.4)	22	165.2 ± 7.42 d (143.2–180.0) 131	51.6 ± 6.96 g (37.6–72.8) 131	77.2 ± 13.45 f (54.4–136.8) 127	135.1 ± 12.72 c d (89.6–166.4) 131	2.0 ± 0.56 e d (1.2–4.1) 131
Murina suilla (29.5, 3.9)	20	165.0 ± 6.63 d (143.2–180.0) 118	55.2 ± 8.52 f (33.6–73.6) 118	85.0 ± 16.56 e (44.8–127.2) 116	135.1 ± 10.83 c d (102.4–153.6) 118	2.0 ± 0.48 e (1.0–3.6) 11

And – calls very low intensity and high frequency (> 200 kHz) – need flight tent + good microphone + sampling rate of detector (Full spectrum)

Bat detectors

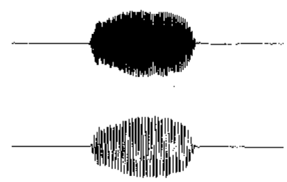
- Full spectrum ---- from Time Expansion or High Speed Sample (aka Real Time Sampling) e.g. Pettersson, EM3, Nano
- Frequency Division --- from zero crossing e.g. Anabat
- Heterodyne --- makes calls audible, no use for analysis.

HETERODYNE

- Converts to audible range
- Can only sample a limited range of frequencies (usually 10kHz around the control setting)
- No analysis use, can be handy for immediate confirmations in the field for hand-held cf bats if different enough for good tuning

FREQUENCY DIVISION/ZERO-CROSSING

- Can sample entire frequency range of detector constantly
- Works in real time
- Ultrasound frequency changed by a constant factor (10) (40kHz→ 4 kHz)
- Frequency division from counting number of "zero-crossings" made by original signal, then 1 output signal for each 10 zero-crossings ==1/10th of original frequency
- **But** this is based on the wave form. Strong harmonic in original signal (as in rhinolophids)→ extra-zero crossings, so



- Output frequency is higher than fundamental
- No harmonic information

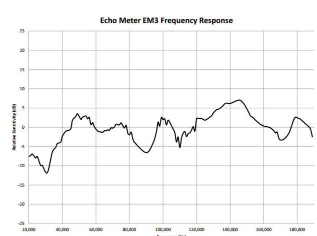
TIME EXPANSION (REAL-TIME SAMPLING/HIGH SPEED SAMPLING/FULL SPECTRUM)

- Can sample entire frequency range of detector constantly
- Signal captured, stored, and replayed at slower speed → stretches time base
- Retains all details (whole waveform, frequency and amplitude) lost in other systems (harmonics etc)
- Best for call descriptions because all details retained
- WAS prohibitively expensive, now new cheaper (USD1000 or so) systems available (Nano, EM3)
- Previously, memory would fill fast (seconds) and you'd need to download (and couldn't record). Flash-based memories now allow for continuous, full-bandwidth real-time recording

SAMPLING FREQUENCY = SAMPLING RATE

- Rate at which call is sampled. Needs to be at 2 x the highest frequency of the call you want to record.
- So if you your bat is calling around 100kHz, fs = 200kHz
- If 200 kHz call (*Coelops/Kerivoula*) = 400kHz, so watch out if detector only gives sample rate options up to 384 kHz (like EM3) – that's c. 150 kHz
- Some detectors you need it higher e.g. D1000x max call 0.4x fs (because anti-aliasing filter), so 200kHz call – 500 kHz fs
- Check the specs of your bat detector that it can do this.
- (note higher fs, larger files)

FREQUENCY RANGE/RECORDING BANDWIDTH



- Range of frequencies over which the detector can record effectively (has a flat response) – this is a property of the microphone, common cut-off 120kHz
- EM3 – 194; Nano is offering a NEUmic to 200kHz, D1000x is custom and > 200 kHz
- So, "best" is going to depend on how high the frequencies you expect from your bats. Unfortunately several rhinos and hippos >120kHz, and all *Kerivoula* other broadband FM bats too high for 120 kHz options
- http://batdetecting.blogspot.com/

The Bottom Line

CF Bats -- Rhinolophidae, Hipposideridae

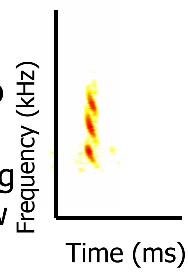
- Record – in the hand (because of doppler shift compensation). Keep an eye on the gain because they are very loud (120dB 1 cm from the mouth), and overloaded calls will be distorted.
- Use – Full spectrum – Problem with FD is that any harmonics (present in Rhinos/Hippos) will be added into the zero-crossing process giving a higher frequency.
- Watch sampling rate and frequency range of microphone
- Measure – Peak frequency (from power spectrum)

Broadband FM Bats – Murininae - Kerivoulinae

- Almost impossible to get repeatable measures that can ➔ species discrimination (use other traits)
- Full spectrum detectors with flat response >>200 kHz
- Flight cage recordings –use calls as bat flying straight towards microphone, because v. low intensity (quiet)
- Start frequency, end frequency, call duration.

Broadband Multiharmonic Bats – Megadermatidae, Nycteridae

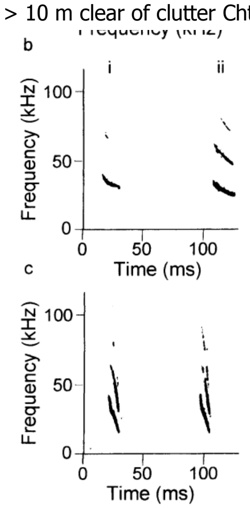
- Very little work on these, but not unlike trying to separate phyllostomids by call characteristics.
- Full spectrum detectors with flat response to 150kHz
- Flight cage recordings –use calls as bat flying straight towards microphone, because v. low intensity (quiet)
- Start frequency, end frequency, call duration, possible of each harmonic (if you can discriminate it). Not sure of consistency from call – call.



CF-FM calls (open-space, edge/gap bats, Molossidae, Emballonuridae, other Vesps)

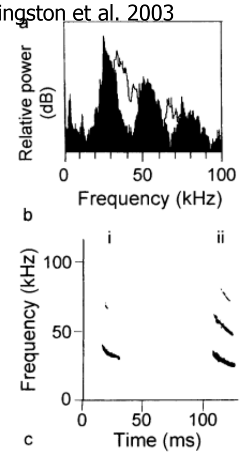
- Calls change a lot depending on context because of avoidance of masking effects.
- Full spectrum detectors with flat response to 130kHz should be OK for most.
- Zip-line or free-flight recordings – need to be in search phase to characterize "trait" properly
- **Peak frequency** will be most species-specific and change least if recording out of **search phase**, but measure others
- BUT……

> 10 m clear of clutter Chto

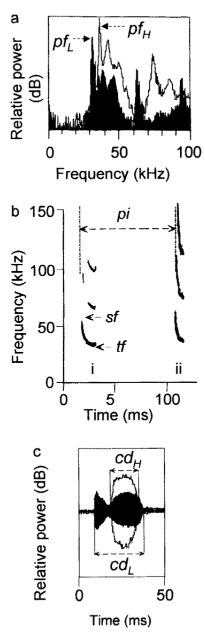


< 5 m - Chto

Cheiromeles torquatus– Kingston et al. 2003



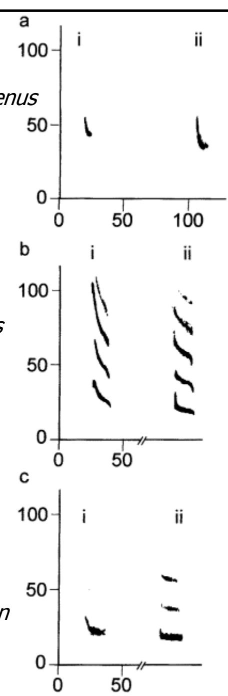
Pipistrellus stenopterus



Hesperoptenus blandfordi

Mops mops

Chaerephon johorensis



Many open-space species use call alternation during search phase – need to characterize both call types.

The Very Bottom Line

- CF calls of Hippos and Rhinos your best bet because v. little intra-individual variation in easily ID'd measurement – Pf.
  - But need full spectrum detector
  - Focusing on Hippos, need to be able to record higher frequencies (sampling rate + microphone response)
- Very easy to do, widely used in publications

- Other groups –much variation in parameters (because of what the bat is doing), recording limitations ➔ value is limited unless you are dedicated to doing it as a major focus of your study.