

REVIEW

Evolution of high duty cycle echolocation in bats

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Summary

Duty cycle describes the relative ‘on time’ of a periodic signal. In bats, we argue that high duty cycle (HDC) echolocation was selected for and evolved from low duty cycle (LDC) echolocation because increasing call duty cycle enhanced the ability of echolocating bats to detect, lock onto and track fluttering insects. Most echolocators (most bats and all birds and odontocete cetaceans) use LDC echolocation, separating pulse and echo in time to avoid forward masking. They emit short duration, broadband, downward frequency modulated (FM) signals separated by relatively long periods of silence. In contrast, bats using HDC echolocation emit long duration, narrowband calls dominated by a single constant frequency (CF) separated by relatively short periods of silence. HDC bats separate pulse and echo in frequency by exploiting information contained in Doppler-shifted echoes arising from their movements relative to background objects and their prey. HDC echolocators are particularly sensitive to amplitude and frequency glints generated by the wings of fluttering insects. We hypothesize that narrowband/CF calls produced at high duty cycle, and combined with neurobiological specializations for processing Doppler-shifted echoes, were essential to the evolution of HDC echolocation because they allowed bats to detect, lock onto and track fluttering targets. This advantage was especially important in habitats with dense vegetation that produce overlapping, time-smeared echoes (i.e. background acoustic clutter). We make four specific, testable predictions arising from this hypothesis.

Key words: Chiroptera, calling behaviour, signal design, Yinpterochiroptera, Yangochiroptera, flutter detection, Doppler shift compensation.

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Introduction

Echolocation is an active sensory system that tightly couples signal production with echo reception. Echolocation has evolved independently in two orders of birds (Caprimulgiformes and Apodiformes) and four orders of mammals [Cetartiodactyla, Chiroptera, Eulipotyphla (Buchler, 1976); and Afrosoricida (Gould, 1965; Thomas et al., 2002)]. The ability to echolocate allows animals to orient in their environment (all echolocators) and detect prey (odontocete whales and laryngeally echolocating bats) in total darkness and other conditions of uncertain lighting (Griffin, 1944; Griffin, 1958). Using differences between pulse and echo, echolocators collect information and form an acoustic image of the environment.

Echolocation works best when the loud outgoing vocalizations do not mask or reduce the listener’s sensitivity to the weaker returning echoes (Jen and Suga, 1976; Suga and Schlegel, 1972; Fenton et al., 1995). Most echolocators avoid forward masking effects by separating pulse and echo in time; however, ~160 species of bats in the families Rhinolophidae and Hipposideridae and the mormoopid *Pteronotus parnellii* separate pulse and echo information in frequency. These different calling strategies correspond to low (LDC) and high duty cycle (HDC) echolocation, respectively.

The duty cycle (DC) of a periodic sound is the ratio of signal duration to signal period ($DC=d/T$). Animals alter the duty cycle of their signals by changing their call duration (d , the time between the onset and offset of a sound) and/or period (T , the time between

the onset of successive sounds). Duty cycle describes the ‘on time’ of a sound relative to the interval of silence between sounds and is a measure of signalling effort.

Fig. 1 shows oscillograms and spectrograms of typical search phase echolocation calls to illustrate the difference in the temporal patterns of call emission for representative LDC and HDC species. Included are two Old World HDC bats (*Rhinolophus hipposideros*, *Hipposideros armiger*) and the one New World HDC bat (*P. parnellii*). Call duty cycle differs dramatically between the bats in these groups, ranging from 6.1% to 9.2% for the three LDC echolocators and from 34.7% to 56.3% for the three HDC echolocators (data in Table 1). Fig. 2 shows oscillograms, spectrograms and power spectra of single search phase echolocation calls from the temporal sequences in Fig. 1 to illustrate why signal duration, call structure (frequency modulated FM versus constant frequency CF) and/or signal bandwidth alone do not uniquely identify LDC from HDC echolocators. We include both spectrograms and oscillograms because the former usefully illustrate call frequency structure and the latter call duration.

LDC and HDC echolocation differ in a number of respects. Most bat species use an LDC calling strategy and avoid forward masking under most natural conditions (Kalko and Schnitzler, 1989). LDC bats typically do not broadcast calls and receive echoes concurrently. Rather, they produce a call and then listen for audible echoes before emitting another call (Holderied and von Helversen, 2003; Holderied et al., 2005). The outgoing calls of LDC echolocators are short in duration (typically 1–20 ms) and are

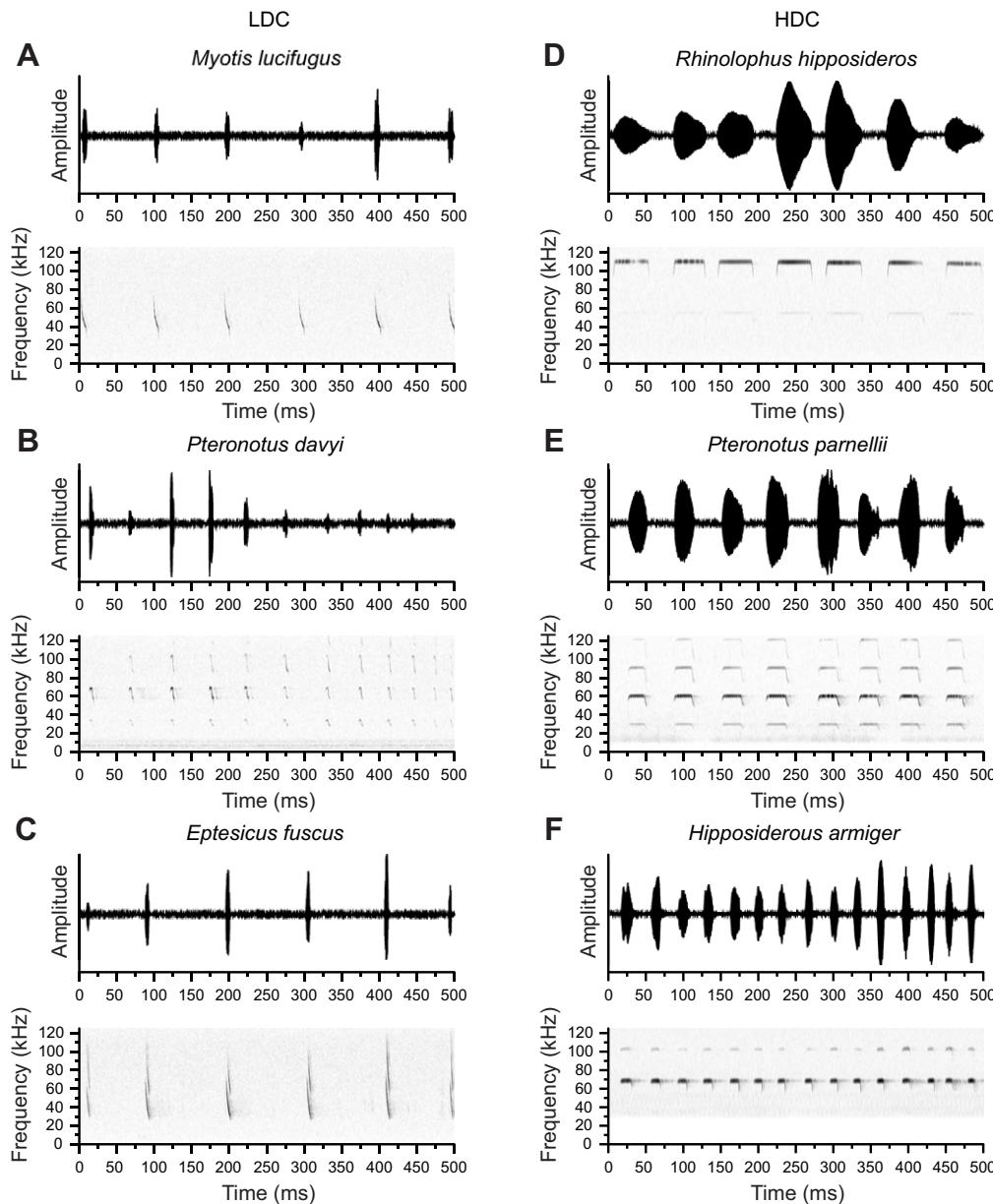


Fig. 1. Temporal pattern of biosonar call emission for low duty cycle (LDC) and high duty cycle (HDC) echolocators. Each panel shows an oscillogram (top) and spectrogram (bottom) and illustrates the typical temporal pattern of call emission during the search phase of echolocation. LDC species like *Myotis lucifugus* (A), *Pteronotus davyi* (B) and *Eptesicus fuscus* (C) emit short duration, broadband frequency modulated (FM) echolocation signals, whereas HDC species like *Rhinolophus hipposideros* (D), *Pteronotus parnellii* (E) and *Hipposideros armiger* (F) emit long duration, narrowband CF signals. Duty cycle data are presented in Table 1. Oscillogram signal amplitude is displayed in arbitrary units.

separated by long intervals of silence (Fig. 1A–C). For the purpose of this paper, we define LDC bats as those producing signals with a duration <25% of their signal period during the search phase of echolocation. Most LDC bats produce echolocation calls with their larynx, although a handful of species in the family Pteropodidae use tongue clicks (Griffin et al., 1958; Yovel et al., 2010).

HDC bats avoid auditory masking by separating pulse and echo in frequency, allowing them to broadcast calls and receive echoes at the same time (Schuller, 1974; Schuller, 1977). HDC bats take advantage of information contained in Doppler-shifted echoes generated by the relative movements of bat and target, including acoustic glints generated by the wingbeats of fluttering insects. Echolocation calls of HDC bats consist of a long CF component followed by a brief, downward FM sweep. In some species, the initial portion of the call also contains a short, upward FM sweep (Henson et al., 1987; Jones and Rayner, 1989). Narrowband calls of HDC bats are typically multi-harmonic with the highest signal energy in the second acoustic element (Pye and Roberts, 1970;

Schnitzler and Denzinger, 2011). HDC bats emit long duration calls (e.g. 10 to >50ms) relative to their call period (Fig. 1D–F). We operationally define HDC bats as those whose signal durations are $\geq 25\%$ of their call periods during the search phase of echolocation. There are ~160 species of HDC echolocators, most of which are in the Old World families Rhinolophidae and Hipposideridae, and one species (*P. parnellii*) in the New World family Mormoopidae. Rhinolophids appear to be the most neurobiologically specialized HDC echolocators and hipposiderids the least specialized, with *P. parnellii* falling in between (Neuweiler, 1990). All HDC bats are laryngeal echolocators. Old World HDC echolocators typically emit sounds through their nostrils, whereas *P. parnellii* emits sounds through its mouth (Schnitzler and Denzinger, 2011). Both LDC and HDC species exhibit echo intensity compensation; that is, bats decrease the sound pressure level (SPL) of vocalizations to compensate for the increase in echo amplitude received during the approach to a target (Kick and Simmons, 1984; Kobler et al., 1985; Hiryu et al., 2008).

Aerial-hawking bats searching for flying insects emit a sequence of calls in which pulse duration decreases and the pulse repetition rate and duty cycle increase from the search to the approach to the terminal phases of hunting (Griffin et al., 1960; Simmons et al., 1979; Kalko et al., 1998). During feeding buzzes, LDC bats actively control the bandwidth and focus of their echolocation beam (Surlykke et al., 2009; Jakobsen and Surlykke, 2010). Furthermore, superfast muscles in the larynx are vital to the production of rapid call sequences during feeding buzzes (Elemans et al., 2011). While it is assumed that HDC echolocators also possess superfast laryngeal muscles (Elemans et al., 2011), it is unknown whether they also control their sonar beam width.

Here, we compare HDC and LDC bats and develop a hypothesis about the origin and evolution of HDC echolocation. We argue that the combination of acoustic and neurobiological specializations that evolved with HDC echolocation improved the ability of bats to detect, lock onto and track fluttering prey. We are not the first students to have arrived at this hypothesis for the evolution of HDC echolocation but, to the best of our knowledge, we are the first to make it explicit and provide a framework of testable predictions.

HDC echolocation

HDC bats have a unique combination of four features. First, they emit echolocation calls with long durations relative to their signal period. Second, the peak call energy is concentrated into a narrow spectral band dominated by a CF component (Neuweiler, 1990; Jones, 1999). Third, the peripheral auditory system of HDC bats contains anatomical modifications in the cochlea and an overrepresentation of afferent neurons each tuned to a narrow frequency range centred on and slightly above the second harmonic of the CF echolocation call component (Pollak et al., 1972; Suga et al., 1976). This 'auditory fovea' results from mechanical specializations of the basilar membrane of the cochlea and a disproportionate representation of sharply tuned neurons at all levels of the central auditory system (Suga and Jen, 1976; Schuller and Pollack, 1979; Rübtsamen et al., 1988; Pollak and Casseday, 1989; Ostwald, 1984; Neuweiler, 1990). Fourth, HDC bats exhibit Doppler shift compensation, which involves lowering the frequency of the next outgoing echolocation call to compensate for the flight-induced Doppler-shifted increase in frequency of the previous call's echo (Schnitzler, 1973; Jen and Kamada, 1982). Details of this behaviour have been documented extensively in laboratory studies with both stationary and moving bats (e.g. free-flying bats recorded with stationary microphones or from bats placed at the end of a moving pendulum). A few studies have also managed to record outgoing biosonar vocalizations and the Doppler-shifted echoes that return to a flying bat by attaching a small microphone and radio transmitter to the head of the animal (Henson et al., 1987; Hiryu et al., 2005; Hiryu et al., 2008). Regardless of the technique, these studies confirm that flying bats adjust the frequency of their sonar emissions to correct for flight-induced Doppler-shifted echoes. Doppler shift compensation ensures the narrowband/CF echo remains centred on the auditory fovea (Schuller and Pollack, 1979; Schnitzler, 1970). Among HDC echolocators, hipposiderids perform less well at Doppler shift compensation than rhinolophids and *P. parnellii* (Habersetzer et al., 1984; Gaioni et al., 1990), perhaps because of the more broadly tuned auditory fovea in the hipposiderids (Schuller, 1980; Habersetzer et al., 1984; Moss and Schnitzler, 1995; Schnitzler and Denzinger, 2011).

The ability to extract information from Doppler-shifted echoes of fluttering insects allowed HDC bats to detect and continuously

Table 1. Call duration, period and duty cycle in laryngeally echolocating bats

Family/Species	<i>d</i> (ms)	<i>T</i> (ms)	DC (%)	Strategy
Suborder Yinpterochiroptera				
Rhinopomatidae				
<i>Rhinopoma hardwickei</i>	5.4	100.1	5.0	LDC
Hipposideridae				
<i>Hipposideros armiger</i>	11.4	34.0	34.7	HDC
<i>Asellia tridens</i>	7.3	28.5	27.9	HDC
Rhinolophidae				
<i>Rhinolophus blasi</i>	38.0	93.1	40.9	HDC
<i>Rhinolophus capensis</i>	31.2	68.9	45.3	HDC
<i>Rhinolophus clivosus</i>	27.3	58.2	46.9	HDC
<i>Rhinolophus euryale</i>	52.9	96.4	56.1	HDC
<i>Rhinolophus ferrumequinum</i>	53.4	93.6	57.1	HDC
<i>Rhinolophus hipposideros</i>	41.3	73.4	56.3	HDC
<i>Rhinolophus mehelyi</i>	50.4	103.5	47.9	HDC
Suborder Yangochiroptera				
Emballonuridae				
<i>Diclidurus alba</i>	13.8	156.4	9.6	LDC
<i>Rhynchonycteris naso</i>	5.1	49.7	10.3	LDC
Noctilionidae				
<i>Noctilio leporinus*</i>	13.5	108.3	12.4	LDC
Mormoopidae				
<i>Mormops blainvilli</i>	3.1	40.3	7.8	LDC
<i>Pteronotus davyi</i>	6.1	66.3	9.2	LDC
<i>Pteronotus gymnonotus</i>	5.2	40.7	12.9	LDC
<i>Pteronotus macleayi</i>	4.3	54.3	8.0	LDC
<i>Pteronotus parnellii</i>	30.9	72.9	43.3	HDC
<i>Pteronotus personatus</i>	4.9	43.3	12.4	LDC
<i>Pteronotus quadricens</i>	3.5	42.7	8.2	LDC
Phyllostomidae				
<i>Monophyllus redmanii</i>	1.7	33.1	5.0	LDC
Vespertilionidae				
<i>Eptesicus furinalis</i>	7.4	325.0	2.3	LDC
<i>Eptesicus fuscus</i>	4.9	81.1	7.9	LDC
<i>Kertivoula</i> spp.	1.4	30.9	6.8	LDC
<i>Lasiurus borealis</i>	9.7	136.7	7.1	LDC
<i>Lasiurus cinereus</i>	11.9	246.1	4.8	LDC
<i>Murina leukogaster</i>	0.7	43.4	1.7	LDC
<i>Myotis evotis</i>	4.0	107.1	3.8	LDC
<i>Myotis lucifugus</i>	5.9	96.3	6.1	LDC
<i>Otonycteris hemprichii</i>	4.3	137.0	3.4	LDC
<i>Perimyotis subflavus</i>	10.8	135.8	8.0	LDC
<i>Pipistrellus</i> sp.	5.2	92.2	5.8	LDC
Molossidae				
<i>Molossus molossus</i>	10.7	97.1	12.5	LDC
<i>Molossus rufus</i>	13.1	176.6	7.4	LDC
<i>Molossus</i> sp.*	14.2	69.3	20.7	LDC
<i>Tadarida brasiliensis</i>	13.4	278.1	4.8	LDC
<i>Tadarida teniotis</i>	12.2	152.5	13.1	LDC

DC, duty cycle; *d*, call duration; *T*, period; DC=(*d*/*T*)×100.

Shown are search phase echolocation data for 37 species of bats free flying in the field or calling from a perch. Low duty cycle (LDC) echolocation is defined as DC <25%; high duty cycle (HDC) echolocation is defined as DC ≥25%. Species marked with an asterisk are reported to have variable duty cycle echolocation.

track prey in dense vegetation and thus forage in areas with high background acoustic (echoic) clutter (Bell and Fenton, 1984). HDC bats may also be more readily attracted to fluttering targets than LDC bats (Goldman and Henson, 1977; Lazure and Fenton, 2011). In these respects, HDC echolocators differ from LDC echolocators.

Echoes returning to a flying bat are Doppler shifted because of changes in the relative velocities of the bat and target (Schnitzler, 1968; Schnitzler, 1970; Schnitzler, 1973). The CF component of the echo becomes shifted up (down) in frequency as the distance between the flying bat and insect decreases (increases). Doppler-

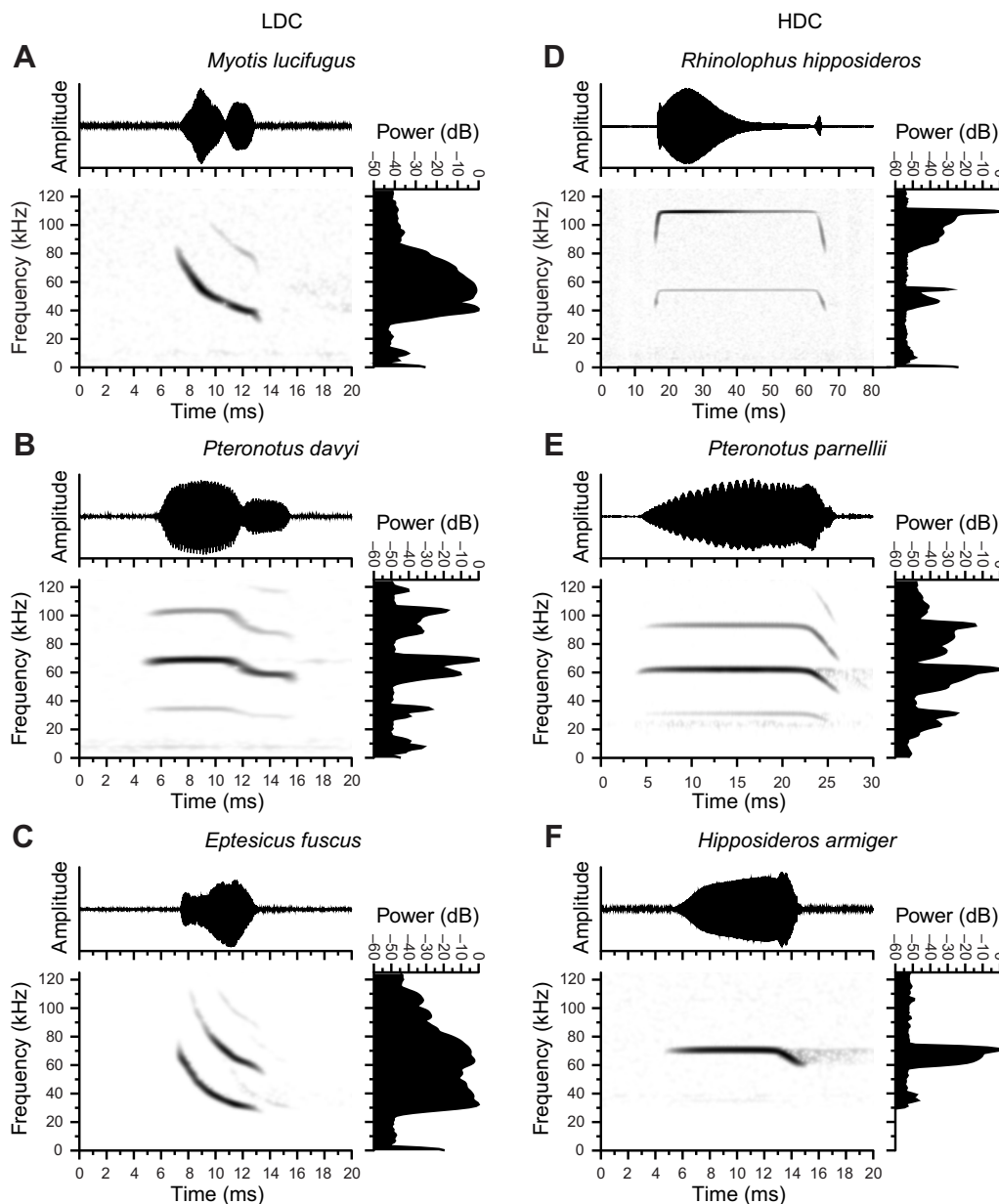


Fig. 2. Echolocation calls of LDC and HDC bats. Comparison of single echolocation calls demonstrates that signal duration, call structure and/or signal bandwidth alone cannot uniquely discriminate LDC from HDC echolocators. (A–C) Single search phase calls from LDC echolocators; (D–F) search phase calls from HDC species. For each call we show an oscillogram (top), a spectrogram (bottom left) and a fast Fourier transform (FFT) power spectrum (bottom right). The calls of *H. armiger* have been high-pass filtered (30 kHz cutoff frequency) to remove background insect noise. Oscillogram signal amplitude is displayed in arbitrary units.

shifted echoes may also contain ‘acoustic glints’ that appear as fluctuations in the amplitude and spectral composition within the CF component. Glints are generated by the rhythmic motion of the insect’s wings relative to the direction of sound propagation from the bat (Schnitzler et al., 1983; Kober and Schnitzler, 1990; Henson et al., 1987). HDC bats do not compensate for Doppler shifts generated by insect wing movements (Trappe and Schnitzler, 1982).

Echoes from the long duration calls of HDC bats may contain multiple amplitude and frequency glints. The time interval between individual glints in the echo corresponds to about the reciprocal of twice the insect’s wingbeat rate (Schnitzler et al., 1983; Koselj et al., 2011). Amplitude glints are produced by changes in the reflective area of the fluttering insect target. Specifically, when the insect’s wings are perpendicular to the direction of sound propagation (typically near the top or bottom of the stroke), this presents a larger reflective surface that can increase echo amplitudes by ≥ 20 dB compared with the body of the insect when the wings are horizontal (Henson et al., 1987; Kober et al., 1985).

Frequency glints are Doppler-shifted spectral broadenings in the CF component of the echo resulting from the motion of insect’s wings towards or away from the bat (Schnitzler et al., 1983). Frequency glints appear as a ± 2 kHz spectral broadening in the CF echo, and the sign of the frequency change (re. the CF component) indicates the direction of wing motion (Schnitzler and Denzinger, 2011). Such brief frequency glints are superimposed on the overall Doppler-shifted CF echo from the insect’s body. *Rhinolophus ferrumequinum* can resolve differences in flutter rate of < 10 Hz for frequencies within its auditory fovea (von der Emde and Menne, 1989).

HDC bats may recognize particular types of insects by wingbeat signatures encoded in the amplitude and frequency glints of returning echoes (Schuller, 1984; Schnitzler, 1987; Kober and Schnitzler, 1990). Wingbeat signatures and other features of prey flight patterns may help determine which items are attacked or ignored by HDC echolocators when a smorgasbord of insects is available (Koselj et al., 2011). Echoes from LDC echolocation calls contain less glint-related information and thus may not provide the

sensory feedback necessary to make precise decisions about prey selection (i.e. to be a 'picky eater'). Echoes from the calls of HDC bats encode the temporal patterning (spacing) of acoustic glints and follow the rhythm of the insect's wingbeat cycle (Schnitzler et al., 1983; Kober and Schnitzler, 1990). Wingbeat rates of flying insects typically range from 10 to 50 Hz ($T=100-20$ ms), so only some HDC bats with CF durations >40 ms (mainly rhinolophids) will frequently receive single echoes containing multiple acoustic glints over several wingbeat cycles. Hipposiderids and *P. parnellii* presumably obtain this information over several successive echoes. Evidence of foraging selectivity comes from observations of several species of HDC bats that responded to and tracked passing insects, but only attacked some of them [e.g. *Hipposideros commersoni* (Vaughan, 1977), *Rhinolophus rouxi* (Neuweiler et al., 1987), *R. ferrumequinum* and *R. hipposideros* (Jones and Rayner, 1989)]. This in contrast to LDC species, some of which attack inanimate objects in the wild (Acharya and Fenton, 1992; Barclay and Brigham, 1994).

Relative to LDC echolocators, HDC bats dramatically increase call duty cycle during prey capture attempts (Vogler and Neuweiler, 1983; Schnitzler et al., 1985; Jacobs et al., 2008), suggesting the increase in duty cycle indicates that a bat has detected a fluttering target and is locking onto the target and/or confirming its identity. Multiple time- and frequency-smear background clutter echoes may make the amplitude and frequency glints of fluttering insects more conspicuous in a manner analogous to stochastic resonance processing in the auditory system (e.g. Henry, 1999). A comparison of search phase echolocation call sequences emitted by LDC and HDC bats free-flying in the field or calling from a perch (Fig. 1) demonstrates that HDC bats have the potential to acquire more detailed and almost continuous data about fluttering targets compared with LDC bats. Table 1 presents typical call duration, period and duty cycle data for search phase echolocation calls of representative bats.

Variable duty cycle echolocation

The distinction between HDC and LDC echolocation is generally consistent (Fig. 1; Table 1), but some foraging molossid (e.g. *Molossus* spp. but typically not *Eumops* spp., *Otomops* spp., *Tadarida* spp.) emit calls with duty cycles between 15% and 30%. As yet, there is no evidence that *Molossus* spp. perform Doppler shift compensation or that they are attracted to fluttering targets. The basilar membrane of *Tadarida brasiliensis* shows a slight expansion (6 mm per octave) in the frequency range used for echolocation, but nothing approaching the overrepresentation specialization of the sensory epithelium associated with the acoustic fovea in HDC bats [40 mm per octave (Vater and Siefert, 1995)]. Furthermore, when flying in the lab, many LDC bats emit calls with a shorter duration and period and an increased duty cycle relative to when they are calling in the field [e.g. *Eptesicus fuscus* (Surlykke and Moss, 2000)]. Hence, most if not all bats increase duty cycle when trying to collect more information about situations in which they are operating, just not to the extent of HDC echolocators (Simmons et al., 1979).

Data from a small molossid (*Molossops temminckii*) recorded in the field reveal duty cycles from ~6% to ~18% (Guillén-Servent and Ibáñez, 2007). The echolocation behaviour of *Noctilio* species (*N. albiventris*, *N. leporinus*; Noctilionidae) demonstrates flexibility in duty cycle among bats previously considered to be LDC echolocators. When foraging, *Noctilio* spp. emit a mixture of calls with just CF, just FM or a combination of CF-FM components and regularly alternate duty cycle between 10% and 40%

(Schnitzler et al., 1994; Kalko et al., 1998). Both *Noctilio* spp. partially compensate for flight-induced (but not target-induced) Doppler shifts in echoes by lowering the CF components of their emitted signals (Wenstrup and Suthers, 1984; Roverud and Grinnell, 1985). Auditory brainstem responses in *N. leporinus* reveal moderately sharp neural tuning near the CF component of its narrowband echolocation calls (Wenstrup, 1984); however, peripheral and central specializations of its auditory system are not known to provide an auditory fovea.

None of the bats categorized as LDC in Table 1 shows the unique combination of the four features we identify as being characteristic of HDC echolocators. The presence of individual features such as narrowband calls, increases in duty cycle during prey capture, narrowly tuned neurons or Doppler shift compensation do not alone represent HDC echolocation as we have identified it. Doppler shift compensation is mainly restricted to HDC echolocators, although among mormoopids both *P. parnellii* (an HDC echolocator) and *Pteronotus personatus* (an LDC echolocator) perform Doppler shift compensation, whereas other LDC mormoopids (e.g. *Mormoops megalophyllus* and *Pteronotus davyi*) do not (Smotherman and Guillén-Servent, 2008). Arguably the situation in molossids, noctilionids and mormoopids other than *P. parnellii* demonstrates that LDC echolocators have tremendous potential to modify patterns of call production and information processing.

Evolution of HDC echolocation

Current morphological and molecular evidence suggests that the monophyletic order Chiroptera is composed of two suborders (Teeling, 2009), each including HDC laryngeal echolocators – the Yinpterochiroptera (Rhinolophidae and Hipposideridae) and Yangochiroptera (Mormoopidae – *P. parnellii*; 1 species). If LDC laryngeal echolocation was the ancestral condition in echolocating bats, then it could have evolved once and persisted in all Yangochiroptera and most Yinpterochiroptera (Fig. 3). In this scenario, laryngeal echolocation was lost within one group (Pteropodidae) of Yinpterochiroptera. In some pteropodid species from the genus *Rousettus* tongue-click echolocation subsequently evolved. This hypothesis is supported by two observations. First, the echolocation signals of all bats except *Rousettus* spp. are tonal and produced in the larynx. Second, in laryngeally echolocating bats the stylohyal bone (part of the mammalian hyoid apparatus) contacts, and sometimes is fused with, the tympanic bone, which surrounds and supports the tympanic membrane. Neither condition – echolocation calls with time-frequency structure or stylohyal-tympanic bone contact – occurs in pteropodid bats, including those that echolocate with tongue clicks (Veselka et al., 2010a).

Alternatively, LDC echolocation could have evolved independently in Yinpterochiroptera and Yangochiroptera. If LDC echolocation was the ancestral condition in bats, then either scenario necessitates the independent evolution of HDC echolocation at least once in both suborders. At present it is not possible to resolve which scenario is correct.

Simmons (Simmons, 1980) suggested that a short duration CF call with multiple harmonics was the ancestral condition in laryngeally echolocating bats, and that the principal trend in the evolution of echolocation was a broadening of signal bandwidth by the introduction of FM components. In this scenario, long duration CF-FM echolocation calls, an auditory fovea with specializations for glint/flutter detection and Doppler shift compensation would be more specialized (derived) conditions that evolved independently

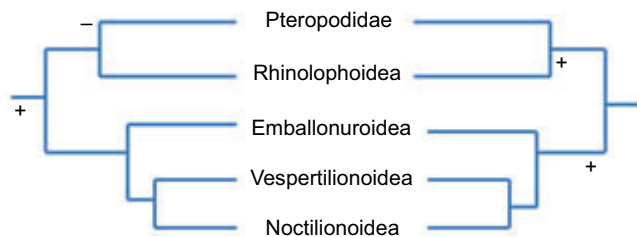


Fig. 3. Evolution of LDC and HDC echolocation in bats. Two equally parsimonious scenarios for the evolution of echolocation in the two currently recognized suborders of bats, the Yinpterochiroptera and the Yangochiroptera. Left, laryngeal echolocation is presumed to be ancestral and has evolved once (+) but was lost (-) in the family Pteropodidae. Right, laryngeal echolocation is presumed to have evolved twice, once in the lineage leading to the Yangochiroptera (+) and again in the lineage leading to the Rhinolophoidea (+). After Fenton and Ratcliffe (Fenton and Ratcliffe, 2010). The superfamily Rhinolophoidea includes the families Rhinolophidae, Hipposideridae, Rhinopomatidae, Craseonycteridae and Megadermatidae. The superfamily Emballonuroidea includes the families Emballonuridae and Nycteridae. The superfamily Vespertilionoidea includes the families Vespertilionidae, Thyropteridae, Natalidae, Furiferidae, Molossididae, Myzopodidae and Miniopteridae. The superfamily Noctilionoidea includes Noctilionidae, Mormoopidae and Phyllostomidae.

in the Rhinolophidae and Hipposideridae (Yinpterochiroptera) and in the mormoopoid *P. parnellii* (Yangochiroptera).

Increasing the strength of the outgoing vocalization from the larynx was an essential adaptation in the evolution of echolocation to track flying insects (Fenton et al., 1995). Echolocation in air is a relatively short-range operation because of the physics of sound propagation through the atmosphere. Two factors are involved. First, geometric spreading (i.e. the inverse square law) reduces energy in both outgoing sounds and returning echoes equally across all frequencies. Second, the absorption of sound energy by water molecules in the atmosphere increases dramatically at frequencies above 30 kHz (Lawrence and Simmons, 1982), compounding attenuation by geometric spreading. Many echolocating bats emit signals with amplitudes in excess of 130 dB SPL (re. 20 μ Pa) at 10 cm in front of the bat's mouth (Holderied et al., 2005; Surlykke and Kalko, 2008). Such high SPLs allow bats to detect insect targets at 20–30 m (Surlykke and Kalko, 2008), much greater detection distances than previously reported [ca. 3–5 m (Kick, 1982)]. Together, detection distance and flight speed have an important impact on foraging by aerial-hawking bats. A bat flying at 5 m s⁻¹ that detects a moth at 30 m has 6 s to react, while one flying at 10 m s⁻¹ has only 3 s to react. Thus, reducing outgoing call strength results in a shorter effective operating range, giving bats less time to detect, track and intercept airborne targets.

The echolocation calls of laryngeally echolocating bats show structured changes in frequency over time. Call frequencies range from ~8 to >200 kHz, and most species emit calls with peak energy between 20 and 60 kHz (Jacobs et al., 2008). Sounds of higher frequency have shorter wavelengths and reflect more efficiently from small targets such as fluttering insects. Bats that emit echolocation calls with a large signal bandwidth have more listening frequencies available to extract details from echoes about the size, shape, velocity and distance to a target (Simmons and Stein, 1980). Conversely, sounds of lower frequencies have longer wavelengths, are less subject to excess attenuation, and provide a greater operating range of echolocation.

Long duration, narrowband calls (Figs 1, 2) are not unique to HDC echolocators as many bats emit long narrowband search phase signals in open habitats (e.g. *E. fuscus*, *Lasiurus cinereus*, *T. brasiliensis*, *Tadarida midas*, *Tadarida teniotis*, *Otomops martiensseni*, *N. leporinus*, *N. albiventris*). The use of long duration narrowband calls is adaptive in these situations because it focuses spectral energy and provides for a larger operating range (Simmons and Stein, 1980). According to Parseval's theorem, power spectral density level increases by 10 dB for every decade reduction in signal bandwidth with no additional costs of call emission (Oppenheim et al., 1999). Flutter detection is not limited to bats using HDC echolocation as some vespertilionids [*Pipistrellus stenopterus* (Sum and Menne, 1988); *Murina* spp. and *Kerivoula* spp. (Lazure and Fenton, 2011)] and both *Noctilio* spp. also have this ability. Both HDC and LDC bats may use passive hearing to detect the fluttering and/or walking sounds of insects on surfaces (e.g. Bell, 1982; Link et al., 1986; Faure and Barclay, 1992).

Bats that employ LDC echolocation are unlikely to receive echoes with multiple acoustic glints (Schnitzler and Denzinger, 2011). Indeed, the echolocation calls of *Kerivoula* spp. and *Murina* spp. are the antithesis of those used by HDC echolocators because they are extremely short (~1 ms), broadband (~100 kHz) FM sweeps (Schmieder et al., 2010). Some *Kerivoula* and *Murina* spp. detect flutter, but the cues they use remain unknown (Lazure and Fenton, 2011).

Temporal overlap between outgoing sounds and returning echoes is an important feature of HDC echolocation. In *P. parnellii*, the beginning of the approach phase is signalled by an increase in pulse duration resulting in prominent pulse–echo overlap (Novick and Vaisnys, 1964). Pulse–echo overlap is well known for the echolocation calls of HDC bats and is essential for proper Doppler shift compensation in *R. ferrumequinum* (Griffin, 1962; Schuller, 1974), whereas the FM component in the CF–FM calls of *R. ferrumequinum* is not necessary for Doppler shift compensation (Schuller, 1977). In theory, a bat could use pulse–echo overlap to detect the presence of and distance to objects (Novick, 1971). Biosonar pulses overlapping with echoes from an insect's body or from stationary targets in the background will generate interference patterns that differ from the acoustical glints generated by fluttering prey. The interference patterns generate amplitude modulations in the echoes corresponding to the frequency difference between overlapping sounds (i.e. pulse and echo, echo and echo), and such signals have an additional cue that may play a role in object detection by HDC bats (Pye, 1960; Pye, 1961; Kay, 1961; Novick and Vaisnys, 1964; Novick, 1971; Henson et al., 1987).

Detailed studies on the neural basis of hearing and HDC echolocation have been performed on two species: the Old World greater horseshoe bat (*R. ferrumequinum*) and the New World moustached bat (*P. parnellii*). Both possess an auditory fovea with mechanical and physiological specializations of the cochlea and extremely sharply tuned neurons in the peripheral and central auditory systems (Bruns, 1976a; Bruns, 1976b; Suga and Jen, 1976; Suga and Jen, 1977; Pollak et al., 1979; Vater, 1982; Henson et al., 1985; Kössl and Vater, 1985). Neurons in the inferior colliculus of *R. ferrumequinum* and *P. parnellii* have specialized response properties that encode signal parameters such as fundamental wingbeat frequency and amplitude and frequency glints present in echoes from fluttering insects (Vater, 1981; Bodenhamer and Pollak, 1983; Schuller, 1984; O'Neill, 1985).

Two populations of cells with specialized response properties may further facilitate combinatorial processing of loud outgoing vocalizations with information contained in later returning weaker

echoes. These are delay-tuned and duration-tuned neurons. Delay-tuned neurons are found in the inferior colliculus and cortex of both LDC and HDC bats, and are thought to be important for extracting information about target range/distance (O'Neill and Suga, 1979; Sullivan, 1982; Schuller et al., 1991; Casseday et al., 1994; Yan and Suga, 1996; Galazyuk and Feng, 1997; Portfors and Wenstrup, 1999). Delay-tuned neurons show a facilitated response and fire maximally when the timing (delay) between two sounds – the outgoing pulse and returning echo – corresponds to the cell's best delay. Duration-tuned neurons are temporally selective cells that respond only when signals of the correct frequency are presented at a specific duration (Faure et al., 2003). Duration-tuned neurons are also tuned in frequency and some are tuned to stimulus amplitude (Fremouw et al., 2005). Because duration-tuned neurons are found in both echolocating and non-echolocating vertebrates, the ability to echolocate cannot be a prerequisite for the evolution of duration selectivity in bats. Nevertheless, this does not preclude a functional role for duration tuning in the neural basis of echolocation (Sayegh et al., 2011; Aubie et al., 2012). Duration-tuned neurons have also been reported from the inferior colliculus of LDC and HDC bats, and in both New World and Old World species (e.g. Casseday et al., 1994; Fuzessery and Hall, 1999; Mora and Kössl, 2004; Luo et al., 2008; Macías et al., 2011).

In short, the brains of echolocating bats have populations of neurons that fire action potentials only in response to stimuli that possess a specific combination of signal duration, frequency, amplitude and/or delay. We hypothesize that this type of temporal-spectral-amplitude response selectivity may be crucial for locking on and tracking flying targets using echolocation.

Advantages of HDC echolocation

The preceding background demonstrates that, compared with LDC bats, the unique combination of features associated with HDC echolocation – long duration calls dominated by a CF component, an acoustic fovea and Doppler shift compensation – allowed bats to detect, lock onto and track fluttering insects. Therefore, we propose that HDC echolocation originated because it allowed hunting bats better access to nocturnal prey, especially in cluttered habitats. The difference in foraging effectiveness reflects the reality that HDC bats may acquire a stream of roughly 2–4 times as much information with the same number of call emissions as LDC bats (Fig. 1; Table 1). The longer duration calls of HDC bats also offer the potential for detecting multiple amplitude and frequency glints generated by fluttering insects. This hypothesis generates four specific and testable predictions.

First, compared with LDC bats, HDC echolocators should respond more often to presentations of fluttering insect targets, especially in areas with increased background clutter. By presenting artificial fluttering targets to foraging bats it is possible to assess the willingness of bats to investigate and attack such targets. By monitoring echolocation calls at the same time, researchers can compare the responses of HDC and LDC echolocators, and identify other strategies that bats may use to detect fluttering targets [e.g. LDC bats in the genera *Murina* and *Kerivoula* (Lazure and Fenton, 2011)].

Second, compared with LDC bats, HDC bats should be better able to exploit wingbeat signatures of fluttering insects and be more likely to show selective foraging. This prediction can be tested by identifying and comparing the diversity of insect prey in the diets of sympatric HDC and LDC bats. Specifically, this can be done using DNA barcodes obtained from insect fragments in faeces in areas where HDC and LDC bats forage sympatrically (Clare et al.,

2009; Clare et al., 2011; Goertlitz et al., 2010). HDC bats are expected to take fewer prey species and show more consistent patterns of prey selection. Hipposiderids appear to feed heavily on moths (Haberseizer et al., 1984; Link et al., 1986). Moths should be preferred prey because many are soft-bodied, medium- to large-sized insects and relatively slow flyers. Fluttering insects that have auditory deficits or that lack bat-detecting ears may be particularly easy targets for 'lock and track' echolocators (Faure and Hoy, 2000).

Third, if delay-tuned and duration-tuned neurons allow HDC bats to better lock onto and track fluttering insects, then the response physiology of these cells should differ between HDC and LDC echolocators. Delay-tuned and duration-tuned neurons occur in both HDC and LDC bats, suggesting a more general role in hearing and echolocation. We speculate that HDC bats should have delay-tuned and duration-tuned neurons tuned to longer pulse intervals and signal durations than LDC bats (e.g. Schuller et al., 1991; Mora and Kössl, 2004; Luo et al., 2008). Moreover, the bandwidth of the frequency tuning curves of duration-tuned and delay-tuned neurons should be narrower in HDC bats, with a high proportion of neurons tuned at or just above the CF resting frequency.

Fourth, HDC bats should spend proportionally more time foraging for insects in cluttered habitats than LDC bats of comparable body size, wing morphology and flight characteristics. In acoustically cluttered habitats, we expect HDC echolocators to have an advantage over most LDC echolocators in detecting, tracking and identifying fluttering insect prey, but this prediction applies only to bats using echolocation to detect prey in cluttered habitats.

There are many records of bats attacking airborne, insect-sized targets, from small pebbles to dry flies used in fishing (Acharya and Fenton, 1992; Barclay and Brigham, 1994). This raises the question: do HDC echolocators sometimes behave as if they were LDC echolocators? If so, like many LDC echolocators, they should sometimes detect, track and attack airborne, non-fluttering insect-sized prey. However, if HDC echolocators are primed to respond to fluttering targets, then we predict that they will not attempt to attack airborne but non-fluttering targets. Field and flight room observations suggest the latter may be the case (Bell and Fenton, 1984; Jacobs et al., 2008), as some HDC bats did not track aerial insect-sized targets whose wings were not moving (Goldman and Henson, 1977; Link et al., 1986).

Disadvantages of HDC echolocation

One obvious disadvantage of using HDC echolocation arises because this strategy involves broadcasting calls over a longer period of time, an important feature for glint detection. Longer duration calls contain more energy, which can increase information leakage and make HDC echolocation signals more conspicuous to conspecifics, predators and prey (Faure et al., 1990; Jacobs et al., 2008). Longer duration calls are presumably more expensive to produce than shorter duration calls of the same frequency. Kingston and Rossiter recognized the potential impact on communication of the echolocation calls used by HDC bats (Kingston and Rossiter, 2004). Focusing signal energy into a narrower bandwidth can also make HDC calls more conspicuous to insects with hearing-based defences (Jacobs et al., 2008). Because the peak spectral frequencies of bats using HDC echolocation are often higher than those using LDC echolocation, the costs of emitting longer duration signals may be offset by the benefits of shifting peak energy to higher frequencies. The ears of bat-detecting insects are typically

most sensitive to sound frequencies ranging from 20 to 60 kHz, which may explain the prevalence of higher frequency sounds in the echolocation calls of HDC bats (Jones, 1999) and supports Fullard's (Fullard, 1987) allotonic frequency hypothesis (e.g. Pavey and Burwell, 1998; Jacobs, 2000). Once an HDC bat has locked onto a flying target, it may be less vulnerable to evasive manoeuvres of prey compared with an LDC bat, in part because of the absence of long intervals between successive target echoes.

The specialization of the thoracic skeleton in some species of HDC echolocators suggests that a high duty cycle approach requires a different pattern and rhythm of respiration than LDC echolocation. It remains to be determined whether the broad flat ribs characteristic of rhinolophids and hipposiderids are morphological specializations associated with HDC echolocation (Desroche et al., 2007). Data on the cost of echolocation call production are all from LDC species (Speakman and Racey, 1991).

The prevalence of LDC echolocation among insectivorous bats demonstrates that this approach to detecting and tracking prey is successful and works well in most situations. There is no evidence of an HDC species adopting an LDC echolocation strategy, although some bats (e.g. *Molossus* spp., *M. temminckii*, *Noctilio* spp.) may alternate between an LDC- and HDC-like signalling strategy (Table 1). The fundamental dichotomy between the strategies may come down to more time-focused (HDC) versus frequency-focused (LDC) analyses by the brains of echolocators. More specific details about patterns of habitat use are required to demonstrate any foraging advantage accruing to HDC bats, especially in cluttered environments.

Evolution of bats

The origin and evolution of flight and echolocation in bats remains a topic of debate (e.g. Fenton et al., 1995; Simmons and Geisler, 1998; Speakman, 2001; Schnitzler et al., 2004). Powered flight is a diagnostic feature that sets bats apart from all other mammals. The evolution of echolocation has profoundly influenced the diversification of Chiroptera, but the ability to echolocate is neither diagnostic of nor unique to bats. Post-cranial anatomy of the earliest known fossil bat, *Onychonycteris finneyi*, reveals that this Eocene species could fly, but whether it could echolocate is unclear (Simmons et al., 2008; Veselka et al., 2010a; Veselka et al., 2010b). There are three points of view about the origin of flight and echolocation in bats: (1) that flight evolved first, giving the ancestors of bats increased mobility in forested/cluttered habitats (Simmons and Geisler, 1998); (2) that echolocation evolved first, giving the gliding ancestors of bats access to a previously under-exploited food source (nocturnal flying insects) in forested/cluttered habitats (Fenton et al., 1995); and (3) that echolocation and flight co-evolved because coordinating the production of repetitive, high amplitude vocalizations with the downstroke of flight reduced the overall costs of sound production (Speakman and Racey, 1991). The possible origins of echolocation in bats has been the topic of some discussion and has repercussions for interpreting chiropteran phylogeny and evolutionary divergence (Teeling, 2009; Simmons et al., 2010; Veselka et al., 2010b).

We agree with the view that the ancestors of bats hunted from perches and glided in pursuit of flying insects that were detected and tracked using LDC laryngeal echolocation. HDC echolocation calls developed as a specialized extension of using long, narrowband echolocation calls that improved the ability of bats with powered flight to detect, lock onto and track flying prey, probably in areas of high clutter. The evolution of HDC echolocation involves considerable anatomical and physiological

specialization over and above LDC echolocation, and this may account for its relative scarcity among insectivorous bats (~160 HDC versus ~900 LDC species). Additional phylogenetic reconstructions and comparative studies are needed to better understand and estimate the pattern of adaptations favouring the evolution of HDC echolocation in bats.

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