The evolution of echolocation in bats: a comparative approach

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Declaration

I, Alanna Collen (née Maltby), confirm that the work presented in this thesis is my own. Where information has been derived from other sources, this is indicated in the thesis, and below:

Chapter 1

This chapter is published in the *Handbook of Mammalian Vocalisations* (Maltby, Jones, & Jones) as a first authored book chapter with Gareth Jones and Kate Jones. Gareth Jones provided the research for the genetics section, and both Kate Jones and Gareth Jones providing comments and edits.

Chapter 2

The raw echolocation call recordings in EchoBank were largely made and contributed by members of the 'Echolocation Call Consortium' (see full list in Chapter 2). The R code for the diversity maps was provided by Kamran Safi. Custom adjustments were made to the computer program SonoBat by developer Joe Szewczak, Humboldt State University, in order to select echolocation calls for measurement.

Chapter 3

The supertree construction process was carried out using Perl scripts developed and provided by Olaf Bininda-Emonds, University of Oldenburg, and the supertree was run and dated by Olaf Bininda-Emonds. The source trees for the Pteropodidae were collected by Imperial College London MSc student Christina Ravinet.

Chapter 4

Rob Freckleton, University of Sheffield, and Luke Harmon, University of Idaho, helped with R code implementation.

Chapter 5

Luke Harmon, University of Idaho, helped with R code implementation.

Chapter 6

Joseph W. Brown, University of Idaho, and Rich FitzJohn, University of British Columbia, helped with R code implementation.

Abstract

The evolutionary history of echolocation in bats is poorly understood, as fossils provide little direct evidence, and most studies into echolocation have taken an ecological approach. Bats use a wide variety of echolocation call structures despite facing similar sensory challenges, and it is not clear how and why these echolocation call types evolved, or what impact they have on other aspects of the evolution of bats.

Here, I use phylogenetic comparative methods and newly-collated echolocation call data from 410 species in 120 genera and all 19 families to investigate the origination and evolution of echolocation in bats (Chiroptera). I construct an updated phylogenetic supertree of the bats using source phylogenies from the literature between 1970 and 2009. I ask three main questions: (1) Are echolocation call structures really a product of present-day ecological conditions, or are they much more constrained by evolutionary history than is currently thought? (2) What did the first echolocation calls sound like? (3) Are echolocation calls 'key innovations' that promote diversification?

I found that early divergences and subsequent constraints in evolutionary history have resulted in a greater variety of bat call structures than appear to be functionally necessary. The structure of the first echolocation calls was predicted to be short duration, multi-harmonic, and narrowband, suggesting that the proto-bat was a slow and manoeuvrable flier with an opportunistic and omnivorous diet, and may have used a perch-hunting foraging strategy. Finally, some echolocation call types were found to correlate with higher diversification rates such that they may be considered key innovations, but, unexpectedly, the most rapidly diversifying clades were those in which species either did not use echolocation at all (Pteropodidae), or where less sensory reliance was placed on echolocation (Stenodermatinae: Phyllostomidae).

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1 Chapter 1: General Introduction

1.1 Introduction

Bats are unique in having evolved both sophisticated laryngeal echolocation and powered flight. It is these attributes that have been proposed as the key innovations that allowed bats to radiate into a niche new to mammals – the night sky (Fenton et al. 1995; Schnitzler, Moss, & Denzinger 2003; Sears et al. 2006; Speakman 2001). Bats are the second most speciose order of mammals, although arguably the most ecologically diverse: their diets range from pollen, nectar and fruit, through insects and other arthropods, to birds, reptiles, amphibians, fish, small mammals, and the blood of birds and large mammals. They roost in foliage, caves and rock crevices, trees and under bark, and various man-made structures, and forage in all terrestrial habitats (Nowak 1994).

Most bats are crepuscular or nocturnal, and, although able to see, must rely on echolocation as their primary sensory modality (Nowak 1994). Echolocation, or biosonar, is the active use of calls and interpretation of their echoes to detect, localise, and classify objects (Griffin 1944; Jones 2005). The echo from an emitted echolocation call contains auditory cues relating to the direction, timing and spectral composition of nearby objects which allow the animal to then perceive, pinpoint and recognise potential prey and obstacles (Pollak & Casseday 1989; Thomas, Moss, & Vater 2004).

Echolocation has evolved in environments where vision is of limited use; the nocturnal niche of bats reduces the efficacy of vision. In toothed whales, the turbidity of the water and the tendency to dive to depths where very little light permeates have contributed to the evolution of echolocation. Echolocating bird species (the oilbird (Steatornithidae) of South America, and members of the cave swiftlets (Apodidae) of Southeast Asia) do so only to orientate in the dark caves in which they roost (Griffin 1958; Medway 1959). Various other species have been proposed as echolocators, including desmans, tenrecs, solenodons, shrews, baleen whales, Weddell seals, and leopard seals (Schusterman *et al.* 2004; Siemers *et al.* 2009), though evidence suggests none of these rely exclusively on echolocation. The

echolocation signals of non-bat echolocators are clicks, unlike the usually longer duration and more complex calls produced in the larynx by bats (Thomas & Jalili 2004).

1.1.1 Echolocation call frequencies

Bat echolocation calls tend to be in the ultrasonic frequency range (sound above the upper limit of human hearing, standardised at 20 kHz (Pumphrey 1950)), although some echolocation calls are audible to humans. The lowest frequencies used in echolocation are emitted by the spotted bat (*Euderma maculatum*, Vespertilionidae), which uses frequencies containing most energy around 9 kHz (Fullard & Dawson 1997). In contrast, the highest known peak energy frequencies reach about 212 kHz in Percival's short-eared trident bat (*Cloeotis percivali*, Hipposideridae) (Fenton & Bell 1981), and are likely to be even higher for non-peak energy harmonics and frequencies, such as the starting frequency of 250kHz in the clear-winged bat (*Kerivoula pellucida*, Vespertilionidae) (Schmieder *et al.* 2010). Ultrasonic frequencies are not a requirement for echolocation, although there are several advantages to using them. Sounds reflect most clearly from objects larger than the wavelength of the sound, and because high-frequency sounds have short wavelengths, they allow strong echoes to be generated from small objects such as flying insects (Houston, Boonman, & Jones 2004). High frequencies are also directional (e.g., Surlykke, Pedersen, & Jakobsen, 2008; see also Brudzynski & Fletcher, 2010) and can limit the spread of echolocation calls so that objects other than the target of interest are not detected. While bats may avoid using low frequencies in echolocation because of the need to detect small targets, extremely high frequencies are also avoided because excess atmospheric attenuation limits the range over which echolocation is effective (Brudzynski & Fletcher 2010; Lawrence & Simmons 1982). Most bats utilise "compromise" frequencies to avoid the costs associated with very high and very low frequencies, and call between 20 and 60 kHz (Fenton, Portfors, et al. 1998).

1.1.2 Diversity in call structure

Bats show considerable diversity in call structure (see Figure 1.1 and Table 1.1). Some bats do not echolocate at all, i.e., most of the bats within the family Pteropodidae (the Old

World fruit bats). Although species in a given family often tend to have similar call structures to one another, selective pressures imposed by the environment appear to have overridden phylogenetic constraints in some cases. For example, the common moustached bat *Pteronotus parnellii* (Mormoopidae) has independently evolved a very similar call structure to bats in the family Rhinolophidae, and even compensates for Doppler shifts caused by varying flight speeds (Schnitzler 1972). In addition, there is much intraspecific variation in call structure, as different structures are suited to different perceptual challenges (e.g., Kalko & Schnitzler, 1993). This plasticity often makes it more difficult to classify taxa by the echolocation call type. However, with some generalization, it is possible to categorise the call types of bats. For example, there are several aspects of call structure that define a bat's call. The first is the duration of the call – calls may be extremely brief (1 ms) as in the broadband tongue clicks of the only echolocating genus in the Pteropodidae (*Rousettus*); relatively short (3-10 ms) as in the calls of some bats in the family Vespertilionidae (e.g., many species in the genus *Myotis*); or long (>10 ms - 80 ms) such as calls emitted by many bats in the families Myzopodidae, Rhinolophidae and some of the Hipposideridae.

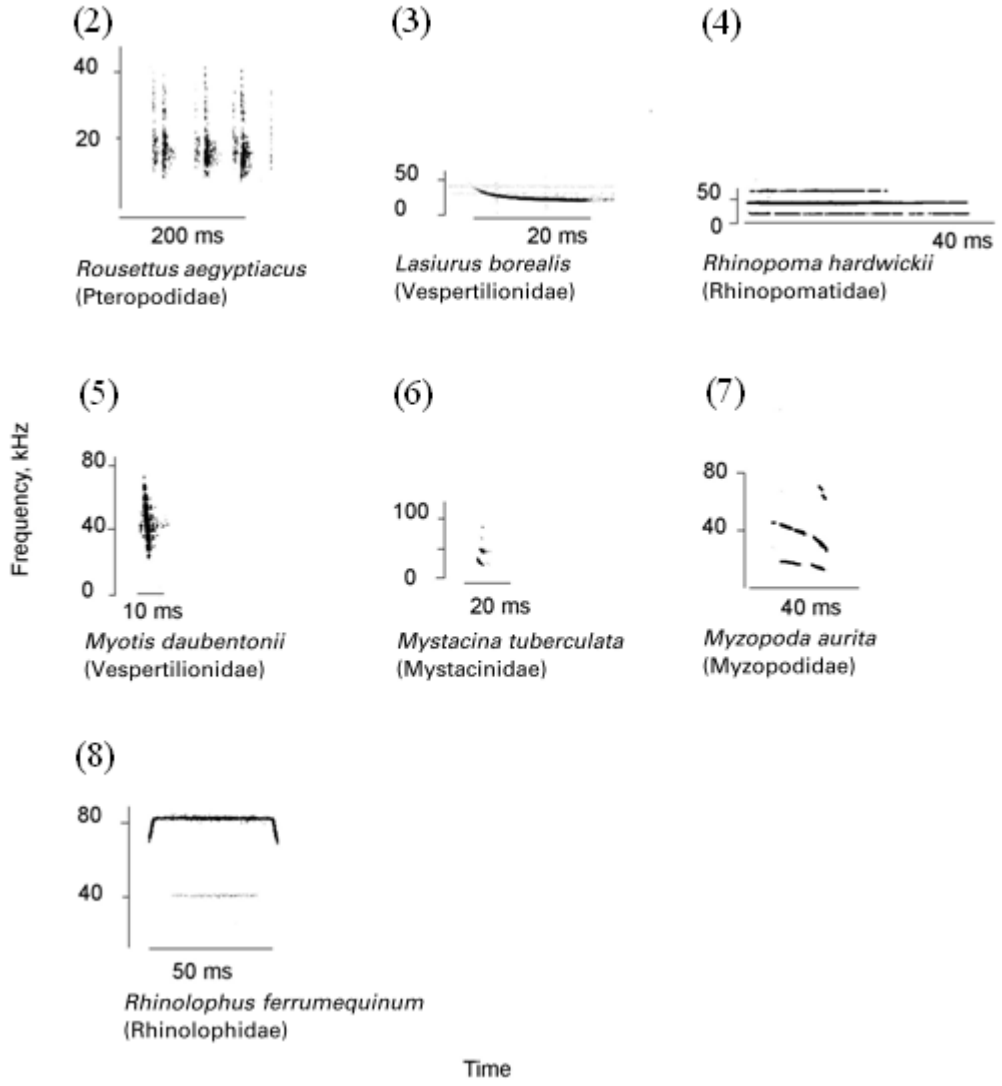


Figure 1.1: The evolution of echolocation in bats. Based on an illustration in Jones & Teeling (2006) ***Trends in Ecology and Evolution*** **21, 149-156. Call types shown in brackets.**

Family	Call type	Clade size
Craseonycteridae (Hog-nosed bat)	4	1
Emballonuridae (Sheath-tailed bats)	4	51
Furipteridae (Smoky bats)	no data	2
Hipposideridae (Old World leaf-nosed bats)	8	81
Megadermatidae (False vampire bats)	6	5
Miniopteridae (Long-fingered bats)	3	19
Molossidae (Free-tailed bats)	3	100
Mormoopidae (Naked-backed bats)	4,8	10
Mystacinidae (Short-tailed bats)	6	2
Myzopodidae (Sucker-footed bats)	7	1
Natalidae (Funnel-eared bats)	6	8
Noctilionidae (Bulldog bats)	5,8	2
Nycteridae (Slit-faced bats)	6	16
Phyllostomidae (New World leaf-nosed bats)	6	160
Pteropodidae (Old World fruit bats)	1, 2	186
Rhinolophidae (Horseshoe bats)	8	77
Rhinopomatidae (Mouse-tailed bats)	4	4
Thyropteridae (Disk-winged bats)	4	3
Vespertilionidae (Vesper bats)	3, 5, 6	388

Table 1.1: Diversity of bat echolocation signals across families. Call types are categorised as follows: 1, no echolocation; 2, brief broadband tongue clicks; 3, narrowband dominated by fundamental harmonic; 4, narrowband multiharmonic; 5, short broadband dominated by fundamental harmonic; 6, short broadband multiharmonic; 7, long broadband multiharmonic; 8, constant frequency as in Figure 1.1. Taxonomy following Simmons (2005) and Miller-Butterworth *et al.* (2007) and echolocation call data from Jones & Teeling (2006).

A further defining aspect is the bandwidth of the call. As wavelength is inversely proportional to frequency, high bandwidth calls allow bats to detect different sized objects. Calls may be very broadband, exceeding 170 kHz in some *Kerivoula* species (Vespertilionidae) (Kingston *et al.* 1999; Schmieder *et al.* 2010), or they may be very narrowband, as in some species in the Rhinopomatidae and Vespertilionidae (e.g., Habersetzer, 1985). Using a narrow bandwidth causes concentration of the sound energy into a smaller range of frequencies, allowing the sound to travel a greater distance before

completely attenuating. Frequencies often change abruptly across the time domain, as in the calls of the Rhinolophidae, which start with a brief upward broadband sweep, followed by a long constant frequency (CF) component, before ending with a downward broadband sweep (e.g., Jones & Rayner, 1989).

Many bats also use several harmonics in their calls, although usually with most of the call's energy concentrated into either the first (the fundamental) or the second harmonic (Jones & Teeling 2006). Each subsequent harmonic is a multiple of the fundamental frequency.

1.1.3 Phylogenetic context

In order to understand how different call types have evolved, for example, whether similar call structures have evolved convergently in phylogenetically distant taxa, it is necessary to place these calls into a context of the evolutionary history of bats. However, any such inferences are dependent on the accuracy of the reconstruction of bat evolutionary relationships. Bat evolutionary history has been, and remains, a hotly debated topic, with disagreements at all levels of the phylogenetic tree, both within the order and regarding the relationship of bats to other mammals. This has made inferences about the evolution of call structures challenging. To place this into context I briefly review the most important issues to shape our understanding of the evolutionary relationships of bats.

Bats (Order Chiroptera) are the second most speciose mammalian order after the Rodentia, comprising around 1,116 species in 202 genera and 18 families (Simmons 2005), although there may be 19 families according to the latest taxonomic revisions (Gunnell & Simmons 2005; Miller-Butterworth *et al.* 2007; Simmons *et al.* 2008). Molecular analyses place the order Chiroptera in a basal position within the superorder Laurasiatheria, along with hedgehogs; shrews; odd-toed ungulates; even-toed ungulates and whales; carnivores; and pangolins, and reject its previous placement with primates, colugos and treeshrews (see Springer & Stanhope 2004). Being certain of the possible sister taxa of bats has important implications for our understanding of the evolution of echolocation in bats. For example, as other taxa in Laurasiatheria are known to echolocate occasionally (e.g., cetaceans and

shrews) (Schusterman *et al.* 2004; Siemers *et al.* 2009), it would be possible to infer how primitive or derived this characteristic is in bats.

1.1.4 The chiropteran monophyly debate

In the 1980s and 1990s, despite previously widespread acceptance that all bats shared a common ancestor, a debate began around the suggestion that bats were diphyletic rather than monophyletic. Pettigrew (1986) discovered that the system of neural connections between the midbrain and the retina of pteropodids (Pteropodidae, formerly classified in the suborder Megachiroptera, see below) was similar to that of primates and colugos, whereas other bats (the former suborder Microchiroptera) showed the putatively "primitive" system of connections, in common with all other mammals. This evidence, in association with other aspects of morphology (Buhl & Dann 1991; Kennedy, Pettigrew, & Calford 1987; Pettigrew 1986; Pettigrew et al. 1989; Smith 1977a; Smith & Madkour 1980) and some early molecular evidence (Kleinschmidt *et al.* 1988) suggested that the megachiropterans evolved from a shared ancestor with primates, in a separate lineage from that which led to the evolution of microchiropterans. The bat diphyly hypothesis proposed that flight evolved on two independent occasions in bats. However, as molecular techniques developed and became more widely used, support for monophyly has proven overwhelming (e.g., Murphy *et al*., 2001; Teeling, Scally, & Kao, 2000; Teeling *et al*., 2005; although see Pettigrew, Maseko, & Manger, 2008). If we accept that bats are monophyletic, then both flight and echolocation may have evolved from a common bat ancestor and diversified into different structures across the clade.

1.1.5 The microchiropteran monophyly debate

Within the 19 currently recognised extant and seven extinct bat families, familial interrelationships have also been debated. Bats had traditionally been placed in two monophyletic suborders, the Microchiroptera and the Megachiroptera (Dobson 1875) (Figure 1.2). Megachiroptera comprise one family, the Old World fruit bats (Pteropodidae) the majority of which do not use echolocation (although some (possibly all) species of *Rousettus* use broadband clicks), whereas Microchiroptera includes all the other families

(which all use some form of echolocation) (see Table 1.1). However, the monophyly of the Microchiroptera is now disputed, as molecular evidence indicates that several of the microchiropteran families are more closely related to Pteropodidae than to the remaining families (see Figure 1.2). The most widely used division of the order places the Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae, Craseonycteridae, and the Rhinopomatidae in a new suborder, initially termed the Yinpterochiroptera. This was formed by the concatenation of "Yinochiroptera" introduced by Koopman (1984) and "ptero" by Springer, Teeling, Madsen, Stanhope, & de Jong (2001), and leaves the remaining families in the suborder Yangochiroptera (Figure 1.2). Yangochiroptera was originally named by Koopman (1984), although at that time it excluded Nycteridae and Emballonuridae (Gunnell & Simmons 2005; Springer, Teeling, & Madsen 2001). Given the recent confusion about the family members of each suborder (Yinpterochiroptera and Yangochiroptera) and the diphyly of the one of the previously used subordinal names (Microchiroptera), Hutcheon & Kirsch (2006) proposed new names for these suborders, using the International Code of Zoological Nomenclature's principles of typification, priority and attribution (International Commission on Zoological Nomenclature 2000). The suborder described above as 'Yangochiroptera' should be known as Vespertilioniformes based on Linnaeus' *Vespertilio* of 1758 and the suborder described as 'Yinpterochiroptera' should be known as Pteropodiformes, based on Brisson's *Pteropus* of 1762. In this thesis, I use Hutcheon and Kirsch's names.

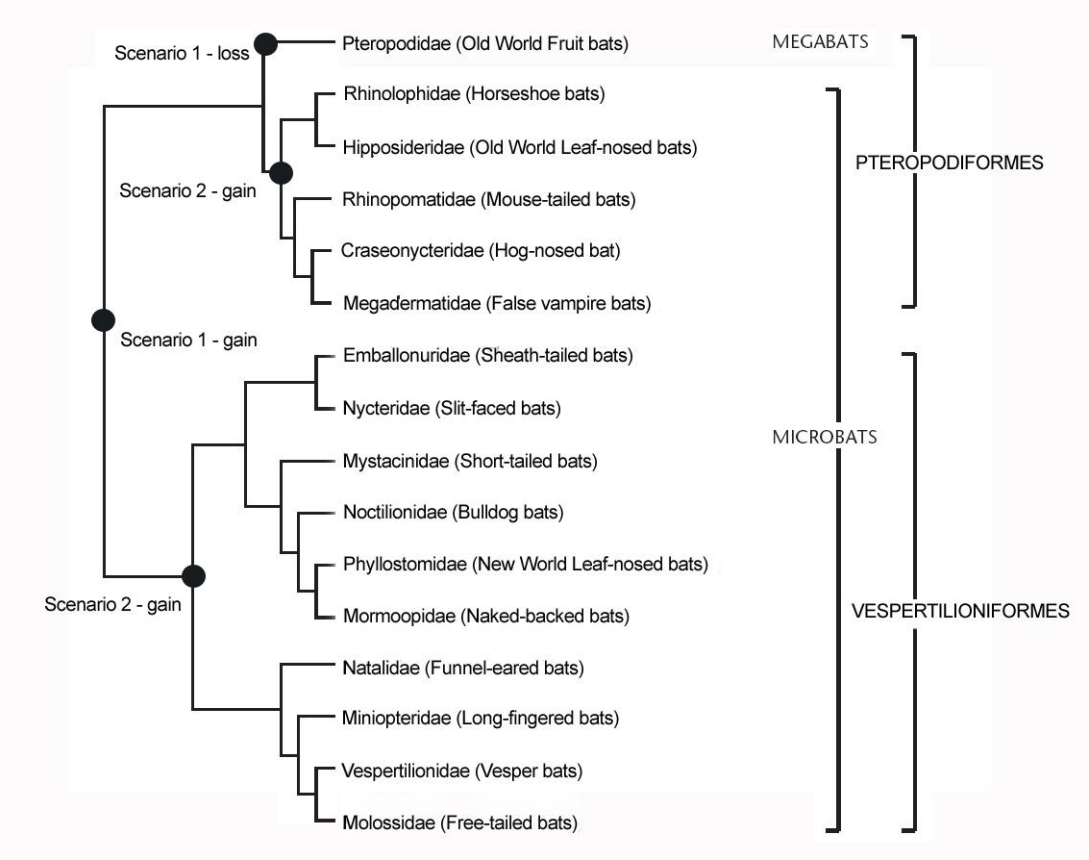


Figure 1.2: Phylogenetic relationships among 16 bat families following Teeling *et al*. (2005). Circles indicate where echolocation may have evolved, either once (Scenario 1) or twice (Scenario 2).

The new understanding of the phylogenetic relationships between families suggests that the most parsimonious explanation under the current phylogeny is that laryngeal echolocation evolved once, at the root of the bat lineage, and was later lost in the Pteropodidae. This would suggest that the pteropodid genus *Rousettus* then independently evolved their broadband tongue clicks. Alternatively, laryngeal echolocation evolved at least twice: once in the ancestors of echolocating Pteropodiformes and independently in Vespertilioniformes (Figure 1.2). However, whether laryngeal echolocation evolved once or more than once in bats remains unresolved: molecular phylogenies that incorporate fossil taxa (placed according to morphological evidence) support a single evolutionary event, while analyses of genes associated with hearing (Li *et al.* 2008) suggest that separate evolutionary events may have occurred (see Section 1.1.9 below).

Reconstructions of the ancestral states of echolocation calls are problematic, given the difficulties imposed by convergence in signal structure across phylogenetically distant taxa. Mapping of call characteristics onto phylogenetic trees suggests that the use of calls dominated by the fundamental harmonic (as in many members of the Vespertilionidae and Molossidae) is a derived state, and that multiharmonic signals are ancestral (see Figure 1.3) (Jones & Teeling 2006). Schnitzler, Kalko, & Denzinger (2004) suggested that early echolocating bats used calls that were tonal, low intensity, short, broadband and multiharmonic. Conversely, Eick, Jacobs, & Matthee (2005) hypothesised that the ancestral proto-bat emitted high intensity calls. Much of the current literature concerning the ancestral echolocation call is based on supposition, and as yet there are no quantitative analyses to support any of the hypotheses.

Some features of bat echolocation have evolved independently on several occasions. I have already described the independent evolution of constant frequency calls and Doppler shift compensation in rhinolophids (Pteropodiformes) and in *Pteronotus parnellii* (Vespertilioniformes). Furthermore, nasal emission of calls has evolved in some vespertilionids (e.g., Rafinesque's big-eared bat *Corynorhinus rafinesqui*) (Griffin 1958), nycterids and phyllostomids within the Vespertilioniformes, and in megadermatids in the Pteropodiformes (Eick *et al.* 2005).

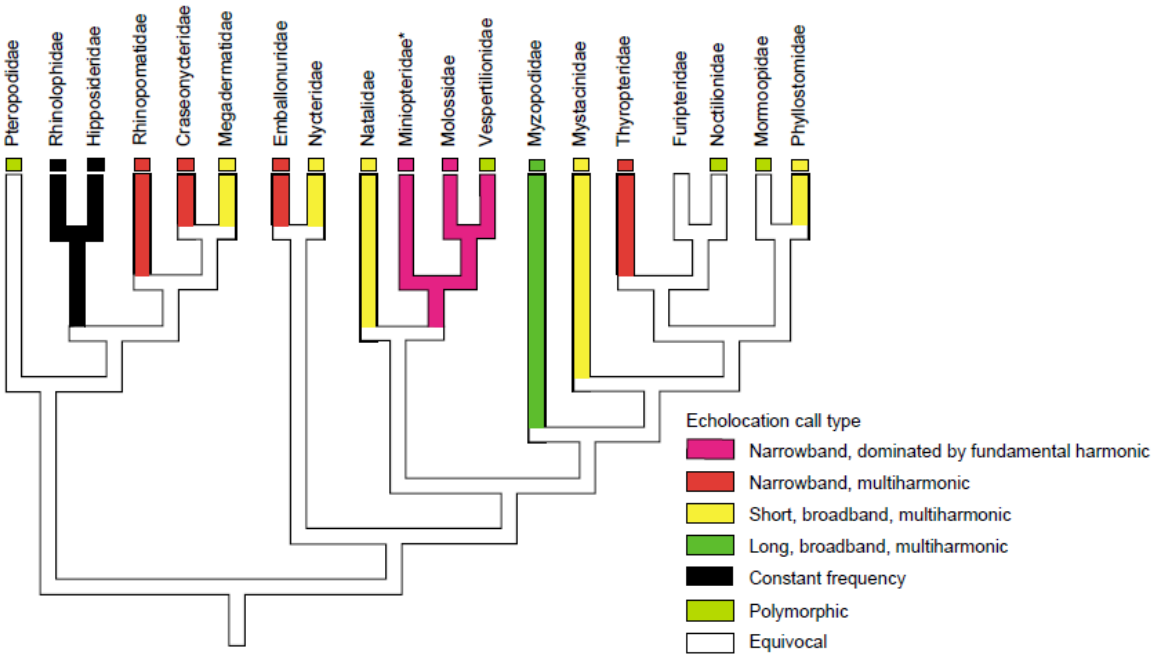


Figure 1.3: Linear parsimony ancestral reconstructions of eight echolocation call types using the family-level molecular phylogeny of Teeling *et al.* (2005) using MacClade v.3.8 (Maddison & Maddison 1992). Adapted from Jones & Teeling (2006). Call types were categorised as in Table 1.1. Different patterns represent either the call type of the family (patterns in the terminal squares at the end of the branches) or ancestral reconstructions of the call types (branch patterns). Some families have more than one call type and this is denoted as polymorphic (i.e., Pteropodidae has call types 1 and 2; Noctilionidae 5 and 8; Mormoopidae 4 and 8; and Vespertilionidae 3, 5 and 6). Branches are denoted as equivocal where it is not possible to estimate the call type ancestral condition. Adapted from Jones & Teeling (2006).

1.1.6 Which came first: flight or echolocation?

Bats are thought to have evolved around between 89 (Bininda-Emonds *et al.* 2007) and 62 million years ago (Jones, Bininda-Emonds, & Gittleman 2005), with the oldest known fossils dated to the Eocene about 53 million years ago (Simmons & Geisler 1998). Whether bats evolved flight before echolocation or vice versa has been hotly debated (summarised in Speakman (2001)). Briefly, there are three hypotheses that have been posited: echolocation first; flight first; and tandem origin (where the ancestral bat uses echolocation calls only for communication and this develops with the ability to fly). The most promising evidence to date to test these hypotheses is from a recent fossil *Onychonycteris finneyi*, dated at around 52.5 million years ago (Simmons *et al.* 2008). Cranial features of this fossil, together with

its relatively small cochlea, initially suggest that bats may have evolved powered flight prior to evolving the ability to echolocate. However, this finding has since been disputed, based on a comparative analysis of stylohyal and tympanic bones (Veselka *et al.* 2010), suggesting that *O. finneyi* was a flying echolocator. Prior to the discovery of *Onychonycteris*, there was no clear evidence in support of any of the three hypotheses for the evolution of echolocation and flight (Speakman 2001), and given the controversy surrounding the new fossil, this has not changed.

1.1.7 Coevolution with insects

There is some evidence that bat echolocation behaviour may have been influenced by interactions with other taxa, for example, the arms race between some bat species and their tympanate moth prey (which can hear ultrasound) (Fullard 1998). Some bats have evolved the use of low echolocation frequencies that are below the range of moth hearing, and this enables them to prey on moths. For example, the European free-tailed bat (*Tadarida teniotis*) calls as low as 11 kHz and the spotted bat (*Euderma maculatum*) calls at around 9 kHz. Both feed mainly on tympanate insects (Fullard & Dawson 1997; Rydell & Arlettaz 1994). Hipposiderid and rhinolophid bats that emit very high frequencies tend to eat more moths than low-frequency congeners (Bogdanowicz, Fenton, & Daleszczyk 1999; Jones 1993). Hence, bats may be able to catch tympanate prey by using echolocation calls at allotonic frequencies (i.e., by calling at frequencies outside the range of moth hearing) (Fenton & Fullard 1979; Schoeman & Jacobs 2003). However, whether bats evolved allotonic frequencies primarily to exploit tympanate prey, or initially for other reasons associated with improving echolocation performance (e.g., for detecting smaller targets by using higher frequencies) is open to question (Waters 2003). In response to the echolocation calls of moth-eating bats, some insects in turn have evolved tympanal organs (ears) which can detect frequencies with highest sensitivity roughly between 20 and 60 kHz, and react to these sounds by changing direction or folding their wings and dropping out of the flight path of the bat (Jones & Rydell 2003). It is clear that predation by echolocating bats is an important selection pressure shaping insect hearing, because sensitivity to ultrasound has evolved in at least six insect orders, including several times independently in

moths (Hoy 1998). Janzen (1980) defines coevolution as '*an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first*'. The evolution of insect hearing followed by the evolution, in response, of a stealth detection mechanism by bats, such as the use of allotonic frequencies, or through dropping call intensity on approach (Goerlitz *et al.* 2010), would therefore constitute coevolution.

1.1.8 Coevolution with plants

Similarly, we may be able to gain insight into the influence that flowering, fruiting and nectar-producing plants have had on the bat echolocation call structure and vice versa. For example, around 1,000 plant species in the Neotropics are pollinated by bats in the family Phyllostomidae. Adaptations of the plants to the bats include outward-facing flowers; large, sturdy petals with exposed stamens; inconspicuously coloured, strong-smelling, night-opening flowers; high protein content pollen; and large volumes of nectar, released in small doses (Dobat & Peikert-Holle 1985). There is some evidence that bats have tailored their echolocation calls to the recognition of the plants they feed on, and it is likely that plants have evolved structures, shapes and textures that help bats to locate them and to feed (von Helversen & von Helversen 1999; von Helversen, Holderied, & von Helversen 2003; Simon *et al.* 2011).

1.1.9 Genes and echolocation

Our attempts to understand the evolutionary history of echolocation may soon be best served by the burgeoning field of genomics, especially following the sequencing of several bat species' genomes (*Myotis lucifugus* (Vespertilionidae), *Rhinolophus ferrumequinum* (Rhinolophidae), *Carollia perspicillata* (Phyllostomidae), and *Pteropus vampyru*s (Pteropodidae)) (International Sequencing Consortium 2011). Two genes have already been identified as likely candidates for serving a role in echolocation. A transcription factor involved in the neural control of orofacial coordination, known as FOXP2, was identified as playing a role in human speech development and language comprehension (Fisher &

Marcus 2006). Although it had previously been thought that *FoxP2* was highly conserved in non-human mammals, studies of this gene in bats have revealed great diversity and accelerated evolution compared with in other vertebrates (Li, Wang, et al. 2007). Exons 7 and 17 show particular diversity, with 17 containing eight non-synonymous mutations in bats, whereas it was invariant in the other eutherian mammals considered by Li *et al.* (2007), except for a single non-synonymous mutation in the pig. *FoxP2* is known to show strong expression in the inferior colliculus of mice (Ferland *et al.* 2003), a brain region that shows enlargement and morphological specialization in bats (Glezer *et al.* 2004), and which is fundamental in bat echolocation (Pollak & Casseday 1989). Recent work (Metzner & Zhang) shows that knocking-down *FoxP2* expression in the anterior cingulated cortex brain region of *Hipposideros armiger* (Hipposideridae) significantly altered the bats' ability to compensate for Doppler shift, but did not alter the frequency used by stationary bats (i.e., without the use of Doppler Shift Compensation). This suggests *FoxP2* is most involved in controlling call parameters during more complex echolocation tasks (Metzner & Zhang).

The second gene of interest is *Prestin*, which is known to be the motor protein of cochlear outer hair cells (OHCs) (Zheng *et al.* 2000). It works significantly quicker than other cellular motor proteins, and amplifies aural sensitivity up to 100-fold (Liberman *et al.* 2002). It is thought to be essential for auditory sensitivity and selectivity, and possibly also for high-frequency hearing in mammals (Liberman *et al.* 2002). When *Prestin*'s role in bats was considered, it was found to have undergone positive selection in the lineage of bats leading to the Rhinolophoidea, members of which use long constant frequency echolocation calls which compensate for Doppler shift (Li *et al.* 2008). These bats have an 'acoustic fovea': a frequency range with extremely fine tuning and sensitivity (Schuller & Pollak 1979), and it is thought that *Prestin* may be partly responsible for this (Li *et al.* 2008). In addition, a phylogeny based on *Prestin* sequences places all echolocating bats as a monophyletic clade to the exclusion of the Old World fruit bats (Pteropodidae). This replicates the old phylogeny of bats based on morphological characters, but is likely to be as a result of convergence in this functional gene (Li *et al.* 2008). Similarly, a phylogeny constructed from *Prestin* sequences for a selection of mammalian species places the bottlenose dolphin alongside the Rhinolophoidea, instead of near its closest relative of the

group, the cow (Li *et al.* 2010; Liu *et al.* 2010). These results suggest that echolocation, or at least high frequency hearing, could be the result of more than one evolutionary origin. However, a whole suite of genes are likely to be involved in echolocation, so further genetic evidence is necessary to elucidate this point.

Genomic comparisons have the potential to lead to further discoveries of genes involved in echolocation, and in combination with the better documentation and understanding of echolocation call diversity in bats, to expose exciting breakthroughs in research on the evolution of echolocation in bats.

1.1.10 Phylogenetic comparative approach

In the absence of further candidate genes, a potentially revealing means of studying the evolution of echolocation in bats is through the use of phylogenetic comparative methods. A review of the diversity in echolocation call structure within the framework of the phylogeny of bats has only been formally attempted once, using a family level tree and a family level descriptor of echolocation call type (Jones & Teeling 2006). The potential for generating further insight using an up-to-date, species level phylogeny and both continuous and discrete measures of echolocation call structures for a large number of echolocating bat species is vast, as it can help us to understand the extent of phylogenetic constraints on echolocation call plasticity, the call structure and ecological niche of the proto-bat, and the impact of echolocation call structure on ecological adaptability and species diversification. In addition, the results of these analyses may influence ongoing postulations regarding the relative timings of the origins of flight and echolocation in bats, and the number of evolutionary origins of laryngeal echolocation.

Similar studies have been carried out to look at the vocalisations of other animal groups. In 1985, in the early days of modern comparative analysis, Ryan & Brenowitz studied the relative roles of body size, phylogeny and ambient noise in the evolution of bird song, and found that body size and phylogeny played a strong role in determining the emphasised frequency of the songs. Devoogd *et al*. (1993) assessed the relationship between song

repertoire size and brain volume (specifically, the high vocal centre) in oscine birds within a phylogenetic framework, and they found a significant correlation between them. Ryan & Rand (1995) reconstructed túngara frog advertisement calls at ancestral nodes and used the results to conduct discrimination experiments using females of each of the túngara species. Ricklefs (2003) looked at the causes of patterns of diversification rates in passerine birds worldwide and found it likely that varied clades size were a result of random processes and extrinsic circumstances rather than intrinsic characteristics such as key innovations. Finally, Cardoso & Mota (2007) carried out an assessment of variation and evolutionary similarity in the songs of canaries and seedeaters (*Serinus*), finding that song characteristics were evolutionarily labile and largely unrelated to body size.

The varied use of comparative methods in studying vocalisations, and many other morphological and behavioural traits, bodes well for its extension to the echolocation calls of bats. Echolocation could be seen to have an additional layer of complexity to vocalisations made for communication reasons alone, as echolocation call structures must respond evolutionarily to the functional pressures associated with sensory tasks, as well as morphological and behavioural pressures. Learning more about the interactions between ecology and evolutionary history in shaping the huge variety of echolocation calls used by modern bats should prove extremely interesting.

1.2 Thesis aims and outline

The overall aim of this thesis is to understand how echolocation originated and diversified in bats, using a large database of echolocation call recordings, an up-to-date supertree, and phylogenetic comparative methods that have hitherto not been used in echolocation research. To do this, I ask the following research questions:

1. Do the echolocation call structures of bats show phylogenetic patterns consistent with the constraints of evolutionary history, rather than present-day ecological pressures, and in what manner have echolocation calls evolved?

2. What was the structure of the earliest echolocation calls of bats and how did this evolve into the diversity of echolocation call structures seen today?
3. Have any echolocation call types acted as key innovations aiding an increased rate of diversification in bats?
4. What do these analyses tell us about the nature of the evolution of echolocation and its impact on other aspects of the evolution of bats?

To answer these questions requires a large amount of echolocation call data, and a dated, comprehensive and well-resolved phylogenetic tree to act as a framework for carrying out comparative analyses. Chapter 2 describes the collection and measurement of the echolocation data, and Chapter 3 describes the construction and dating of a new phylogenetic supertree of bats. The following three chapters are analyses concerning the research questions above, followed by a set of general conclusions about the state of our understanding of the evolution of echolocation in bats.

Chapter 4: Evolutionary constraint in echolocation call structure

In Chapter 4, I investigate the degree to which echolocation call structure is constrained by evolutionary history. The variety of echolocation call structures is greater than would be expected if the sounds were shaped purely by the ecological pressures facing extant bats, suggesting that evolution has taken different routes in shaping bat calls that function in a very similar way. In this chapter I (1) review the variation across the order, (2) assess phylogenetic and spatial signal (autocorrelation), (3) estimate the most likely manner of evolutionary change, and (4) determine the best model of evolution (between Brownian motion (BM), Ornstein-Uhlenbeck (OU), and Early Burst (EB)), for eight echolocation call parameters. I find a high degree of convergent evolution in echolocation call functionality, with differences in call structure suggestive of independent evolutionary pathways and a constraining force. I conclude that all call parameters show greater influence from evolutionary history, a lower degree of influence from environmental conditions, and a tendency towards species-specific, punctuational, and directional evolution.

Chapter 5: The origin of echolocation calls in bats: what did the first echolocation calls sound like?

In Chapter 5, I consider the evolutionary origin of echolocation and the subsequent diversification of bat echolocation calls. I use present-day echolocation call diversity to (1) reconstruct the evolutionary history of echolocation call structure using contemporary phylogenetic comparative methods, (2) consider the other evidence for ancestral echolocation call structure, and (3) infer the ancestral bat's habitat, wing morphology, foraging style, and prey type from the predicted ancestral call type. All ancestral reconstruction techniques, discrete analyses and further evidence suggest an ancestral call type that was fairly short in duration, multi-harmonic, and narrowband as the ancestral echolocation call of bats. This call type suggests that the proto-bat was a slow and manoeuvrable flier with an opportunistic and omnivorous diet and that it may have used a perch-hunting foraging strategy.

Chapter 6: Which echolocation call structures are 'key innovations' that promote diversification?

In Chapter 6, I explore whether the bat phylogeny shows any evidence of 'up-shifted' clades that have undergone increased rates of diversification. I ask whether these clades are up-shifted as result of the echolocation call types used by the species they contain, and I explore the possible ecological models that might substantiate a link between echolocation call types and increased speciation rates. I find that there were two significant up-shifts in speciation rate, one at the root of a clade of 80 species of Old World fruit bat (Pteropodidae), and the other at the root of the New World fruit bat sub-family Stenodermatinae (Phyllostomidae). I also find that call types 1 and 9 (vision, and a multiharmonic, short duration, high bandwidth call), used by the two up-shifted clades, show increased rates of speciation compared to other call types. Analysis of speciation rates for all echolocation call types also highlights four other call types as causing increased speciation rates. I suggest that these echolocation call types should be considered key innovations, as (1) they are associated with increased rates of diversification; (2) I put forward an ecological model explaining the link between the traits and increased speciation; and (3) an analogous trait in toothed whales shows a similar pattern of diversification.

2 Chapter 2: General Methods

2.1 Introduction

The analyses described in chapters 4 to 6 are based on two main sets of data; a database of bat echolocation calls (EchoBank) and a new phylogenetic supertree of the bats (see Chapter 3). This chapter details how the first of these datasets, EchoBank, was compiled, and how measurements of search phase echolocation calls were extracted from the recordings it contains. Any methods and data specific to each of the analyses are described within each of the analysis chapters.

2.2 Call consortium

Since echolocation was discovered in the 1940s (Griffin & Galambos 1941), the calls of hundreds of species of bats have been recorded. Recordings have largely remained in the possession of recordists, or in small, incomplete online databases (see Table 2.1), the largest of which allows only listening access rather than the ability to view the spectral content of recordings using sound analysis software. Among the bat echolocation community, interest in a centralised online database, or reference library, has been growing as recordings accumulate (Korine & Kalko 2001). Research looking at echolocation in a phylogenetic, rather than geographic or purely ecological context, has been hampered by the time and cost involved in collecting echolocation calls from a group of related, yet perhaps widely dispersed, species. The nature of the analyses in this thesis is such that large numbers of calls representing a wide sample of bat families, genera and species, distributed across the world, were required.

Library Name	Citation	Number of Records	Number of Named Species	Recording Method
British Sound Archive	British Sound Archive, 2008	~700	139	time expansion
www.batcalls.org	Wenzel 2008	91	42	time expansion
BatCall	Museum of Southwestern Biology, 2008	3821	22	frequency division
Wyoming Bat Call Library	Keinath 2008	73	14	frequency division
Pacific Northwest Bat Call Library	Erikson & West 2008	33	10	frequency division
South-eastern Australian Bat Call Library	Herr & Klomp 2008	31	9	frequency division
Macaulay Library	Cornell Lab of Ornithology, 2008	72	1	time expansion

Table 2.1: Sound libraries containing bat echolocation call recordings. Only calls recorded using the time expansion or real-time method are suitable for detailed analyses - see section 2.2.2 for an explanation of the terms 'time expansion', 'real-time' and 'frequency division'.

To create such a collection, a call consortium (for members see Table 2.2) was formed from a group of bat researchers who had recorded the echolocation calls of large numbers of bat species using methods appropriate for detailed sound analysis (see section 2.3). The call consortium agreement states that each consortium member will contribute their calls to the database, known as EchoBank, and grant access to the original sound files to all other members. Publications that make use of the recordings must be agreed on by all members. New members, who are often recommended by original members, are added only in the absence of objections from existing members, as this effectively provides a 'peer review' system of recordist quality, ensuring that species are competently identified and that recordings are made using suitable techniques and equipment.

Name	Institution
Michel Barataud	Independent researcher, France
Roger Coles	University of Queensland, Australia
Christian Dietz	University of Tuebingen, Germany
Brock Fenton	University of Western Ontario, Canada
Dai Fukui	Hokkaido University, Japan
David Jacobs	University of Cape Town, South Africa
Richard Jenkins	Madagasikara Voakajy, Madagascar
Nancy Jennings	Dotmoth Ecological Consultancy, UK
Gareth Jones	University of Bristol, UK
Elisabeth Kalko	University of Ulm, Germany
Alanna Collen	Zoological Society of London, UK
Martin Obrist	Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland
Stuart Parsons	University of Auckland, New Zealand
Sebastien Puechmaille	University College Dublin, Republic of Ireland

Table 2.2: Contributors to the EchoBank Call Consortium.

2.3 Recording echolocation calls

There are a wide range of equipment types, data capture techniques, and bat handling methods that can affect the quality and comparability of echolocation call reference recordings for a call library. In general, sound entering a *microphone* is captured and processed by a *detector* and recorded onto a *media type* in a *recorder*. Sets of equipment may keep some or all of these elements separate, whereas others incorporate all the elements into a single device. Detectors may have options for the data capture stage, such as *time expansion factor*, *sampling rate* and *sample size*. Microphones can vary in their *frequency response*. Recorders can vary in the *media type* on to which they record. Different media types may or may not require digitisation. Those that do are analogue and vary in their susceptibility to deterioration with age, and those that do not are digital and may be able to record various file types.

Additionally, a recording of a bat's calls can be made in several different ways and must take into account the bat's *echolocation style*. The *release type* specifies the way in which the bat is being handled as the recording is made and the *surroundings* indicate the degree of clutter around the bat.

The following show the impact that choices in each of these italicised categories can have on the recording, and the range that exist within the EchoBank database:

1. *Equipment and data capture*
    a. *Detector*

EchoBank contains recordings from 10 different detectors made by four different manufacturers (see Table 2.3). The data capture settings below determine the differences between these detectors.

Detector	Recording Device	Media	Microphone	Recording Method	Frequency Response (kHz)	Reference
UltraSound Advice S-25	Laptop with DAQ card	Hard Disk	Integrated	Time expansion	10-180	Lemasson *et al.*, 2005
UltraSound Advice S-25	Sony WM-D6C	Cassette Tape	Integrated	Time expansion	10-180	Lemasson *et al.*, 2005
UltraSoundGate 416-200	Laptop no DAQ card	Hard Disk	Avisoft CM16/CMPA	Time expansion	20-370	Specht, 2011
UltraSoundGate Unknown	Laptop no DAQ card	Hard Disk	AKG	Time expansion	Unknown	-
Laar Bridge Box	Sony TCD-D7	DAT Tape	AKG	Time expansion	20-170	Budenz, 2009
Pettersson D240	Sony TCD-D100	DAT Tape	Integrated	Time expansion	10-120	Alana Ecology, 2011
Pettersson D240X	NET MZ-N510 Type S	MiniDisc	Integrated	Time expansion	10-120	Pettersson, 2011
Pettersson D240X	Sony TCD-D100	DAT Tape	Integrated	Time expansion	10-120	Pettersson, 2011
Pettersson D960	Sony WM-D6C	Cassette Tape	Integrated	Time expansion	10-150	Arak & Eiriksson, 1992
Pettersson D980	Laptop with DAQ card	Hard Disk	Integrated	Time expansion	10-200	Alana Ecology, 2011
Pettersson D980	Marantz CP 230	Cassette Tape	Integrated	Time expansion	10-200	Alana Ecology, 2011
Pettersson D980	Sharp MD	MiniDisc	Integrated	Time expansion	10-200	Alana Ecology, 2011
Pettersson D980	Sony TCD-D8	DAT Tape	Integrated	Time expansion	10-200	Alana Ecology, 2011
Pettersson D1000X	Integrated in bat detector	Flash Card	Integrated	Direct sampling	5-307.2	Pettersson, 2011
University of Tuebingen PC Tape	Integrated	Unknown	Integrated	Time expansion	18-200	Koblitz, 2010

Table 2.3: Detectors, recording devices and microphones used to make recordings stored in EchoBank. DAQ = Data Acquisition; DAT = Digital Audio Tape.

i. time expansion factor

Echolocation calls range in frequency from around 9 kHz (Leonard & Fenton 1984) to around 212 kHz (Fenton & Bell 1981). The upper limit of human hearing is about 20 kHz (Pumphrey 1950), so techniques have been developed to record the high frequency sounds of bats as audible sounds. These techniques include time expansion, frequency division, heterodyne, and real-time recordings. Recordings of echolocation calls in EchoBank were recorded using either time expansion or real-time techniques. Time expansion records high frequency sound as audible to humans by slowing down the recording by a pre-determined 'time expansion factor' (most often 10), whereas real-time recordings use analogue-to-digital cards that operate at high sampling rates to record high frequencies directly, so they remain largely inaudible unless played back at reduced speed. Both of these techniques yield high quality sound recordings that most reliably reproduce the original sound, and are suitable for detailed sound analysis, though the true signal will always be illusory (Pye 1993).

The two other methods used to record bat sounds, frequency division and heterodyne, are not suitable for detailed sound analysis (see Parsons, Boonman, & Obrist, 2000). Frequency division makes high frequency sound audible by dividing the frequency by a predetermined ratio, so using a factor of 10 would make an inaudible frequency of 120 kHz into an audible frequency of 12 kHz. This method can produce a misleading output signal that does not show harmonic content reliably, and also typically contains no relative amplitude information (Parsons *et al.* 2000). Heterodyning produces a sound that is the difference between the frequency set on the heterodyne recorder and the frequency entering the microphone, and is therefore not a reliable representation of the original sound (Parsons *et al.* 2000).

Time expansion factors in EchoBank range from 1 (≡ real-time) through 5, 8, 10, 15, and 16, to 20. Approximately 55% of recordings were made at factor 10 and a further 35% at factor 1. Using lower time expansion factors requires a higher sampling rate (due to the

Nyquist-Shannon sampling theorem, explained below), and a faster processor, which allows greater precision. Once sampling rate (see below) has been accounted for, time expansion factor has no impact on the quality or comparability of the calls (L. Pettersson, Personal Communication, 2010).

ii. sampling rate

The sampling rate (kHz) is the frequency with which the sound is sampled. In order to sample a complete sound, the sampling rate must be at least twice the value of the highest frequency in the sound (the Nyquist-Shannon sampling theorem). If it is not, aliasing will occur, where different aspects of the signal become indistinguishable from one another (Nyquist 1928).

Higher sampling rates produce more detailed recordings, similar to resolution in photographic images, and also improve the signal-to-noise ratio of the recording. Whilst all recordings made above the Nyquist limit are accurate, recordings with higher frequencies are more precise.

In EchoBank, sampling frequencies used range from 11.025kHz to 500kHz. Sampling frequency is the number of samples per second as the recording is made, so the sound made by the bat is actually sampled at this rate multiplied by the time expansion factor. For example, 5 seconds of bat calls might be time-expanded 10 times, resulting in a 50 second recording, for which each second is sampled at 44,100 times, or 44.1kHz. This means the original 5 seconds of sound have been sampled 441,000 times per second, or 441kHz. Taking time expansion into account, the sampling frequencies used in EchoBank range from 192kHz to 882kHz, with ~45% of recordings made with an effective sampling frequency of 441kHz, and a further ~40% at 500kHz, 384kHz, and 250kHz. A recording may be subjected to a further round of sampling as it reaches the recording device. However, all recording devices used for EchoBank recordings that are independent of the

bat detector have a sampling rate of at least 44.1kHz, and given that the recordings have been time expanded, none exceed the Nyquist limit.

Recordings made at different sampling rates are broadly compatible as long as the sampling rate is above the Nyquist limit and anti-aliasing filters are adequate (L. Pettersson, Personal Communication, 2010).

iii. Sample size

The sample size is the amount of computer memory allocated to each sample of the sound and is measured in bits. Eight bits are equivalent to 1 byte, so a recording of 1 second in length made at a sampling frequency of 500kHz and a bit rate of 16 has a file size of 500,000 * 16 = 8,000,000 bits ≡ 1,000,000 bytes ≡ 0.95Mb (since 1Mb = 1024^2 bytes). The bit rate (kbps – kilobits per second) of this file is the sample size multiplied by the sample rate (kHz): 16 * 500 = 8,000kbps.

All but three recordings contained in EchoBank have a sample size of either 8 or 16 bits (the others are 24 bits). 16 bit sample sizes give greater precision and less noise than 8 bit sample sizes, but the two are comparable nonetheless (L. Pettersson, Personal Communication, 2010).

b. Microphone

Table 2.3 shows that most of the microphones used in making recordings in EchoBank were integrated within the bat detector. Microphones vary in many ways, but the major impact to recordings of bat echolocation calls are differences in the frequency response of different microphones.

i. frequency response

The frequency response of a microphone is a measure of the output produced from a given input. A frequency response curve can be made by testing the volume (in decibels) of the

output for a given input volume over a range of frequencies (a Bode plot). Microphones vary in their responses to different frequencies and this can affect measures of relative amplitude both within recordings and between microphones (see Table 2.3 for frequency responses of detectors used for recordings in EchoBank).

c. Recorder

Nine different models of recorder were used in making the recordings in EchoBank: two cassette recorders, three DAT (Digital Audio Tape) recorders, two MiniDisc recorders, and two high-speed digital recorders. Recorder type can influence the quality and comparability of the recordings through the media type upon which it relies.

i. media type

Recordings in EchoBank were recorded onto cassette, DAT, MiniDisc, flash memory card or hard disk. Approximately 70% were recorded onto flash memory or hard disk. Cassettes and DATs are prone to degeneration with age and require digitization (outlined in section 2.4). Data compression methods are used with some media types to reduce the amount of storage space used by a recording. Some compression techniques, known as 'Lossy data compression' are less suitable for recording echolocation calls to the quality needed for detailed call analysis because they remove frequencies above the upper limit of human hearing, but others (Lossless data compression) encode all the information in a way that can be perfectly reconstructed. Where lossy data compression has been in use, as is often the case in MiniDisc recordings, recordings must be made using time expansion and for relatively low frequency calls, to ensure aspects of the call are not lost (Specht 2011b).

2. Bat handling

Aside from the range of technical choices available to a bat call recordist, there are several practical procedures to follow and choices to make when recording bat calls. The best methods to use depend on the echolocation style used by the bat and the surroundings in which the bat normally echolocates.

a. Echolocation style

Bats in the families Hipposideridae (Old World leaf-nosed bats) and Rhinolophidae (horseshoe bats) as well as *Pteronotus parnellii* (Mormoopidae – moustached bats) in the New World, compensate for Doppler shifts on their echolocation calls induced by motion by altering the frequency of the emitted call. This causes the echoes of interest returning to the bat to be at a steady frequency; that which is best detected by the acoustic fovea (Schuller & Pollak 1979). Stationary bats do not normally alter their call frequency as Doppler shifts are less likely. This frequency is known as the resting frequency and to record it, bats with Doppler Shift Compensation (DSC) should be recorded for approximately 60 – 120 seconds whilst they are hanging free from a cave roof, hanging in a bat bag, or being held in the hand. It should be noted that these calls will not be representative of the entire repertoire of the bat, since in flight calls will be shifted downwards in frequency.

Species belonging to all other bat families do not compensate for Doppler shift and produce good quality calls when in free flight. They should be released approximately 10 metres from the bat detector, at approximately 2 metres above ground level. The microphone is aimed at the bat for as long as it is in the range of the bat detector, to collect a sequence of echolocation calls. Calls recorded immediately after the bat's release are ignored, to avoid echolocation calls that are not representative of free flight call types.

b. Surroundings

Bats alter the structure of their echolocation calls according to the surroundings in which they are flying (Schnitzler & Kalko 2001). In open habitats with few objects to avoid, bats use lower frequencies, smaller bandwidths, longer call durations, and fewer harmonics. In cluttered habitats, bats use higher frequencies, larger bandwidths, shorter call durations and pulse intervals, and more harmonics. Most bats are adapted to spend most of their time in habitats with a certain amount of clutter, producing mainly one kind of call structure in

search phase flight (Schnitzler & Kalko 2001). It is this kind of call structure, reflecting the bat's normal behaviour that should be recorded for use in a reference library. This can be achieved most easily by recording bats in the habitat in which they are caught. The kind of surroundings should be noted: EchoBank categories include *open, edge, cluttered, in roost,* and *roost emergence* stating whether or not these were *over water*. Open habitats contain very few obstacles, edge habitats often have a tree line on one side of the foraging area but are otherwise open, and cluttered habitats, such as forests, have a large number of different sized obstacles. It is useful to know whether recordings are made over water or not, as water can cause interference in the recording (Kalko & Schnitzler 1989).

c. Release type

As mentioned above, when making reference recordings bats with DSC should be stationary and all other species should be in free flight. Recordists use a range of release techniques to get good quality recordings, depending on circumstances. Release types used for recordings in EchoBank include: *in hand, in bat bag, free stationary, in net* (all stationary 'release types'), *hand release, zip line, light tagged, flight cage, free flying, ground release, artificial roost site, test room/laboratory, leaving roost* (all in flight release types), *in hand followed by free flight, free flying and hanging* (mixed stationary and in flight release types). These terms are explained in Table 2.4.

Release Type	Explanation
In Hand	Bat is recorded whilst held in the hand.
In Bat Bag	Bat is recorded whilst hanging or lying in a bat bag.
Free Stationary	Bat is recorded whilst hanging or lying without restraint.
In Net	Bat is recorded whilst caught in a net.
Hand Release	Bat is recorded flying out of the hand until out of range of the detector.
Zip Line	Bat is recorded whilst tethered to a line allowing it to fly back and forth but not escape. This technique is particularly used when the bat is needed after the echolocation call has been recorded.
Light Tagged	Bat is recorded flying out of the hand but has a glowing light tag attached to its underside to allow the recordist to follow it in flight for as long as possible.
Flight Cage	Bat is recorded flying in a flight cage.
Free Flying	Bat is recorded in free flight.
Ground Release	Bat is recorded flying off the ground until out of range of the detector.
Artificial Roost Site	Bat is recorded hanging or lying in an artificial roost.
Test Room/Laboratory	Bat is recorded flying in a test room/laboratory.
Leaving Roost	Bat is recorded in free flight whilst leaving its roost.
In Hand followed by Free Flight	Bat is recorded in the hand and then flying out of the hand.
Free Flying and Hanging	Bat is recorded both free flying and hanging.

Table 2.4: Explanations for release types (what the bat is doing during the recording) of recordings stored in EchoBank.

2.4 Digitisation

Echolocation call recordings in EchoBank had been made onto compact cassette tape, digital audio tape (DAT), and as digital wave files stored on hard disk drives and MiniDiscs. Compact cassette tape and DAT recordings were played through a portable cassette player and an external sound card and were then digitised onto an external hard

disk drive using BatSound (Pettersson 2008) or Avisoft-RECORDER (Specht 2008) (sound analysis software). Digital wave files were simply transferred to the external hard disk drive for storage.

2.5 Field methods

An assessment of the geographic and taxonomic coverage of the echolocation call recordings in EchoBank in September 2008 showed a paucity of data from Australia and Papua New Guinea (see Figure 2.1 – made in R (The R Core Development Team, 2010)), and from the many endemic taxa in that region, such as the genera *Vespadelus*, *Chalinolobus*, *Nyctophilus* and *Scotorepens* (Chiroptera: Vespertilionidae). I expected to receive further data from recordists working in South America and Africa, leaving Papua New Guinea and Australia the most under-represented areas. The lack of call recordings made of species found in this region is due to the popularity of the frequency division technique of call recording amongst Australian bat researchers, as opposed to the time expansion or real-time methods (R. Coles, Pers. Comm., 2009).

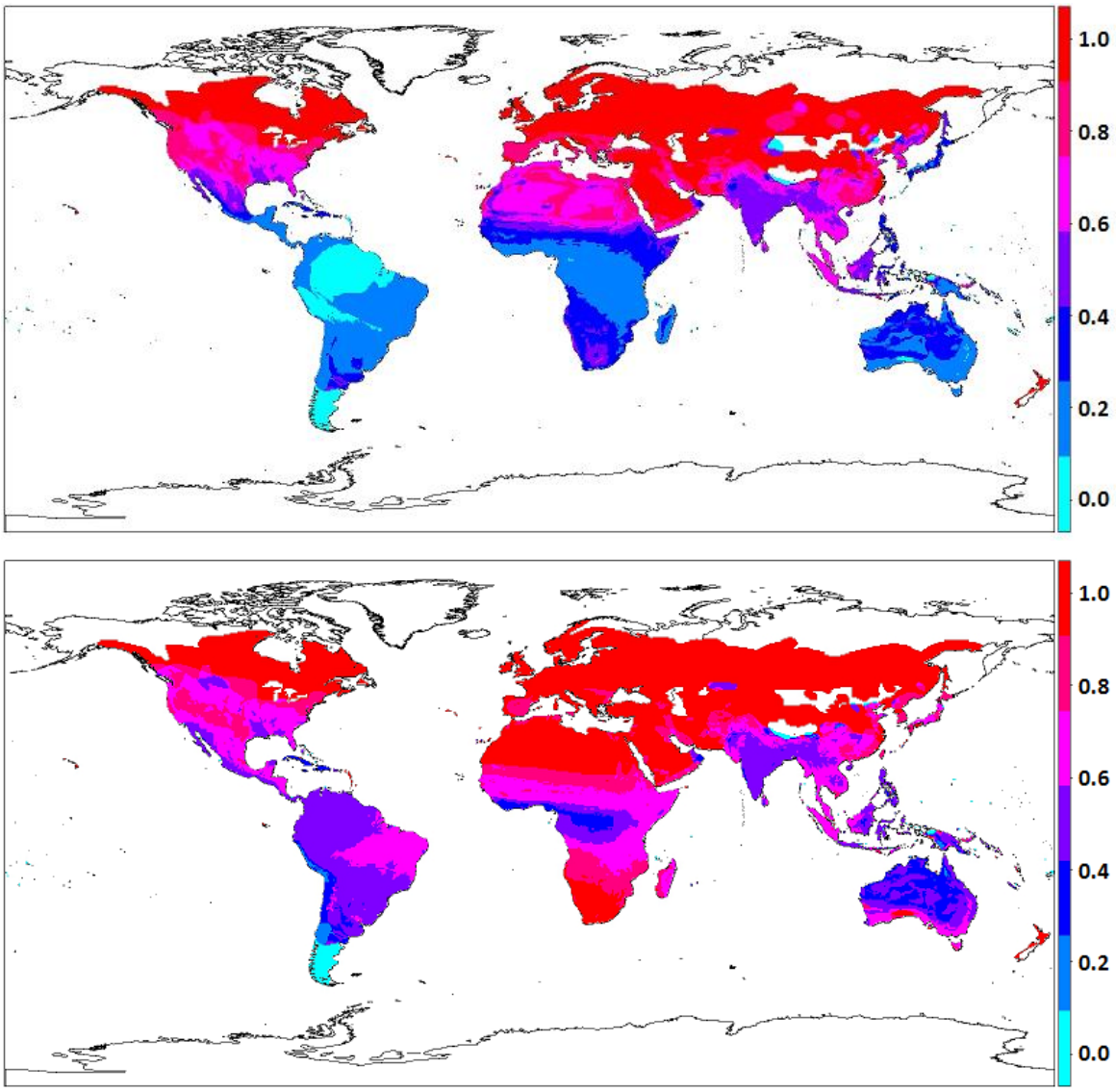


Figure 2.1: Top: The proportion of species held in EchoBank in September 2008 (when geographic coverage was assessed) out of those present in any given range according Grenyer *et al*. (2009). Bottom: The proportion of species held in EchoBank in November 2010 out of those present in any given range according to Grenyer *et al*. (2009). The map is comprised of overlapping species' range maps for 899 echolocating bat species, and each 250km^2 grid square is shaded according to the proportion of species present in that grid square that are represented in EchoBank. Redder areas of the map show good EchoBank coverage relative to species diversity, whereas paler blue areas show poor EchoBank coverage.

I conducted fieldwork to make recordings of the under-represented taxa mentioned above, and any other species caught. This fieldwork took place in the Southern Highlands Province of Papua New Guinea and in Queensland and New South Wales, Australia. Bats were caught using harp traps and mist nets, and by hand in caves. They were identified to species level, with identities confirmed by experts Dr Kris Helgen in Papua New Guinea (Smithsonian Institution, Washington DC, USA), Dr Lindy Lumsden in New South Wales (Arthur Rylah Institute, Victoria State Government, Australia) and Dr Roger Coles in Queensland (University of Queensland, Australia). The bats were recorded at night using a Pettersson D1000X bat detector with integrated microphone and compact flash card at a sampling rate of 384 kHz and time expansion factor 1 (real-time). Bats in the families Hipposideridae (Old World leaf-nosed bats) and Rhinolophidae (horseshoe bats) were recorded for approximately 60 – 120 seconds whilst they were hanging free from a cave roof, hanging in a bat bag, or being held in the hand. Species belonging to all other bat families were released approximately 10 metres from the bat detector, at approximately 2 metres above ground level in the habitat in which they were caught. The microphone was aimed at the bat for as long as it was in range, to collect a sequence of echolocation calls. Calls recorded immediately after the bat's release were ignored, to avoid echolocation calls that are not representative of free flight call structures. The metadata data described in section 2.6 were also recorded. The species recorded are listed in Table 2.5. Two species are thought to be new to science, and, although they are in EchoBank, they could not be included in my analyses as they are not yet listed in Mammal Species of the World (Simmons 2005). Following this fieldwork, and the receipt of recordings from South America and Africa, the geographic coverage of the recordings in EchoBank was much more even (see Figure 2.1).

Family	Genus	Species	Country	Sample size	In analysis?
Emballonuridae	*Emballonura*	*dianae*	Papua New Guinea	15	Yes
	Emballonura	*furax*	Papua New Guinea	8	Yes
	Tadarida	*australis*	Australia	3	Yes
Hipposideridae	*Aselliscus*	*tricuspidatus*	Papua New Guinea	1	Yes
	Hipposideros	*ater*	Papua New Guinea	1	Yes
	Hipposideros	*calcaratus*	Papua New Guinea	12	Yes
	Hipposideros	*cervinus*	Papua New Guinea	5	Yes
	Hipposideros	*maggietaylorae*	Papua New Guinea	5	Yes
	Hipposideros	*wollastoni*	Papua New Guinea	3	Yes
Miniopteridae	*Miniopterus*	*australis*	Australia	5	Yes
	Miniopterus	*sp. nov.*	Papua New Guinea	1	No
Rhinolophidae	*Rhinolophus*	*euryotis*	Papua New Guinea	15	Yes
	Rhinolophus	*megaphyllus*	Australia	5	Yes
	Rhinolophus	*sp. nov.*	Papua New Guinea	2	No
Vespertilionidae	*Chalinolobus*	*gouldii*	Australia	7	Yes
	Chalinolobus	*morio*	Australia	3	Yes
	Myotis	*macropus*	Australia	1	Yes
	Nyctophilus	*geoffroyi*	Australia	4	Yes
	Vespadelus	*darlingtoni*	Australia	1	Yes
	Vespadelus	*regulus*	Australia	3	Yes
	Vespadelus	*vulturnus*	Australia	9	Yes

Table 2.5: Species caught during fieldwork in Papua New Guinea and Australia in 2009.

2.6 The EchoBank database

EchoBank is a Microsoft Access database storing recordings and metadata. The metadata categories pertaining to each recording are shown in Table 2.6. The taxonomic contents of EchoBank can be seen in Appendix A.

Individual	Life Stage
	Sex
	Species
	Reproductive Status
Recording	File name
	Surroundings (see section 2.3, sub-section 2b)
	Release Type (see section 2.3, sub-section 2c)
	Date
	Time
	Country
	Locality
	Latitude
	Longitude
	Sampling Rate
	Bit Rate
	Filters Used
Recordist	Title
	First Name
	Last Name
	Institution
	Department
	Email Address
	Website
Equipment	Bat Detector
	Recording Device
	Microphone
	Media Type
	Other (filters, calibrations, etc.)
Other	Notes

Table 2.6: Metadata collected and stored in EchoBank.

2.7 Parameterisation

Bat echolocation calls can be viewed using sound analysis software programmes, which display sound as two-dimensional images. These images can be sonograms (or spectrograms) of frequency against time, or oscillograms of amplitude against time, or power spectra of power (energy/time) against frequency. Commonly, sonograms display frequency against time with amplitude indicated using a colour scale. Using these images, various parameters of each echolocation call can be measured.

Before the echolocation calls in EchoBank were measured, each of the 5784 recordings in the database was checked for quality. Recordings with too many species present, or containing two species with overlapping echolocation call frequencies, were removed. The time expansion factor was checked, and the time-in-file of any social calls, approach phase calls, or feeding buzzes was noted, since only search phase calls (when the bat is not approaching an object: see Figure 2.2) were measured.

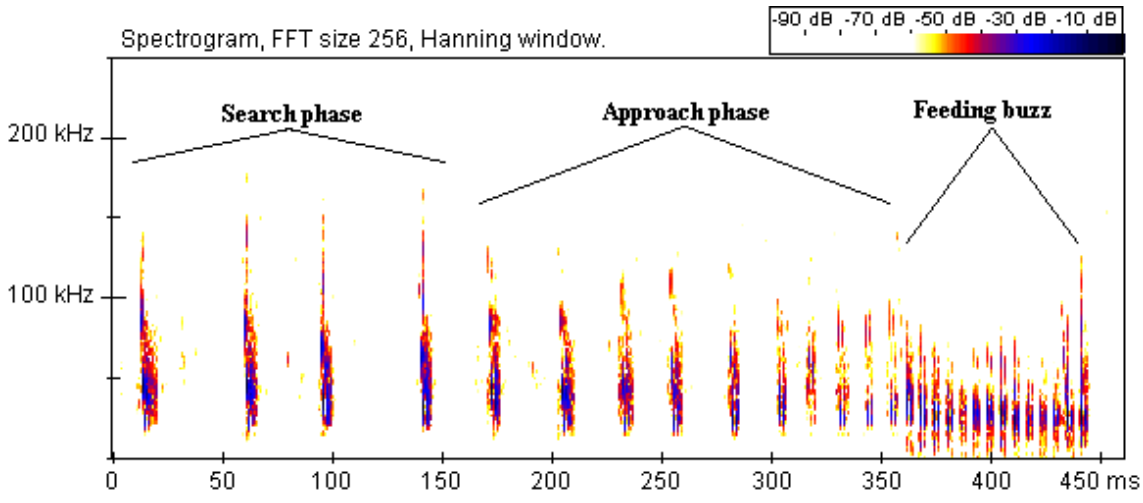


Figure 2.2: A sequence of *Myotis tricolor* split into search phase, approach phase and feeding buzz, showing the different call types used for each task.

I used a customised version of SonoBat v3 (Szewczak 2010) to measure the 76 echolocation call parameters shown in Table 2.7 for the harmonic containing the most energy in each call. These parameters are taken as standard by SonoBat.

Parameter	Explanation
PrecedingIntrvl	Time between the current call and the previous call (milliseconds).
CallsPerSec	Mean calls per second of the recording or section of recording displayed. The accuracy of the reported value depends both on the quality of the recording and the absence of other bats and other signals in the recording. Any other signal components that pass through the discrimination logic will be counted as calls and contribute to (and reduce the accuracy of) the calculation.
CallDuration	Duration of the call (milliseconds).
Fc	Characteristic frequency of the call. Determined by finding the point in the final 40% of the call having the lowest slope or exhibiting the end of the main trend of the body of the call (kHz).
HiFreq	Highest apparent frequency of the call (kHz).
LowFreq	Lowest apparent frequency of the call (kHz).
Bndwdth	Total frequency spread of the call. Calculated from the difference between the highest and lowest frequency (kHz).
FreqMaxPwr	The frequency of the maximum amplitude of the call (kHz).
PrcntMaxAmpDur	Percentage of the entire call duration at which the maximum amplitude occurs.
TimeFromMaxToFc	Time from the point at which the maximum amplitude occurs to the point in the call of the characteristic frequency (ms).
FreqKnee	Frequency at which the initial slope of the call most abruptly transitions to the slope of the body of the call (kHz).
PrcntKneeDur	Percentage of the entire call duration at which the knee occurs, i.e., the point at which the initial slope of the call most abruptly transitions to the slope of the body of the call.
StartF	Frequency of the start of the call. Typically the same point as the highest frequency, but different if the call initially rises in frequency (kHz).
EndF	Frequency of the end of the call. Typically the same point as the lowest frequency, but different if the call ends with a rise in frequency (kHz).

DominantSlope	Slope of the longest sustained trend in slope of the call. Determined by finding the segment of the call having the minimum residue for a linear regression of a segment of the call of 20% the duration of the call (kHz/ms).
SlopeAtFc	Instantaneous slope at the point of the characteristic frequency (kHz/ms).
StartSlope	Slope at the start of the call, calculated from the first 5% of the call duration (kHz/ms).
EndSlope	Slope at the end of the call, calculated from the final 5% of the call duration (kHz/ms).
SteepestSlope	Steepest slope of the call, calculated from a linear regression of a segment of 10% the duration of the call (kHz/ms).
LowestSlope	Lowest slope of the call, calculated from a linear regression of a segment of 10% the duration of the call (kHz/ms).
TotalSlope	Total slope of the call, calculated from the difference in frequency and time from the point of highest frequency to the point of the characteristic frequency (kHz/ms).
HiFtoKnSlope	Slope of the call calculated from the difference in frequency and time from the point of highest frequency to the point of the knee (kHz/ms).
KneeToFcSlope	Slope of the call calculated from the difference in frequency and time from the point of the knee to the point of the characteristic frequency (kHz/ms).
CummNmlzdSlp	Average of the instantaneous slopes of the call (kHz/ms).
HiFtoFcExpAmp	Amplitude parameter of an exponential fit of the call from the point of high frequency to the point if the characteristic frequency.
HiFtoFcDmp	Damping parameter of an exponential fit of the call from the point of high frequency to the point if the characteristic frequency.
KnToFcExpAmp	Amplitude parameter of an exponential fit of the call from the point of the knee to the point if the characteristic frequency.
KnToFcDmp	Damping parameter of an exponential fit of the call from the point of the knee to the point if the characteristic frequency.
HiFtoKnExpAmp	Amplitude parameter of an exponential fit of the call from the point of the high frequency to the point if the characteristic frequency.
HiFtoKnDmp	Damping parameter of an exponential fit of the call from the point of the high frequency to the point if the characteristic frequency.
FreqLedge	Frequency of the ledge, i.e., the most abrupt transition to the most extended flattest slope section of the body of the call preceding the characteristic frequency, also referred to as the “ledge” of the call (kHz).

LedgeDuration	Duration of the ledge, i.e., the most extended flattest slope section of the body of the call preceding the characteristic frequency (ms).
FreqCtr	Frequency at the center of the duration of the call (kHz).
Fbak32dB	Frequency of the call 32 dB below the point of maximum amplitude of the call, and preceding the point of maximum amplitude of the call (kHz).
FFwd32dB	Frequency of the call 32 dB below the point of maximum amplitude of the call, and after the point of maximum amplitude of the call (kHz).
Fbak20dB	Frequency of the call 20 dB below the point of maximum amplitude of the call, and preceding the point of maximum amplitude of the call (kHz).
FFwd20dB	Frequency of the call 20 dB below the point of maximum amplitude of the call, and after the point of maximum amplitude of the call (kHz).
Fbak15dB	Frequency of the call 15 dB below the point of maximum amplitude of the call, and preceding the point of maximum amplitude of the call (kHz).
FFwd15dB	Frequency of the call 15 dB below the point of maximum amplitude of the call, and after the point of maximum amplitude of the call (kHz).
Fbak5dB	Frequency of the call 5 dB below the point of maximum amplitude of the call, and preceding the point of maximum amplitude of the call (kHz).
FFwd5dB	Frequency of the call 5 dB below the point of maximum amplitude of the call, and after the point of maximum amplitude of the call (kHz).
Bndw32dB	The total bandwidth covered from the point of the call 32 dB below and before the point of maximum amplitude and the point of the call 32 dB below and after the point of maximum amplitude of the call (kHz).
Bndw20dB	The total bandwidth covered from the point of the call 20 dB below and before the point of maximum amplitude and the point of the call 32 dB below and after the point of maximum amplitude of the call (kHz).
Bndw15dB	The total bandwidth covered from the point of the call 15 dB below and before the point of maximum amplitude and the point of the call 32 dB below and after the point of maximum amplitude of the call (kHz).
Bndw5dB	The total bandwidth covered from the point of the call 5 dB below and before the point of maximum amplitude and the point of the call 32 dB below and after the point of maximum amplitude of the call (kHz).
DurOf32dB	The duration of the call from the point of the call 32 dB below and before the point of maximum amplitude and the point of the call 32 dB below and after the point of maximum amplitude of the call (ms).
DurOf20dB	The duration of the call from the point of the call 20 dB below and before the point of maximum amplitude and the point of the call 32 dB below and after the point of maximum amplitude of the call (ms).

DurOf15dB	The duration of the call from the point of the call 15 dB below and before the point of maximum amplitude and the point of the call 32 dB below and after the point of maximum amplitude of the call (ms).
DurOf5dB	The duration of the call from the point of the call 5 dB below and before the point of maximum amplitude and the point of the call 32 dB below and after the point of maximum amplitude of the call (ms).
Amp1stQrtl	Total amplitude of the first quartile of the call (relative units).
Amp2ndQrtl	Total amplitude of the second quartile of the call (relative units).
Amp3rdQrtl	Total amplitude of the third quartile of the call (relative units).
Amp4thQrtl	Total amplitude of the fourth quartile of the call (relative units).
Amp1stMean	Mean of the first quartile amplitude (relative units).
Amp2ndMean	Mean of the second quartile amplitude (relative units).
Amp3rdMean	Mean of the third quartile amplitude (relative units).
Amp4thMean	Mean of the fourth quartile amplitude (relative units).
LnExpA_StartAmp	Amplitude parameter of an exponential fit of the time-amplitude trend of the call from the start of the call to the point of maximum amplitude.
LnExpB_StartAmp	Damping parameter of an exponential fit of the time-amplitude trend of the call from the start of the call to the point of maximum amplitude.
AmpStartLn60ExpC	Time parameter of an exponential fit of the time-amplitude trend of the call from the start of the call to the point of maximum amplitude.
LnExpA_EndAmp	Amplitude parameter of an exponential fit of the time-amplitude trend of the call from the point of maximum amplitude to the end of the call.
LnExpB_EndAmp	Damping parameter of an exponential fit of the time-amplitude trend of the call from the point of maximum amplitude to the end of the call.
AmpEndLn60ExpC	Time parameter of an exponential fit of the time-amplitude trend of the call from the point of maximum amplitude to the end of the call.
AmpK@start	Slope of a logarithmic plot of the time-amplitude trend of the call from the start of the call to the point of maximum amplitude (kHz/ms).
AmpK@end	Slope of a logarithmic plot of the time-amplitude trend of the call from the point of maximum amplitude to the end of the call (kHz/ms).
AmpKurtosis	Kurtosis of the time-amplitude trend.
AmpSkew	Skew of the time-amplitude trend.
AmpVariance	Variance of the time-amplitude trend.
AmpMoment	Moment of the time-amplitude trend.
AmpGausR2	R-squared of a Gaussian fit of the time amplitude trend.

Quality	Quality rating (0 to 1) of the call based on the total points of the sonogram above a threshold value. SonoBat uses this synthesised measure to assist in the call trending analysis of strong and weak call signals.
HiFminusStartF	High frequency minus start frequency. This measure may be used as a quality control check to sort and reject improperly trended calls. For typical frequency modulated calls, a value greater than zero (i.e., start frequency less than high frequency) may indicate an improperly trended call (kHz).
FcMinusEndF	Characteristic frequency minus start frequency. This measure may be used as a quality control check to sort and reject improperly trended calls. Use as appropriate for different types of calls. For example, most calls from the genus Myotis should have a positive value for this measure indicating the end frequency is less than the characteristic frequency. A negative value might indicate an improper trend as the result of a poor signal or excessive echo obscuring the end of the call (kHz).
RelPwr2ndTo1st	Ratio of the strength of the harmonic that SonoBat trended (typically the first or primary harmonic) to the strength of the next higher harmonic (typically the second harmonic). A ratio of the 3rd harmonic that exceeds the 2nd harmonic's ratio typically indicates a saturated or "clipped" signal. Such calls will render inaccurate assessments of power distribution through the call, although the time-frequency trend will remain reliable.
RelPwr3rdTo1st	Ratio of the strength of the harmonic that SonoBat trended (typically the first or primary harmonic) to the strength of the second higher harmonic (typically the third harmonic). A ratio of the 3rd harmonic that exceeds the 2nd harmonic's ratio typically indicates a saturated or "clipped" signal. Such calls will render inaccurate assessments of power distribution through the call, although the time-frequency trend will remain reliable.
Harmonic	Harmonic measured. Always the harmonic with the greatest energy in each call. This parameter is noted manually, after processing the call using SonoBat.

Table 2.7: Parameters taken by SonoBat for each echolocation call.

The customisation of the SonoBatch automatic measurement feature of SonoBat v.3 allows calls to be accepted (written to an output file) or rejected (not written to the output file). Sounds are rejected if (1) they are not bat calls, (2) the measurement line includes echo or background noise, (3) the measurement line fails to fit to the curve of the call, (4) the calls are overloaded (too loud for the microphone to capture the signal), (5) calls have low

signal-to-noise ratio (the signal is hidden amongst other sounds). SonoBat has an anti-aliasing feature which automatically calculates the true position of harmonics up to 350 kHz, so aliased calls could be included without comprising the quality of the measurements.

Calls from all sequences (sound files) for each species were parameterised, except in the family Rhinolophidae (horseshoe bats) where a maximum of 30 files were measured, since a very large number of recordings were in EchoBank for nine of these species and 30 recordings provided sufficient data. A total of 3,534 sequences and 53,086 calls were measured for each of 296 species in 95 genera and 19 families, representing 31% of echolocating species, 57% of echolocating genera, and 100% of families. The results were stored in EchoBank.

The parameters for each species were checked for errors, such as time expansion factor mistakes, by viewing a graph of call duration against either maximum or minimum frequency. The calls pertaining to any extreme outliers were checked for each species in case of mistakes. A mean, median and variance were taken for each sound file of each species, and then a mean of each of these for the species as a whole, so that each of the 76 parameters in Table 2.7 was summarised as a mean, median and variance for each species.

All records in EchoBank were conformed to the taxonomy of the 3rd Edition of Wilson and Reeder's Mammal Species of the World (Simmons 2005). Any recordings made of newly discovered species were stored in EchoBank as database 'orphans' and were not measured for my analyses. Any species noted under a synonym were updated to the appropriate name in the current taxonomy (Simmons 2005).

2.8 Echolocation data from the literature

To augment the echolocation data collected from members of EchoBank, I collected data from the literature (see Appendix B for reference list) for species not present in the data set following the parameterization of EchoBank recordings. Every species name was searched in conjunction with the word *echolocation* in Web of Science, BIOSIS Previews and Zoological Record. In addition, bat field guides were searched for echolocation data. This literature search resulted in echolocation data for an additional 115 species in 60 genera (27 new) and 13 families (1 new). The echolocation data in the literature conform to the same standard as the EchoBank data. This took the total echolocation data for analysis to 410 species in 120 genera and 19 families (see Appendix A for species list). This represents 44% of species, 74% of genera, and 100% of families of echolocating bats. The geographic and phylogenetic coverage are both comprehensive (see Figure 2.3 and Figure 2.4).

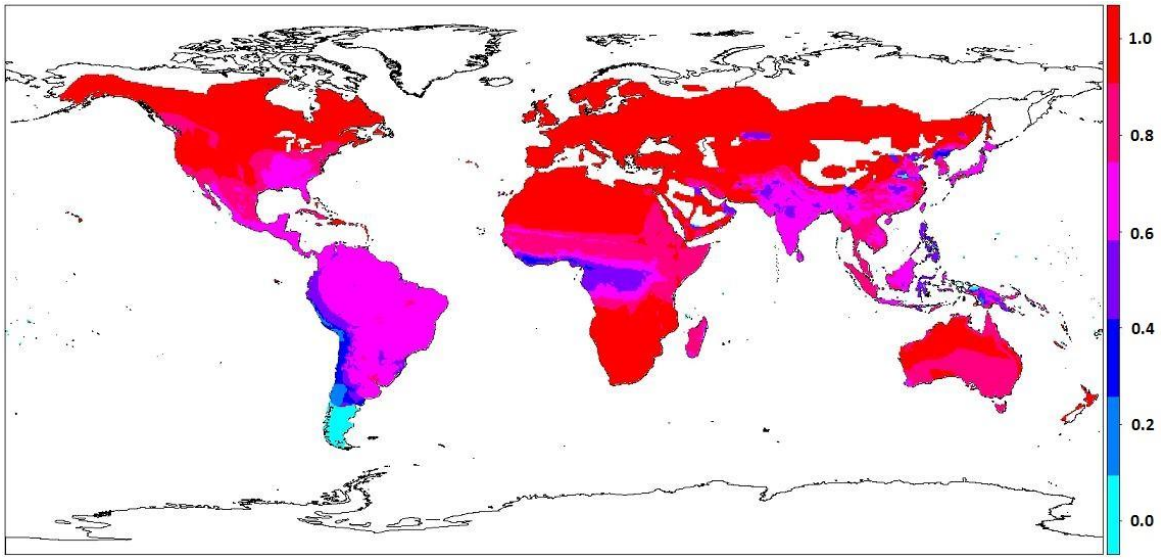


Figure 2.3: The proportion of species used in my analyses out of those present in any given range according to Grenyer *et al*. (2009). The map is comprised of overlapping species' range maps for 899 echolocating bat species, and each 250km^2 grid square is shaded according to the number of species present in that grid square that are represented in EchoBank. Redder areas of the map show good EchoBank coverage relative to species diversity, whereas paler blue areas show poor EchoBank coverage.

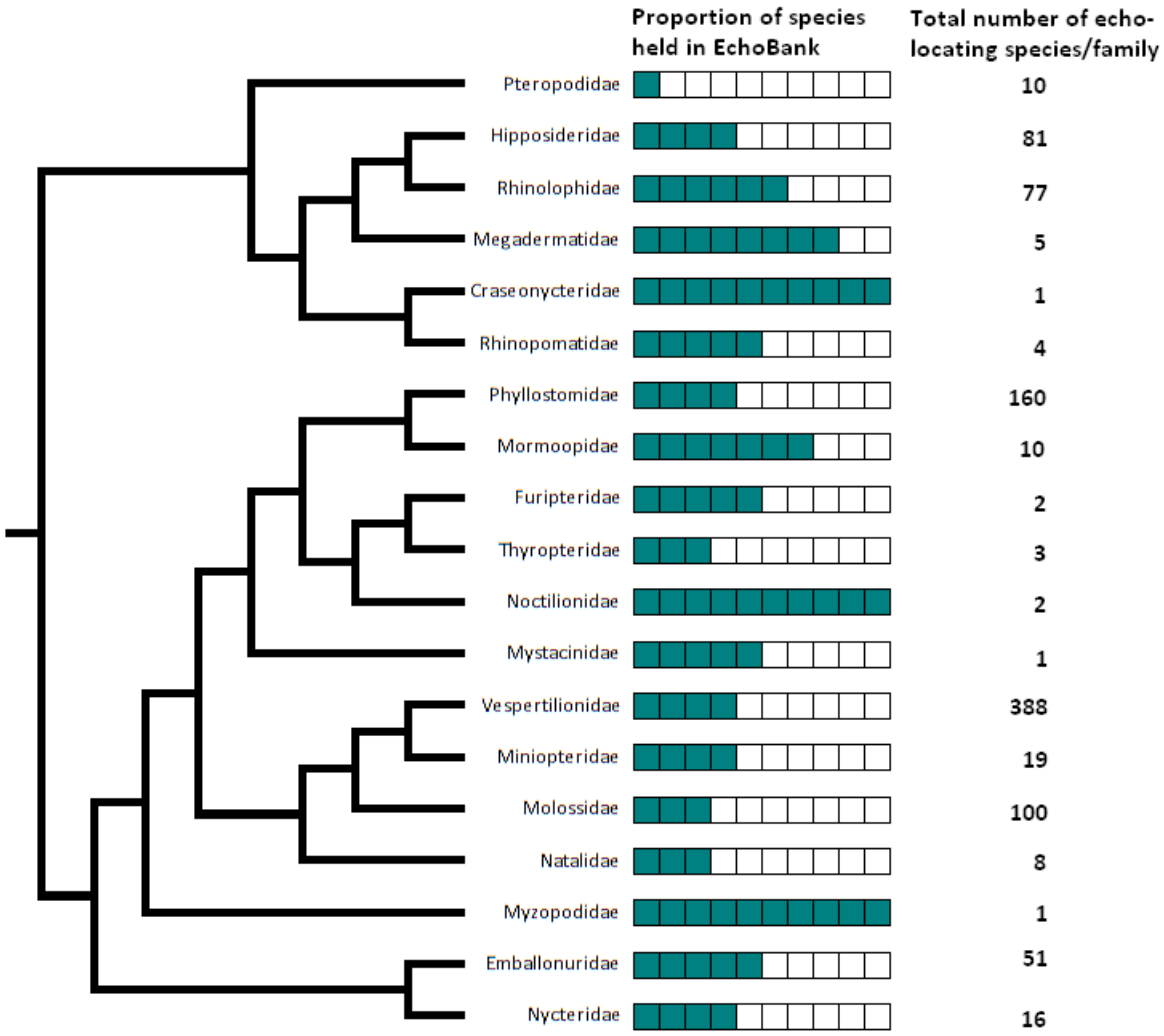


Figure 2.4: The phylogenetic coverage of the species used in my analyses as a proportion of the total number of echolocating species in the 2005 edition of Mammal Species of the World (Simmons 2005), shown on a family level tree, collapsed from the supertree reported in Chapter 3 of this thesis.

Echolocation call parameters were extracted from the literature if they matched with any of the parameters measured by SonoBat but did not overlap with the species in EchoBank (Table 2.7). The sample size, method of averaging, and metadata shown in Table 2.6 were also extracted, so that the data could be integrated with EchoBank data.

2.9 Echolocation data for analyses

I chose to use a subset of the parameters measured by SonoBat in my analyses, since many of the SonoBat parameters are extremely similar to one another. The eight parameters I selected represent the two main dimensions of a sound: time and frequency, and summarise the outline features of echolocation call structure. They correspond well to parameters commonly reported in the literature (Bayefsky-Anand, Skowronski, M. B. Fenton, Korine, & Holderied, 2008; O. Berger-Tal, R. Berger-Tal, Korine, Holderied, & M. B. Fenton, 2008; A. Boonman & H. U. Schnitzler, 2005; Fukui, Agetsuma, & Hill, 2004; Jones, 1999; Jung, E. K. V. Kalko, & von Helversen, 2007; Kingston, Jones, Akbar, & Kunz, 1999; Kingston *et al*., 2003; Ma, Liang, Zhang, & Metzner, 2008; Preatoni *et al*., 2005; Tian & H. U. Schnitzler, 1997; Vaughan *et al*., 1997; Yoshino *et al*., 2006; Zhao, Zhang, Zuo, & Zhou, 2003), and are functionally important and biologically meaningful. They, and a ninth parameter I recorded myself, are summarised in Table 2.8 and Figure 2.5.

One issue is of particular note regarding two of these parameters. Measuring maximum and minimum frequency can be somewhat subjective, since the amplitude of the call can impact on the values of these two parameters. This is especially true of maximum frequency, to which attenuation and directionality effects make quantification even more difficult. Some researchers use an amplitude value relative to the peak to define the maximum and minimum frequencies, but I feel this adds an *a priori* assumption that influences the values unduly. I chose to use the direct measures of maximum and minimum frequency since the large amount of data measured should produce reasonably reliable averages.

Call parameter	Description	Functional interpretation	Sample size (species)
Bandwidth	Maximum frequency – minimum frequency of the harmonic with the maximum energy (kHz)	High bandwidths allow greater resolution of different size classes. Low allow concentration of energy and increased range	365
Call Duration	Total duration of the harmonic with the maximum energy (ms)	Short durations give better localisation performance and long durations give more temporal informtation	392
Characteristic Frequency	The frequency measure with the lowest variance for each species out of maximum frequency, minimum frequency, and peak frequency (kHz). This value is more consistent than peak frequency at best representing all families	Lower frequencies travel further and higher frequencies give greater resolution – shows where main energy is placed	407
Dominant Slope	Slope of the longest sustained trend in slope of the call (kHz/msec)	Greater slope gives greater resolution and localisation, and lower slopes give greater range and more temporal information	290
Maximum Frequency	Highest frequency in the harmonic with the maximum energy (kHz)	Lower frequencies travel further and higher frequencies give greater resolution	353
Minimum Frequency	Lowest frequency in the harmonic with the maximum energy (kHz)	Lower frequencies travel further and higher frequencies give greater resolution	353
Peak Frequency	Frequency with the maximum energy (amplitude) in the harmonic with maximum energy (kHz)	Lower frequencies travel further and higher frequencies give greater resolution	407
Total Slope	Total slope of the call, calculated from the point of highest frequency to the point of the characteristic frequency (*sensu* SonoBat) (kHz/msec)	Greater slope gives greater resolution and localisation, and lower slopes give greater range and more temporal information	289
Peak Harmonic	Harmonic that most frequently has the maximum energy	Energy placement amongst harmonics allows movement on frequency scale	410

Table 2.8: The echolocation call parameters selected for analysis.

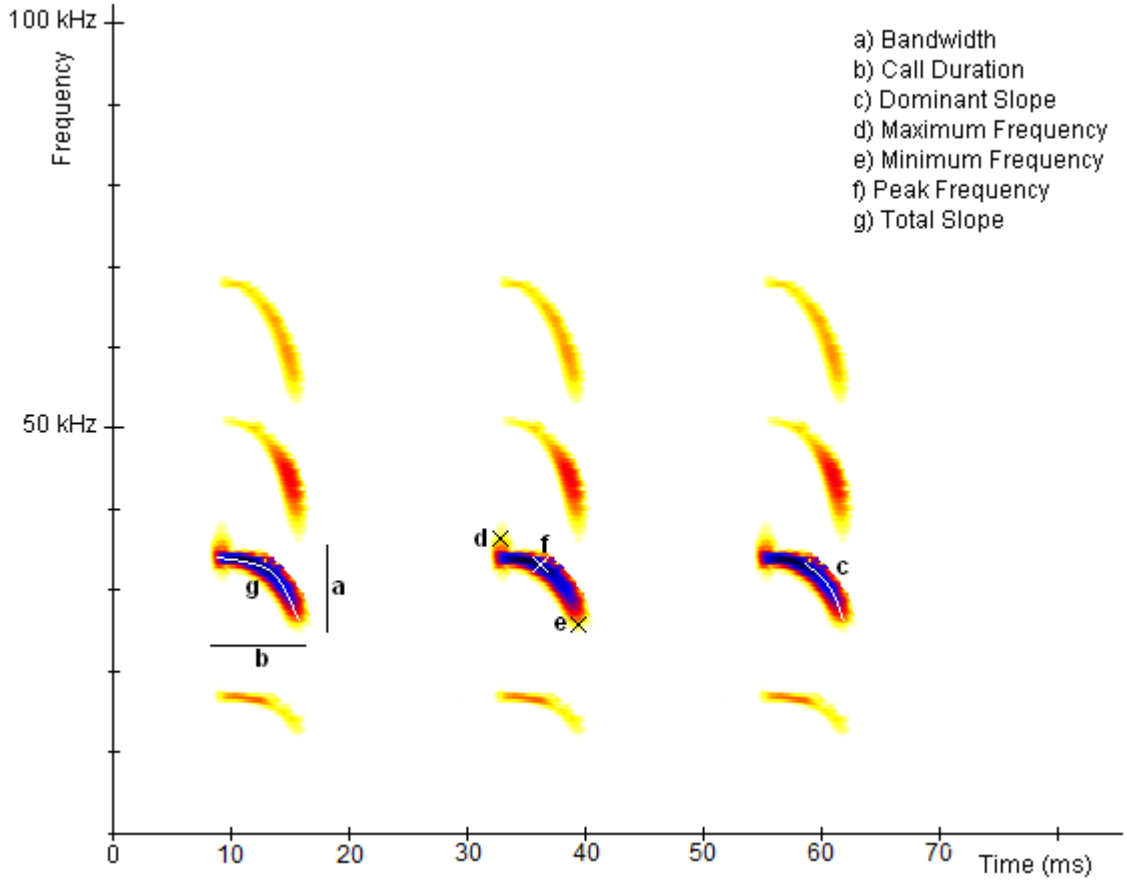


Figure 2.5: A spectrogram showing the echolocation call parameters selected for analysis. In this species (*Emballonura dianae*, Emballonuridae) Characteristic Frequency was equal to Maximum Frequency.

Since the echolocation data (and body mass data) were not normally distributed, I transformed each parameter using $\log_{10}$, natural log, and square root (or square root(parameter+1) where some values were less than 1), and chose the transformation that gave the most normal distribution, judged by the shape of a histogram. The transformations used for the parameters are shown in Table 2.9.

Parameter	Transformation
Bandwidth	square root(Bandwidth+1)
Body Mass	natural log
Call Duration	natural log
Characteristic Frequency	natural log
Dominant Slope	square root(DominantSlope+1)
Maximum Frequency	square root
Minimum Frequency	natural log
Peak Frequency	natural log
Total Slope	square root(TotalSlope+1)

Table 2.9: The transformations used for the parameter data analysed in subsequent chapters.

2.10 Conclusions

EchoBank contains 5784 recordings of 322 species in 101 genera and 19 families, recorded by 15 data contributors, including 106 recordings of 19 species in 10 genera and 6 families that I recorded myself. As shown in Figure 2.6, these range from a single recording for each of 48 species, to 291 recordings for one species (*Rhinolophus swinnyi*, Rhinolophidae). Of these, 53086 calls in 3534 recordings of 295 species in 94 genera and 18 families were of high enough quality to extract parameter measurements using SonoBat (Szewczak 2010). A median value of each parameter was calculated for each individual, and a mean of these was calculated for each species, resulting in a median value for each parameter of each species. To these I added the echolocation data from the literature (mainly means, with some medians) taking the total echolocation data for analysis to 410 species in 120 genera and 19 families.

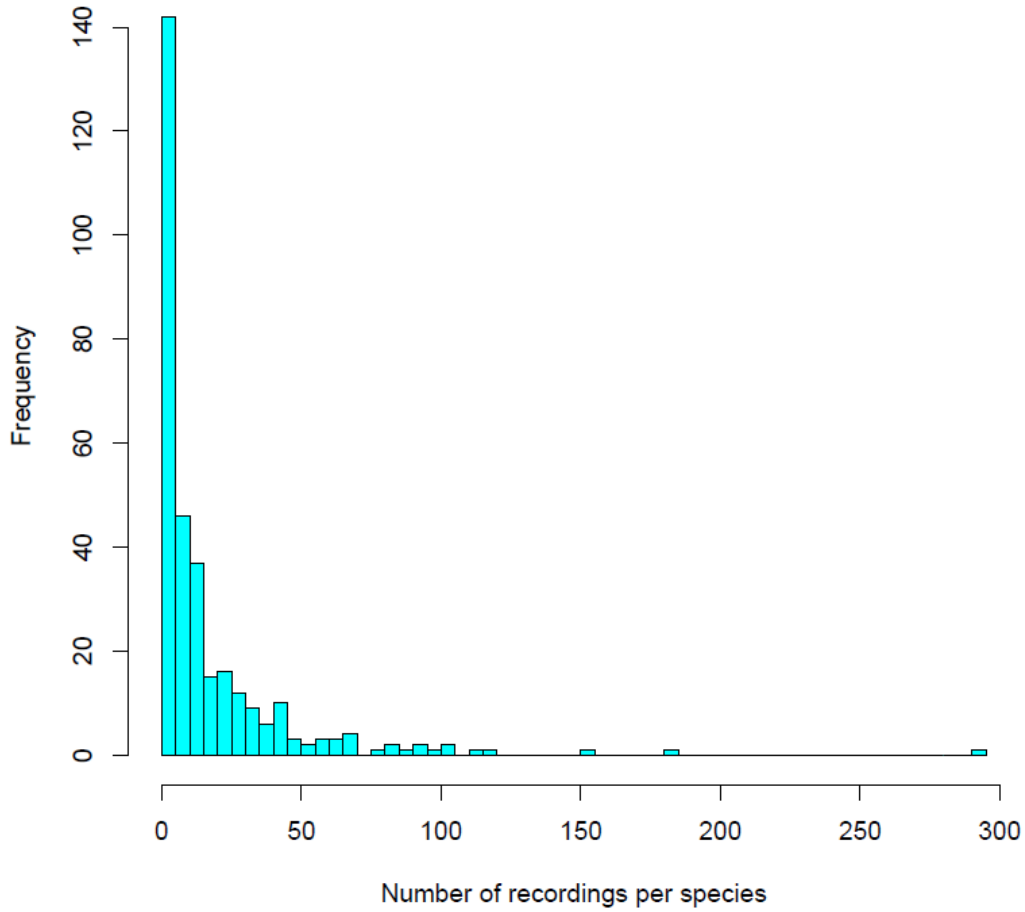


Figure 2.6: The frequency distribution of number of recordings per species.

3 Chapter 3: A new supertree of bats (Chiroptera)

3.1 Abstract

I present an updated estimate of the phylogenetic relationships among all 1116 recognised extant and recently extinct species of bats (Mammalia: Chiroptera). The phylogeny was assembled by combining 204 estimates of bat phylogenetic relationships published between 1970 and 2009 using the Matrix Representation with Parsimony (MRP) supertree construction technique. Since the first bat supertree, systematic studies have covered the order more evenly, with families receiving attention roughly in proportion to their speciosity. However, 36% of all bat species have yet to be included in a phylogenetic study. Resolution for a strict consensus tree has fallen since the 2002 supertree, from 46.4% to 34.7%, which is possibly due to the contradictions often seen between trees built from morphological characters and molecular characters. The new bat supertree supports microchiropteran paraphyly with respect to Megachiroptera, whereas the 2002 analysis did not. This shift is due to the great increase in published phylogenies supporting the change since 2000. Although the supertree is not a substitute for comprehensive total evidence phylogeny based on raw character data, it supplies us with a well-supported tool for large-scale phylogenetic comparative analyses.

3.2 Introduction

3.2.1 History of the bat phylogeny

Chiroptera (bats) is the second most speciose mammalian order, after Rodentia (rodents), comprising around 1116 species in 204 genera and 19 families (Gunnell & Simmons 2005; Hoofer & Van den Bussche 2003; Miller-Butterworth et al. 2007; Simmons 2005). Although bats comprise over one fifth of all mammalian species, it has only been in the last decade or so that evolutionary relationships have become clear. The lack of reliable, comprehensive and detailed phylogenies of the bats has hampered efforts to understand evolutionary patterns and processes using comparative methods, with many studies

focusing on either small groups of related species from a single geographic area, or on higher-level taxa. The burgeoning use of molecular techniques to uncover evolutionary relationships (see Figure 3.1) has improved our understanding of both the relationships of bats at the family level, and the species-level detail (e.g., Hoofer & Van den Bussche (2003); Teeling *et al*. (2000)).

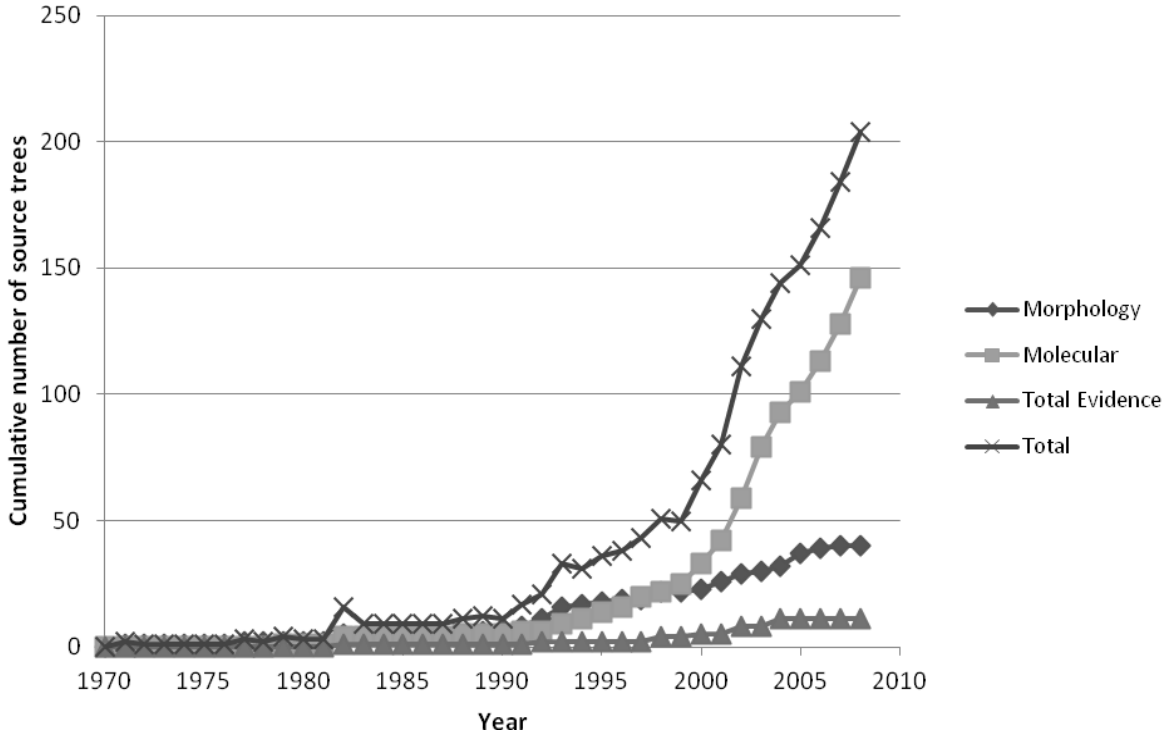


Figure 3.1: Cumulative number of source trees appropriate for inclusion in a bat supertree-building process, published between 1970 and 2008. Note that the number of trees per source can be greater than one, and so the number of unique sources is lower.

In the 1980s, despite previously widespread acceptance that all bats shared a common ancestor, a debate began around the possibility that bats were diphyletic. Pettigrew (1986) found that the system of neural connections between the mid-brain and the retina of the Megachiroptera (*sensu lato*) matched that of the primates, whereas the Microchiroptera (*sensu lato*) showed the putatively 'primitive' system of connections, in common with all other mammals. This evidence, in association with other pieces of morphological evidence (Buhl & Dann 1989, 1991; Kennedy 1987; Pettigrew 1986; Pettigrew et al. 1989; Smith

1977b; Smith & Madkour 1980) and some molecular evidence (Bennett *et al.* 1988; Kleinschmidt *et al.* 1988) indicated that the megabats evolved from the primate lineage, in a separate evolutionary event from that of the origin of the microbats. However, as molecular techniques developed and became more widely used, support has returned for the original monophyly hypothesis (Ammerman & Hillis 1992; Bailey, Slightom, & Goodman 1992; Baker, Honeycutt, & Van Den Bussche 1991; Baker, Novacek, & Simmons 1991; Bennett et al. 1988; Kirsch et al. 1995; Simmons, Novacek, & Baker 1991; Thewissen & Babcock 1991).

Within the 19 extant bat families (Gunnell & Simmons 2005; Hoofer & Van den Bussche 2003; Miller-Butterworth et al. 2007; Simmons et al. 2008), interrelationships have also been in debate. Bats were previously placed in two monophyletic sub-orders, the Microchiroptera and the Megachiroptera (Dobson 1875). The Megachiroptera contained a single family of Old World fruit bats that do not use laryngeal echolocation (Pteropodidae), whereas the Microchiroptera included the remaining 18 families of echolocating bats.

However, the monophyly of the Microchiroptera is now disputed, as molecular evidence suggests that several of the microchiropteran families are more closely related to the Megachiroptera than to the remaining families (Teeling *et al.* 2005). The most widely used division of the order places the Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae, Craseonycteridae, and the Rhinopomatidae in a new suborder, the Yinpterochiroptera (formed by the concatenation of 'Yinochiroptera' (introduced by Koopman (1984)) and 'ptero' (by Springer *et al.* (2001)), and leaves the Nycteridae, Emballonuridae, Myzopodidae, Mystacinidae, Phyllostomidae, Mormoopidae, Noctilionidae, Miniopteridae, Thyropteridae, Furipteridae, Natalidae, Molossidae, and Vespertilionidae in the sub-order Yangochiroptera (named by Koopman (1984) at which time it excluded Nycteridae and Emballonuridae) (Gunnell & Simmons 2005; Springer, Teeling, & Madsen 2001) (see Figure 3.2).

Given the recent confusion about the family members of each suborder (Yinpterochiroptera and Yangochiroptera) and the diphyly of the one of the previously used subordinal names

(Microchiroptera), Hutcheon & Kirsch (2006) have proposed new names for these suborders, using the International Code of Zoological Nomenclature's principles of typification, priority and attribution (International Commission on Zoological Nomenclature 2000). The suborder described above as 'Yangochiroptera' should be known as Vespertilioniformes based on Linnaeus' *Vespertilio* of 1758 and the suborder described as 'Yinpterochiroptera' should be known as Pteropodiformes, based on Brisson's *Pteropus* of 1762. In this thesis, I use Hutcheon and Kirsch's names.

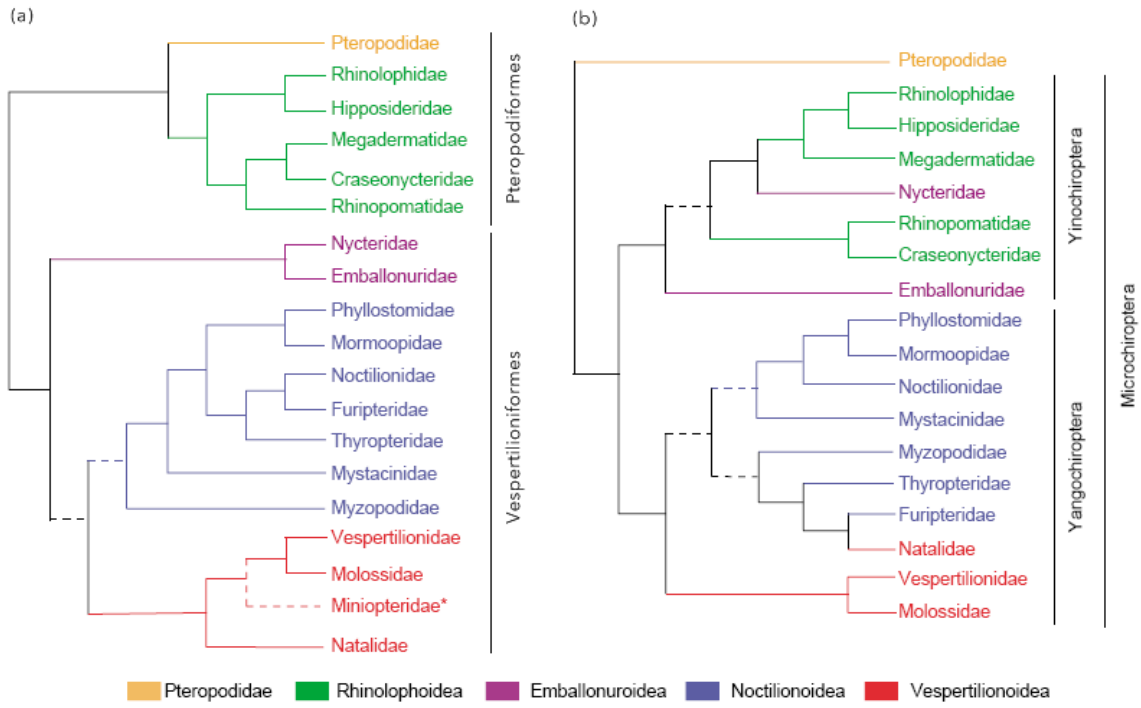


Figure 3.2: (a) Relationships amongst Chiropteran families based on more recent molecular work (Teeling et al. 2005); (b) The old topology, with the Pteropodidae basal to all other Chiropteran families (Gunnell & Simmons 2005). Figure adapted from Jones & Teeling 2006.

3.2.2 Phylogenetic supertrees

Phylogenetic supertrees are a somewhat controversial means of inferring evolutionary relationships between large numbers of taxa. Instead of analyzing molecular or morphological character data directly, the supertree approach takes topologies created from primary character data and combines them to form a more comprehensive phylogeny

(Bininda-Emonds 2004). The value in obtaining a complete phylogeny for a particular group was made evident in a macro-evolutionary study of the primates, based around a primate supertree (Purvis, Nee, & Harvey 1995), and this has been followed by numerous other studies, including a study of diversification rates in bats (Jones *et al.* 2005), an assessment of the factors increasing extinction risk in mammals (Fritz 2009), and a study of the adaptive significance of colouration in lagomorphs (Stoner, Bininda-Emonds, & Caro 2003).

One advantage of the supertree method in tree-building involving as many species as the Chiropteran tree (1116 species), is that it can incorporate species for which there are mismatched, or a complete lack of, primary character data. Alternative methods such as the supermatrix approach make use of a consistent set of character data to infer phylogeny, but until sequences of one or more particular genes are available for every species of bat, different character data sets will need to be combined to construct a complete phylogeny (Bininda-Emonds 2004). The supertree method makes this possible, and allows the incorporation of species for which there are *no* character data (and that therefore are not featured on any published topology) through the use of a reference taxonomy (Bininda-Emonds 2004).

In 2002, Jones *et al*. published a complete phylogenetic supertree of the bats (subsequently included in a supertree of mammals with no alterations (Bininda-Emonds *et al.* 2007), and followed by an update with branch lengths (Jones *et al.* 2005)) using source trees published between 1970 (start date chosen by Jones *et al*. (2002) to facilitate exclusion of less analytically robust studies) and 2000, and with a taxonomy corresponding to the second edition of the Mammal Species of the World (Koopman 1993). Since 2000 many phylogenetic studies of bats have been published, and the majority are based on molecular data. These phylogenies resolve many of the polytomies found in the 2002 supertree. In addition, an updated taxonomy has been published, taking the number of accepted bat species from 916 to 1116 (Simmons 2005). Amongst the new studies, molecular trees supporting microbat paraphyly have all but outweighed previous evidence in favour of megabats as an ancestral clade to the microbats. Because of the interfamilial

rearrangements, the extra resolution within several large genera, and changes in taxonomy, I have updated the 2002 supertree of Jones *et al*.

3.3 Methods

I updated the 2002 supertree using sources trees published in the literature between 2000 and the end of April 2009 for all families except for one: The supertree for the third most speciose family of bats, the Phyllostomidae (New World leaf-nosed bats) was updated from the 2002 supertree by Cooper & Purvis (2009) using further source trees from the literature between 2000 and the end of March 2007. To ensure consistency throughout the supertree, I used the source trees found by Cooper & Purvis 2009, but followed the methods outlined below (in section 3.3.2) when reconstructing the topology of the Phyllostomidae.

3.3.1 Source tree selection

I searched for source trees between 2000 and the end of April 2009 in Web of Science, BIOSIS Previews and Zoological Record. The search terms used were: vespertilionid*, myotis, kerivoula, pipistrellus, hypsugo, lasiurus, and eptesicus, chiropter*, rhinolophid*, hipposiderid*, megadermatid*, rhinopomatid*, craseonycterid*, emballonurid*, nycterid*, myzopodid*, mystacinid*, mormoopid*, noctilionid*, furipterid*, thyropterid*, natalid*, and molossid*, where * represents a wildcard – any letters in use here will produce results. Each of these search terms was, in turn, combined with each of the following additional search terms: phylogen*, systematic*, cladistic*, classif*, taxonom*, cladogram*, phenogram*, and fossil*.

I used source trees that resulted from valid analyses, as defined by Bininda-Emonds *et al*. (2004), but I did not include trees constructed using phenetic, rather than cladistic, methods. Phenetics is a means of classifying species based on similarity (often morphological similarity) regardless of evolutionary relationships, and as such, I do not consider its output appropriate for inclusion in a phylogenetic supertree. New sources were combined with pre-2000 sources from Jones *et al*. (2002), excluding those that were

phenetic or taxonomic, to assess independence using the protocol of Bininda-Emonds *et al*. (2004), as described below. Source trees must only be entered into supertree construction if they have data sets (taxon sets and character sets) that do not completely overlap (i.e., at least some characters or taxa are different) to prevent duplication of data that might lead to spurious signal enhancement of the duplicated clades (Bininda-Emonds 2004). When the taxon sets of each respective pair of trees were independent, the trees were both included in the analysis. For matching taxon sets, only those with independent character sets were included in the analysis. Character sets could be composed of morphological or molecular characters. Trees constructed from character sets combining several genes or morphological character subsets were considered independent of trees constructed from character sets including one of those genes or subsets.

Where source trees were non-independent, the tree with the largest taxon set was included. If trees were non-independent and equally comprehensive (common when trees are the result of a single study), the tree explicitly preferred by the authors was included. If no tree was preferred, the consensus tree was included. If there was no consensus tree, both/all trees were included, but down-weighted proportionally. See Appendix C for a list of source trees included in the supertree matrix.

The taxonomy of all terminal taxa was standardised using a source tree created from the reference taxonomy of Simmons (2005). This tree grouped genera, subfamilies and families, with the intention of incorporating all recognised species not present in the source trees and placing them in a likely position, i.e., with members of the same genus. All terminal taxa in the source trees were aligned with the species names given in the reference taxonomy; synonyms were brought up to date and unrecognised names were highlighted for corrections. This was done using a Perl script, 'SynonoTree.pl v2.2', (see Bininda-Emonds (2010)) written by Olaf Bininda-Emonds (OBE).

Any taxa present on the source trees which were not defined to species level were standardised to the reference taxonomy: where a genus name is present, the type species for that genus was assigned, unless monophyly of the genus is in question, in which case it was

removed; where a terminal taxon contains a cf. e.g. *Myotis cf. punicus*, or a 'sp., e.g. *Myotis sp.*, the taxon is deleted.

3.3.2 Matrix construction

There are a large number of supertree construction methodologies, some of which are tailored to specific challenges, such as reproducing branch-length information. The most commonly used method is Matrix Representation with Parsimony (MRP). This technique allows multiple 'source' trees to be combined, despite their origins in different primary character data sets and the inclusion of different taxon sets.

All source trees were redrawn in Mesquite v2.6 (Maddison & Maddison 2009). The collection of source trees was converted into a single MRP (Matrix Representation using Parsimony) matrix using a Perl script written by OBE, 'SuperMRP.pl v1.2.2' (Bininda-Emonds 2010). This script operates by creating a matrix containing columns which represent characters, each of which pertains to a single node in the phylogeny. For each species, the value in the column is '1' if the species is present in the branches subtending that node, '0' if it is not present in those branches, and '?' (missing data) if the species is not present in the source tree at all.

3.3.3 Source tree weighting scheme

Source trees entering the tree building stage of supertree construction were differentially weighted to encourage balance between different data types used in source tree construction, and to prevent less reliable primary data types unduly influencing the supertree topology. The source trees were split into the following groups according to the data that were used to generate them: pure morphology, pure mitochondrial DNA, pure nuclear DNA, mitochondrial DNA + nuclear DNA, morphology + DNA, karyotypes and chromosomes, other. Each of these categories was weighted equally.

3.3.4 Tree building

Searches were performed in PAUP* v4.0b10 (Swofford 2010) on the MRP matrix (of all source trees) using four independent parsimony ratchets created by a Perl script written by OBE; perlRat.pl v2.0b (Bininda-Emonds 2010). The parsimony ratchet is a method of branch swapping during tree searching that maximises the number of tree search starting points so that the search does not become trapped on a small number of potentially suboptimal tree 'islands' in tree space (Nixon 1999). This means that large taxon sets can be analysed in a much shorter time, with the same outcome in terms of tree length. Each ratchet performed 50 independent batches of 200 reweighting iterations, which generated 10050 trees. These trees were used as input trees for four heuristic searches using the Tree Bisection and Reconnection (TBR) branch swapping technique to speed up the analysis, each producing a maximum of 20,000 equally most parsimonious solutions. Of the 80,000 output trees, 49,914 were equally the most parsimonious, and the final supertree was a 95% majority rule tree of these trees. 95% majority rule was preferred as a consensus method over strict consensus because tree searching resulted in a large number of equally most parsimonious trees and strict consensus therefore results in a poorly resolved tree, whereas 95% majority rule provides a highly resolved tree; more appropriate for comparative analysis (Purvis & Garland 1993).

3.3.5 Assessing support

The degree of support for each node of the supertree was assessed using the relative Quantitative Support (rQS) index (Bininda-Emonds 2003) which was expressly designed for supertree analyses as it accounts for the non-independence of the characters in the MRP matrix, using the Perl Script QualiTree.pl v1.2.1. It compares each source tree with the supertree, pruned to the same taxa, and calculates the combined degree of support that the source trees give to the supertree at each node, normalised to between -1 (conflict) and +1 (support). Nodal support values for each node are shown in Appendix D.

3.3.6 Supertree dating

The supertree was dated by Olaf Bininda-Emonds using the techniques outlined here (and in the supplementary material of Bininda-Emonds *et al*. (2007)). Modifications to the Bininda-Emonds (2007) technique are detailed below. Relevant data for the 1949 nodes in the supertree were derived from three sources: (1) sequence data; (2) fossil data; and (3) relative and interpolated dates.

Sequence data

The sequence data used to obtain the relative molecular dates were based on an updated version of the aligned data sets used to date the mammal supertree of Bininda-Emonds *et al*. (2007) with additional sequence data that have since been added to GenBank (Benson *et al.* 2010) which was mined using the Perl script GenBankStrip.pl v2.1 (Bininda-Emonds 2010). The following genes had sufficient species coverage among Chiroptera (≥20 species) to be included: the mitochondrial genes MT-CYB (cytochrome b), MT-ND1, MT-RNR1 (12S rDNA), and MT-RNR2 (16S rDNA), and the nuclear genes C-MOS, RAG2, and VWF. The additional sequence data were aligned to the existing data set by eye. Taxon names were updated to match the taxonomy of Simmons (2005) using the Perl script seqCleaner.pl v1.2 (Bininda-Emonds 2010), which also ensured that all sequences in a data set were pairwise overlapping by at least 100 base pairs. *Homo sapiens* and *Canis lupus* were used as outgroups because both species were available for all data sets. Thereafter, each data set was fitted to the topology of the supertree under the most appropriate model of evolution, determined using PHYML v3.0 (Guindon & Gascuel 2003) using the Perl script autoMT.pl v2.0 (Bininda-Emonds 2010) to direct the process. This procedure simultaneously yielded the branch length data needed to determine the relative branch lengths. In a subsequent step, the Perl script batchRAXML.pl v1.2 (Bininda-Emonds 2010) was used to direct the PTHREADS variant of RAxML v7.2.6 (Stamatakis 2006) to determine 1000 bootstrap trees for each gene. This information was used to weight the relative dates according to how strongly each data set supported the supertree topology (see below).

Fossil data

Fossil dates were taken from Eiting & Gunnell's (2009) summary of all known fossil bats, with greater dating precision provided by the author (T. Eiting, pers. comm., 2010) (see Appendix E for taxa and dates used). The midrange value was taken for all dates given as ranges. The oldest known bat, *Onychonycteris finneyi*, was used to date the root node for Chiroptera using the date given in (Simmons *et al.* 2008). Fossil taxa were assigned to nodes on the supertree following Renner (2005), with the oldest fossil for a given group being used to estimate the divergence date of the parent node for that group. Thus the oldest known fossil for Vespertilionidae was used to calibrate the divergence date for the node immediately ancestral to all vespertilionid species in the tree. If a node had several date estimates, the earliest date was used, since most fossil date estimates are underestimates of the real divergence date. If a daughter node was found to have an older date assigned to it than its parent node, the date on the parent node was discarded. All fossil dates were used as minimal age constraints with no upper limit.

Relative and interpolated dates

The combination of molecular branch lengths and fossil data was then used to obtain an initial set of divergence date estimates for the bat supertree using the Perl script relDate.pl v3.0. Briefly, the relDate procedure converts the molecular branch lengths from each gene tree into relative branch lengths, where the age of a given node is expressed as a percentage of the age of an ancestral node based on the relative heights of the two nodes. Absolute ages are then obtained using the fossil data to calibrate the relative branch lengths. For a given node, the initial divergence date estimate was taken to be the median of all relative branch lengths and any fossil calibration points for that node. In cases where the median was younger than the calibration point, the date was taken to be the calibration point, thereby enforcing the latter as minimum age constraints. The standard errors (SEs) of these estimates were used to derive the upper and lower 95% confidence intervals (CIs) on the dates (as ±2 * SE). One change to the procedure provided in Bininda-Emonds *et al*. (2007) was that the individual relative branch lengths were weighted by the bootstrap frequencies for the focal node to account for differential support among and within the gene trees for the supertree topology. Agreement between the data set and the supertree topology would

therefore be reflected by high bootstrap values and therefore proportionately more weight in the analysis for the corresponding relative branch length. In this case, the initial estimate for a given node (and the 95% CIs) was calculated as the weighted average of all estimates contributing to it, with any fossil calibration data being given a neutral weight (equal to the average of the bootstrap frequencies for all the relative branch lengths for that node).

Thereafter, the initial date estimates were corrected for any negative branch lengths that might have been generated as well to interpolate divergence times for nodes missing such estimates (divergence time estimates are only possible for clades where all subtending lineages have at least one species with sequence data). For the latter clades, the interpolated date is derived from the number of species it possesses relative to ancestral and/or daughter clades using a birth-death model (following Purvis *et al*. (1995)). Interpolated dates were derived from immediate daughter nodes and/or from ancestral nodes up to five levels more inclusive than the focal node. In all cases, dates for reference nodes could not themselves be interpolations but based directly on either molecular and/or fossil data.

3.4 Results and Discussion

3.4.1 Taxonomic coverage, resolution, support and dates

The number of useable unique sources (each of which may contain more than one tree (as displayed in Figure 3.1)) for supertree construction increased considerably between the sampling end-point for the 2002 supertree (Jones *et al.* 2002) and the sampling end-point for this supertree, rising from 105 useable sources (only 61 of which were re-used) in 2000 to 146 useable sources in April 2009. Coverage per species is still poor (0.13 sources per species in 2009) when compared to the 0.6 sources per species found for primates and 0.7 sources per species for carnivores (see Jones *et al*. (2002)), especially when taking into account sampling end-points of the primate and carnivore supertrees (1993 and 1996 respectively). However, the number of published phylogenies containing bat species is growing exponentially (see Figure 3.1).

Systematic studies of bats have not been distributed evenly across the order, with six families receiving a greater proportion of the total number of studies than the family represents as a proportion of the total number of species of bats. These are Megadermatidae, Thyropteridae, Emballonuridae, Miniopteridae, Natalidae, and Rhinopomatidae. The remaining families received less attention than their speciosity warrants.

The phylogenetic supertree of the bats contains 1116 species and 834 nodes, which is 74.8% of a fully bifurcating solution. This cannot easily be compared to other supertrees, since it was produced using 95% majority rule, rather than strict consensus. However, a strict consensus tree produced from the same data was 34.7% resolved, indicating an increase in disagreement between sources trees from the 2002 supertree, which was 46.4% resolved. Four hundred and three species out of the total 1116 were not represented in a single source tree. The degree of resolution is fairly constant in different clades, with 11 families completely bifurcating and a further four families showing greater than 75% bifurcation. Four families stand out as being particularly badly resolved: Nycteridae (40%), Molossidae (52.5%), Vespertilionidae (65.1%) and Rhinolophidae (65.8%). Interestingly, Jones *et al*. (2002) found Molossidae to be particularly well resolved, with 65% bifurcation. The drop in the degree of bifurcation indicates a fall in congruence between source phylogenies, perhaps due to conflict between morphological and molecular topologies.

The reduced Quantitative Support (rQS) index for the clades in the supertree are presented in Appendix B. 79.5% of the nodes have positive rQS values, 11.9% are equivocal and 8.6% have negative rQS values, showing a broad degree of support for the supertree topology.

Tree dating (see Figure 3.3) indicates that bats originated 54.1 million years ago (mya), and that the suborders, Pteropodiformes and Vespertilioniformes, diverged 54.0 mya. These estimates are considerably younger than any previous estimates (Delsuc, Vizcaino, & Douzery 2004; Eick et al. 2005; Jones et al. 2005; Springer, Murphy, & Eizirik 2003; Teeling et al. 2003, 2005), including both versions of the 2005 dated bat supertree (Jones *et*

al. 2005) and its inclusion in the dated mammal supertree (Bininda-Emonds *et al.* 2007) (see Table 3.1). The oldest calibration point for the new supertree is 52.5 Mya, as indicated by the fossil bat *Onychonycteris finneyi* (Simmons & Geisler 1998). Other trees have used calibration points outside the bats, resulting in older estimates for the origin of bats (see Table 3.1).

The timing of the initial splitting of each of the superfamilies and of Pteropodidae shown by the new supertree correspond well with previous estimates, except in the case of Noctilionoidea (Phyllostomidae, Mormoopidae, Furipteridae, Thyropteridae, Noctilionidae, and Mystacinidae), where the estimate on the new supertree is on average 15 million years younger than previous estimates. This is a result of the younger root node forcing downstream nodes to appear younger.

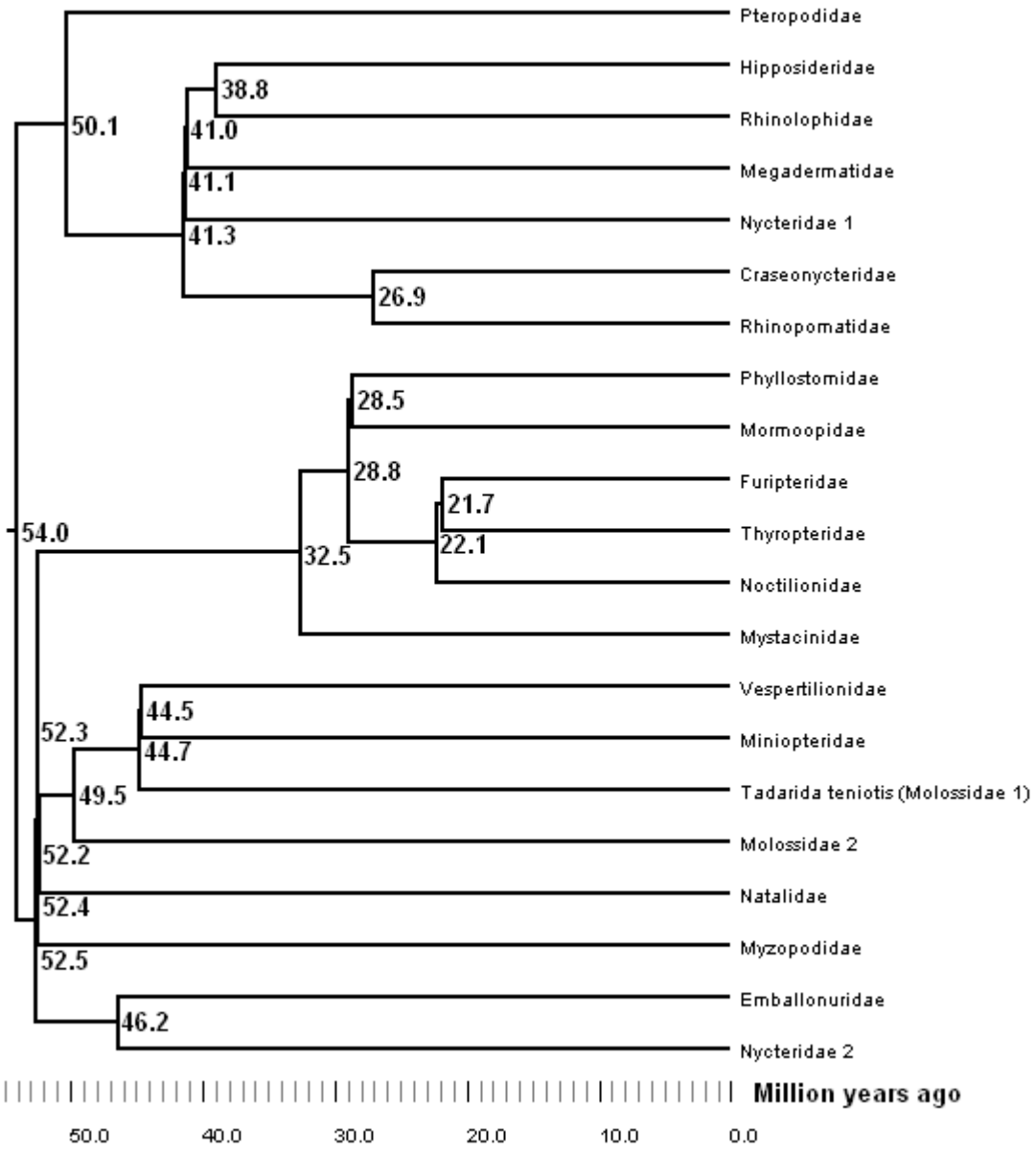


Figure 3.3: New dated bat higher-level supertree. Branches are proportional to time (millions of years). The number next to each node represents the divergence time (million years ago). Node numbers are shown in Figure 3.4.

Node	Date at node for each source tree (mya)								
	New dates	**Bininda-Emonds 2007**	**Jones 2005 - Original topology**	**Jones 2005 - Teeling topology**	**Eick 2005**	**Teeling 2005**	**Delsuc 2004**	**Springer 2003**	**Teeling 2003**
Origination of Chiroptera	54.1	89	62	58	65	-	81	84	81
Split between suborders	54.0	-	-	56	62	64	63	65	67
Split of Pteropodidae	26.1	-	-	-	-	24	22	21	24
Split of Rhinolophoidea	41.3	-	-	43	54	52	52	-	56
Split of Noctilionoidea	32.5	-	-	52	44	52	-	-	47
Split of Vespertilionoidea	52.2	-	-	51	50	50	-	-	35
Split of Emballonuroidea	46.2	-	-	52	50	52	-	-	43

Table 3.1: Comparison of date estimates at major nodes between trees in the recent literature, to the nearest million years for dates from the literature.

3.4.2 Higher-level relationships

The family-level relationships in the new supertree are shown in Figure 3.4. The 95% majority rule tree places Pteropodidae as a member of the suborder Pteropodiformes, rather than placing it as a basal group and leaving the 'microbats' as a monophyletic group. This is due to an increase in the number of sources which found it to cluster with the Rhinolophoidea, producing a diphyletic Microchiroptera (e.g. Eick *et al*. 2005; Miller-Butterworth *et al*. 2007; Teeling *et al*. 2003; Teeling *et al*. 2005).

The composition of each sub-clade does not reflect the two suborders (Pteropodiformes and Vespertilioniformes), due to the splitting of the Nycteridae, which, in the new supertree, fall partly in the Vespertilioniformes (five species) and partly in the Pteropodiformes (11 species). All other family-level topologies that include Nycteridae place it next to Emballonuridae as part of the Vespertilioniformes (see Figure 3.5). It appears that one species, *Nycteris hispida*, which in most source trees is representing its family (as it is the type species), is found in the Pteropodiformes in five sources trees, but is not found in the Vespertilioniformes in any source trees. Because it is the type species of the family, all members of Nycteridae which are not found in a source tree (10 species) are linked to *N. hispida* and are therefore also placed in the Pteropodiformes. Four of the five source trees that place Nycteridae in the Pteropodiformes are morphological, and one is based on the gene cytochrome *b*. Only one (Lim *et al.* 2008) other out of 16 molecular source tree places any nycterid species in the Pteropodiformes, but four morphological source trees do, suggesting the morphology of Nycteridae is misleading in systematics.

Other than the presence of Nycteridae, the topology of the Pteropodiformes (Pteropodidae and superfamily Rhinolophoidea (composed of Hipposideridae, Rhinolophidae, Megadermatidae, Craseonycteridae and Rhinopomatidae)) is broadly similar to that seem in other family-level trees, except Megadermatidae tends to be more closely related to Rhinopomatidae and Craseonycteridae in the family-level source trees, whereas in the new supertree it is more closely related to Hipposideridae and Rhinolophidae (see Figure 3.5). This topology is the result of the source trees presented in Giannini & Simmons (2005),

Giannini & Simmons (2007), Gunnell & Simmons (2005), Hulva (2002), Simmons & Geisler (1998), Springer, Hollar, & Kirsch (1995), and Springer, Teeling, & Stanhope (2001). These source trees are a mixture of morphological, molecular, and mixed analyses, suggesting that the true topology remains uncertain.

The Vespertilioniformes suborder is, according to Teeling *et al*. (2005) composed of three superfamilies: Noctilionoidea (Phyllostomidae, Noctilionidae, Mormoopidae, Furipteridae, Thyropteridae, Mystacinidae, and Myzopodidae), Vespertilionoidea (Vespertilionidae, Miniopteridae, Molossidae and Natalidae), and Emballonuroidea (Emballonuridae and Nycteridae). These groupings have yet to be agreed upon, particularly with respect to the placement of Myzopodidae, and hence the superfamily definitions await further study and are not in use in the third edition of Mammal Species of the World (Simmons 2005). The new supertree corroborates the grouping of all member families in Noctilionoidea *sensu* Teeling *et al*. (2005), except for Myzopodidae, which has been influenced by several other studies (including Eick *et al*. 2005; Hoofer *et al*. 2003), and has joined the Vespertilionoidea superfamily (see Figure 3.5).

The composition of Vespertilionoidea reflects the sources trees well (see Figure 3.5), with just one anomalous point: one species of Molossidae (*Tadarida teniotis*) has fallen out of the family, and lies polyphyletically between Miniopteridae and Molossidae (see Figure 3.4). This is due to a single source tree, in which *T. teniotis* is found to more closely related to three species of Vespertilionidae than to another species of Molossidae (Giannini *et al.* 2008). This is the only occurrence of *T. teniotis* in all the source trees, and this particular tree was constructed from characters derived from premaxillae morphology alone.

The superfamily Emballonuroidea is composed of families Emballonuridae and Nycteridae in all family-level trees containing both families (see Figure 3.5), and the new supertree reflects this. Apart from the splitting of Nycteridae (explained above), the composition and position of this superfamily is in line with current understanding (Teeling 2011, pers. comm.)

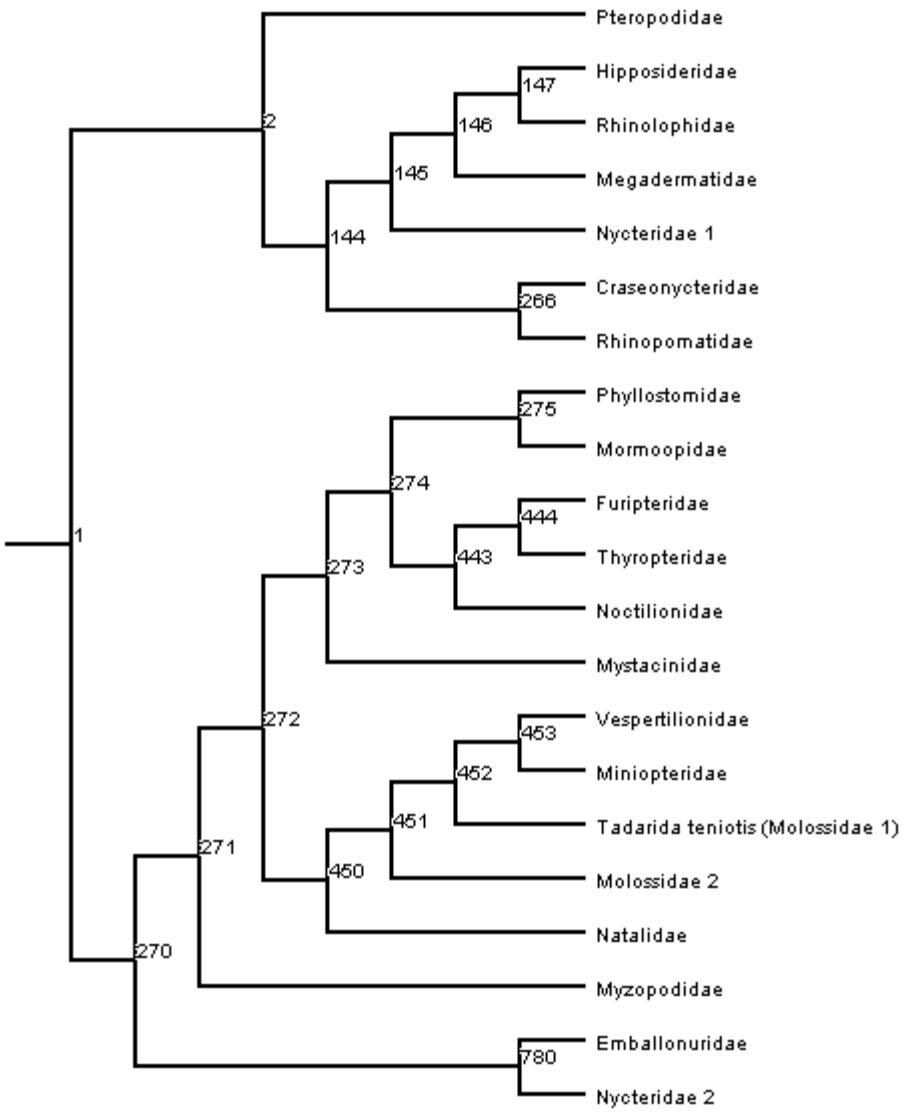


Figure 3.4: The new supertree for family-level relationships.

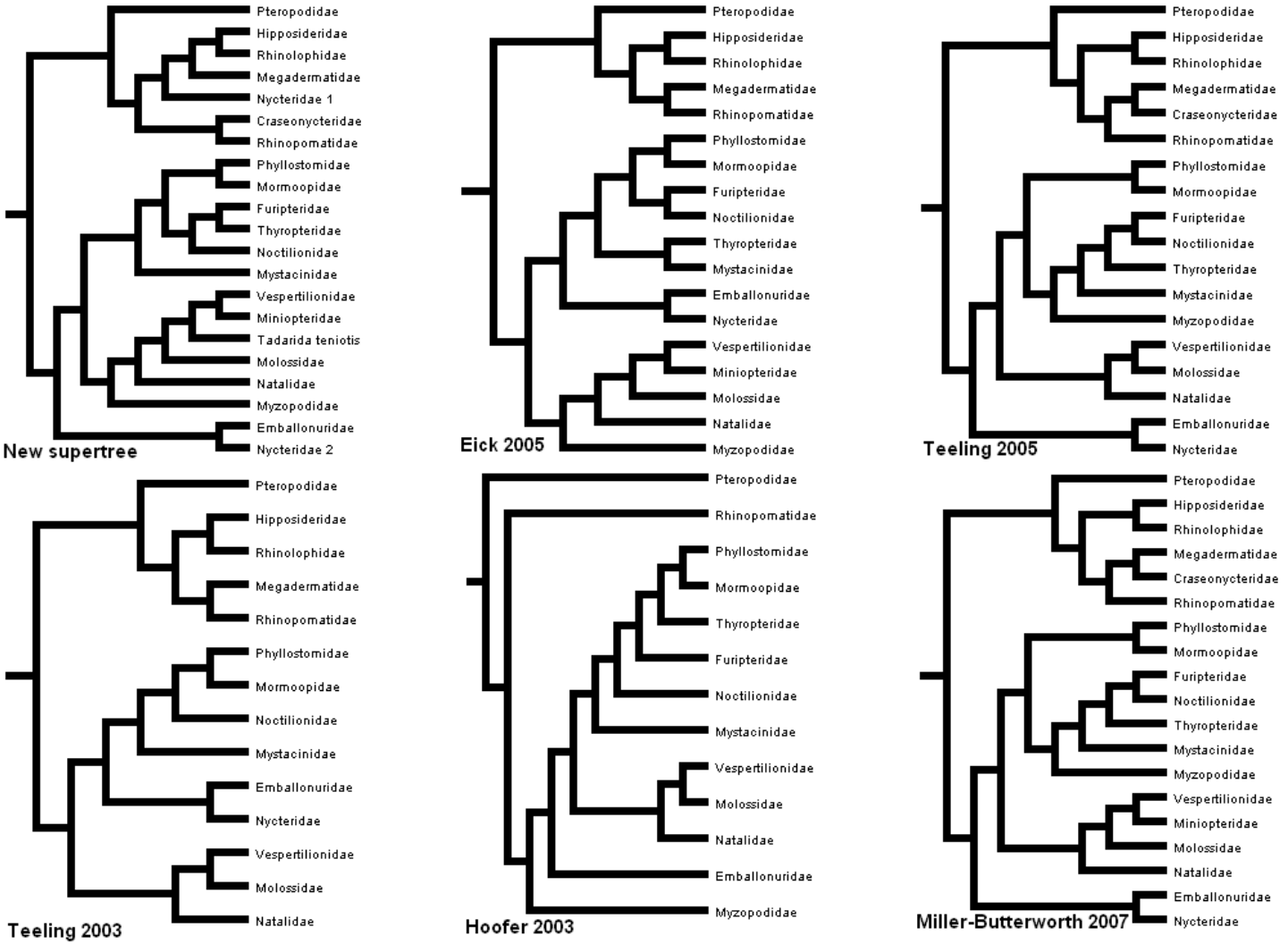


Figure 3.5: A comparison of the new supertree family-level topology with published family-level topologies.

3.4.3 Pteropodidae

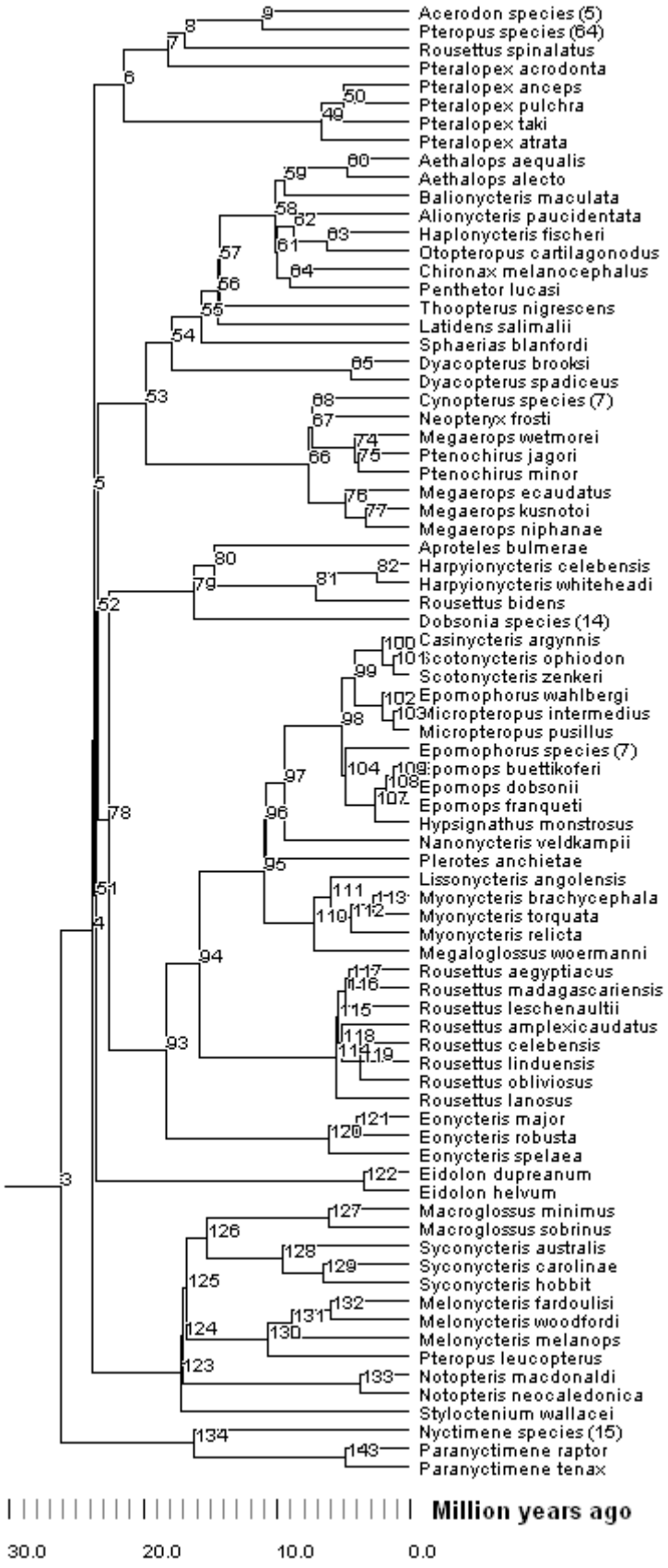
The Pteropodidae supertree is shown in Figure 3.6, with collapsed genera *Pteropus*, *Nyctimene*, *Dobsonia*, *Epomorphorous*, *Cynopterus*, and *Acerodon* shown in Figure 3.7 to Figure 3.12. Several subfamilial schemes have been defined in the past, but currently none are in place in the third edition of Mammal Species of the World (Simmons 2005). The new supertree does not support the subfamilies of Koopman & Jones (1970), Macroglossinae and Pteropodinae, nor the replacement subclades of Koopman (1994). It does, however, support Corbet & Hill (1992) two small subfamilies (proposed in addition to Koopman & Jones' (1970) subfamilies): Harpyionycterinae (*Harpionycteris* only) and Nyctimeninae (*Nyctimene* and *Paranyctimene*).

Amongst genera, most are monophyletic, including all that contain just two or three species, but for several of the larger genera, monophyly is not supported by the supertree. In particular, 64 of the 65 *Pteropus* species are placed together, but one species (*Pteropus leucopterus*) falls with *Melonycteris* species instead, due to the source trees of Esselstyn *et al*. (2008). Additionally, one species of *Megaerops* (*M. wetmorei*) does not cluster with the other three species in the genus due to Almeida *et al*. (2009), which showed *M. wetmorei* with *Ptenochirus jagori*. *Pteralopex acrodonta* is found with *Rousettus spinalatus*, *Pteropus spp.*, and *Acerodon* spp. because of the influence of Colgan & da Costa 2002; Colgan & Flannery 1995; O'Brien *et al*. 2009.

Of particular interest in the context of echolocation is the polyphyly of the genus *Rousettus*, of which at least three species (*R. amplexicaudatus*, *R. aegyptiacus*, and *R. spinalatus*) use tongue-clicking echolocation to navigate in caves (Nowak 1999), and it is generally assumed that all *Rousettus* species do. In the supertree this genus is fragmented, with a core group of eight species (including two of the known echolocators (*R. amplexicaudatus* and *R. aegyptiacus*), and two lone species: the remaining known echolocator *R. spinalatus* is found with genera *Acerodon* and *Pteropus*, and *R. bidens* is found with the genus *Harpionycteris*. The position of *R. spinalatus* appears to be due to its use as an outgroup to *Pteropus* species in Esselstyn *et al*. (2008), whereas *R. bidens* is considered by some

authors to be a separate genus (*Boneia*) (e.g., Andersen 1912; Koopman 1993), and is found polyphyletically to other *Rousettus* species in source trees in Giannini, Cunha Almeida, & Simmons (2009) and Romagnoli & Springer (2000). Since a direct analysis of the relationships between all *Rousettus* species and their position within Pteropodidae has not been carried out, it is possible the splitting of the genus in the supertree is an artefact, and has no bearing on the evolution of tongue-clicking echolocation in this family.

Figure 3.6 (Next page): Pteropodidae supertree, with six genera collapsed. The supertrees for these genera are shown in Figure 3.7 (*Pteropus*), Figure 3.8 (*Nyctimene*), Figure 3.9 (*Epomorphorus*), Figure 3.10 (*Cynopterus*), Figure 3.11 (*Dobsonia*), and Figure 3.12 (*Acerodon*).


Acerodon species (5)
Pteropus species (64)
Rousettus spinalatus
Pteralopex acrodonta
Pteralopex anceps
Pteralopex pulchra
Pteralopex taki
Pteralopex atrata
Aethalops aequalis
Aethalops alecto
Balionycteris maculata
Alionycteris paucidentata
Haplonycteris fischeri
Otopteropus cartilagonodus
Chironax melanocephalus
Penthetor lucasi
Thoopterus nigrescens
Latidens salimalii
Sphaerias blanfordi
Dyacopterus brooksi
Dyacopterus spadiceus
Cynopterus species (7)
Neopteryx frosti
Megaerops wetmorei
Ptenochirus jagori
Ptenochirus minor
Megaerops ecaudatus
Megaerops kusnotoi
Megaerops niphanae
Aproteles bulmerae
Harpyionycteris celebensis
Harpyionycteris whiteheadi
Rousettus bidens
Dobsonia species (14)
Casinycteris argynnis
Scotonycteris ophiodon
Scotonycteris zenkeri
Epomophorus wahlbergi
Micropteropus intermedius
Micropteropus pusillus
Epomophorus species (7)
Epomops buettikoferi
Epomops dobsonii
Epomops franqueti
Hypsignathus monstrosus
Nanonycteris veldkampii
Plerotes anchietae
Lissonycteris angolensis
Myonycteris brachycephala
Myonycteris torquata
Myonycteris relicta
Megaloglossus woermanni
Rousettus aegyptiacus
Rousettus madagascariensis
Rousettus leschenaultii
Rousettus amplexicaudatus
Rousettus celebensis
Rousettus linduensis
Rousettus obliviosus
Rousettus lanosus
Eonycteris major
Eonycteris robusta
Eonycteris spelaea
Eidolon dupreanum
Eidolon helvum
Macroglossus minimus
Macroglossus sobrinus
Syconycteris australis
Syconycteris carolinae
Syconycteris hobbit
Melonycteris fardoulisi
Melonycteris woodfordi
Melonycteris melanops
Pteropus leucopterus
Notopteris macdonaldi
Notopteris neocaledonica
Stylocteniumwallacei
Nyctimene species (15)
Paranyctimene raptor
Paranyctimene tenax
Million years ago
30.0
20.0
10.0
0.0

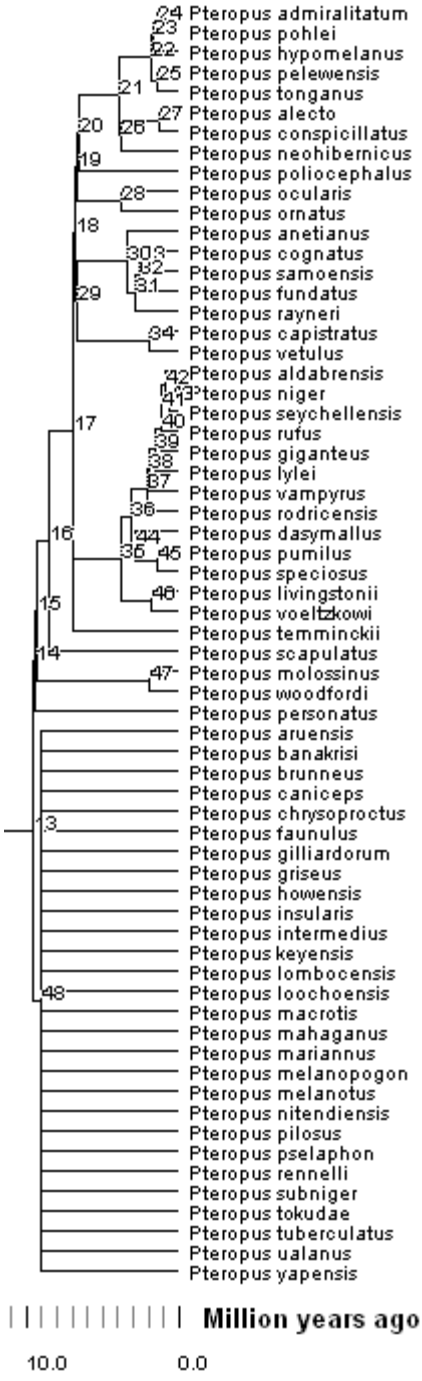


Figure 3.7: *Pteropus* supertree.

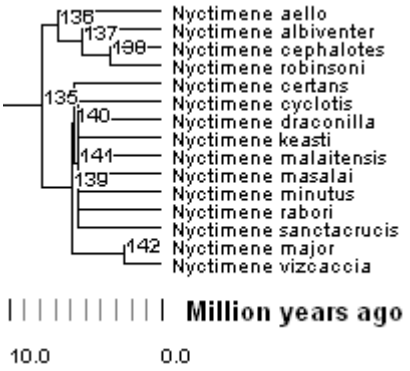


Figure 3.8: *Nyctimene* supertree.

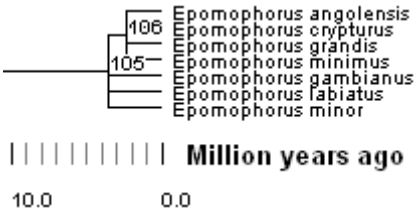


Figure 3.9: *Epomorphorus* supertree.

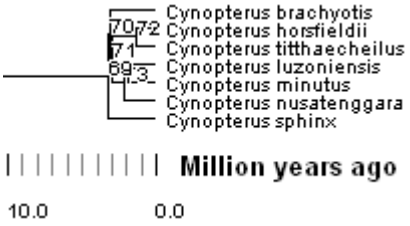


Figure 3.10: *Cynopterus* supertree.

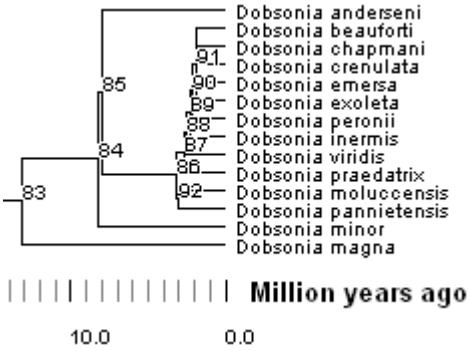


Figure 3.11: *Dobsonia* supertree.

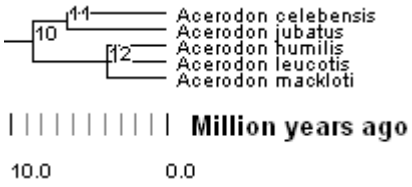


Figure 3.12: *Acerodon* supertree.

3.4.4 Hipposideridae

The Hipposideridae supertree is presented in Figure 3.13. It is fully resolved for species that were represented in the source trees, indicating a high level of agreement (Bogdanowicz & Owen 1998; Van Den Bussche & Hoofer 2004; Eick et al. 2005; Gu, He, & Ao 2008; Guillen-Servent & Francis 2006; Kawai et al. 2002; Li, Liang, et al. 2007; Vallo et al. 2008; Wang et al. 2003; Zhou et al. 2009). Twenty-one species are not found in any source tree. The monophyly of all genera except *Hipposideros* are preserved (as a result of the morphology-based source tree of (Bogdanowicz & Owen 1998)), and the tribes Coelopsini (*Coelops* and *Paracoelops*) and Hipposiderini (*Anthops*, *Asellia*, *Aselliscus*, *Cloeotis*, *Rhinonicteris*, *Triaenops*, and *Hipposideros*) are not supported.

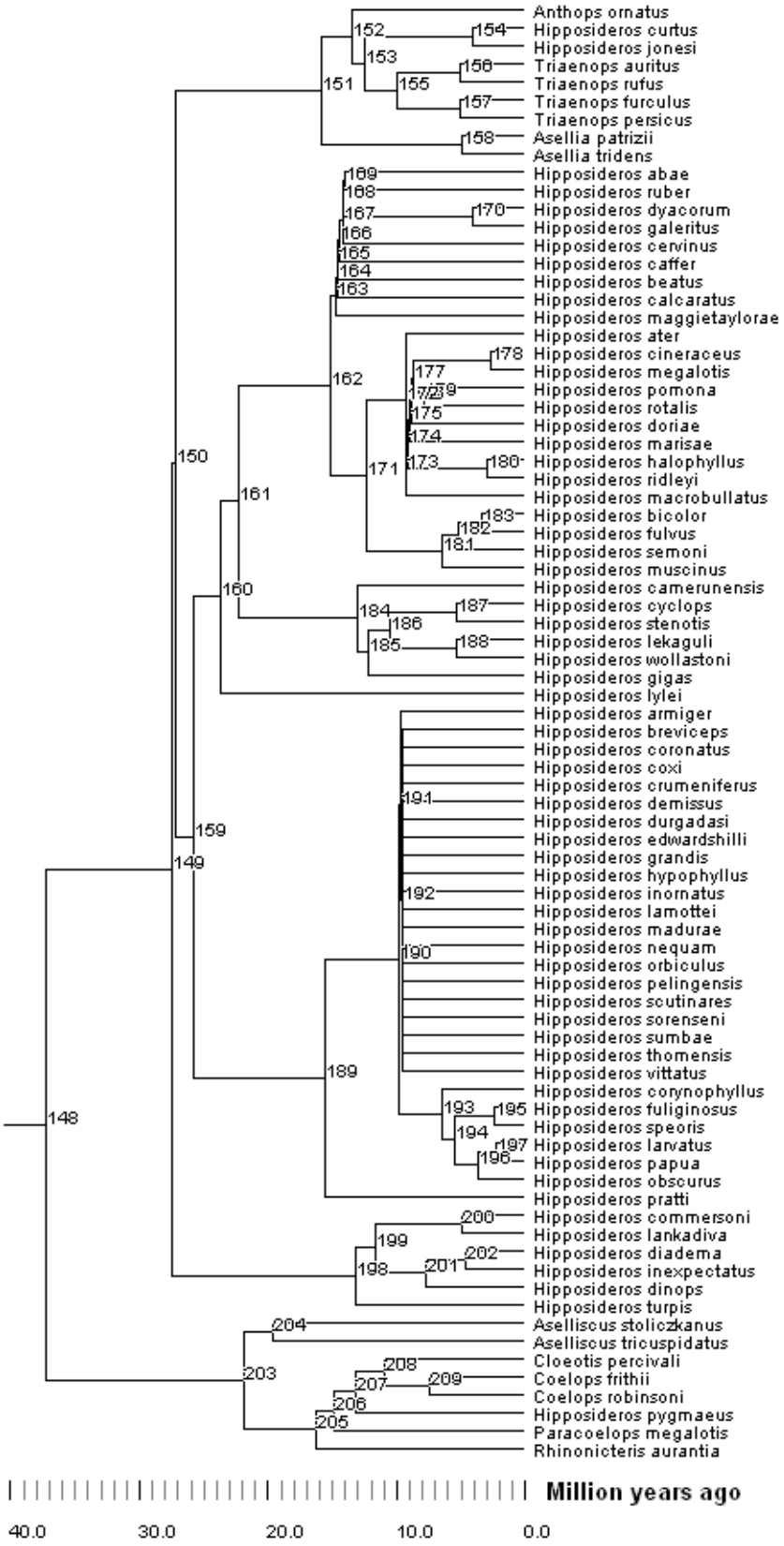


Figure 3.13: Hipposideridae supertree.

3.4.5 Rhinolophidae

The Rhinolophidae supertree is presented in Figure 3.14. Twenty-six species of *Rhinolophus* (the only genus in the family) were not found in any source tree, and are therefore seen as a polytomy. Amongst the remaining 51 species resolution is extremely high, indicating high congruence between sources (Csorba, Ujhelyi, & Thomas 2003; Eick et al. 2005; Gu et al. 2008; Li et al. 2006; Li, Liang, et al. 2007; Maree & Grant 1997; Springer, Teeling, & Madsen 2001; Sun et al. 2008; Wang et al. 2003). Rhinolophidae is split into 15 species groups (Csorba *et al*. (2003) – *adami*, *capensis*, *euryale*, *euryotis*, *ferrumequinum*, *fumigatus*, *hipposideros*, *landeri*, *maclaudi*, *megaphyllus*, *pearsoni*, *philippinensis*, *pusillus*, *rouxi*, *trifoliatus*), the largest of which contains 11 species and the smallest, just one species. Only four of these species groups are monophyletic on the supertree: *euryotis* (six species monophyletic but three species not found in source trees), *fumigatus* (all three species monophyletic), *euryale* (both species together), and *rouxii* (all three species monophyletic).

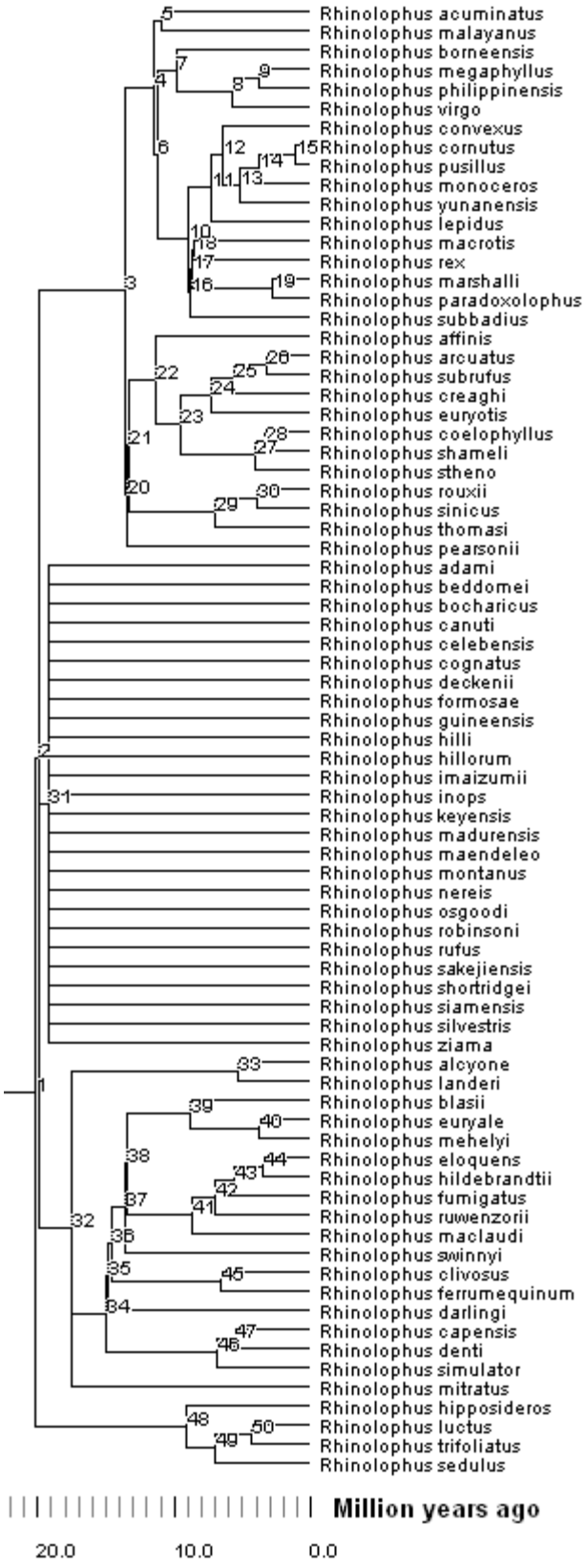


Figure 3.14: Rhinolophidae supertree.

3.4.6 Megadermatidae

The Megadermatidae supertree is presented in Figure 3.15. Three source trees have contributed to its topology, two containing three species (Eick *et al.* 2005; Giannini & Simmons 2007), and one containing all five (Griffiths, Truckenbrod, & Sponholtz 1992). Only the tree presented in Griffiths *et al*. (1992) influences the topology seen in the supertree, which contradicts both other sources, one of which finds *Cardioderma cor* and *Megaderma spasma* to be mostly closely related, with *Megaderma lyra* basal, and the other finds *Macroderma gigas* and *Megaderma spasma* to be most closely related, with *Cardioderma cor* basal.

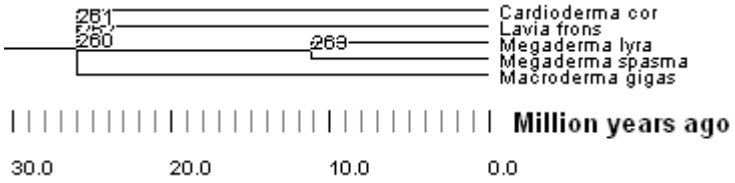


Figure 3.15: Megadermatidae supertree.

3.4.7 Rhinopomatidae

The Rhinopomatidae supertree is presented in Figure 3.16. Just one source tree contributes to its topology (Hulva, Horáček, & Benda 2007), presenting the relationship shown in Figure 3.16, but without *Rhinopoma macinnesi*, which, prior to the 2005 edition of Mammal Species of the World, was considered to be a subspecies of *R. hardwickii* (Simmons 2005).

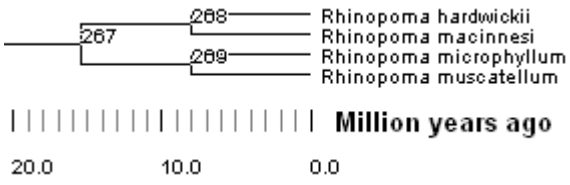


Figure 3.16: Rhinopomatidae supertree.

3.4.8 Phyllostomidae

The Phyllostomidae supertree is shown in Figure 3.17, with subfamilies shown fully in Figure 3.18, Figure 3.19, and Figure 3.20. The Phyllostomidae supertree is extremely well resolved, and the monophyly of four of the seven subfamilies is preserved (Stenodermatinae, Brachyphyllinae, Phyllonycterinae, and Desmodontinae). The remaining polyphyletic subfamilies are Phyllostominae and Glossophaginae, which are distributed amongst the other subfamilies and each other, and Carollinae, which has lost *Rhinophylla* to Stenodermatinae. This is due to the source trees of Baker *et al*. (2003), Baker *et al*. (2000), and Lim & Engstrom (1998), which over-ride the monophyly of Carollinae seen in the topology of Gimenez (1993) and Wetterer, Rockman, & Simmons (2000). Otherwise, all genera are monophyletic.

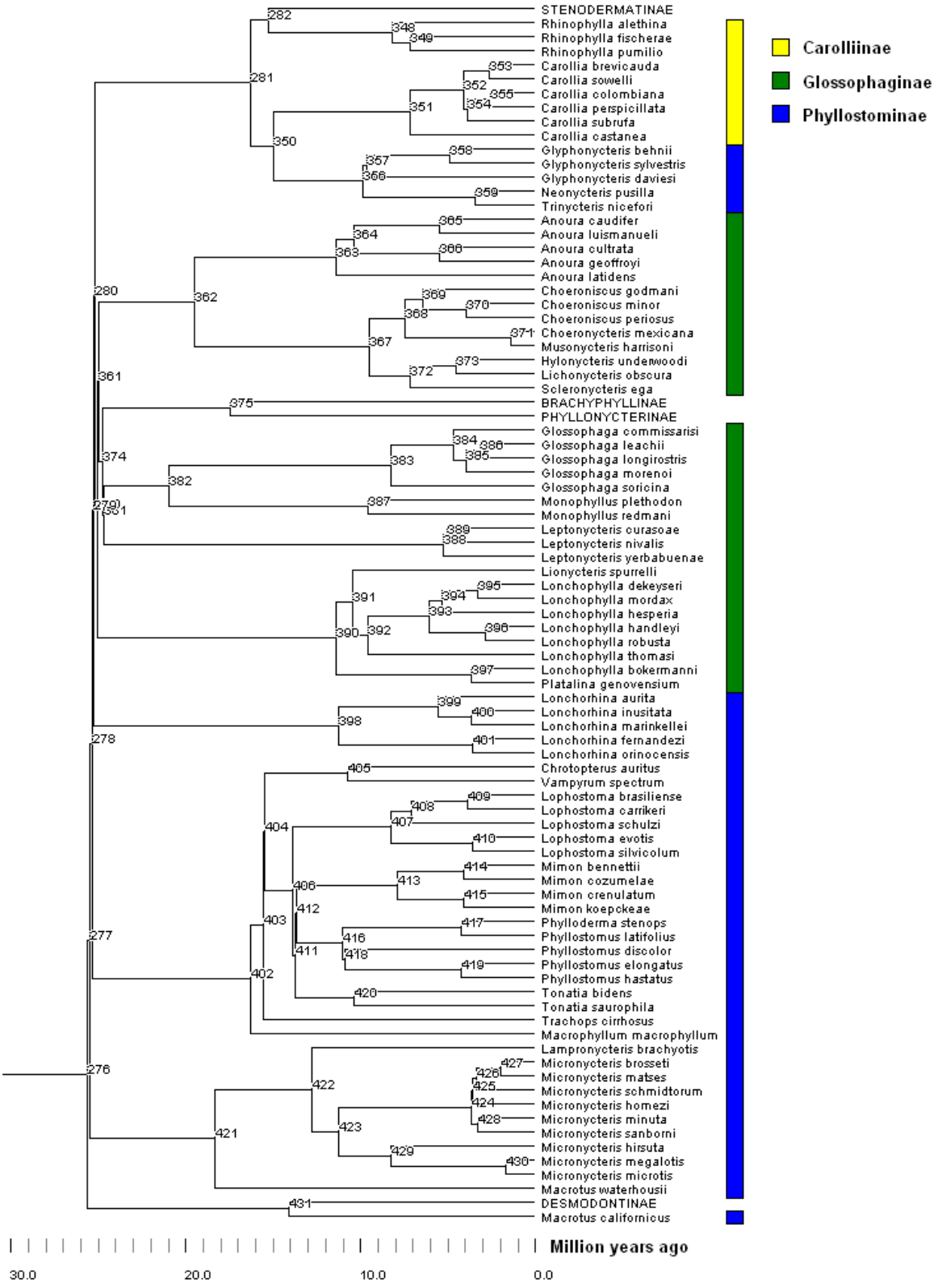


Figure 3.17: The supertree for Phyllostomidae with several subfamilies collapsed. Relationships within these clades are shown in Figure 3.18, Figure 3.19, and Figure 3.20.

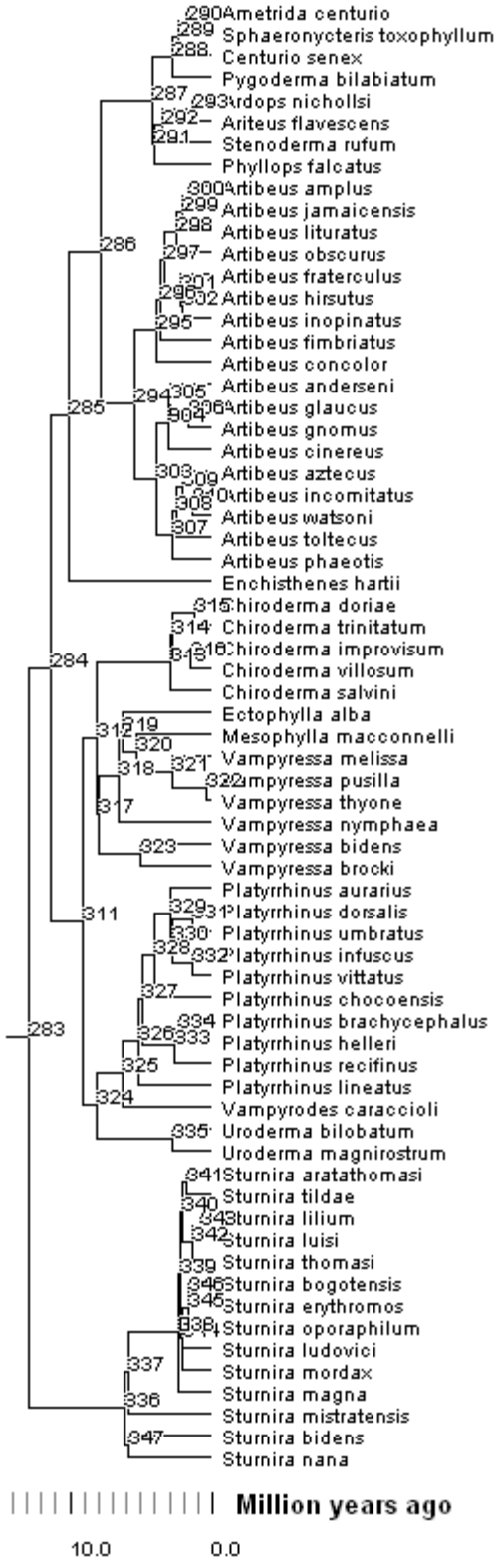


Figure 3.18: Stenodermatinae supertree.

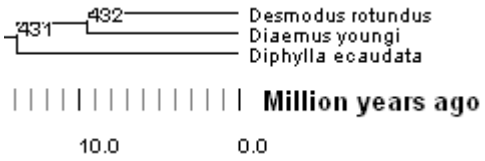


Figure 3.19: Desmodontinae supertree.

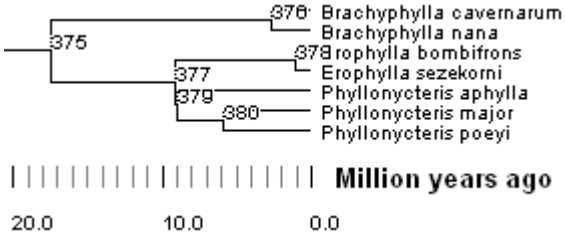


Figure 3.20: Brachyphillinae and Phyllonycterinae supertree.

3.4.9 Mormoopidae

The Mormoopidae supertree is presented in Figure 3.21. Fifteen source trees in six papers contribute to its fully resolved topology. All agree on the placement of the three *Mormoops* species basal to the seven *Pteronotus* species. No source tree (except the reference taxonomy) includes *Mormoops magna*. Amongst the *Pteronotus* species, the subgenus *Pteronotus* (*P. davyi* and *P. gymnonotus*) was upheld by all source trees and the supertree, as is the subgenus *Chilonycteris* (*P. macleayi* and *P. quadridens*) excluding *P. personatus* as intimated by Simmons (2005). The final subgenus, *Phyllodia*, is comprised of *P. pristinus* and *P. parnellii*, but *P. pristinus* does not feature in any of the source trees, hence this subgenus is not upheld in the supertree. The topology of the seven *Pteronotus* species is upheld by 12 of the 16 source trees in four of the six papers (Arnold *et al*. 1982; Davalos 2006; Lewis-Oritt, Porter, & Baker 2001; Van Den Bussche & Weyandt 2003 vs. Simmons & Conway 2001; Van Den Bussche, Hoofer, & Simmons 2002).

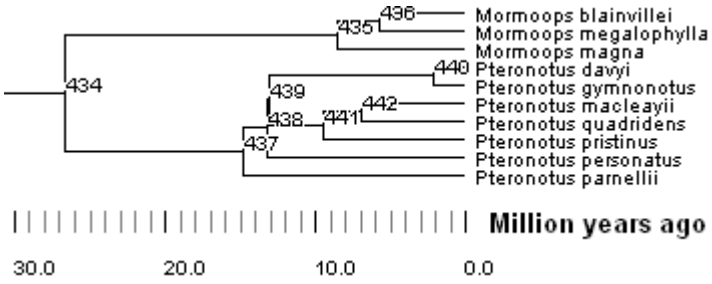


Figure 3.21: Mormoopidae supertree

3.4.10 Thyropteridae

The Thyropteridae supertree is presented in Figure 3.22. Two source trees contribute to the topology, and both are congruent (Gregorin et al. 2006; Solari et al. 2004).

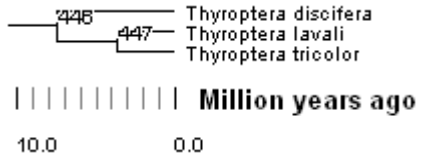


Figure 3.22: Thyropteridae supertree.

3.4.11 Vespertilionidae

The monophyly of the largest family of bats (388 species), Vespertilionidae, is supported by the supertree analysis (*sensu* Simmons 2005), and above genus level the topology is well resolved, reflecting the large number of sources tackling this family (Appleton, McKenzie, & Christidis 2004; Baird et al. 2008, 2009; Baker et al. 1988; Barratt et al. 1995, 1997; Bickham 1979; Bickham et al. 2004; Bogdanowicz, Kasper, & Owen 1998; Castella et al. 2000; Frost & Timm 1992; Goodman et al. 2007; Hoofer & Van Den Bussche 2001; Hoofer et al. 2003; Hulva, Benda, et al. 2007; Hulva et al. 2004; Jones et al. 2006; Juste et al. 2004; Kawai et al. 2003; Kearney et al. 2002; Kiefer et al. 2002) and (Miller-Butterworth et al. 2005; Morales & Bickham 1995; Pestano et al. 2003; Piaggio & Perkins 2005; Piaggio et al. 2002; Qumsiyeh & Bickham 1993; Ruedi & Mayer 2001; Salgueiro et al. 2007; Stadelmann, Herrera, et al. 2004; Stadelmann et al. 2007; Stadelmann, Jacobs, et al. 2004; Thabah et al. 2007; Tumlison & Douglas 1992; Volleth & Heller 1994; Weyeneth

et al. 2008) (see Figure 3.23), most of which were published since the previous bat supertree (Jones *et al.* 2002). Of the five subfamilies, the three smallest, Antrozoinae, Kerivoulinae, and Murininae, were found to be monophyletic, with Kerivoulinae and Murininae forming sister clades. Myotinae (composed of the largest genus *Myotis*, as well as *Cistugo* and *Lasionycteris*) and the largest subfamily, Vespertilioninae, were both polyphyletic.

The supertree of the subfamily Kerivoulinae, shown in Figure 3.24, maintains monophyly of each genus, *Kerivoula* and *Phoniscus*, since no source tree investigates both genera simultaneously. The subfamily is poorly resolved due to a lack of information regarding all but five of the 23 species. The supertree of subfamily Murininae, shown in Figure 3.25, maintains monophyly of each genus, *Murina* and *Harpiocephalus*, and appears to uphold Koopman's (1994) subgenera *Murina* and *Harpiola*, though due to a lack of information for 10 of the 17 species, this is not clearly defined because of the low degree of resolution in this clade.

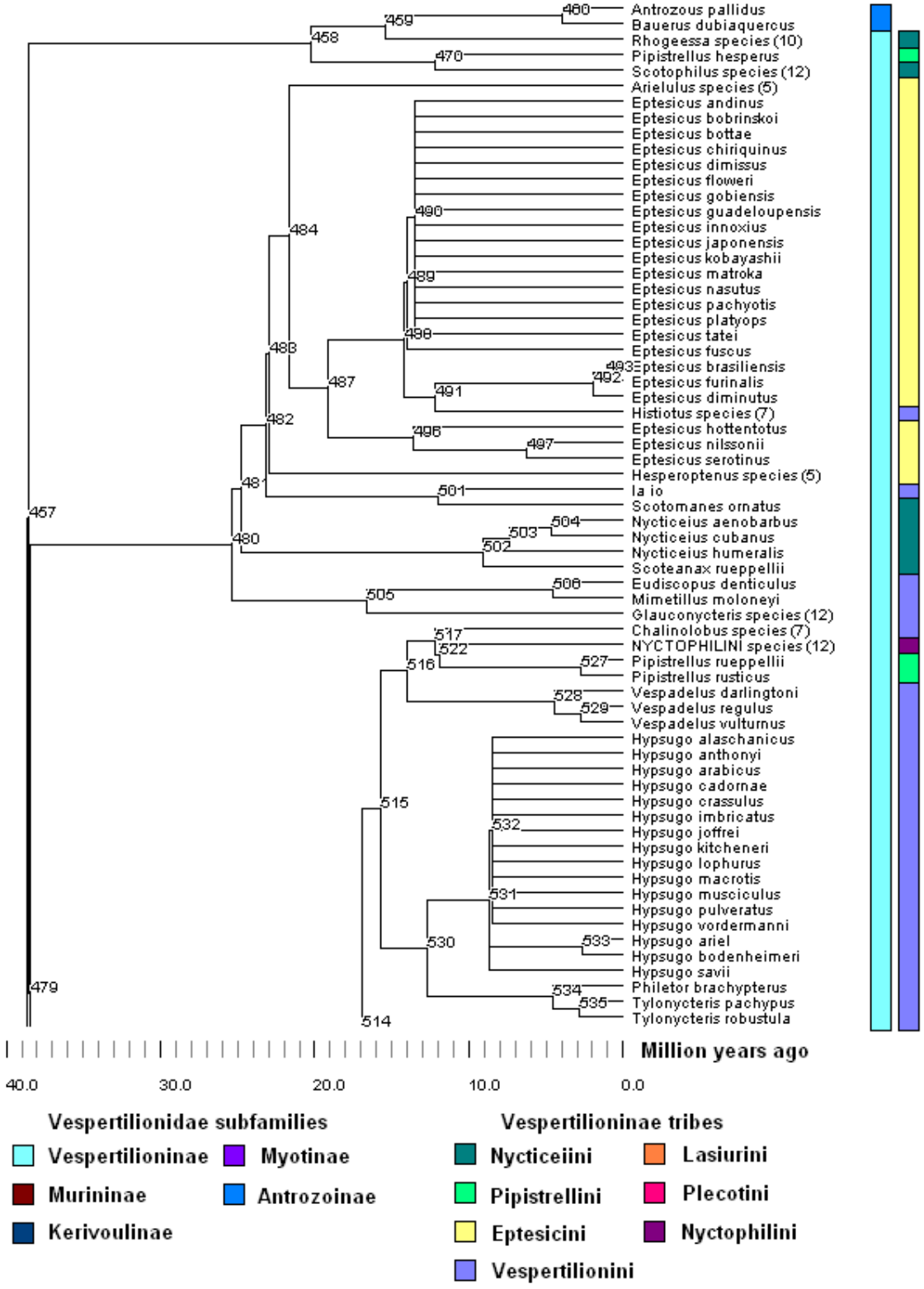
The subfamily Myotinae includes genera *Myotis*, *Cistugo*, and *Lasionycteris*. The genus *Myotis* is monophyletic (see Figure 3.26), but the genera *Cistugo* and *Lasionycteris* do not cluster with it. In fact the two species of *Cistugo* form the most basal taxa of the Vespertilionidae supertree (see Figure 3.23), and their distance from *Myotis* is supported by every source tree in which they appear (Bickham et al. 2004; Eick et al. 2005; Jacobs et al. 2004; Miller-Butterworth et al. 2005; Stadelmann, Jacobs, et al. 2004)

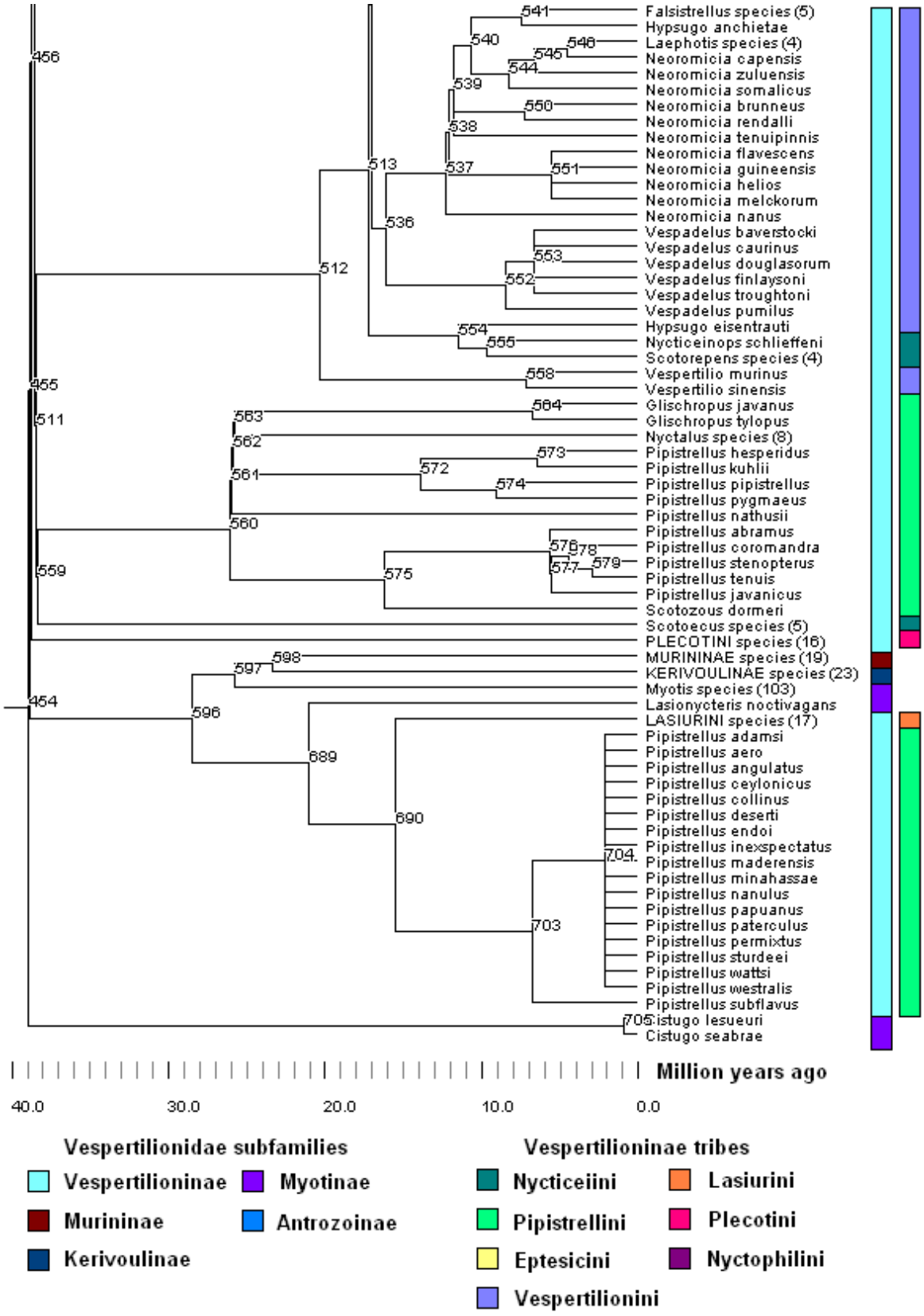
The subfamily Vespertilioninae contains 238 species in seven tribes: Eptesicini, Lasiurini, Nycticeiini, Nyctophilini, Pipistrellini, Plecotini, and Vespertilionini. The supertree finds the subfamily to be polyphyletic (see Figure 3.23), but finds support for the monophyly of the three least speciose tribes: Lasiurini, Nyctophilini and Plecotini, echoing the findings of the original bat supertree (Jones *et al.* 2002). Lasiurini is mono-generic (*Lasiurus*) and has universal support and agreement from the three contributing source trees (Baker et al. 1988; Hoofer & Van den Bussche 2003; Morales & Bickham 1995) (see Figure 3.27). Amongst the species which appear in a source tree, there is also support for the subgenera *Lasiurus*

and *Dasypterus* (*sensu* Koopman (1994)). The tribe Nyctophilini contains genera *Nyctophilus* and *Pharotis* and is amongst completely unresolved, except for two species (see Figure 3.36) which reflect the source tree in Hoofer & Van den Bussche (2003). The tribe Plecotini contains six genera and the supertree shows very high resolution (see Figure 3.39) and broad agreement between the 10 sources (Bogdanowicz et al. 1998; Van Den Bussche & Hoofer 2004; Frost & Timm 1992; Hoofer & Van den Bussche 2003; Hoofer & Van Den Bussche 2001; Juste et al. 2004; Kiefer et al. 2002; Pestano et al. 2003; Qumsiyeh & Bickham 1993; Tumlison & Douglas 1992).

The other tribes within Vespertilioninae were found to be polyphyletic (Eptesicini, Nycticeiini, Pipistrellini, and Vespertilionini) (see Figure 3.23), as were the genera *Eptesicus*, *Pipistrellus*, *Hypsugo*, *Neoromicia* and *Vespadelus*. As a result, neither of Hill & Harrison's (1987) two putative sister clades (one containing *Eudiscops*, *Pipistrellus*, *Nyctalus*, *Glischropus*, *Laephotis*, *Philetor*, *Hesperoptenus*, and *Chalinolobus*, and the other containing *Ia*, *Vespertilio*, *Histiotis*, *Tylonycteris*, *Mimetillus*, and *Eptesicus*) were supported. All other genera in these four tribes were monophyletic (see Figure 3.23 and Figure 3.27 to Figure 3.41) though most had poor resolution and were monophyletic due to the influence of the Simmons (2005) reference taxonomy.

Figure 3.23: (Next two pages) Vespertilionidae supertree, with several subfamilies, tribes and genera collapsed. These clades are shown in Figure 3.24 to Figure 3.41.




Falsistrellus species (5)
Hypsugo anchietae
Laephotis species (4)
Neoromicia capensis
Neoromicia zuluensis
Neoromicia somalicus
Neoromicia brunneus
Neoromicia rendalli
Neoromicia tenuipinnis
Neoromicia flavescens
Neoromicia guineensis
Neoromicia helios
Neoromicia melckorum
Neoromicia nanus
Vespadelus baverstocki
Vespadelus caurinus
Vespadelus douglasorum
Vespadelus finlaysoni
Vespadelus troughtoni
Vespadelus pumilus
Hypsugo eisentrauti
Nycticeinops schlieffeni
Scotorepens species (4)
Vespertilio murinus
Vespertilio sinensis
Glischropus javanus
Glischropus tylopus
Nyctalus species (8)
Pipistrellus hesperidus
Pipistrellus kuhlii
Pipistrellus pipistrellus
Pipistrellus pygmaeus
Pipistrellus nathusii
Pipistrellus abramus
Pipistrellus coromandra
Pipistrellus stenopterus
Pipistrellus tenuis
Pipistrellus javanicus
Scotozous dormeri
Scotoecus species (5)
PLECOTINI species (16)
MURININAE species (19)
KERIVOULINAE species (23)
Myotis species (103)
Lasionycteris noctivagans
LASIURINI species (17)
Pipistrellus adamsi
Pipistrellus aero
Pipistrellus angulatus
Pipistrellus ceylonicus
Pipistrellus collinus
Pipistrellus deserti
Pipistrellus endoi
Pipistrellus inexspectatus
Pipistrellus maderensis
Pipistrellus minahassae
Pipistrellus nanulus
Pipistrellus papuanus
Pipistrellus paterculus
Pipistrellus permixtus
Pipistrellus sturdeei
Pipistrellus wattsi
Pipistrellus westralis
Pipistrellus subflavus
Cistugo lesueuri
Cistugo seabrae
Million years ago
40.0
30.0
20.0
10.0
0.0
Vespertilionidae subfamilies
Vespertilioninae
Myotinae
Murininae
Antrozoinae
Kerivoulinae
Vespertilioninae tribes
Nycticeiini
Lasiurini
Pipistrellini
Plecotini
Eptesicini
Nyctophilini
Vespertilionini

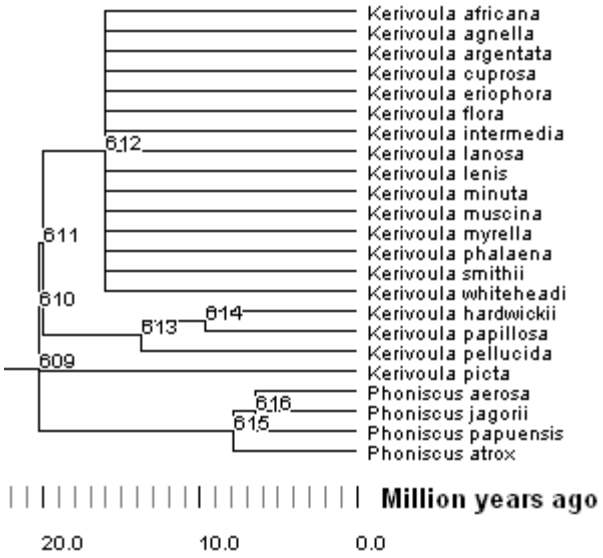


Figure 3.24: Kerivoulinae supertree.

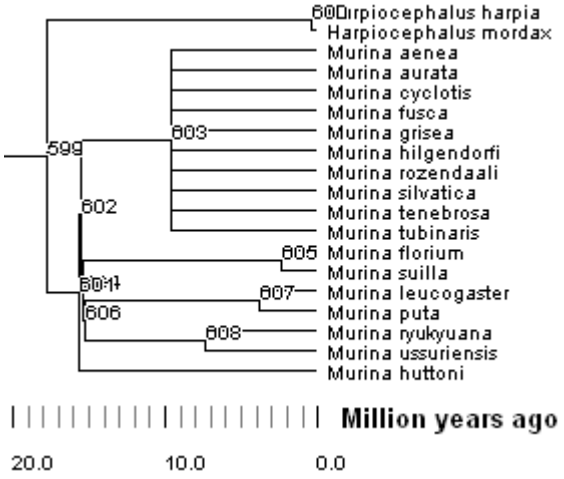
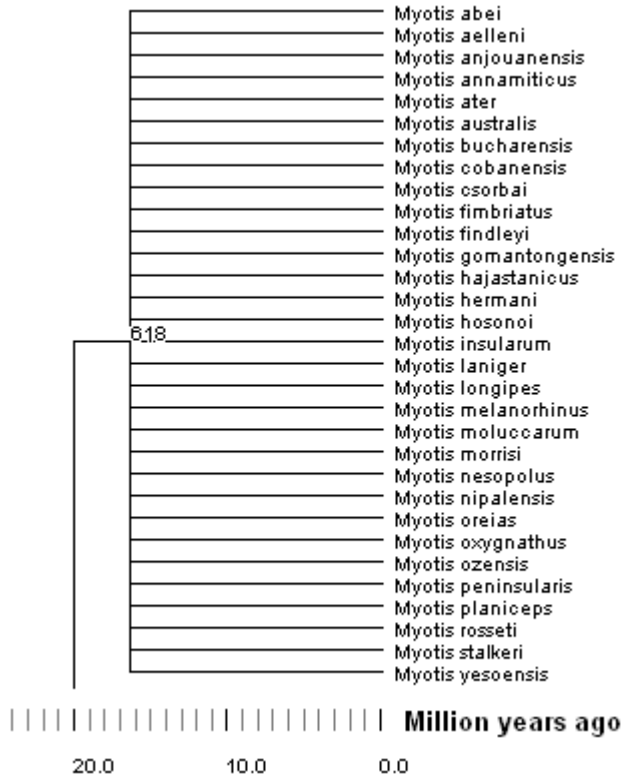
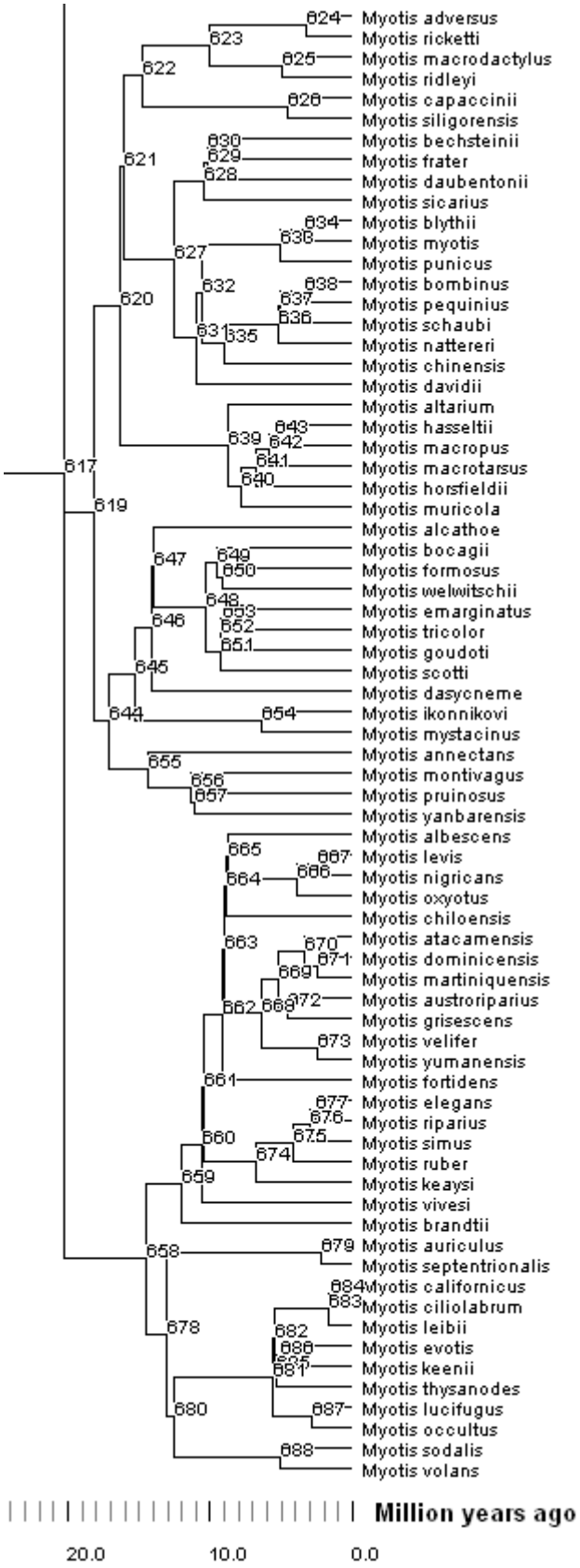


Figure 3.25: Murininae supertree.

Figure 3.26: (This and next page) *Myotis* supertree.




624
Myotis adversus
623
Myotis ricketti
625
Myotis macrodactylus
622
Myotis ridleyi
626
Myotis capaccinii
Myotis siligorensis
630
Myotis bechsteinii
621
629
Myotis frater
628
Myotis daubentonii
Myotis sicarius
634
Myotis blythii
636
Myotis myotis
627
Myotis punicus
632
638
Myotis bombinus
620
637
Myotis pequinius
636
Myotis schaubi
631
635
Myotis nattereri
Myotis chinensis
Myotis davidii
Myotis altarium
643
Myotis hasseltii
639
642
Myotis macropus
641
Myotis macrotarsus
617
640
Myotis horsfieldii
619
Myotis muricola
Myotis alcathoe
649
Myotis bocagii
647
650
Myotis formosus
Myotis welwitschii
648
653
Myotis emarginatus
646
652
Myotis tricolor
651
Myotis goudoti
645
Myotis scotti
Myotis dasycneme
644
654
Myotis ikonnikovi
Myotis mystacinus
Myotis annectans
655
Myotis montivagus
656
Myotis pruinosus
657
Myotis yanbarensis
Myotis albescens
665
667
Myotis levis
664
666
Myotis nigricans
Myotis oxyotus
Myotis chiloensis
663
670
Myotis atacamensis
671
Myotis dominicensis
669
Myotis martiniquensis
662
668
672
Myotis austroriparius
Myotis grisescens
673
Myotis velifer
Myotis yumanensis
661
Myotis fortidens
677
Myotis elegans
676
Myotis riparius
660
675
Myotis simus
674
Myotis ruber
659
Myotis keaysi
Myotis vivesi
Myotis brandtii
658
679
Myotis auriculus
Myotis septentrionalis
684
Myotis californicus
683
Myotis ciliolabrum
678
682
Myotis leibii
686
Myotis evotis
681
Myotis keenii
Myotis thysanodes
680
687
Myotis lucifugus
Myotis occultus
688
Myotis sodalis
Myotis volans
Million years ago
20.0
10.0
0.0

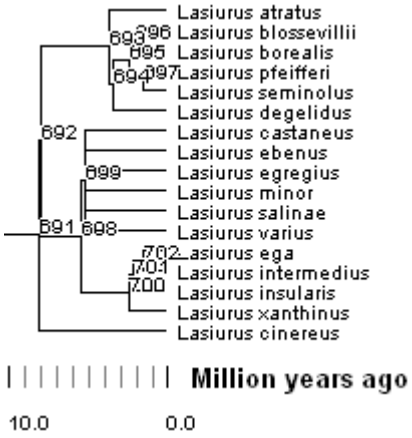


Figure 3.27: *Lasiurus* supertree.

Figure 3.28: *Arielulus* supertree.

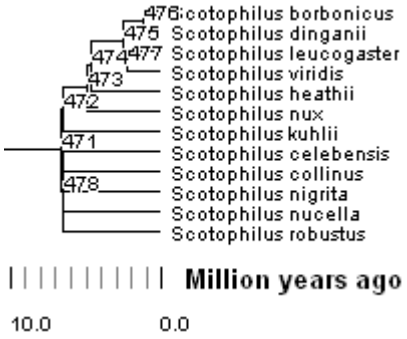


Figure 3.29: *Scotophilus* supertree.

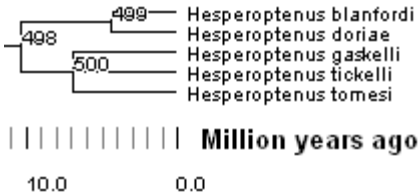


Figure 3.34: *Hesperoptenus* supertree.

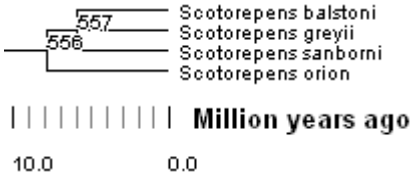


Figure 3.30: *Scotorepens* supertree.

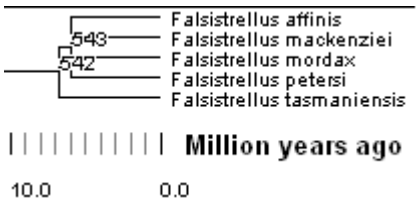


Figure 3.31: *Falsistrellus* supertree.

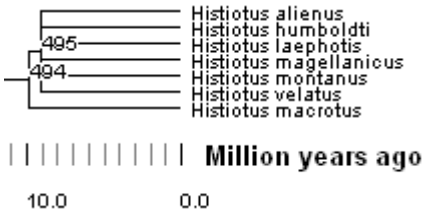


Figure 3.32: *Histiotus* supertree.

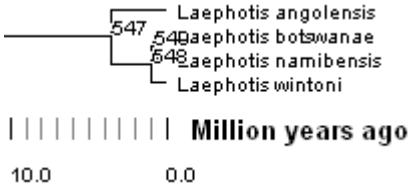


Figure 3.33: *Laephotis* supertree.

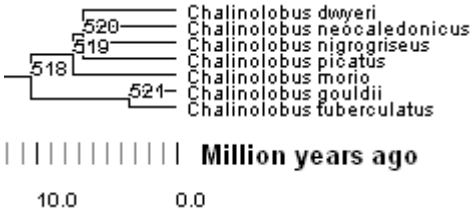


Figure 3.35: *Chalinolobus* supertree.

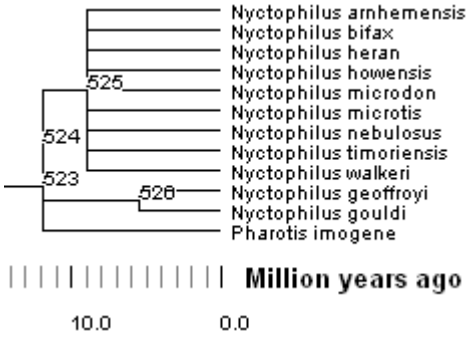


Figure 3.36: Nyctophilini supertree.

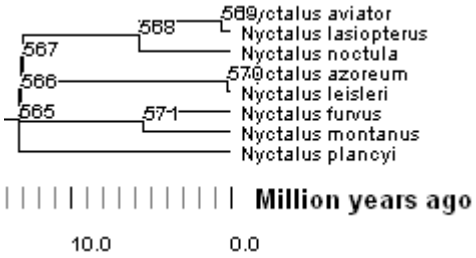


Figure 3.37: *Nyctalus* supertree.

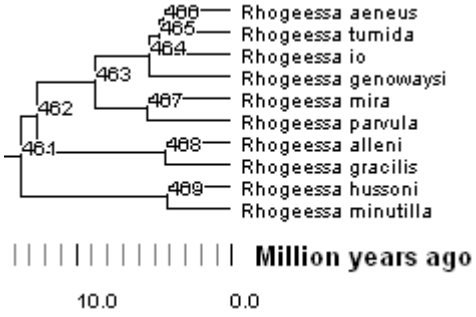


Figure 3.38: *Rhogeessa* supertree.

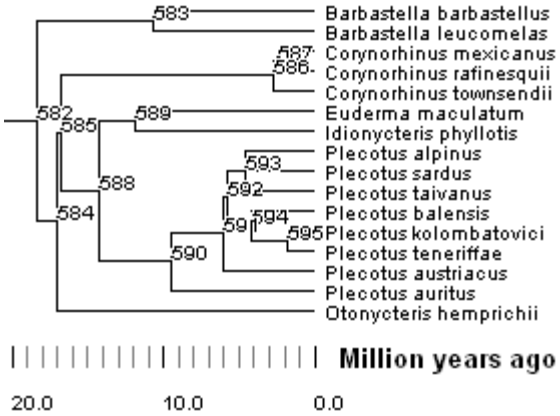


Figure 3.39: Plecotini supertree.

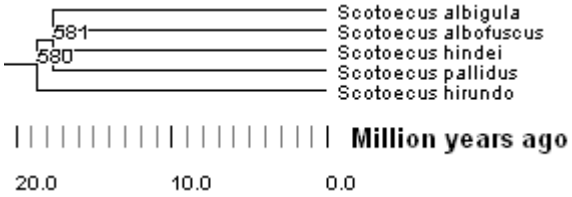


Figure 3.40: *Scotoecus* supertree.

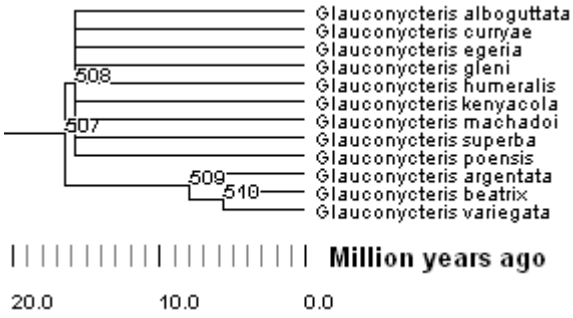


Figure 3.41: *Glauconycteris* supertree.

3.4.12 Miniopteridae

The Miniopteridae supertree is presented in Figure 3.42. It is well resolved (89%), reflecting general agreement among the source trees. *Miniopterus paululus*, *M. robustior* and *M. shortridgei* do not appear in any source trees (except the reference taxonomy), hence their basal position and unresolved topology.

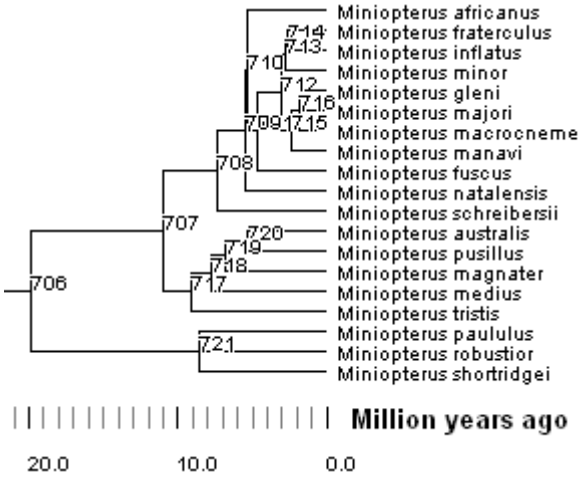


Figure 3.42: Miniopteridae supertree.

3.4.13 Molossidae

The Molossidae supertree is presented in Figure 3.43. The topology has fairly poor resolution (50%). The two subfamilies (Simmons 2005), Tomopeatinae (*Tomopeas* only) and Molossinae (all other Molossidae genera), are supported, with *Tomopeas ravus* falling basal to the Molossinae. Neither Freeman's (1981) two subclades nor Legendre's (1984) three subfamilies are supported by the supertree topology. The monophyly of all genera are supported except for *Tadarida* and *Mops*. *Tadarida teniotis* is left out of the Molossidae supertree and the reasons for this are explained in Section 1.1.1 above. *Mops trevori* does not cluster with the other *Mops* species, due to its placement with *Eumops*, *Nyctinomops* and *Molossus* in the source tree of Hoofer *et al.* 2003.

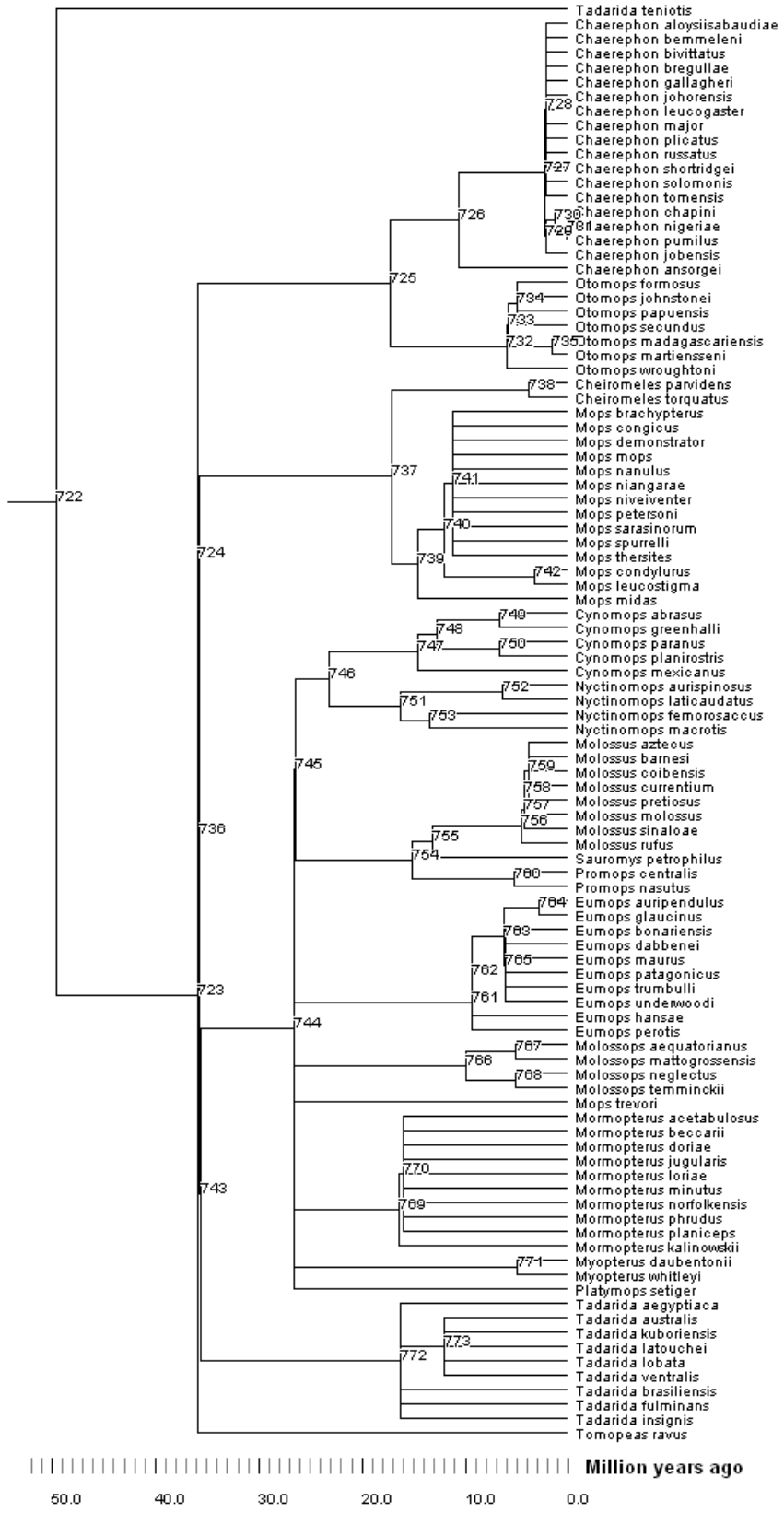


Figure 3.43: Molossidae supertree.

3.4.14 Natalidae

The Natalidae supertree is presented in Figure 3.44. The two source trees contributing to it contain seven species, excluding *Natalus primus* (Davalos 2005), and six species, excluding *N. primus* and *N. jamaicensis* (Morgan & Czaplewski 2003). They are congruent and their topologies are seen in the supertree, with the addition of *N. primus*.

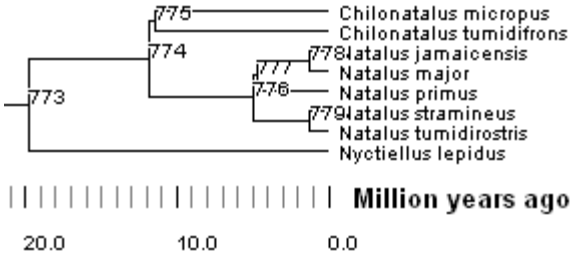


Figure 3.44: Natalidae supertree

3.4.15 Emballonuridae

The Emballonuridae supertree is presented in Figure 3.45. The tree is fully resolved since all the source trees and the new supertree agree on the division between the two subfamilies, Taphozoinae (*Taphozous* and *Saccolaimus*) and Emballonurinae (all remaining emballonurid genera) (Dunlop 1998; Griffiths, Koopman, & Starrett 1991; Griffiths & Smith 1991; Lim et al. 2008). Within Taphozoinae, the supertree supports the monophyly of the two genera. Within Emballonurinae, the supertree supports the monophyly of both the Old World tribe Emballonurini (*Emballonura*, *Mosia*, and *Coleura*) and the New World tribe Diclidurini (*Cyttarops*, *Diclidurus*, *Rhynchonycteris*, *Cormura*, *Saccopteryx*, *Balantiopteryx*, *Peropteryx* and *Centronycteris*). The monophyly of all genera is supported in the supertree.

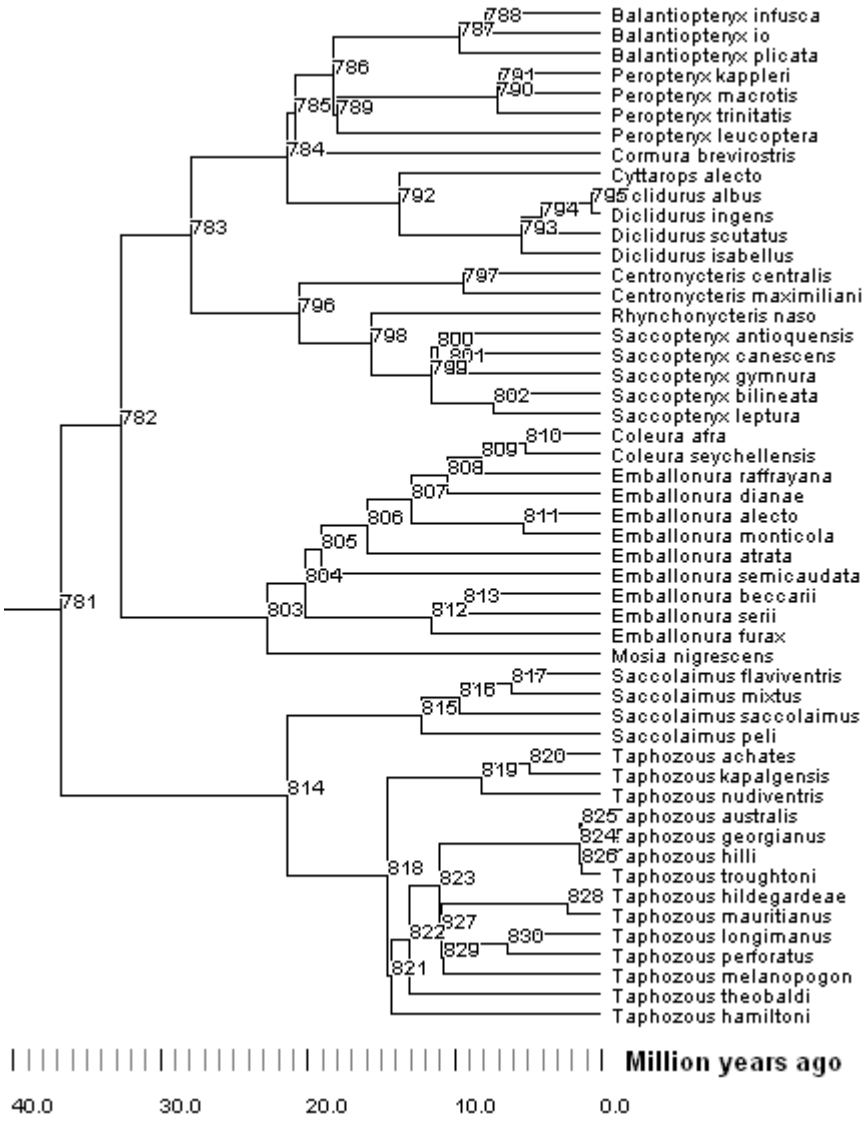


Figure 3.45: Emballonuridae supertree

3.4.16 Nycteridae

The Nycteridae supertrees are presented in Figure 3.46 and Figure 3.47. The family has been split, with the species in Figure 3.46 appearing in the suborder Pteropodiformes, and the species in Figure 3.47 appearing in the Vespertilioniformes suborder. The reasons for this split are explained in Section 1.1.1 above. The species forming the polytomy in Figure 3.46 do so because they are not found in any source tree. The topology in Figure 3.47 is largely due to a single source tree (Eick *et al.* 2005) which contributes all the species except

Nycteris arge. This final species is brought in by another source tree (Van Den Bussche & Hoofer 2004).

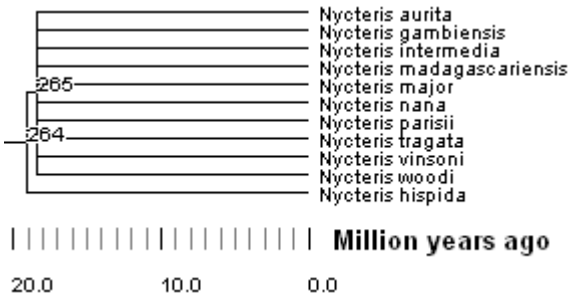


Figure 3.46: Nycteridae 1 supertree – species appearing in the Pteropodiformes suborder.

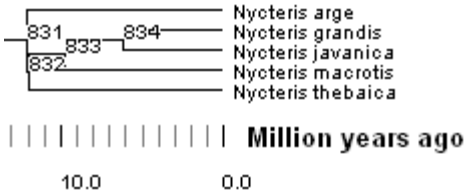


Figure 3.47: Nycteridae 2 supertree – species appearing in the Vespertilioniformes suborder.

3.5 Conclusions

The bat supertree presented here is not intended as a definitive work on the phylogenetic relationships of bats that overrules previous phylogenetic analyses of molecular and morphological data. However, the lack of comparable data from each species of bat and the difficulty in analysing large numbers of characters and taxa simultaneously means the most robust methods for phylogenetic estimation are not able to compute a phylogeny that incorporates all bat species. Instead, this supertree allows the macro-scale comparative analysis of trait data using a comprehensive working hypothesis that summarises the consensus view of many smaller, more detailed systematic studies.

As well as providing a phylogenetic framework for addressing comparative questions in bat biology, the new supertree allows the identification of clades that are in particular need of further taxonomic and systematic study. For example, the families Nycteridae, Molossidae,

Vespertilionidae and Rhinolophidae show the poorest resolution and would benefit most from increased attention.

As predicted by Jones *et al*. (2002), the impact of the previous decade of phylogenetic analysis has been to shift the balance of the most fundamental aspects of tree topology, in that the new supertree now reflects the more recent evidence in favour of the inclusion of Pteropodidae into the 'microbats', refuting previous ideas about the basal nature of the Old World fruit bats. In most cases the vast majority of systematic studies on any particular clade show broad agreement, giving an increasingly clear picture of evolutionary relationships.

Jones *et al*. (2002) hoped that in 20 years a complete phylogeny of bats based on simultaneous analysis of molecular and morphological data would converge on a single well-supported topology. The vast number of studies completed between 2000 and 2009, and the increasingly large numbers of taxa covered in each offer much encouragement, but far too many species are neglected, with 36% of bat species having not been included in a systematic study between 1970 and 2009. Despite this, the supertree offers a consensus of previous work, and allows a new level of detailed study in the comparative analysis of bats.

4 Chapter 4: Evolutionary constraint in echolocation call structure

4.1 Abstract

The functional roles of the different types of echolocation call are now well understood, and the role of habitat in shaping these structures has been established and emphasised. However, the impact of evolutionary history on the variation in echolocation call structures seen in bats is rarely acknowledged and has never been quantified. The variety of echolocation call structures is greater than what would be expected if the sounds were shaped purely by the ecological pressures facing extant bats, suggesting that evolution has taken different routes in shaping bat calls that function in a very similar way. Here I use echolocation call data from 410 species (44%), 120 genera (74%) and all 19 families of echolocating bats, and a complete, species-level phylogeny to (1) review the variation across the order, (2) assess phylogenetic and spatial signal (autocorrelation), (3) to estimate the most likely manner of evolutionary change, and (4) to determine the best model of evolution (between Brownian motion (BM), Ornstein-Uhlenbeck (OU), and Early Burst (EB)), for eight echolocation call parameters. I find a high degree of convergent evolution in echolocation call functionality, with differences in call structure suggestive of independent evolutionary pathways and a constraining force. Call parameters appear to have evolved in two ways: one set (peak frequency, characteristic frequency, call duration and bandwidth) has been more constrained by evolutionary history, less influenced by habitat, and has evolved more gradually in a directional manner towards a single selective optimum (OU). These parameters are more strongly associated with body mass. The other set of call parameters (maximum frequency, minimum frequency, total slope and dominant slope) are less constrained by evolutionary history, more influenced by habitat, and have evolved in a punctuational and directional manner towards several selective optima (modified OU). These parameters appear to be more important in giving echolocation calls task-based functionality. All call parameters show greater influence from evolutionary history, a lower degree of influence from environmental conditions, and a tendency towards species-specific, punctuational, and directional evolution.

4.2 Introduction

4.2.1 Background

Many studies of echolocation in bats have aimed to understand the functionality of different echolocation call structures, and how these relate to the range of sensory tasks encountered by bats (e.g. Aldridge & Rautenbach 1987; Jones & Rayner 1988; Kalko 1995; Kalko & Schnitzler 1993; Neuweiler 1984; Obrist 1995; Schnitzler & Kalko 2001; Schnitzler, Moss, & Denzinger 2003; Simmons, Fenton, & OFarrell 1979; Surlykke & Moss 2000). From these studies, we have a good comprehension of the necessary attributes of an echolocation call for any given task: for example, a particular bat call structure results from an interplay of factors such as the influence of target size on call frequency, target proximity on pulse duration and interval and clutter on bandwidth (see Table 4.1) (Jones & Holderied 2007). It is also clear what intrinsic and extrinsic factors influence, and interact to determine, the structure of an echolocation call: habitat, wing morphology, and prey type (Kalko & Schnitzler 1993; Schnitzler *et al.* 2003). Studies repeatedly reaffirm the influence of habitat (which in turn influences wing morphology and prey type) on call structure, often splitting bat species into 'guilds': groups that forage in a similar way, either for the same food source, or in habitats with the same degree of clutter, or a combination of both (Aldridge & Rautenbach 1987; Fenton 1995; Neuweiler 1990; Schnitzler & Kalko 2001, 1998). However, in these studies, the role of phylogeny, evolutionary history, and evolutionary constraints is rarely acknowledged to have an impact on echolocation call structure, and is thus relegated in importance compared to habitat and sensory tasks.

Call characteristic	Value	Advantage	Disadvantage
Frequency	Low	Travels further	Poorer resolution
	High	Greater resolution	Travels less far
Duration	Short	Better localisation performance, and less call-echo overlap	Less temporal information
	Long	More temporal information	Poorer localisation performance, and call-echo overlap at close range
Bandwidth	Narrow	Energy concentrated - intensity high	Poorer resolution of different size classes
	Broad	Greater resolution of different size classes	Energy spread - intensity reduced

Table 4.1: The impact of variation in the three major components of echolocation call structure on functionality.

In several other fields, the impact of evolutionary history has been assessed alongside the role of current ecological conditions. For example, Edwards & Naeem (1993) looked at the phylogenetic pattern of cooperative breeding in perching birds, and in doing so, defined *phylogenetic inertia* as the 'tendency for traits to resist evolutionary change despite environmental perturbations'. Similarly, Diniz *et al.* (1999) considered the impact of evolutionary history on phenotypes in honey bees, and Morales (Morales 2000) studied demographic and morphological characters in plants. Such comparative studies add an evolutionary perspective to studies of ecology and physiology, and can enable greater understanding of both pattern and process.

The influence of evolutionary history on the current diversity of echolocation calls in bats has been hinted at. For example, Schnitzler *et al.*'s (Schnitzler *et al.* 2004) *vocal plasticity* hypothesis is based on the idea that "echolocation signals reflect a phylogenetically determined basic call structure shaped by specific ecological conditions". However, most 'comparative studies' cited by Schnitzler do not comment on evolution, and often look at

only a single species. Evolutionary history is likely to be much more prominent in shaping echolocation calls than we have acknowledged.

If habitat were solely responsible for shaping the call variation seen today, we would expect to see a single echolocation call type in use in search phase flight by each guild. For example, in Schnitzler and Kalko's (1998) three-guild model of bats that forage in (1) uncluttered space, (2) background-cluttered space, and (3) highly cluttered space, we would expect three call types based on the requirements outlined in Table 4.1: (1) low frequency, long duration, low bandwidth calls, (2) mid frequency, mid duration, mid bandwidth calls, and (3) high frequency, short duration, high bandwidth calls. In fact, taking the final guild as an illustration, we see a number of different call types, most of which correspond with these requirements in outline, but differ in composition. They include the calls of species in the genus *Myotis* (Vespertilionidae) which are high bandwidth by virtue of an increase in the maximum frequency of the fundamental harmonic, as well as the calls of species in the family Phyllostomidae which achieve a high bandwidth by using a multiharmonic structure and spreading the energy over all harmonics, and also the very long, largely constant frequency calls of the family Rhinolophidae, which circumvent the need for a high bandwidth by detecting the movement of prey against a stationary background (Schnitzler & Kalko 1998).

To determine the real impact of evolutionary history relative to current ecological conditions on echolocation call structures, we need to quantify the relationship between the bat phylogeny and the traits of interest. By using the new, complete and well resolved bat supertree, and measurements describing the echolocation call structures of 44% of echolocating bat species in 74% of genera and every family, it is possible to use phylogenetic comparative methods to understand the patterns and processes involved in the evolutionary path of echolocation in bats.

One way of assessing the relative contributions of the environment and shared evolutionary history to the design of echolocation calls is to calculate the strength of phylogenetic signal for characteristic aspects of call structure. In the purest sense, phylogenetic signal is the

statistical non-independence of species trait values due to their phylogenetic relatedness (Revell, Harmon, & Collar 2008) – high signal indicates that trait values are very similar among related species. Biologically, it may be interpreted as measure of the impact of shared evolutionary history on a particular trait, since sister species must have shared a trait value in their most recent common ancestor. The remainder of the variation can be thought of as a result of recent selective pressures due to environmental conditions.

One major criticism of comparative methods is the assumption of negligible variance in the intra-species variation of the traits in question (Garland, Bennett, & Rezende 2005; Ives, Midford, & Garland 2007; Martins & Hansen 1996; Rohlf 2001, 2006). This is a particular concern for bat echolocation call data, since the variability in call parameters within species is well documented, both due to geographic variation (Barclay, Fullard, & Jacobs 1999; Murray, Britzke, & Robbins 2001; Thomas, Bell, & Fenton 1987), sex and age (Jones & Kokurewicz 1994), and differing functional tasks (Schnitzler & Kalko 1998). To combat this potential source of error, the phylogenetic signal analysis is bootstrapped using randomly selected raw echolocation data, rather than species averages.

When using comparative data relating to a large number of species, phylogeny is not the only source of statistical non-independence. Spatial autocorrelation may also be responsible for similar trait values among species found in close proximity (Freckleton & Jetz 2009). This is usually due to shared environmental conditions as a result of climate and geology, which may then determine habitat types and species assemblages. When assessing the relative contributions of shared evolutionary history and environment on echolocation calls, spatial autocorrelation must also be included.

It is also useful to look at the tempo and mode of evolution in echolocation calls leading to the diversity seen today. At present, very little is understood about how changes to the structure of echolocation calls evolve. Here I investigate the tempo using Pagel's kappa, which estimates whether evolution proceeded gradually or in bursts associated with speciation, and Pagel's delta, which estimates whether evolutionary change occurred early

in the tree (consistent with adaptive radiation), or late (indicating species-specific changes) (Pagel 1999a).

I also consider the mode of evolution by evaluating three main models: (1) the Brownian motion model (BM), (2) the Ornstein-Uhlenbeck model (OU), and (3) the Early Burst model (EB) (see Blomberg, Garland, & Ives 2003; Felsenstein 1973; Hansen 1997). BM describes a 'random walk' where evolution can proceed in any direction away from the starting value of a trait, leading to trait variance increasing over time (Felsenstein 1973). It is often assumed to be the mode of evolution in action in comparative studies, though its random nature makes this unlikely, since the subject of most comparative studies are traits that are likely to impact the fitness of the organism under study (Butler & King 2004). OU is a modified BM model, including a non-neutral parameter α, that specifies the value of a selective optimum for the trait, and which exerts a restraining force, pulling the value of the trait towards it (Felsenstein 1988). EB is characterised by change early in a lineage, such might occur in adaptive radiations. This early change is followed by a decreased rate of diversification (of species) and associated disparification (diversity of trait values - Evans & Smith 2009) as niches fill up.

4.2.2 Hypotheses

I would expect a high phylogenetic signal in body mass, as body mass values appear to be similar amongst more closely related bat taxa. I would also expect high phylogenetic signal in echolocation call parameters that are closely associated with body mass, i.e. peak frequency, characteristic frequency, and call duration. The call parameters more closely linked to habitat differences, i.e. maximum frequency, minimum frequency, and the measures of call slope (Jones & Holderied 2007; Schnitzler & Kalko 1998), should have a lower phylogenetic signal.

For spatial signal, I would expect to see a reversal of the pattern to that seen in phylogenetic signal, so that call parameters closely linked to habitat show greater spatial signal, and those more closely related to body mass show lower spatial signal.

I would hypothesise that change in call parameters would be somewhat punctuational, since intermediate call values may be non-functional. However, for call parameters linked to body mass, such as peak frequency, characteristic frequency and call duration, I would expect a more gradual course of evolutionary change. I predict that, in terms of the timing of evolutionary changes in call parameters, most parameters would show late, species-specific change, since the high diversity of call structures would not be expected if call parameters had evolved early in the history of bats, and had remained relatively unchanged since.

Since echolocation is a highly functional trait, I would not expect to see a BM model of evolution. The importance of the call parameter values in the fitness of each species leads me to expect an OU model, with constraining selective optima. Just as I suspect evolutionary change occurred late in the phylogeny, I also would not expect the EB model of evolutionary change, as it hints at early diversification and disparification, followed by relative stasis.

4.2.3 Chapter aims

The aims of this study are threefold: (1) To illustrate the variation in echolocation call design from species level to family level using data from up to 410 species (44%), 120 genera (74%) and 19 families (100%), (2) To determine to phylogenetic, spatial and independent components of these measures, (3) To assess the evolutionary process underpinning the evolution of echolocation call traits.

4.3 Methods

4.3.1 Data

4.3.1.1 Bat call data

I collated and measured the echolocation call data as described in Chapter 2: section 2.2. The echolocation data used included data from species found in EchoBank that could be

successfully measured (see Appendices A and E), and data from species reported in the literature (see Appendix B). I used the parameters chosen in section 2.2.8 in Chapter 2: bandwidth, call duration, characteristic frequency, maximum frequency, minimum frequency, peak frequency, dominant slope and total slope. Transformed data (according to Table 2.9 in Chapter 2 section 2.9) were used in all analyses.

4.3.1.2 Supertree

I constructed the supertree as described in Chapter 2: section 2.3. I used the EchoBank and Literature version of the tree, pruned to the 410 species for which I have echolocation data from either EchoBank or the literature. I altered the topology, however, moving the Molossidae species *Tadarida teniotis* from its location paraphyletic to the Molossidae, to being allied with the other *Tadarida* species, because this species had fallen out of its family due to its presence in a single morphological source tree that found it to be more closely related to species of Vespertilionidae than another species of Molossidae (Giannini *et al.* 2008). I also moved the Nycteridae species found amongst the Pteropodiformes to join the other Nycteridae species in the Vespertilioniformes. This latter topology reflects current consensus much more closely (Eick, Jacobs, & Matthee 2005; Miller-Butterworth *et al*. 2007; Teeling *et al*. 2003, 2005, pers. comm.). I chose to make these changes to ensure that the analyses of echolocation data are as relevant and current as possible.

4.3.1.3 Body mass and spatial data

Adult body mass data (averaged over both sexes) (see Appendix F) and spatial data (mid-range latitude and longitude values for each species) were taken from the PanTHERIA database – a database of life history traits for mammalian species (Jones *et al.* 2009) according to the taxonomy of the Mammal Species of the World 2005 (Simmons 2005). PanTHERIA includes a value for 'Extrapolated Adult Body Mass', calculated from either adult head-body length, adult forearm length, or both, and where a direct value for body mass was unavailable for a species, the extrapolated body mass value was used instead. For the complete species list used in these analyses, 8% of body mass values were extrapolated in this way. Spatial data were available for 401 of the 410 species.

4.3.1.4 Combined data sets

The data sets used for each analysis in this chapter are subsets of the total data set of 410 species. There are missing data points in the EchoBank data set, where SonoBat (Szewczak 2010) was unable to measure a particular parameter; in the Literature, where parameters were not reported; and in PanTHERIA, where data were unavailable (see Chapter 2 section 2.9 for details and Appendix F for species list). In each analysis, the phylogeny was pruned to include only those species which were represented by data for every parameter involved in the analysis.

4.3.2 Analysis

All data analysis was performed using R version 2.12.0 (The R Core Development Team 2010).

4.3.2.1 Echolocation Call Variation

I reviewed the variation in echolocation calls across the order visually, considering each family independently by placing a call for each species represented in EchoBank on a composite sonogram. Each sonogram was produced using BatSound (Pettersson 2002), keeping the time frame and frequency axis constant. Each figure uses a Hanning 1024 Fast Fourier Transform window and the sound threshold is set to produce images where echolocation calls are of roughly comparable intensity. However, the intensity shown in the figures does not represent relative intensities between species, merely relative amplitudes within a single call. Where a species has calls of alternating frequencies, such as in *Saccopteryx bilineata*, all calls in a series are shown, but the interpulse duration is not scaled.

I used these sonograms to group similar calls and to assess the suitability of the echolocation call categories outlined in Jones & Teeling (2006).

I also compared differences in frequencies used, characteristic frequency, bandwidth and call duration, family-by-family, across the order.

4.3.2.2 Patterns of Phylogenetic and Spatial Signal

The analyses below assess the variation seen in echolocation call structures in a quantitative manner. They concentrate on understanding the patterns of trait variation across the phylogeny.

- Pagel's Lambda

I estimated Pagel's lambda (λ) values (Pagel 1999a) for each echolocation call parameter and for the residuals of each echolocation call parameter following a phylogenetic generalised least squares analysis (PGLS) run using the 'gls' function of the package *nlme* in R (The R Core Development Team 2010), using an Ornstein-Unlenbeck correlation structure where alpha was equal to the values estimated in section 4.3.2.3 below. Lambda is a measure of the phylogenetic signal in the data, i.e. how clumped or over-dispersed values are on the phylogeny, with values close to one indicating high similarity in trait values among closely related species, and values close to zero indicating random dispersion of trait values across the tree. Lambda was estimated using the 'fitContinuous' function of the package *geiger* in R (The R Core Development Team 2010). This function scales branch lengths according to the different value of lambda and uses maximum likelihood to estimate the most likely value for each parameter. To check the validity of using a median value for each species, I ran a second estimation of lambda using 100 bootstraps of randomly picked individual calls.

- Freckleton and Jetz test

Since the echolocation data in this study come from a worldwide distribution of bat species, phylogenetic autocorrelation is likely not to be the only source of statistical non-independence affecting the dispersal of trait values. Species which occupy overlapping or nearby geographic ranges may have similar traits due to the impact of shared environmental conditions. Freckleton and Jetz (2009) developed a means of incorporating phylogenetic

and spatial autocorrelation into a single test, enabling the estimation of three concomitant parameters: lambda prime (λ′ - contribution of phylogeny (an adjusted lambda value)), phi (φ - contribution of space), and gamma (γ – independent/unknown). I used the custom-built function 'distance2', written by Freckleton and Jetz and implemented in the *ape* package of R to estimate lambda′, phi and gamma.

4.3.2.3 Processes of Evolution

The following analyses estimate the likely processes of evolution that have been in operation to produce the patterns found in echolocation call structure and the distribution of traits over the phylogeny of bats.

- Pagel's Kappa and Delta

I estimated Pagel's kappa (κ) and delta (δ) values (Pagel 1999a) for each echolocation call parameter and for the residuals of each echolocation call parameter following a phylogenetic generalised least squares analysis (PGLS) run using the 'gls' function of the package *nlme* in R (The R Core Development Team 2010), using an Ornstein-Unlenbeck correlation structure where alpha was equal to the values estimated in section 4.3.2.3 above. I also estimated kappa and delta for bat body mass for comparison. Kappa gives an indication of how gradual or punctuated change in trait values is on the phylogeny, with values greater than one indicating that longer branches in the phylogeny contribute more to trait evolution (change is gradual), and values below one suggesting that trait evolution is less dependent on branch length, and therefore more 'punctuational'. Delta indicates which changes in traits occur early or late in the course of evolution over the phylogeny, with values greater than one indicating accelerating evolution over time, and values less than one suggesting that trait change occurred early in the phylogeny. Both parameters were estimated using the 'fitContinuous' function of the package *geiger* in R (Harmon *et al.* 2009). This function scales branch lengths according to the different values of kappa and delta and uses maximum likelihood to estimate the most likely value for each parameter. Again, to check the validity of using a median value for each species, I ran a second estimation of kappa and delta using 100 bootstraps of randomly picked individual calls.

- Mode of Evolution

I compared three models of evolution; Brownian Motion (BM), Ornstein-Uhlenbeck (OU), and Early Burst (EB), using the function 'fitContinuous' in the package *geiger* in R (Harmon *et al.* 2009). I compared corrected Akaike Information Criterion (AICc) scores to select the best performing model for each echolocation call parameter. Although the OU model is more complex than BM, in that it adds a selective optimum (α) for the trait to tend towards, it only specifies a single selective optimum for all the species on the phylogeny. Since it is possible that each echolocation call parameter could be tending towards more than one selective optimum across up to 410 species, I also tested between BM, OU with one selective optimum, and five 'Hansen' models (Butler & King 2004): OU models with more than one selective optimum. The five models contained 2, 19, 23, 30 and 38 selective optima, based on splitting the phylogeny according to (1) suborders (*sensu* Teeling *et al.* (2005)), (2) families, (3) families but with Vespertilionidae (the most speciose family) broken into subfamilies, (4) subfamilies, and (5) tribes, respectively (*sensu* Simmons (2005)). To do this I used the package *ouch* in R (King & Butler 2009). Again, I compared Akaikie Information Criterion (AIC) and Bayesian Information Criterion (BIC) scores to select the best performing model for each echolocation call parameter.

4.4 Results

4.4.1 Echolocation Call Variation

Echolocation call structures across all 18 families of laryngeally echolocating bats vary dramatically and include near-vertical sweeps from high to low frequency over just a couple of milliseconds (for example in the genus *Kerivoula*, Vespertilionidae) constant frequency calls of up to 81 ms in duration (in the Rhinolophidae), and calls with several elements, either as repeated sounds at slightly different frequencies (such as in Emballonuridae) or as two different sound structures (Myzopodidae). Examples of a call from all collected species in all laryngeally-echolocating families are shown in Figure 4.1 to Figure 4.9 according to the phylogenetic relationships found in the supertree, except for the largest family Vespertilionidae, for which a call for each genus is shown. Branch

lengths in the figures correspond roughly to divergence times – see Chapter 3 for accurately dated figures of the supertree.

A large amount of variation in call structures between species is evident in the Emballonuridae (Figure 4.1), Molossidae (Figure 4.4) and amongst the species of the smaller families (Craseonycteridae, Furipteridae, Natalidae, Myzopodidae, Mystacinidae, Noctilionidae, Nycteridae, Rhinopomatidae, Mormoopidae, Thyropteridae, and Megadermatidae (Figure 4.9)). However, a surprisingly small degree of variation between species is seen in the Hipposideridae (Figure 4.2), Miniopteridae (Figure 4.3), Phyllostomidae (Figure 4.5), Rhinolophidae (Figure 4.6) and Vespertilionidae (Figure 4.7), particularly within the genus *Myotis* (Figure 4.8). There are several examples of putative convergent evolution, most notably in the call of *Hipposideros semoni* (Hipposideridae), which shows a constant-frequency structure more similar to that of the Rhinolophidae than the Hipposideridae, as does *Pteronotus parnellii* (Mormoopidae). To find this call structure in a species of Hipposideridae is extremely surprising, and due to the possibility that the recording had been mislabeled, or the bat misidentified, I checked the literature for independent verification of this species' unusual call type. I found two references by different authors containing spectrograms confirming the call's rhinolophid-like structure (Churchill 2010; de Oliveira & Schulz 1997).

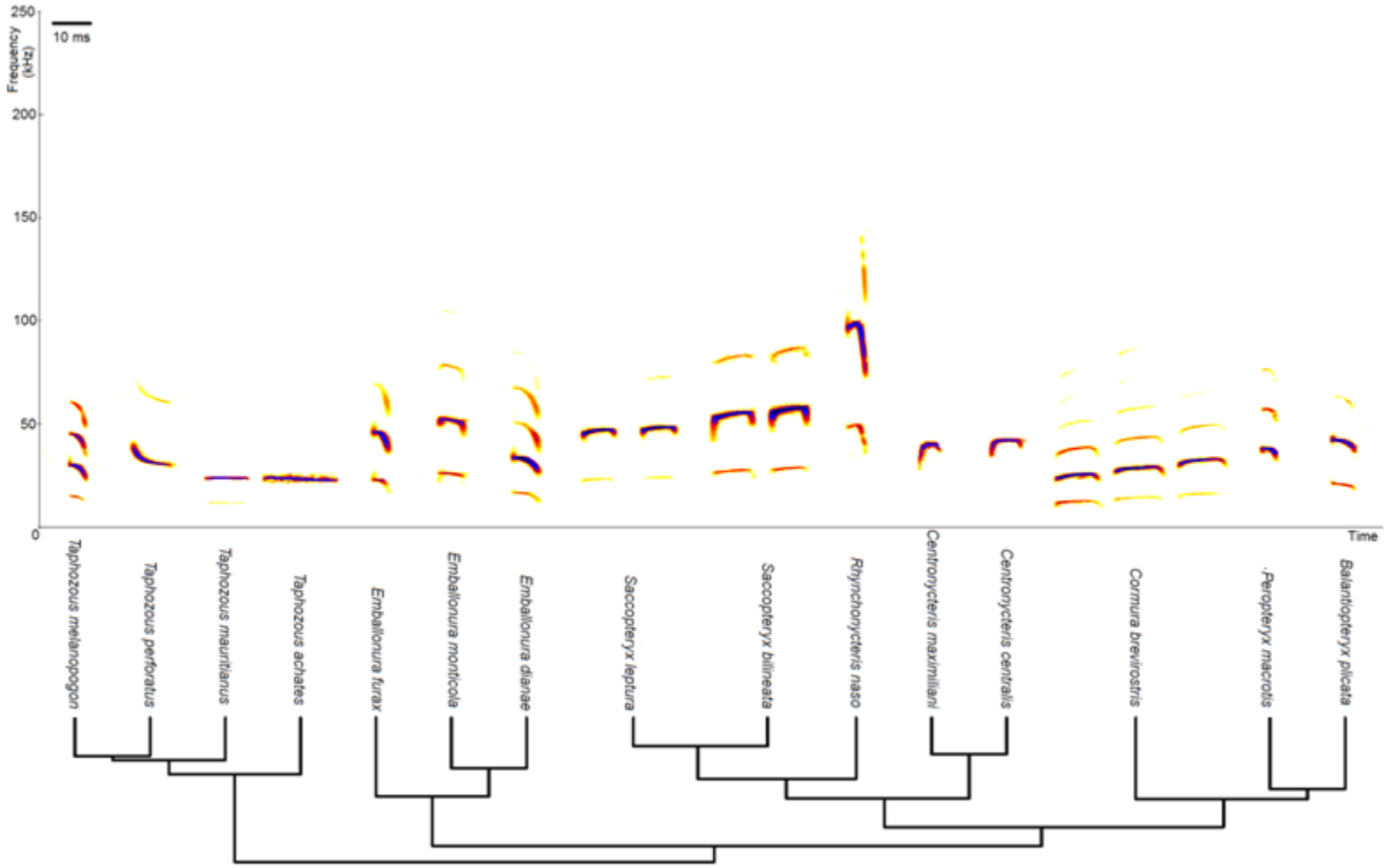


Figure 4.1: Sonograms of search phase echolocation calls in 15 species of Emballonuridae. Pulse intervals are not scaled.

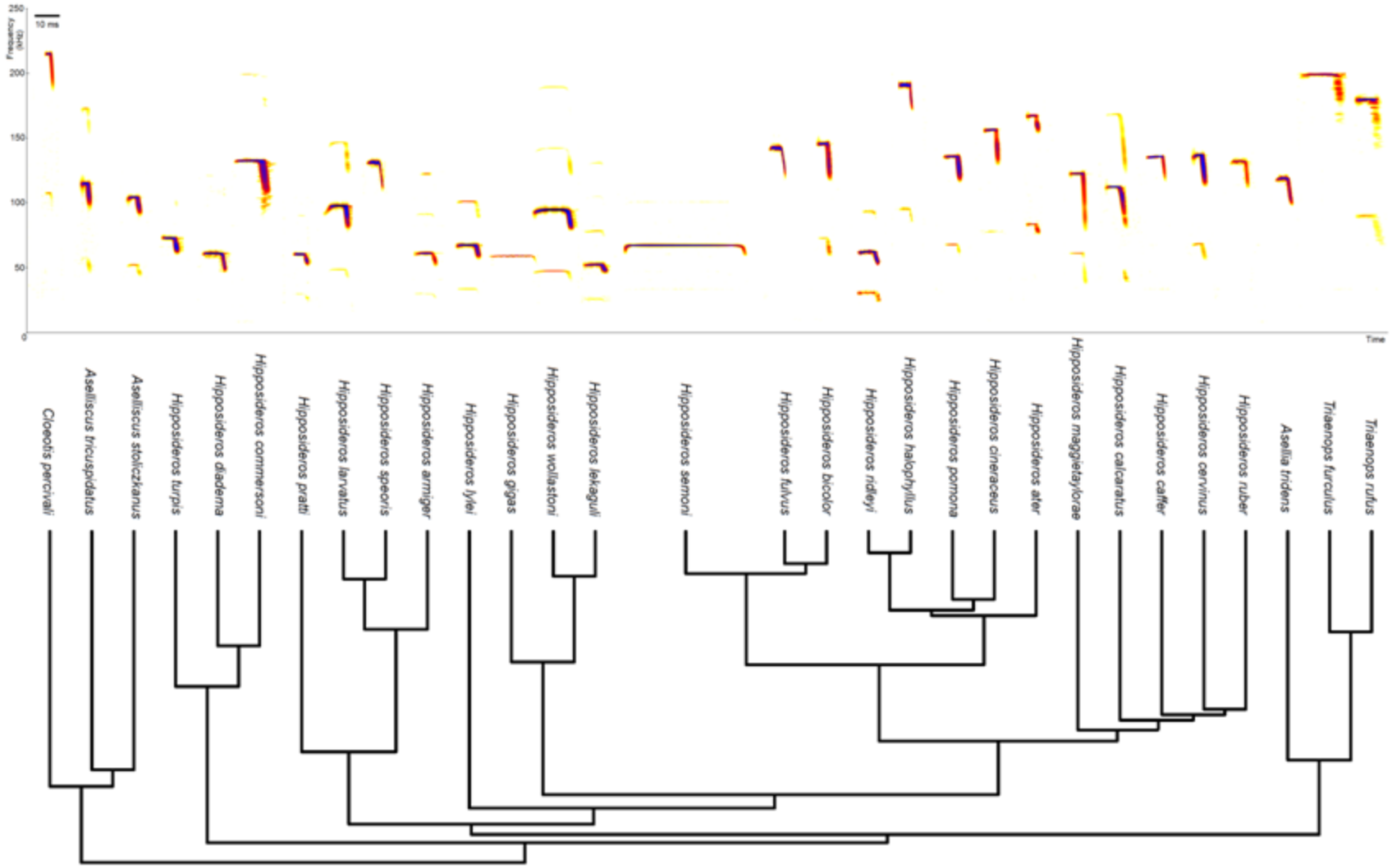


Figure 4.2: Sonograms of search phase echolocation calls emitted in 30 species of Hipposideridae.

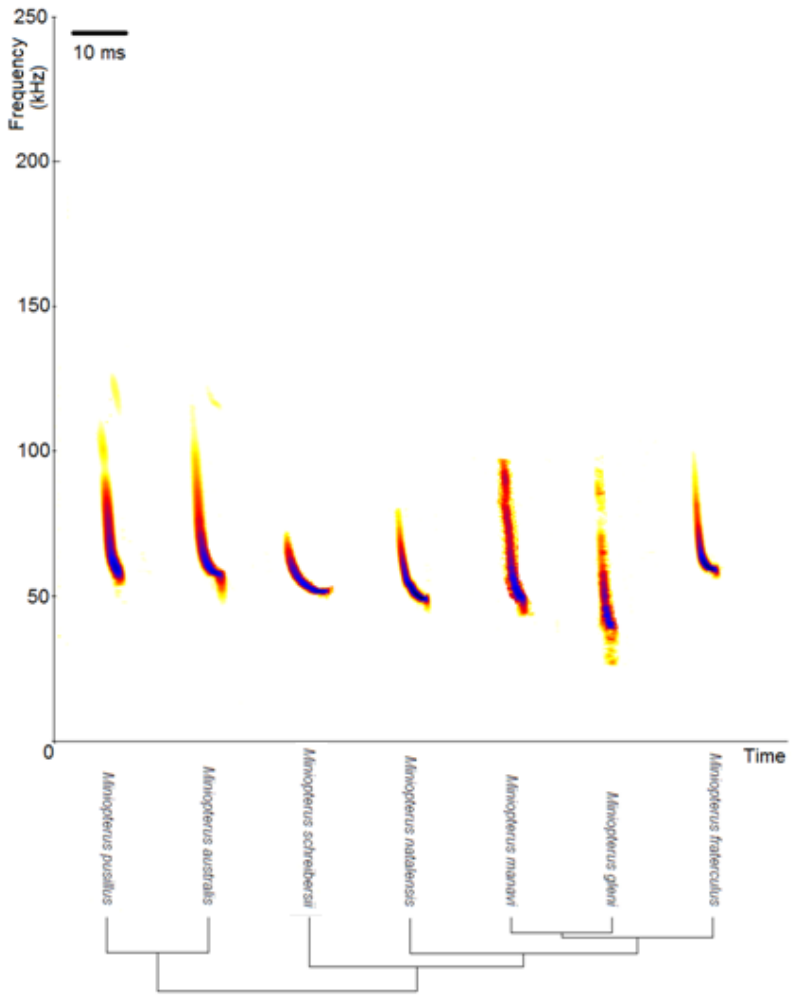


Figure 4.3: Sonograms of search phase echolocation calls emitted in seven species of Miniopteridae.

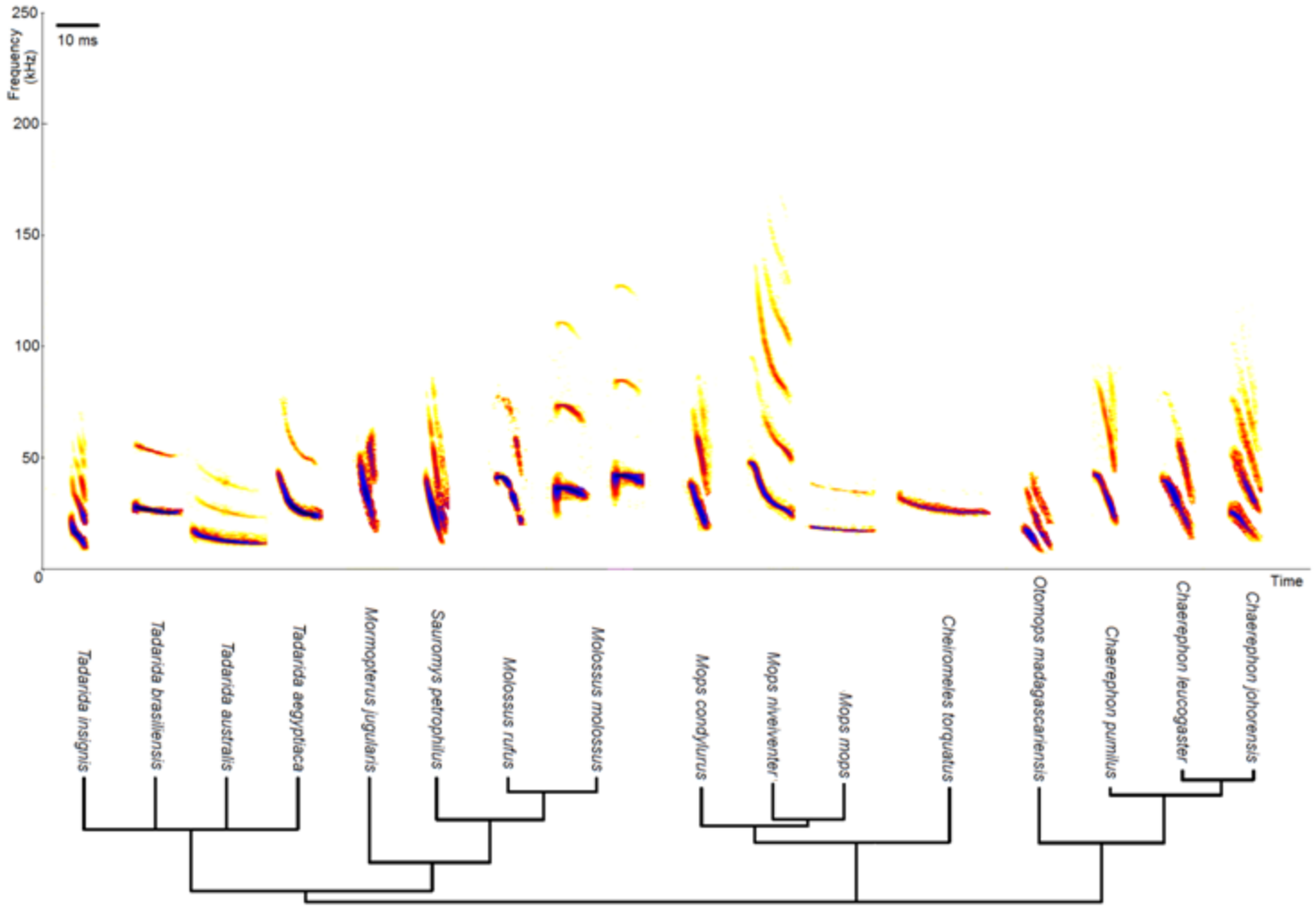


Figure 4.4: Sonograms of search phase echolocation calls emitted in 16 species of Molossidae.

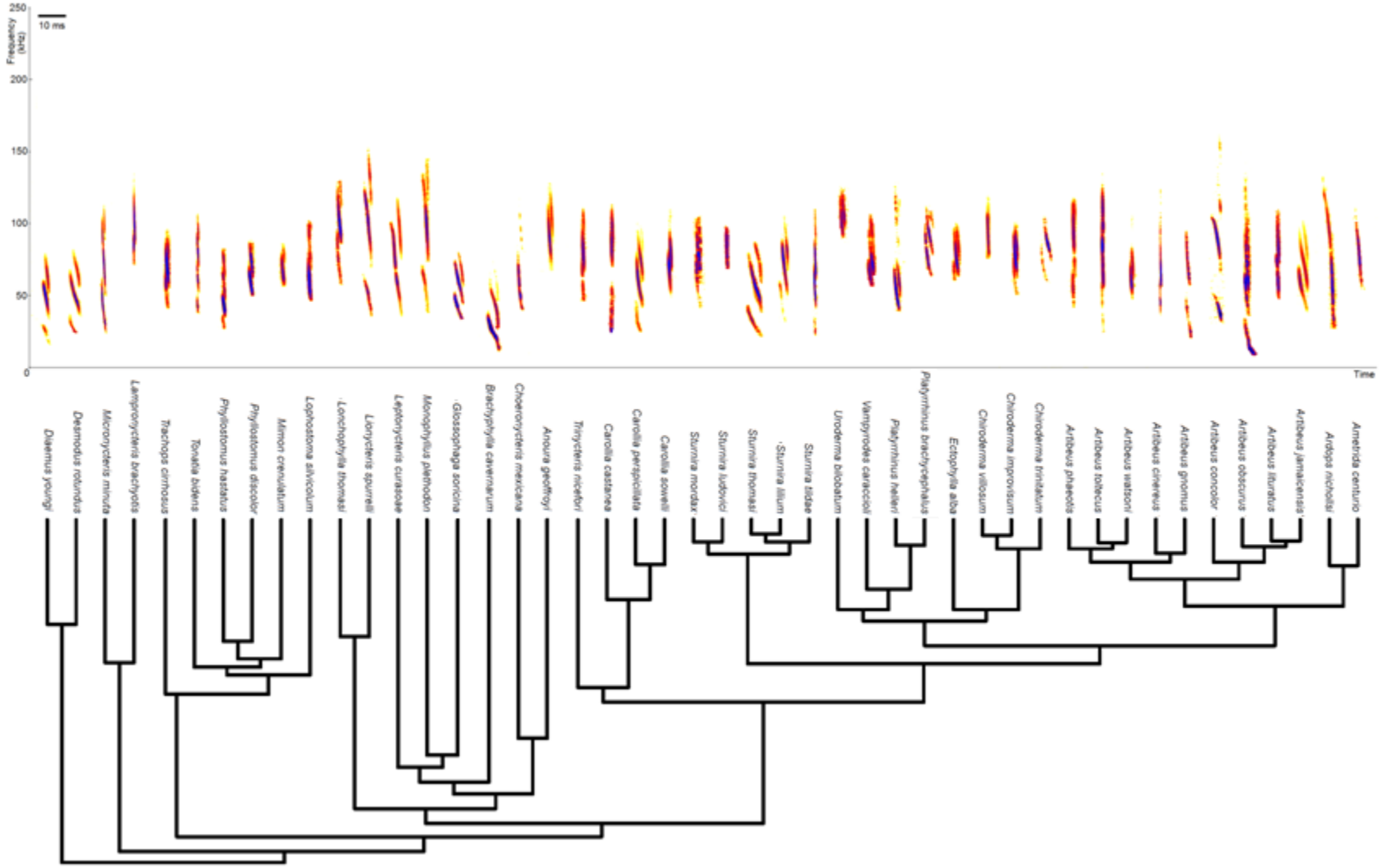


Figure 4.5: Sonograms of search phase echolocation calls emitted in 46 species of Phyllostomidae.

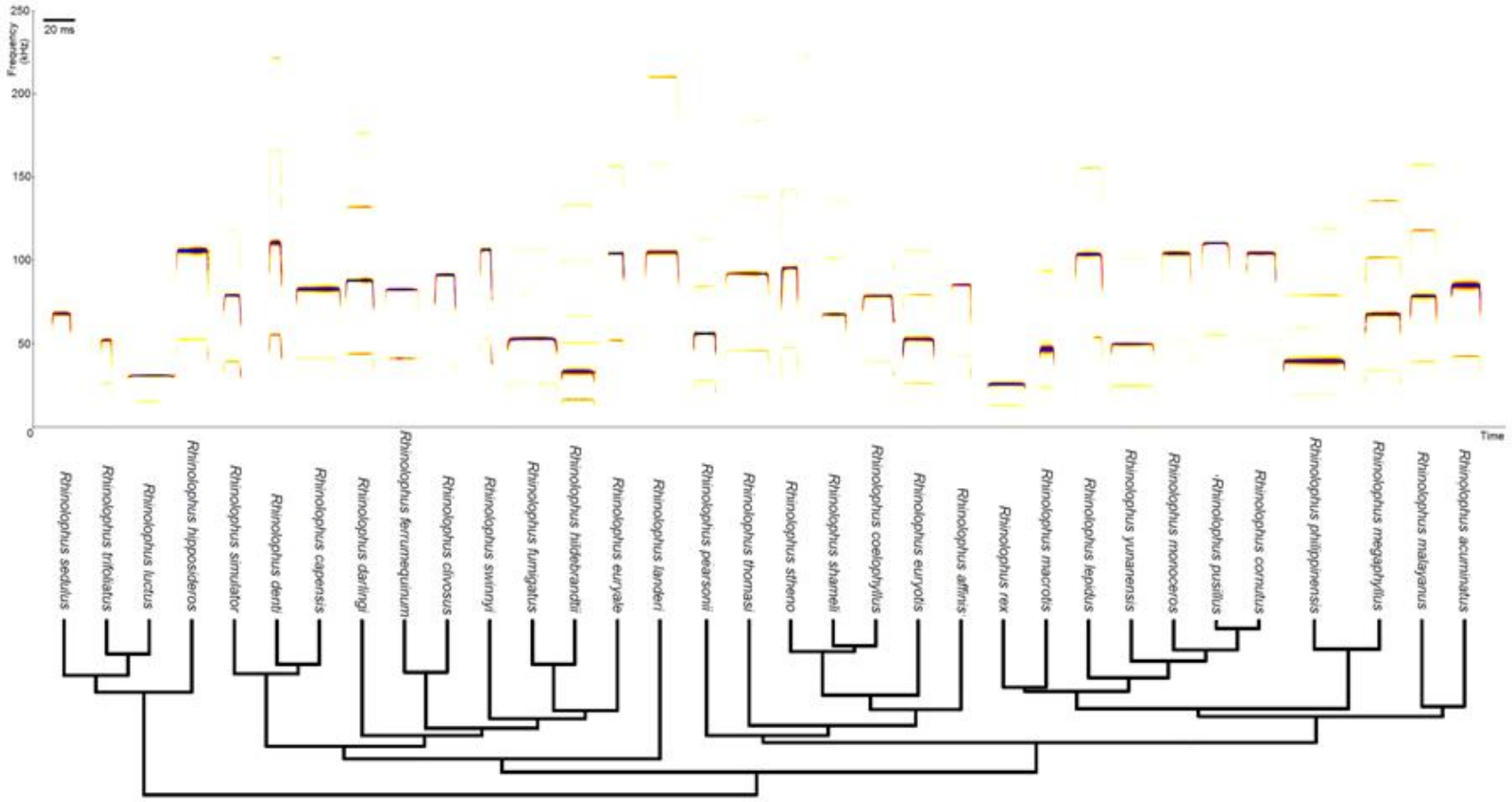


Figure 4.6: Sonograms of search phase echolocation calls emitted in 33 species of Rhinolophidae.

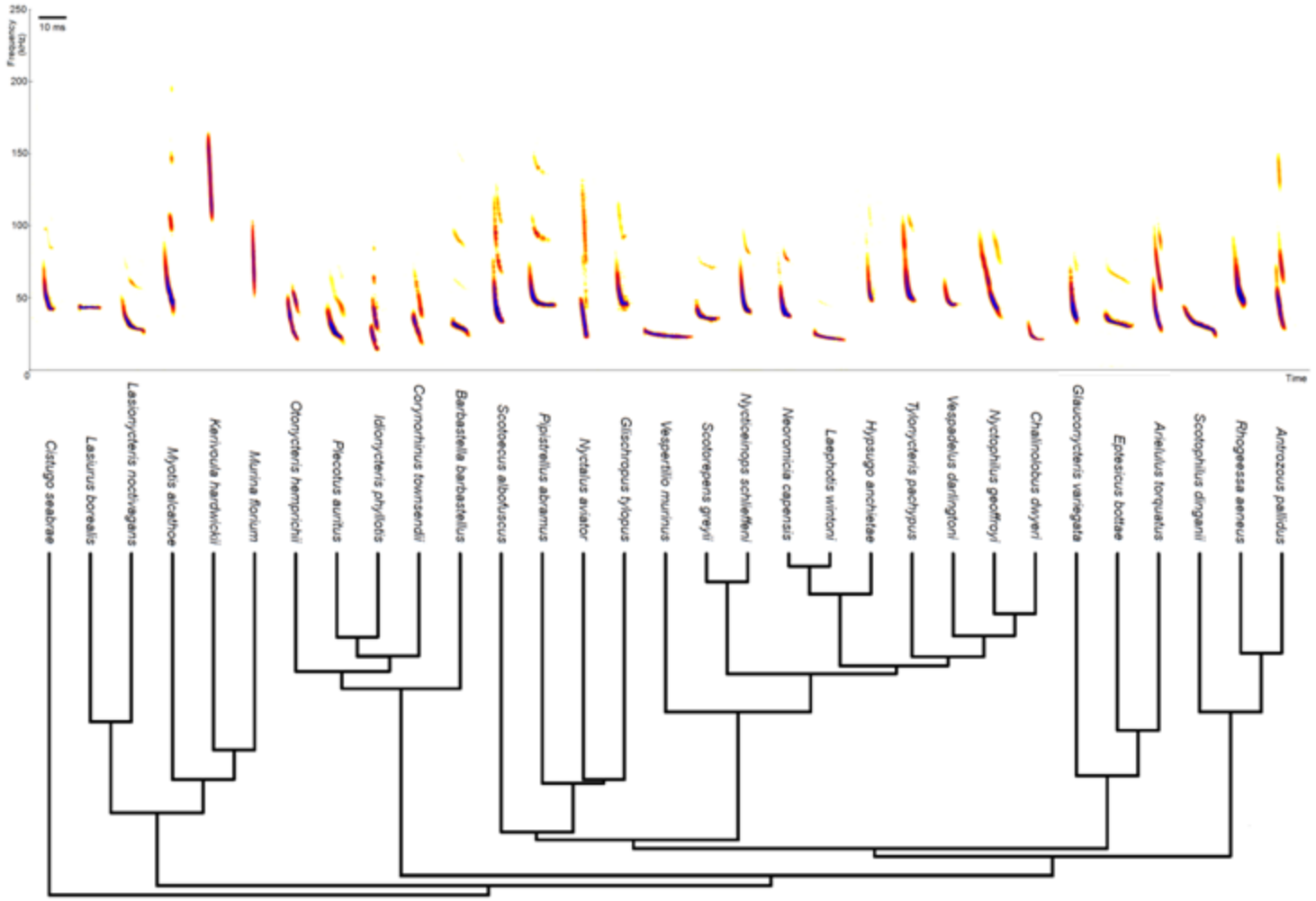


Figure 4.7: Sonograms of search phase echolocation calls emitted in 31 species of Vespertilionidae, each representing a single genus.

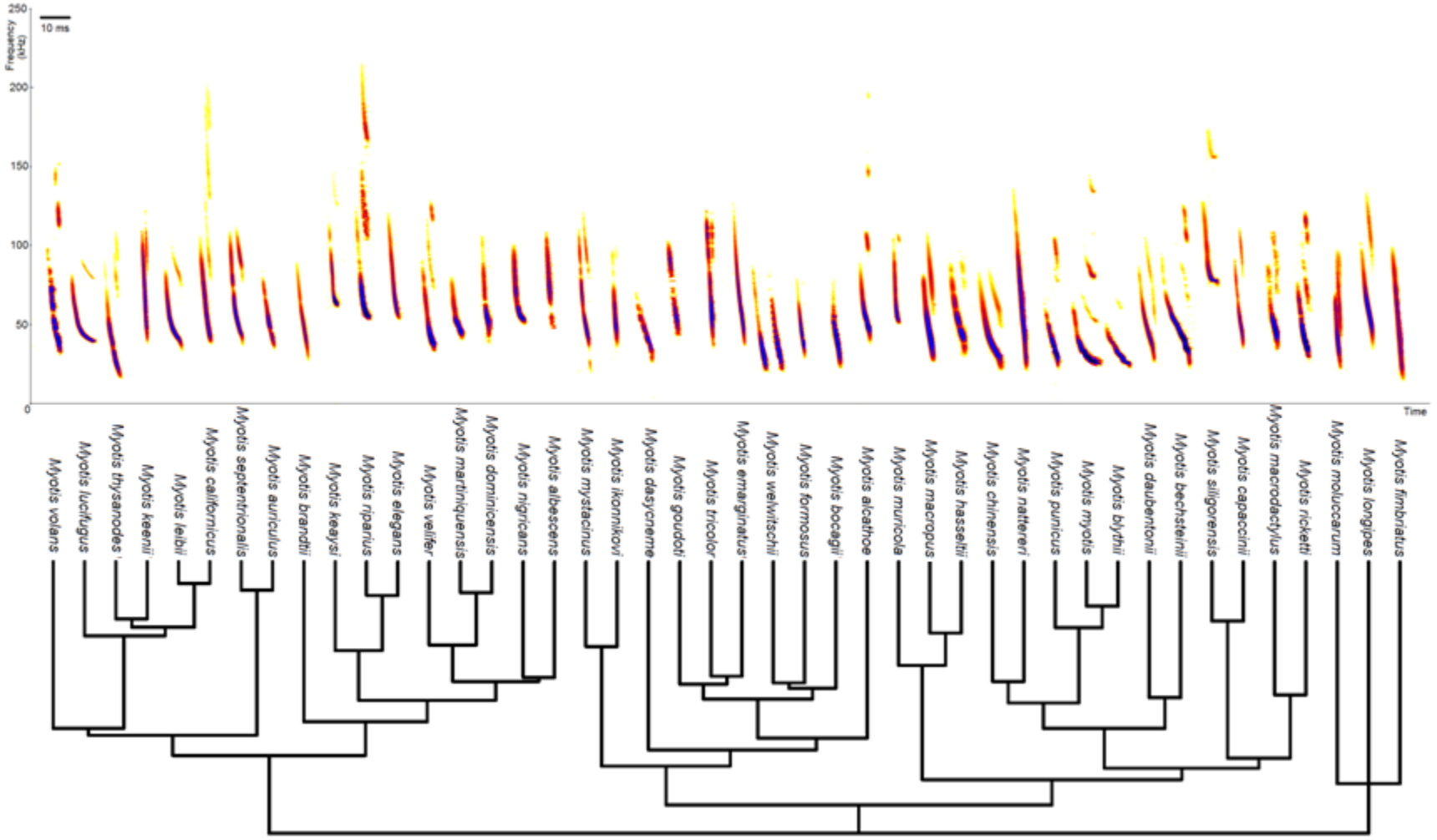


Figure 4.8: Sonograms of search phase echolocation calls emitted in 44 species of the genus *Myotis* (Vespertilionidae).

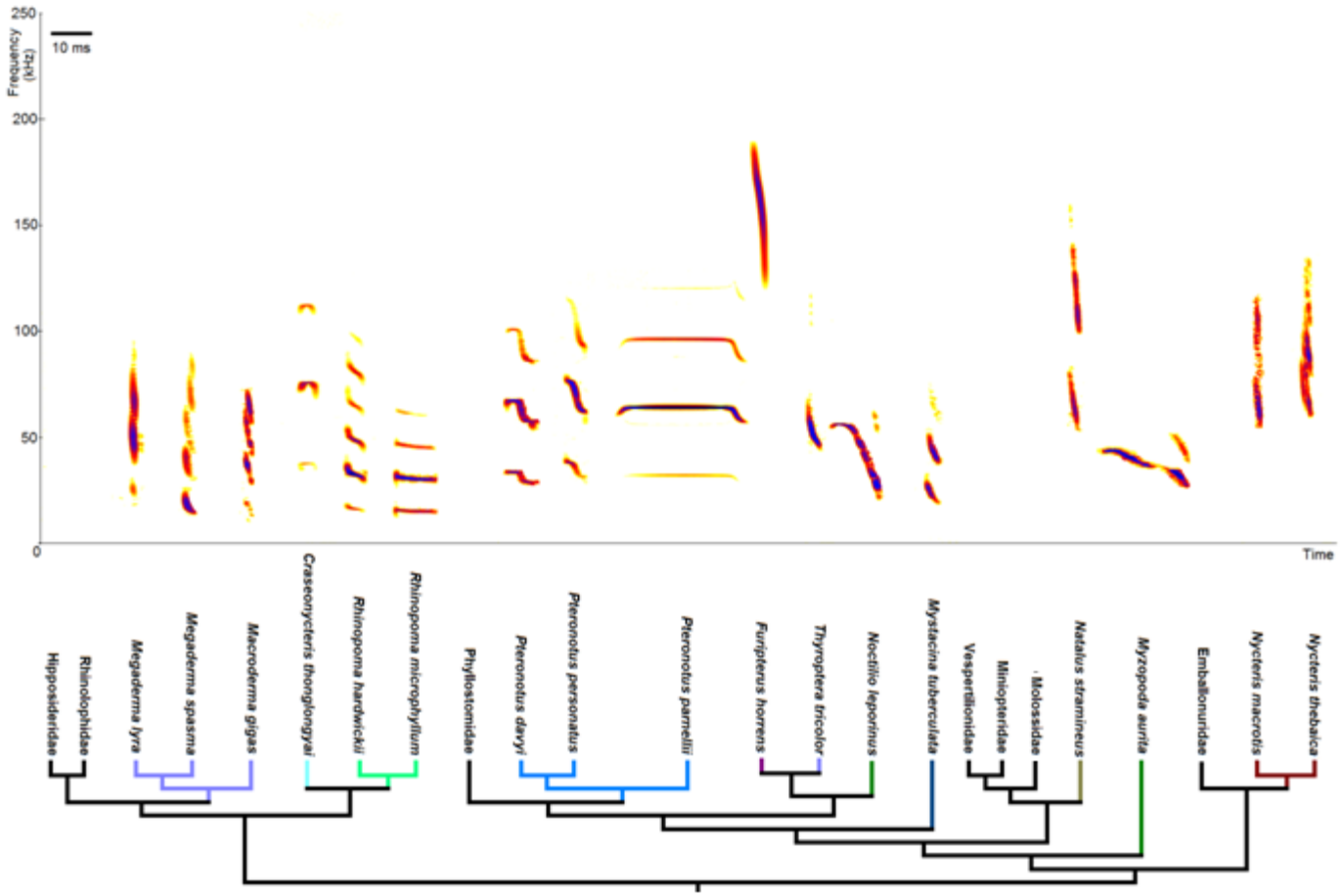


Figure 4.9: Sonograms of search phase echolocation calls emitted in one species of each of Craseonycteridae, Furipteridae, Thyropteridae, Noctilionidae, Mystacinidae, Natalidae, and Myzopodidae, two species of each of Rhinopomatidae and Nycteridae, and three species of each of Megadermatidae and Mormoopidae.

On comparison with the echolocation call categories designated by Jones and Teeling (2006), I found several opportunities for further divisions that I consider to be functionally and evolutionarily relevant (see Table 4.2). I found total agreement between Jones and Teeling's call types (a) and (b) with my call types (1) and (2). I modified the description of call type (c) to my call type (3) and excluded Miniopteridae (which I found to be broadband, not narrowband), and instead included members of Emballonuridae. I split call type (d) into my call types (4), (5), and (6), reflecting the different types of curvature found under the description of 'narrowband, multiharmonic'. I also split call type (e) into my call types (7) and (8), since (e) excluded broadband calls of >5ms that did not fit into any of Jones and Teeling's other categories. Call type (8) absorbs the Miniopteridae that I removed from group (c)/(3). Call type (f) does not distinguish between the dominant harmonics used in short, broadband, multiharmonic calls, so I split this group into call types (9) and (10), and I included members of Molossidae in (10). Call type (g) includes only *Myzopoda aurita* (Myzopodidae), but I found similarities in call structure between the calls of this species and those of species in Mormoopidae and Molossidae, so I have included these in my call type (11). Call type (h) does not distinguish between brief frequency-modulated up-sweep, long constant-frequency section, brief frequency-modulated down-sweep calls, and brief frequency-modulated up-sweep, mid-length constant-frequency section, and broadband down-sweep calls. I have done this, by creating call types (12) for the former, and (13), for the latter. Call type (12) includes all Rhinolophidae, *Pteronotus parnellii* (Mormoopidae), and some species of Hipposideridae. Call type (13) includes most species of Hipposideridae, as well as *Rhychonycteris naso* (Emballonuridae), *Molossus rufus* (Molossidae) and Noctilionidae.

Table 4.2: The diversity of echolocation calls in bats: a comparison between the categories of Jones and Teeling 2006 (left hand column), and proposed new categories (right hand column). The right hand column includes a spectrogram for every family with calls belonging in a call type, but may not be limited to the species mentioned. Figure adapted from Jones & Teeling 2006.

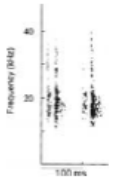
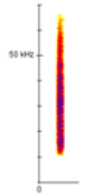
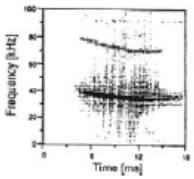
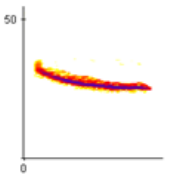
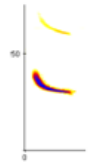
Echolocation call categories outlined in Jones and Teeling 2006		Proposed new echolocation call categories	
Echolocation call type	Bat families Spectrogram	Echolocation call type	Bat families Spectrogram
(a) No echolocation	Pteropodidae, except *Rousettus*	(1) No echolocation	Pteropodidae, except *Rousettus*
(b) Brief, broadband tongue clicks	*Rousettus*, Pteropodidae  *Rousettus aegyptiaca*	(2) Brief, broadband tongue clicks	*Rousettus*, Pteropodidae  *Rousettus aegyptiaca*
(c) Narrowband, dominated by fundamental harmonic	Vespertilionidae  *Lasiurus borealis* "Many open space bats in Vespertilionidae, Molossidae and Miniopteridae. Limited frequency modulation, >5ms."	(3) Narrowband, dominated by a single harmonic	Vespertilionidae  *Lasiurus borealis* Molossidae  *Cheiromeles torquatus* Emballonuridae  *Taphozous perforatus*

Table 4.2 continued:

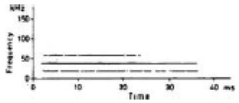
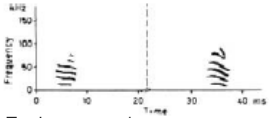
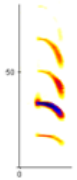
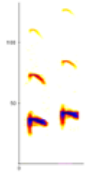
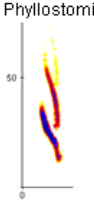
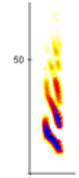
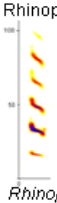
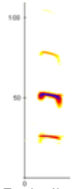
Echolocation call categories outlined in Jones and Teeling 2006			Proposed new echolocation call categories		
Echolocation call type	Bat families Spectrogram		Echolocation call type	Bat families Spectrogram	
(d) Narrowband, multiharmonic	Rhinopomatidae  *Rhinopoma hardwickii*	Emballonuridae  *Taphozous melanopogon*	(4) Multiharmonic decurve	Emballonuridae  *Emballonura dianae*	Molossidae  *Molossus molossus*
"Open-space bats in the families Craseonycteridae, Rhinopomatidae, Emballonuridae, Moormopidae and Thyropteridae. Usually dominated by a harmonic other than the fundamental."			(5) Multiharmonic down-sweep into decurve	Phyllostomidae  *Brachyphylla cavernarum*	Molossidae  *Tadarida insignis*
				Rhinopomatidae  *Rhinopoma hardwickii*	
			(6) Multiharmonic, brief up-sweep, short narrowband centre, brief down-sweep	Emballonuridae  *Emballonura monticola*	Craseonycteridae  *Craseonycteris thonglongyai*

Table 4.2 continued:

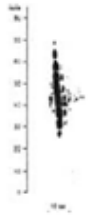
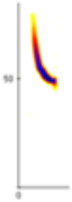
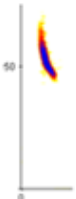
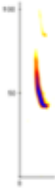
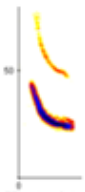
Echolocation call categories outlined in Jones and Teeling 2006		Proposed new echolocation call categories		
Echolocation call type	Bat families Spectrogram	Echolocation call type	Bat families Spectrogram	
(e) Short, broadband dominated by fundamental harmonic	Vespertilionidae  *Myotis daubentonii* "Found only in the Vespertilionidae in cluttered habitats. <5ms."	(7) Very short, broadband, dominated by a single harmonic	Vespertilionidae  *Kerivoula hardwickii*	Furipteridae  *Furipterus horrens*
		(8) Short, broadband, dominated by a single harmonic, mostly FM, but short narrowband ending	Miniopteridae  *Miniopterus natalensis*	Thyropteridae  *Thyroptera tricolor*
			Vespertilionidae  *Cistugo seabrae*	Molossidae  *Tadarida aegyptiaca*

Table 4.2 continued:

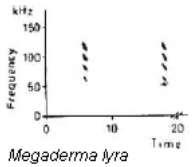
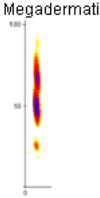
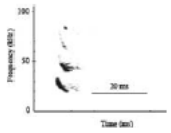
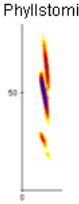
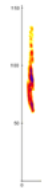
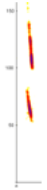
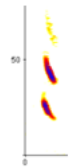
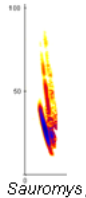
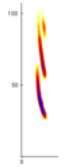
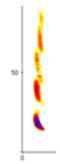
Echolocation call categories outlined in Jones and Teeling 2006			Proposed new echolocation call categories		
Echolocation call type	Bat families	Spectrogram	Echolocation call type	Bat families	Spectrogram
(f) Short, broadband multiharmonic	Megadermatidae	 *Megaderma lyra*	(9) Very short, broadband, multiharmonic, peak harmonic is not the fundamental	Megadermatidae	 *Megaderma lyra*
	Mystacinidae	 *Mystacina tuberculata*		Phyllstomidae	 *Diaemus youngi*
	"Found in a range of families: Megadermatidae, Nycteridae, Phyllostonidae, Mystacinidae, Vespertilionidae, and Natalidae. Varying dominant harmonic."			Nycteridae	 *Nycteris thebaica*
				Natalidae	 *Natalus stramineus*
				Mystacinidae	 *Mystacina tuberculata*
			(10) Very short, broadband, multiharmonic, peak harmonic is the fundamental	Molossidae	 *Sauromys petrophilus*
				Vespertilionidae	 *Arielulus torquatus*
				Megadermatidae	 *Megaderma spasma*

Table 4.2 continued:

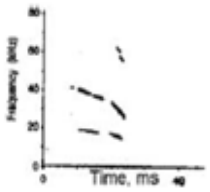
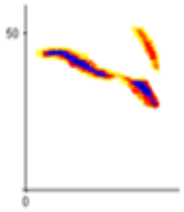
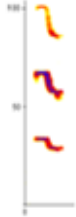
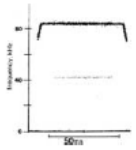
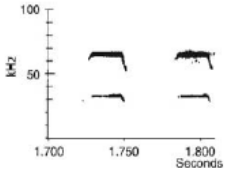
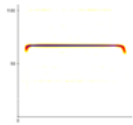
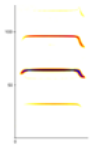
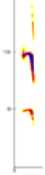
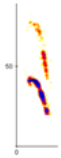
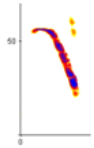
Echolocation call categories outlined in Jones and Teeling 2006		Proposed new echolocation call categories		
Echolocation call type	Bat families Spectrogram	Echolocation call type	Bat families Spectrogram	
(g) Long, broadband, multiharmonic	Myzopodidae  *Myzopoda aurita* "Long duration multiharmonic calls found only in *Myzopoda aurita*, with a dominant second harmonic, up to 23ms long."	(11) Multiharmonic decurve into down-sweep	Myzopodidae  *Myzopoda aurita* Molossidae  *Mops niveiventer*	Mormoopidae  *Pteronotus davyi*

Table 4.2 continued:

Echolocation call categories outlined in Jones and Teeling 2006			Proposed new echolocation call categories		
Echolocation call type	Bat families	Spectrogram	Echolocation call type	Bat families	Spectrogram
(h) Constant frequency	Rhinolophidae	 *Rhinolophus ferrumequinum*	(12) FM up-sweep, mid-length to long CF, FM down-sweep	Rhinolophidae	 *Rhinolophus capensis*
	Mormoopidae	 *Pteronotus parnellii*		Hipposideridae	 *Hipposideros semoni*
	"Pure tones with no bandwidth found in the Rhinolophidae, Hipposideridae, and *Pteronotus parnellii* (Mormoopidae)."			Mormoopidae	 *Pteronotus parnellii*
			(13) Mid-length CF, broadband FM down-sweep	Hipposideridae	 *Hipposideros bicolor*
				Emballonuridae	 *Rhynchonycteris naso*
				Molossidae	 *Molossus rufus*
				Noctilionidae	 *Noctilio leporinus*

Bats use a wide range of frequencies from ~7.5kHz in *Euderma maculatum* (Vespertilionidae) to ~210kHz in *Cloeotis percivali* (Hipposideridae) (see Figure 4.10). In a single call, some bats are able to span ~95kHz (e.g., *Kerivoula hardwickii*, Vespertilionidae), or remain at such a constant frequency that the bandwidth is ~0.5kHz (*Taphozous achates*, Emballonuridae) (see Figure 4.11A). Call durations can be as short as 0.1ms (*Lampronycteris brachyotis*, Phyllostomidae) and longer than 81ms (*Rhinolophus luctus*, Rhinolophidae) (see Figure 4.11B). Finally, bats use between one and four harmonics (doublings in frequency), sometimes extending as high as the fifth harmonic (see Figure 4.12). Most families (12 out of 18) are able to switch the energy in the call between at least two different harmonics. Of the six families that never place the maximum energy in more than one harmonic, Noctilionidae, Miniopteridae, and Myzopodidae use the first harmonic (i.e., the fundamental), and Natalidae and Rhinolophidae use the second harmonic, and Furipteridae use the third. Seven families use one harmonic as the main harmonic (with most energy) more than 90% of the time, but not exclusively: for Molossidae and Vespertilionidae it is the first harmonic, and for Craseonycteridae, Emballonuridae, Hipposideridae, Mormoopidae and Rhinopomatidae it is the second harmonic. The remaining five laryngeal-echolocating families studied switch the harmonic with the maximum energy between three or four different harmonics: Megadermatidae and Phyllostomidae use harmonics one to four; Thyropteridae and Mystacinidae use harmonics one to three, and Nycteridae use harmonics two to five.

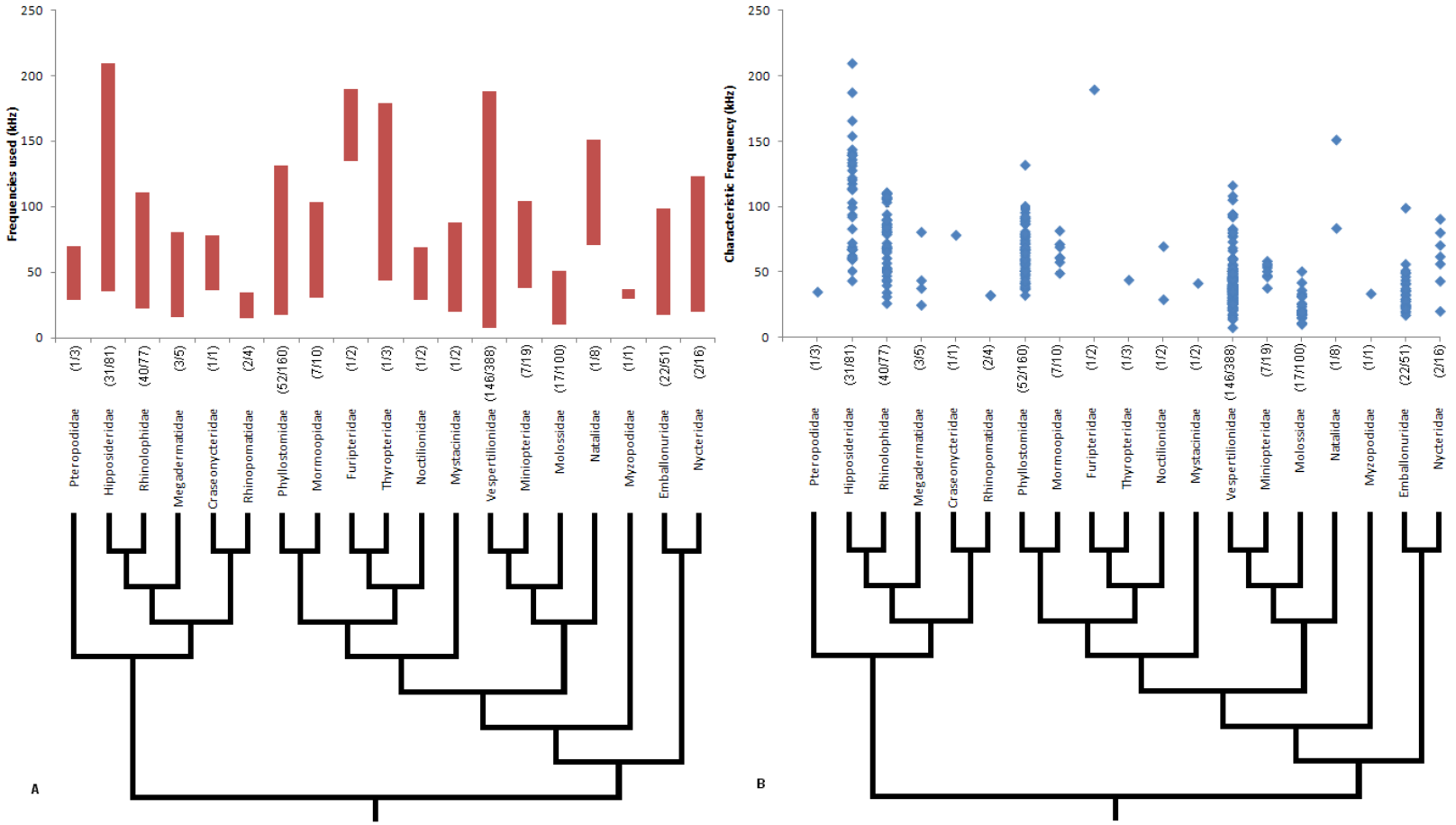


Figure 4.10: (A) shows the range of frequencies (kHz) used by each family, from the median minimum frequency used by any species in any harmonic, to the median maximum frequency used by any species in any harmonic. (B) shows the median characteristic frequencies (kHz) used by each species, grouped by family.

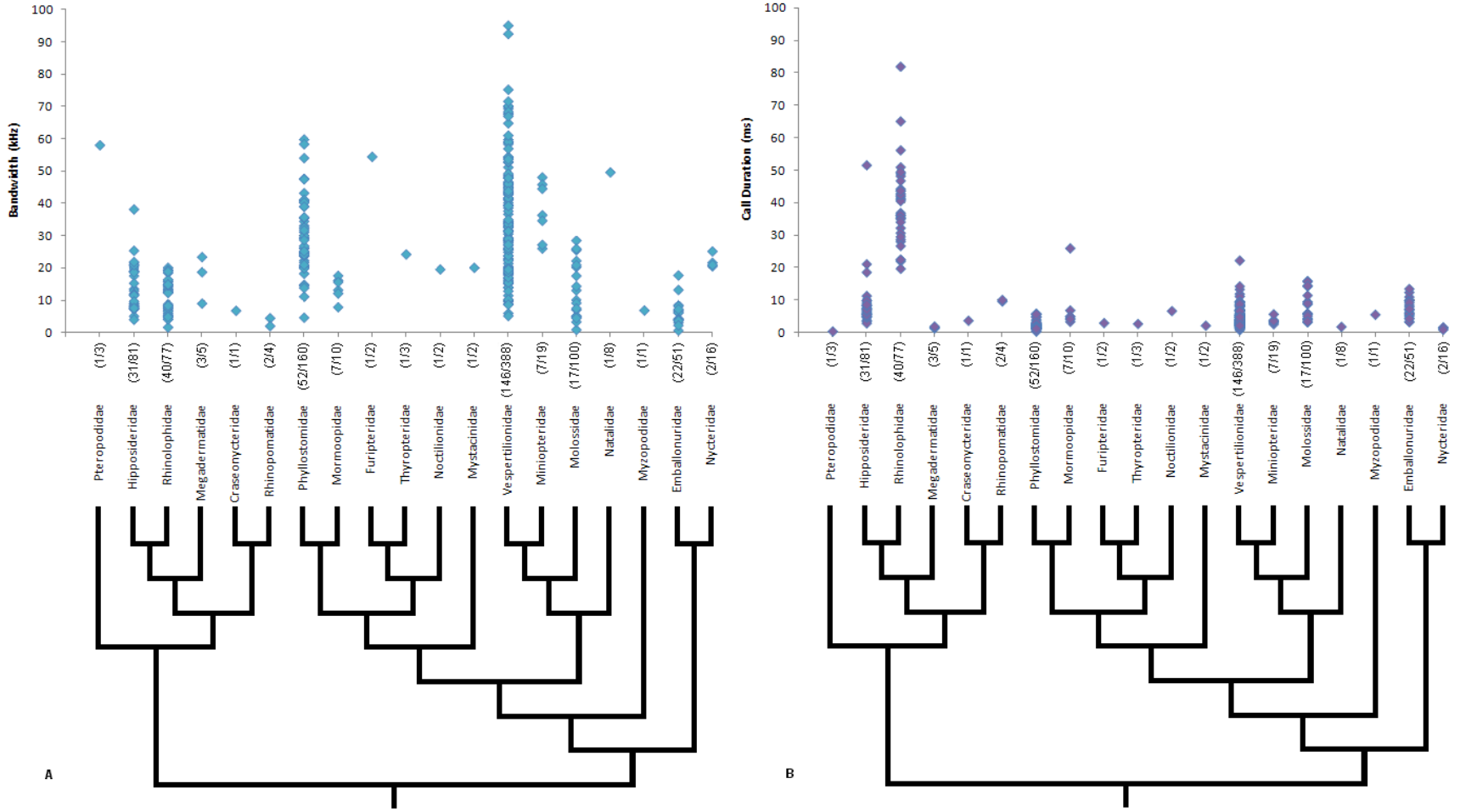


Figure 4.11: (A) shows the median bandwidths used by each species, grouped by family. (B) shows the median call durations used by each species, grouped by family.

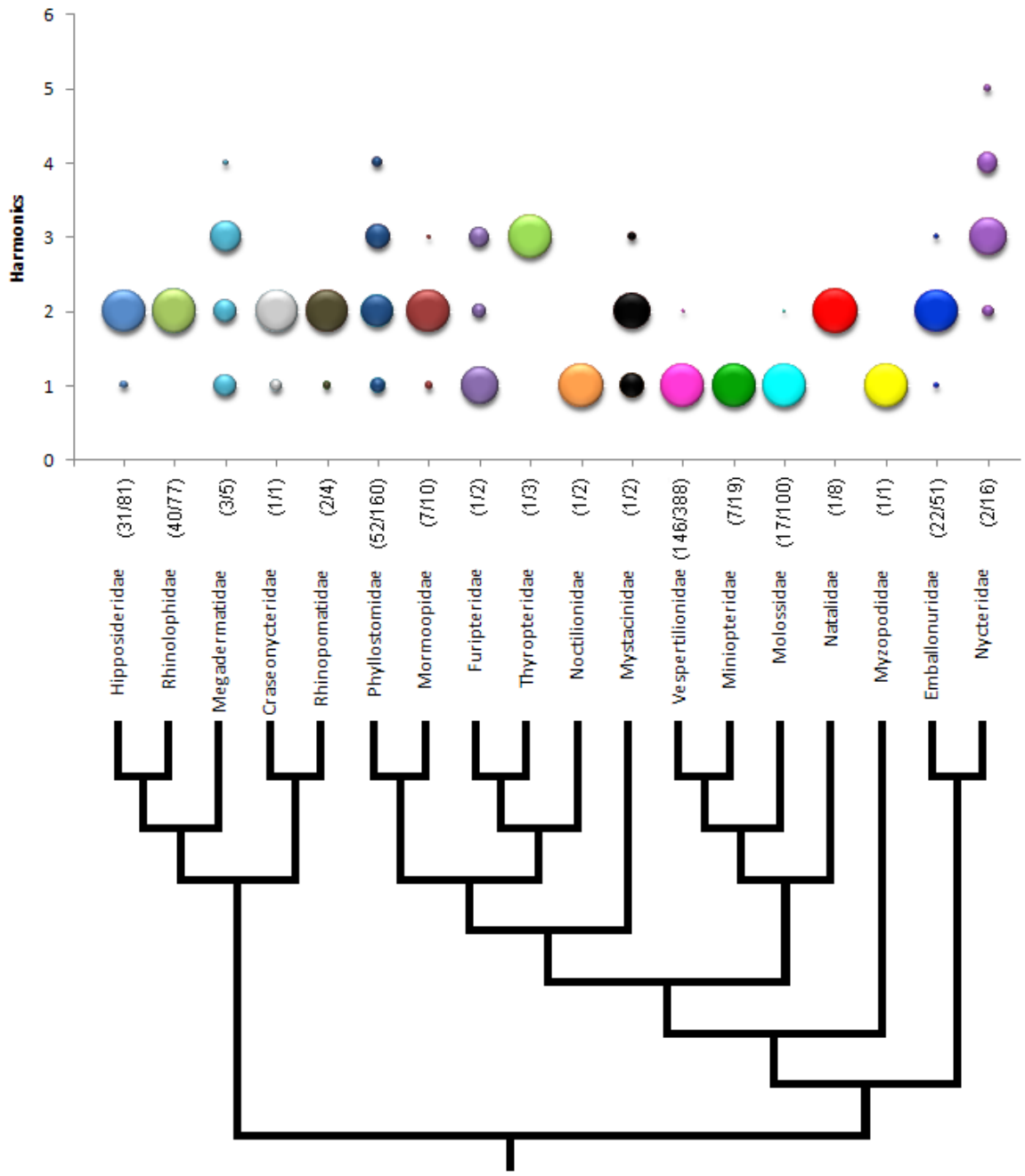


Figure 4.12: The harmonic usage by each family: bubble area represents the usage of each harmonic as the harmonic with the maximum energy, as a proportion of all harmonics used in each family.

4.4.2 Patterns of Phylogenetic and Spatial Signal

The estimated lambda values for each echolocation call parameter, and body mass, indicate a moderately high to very high degree of phylogenetic signal for all echolocation call

parameters (see Figure 4.13). The residuals (the value of the echolocation call parameters after accounting for body mass) show very similar phylogenetic signal values to those of the uncorrected echolocation call parameters, although the phylogenetic signal seen in bandwidth is somewhat lower when body mass is accounted for.

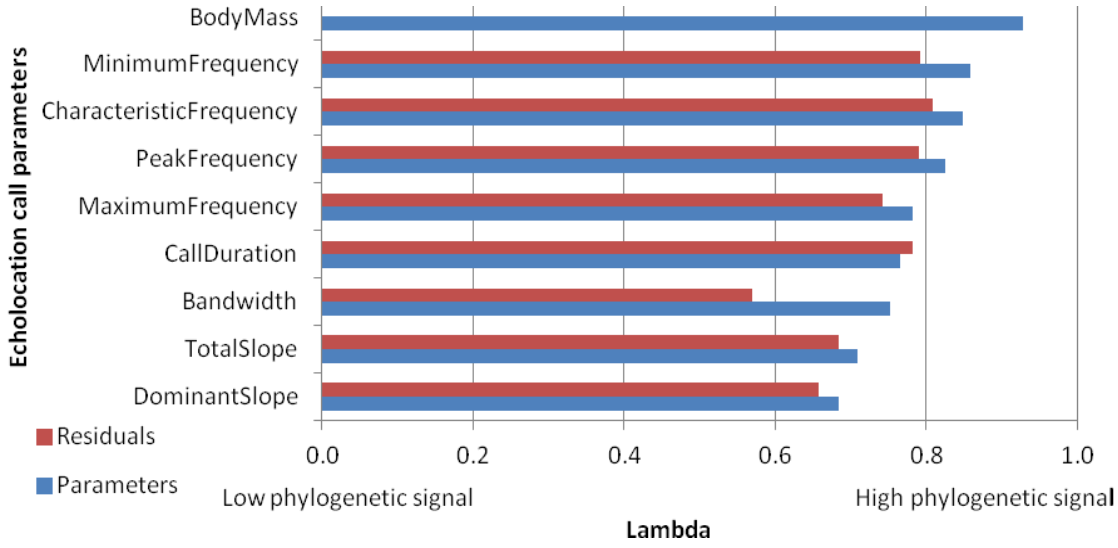


Figure 4.13: Degree of phylogenetic signal shown by body mass and eight echolocation call parameters using Pagel's Lambda.

The lambda values produced by median call parameters are very similar to the values produced by 100 randomly selected individual calls for each species (see Figure 4.14). Most call parameters actually show a small increase in phylogenetic signal, suggesting that median values are fairly conservative.

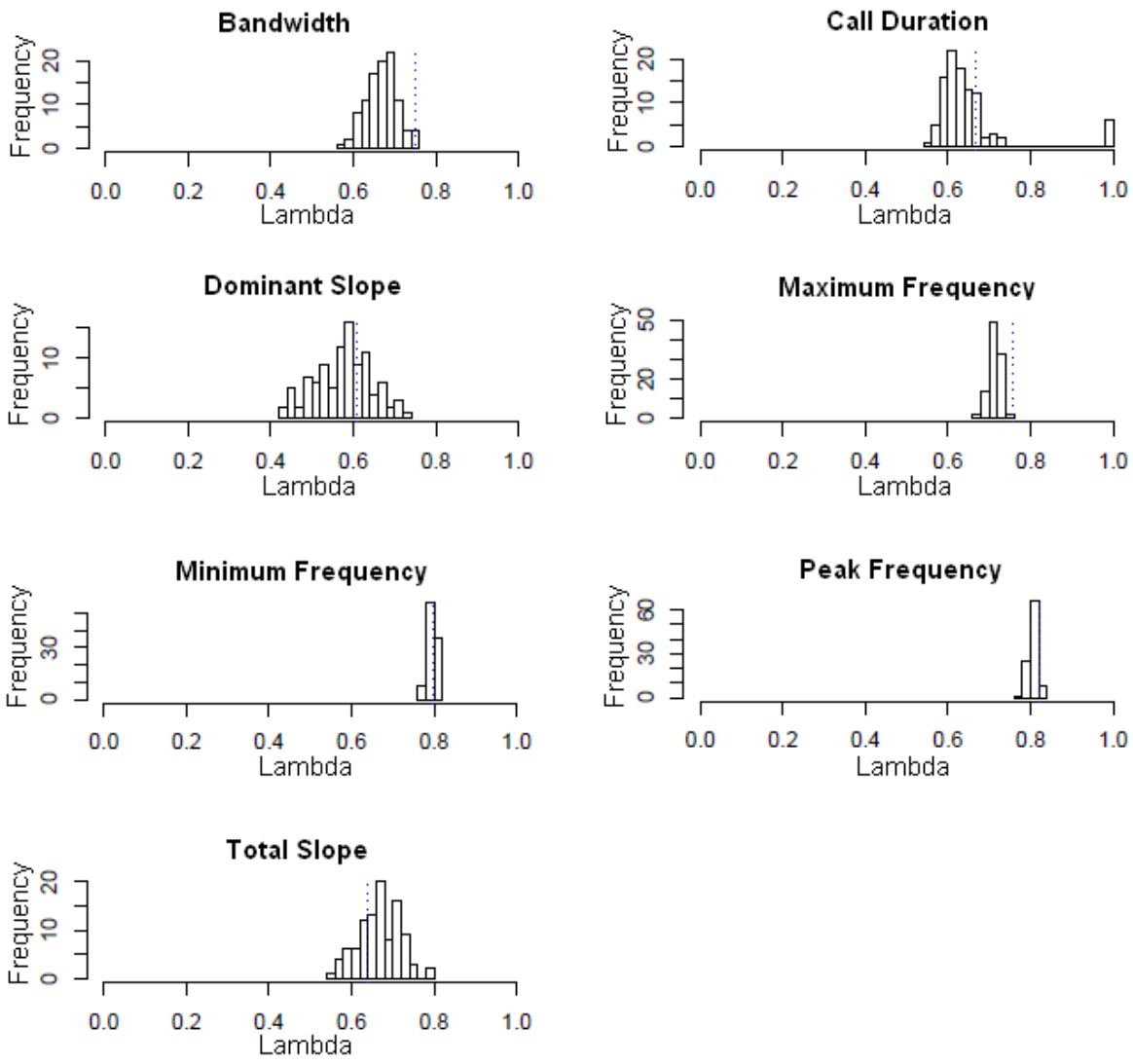


Figure 4.14: Frequency distributions of the lambda values for 100 bootstraps of individual call parameters, compared to the lambda score for the median values of the EchoBank calls only (as opposed to EchoBank calls and literature values shown in Figure 4.13), shown as a dotted blue line.

Some signal seen in the echolocation parameters may be due to species proximity in space as well as, or instead of, their degree of relatedness. Freckleton and Jetz's method (Freckleton & Jetz 2009) allows signal to be further partitioned to account for spatial signal as well as phylogenetic signal. This test showed that the majority of the similarity between species is still due to phylogenetic signal for all echolocation call parameters (see Figure 4.15). However, spatial autocorrelation has a varying impact on different parameters,

tending to influence the minimum and maximum frequencies and the slope of echolocation calls most.

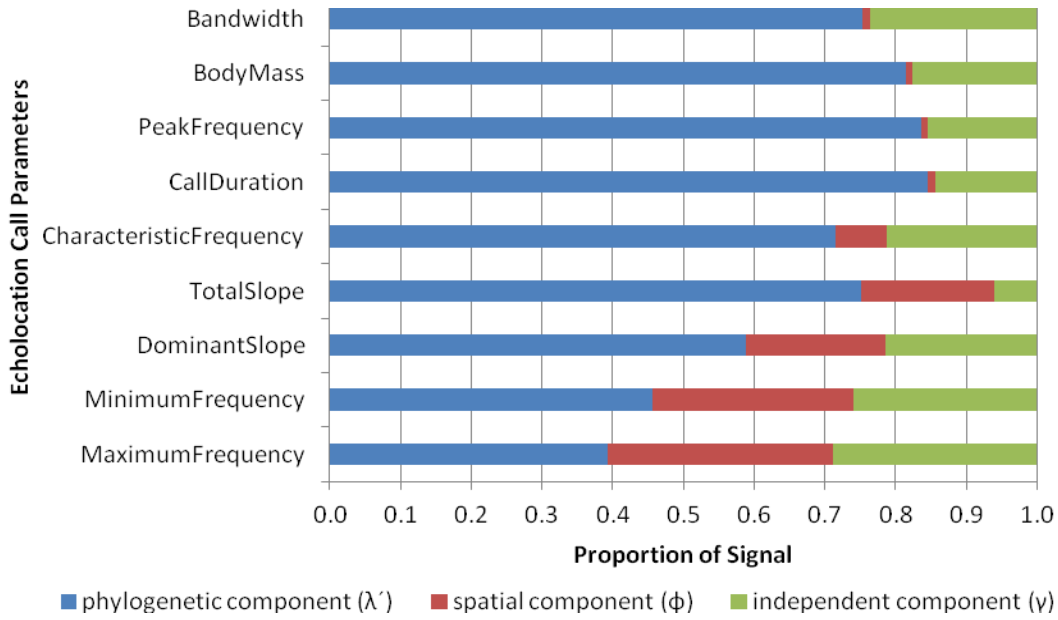


Figure 4.15: Proportional phylogenetic and spatial contributions to echolocation call parameter values.

4.4.3 Processes of Evolution

The estimated kappa values for each echolocation call parameter, and body mass, as well as the echolocation call parameters accounting for body mass, are typically low (see Figure 4.16), indicating that the evolution tends to have been punctuational for most echolocation call parameters, particularly for the slope values, call duration and bandwidth. However, measurement error could reduce kappa values in variables that have evolved under a Brownian Motion model.

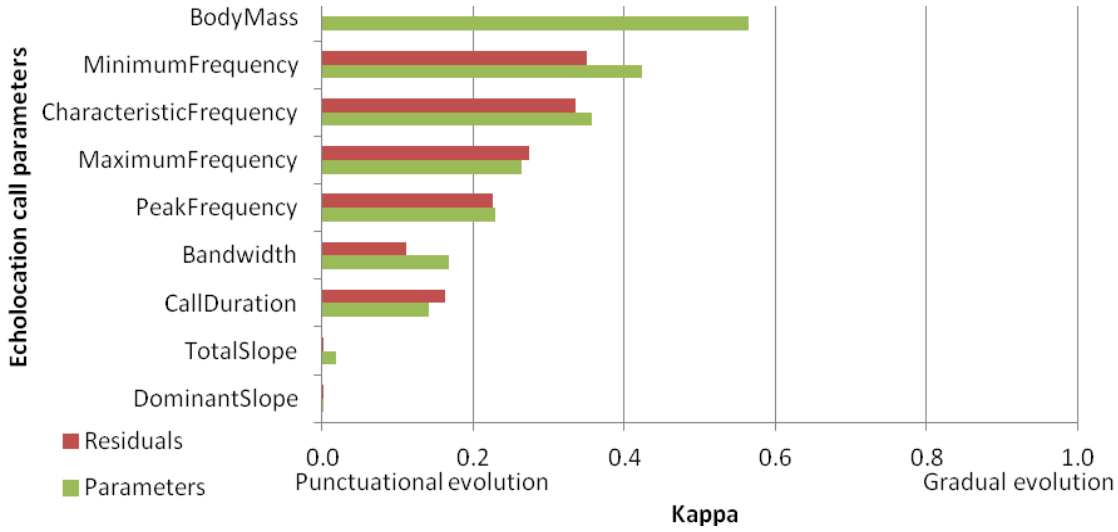


Figure 4.16: Degree of evolutionary gradualism shown by body mass and eight echolocation call parameters using Pagel's Kappa.

The bootstrap analysis (see Figure 4.17) shows that the kappa values produced by 100 randomly selected individual calls for each species are somewhat lower than the values produced by median call parameters, except for the three frequency parameters, which were kappa = 1 regardless of the values used. The results for the both the median value and the bootstrapped values shown in Figure 4.17 are quite different to those for the median values shown in Figure 4.16. The two analyses were performed on different data sets: bootstrapping was performed only on EchoBank data since these data included raw measurements from single calls, whereas the echolocation data from the literature were averages from many calls. The median values presented in Figure 4.17 are from EchoBank data only as well, whereas the much larger data set used for the analysis in Figure 4.16 included both EchoBank data and echolocation data from the literature (see Appendix A for details). Because the results presented in Figure 4.16 are from a larger data set, they are more reliable, though the variability shown between these analyses indicates the unpredictable nature of kappa as an indicator of evolutionary gradualism.

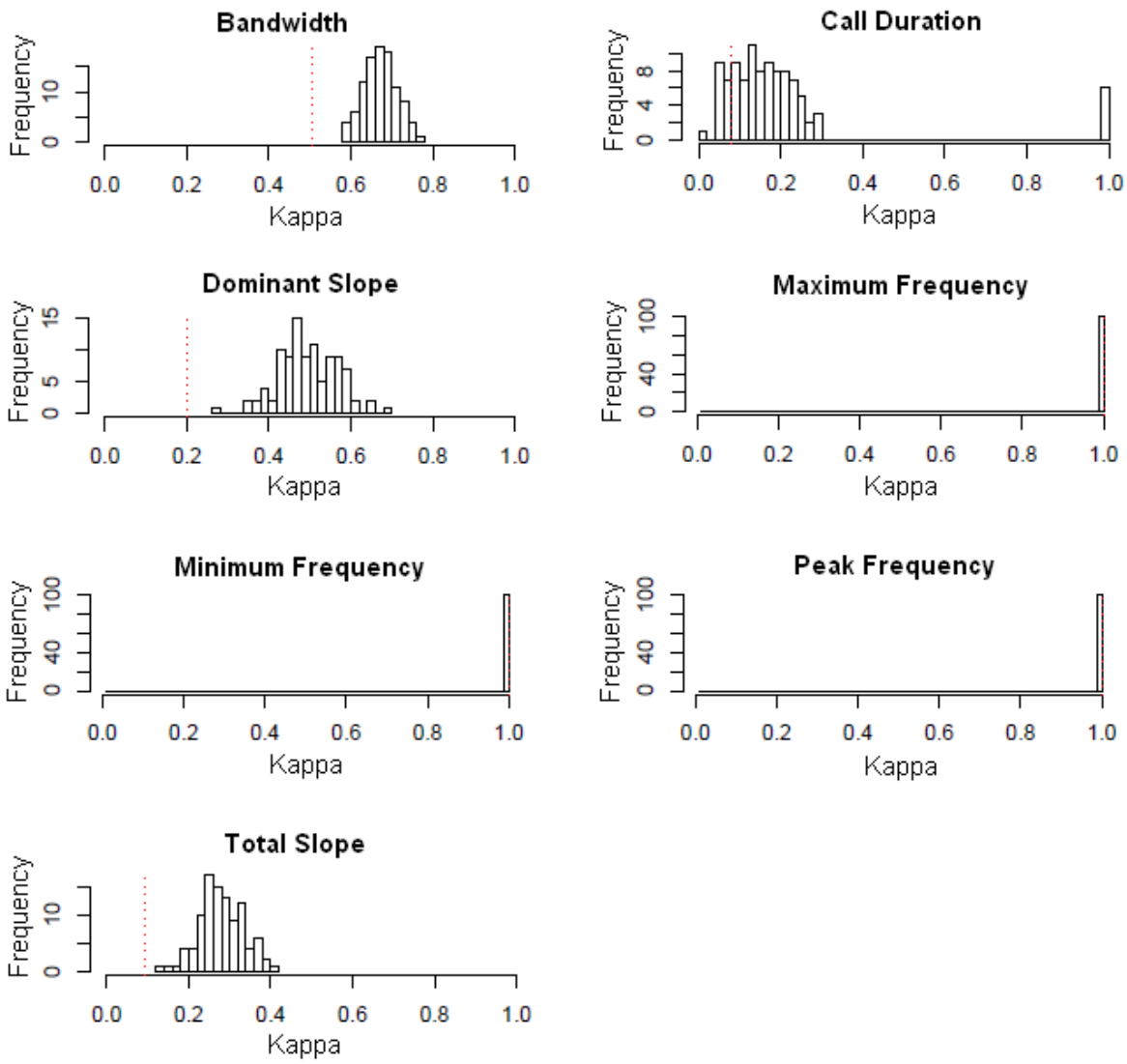


Figure 4.17: Frequency distributions of the kappa values for 100 bootstraps of individual call parameters, compared to the kappa score for the median values of the EchoBank calls only (as opposed to EchoBank calls and literature values shown in Figure 4.16), shown as a dotted red line.

The estimated delta values for each echolocation call parameter, and body mass, as well as the echolocation call parameters accounting for body mass, all have delta scores that indicate species-specific adaptation (see Figure 4.18). Although, minimum frequency has a lower score than the other parameters, it still strongly indicates species-specific adaptation.

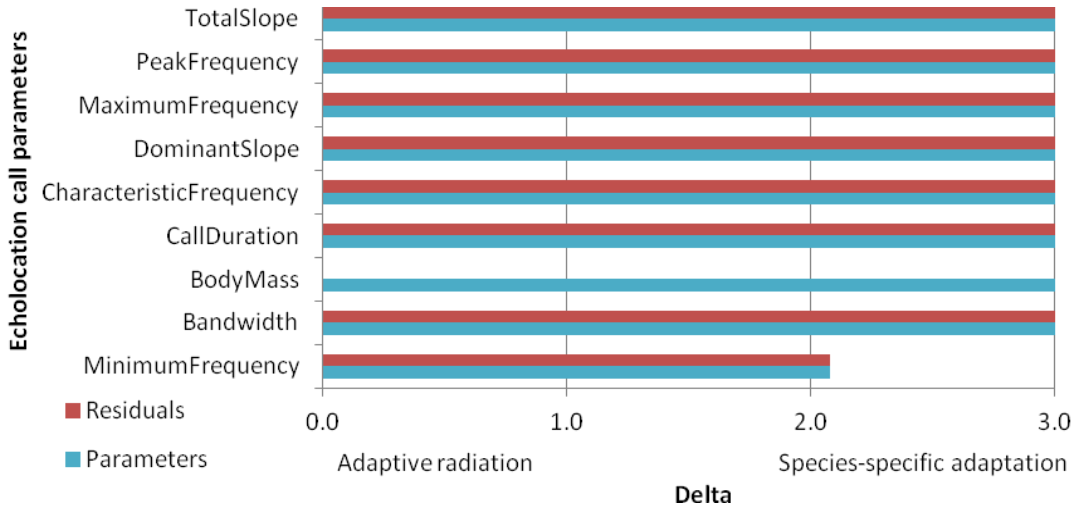


Figure 4.18: Timing of evolutionary change shown by body mass and eight echolocation call parameters using Pagel's Delta.

The bootstrap analysis shows that the delta values produced by median call parameters are very similar to the values produced by 100 randomly selected individual calls for each species (see Figure 4.19), and make no difference to the interpretation of the timing of evolutionary change.

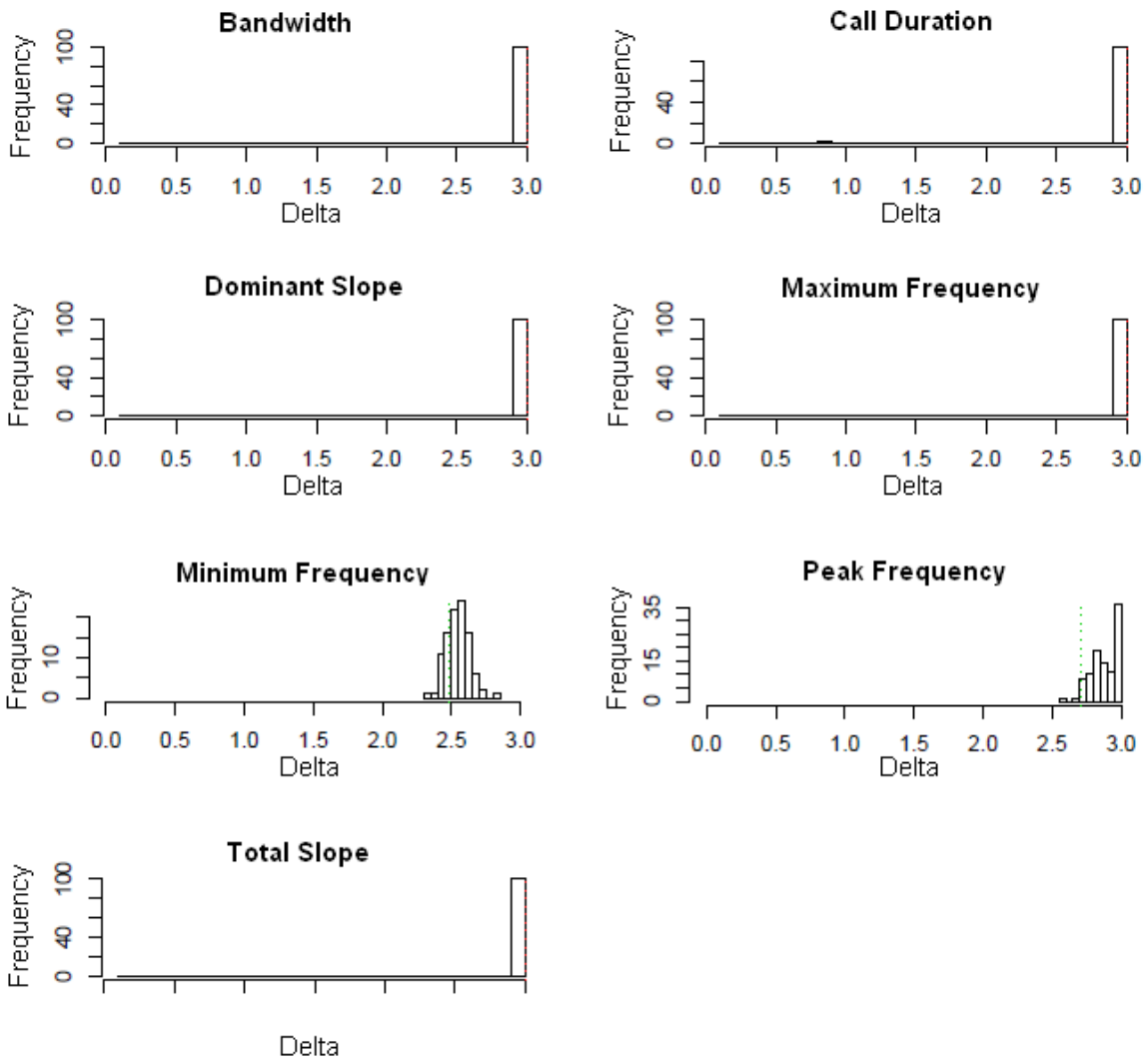


Figure 4.19: Frequency distributions of the delta values for 100 bootstraps of individual call parameters, compared to the delta score for the median values of the EchoBank calls only (as opposed to EchoBank calls and literature values shown in Figure 4.18), shown as a dotted green line.

In the initial test between three models of evolution; Brownian Motion (BM), Ornstein-Uhlenbeck (OU) and Early Burst (EB), all eight echolocation call parameters and body mass were indicated to have evolved under an OU process (see Table 4.3).

		AICc Weights for Evolutionary Model		
		BM	**OU**	**EB**
Parameters	**Bandwidth**	2.99E-17	1.00	1.08E-17
	Body Mass	2.14E-10	1.00	7.75E-11
	Call Duration	7.36E-28	1.00	2.67E-28
	Characteristic Frequency	2.07E-08	1.00	7.52E-09
	Dominant Slope	1.70E-16	1.00	6.14E-17
	Maximum Frequency	1.90E-09	1.00	6.86E-10
	Minimum Frequency	8.62E-05	1.00	3.12E-05
	Peak Frequency	7.19E-16	1.00	2.60E-16
	Total Slope	2.83E-15	1.00	1.02E-15

Table 4.3: The relative weights for the corrected Akaike Information Criterion scores for the three competing evolutionary models: Brownian Motion, Ornstein-Uhlenbeck and Early Burst.

Upon further investigation of the number of selective optima in the OU process, the Bayesian Information Criterion (BIC) indicated that Bandwidth, Call Duration, Dominant Slope, Maximum Frequency, Peak Frequency and Total Slope were most likely to have evolved under an OU process with a different selective optimum (α) for each family, except within the Vespertilionidae where there is a different selective optimum for each subfamily. However, for Body Mass, Characteristic Frequency and Minimum Frequency, the BIC indicated that the most likely evolutionary process was OU with a single selective optimum (see Table 4.4).

Parameters	Model						
	BM	OU All	OU Suborders	OU Families	OU Families, but Vespertilionidae Subfamilies	OU Subfamilies	OU Tribes
Bandwidth	1084.5	1035.5	1043.7	1078.6	986.2	999.3	1030.9
Body Mass	607.9	600.3	610.5	674.4	689.0	714.1	743.7
Call Duration	828.3	765.4	776.1	669.5	634.6	642.5	660.2
Characteristic Frequency	348.6	335.5	339.3	379.1	367.7	388.2	405.7
Dominant Slope	1084.7	1016.0	1018.9	1064.2	919.8	944.6	981.9
Maximum Frequency	1233.7	1197.0	1203.8	1245.0	1187.5	1202.7	1227.0
Minimum Frequency	310.3	297.8	301.1	337.7	334.6	354.2	363.3
Peak Frequency	372.0	338.0	340.4	369.8	323.3	329.1	344.2
Total Slope	1018.6	955.7	956.5	972.8	826.8	850.1	887.3

Table 4.4: The relative weights for the Bayesian Information Criterion scores for the competing evolutionary models: Brownian Motion, Ornstein-Uhlenbeck with a single selective optimum and five models based on Ornstein-Uhlenbeck with multiple selective optima. Numbers highlighted in yellow are the best performing models for each echolocation call parameter.

4.5 Discussion

4.5.1 Echolocation Call Variation

The great diversity of echolocation call structures produced by bats can be seen in Figures 4.1 to 4.9, with variations in duration, bandwidth, frequencies emphasised, harmonic composition, and overall shape. Some families show a remarkable consistency in the structure of echolocation calls between species. In particular, Hipposideridae (Figure 4.2), Miniopteridae (Figure 4.3), Phyllostomidae (Figure 4.5), and Rhinolophidae (Figure 4.6) all demonstrate a family-specific call type (see call types 8, 13, 9, and 12, respectively, in Table 4.2), with only a couple of exceptions. The Vespertilionidae (Figure 4.7) could also

be considered to show a large degree of similarity between species, despite its calls being classified as four different types (3, 7, 8, and 10 in Table 4.2), since these probably represent a continuum of oppositely changing parameters: long duration, low bandwidth calls (3) providing long distance detection, to short duration, high bandwidth calls (7 and 10) which allow precise localization and high resolution interpretation (see G. Jones & Holderied, 2007). Indeed, intra-individual variation can span these call types as a bat contends with different habitats and spatial tasks (Kalko 1995). Figure 4.8 shows one genus of the Vespertilionidae: the *Myotis*. This is by far the most speciose genus in the order Chiroptera and the consistency of the echolocation call structure across the taxon is notable (call types 7 and 8 in Table 4.2).

The potential for variability in echolocation call structure between species of the same family is evident in the Emballonuridae (Figure 4.1), Molossidae (Figure 4.4) and amongst the species of the smaller families (Craseonycteridae, Furipteridae, Natalidae, Myzopodidae, Mystacinidae, Noctilionidae, Nycteridae, Rhinopomatidae, Mormoopidae, Thyropteridae, and Megadermatidae (Figure 4.9)). Some of this variation is likely to be in response to the different habitat types occupied by each species (Fenton 1988; Fenton, Rautenbach, et al. 1998; Jennings & Parsons 2004; Obrist 1995), but rather than showing a continuum of call types as in the Vespertilionidae, these families display apparently discretely different call structures. For example, the Molossidae use call types 3, 4, 5, 8, 10, 11, and 13, and Emballonuridae use call types 3, 4, 6, and 13 (Table 4.2). These call types are not all concurrent alterations of the opposite parameters of a call structure, but rather entirely different call shapes.

Some of the call types illustrated in Table 4.2 demonstrate alternative echolocation call structures for dealing with the same functional tasks. For example, bats searching for food items in cluttered environments need to distinguish targets from other objects. One means to do this is for the bat to emit a narrowband call with a long duration, enabling detection of the fluttering wings of an insect against a still background (approach (a)) (call type 12 in Table 4.2). Alternatively the bat can increase the bandwidth of the echolocation call, which is the equivalent of increasing the range of wavelengths emitted, and helps the bat to

resolve different size classes: insect vs. leaves vs. branches, for example. There are several ways to increase bandwidth: (b) increase the bandwidth of the fundamental harmonic by increasing the maximum frequency, as in call types 7 and 8; (c) increase the bandwidth of all the harmonics, as in call types 9 and 10; (d) increase the energy placed in the non-dominant harmonics, as in call types 4, 5, 6, 11, and sometimes 13 (see Table 4.2). Which approach is used by a species is usually a result of its evolutionary history. For example, Rhinolophidae only ever use approach (a), Miniopteridae only use approach (b), and Vespertilionidae mostly use approaches (b) and (c).

However, some species approach such tasks in a manner that is not typical of their own family, and instead use a call structure that results from a process of convergent evolution. There are several examples of convergent evolution, most famously in the calls of *Pteronotus parnellii* (Mormoopidae), which shows a constant-frequency structure which is extremely similar to that of the Rhinolophidae. The calls of *Hipposideros semoni* and *Hipposideros stenotis* (Hipposideridae) are noted here for the first time to be additional examples of calls converging on the structure typical of rhinolophid calls. These unusual Hipposideridae calls are considerably longer than other hipposiderid calls, and share the short FM initial up-sweep and terminal down-sweep of the rhinolophid call (call type 12, Table 4.2), rather than the high-bandwidth down-sweep typical of hipposiderid calls (call type 13, Table 4.2). Although the calls of these two species have been published previously in a bat identification book (Churchill 2010) and the memoirs of a museum (de Oliveira & Schulz 1997), no attention had previously been drawn to their non-typical structure, and many echolocation experts are unaware of them (Jones, 2011, pers. comm.).

Additionally, *Rhynchonycteris naso* (Emballonuridae), *Molossus rufus* (Molossidae), and the two species of Noctilionidae, have a call type similar to that of the Hipposideridae (call type 13, Table 4.2), although less angular, and therefore not a pure constant frequency tone, indicative of multiple convergent origins. The sole species of Craseonycteridae and some members of Emballonuridae have both demonstrated use of call type 6, and members of Megadermatidae, Phyllostomidae, Nycteridae, Natalidae, and Mystacinidae have converged upon call type 9 (Table 4.2). These examples of convergent evolution indicate the flexible

nature of echolocation call structures and the influence of ecological conditions such as habitat and prey type (Schnitzler & Kalko 1998).

The echolocation call of *Myzopoda aurita* (Myzopodidae) is very unusual. I have classified it as call type 11: a multiharmonic decurve into down-sweep. It is considerably longer than other calls of its type, at around 23ms. However, most calls emitted by *Myzopoda aurita* have a silent section in the centre of this 23ms period, suggesting that the call is actually composed of two calls that merge together. The first resembles call type 13, and the second call type 4 (Table 4.2). When this call was first reported, it was described as being composed of four elements; three in the first half of the call and one decurve in the second half (Gopfert & Wasserthal 1995). Understanding more about the phylogenetic relationship of the Madagascan endemic species to other bat families may reveal a lot about how echolocation originated and diversified.

Of additional note is the use by some families of very high frequencies - in particular members of Hipposideridae, Furipteridae and Natalidae which can have characteristic frequencies of over 150 kHz, giving a wavelength of less than approximately 2.5mm.

Only one other study has attempted a systematic review of the diversity in bat calls in recent years, taking parameters and spectrograms of species belonging to all but one family from the literature (Jones & Teeling 2006). In Table 4.2 I compared my classification of echolocation calls to the categories used by Jones and Teeling, and I found a broad degree of agreement, but some areas of disagreement, particularly regarding the members of each category.

Essentially, the categories designated both by Jones and Teeling and by this study are somewhat arbitrary, placing false divisions between call structures that often differ in a continuous manner. In attempting to clarify the divisions between different call types, I ran several phylogenetically-corrected Principal Component Analyses (PCAs) (Revell 2009) between various combinations of echolocation call parameters. However, no combination produced results which were suggestive of any particular groupings, other than between

call type 12 and all other call types, based on the different call durations. Groupings using continuous measures of calls leave out the limited combinations of call parameters that appear as overall call shape, and prevent effective groups from being distinguish using PCA. This emphasises the difficulty of attempting to understand, and especially to reconstruct, the evolutionary history of echolocation using categories, particularly at family level. This is further emphasised by the degree of polymorphism shown by some families using my new categories, which would lead to even more 'equivocal' branches in the reconstruction shown in Jones & Teeling 2006 (see Figure 4.20).

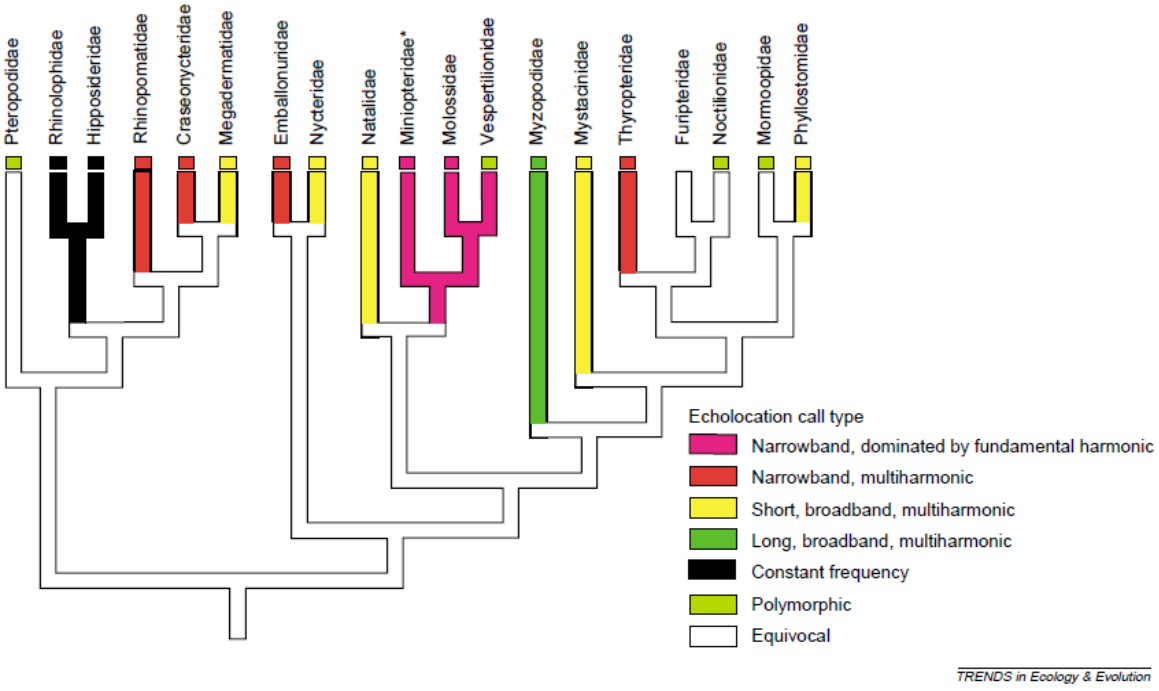


Figure 4.20: Ancestral reconstruction of echolocation call types taken from Jones and Teeling 2006.

4.5.2 Patterns of Phylogenetic and Spatial Signal

I found high phylogenetic signal ($\lambda \geq 0.684$) for all eight echolocation call parameters, though none was as high as for body mass ($\lambda=0.927$). The four measures of frequency had the highest phylogenetic signal ($0.782 \leq \lambda \leq 0.859$), and this is likely to be because of the relationship between call frequency and body mass (Jones 1999). The larger the body size, the larger the larynx, and the lower the sounds it produces (Pye 1979).

Call duration and bandwidth have the next highest phylogenetic signal (λ=0.765, λ=0.751 respectively). Call duration has also been shown to have a relationship to body size (Jones 1999), though less closely than measures of frequency. Both parameters are likely to respond to differences in habitat, as call duration relates to the proximity of objects to the bat, and bandwidth to the degree of resolution necessary to discriminate between objects of different sizes. Because of this environmental pressure on these call parameters, the values have been pushed away from those expected from the phylogeny, and hence the phylogenetic signal is lower.

Total slope and dominant slope had the lowest phylogenetic signal of all the parameters (λ=0.709, λ=0.684). Measurements of the slope of the call co-vary with the bandwidth and call duration, and are likely to be closely related to habitat (Jones & Holderied 2007).

Testing for phylogenetic signal in the echolocation call parameters after removing the effects of body mass did not significantly alter the results, simply reducing the signal slightly in each case.

Lambda scores quantify the similarity between trait values in neighbouring species on a phylogeny, but they do not account for alternative causes of similarity, other than the impact of evolutionary history. The Freckleton and Jetz test (Freckleton & Jetz 2009) partitions this similarity into two sources: that due to sharing an evolutionary history (true phylogenetic signal – λ'), and that due to sharing ecological condition (spatial signal – φ). I expect to find a large portion of the phylogenetic signal revealed by the lambda scores re-assigned to spatial signal in those parameters that are more closely related to habitat: bandwidth, call duration, dominant slope, total slope, minimum frequency, and maximum frequency. I would expect a lower degree of spatial signal in those parameters that are closely associated with body mass: peak frequency and characteristic frequency.

In fact, virtually no spatial signal is found in body mass, bandwidth, peak frequency and call duration. Similarly, body mass showed very low spatial signal in carnivores,

artiodactyls and primates in one study (Freckleton & Jetz 2009), and again in bats, rodents, carnivores and primates in another similar study (Safi, Meri, & Jones 2011). The lack of spatial signal in body mass may be due to the dominance of phylogenetic forces, since body mass is well known to be closely linked to many life history traits in mammals (Charnov 1991), though the relationship is thought to be weaker in bats (Purvis & Harvey 1995). Peak frequency has been shown to be highly correlated with body mass, due to the scaling of the larynx with body size (Jones 1999) and hence spatial signal should be similar for body mass and peak frequency. Call duration has also been shown to be related to body mass, specifically in bats that emit narrowband calls (sometimes known as quasi-constant frequency or QCF) and in Hipposideridae, i.e. call types (3), (4), (5), (6), and (13), since larger bats have a higher wing loading which results in faster flight, allowing the bats to cover greater distances and therefore to need to detect more distant objects. This gives the bats more time between emitting a call and receiving the echo, and therefore allows the use of longer duration calls (Jones 1999). This relationship between body mass and call duration explains the low spatial signal seen in call duration.

The low spatial signal seen in bandwidth (= maximum frequency – minimum frequency) apparently contradicts the high spatial signal seen in both minimum and maximum frequency. Maximum and minimum frequency show high spatial signal because the values of these parameters relate to the degree of clutter in the habitat of each species. Forest bats use higher maximum frequencies because they give greater resolution of small objects, and open-spaced bats use lower minimum frequencies because they attenuate less quickly. Habitat types are clustered in space, resulting in higher spatial signal in the related call parameters. The spatial signal seen in bandwidth, however, is masked, because of the two mechanisms by which bats cope with clutter: most families increase bandwidth to improve the depth of field, but Rhinolophidae maintain a very low bandwidth, and increase call duration, to detect the fluttering wings of insects.

Characteristic frequency also shows low spatial signal. This parameter is derived from the primary parameters of peak, minimum and maximum frequency, depending which showed the lowest variance in each species. It is possible that its inherent low variance is a result of

the close relationship between this parameter and body mass. This might explain why it shows only marginally more spatial signal than body mass.

Total slope and dominant slope show fairly high spatial signal. This corroborates the low lambda scores they showed, and may be due to the impact of habitat on the slope of echolocation calls. Steeper slopes are used in cluttered habitats, such as forests, and shallower slopes in more open habitats, because of the advantageous combination of short call durations and high bandwidths in clutter, and of long call durations and low bandwidths in open space (see Table 4.1) (Jones & Holderied 2007; Fenton 1990; Kalko 1995; Kalko & Schnitzler 1993).

We have seen that there is a strong phylogenetic influence on the values seen in the eight key echolocation parameters, and particularly in bandwidth, call duration, peak frequency and characteristic frequency. These parameters are likely to be strongly linked to body mass, and thus are more constrained to reflect phylogenetic relationships, and have less need to respond to ecological pressures.

It is extremely difficult to decouple the impact of evolutionary history and current ecological conditions when interpreting phylogenetic signal (Revell *et al.* 2008). Evolutionary history represents the trait values held by the ancestors of extant species, and is a result of even older evolutionary history, and past ecological conditions, which exert both constraints and selective pressures on any given trait. Current ecological conditions are related to, and a consequence of, previous ecological conditions, and trait values are thus an accumulation of changing selective pressures and subsequent constraints over evolutionary time. In finding a trait with extremely high phylogenetic signal, we cannot conclude that current ecological conditions are having no impact on the value of that trait, because those conditions might be having the same impact on that trait in all species equally. Likewise, a trait with no phylogenetic signal may not be responding to current ecological conditions, but instead may be free from selective pressures and subject entirely to genetic drift. Hence, evolutionary history is acting in having released any previous constraints.

However, the value of assessing the phylogenetic signal and inferring the relative impact of evolutionary history and current ecological conditions can be found in making comparisons between the different degrees of signal found between traits, without attempting to conclude that a trait with high signal is never subject to selective pressures imposed by its environment, and acknowledging the possibility of overlap between historical and current conditions (Revell *et al.* 2008).

In addition to these limitations, measures of phylogenetic signal may have been over-interpreted in the past. In particular, judgments concerning the evolutionary process or rate have often been attributed to values of phylogenetic signal. For example, high phylogenetic signal has been linked to strong stabilizing selection, niche (or evolutionary) conservatism and a low rate of evolution (Swenson et al. 2007; Zanne, Chapman, & Kitajima 2005), and low phylogenetic signal has been assumed to result from evolutionary lability or rapid evolutionary change (Blomberg et al. 2003; Gittleman et al. 1996). Recent work on simulations of evolutionary rate and process suggest these interpretations may be inappropriate, as low, medium and high values of phylogenetic signal can all result from various combinations of rates and processes of evolution (Ackerly 2009; Revell et al. 2008).

Adding spatial signal also presents complications as it is difficult to disentangle the spatial and environmental contributions to a pattern of trait values, since spatial autocorrelation is a result of many of the same factors as variation caused by the environment (many of which may be adaptive). Spatial signal is usually assumed to be due to shared adaptive evolutionary change between species living in close proximity (Safi *et al.* 2011), and hence measuring phylogenetic and spatial autocorrelation in trait data reveals three components of the total variation: that due to shared evolutionary history, that due to the environment, and the unexplained (or ‘independent’) component.

4.5.3 Processes of Evolution

Having reviewed the patterns in the diversity and phylogenetic distribution of echolocation call structures both qualitatively and quantitatively, we can now assess the processes of evolution that have taken place to produce the patterns.

The first two analyses looked at how change in echolocation traits was distributed over time, i.e. along the branches of the phylogeny. Firstly, Pagel's kappa was estimated, to determine whether change was gradual ($\kappa = 0$) or punctuational ($\kappa = 1$). Punctuational change is expected to be concentrated at the nodes, as speciation occurs, whereas gradual change is distributed more evenly along the branches, throughout the history of a species. I expected to find a tendency towards punctuational change, as echolocation call structures are most likely to change in response to a change in another aspect of a bat species' biology, for example, in body mass, habitat, or community structure (Kingston & Rossiter 2004; Rice & Hostert 1993; Schluter 2001; Via 2001). Gradual change seems unlikely as echolocation call structure is functionally constrained. I would expect those parameters associated most closely with habitat to have the strongest punctuational trends, i.e. those parameters that showed the least phylogenetic signal. Those that are more closely linked to body mass, I would expect to change in a more gradual manner.

The kappa scores showed that only body mass showed any tendency towards gradual change, and, as expected, the four measures of frequency with the highest phylogenetic signal (lambda), were most similar to body mass, although they tended towards a punctuational model of evolutionary change. The other echolocation call parameters showed increasing degrees of punctuational change, from bandwidth through call duration and total slope to dominant slope, which scored 0 – total punctuational change. This indicates that changes in body mass are unlikely to be precipitating speciation events, such as is suggested by Kingston and Rossiter (Kingston & Rossiter 2004), whereas echolocation parameters that are closely linked to habitat and sensory function are associated with speciation. Controlling for the effect of body mass on the echolocation call parameters had little impact on the degree of gradualism, with most parameters very similar with and without the effect of body mass.

The second indicator of the distribution of trait change over time was Pagel's delta. This parameter estimates the point at which most trait change occurred over the phylogeny as a whole. Scores of $\delta < 1$ indicate early change, as in adaptive radiations, and when $\delta > 1$, change was late, indicating species-specific change. Although bats have been cited as an example of adaptive radiation due to the key innovations of flight and echolocation (Barton 1995; Heithaus 1982; Jones & Teeling 2006; Seehausen 2004), I would not expect to find early change in echolocation parameters, because the diversity of call types seen would not be present if the majority of change had taken place in early bat lineages. However, all echolocation parameters and body mass showed delta values of considerably greater than one. All but one parameter had a score of $\delta = 3$, and the remaining parameter, minimum frequency scored $\delta = 2.079$; still significantly over 1. These scores indicate that changes in body mass and echolocation call parameters occur late in the phylogeny in a species-specific manner, i.e. echolocation call structure was not determined prior to the diversification of bats. Controlling for the effect of body mass on the echolocation call parameters had no impact at all on the timing of evolutionary change.

Across the bat family, the Ornstein-Uhlenbeck (OU) model is the most likely mode of evolution for body mass and all eight echolocation call parameters. This suggests that one or more selective optima have constrained these traits over the course of evolution. OU has been found to best explain body mass evolution in bats in a previous study using the same body mass dataset but an earlier derivation of the phylogenetic supertree (Cooper & Purvis 2010). This result was in contrast to the finding of an Early Burst (EB) model in all mammals as a group. Cooper & Purvis (2010) suggested that the different evolutionary process might be the result of constraints on body size imposed by the demands of flight. Further to this, I suggest that the finding of an OU model in the evolution of echolocation is at least partially a consequence of the link between body mass and echolocation call parameters.

Additionally, I suggest it would be extremely unlikely to find that either of the alternatives to OU is favoured. Echolocation is a functional trait that should affect the fitness of the

individuals using it, and is of interest because it is likely to be adaptive. If the mode of evolution had been Brownian Motion (BM), that would have suggested that either changes to the traits were a result of genetic drift, or that the selective optimum for each trait had changed randomly over time (Felsenstein 1988 (see Harmon *et al*. 2010)), which is unlikely for a functional trait unless there are random changes to environmental conditions. Early Burst (EB) has been found to be rare in the evolution of body size and shape (Harmon *et al.* 2010), although Cooper & Purvis (2010) found it was favoured when explaining the evolution of mammalian body mass. EB predicts that younger subclades will show less variation than older, more inclusive subclades – indicating adaptive radiation, which was not supported by Pagel's delta scores.

Exploring the mode of evolution further confirmed the finding of OU as the most likely mode of evolution for all echolocation call parameters, and once again divided the parameters into two groups: those that are more closely linked with body mass, and those that are more responsive to changes in ecological conditions. Body mass, characteristic frequency and minimum frequency favoured an OU model with a single selective optimum (α), mirroring the Pagel's kappa scores which indicate that these three parameters show the most gradual evolutionary change. The remaining parameters favoured an OU model with a different selective optimum for each family, except Vespertilionidae, with a different selective optimum for each subfamily. This may not indicate that a particular adaptive regime is confined to these subclades, but rather that this roughly represents the number and spread of selective optima brought about by other traits.

4.6 Conclusions

Echolocation calls vary in a continuous manner, with parameters 'trading off' against one another to produce functionally relevant call shapes. These convergent call shapes can often be formed in different ways, having followed unique evolutionary pathways. Deconstruction of echolocation calls into component parameters reveals which aspects of calls are more constrained by evolutionary history, and which are more pliable by ecological conditions.

One set of call parameters are more constrained by evolutionary history (higher lambda scores), less influenced by habitat (lower phi scores), and evolve more gradually (higher kappa scores) in a directional manner towards a single selective optimum (OU model with single alpha). These parameters are peak frequency, characteristic frequency, call duration and bandwidth, and they are strongly associated with body mass.

The other set of call parameters are less constrained by evolutionary history (less high lambda scores), more influenced by habitat (higher phi scores), and evolve in a punctuational (lower kappa scores) and directional manner towards several selective optima (OU model with multiple alphas). These parameters are maximum frequency, minimum frequency, total slope and dominant slope.

All the call parameters show a greater than average degree of influence from evolutionary history, a lower than average degree of influence from environmental conditions, and a tendency towards species-specific, punctuational, and directional evolution. In addition, whilst habitat and functionality determine some aspects of the outline structure of an echolocation call, evolutionary history has left its mark of constraint in producing so many different solutions to the same echolocation tasks.

5 Chapter 5: The origin of echolocation in bats: what did the first echolocation calls sound like?

5.1 Abstract

A major challenge for evolutionary biologists is to understand the origin and development of complex traits. Laryngeal echolocation in bats is one such trait and until now no quantitative study regarding the ancestral echolocation call has been attempted. Here I use echolocation call data from up to 410 species (44% of all currently described taxa), 120 genera (74%) and all 19 families of echolocating bats, and a complete, species-level phylogeny to (1) reconstruct the evolutionary history of echolocation call structure using contemporary phylogenetic comparative methods, (2) consider other evidence for ancestral echolocation call structure, and (3) infer the ancestral bat's habitat, wing morphology, foraging style, and prey type from the predicted ancestral call type. I used four ancestral character estimation techniques (squared-change parsimony, least squares phylogenetic independent contrasts, maximum likelihood and generalised least squares) to analyse continuous frequency and time variables of echolocation calls and principal component scores generated from these. The continuous parameters used were bandwidth, call duration, characteristic frequency, dominant slope, maximum frequency, minimum frequency, peak frequency, and total slope. I also used maximum likelihood to compare the results of discrete estimations using three alternative rate matrices, first using the call type categories described in Chapter 4, second using harmonic structure, and third considering bandwidth, call duration, characteristic frequency, and total slope in discrete categories. I also reviewed the output of the mammalian larynx, the variation in the vocalizations of a selection of species from each mammalian order, and the ontogenetic development of echolocation calls in bats. All ancestral reconstruction techniques, discrete analyses and further evidence suggested an ancestral call type that was fairly short in duration, multi-harmonic, and narrowband as the ancestral echolocation call of bats. This work corroborates and justifies the predictions of several previous workers. This call type suggests that the proto-bat was a slow and manoeuvrable flier with an opportunistic and omnivorous diet and may have used a perch-hunting foraging strategy.

5.2 Introduction

5.2.1 Background

One of the great challenges in evolutionary biology is in elucidating the small steps involved in the evolution of complex traits (Raff 1996; Riska 1986). Laryngeal echolocation in bats is one such trait, as it requires the correlated evolution of the larynx, cochleae, pinnae (external ears) and the auditory regions of the brain (Teeling 2009). Whilst the skull, ear bones and laryngeal bones can be seen in fossilised bats (Gunnell & Simmons 2005; Simmons & Geisler 1998), the sounds used by bats at the time of their origin 83 to 58 million years ago (Springer, Teeling, & Madsen 2001) and during their subsequent proliferation are unrecoverable. Gaining insight into the structure of the earliest echolocation calls, and the manner in which they have evolved into the current pattern of diversity requires us to look elsewhere than the fossil record.

There has been great debate of the origin and evolution of echolocation, ranging from the relative timing of the evolution of flight and echolocation (Arita & Fenton 1997; Denzinger, Kalko, & Jones 2004; Gunnell & Simmons 2005; Schnitzler et al. 2004; Simmons & Geisler 1998; Simmons et al. 2008; Speakman 2001; Springer, Teeling, & Madsen 2001; Veselka et al. 2010), through the number of origins of echolocation (Eick et al. 2005; Jones & Teeling 2006; Springer, Teeling, & Madsen 2001; Teeling 2009; Teeling, Madsen, & Van 2002; Teeling et al. 2000), to the structure and function of the first echolocation call (Arita & Fenton 1997; Eick et al. 2005; Fenton 1984; Fenton et al. 1995; Jones & Teeling 2006; Pye 1980; Schnitzler et al. 2004; Simmons 1979; Simmons, Kick, & Lawrence 1984; Simmons & Stein 1980). Changing views on these questions over time have mainly been due to changes in our understanding of bat and order-level mammalian phylogenies (Simmons & Geisler 1998) as molecular phylogenetics uncovered many of the homoplasies mistaken for homologies during the era of morphology-only phylogenetics. As Teeling *et al*. (2002) point out, resolving the disagreements in the relationships among families of bats, and between bats and other mammalian families, is a necessary first step in understanding the evolution of echolocation.

The remarkable diversity, and frequent convergence, seen in the duration, frequencies, harmonic composition and bandwidth of the echolocation calls used by the 930 extant species of laryngeally echolocating bats hints at the difficulty in reconstructing the evolutionary history of echolocation. However, this diversity can also be used to extract clues about the morphology, ecology and behaviour of the proto-bat from the ancestral reconstruction of its echolocation call. Reconstructions can inform our understanding of the precursor to echolocation: for example, did echolocation arise from communication calls or independently? Comparisons with extant species might suggest whether the proto-bat was arboreal or terrestrial; an insectivore or otherwise; a glider, a flier, or non-volant; and, if volant, a perch hunter (waiting on a branch for prey to pass), gleaner (plucking stationary prey from leaves, branches, or the forest floor) or aerial hunter (catching flying prey on the wing).

Our current knowledge is scant, though there has been a great deal of supposition regarding the early evolution of bats. The fossil record is relatively poor for bats, as bat bones do not fossilise well (Thewissen & Babcock 1992). Of the bat fossils that have been found, none are clear transitional forms, and all have fully formed wings that appear to be capable of flapping flight (Simmons et al. 2008; Thewissen & Babcock 1992). The wings of fossil bats tend to be short and broad, which is commensurate with evolution from a gliding ancestor, and also suggests that proto-bats were slow-flying and manoeuvrable: traits suitable for forested habitats (Norberg 1994).

Cochlear and hyoid morphology indicate that all early bats were capable of echolocation, but the fossils do not give away many hints as to the kinds of calls early bats may have emitted, except for the likelihood, based on moderate cochlear size, that echolocation was low-duty (i.e., short calls with relatively long periods of intervening silence) (Springer, Teeling, & Madsen 2001).

Our current understanding of bat phylogeny makes the three hypotheses of the origination of flight and echolocation (‘flight-first’, ‘echolocation-first’ and ‘tandem evolution’: see

Speakman (2001)) equally likely. The recent discovery of an early fossil bat, *Onychonycteris finneyi* (52.5 mya), was followed by the revelation that whilst it could have flown, it could not echolocate (Simmons *et al.* 2008). However, this finding has since been disputed, based on a comparative analysis of stylohyal and tympanic bones (Veselka *et al.* 2010), suggesting that *O. finneyi* was a flying echolocator.

Regarding the number of origins of echolocation, our current understanding of the phylogeny of bats indicates that laryngeal echolocation either arose once, in the ancestor of all bats, and was secondarily lost in the Pteropodidae (with subsequent gain of tongue-clicking in some species), or that there were at least two independent gains of laryngeal echolocation, once in the ancestor of the Vespertilioniformes, and once in the ancestor of the Rhinolophoidea (Teeling 2009) (see Figure 5.1). Most early studies assume a single origin of laryngeal echolocation because prior to Teeling *et al*.'s molecular analysis in 2000, laryngeal echolocators were thought to form a monophyletic group. Now that the monophyly of bats has been broadly accepted, support for a single origin and secondary loss (Jones & Teeling 2006; Springer, Teeling, & Madsen 2001; Teeling et al. 2000) seems roughly equal in strength to evidence for two independent origins (Eick et al. 2005; Li et al. 2008; Li, Wang, et al. 2007; Teeling et al. 2000), though further molecular evidence may help to resolve the argument.

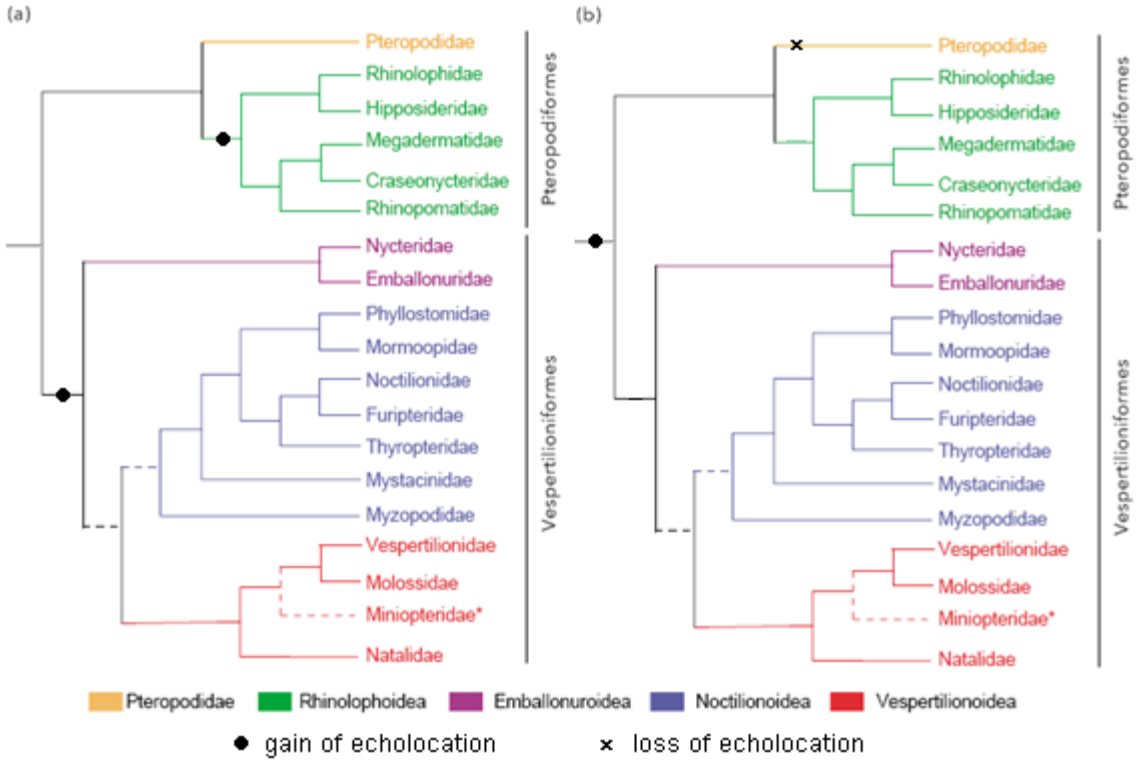


Figure 5.1: Alternative evolutionary scenarios for the origination of echolocation; (a) Two independent gains of echolocation; (b) Single gain and subsequent loss of echolocation. Figure adapted from Jones & Teeling 2006.

The possible structure and function of the ancestral echolocation call has been less contentious than the debate on the relative timing of the evolution of flight and echolocation in bats, though it has been the subject of less research. Most researchers agree that the proto-bat used a low duty cycle, multi-harmonic, short duration, narrowband call (see Figure 5.2) (Fenton 1984; Fenton *et al*. 1995; Jones & Teeling 2006; Pye 1980; Simmons 1979; Simmons *et al*. 1984; Simmons & Stein 1980; Simmons & Geisler 1998b; Springer *et al*. 2001), except Schnitzler *et al*. (2004), who propose that it was broadband, rather than narrowband. This call structure was initially put forward by Simmons in 1979 and was explained as the ancestral call since the larynx normally produces harmonically-structured sounds (Simmons & Stein 1980), but since then little justification for this assumption has been presented.

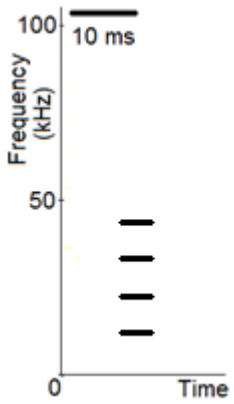


Figure 5.2: The hypothesised ancestral echolocation call: a multi-harmonic, short duration, narrowband call.

In Simmons' (1979) analysis, he used the diversity of echolocation call structures exhibited by 25 species of extant bats in 22 genera and 11 families to create a cladogram based on call structures (see Figure 5.3), radiating out from the hypothesised ancestral call to extant call types, based on qualitative features of calls.

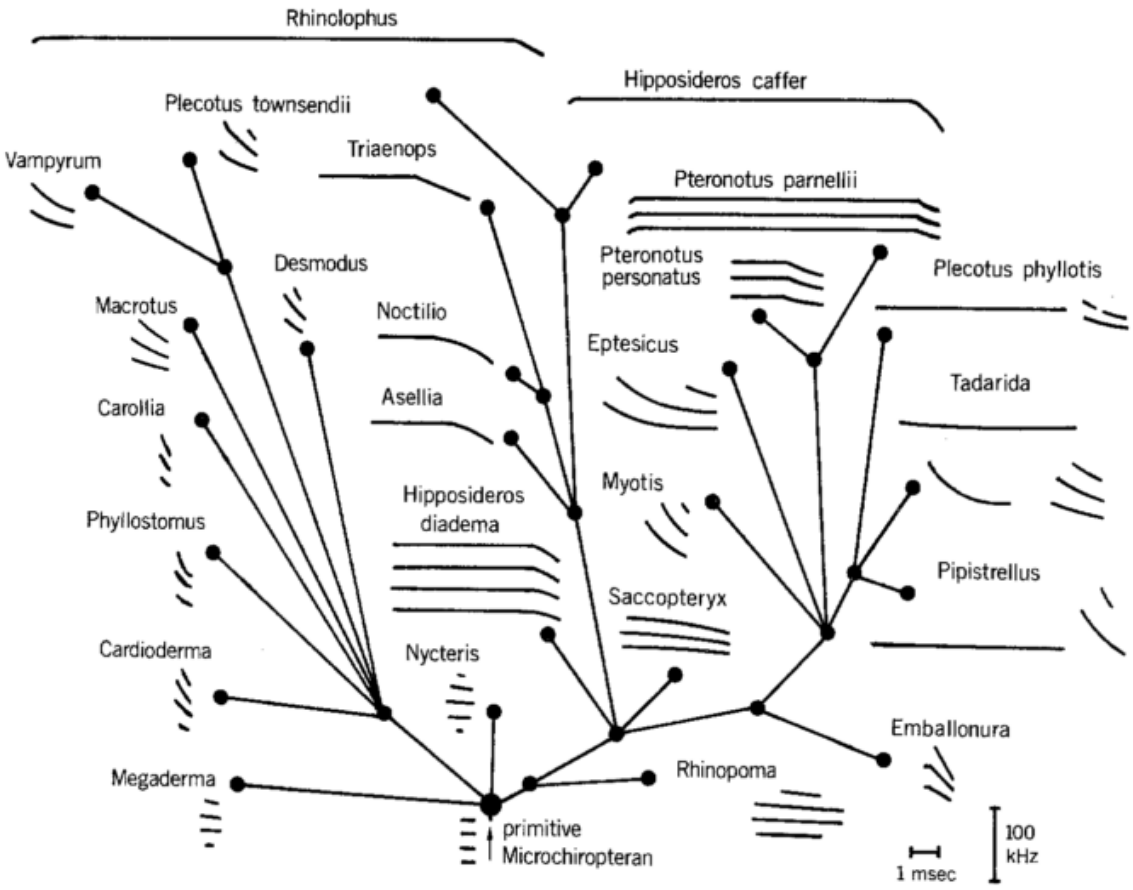


Figure 5.3: Copied from Simmons 1979: A cladogram obtained using the family structure for the sonar sounds of twenty-five species of bats by graphing their relative similarities on seven descriptive dimensions with respect to a hypothetical primitive orientation sound.

Simmons' ideas can be empirically and more thoroughly addressed through the use of modern comparative methods, using a phylogeny constructed not from the calls themselves, but from an independently generated dataset of morphological and molecular characters, and assessing the echolocation call structures of bats given this phylogenetic framework. In particular, the use of ancestral character estimation methods allows the reconstruction of the evolutionary history of bat calls based on the diversity and distribution of current traits and an independently derived phylogeny (Frumhoff & Reeve 1994; Schluter *et al.* 1997).

Due to the poor estimates of phylogeny prior to the use of molecular techniques, there was confusion in the interpretation of the pattern of echolocation call structures produced by

bats. Bats in the families Phyllostomidae, Megadermatidae, Nycteridae, and Rhinopomatidae were all named as having primitive call structures (Simmons & Stein 1980), and the Emballonuridae was thought to be a stem family, responsible for the great diversity of call structures seen across Chiroptera (see Figure 4.1 of Chapter 4, section 4.1.1) (Pye 1980; Simmons *et al.* 1984). Mystacinidae was thought to be an 'advanced' family with a primitive echolocation call structure (Pye 1980).

Molecular analyses place the order Chiroptera in a basal position within the superorder Laurasiatheria, along with hedgehogs, shrews, odd-toed ungulates, even-toed ungulates and whales, carnivores, and pangolins, and reject its previous placement with primates, colugos and treeshrews (see Springer & Stanhope 2004). Additionally, the major relationships between families of bats have been resolved, placing the Old World fruit bats (Pteropodidae) alongside the superfamily Rhinolophoidea, thereby splitting the microbats into two subfamilies – Pteropodiformes and Vespertilioniformes (reviewed in Springer & Stanhope 2004). Given this well-supported phylogeny, reconstructed by the supertree presented in Chapter 3, and echolocation data from 410 species of extant bats, ancestral character estimation techniques can be used to empirically reconstruct the evolutionary history of echolocation in bats and the ancestral bat call.

5.2.2 Hypotheses

Here I use four different statistical methods (squared change parsimony, maximum likelihood, least-squares phylogenetic independent contrasts, generalised least squares and incorporating different models of evolution (Brownian Motion and Ornstein-Uhlenbeck)) to reconstruct the evolutionary history of eight echolocation call parameters and the principal components of those parameters. Only the method referred to as generalised least squares uses the Ornstein-Uhlenbeck model of evolution found to be most likely in Chpater 4, but I include the other methods for comparison. I also use three kinds of discrete call descriptions and varying rate matrices to reconstruct calls without the potential for spurious reconstructions. I chose to use these seven different techniques as ancestral reconstruction

techniques can be unreliable and inaccurate, and this can be compensated for by using a number of different methods (Cunningham 1999; Losos 1999).

If ancestral character techniques produce a reliable prediction of the ancestral call type, I predict a similar call to that hypothesised by previous workers (Pye 1980; Simmons 1979; Simmons & Stein 1980): fairly short, multi-harmonic, and narrowband. However, since reconstructing continuous traits may lead to combinations of characters that are non-functional, continuous methods may reconstruct a non-functional ancestral call type. The methods I have used to reconstruct discrete characters are restricted to the values found in extant taxa, and therefore I predict a reconstruction of a call type that is unlikely to be a realistic estimate of the simple, early calls used by proto-bats. I also predict that the most well-represented call type amongst the extant taxa will be reconstructed as the ancestral call type, due to the algorithms used by ancestral reconstruction techniques (Webster & Purvis 2002).

As well as using a large taxon set and a wide range of methods, considering the results in the context of other evidence should improve the reliability of ancestral reconstructions. Key to reconstructing the origin of echolocation is an understanding of the precursor to echolocation, and its mode of production. Since laryngeal echolocation calls are likely to be derived from communication calls (Schnitzler *et al.* 2004), laryngeal physiology and the fundamental structure of the communication calls of mammals could indicate the likely pre-cursor to echolocation in bats. In addition the ontogenetic development of bats from birth to maturation shows a progression from communication-like sounds to echolocation sounds (Moss 1988). An examination of the initial sounds in a series of species producing different call types, and the changes over time to adult echolocation calls, can reveal a possible evolutionary history. Therefore, further to the analyses, and in support of the hypothesis of ancestral call type above, I investigate several additional lines of evidence to support my position: this call type is (1) the sound produced when air flows through a typical mammalian larynx; (2) the basic sound used by most mammals; (3) produced in the first days of a bat's life and develops into the echolocation calls used by an adult bat in a predictable manner.

5.2.3 Chapter aims

The aims of this study are threefold: (1) To estimate the ancestral echolocation call type using contemporary phylogenetic comparative methods, (2) To consider the other evidence for the ancestral echolocation call structure, (3) To infer the ancestral bat's habitat, wing morphology, foraging style, and prey type from the predicted ancestral call type.

5.3 Methods

5.3.1 Data

5.3.1.1 Bat call data

I collated and measured the echolocation call data as described in Chapter 2: section 2.2. The echolocation data used included data from species found in EchoBank that could be successfully measured, and data from species reported in the literature. I used the parameters chosen in section 2.2.8 in Chapter 2. The full list of species data is shown in Appendices A and E.

5.3.1.2 Supertree

I constructed the supertree as described in Chapter 2: section 2.3. I used the full supertree containing all 1116 bat species as in Chapter 4. The supertree was resolved randomly 100 times in the ancestral character estimation analyses using phylogenetic independent contrasts, generalised least squares and maximum likelihood for discrete states as these techniques require fully dichotomous phylogenies. In these cases, the results presented are the mean values for the 100 trees.

5.3.1.3 Combined data sets

The data sets used for each analysis in this chapter are subsets of the total data set of 410 species. There are missing data points in the EchoBank data set, where SonoBat (Szewczak 2010) was unable to measure a particular parameter, and in the literature, where parameters

were not reported. See Chapter 2 for a fuller description of data collection. In each analysis, the phylogeny was pruned to include only those species which were represented by data for every parameter involved in the analysis. The sample size used for each parameter is shown in Appendix F.

5.3.2 Analysis

Data analysis was performed using R version 2.12.2 (The R Core Development Team 2010) and the function *ace* of the R package 'ape' (Paradis, Claude, & Strimmer 2004) for analyses using phylogenetic independent contrasts, generalised least squares or maximum likelihood for discrete traits. Analyses using squared change parsimony and maximum likelihood for continuous traits were carried out using Mesquite version 2.74 (Maddison & Maddison 2011).

5.3.2.1 Ancestral Character Estimation using Echolocation Call Parameters

A continuous ancestral character estimation was performed for each of the eight echolocation call parameters independently, using four methods: squared change parsimony (SCP) (Maddison 1991), maximum likelihood (ML) (Pagel 1999b), least-squares phylogenetic independent contrasts (PIC) (Felsenstein 1985), and the method referred to by the R package 'ape' as generalised least squares (GLS) (Martins & Hansen 1997). The first three methods assume a Brownian Motion (BM) model of evolution, but as GLS offers the opportunity to specify an Ornstein-Uhlenbeck (OU) model, I did so, using the alpha values estimated in Chapter 4 section 4.3.2.3, since this was found to be the preferred model in that analysis. I include the other methods (using BM) for comparison.

5.3.2.2 Ancestral Character Estimation using Principal Components

A "phylogenetically-corrected" principal components analysis was performed on all eight echolocation call parameters using the R code of Liam Revell (Revell 2009). Many studies use principal components analysis to look at the variation in a group of related traits, but most do not take account of the non-independence of related species. Revell (2009)

developed a method to account for the non-independence of inter-species data due to phylogeny in principal components analysis, which has been used in this chapter. Using PCA values rather than raw data ties the echolocation call parameters together and avoids the reconstruction of spurious calls. Principal components one through eight were determined for each species and a continuous ancestral character estimation was performed using these values, again using squared change parsimony (SCP) (Maddison 1991), maximum likelihood (ML) (Pagel 1999b), least-squares phylogenetic independent contrasts (PIC) (Felsenstein 1985), and generalised least squares (GLS) (Martins & Hansen 1997) in which an Ornstein-Uhlenbeck (OU) model with the alpha values estimated in Chapter 3 section 4.3.2.3 was specified.

5.3.2.3 Ancestral Character Estimation using Discrete Echolocation Call Types

Finally, I estimated ancestral characters using discrete echolocation call types, using three alternative rate matrices: equal rates (ER), symmetrical rates (SYM), and all rates different (ARD) and maximum likelihood estimation. In an equal rates matrix, the probability of character change from any character to any other character is equal, and reversals are possible. In a symmetrical rates matrix, the rates of forward and backward change between any two character states are equal to one another, but different for each state, and change is reversible. In an all rates different matrix, each character state change can have a different rate, and change is reversible. Using these three alternative rate matrices allows for exploration of the types of changes that can occur between different character states. Equal Rates is a simple, but unlikely, model, since it suggests that the rate at which each call type can transition to a different call type is the same for all combinations of call type. Some call types are more similar to one another, and therefore transitions between these types should be easier than between less similar call types. Symmetrical Rates is a more realistic model, though with more parameters, as it differentiates between the rates of transition between different call types. All Rates Different suggests that a change from one trait to another may be easier than the same transition in the opposite direction. See Figure 5.4 for an illustration of the rate matrices.

	A	B	C
A	0	1	1
B	1	0	1
C	1	1	0

ER

	A	B	C
A	0	1	2
B	1	0	3
C	2	3	0

SYM

	A	B	C
A	0	3	5
B	1	0	6
C	2	4	0

ARD

Figure 5.4: Examples of three rate matrices (equal rates (ER), symmetrical rates (SYM), and all rates different (ARD)) for a single character with three states: A, B, and C.

I ran three analyses. The first had two parts: in one I used the 13 new call types defined in Chapter 4 section 4.4.1, and in the second I used the same call types, but included only one representative species per call type per family. I did this to reduce the influence of large numbers of species using the same call type, in case this biased the results towards more speciose families. The second analysis looked at harmonic use: the first part had two alternatives – single or multiple harmonic calls, and the second part considered which of the first four harmonics had maximum energy. In the third analysis I used discrete call categories for four echolocation call parameters based on the divisions shown in Table 5.1.

Parameter	Small	Medium	Large
Bandwidth (kHz)	<10	10-30	>30
Call Duration (ms)	<10	10-25	>25
Characteristic Frequency (kHz)	<50	50-100	>100
Total Slope (kHz/ms)	<1	1-10	>10

Table 5.1: Discrete categories used in ancestral character estimation.

These divisions were chosen based on the different functionality that each category provides, rather than based on equal species numbers in each category. For example, a call duration of less than 10 ms is typically associated with bats that forage in cluttered space, whereas a call duration of 10-25 ms allows bats to forage in open space because signals only overlap with echoes when targets are 1.7 – 4.3m away. A call duration of over 25 ms is typical of a constant frequency call that reveal the fluttering wings of insects against a background of clutter.

5.3.2.4 Additional Evidence

To put the phylogenetic comparative analyses above into a physiological and developmental context, I reviewed further evidence pertaining to the evolution and development of vocalizations in mammals. First, I reviewed the output of the mammalian larynx. Second, I considered the variation in the vocalizations of a selection of species from each mammalian order, chosen from recordings available on the Macaulay Library (Cornell Lab of Ornithology 2011), and created comparable sonograms using BatSound v3.1 (Pettersson 2008) using a Hanning Fast Fourier Transform (FFT) window and an FFT size of 1024. Third, I reviewed the literature concerning the ontogenetic development of echolocation calls in bats, and reproduced the sonograms from all available species.

5.4 Results

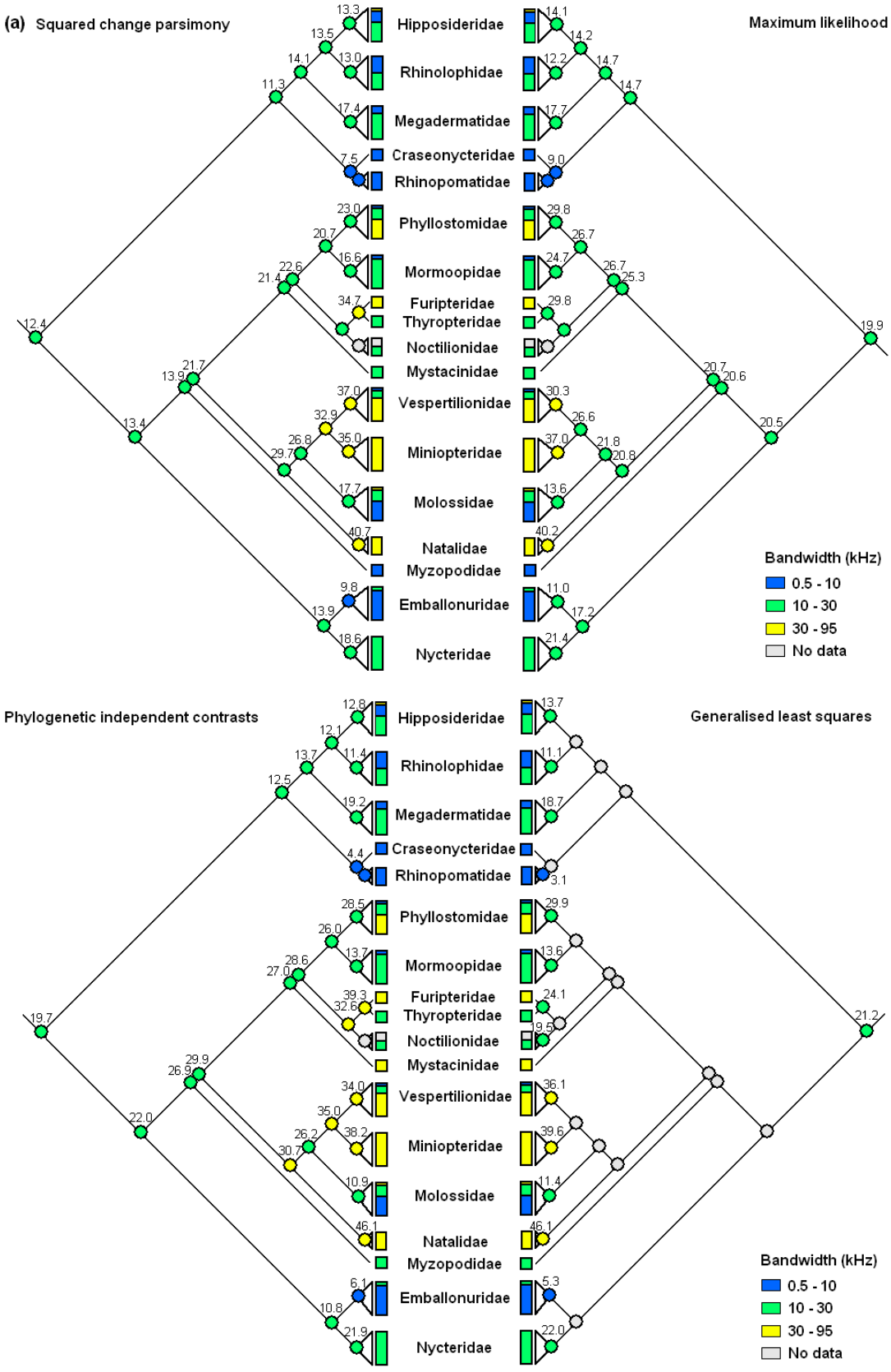
5.4.1 Ancestral Character Estimation using Echolocation Call Parameters

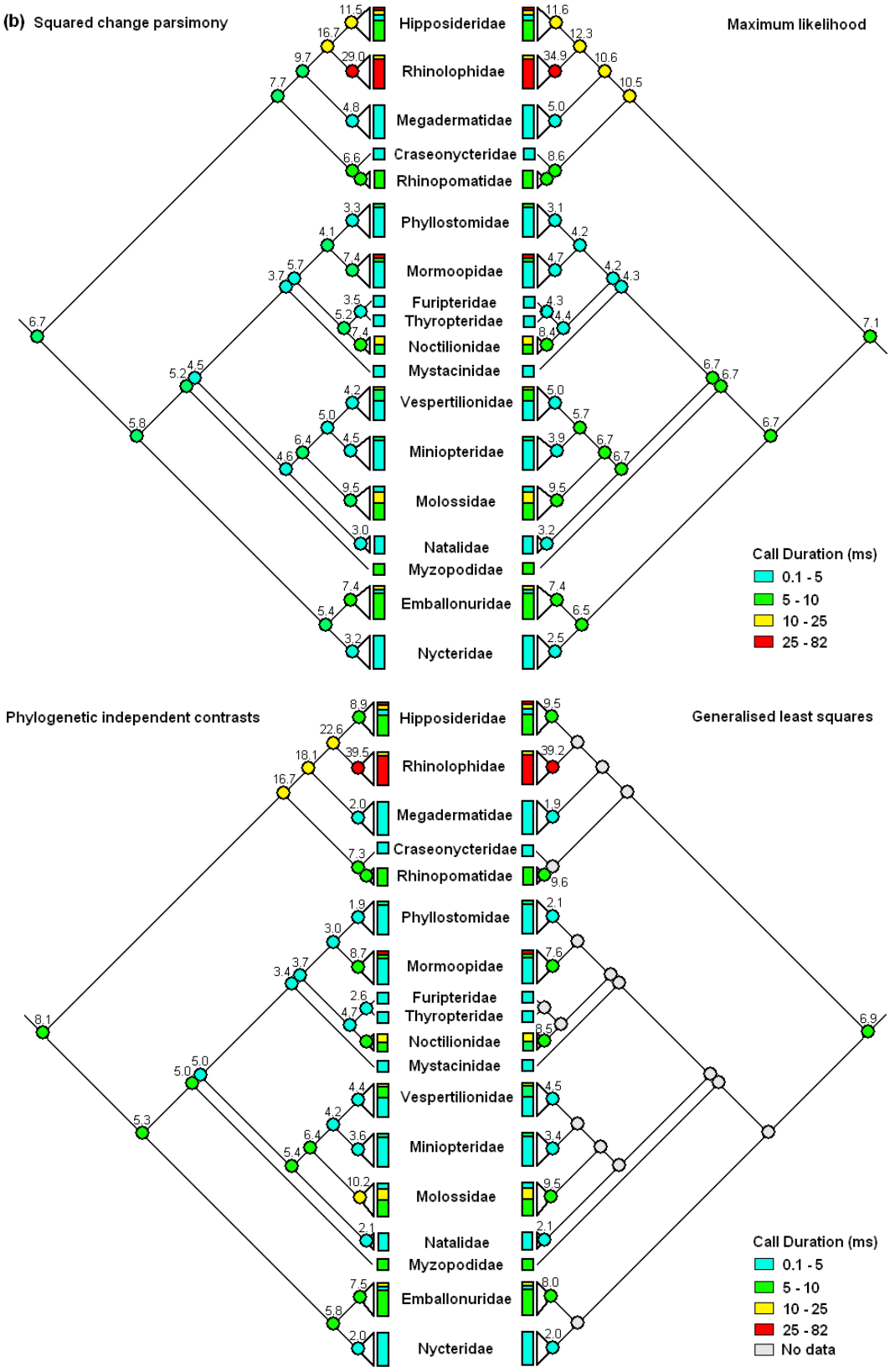
All four continuous trait ancestral reconstruction methods predict an intermediate value at the root node for each echolocation call parameter, resulting in a medium bandwidth (12.4 to 21.2 kHz), medium frequency (49 to 76 kHz), medium slope (4.8 to 8.0 kHz/ms), and short duration (6.7 to 8.1 ms) for the ancestral call. These estimates are not entirely compatible with one another, as the slope is a measure of change in frequency over time, and so it should correspond to bandwidth divided by call duration, which it does not. This is a problem with reconstructing related traits independently, and my other analyses attempt to deal with this (using principal components analysis and discrete traits). Patterns of character change from the tips to the root of the tree are similar, regardless of the method used, though longer branches have a greater influence in ML reconstructions, and the values at more basal nodes exert a greater influence in PIC reconstructions (see Figure 5.5).

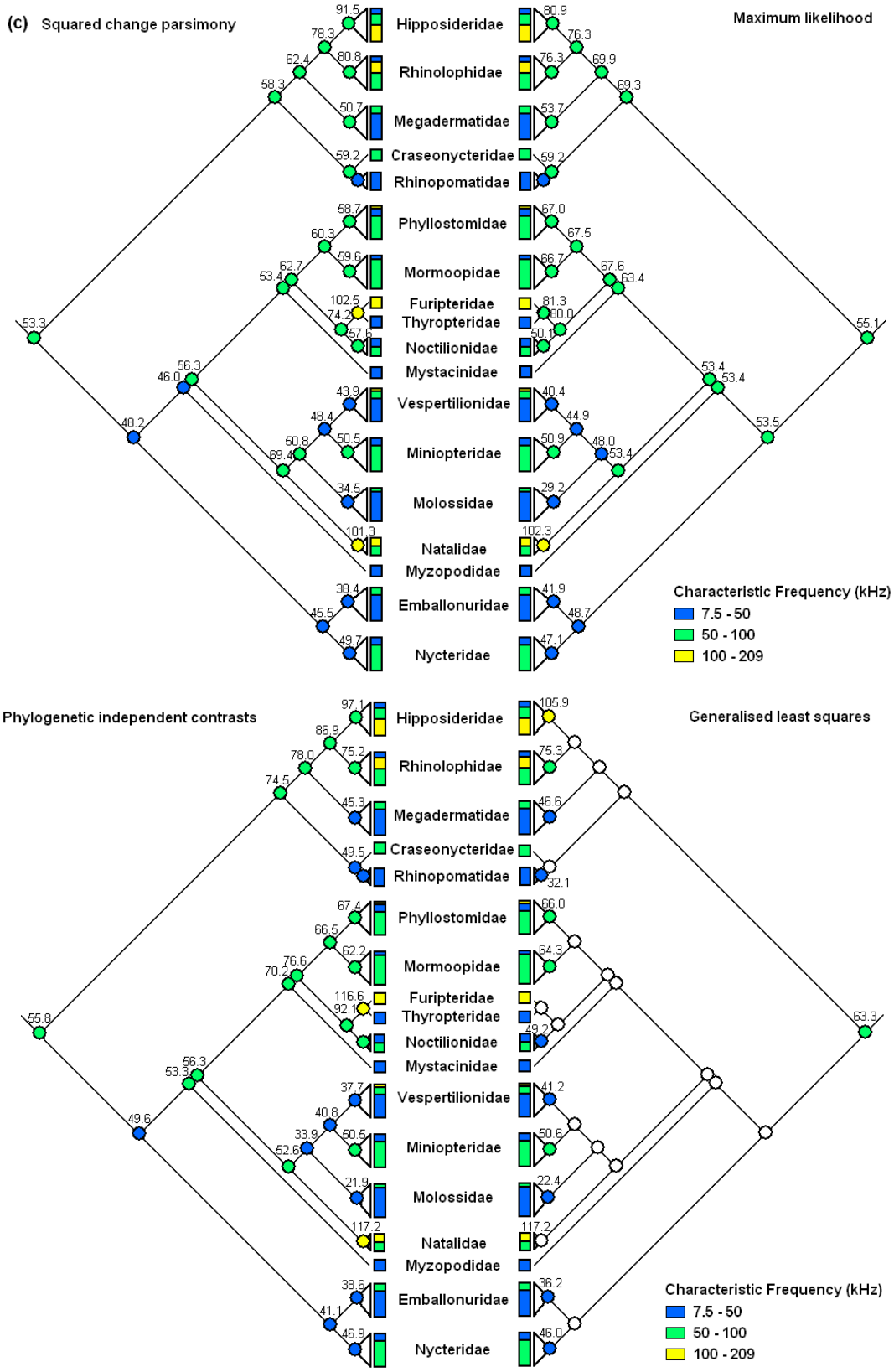
The reconstructed values show that the ancestors of both subfamilies, Pteropodiformes and Vespertilioniformes, had already diverged considerably from the values at the root node for all echolocation call parameters. This suggests that the call types took different evolutionary routes early in the history of bats, with the calls of the Pteropodiformes

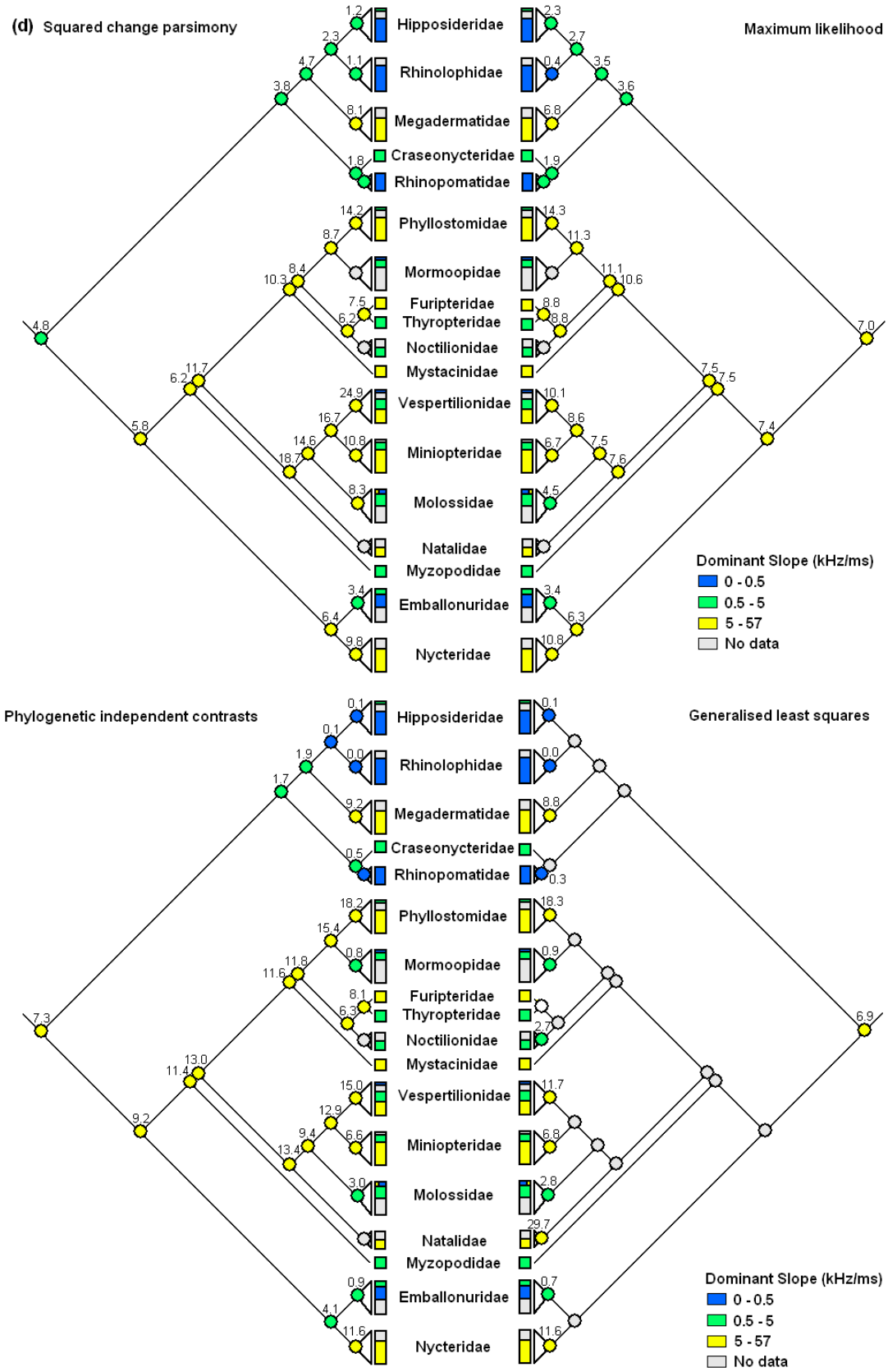
becoming more narrowband, longer, and higher frequency than those of the Vespertilioniformes (see Figure 5.5).

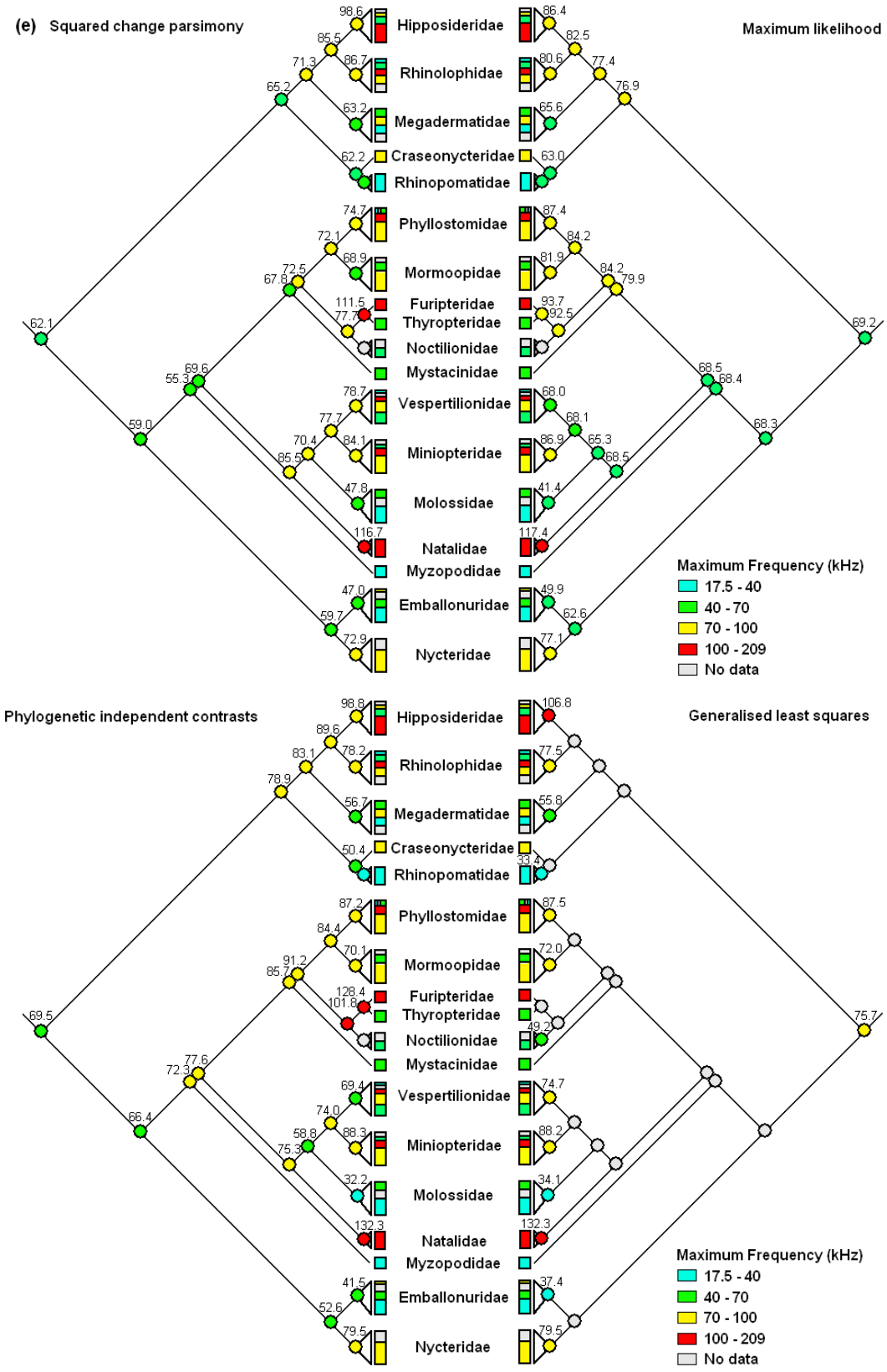
Figure 5.5 (below): Estimated ancestral values across the bat supertree for each echolocation call parameter, using four ancestral reconstruction methods: SCP (squared change parsimony), ML (maximum likelihood), PIC (phylogenetic independent contrasts), and GLS (generalised least squares). The rectangles at the tips of the tree show the rough proportions of traits across each family, and the circular nodes show estimated ancestral values, with the exact value above. (a) Bandwidth; (b) Call Duration; (c) Characteristic Frequency; (d) Dominant Slope; (e) Maximum Frequency; (f) Minimum Frequency; (g) Peak Frequency; (h) Total Slope.

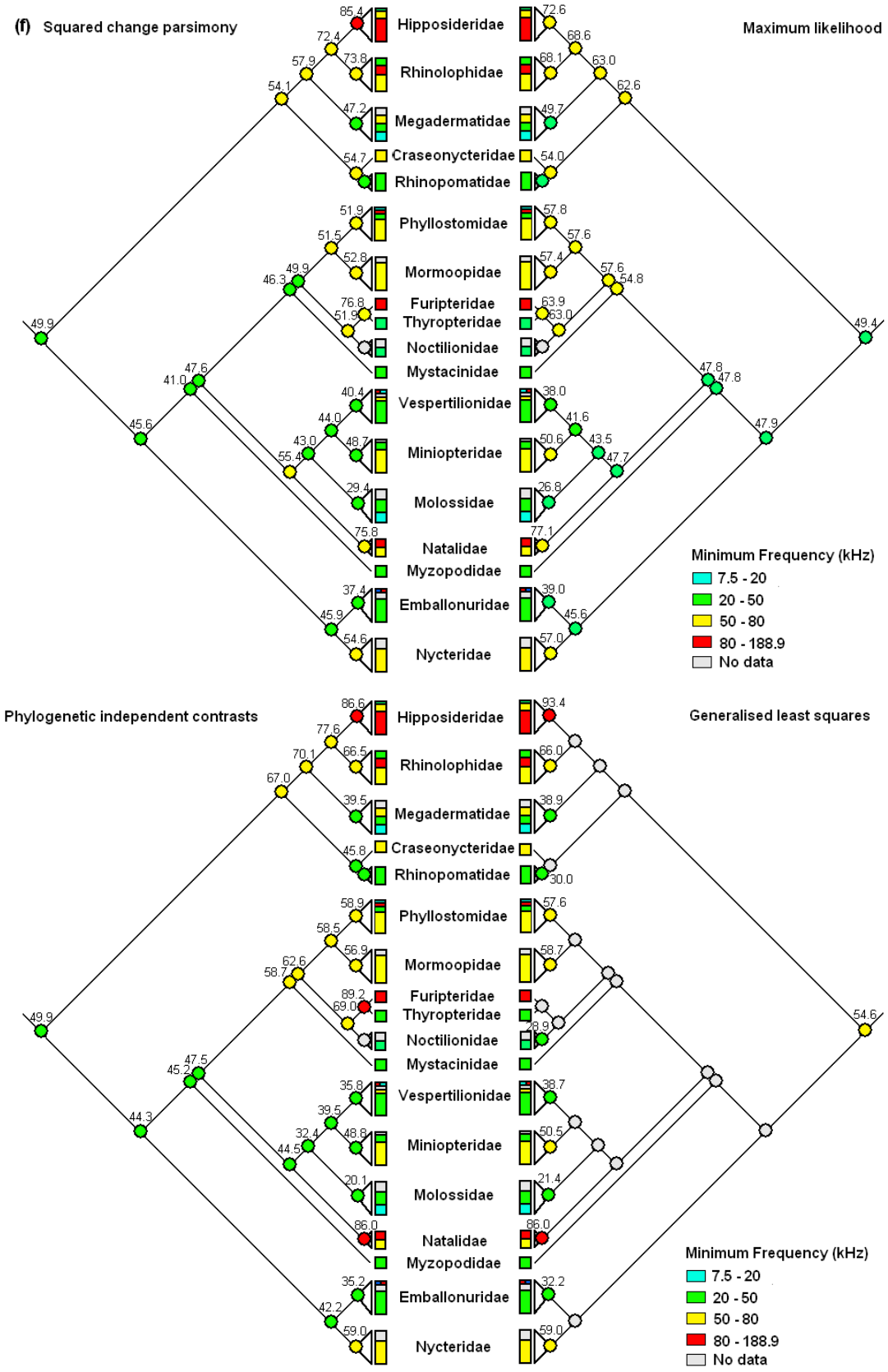

(a) Squared change parsimony
Maximum likelihood
Hipposideridae
Rhinolophidae
Megadermatidae
Craseonycteridae
Rhinopomatidae
Phyllostomidae
Mormoopidae
Furipteridae
Thyropteridae
Noctilionidae
Mystacinidae
Vespertilionidae
Miniopteridae
Molossidae
Natalidae
Myzopodidae
Emballonuridae
Nycteridae
Bandwidth (kHz)
0.5 - 10
10 - 30
30 - 95
No data
Phylogenetic independent contrasts
Generalised least squares

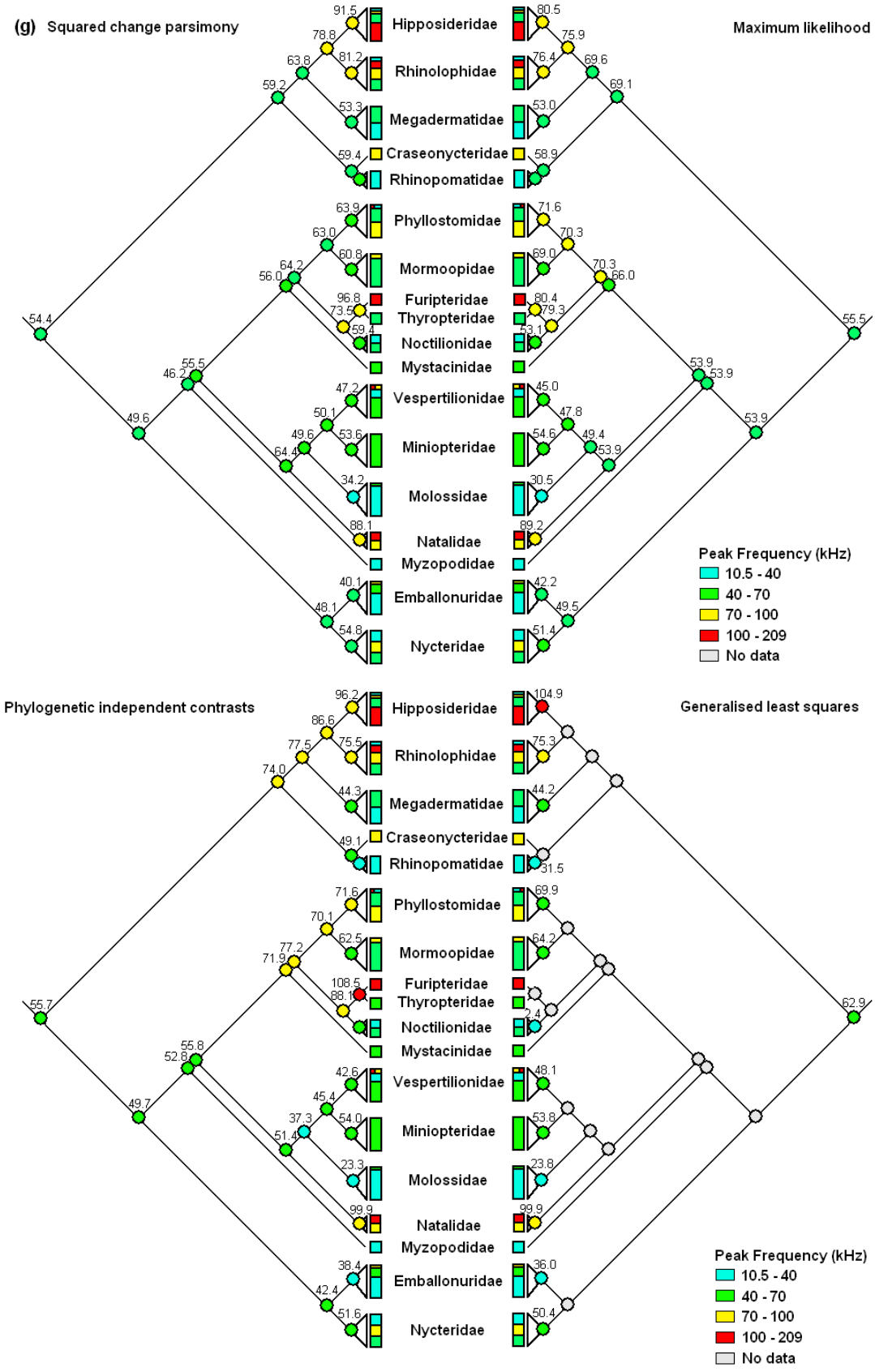

(b) Squared change parsimony
Maximum likelihood
Phylogenetic independent contrasts
Generalised least squares
Hipposideridae
Rhinolophidae
Megadermatidae
Craseonycteridae
Rhinopomatidae
Phyllostomidae
Mormoopidae
Furipteridae
Thyropteridae
Noctilionidae
Mystacinidae
Vespertilionidae
Miniopteridae
Molossidae
Natalidae
Myzopodidae
Emballonuridae
Nycteridae
Call Duration (ms)
0.1 - 5
5 - 10
10 - 25
25 - 82
No data

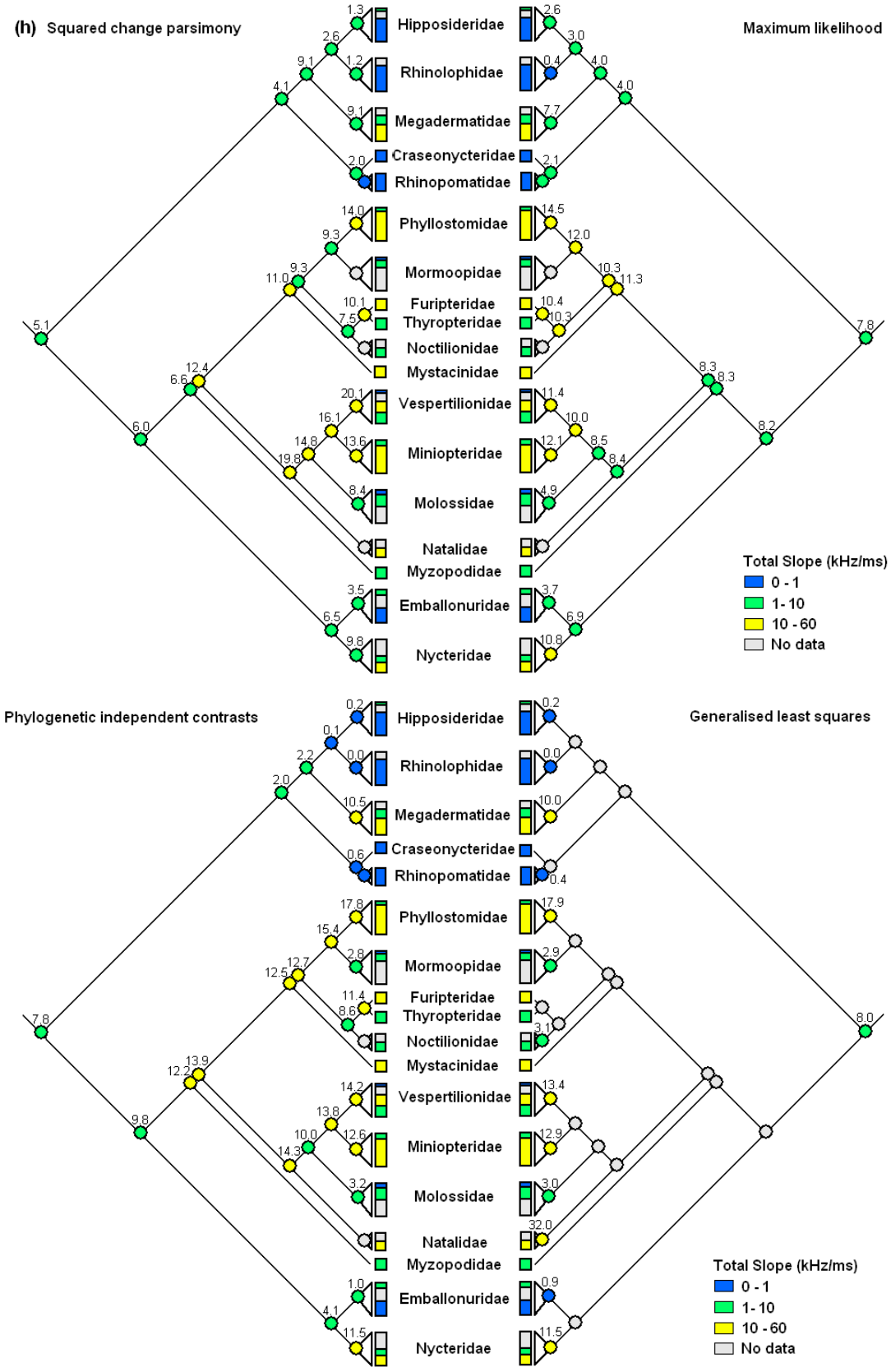

(c) Squared change parsimony
Maximum likelihood
Hipposideridae
Rhinolophidae
Megadermatidae
Craseonycteridae
Rhinopomatidae
Phyllostomidae
Mormoopidae
Furipteridae
Thyropteridae
Noctilionidae
Mystacinidae
Vespertilionidae
Miniopteridae
Molossidae
Natalidae
Myzopodidae
Emballonuridae
Nycteridae
Characteristic Frequency (kHz)
7.5 - 50
50 - 100
100 - 209
Phylogenetic independent contrasts
Generalised least squares


(d) Squared change parsimony
Maximum likelihood
Hipposideridae
Rhinolophidae
Megadermatidae
Craseonycteridae
Rhinopomatidae
Phyllostomidae
Mormoopidae
Furipteridae
Thyropteridae
Noctilionidae
Mystacinidae
Vespertilionidae
Miniopteridae
Molossidae
Natalidae
Myzopodidae
Emballonuridae
Nycteridae
Dominant Slope (kHz/ms)
0 - 0.5
0.5 - 5
5 - 57
No data
Phylogenetic independent contrasts
Generalised least squares


(e) Squared change parsimony
Maximum likelihood
Phylogenetic independent contrasts
Generalised least squares
Hipposideridae
Rhinolophidae
Megadermatidae
Craseonycteridae
Rhinopomatidae
Phyllostomidae
Mormoopidae
Furipteridae
Thyropteridae
Noctilionidae
Mystacinidae
Vespertilionidae
Miniopteridae
Molossidae
Natalidae
Myzopodidae
Emballonuridae
Nycteridae
Maximum Frequency (kHz)
17.5 - 40
40 - 70
70 - 100
100 - 209
No data


(f) Squared change parsimony
Maximum likelihood
Phylogenetic independent contrasts
Generalised least squares
Hipposideridae
Rhinolophidae
Megadermatidae
Craseonycteridae
Rhinopomatidae
Phyllostomidae
Mormoopidae
Furipteridae
Thyropteridae
Noctilionidae
Mystacinidae
Vespertilionidae
Miniopteridae
Molossidae
Natalidae
Myzopodidae
Emballonuridae
Nycteridae
Minimum Frequency (kHz)
7.5 - 20
20 - 50
50 - 80
80 - 188.9
No data


(g) Squared change parsimony
Maximum likelihood
Hipposideridae
Rhinolophidae
Megadermatidae
Craseonycteridae
Rhinopomatidae
Phyllostomidae
Mormoopidae
Furipteridae
Thyropteridae
Noctilionidae
Mystacinidae
Vespertilionidae
Miniopteridae
Molossidae
Natalidae
Myzopodidae
Emballonuridae
Nycteridae
Peak Frequency (kHz)
10.5 - 40
40 - 70
70 - 100
100 - 209
No data
Phylogenetic independent contrasts
Generalised least squares


(h) Squared change parsimony
Maximum likelihood
Hipposideridae
Rhinolophidae
Megadermatidae
Craseonycteridae
Rhinopomatidae
Phyllostomidae
Mormoopidae
Furipteridae
Thyropteridae
Noctilionidae
Mystacinidae
Vespertilionidae
Miniopteridae
Molossidae
Natalidae
Myzopodidae
Emballonuridae
Nycteridae
Total Slope (kHz/ms)
0 - 1
1 - 10
10 - 60
No data
Phylogenetic independent contrasts
Generalised least squares

Of the four methods used to estimate ancestral characters, maximum likelihood and phylogenetic independent contrasts generated extremely similar results across the echolocation call parameters: the values at the root node suggest a fairly short duration, low bandwidth, mid-frequency call (see Table 5.2). SCP tended to produce the lowest values, and GLS the highest. Although the estimated ancestral values were often similar to the mean and median, there was no consistent pattern between the values.

Echolocation Call Parameters	Mean	Median	SCP	ML	PIC	GLS	Sample size (n species)
Bandwidth (kHz)	25.8	22.1	12.4	19.9	19.7	21.2	366
Call Duration (ms)	8.4	4.6	6.7	7.1	8.1	6.9	393
Characteristic Frequency (kHz)	54.1	45.0	53.3	55.1	55.8	63.3	407
Dominant Slope (kHz/ms)	8.7	3.5	4.8	7.0	7.3	6.9	291
Maximum Frequency (kHz)	75.5	72.2	62.1	69.2	69.5	75.7	354
Minimum Frequency (kHz)	49.1	43.4	49.9	49.4	49.9	54.6	355
Peak Frequency (kHz)	57.6	50.7	54.4	55.5	55.7	62.9	408
Total Slope (kHz/ms)	9.6	6.2	5.1	7.8	7.8	8.0	291

Table 5.2: Estimated ancestral values at the root node for each of the echolocation call parameters, using four ancestral reconstruction methods: SCP (squared change parsimony), ML (maximum likelihood), PIC (phylogenetic independent contrasts), and GLS (generalised least squares). The mean and median values for the call parameters are shown for comparison.

Approximately reconstructed using the estimated values for maximum, minimum and peak frequencies, and either call duration or total slope, the ancestral echolocation call at the root node can be seen in Figure 5.6. Due to the conflict between the reconstructed call durations and slopes, two alternative reconstructions are presented: (a) and (b). In (a), the

reconstructed call durations are assumed to be reliable, and the slopes are ignored. Based on the echolocation calls of extant bat species, calls of this duration tend to be curved. In (b), the reconstructed total slopes are assumed to be reliable and the call durations are ignored. Echolocation calls of the resulting call duration (~3ms) tend to be straight.

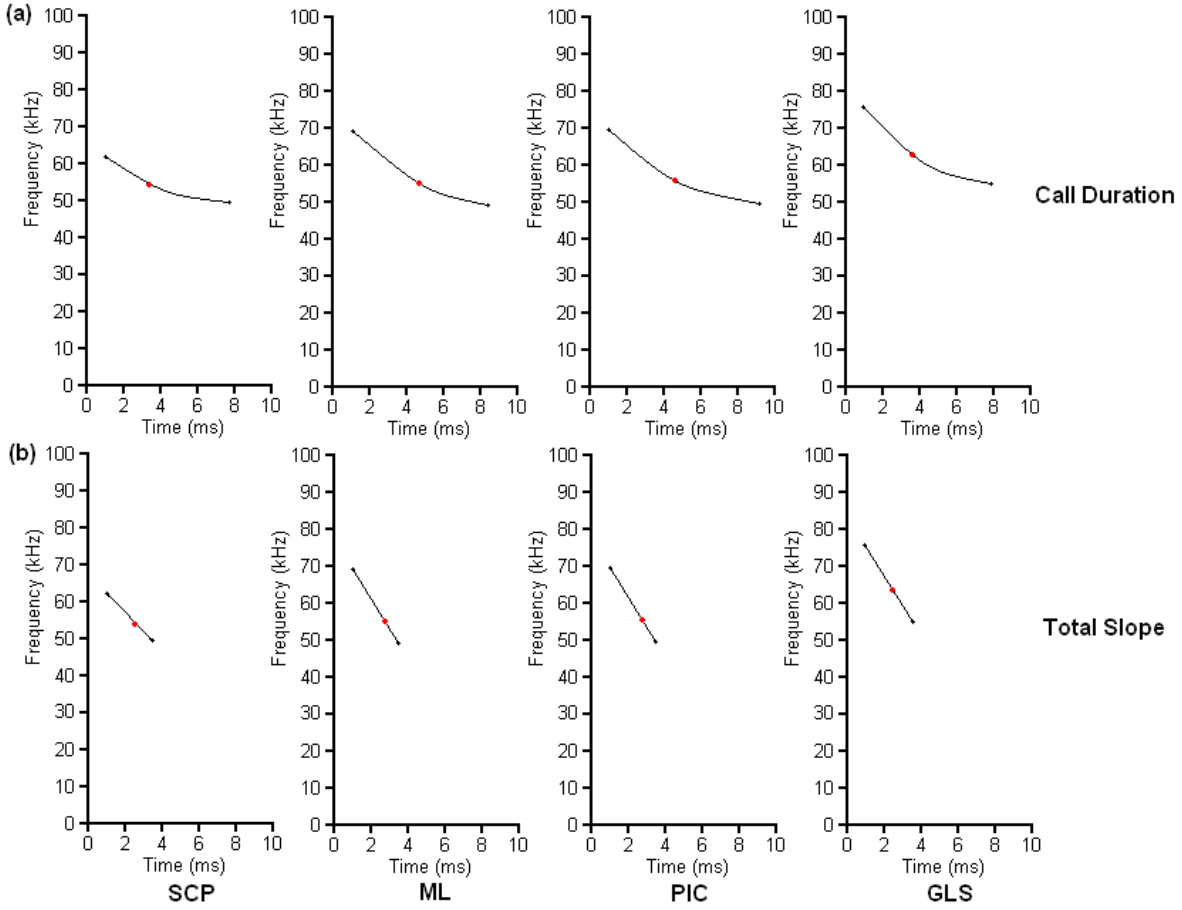


Figure 5.6: Reconstructions of the ancestral echolocation call at the root node for each of the four ancestral character estimation methods using the maximum and minimum frequencies and (a) the reconstructed call duration, or (b) the reconstructed total slope. The red dots show the location of the reconstructed peak frequency value. The different call durations in (a) and (b) make the curved call shape more likely in (a) and the straight call more likely in (b).

The most similar echolocation calls seen in extant bats are of the call types 8 and 9, as presented in Chapter 4 section 4.4.1 (see Figure 5.7).

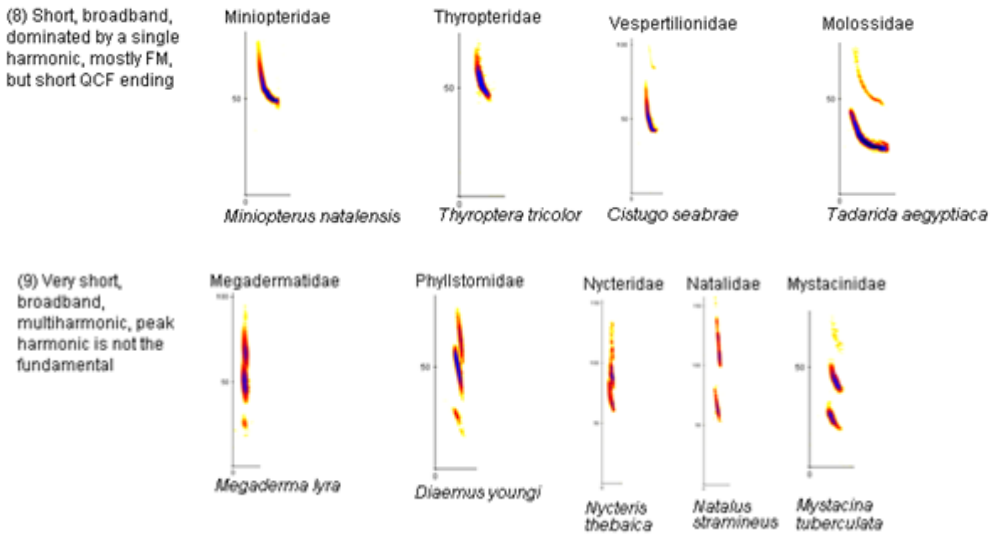


Figure 5.7: Call types 8 and 9, as described in Chapter 4 section 4.4.1.

5.4.2 Ancestral Character Estimation using Principal Components

The eight principal component (PC) scores of all eight echolocation call parameters were entered into ancestral character estimation analyses. PC1 accounted for 62% of the variation in the calls, PC2 for an additional 24% and PC3 for a further 4%, meaning that 91% of the variation in call structure was in the first three principal components. The PC loadings show that changes across PC1 are mostly due to changes in bandwidth, maximum frequency and total slope (see Table 5.3). This represents the change from calls suitable for open space to calls suitable for cluttered space – from a narrowband call (low maximum frequency, shallow slope) to a broadband call (high maximum frequency, steep slope). Across PC2 minimum frequency, characteristic frequency and peak frequency load most heavily. This indicates the position of calls on the frequency scale, regardless of call type. PC3 was representative of changes in bandwidth, characteristic frequency and minimum frequency. See Table 5.3 for full details.

	PC1 (62%)	PC2 (24%)	PC3 (4%)
Bandwidth	0.920	0.115	0.372
Call Duration	-0.514	-0.574	0.234
Characteristic Frequency	0.540	-0.729	-0.339
Dominant Slope	0.746	0.600	-0.213
Maximum Frequency	0.851	-0.520	-0.057
Minimum Frequency	0.581	-0.730	-0.310
Peak Frequency	0.673	-0.673	-0.241
Total Slope	0.821	0.545	-0.060

Table 5.3: Loadings of the eight call parameters onto the first three principal components (with percentage variance accounted for shown in brackets). High absolute numbers are high loadings.

As above, all four ancestral estimation methods produced extremely similar results for the value at the root node (see Figure 5.8 and Table 5.4).

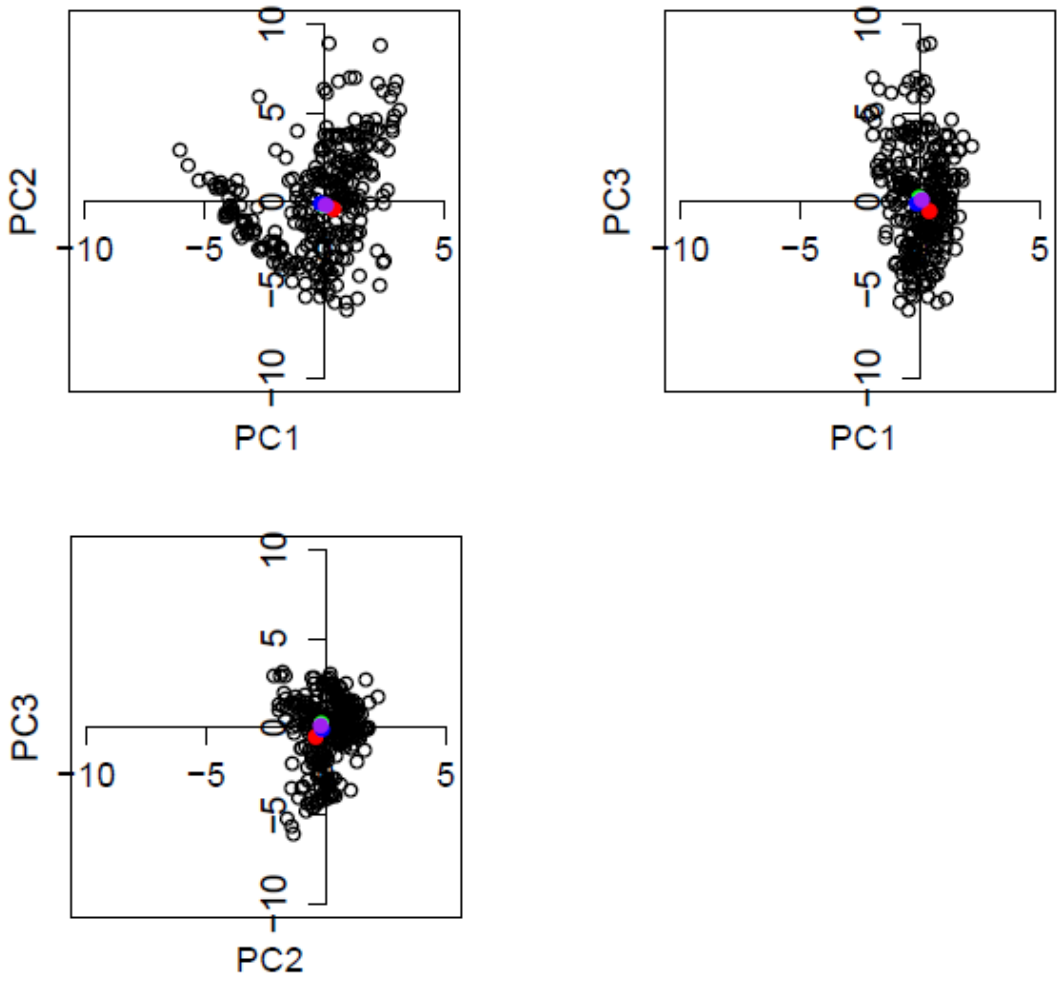


Figure 5.8: Plots of PC1, PC2 and PC3 scores for all species. The ancestral character estimations using squared-change parsimony are shown in red, those using maximum likelihood are shown in blue, those using phylogenetic independent contrasts are shown in green, and those using generalised least squares are shown in purple.

	SSP	ML	PIC	GLS
PC1	0.366	-0.148	-0.046	0.058
PC2	-0.444	-0.166	-0.199	-0.236
PC3	-0.544	-0.150	0.161	0.064

Table 5.4: The reconstructed PCA scores at the root node using four ancestral reconstruction methods: SCP (squared change parsimony), ML (maximum likelihood), PIC (phylogenetic independent contrasts), and GLS (generalised least squares).

Taking the root node estimates for principal components 1, 2, and 3 and comparing them to the PC scores at the tips results in four species that best resemble the root node estimate (within 0.5 of the estimate at each PC) (see Figure 5.9). *Phyllostomus discolor* (Phyllostomidae) matched the score estimated by SCP, *Chiroderma improvisum* (Phyllostomidae) matched scores estimated by SCP and GLS, *Nycticeinops schlieffeni* (Vespertilionidae) matched scores estimated by PIC and GLS, and *Thyroptera tricolor* (Thyropteridae) matched scores estimated by ML, PIC, and GLS. The first two of these species belong to call type 9 and the second two to call type 8, shown in Figure 5.9.

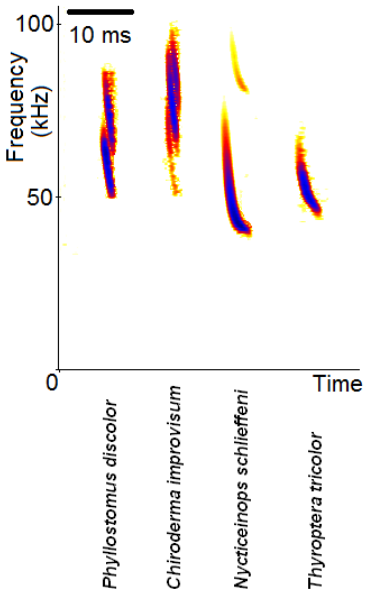


Figure 5.9: The four species with corresponding (within 0.5 of the estimated value) principal components 1, 2, and 3 to the estimated ancestral PC scores.

5.4.3 Ancestral Character Estimation using Discrete Echolocation Call Types

Estimating the ancestral echolocation call type at the root node using the call types described in Chapter 4 section 4.4.2 gives the same best estimation - call type 9 - using all species (total – Equal Rates model) and using a single representative species of each call type per family (representative – All Rates Different model) (see Table 5.5). This analysis also suggested that the ancestor of the Pteropodiformes used call type 13 (a Hipposideridae type call) and the ancestor of the Vespertilioniformes used call type 9 (see Figure 5.10).

The ‘All Rates Different’ model performed best in the ancestral character estimations of the four discrete parameters: bandwidth, call duration, characteristic frequency and total slope (see Table 5.5). The bandwidth at the root node was estimated to be large (>30 kHz), which is somewhat higher than the estimates from the continuous echolocation call parameters in section 5.4.1 above. The call duration and characteristic frequency were both estimated to be medium (10-25 ms and 50-100 kHz respectively), which roughly support the findings in section 5.4.1. The total slope value at the root node was estimated to be small (<1 kHz/ms) which is considerably lower than the estimates in section 5.4.1 and would suggest a constant frequency call typical of the Rhinolophidae (call type 12, see Chapter 4, section 4.4.2), or a narrowband call (call type 3, see Chapter 4 section 4.4.2). As above, the call duration, bandwidth and total slope estimates provided here are incompatible in a single call.

Ignoring the estimates for total slope and call duration, and reviewing the raw data for the call types of the species with calls matching the remaining categories estimated here results in species using call types 8 and 9, shown in Figure 5.9. Including either of the estimates for total slope or call duration produces a spurious call, with no examples in extant bats.

The ancestral call was predicted to be multi-harmonic, regardless of the model used (see Table 5.5). The peak harmonic of the ancestral call was found to be the third harmonic, with ‘All Rates Different’ the most likely model.

Analysis	Equal Rates		Symmetrical		All Rates Different	
	State	Log-likelihood	State	Log-likelihood	State	Log-likelihood
Chapter 4 call types - total	9	-395	5	-414	9	-508
Chapter 4 call types - representative	All equal	-108	8	-103	9	-102
Harmonics – single or multiple	Multiple	-71	Multiple	-71	Multiple	-69
Peak Harmonic	2	-138	2	-118	3	-98
Bandwidth	Medium	-250	Medium	-233	Large	-227
Call Duration	Small	-96	Small	-89	Medium	-82
Characteristic Frequency	Large	-202	Large	-186	Medium	-178
Total Slope	Small	-193	Medium	-177	Small	-170

Table 5.5: Summary of the ancestral character estimates at the root node for the discrete echolocation call types. The preferred models (log-likelihood values closest to zero) are highlighted.

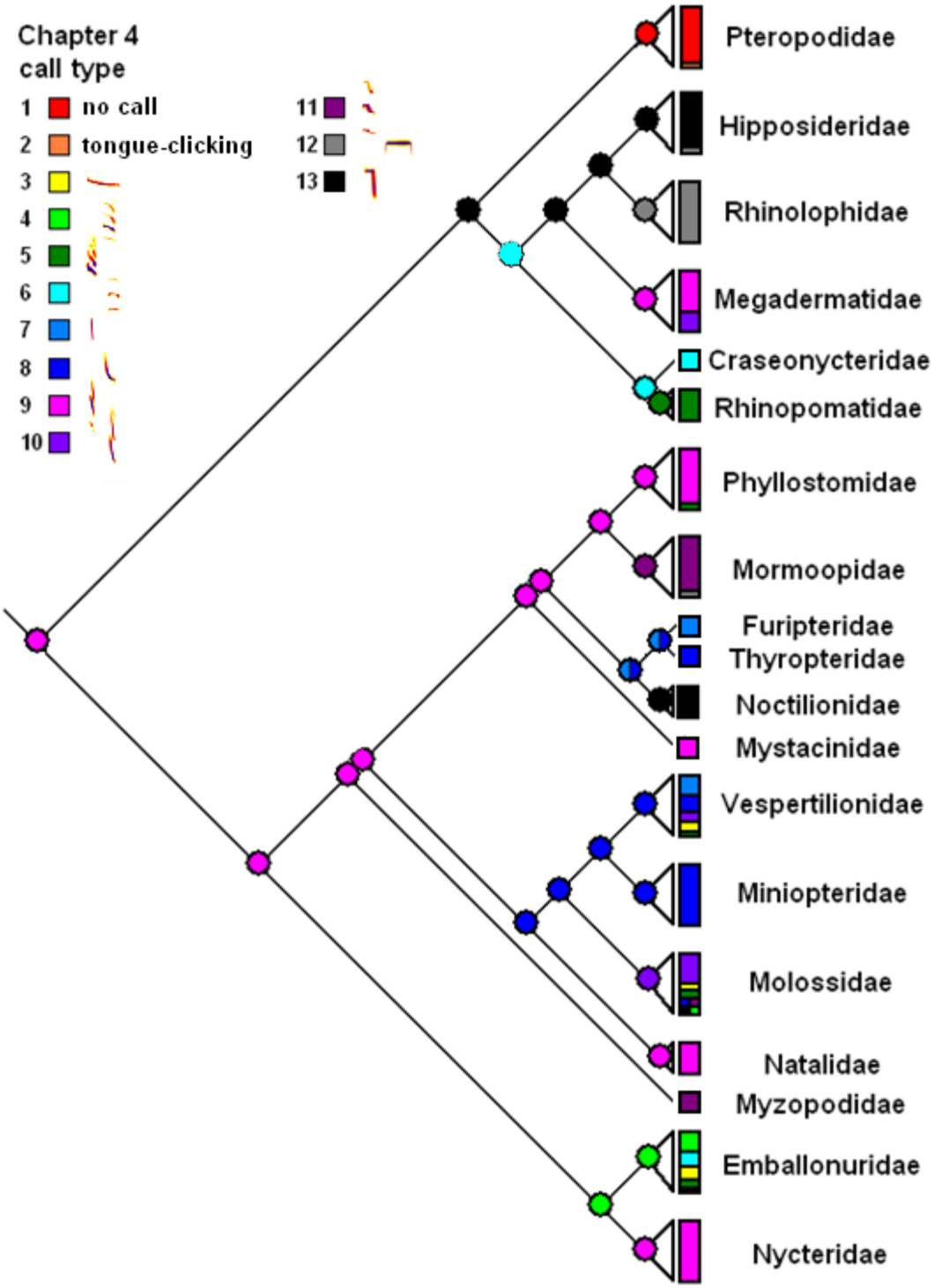


Figure 5.10: Estimated ancestral values across the bat supertree for the discrete call types described in Chapter 4, using an Equal Rates model. The rectangles at the tips of the tree show the rough proportions of each call type seen in extant bats across each family, and the circular nodes show estimated ancestral values.

5.4.4 Additional Evidence

The laryngeal vocalizations of a selection of other mammals are presented in Figure 5.11 as spectrograms. They demonstrate the repeated use of harmonic series as the basic output from the larynx. It can also be seen that echolocation is present in three of the six orders of the Laurasiatheria, compared to just two of the remaining 12 placental mammal orders.

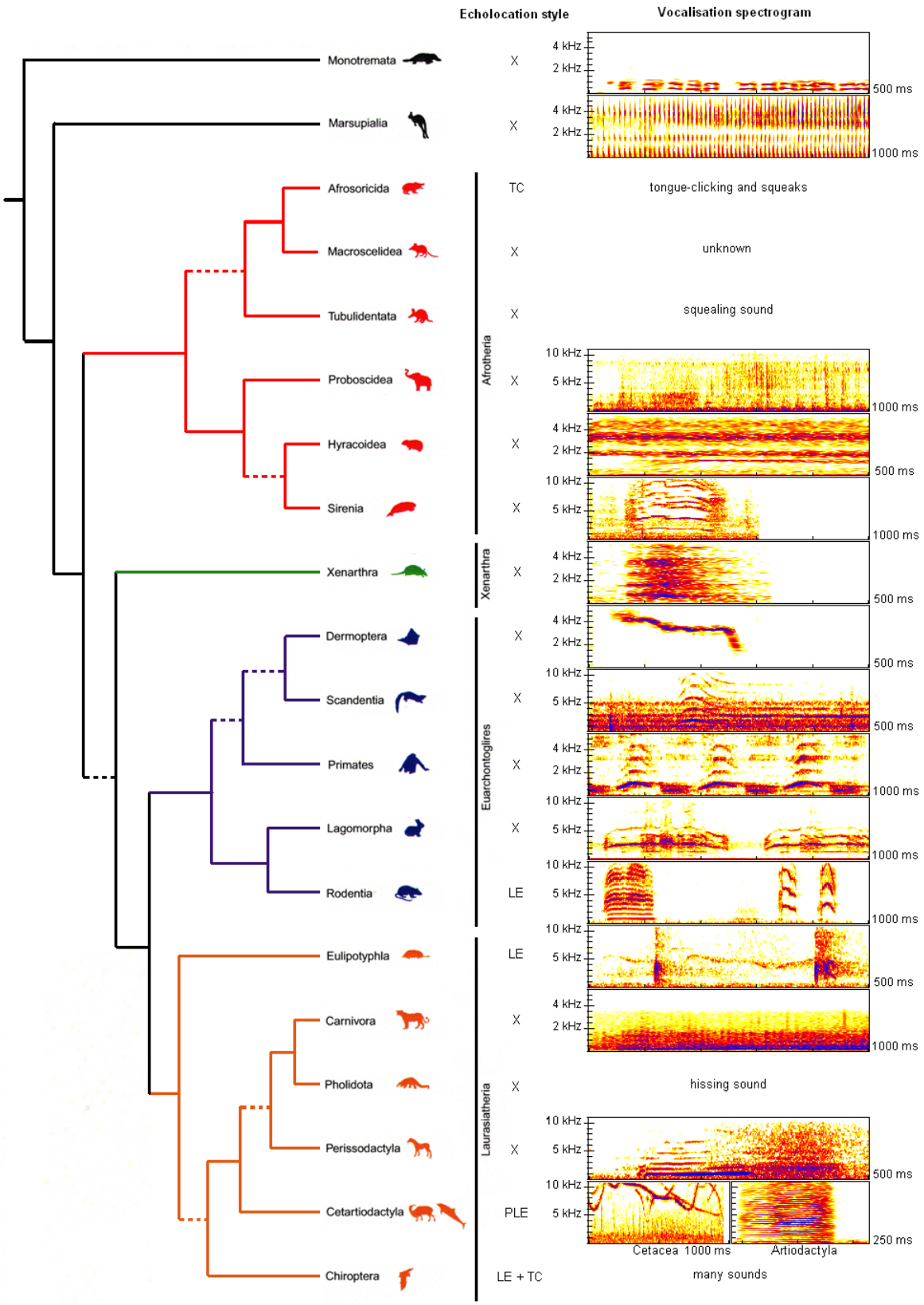
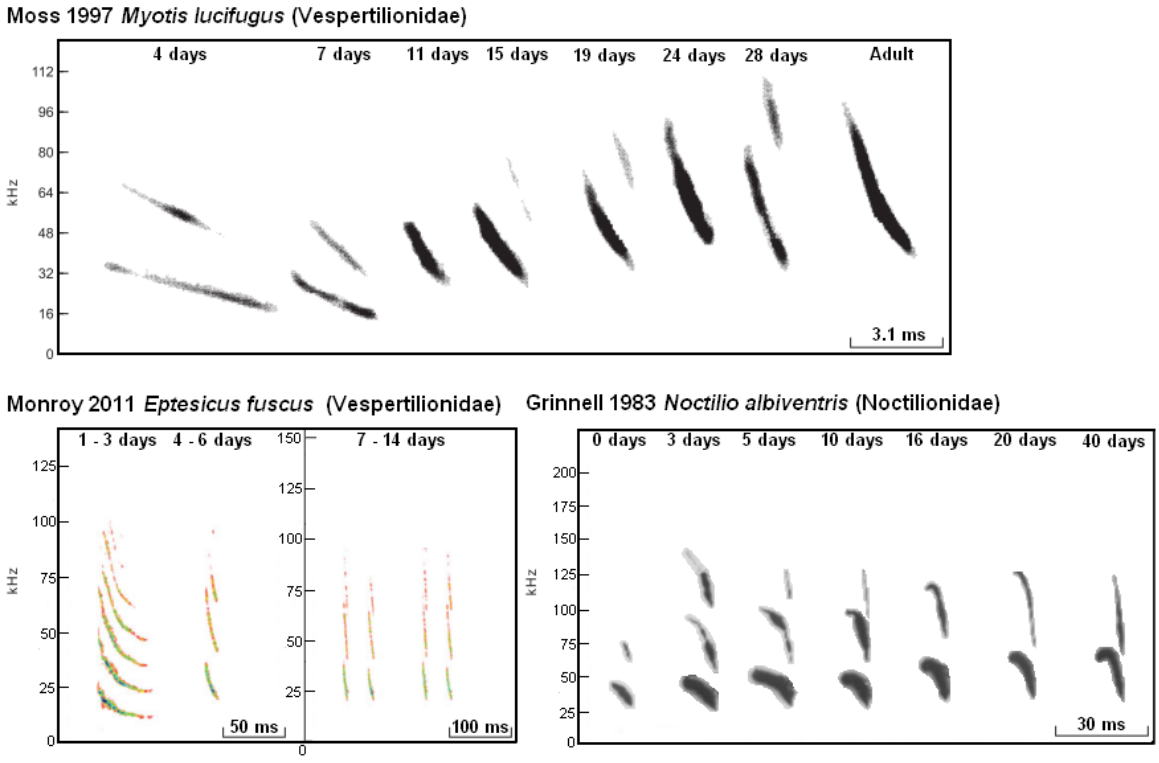
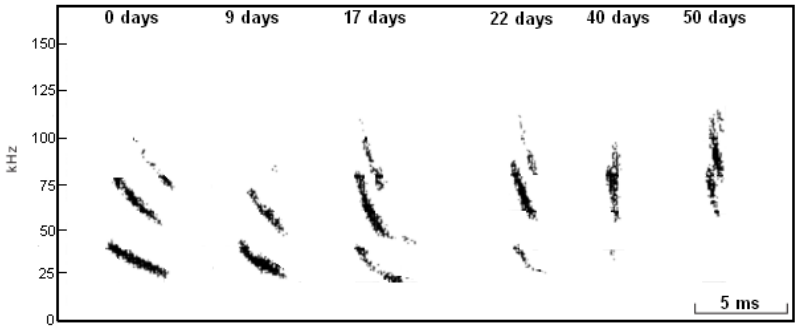

Echolocation style
Vocalisation spectrogram
Monotremata
Marsupialia
Afrosoricida
Macroscelidea
Tubulidentata
Proboscidea
Hyracoidea
Sirenia
Xenarthra
Dermoptera
Scandentia
Primates
Lagomorpha
Rodentia
Eulipotyphla
Carnivora
Pholidota
Perissodactyla
Cetartiodactyla
Chiroptera
Afrotheria
Xenarthra
Euarchontoglires
Laurasiatheria
X
TC
LE
PLE
LE + TC
tongue-clicking and squeaks
unknown
squealing sound
hissing sound
many sounds
4 kHz
2 kHz
10 kHz
5 kHz
500 ms
1000 ms
250 ms
Cetacea
Artiodactyla

Figure 5.11: (Previous page) Laryngeal vocalisations produced by example species from each order of mammals. Diagram adapted from Springer & Stanhope (2004). Echolocation style key: X – no echolocation; TC – tongue-clicking; LE – laryngeal echolocation; PLE – phonic lips echolocation. See Appendix G for list of species and references.

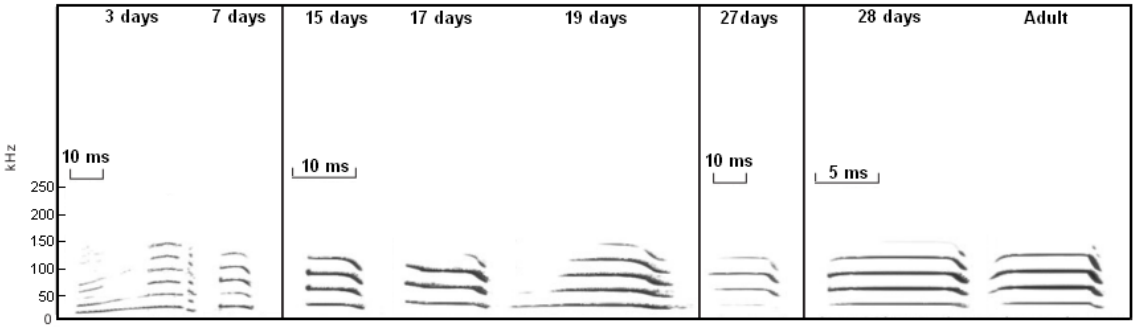
Reviewing the ontogenetic development of echolocation in eight species of bats in six families reveals a similar early call type and a parallel pattern of changes with age (see Figure 5.12). Early calls tend to be low frequency, multi-harmonic and relatively narrowband. With age, the young bats produce fewer harmonics and raise the frequency of the fundamental harmonic. Some families reduce the duration of the calls (Vespertilionidae, Phyllostomidae) and others increase it. Modifications to the call shape are introduced after several days, such as down-sweeps and up-sweeps.



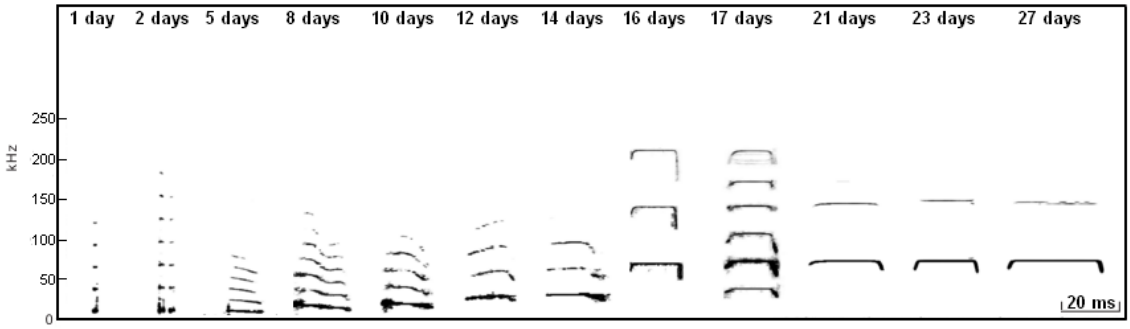
Sterbing 2002 *Carollia perspicillata* (Phyllostomidae)



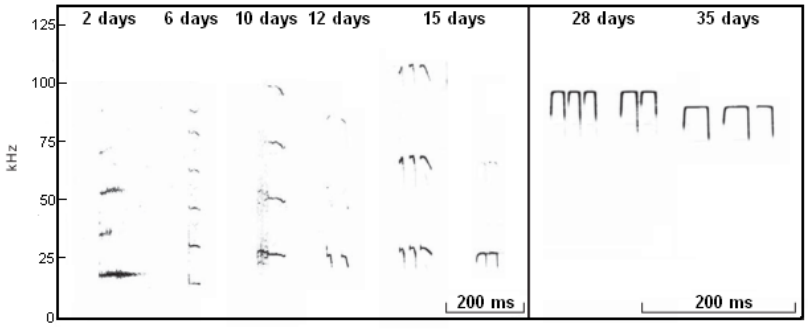
Vater 2003 *Pteronotus parnellii* (Mormoopidae)



Liu 2007 *Rhinolophus ferrumequinum* (Rhinolophidae)



Funakoshi 2010 *Rhinolophus cornutus* (Rhinolophidae)



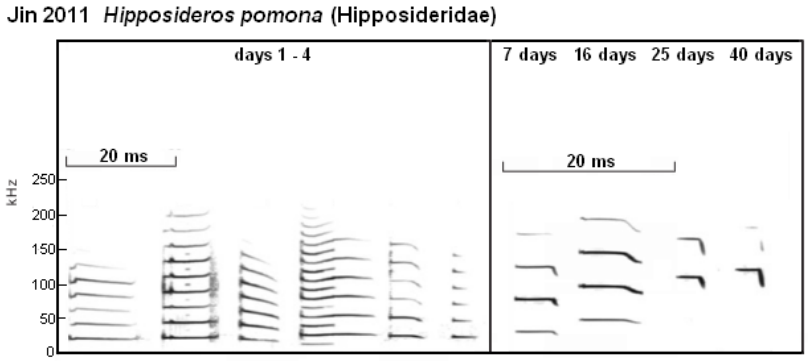


Figure 5.12: Ontogenetic sequences of echolocation development in several species of bats. Figures adapted from the original papers (Funakoshi, Nomura, & Matsukubo 2010; Grinnell 1983; Jin et al. 2011; Liu & Feng 2007; Monroy, Carter, & Miller 2011; Moss, Redish, & Gounden 1997; Sterbing 2002; Vater et al. 2003)**.**

5.5 Discussion

5.5.1 The Ancestral Echolocation Call

All the ancestral character estimation analyses indicated that the ancestral laryngeal echolocation call was of type 8 or 9, as described in Chapter 4, section 4.4.2. Call type 8 is typical of edge-space aerial insectivores such as those in the Vespertilionidae, consisting of a medium-short duration, single harmonic call descending through a medium range of frequencies and ending with a more narrowband downwardly curved tail into which most of the call's energy is placed. Call type 9 is typical of the ecologically-varied bats of the Phyllostomidae, and consists of a short duration call descending abruptly through a medium range of frequencies, and consisting of three to five harmonics. This is consistent with my hypothesis, and the predictions of previous workers.

The first analysis estimated medium values for each of the eight raw echolocation call parameters. The estimates for the maximum, minimum, characteristic and peak frequencies, and bandwidth did not conflict with one another, and indicated an ancestral call already well into the ultrasonic range (49.4 – 75.7 kHz – producing a peak wavelength of 6 – 7 mm). However, as hypothesised, the estimates for call duration and dominant and total slopes contradicted one another, highlighting one of the challenges produced by ancestral

reconstruction methods. The estimates for call duration were too long to accommodate the steepness indicated by the estimates for the slopes. Ignoring the estimates for slope suggested the reconstruction of call type 8 at the root node, whereas ignoring the estimates for call duration indicated the use of call type 9 at the root node (see Figure 5.7).

Reconstruction using principal component scores was employed to avoid the problem of the non-viable call structures produced by estimating the evolutionary history of each call parameter independently and without the constraint of functionality. Principal components analysis re-aligns the axes of the variation in the eight raw call parameters in such a way that produces values that realistically combine elements of the original parameters and prevents the estimation of non-viable call structures. Using this technique, and comparing the PC scores estimated in the ancestral reconstruction analyses with the PC scores of the calls of extant bats indicated the ancestral bat at the root node used a call similar to those of *Phyllostomus discolor* (Phyllostomidae), *Chiroderma improvisum* (Phyllostomidae), *Nycticeinops schlieffeni* (Vespertilionidae), and *Thyroptera tricolor* (Thyropteridae). The first two of these four bats use call type 9 and the others use call type 8, upholding the findings of the analysis of raw call parameters.

The final analysis considered the calls as discrete entities, tying together not only the call parameters, but also the call shapes and harmonic patterns. Using the call types 1 to 13 described in Chapter 4 resulted in a root node estimate of call type 9. This result clarifies the findings above, suggesting that the ancestral character estimations for the slopes are more reliable than those for call duration. Seeking further clarification through the analysis of four echolocation call parameters partitioned into discrete categories results in estimates of the bandwidth and characteristic frequency at the root node that are compatible with call type 9, but again, slopes are estimated to be flatter and call durations longer than are seen in call type 9. Looking independently at the harmonic structure of the ancestral echolocation call revealed that it was multi-harmonic, and most likely dominated by the third harmonic. This result again suggests that call type 9 is a superior estimate, given its multi-harmonic structure and the placement of the majority of energy into the third harmonic.

As well as the non-functional characters produced when trying to combine ancestral character estimates, ancestral reconstruction methods suffer from an array of other problems. In discrete analyses, the states at ancestral nodes are constrained to the range of states present at the tips, implying that the ancestor of interest had already evolved a present-day character state, even, in this case, 83 – 58 million years previously (Springer, Teeling, & Madsen 2001). Additionally, there is a tendency for ancestral estimates to be extremely similar to, and even less accurate than averages of the contributing tip data (Webster & Purvis 2002).

The most serious problem with ancestral reconstruction methods is their inaccuracy in the face of evolutionary trends (Cunningham 1999; Martins 1999; Oakley & Cunningham 2000; Polly 2001; Schluter et al. 1997; Webster & Purvis 2002). In particular, changes in micro-evolutionary rates (Martins 1999; Oakley & Cunningham 2000; Schluter et al. 1997), directionality (including stabilizing selection) (Cunningham 1999; Martins 1999; Oakley & Cunningham 2000; Polly 2001), fluctuating environments (Martins 1999), and bursts of change such as in adaptive radiations (Martins 1999; Schluter et al. 1997) result in considerable inaccuracies. When working with characters that are thought to be under selection, it is thought to be advisable to increase taxon sampling (Salisbury & Kim 2001) and to use a variety of different methods (Cunningham 1999; Losos 1999), as implemented here.

The results of the ancestral reconstructions of the continuous datasets do not clearly reflect the findings of Chapter 4, although they do not contradict them either. There is no evidence for a difference in the mode of evolution of the two different sets of call parameters identified in Chapter 4. The parameter set that was found to be more constrained, gradual and directional towards a single optimum did not produce noticeably different patterns of evolution in the ancestral reconstruction from the parameter set that was found to be less constrained, punctional and directional towards several optima in Chapter 4. It is not clear why not.

As well as using a large taxon set and a wide range of methods, considering the results in the context of other evidence should improve the reliability of ancestral reconstructions. Key to reconstructing the origin of echolocation is an understanding of the precursor to echolocation, and its mode of production. Since laryngeal echolocation calls are likely to be derived from communication calls (Schnitzler *et al.* 2004), laryngeal physiology and the fundamental structure of the communication calls of mammals can indicate the likely precursor to echolocation in bats (see Figure 5.10). In addition the ontogenetic development of bats from birth to maturation shows a progression from communication-like sounds to echolocation sounds (Moss 1988). An examination of the initial sounds in a series of species producing different call types, and the changes over time to adult echolocation calls, reveals a possible evolutionary history (see Figure 5.12). Finally, reviewing echolocation diversity offers some clues as to transitional forms and processes of change.

All mammals are capable of producing sound using the airflow through the larynx, which produces harmonic spectra, where each harmonic in the sound is a multiple of the fundamental (or first) harmonic (Berke & Long 2009). The basic mammalian sound consists of layers of narrowband harmonics, which can be modulated to produce vocalizations that are longer (e.g., Lagomorpha), more tonally complex (e.g., Primates), purer (e.g., Dermoptera), or more tightly packed (e.g., Rodentia). In general, increased tonal complexity and harmonic layering appears to improve the short-distance communication function of the sound, whereas purer sounds, with fewer harmonics are used by bats in echolocation. When air is passed across an excised mammalian larynx, a multi-harmonic, narrowband sound is emitted (Muller 1848). Bats share the basic mammalian larynx, but different species have different modifications to the laryngeal structure, which may be related to echolocation call types (Schuller & Moss 2004). The presence of echolocation in three of the six orders of the Laurasiatheria raises the possibility that some of the molecular, auditory and physiological architecture needed for echolocation may have evolved at the base of the superorder, allowing the final evolutionary steps to take place later, perhaps after the orders had separated.

The ontogenetic changes seen in the vocalizations of various bat species in the first days and weeks after birth can illuminate our understanding of the way in which echolocation call structures take shape. Figure 5.12 shows the development of echolocation in bat pups of eight species in six families, from birth to maturation. The first calls shown for each species are from days 0 to 4, and all share a similar form: low frequency, multi-harmonic, and narrowband. These vocalizations are similar to that sound produced by an excised larynx when air is passed through it, and represent a phase of development prior to the maturation of the larynx, its muscles and its innervation (Gould 1975). One recent study found that echolocation calls in the big brown bat, *Eptesicus fuscus* (Vespertilionidae) appear to develop from isolation calls: calls a young bat uses to attract its mother (Monroy *et al.* 2011). This would lend weight to the idea that echolocation is a specialization of communication calls, though many other ontogenetic studies of bats did not find that echolocation calls developed from isolation calls (Grinnell 1983; Jin *et al*. 2011; Jones, Hughes, & Rayner 1991; Knornschild, Von, & Mayer 2007; Liu & Feng 2007; Rubsamen 1987; Sterbing 2002).

In the first few days of life, the vocalizations rise in frequency and consequently the harmonics spread out. As maturation takes place, the call structures produced by each family begin to differentiate. The echolocation calls of Vespertilionidae and Phyllostomidae decrease in duration and increase in bandwidth, tilting from near-horizontal to near-vertical. The calls of the two Vespertilionidae species show a concentration of the energy in the fundamental harmonic, thereby reducing the amplitude of the higher harmonics (to almost nothing in *Myotis lucifugus*), whereas the calls of the phyllostomids show a shift of the energy from the fundamental harmonic to the second harmonic, but maintain some amplitude in the third and fourth harmonics. Calls from *Noctilio albiventris* (Noctilionidae) appear to develop in a similar way but rather than extending the bandwidth upwards, it drops downwards. The calls of species of Hipposideridae and Rhinolophidae and of *Pteronotus parnellii* (Mormoopidae) show an alternative pattern of development; changing from narrowband to constant frequency and increasing in duration over time. Between day 7 and day 14, the calls develop up-sweeps and down-sweeps in tandem with

the process of filtering to reduce the amplitude of the fundamental, third and fourth harmonics.

These ontogenetic changes indicate that the echolocation call structures of adult bats can be developed from the hypothesised primitive call: a short, multi-harmonic, narrowband sound, lending further weight to the ancestral call structure hypothesis. They also suggest that development can progress either through tilting the call to increase bandwidth and reduce duration, or alternatively by lengthening the duration. These two alternatives are supported by the results of the discrete ancestral state reconstruction, in which the ancestor to the Pteropodiformes used a long duration, narrowband call (call type 13) and the ancestor to the Vespertilioniformes used a short duration, multi-harmonic, high bandwidth call (call type 9) (see Figure 5.10).

Finally, some changes in call type within families can indicate closely related call structures. *Pteronotus parnellii* is unique in its family (Mormoopidae) and suborder (Vespertilioniformes) for having evolved a long duration, constant frequency call (call type 12). Other members of the family use call type 11 (multi-harmonic decurve into down-sweep). Similarly, at least two hipposiderid species (*Hipposideros semoni* and *H. stenotis*) use call type 12, where other members of the family use call type 13; a medium duration, constant frequency call with a broad frequency-modulated down-sweep. There is evidence that call types 11 and 12 are evolutionary intermediates that have partial functionality as high duty cycle, Doppler Shift Compensating echolocation calls (Lazure & Fenton 2011).

In summary, the ancestral reconstruction analyses indicate that the ancestral echolocation call is similar to call type 9; a short duration, multi-harmonic call, though likely more narrowband and longer in duration. The other evidence supports this finding, and confirms the hypothesised ancestral echolocation call as being a fairly short duration, multi-harmonic, narrowband call.

5.5.2 Biology of the proto-bat

It is possible to elicit further information about the 'ancestral' bat by considering the ecology of extant bats using a similar call structure. The functionality of the call is relatively basic (see Figure 5.13), allowing the bat a reasonable perceptual image and location for an object of interest. Increasing the frequency modulation of the harmonics, as in call type 9, improves localization performance (Simmons 1979).

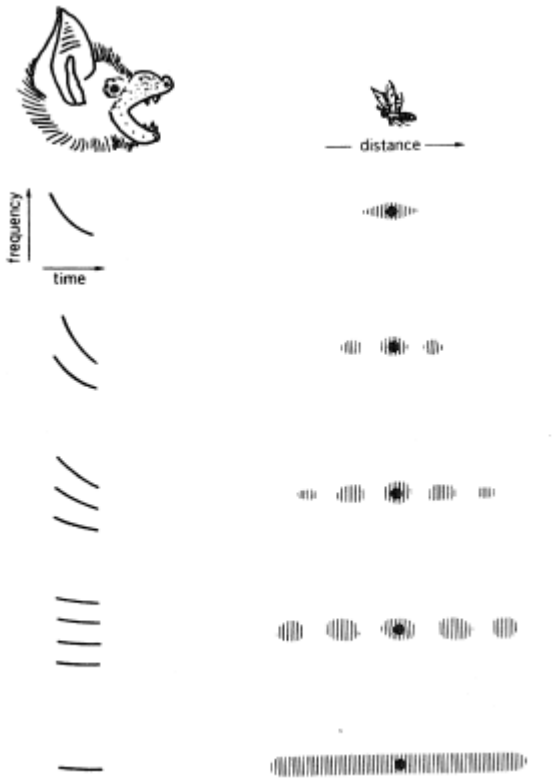


Figure 5.13: Copied from Simmons (1979): A diagram of the relationship between bandwidth and number of harmonics in a sonar sound and the perceived position of a target in range, or target distance. The true position of the target is indicated by a dot, and the distribution of the region in which the target is perceived is shaded.

Echolocation call structures are well known to correlate strongly with habitat use, prey type, and hunting style (Aldridge & Rautenbach 1987; Jones & Rayner 1988; Kalko 1995; Kalko & Schnitzler 1993; Neuweiler 1984; Obrist 1995; Schnitzler & Kalko 2001; Schnitzler et al. 2003; Simmons et al. 1979; Surlykke & Moss 2000). Using call type 9 as

the nearest modern comparison to the proposed ancestral call type points towards the behaviour and ecology of the five families that primarily use this call type as being most similar to that of the proto-bat: Phyllostomidae, Natalidae, Megadermatidae, Nycteridae, and Mystacinidae.

Bats in four of these five families have extremely diverse diets. Phyllostomid species' diets range from insects through pollen, nectar and fruit, to frogs, birds, and other bats, and the blood of mammals and birds (Nowak 1994). Many species are not restricted to any one food type, feeding somewhat opportunistically, taking insects as well as pollen, nectar and fruit. Species in both the families Megadermatidae and Nycteridae feed on arthropods and vertebrates, including other bats, rodents, birds, frogs, reptiles and fish (Nowak 1994). Mystacinid species feed on arthropods, fruit, nectar, pollen and even vertebrate carcasses (Nowak 1994). Members of the Natalidae, however, are thought to be entirely insectivorous (Nowak 1994; Tejedor 2005). These mainly wide-ranging diets suggest that the proto-bat's diet was also very diverse and probably opportunistic, spanning plants and animals, both vertebrates and invertebrates, and giving the proto-bat great flexibility of diet. Previous workers have invoked an insectivorous proto-bat (Arita & Fenton 1997; Fenton 1984; Fenton et al. 1995; Hill & Smith 1984; Simmons & Stein 1980), though Speakman (2001) suggested that it was frugivorous. Fossils of extinct early bats have insectivorous dentition (Freeman 2000; Gunnell & Simmons 2005; Rydell & Speakman 1995; Simmons & Geisler 1998), though it is possible that the first bats evolved up to 25-30 million years prior to the existence of these fossils (Springer, Teeling, & Madsen 2001) leaving ample time for the evolution of insectivory from omnivory. Omnivory is a highly plausible dietary system for the proto-bat, since many other small, nocturnal mammalian taxa feed opportunistically and omnivorously (mouse and rat-like rodents, shrews, hedgehogs, and tenrecs), including bats' close relatives, the order Eulipotyphla, which contains the shrews, moles and hedgehogs (MacDonald 2004). Additionally, high frequencies are necessary to detect small insects using echolocation (higher frequencies have smaller wavelengths), so insectivory may be a derived condition, evolving with high frequency echolocation calls.

The five families using call type 9 also show diversity in their habitat use. Phyllostomids, in particular, are found in desert scrub, prairies, pastures, marshes, orchards, and sub-tropical and tropical forests (Nowak 1994). The other four families are more restricted to forested habitats (Nowak 1994). All five families have wing morphologies that are most suitable for slow, manoeuvrable flight in cluttered conditions. Some use a perch-hunting strategy: hanging on a branch and then dropping onto a prey item, and others a gleaning strategy: snatching prey from surfaces such as leaves and tree trunks whilst in flight (Norberg & Rayner 1987). Some bats in the family Phyllostomidae also hover to access fruit, pollen and nectar, and *Mystacina tuberculata* (sole species of Mystacinidae) is particularly unusual in that it mainly forages on the ground, rather than in flight (Jones 2003; Nowak 1994). The proto-bat is thought to have evolved in a forested habitat (Fenton et al. 1995; Gunnell & Simmons 2005; Schnitzler et al. 2004; Simmons & Stein 1980), and various foraging strategies have been postulated, such as gleaning followed by perch hunting (Speakman 2001) and short flights to the ground, capturing prey by forcing it down using the wings (Schnitzler *et al.* 2004). Both these proto-bat hunting strategies are compatible with those seen in bats using call type 9.

The echolocation calls of the species in these five families are extraordinarily similar, considering the diversity of habitats and prey types they use. Even the three species of sanguivorous bats of the subfamily Desmodontinae (Phyllostomidae), and the frog-eating species, *Trachops cirrhosus* (Phyllostomidae), *Megaderma lyra* (Megadermatidae), *Nycteris grandis* (Nycteridae) use the same multiharmonic, frequency-modulated call. In the phyllostomids, the lack of relationship between their morphology, diet or habitat and their echolocation calls has been noted, and the role of echolocation in the Phyllostomidae questioned (Bogdanowicz, Csada, & Fenton 1997). Functionally, echolocation calls of this type allow great flexibility: the multiharmonic structure provides bats with the opportunity to alter the harmonic of maximum energy, and hence focus on objects of various different sizes.

For the proto-bat, fairly short duration, multi-harmonic, narrowband calls offer the opportunity to benefit from a wide range of prey items using simple foraging techniques

that might have been available using the broad, short wings of the proto-bat living in the understory of a forest. Small alterations to the echolocation call structure could then lead to improved localization and detection, and more specialised diets and foraging strategies in subsequent species.

5.6 Conclusions

Despite concerns about flaws in ancestral reconstruction methodologies, all eight techniques used indicated a similar ancestral echolocation call for bats. Call types 8 and 9 both appeared to be plausible according to reconstructions of continuous characters and principal component scores, though further analyses of discrete characters made call type 9 (a short, multi-harmonic, broadband call) more likely as the ancestral echolocation call. Further evidence regarding the structure of the mammalian larynx, typical mammal sounds, and the ontogenetic development of echolocation calls in bats supports the finding of a short, multiharmonic, broadband call as the ancestral call, but suggest that early bats would have used a narrowband structure, rather than the broadband structure of call type 9, with a later progression to a true call type 9 structure.

Using information about extant users of the nearest call type to that of the ancestral bat, call type 9, it is likely that the proto-bat was a slow and manoeuvrable flier with an opportunistic and omnivorous diet and a perch hunting foraging strategy, living in a forest habitat.

6 Chapter 6: Are echolocation call structures 'key innovations' that promote diversification?

6.1 Abstract

One of the fundamental questions in evolutionary biology concerns the uneven distribution of species among taxa in taxonomic groups, and the causes of differences in diversification rates. Novel traits that make new niche space available, known as key innovations, have long been hypothesised to be responsible for the rapid evolution and diversification of some clades. In this chapter I explore whether the bat phylogeny shows any evidence of such 'up-shifted' clades (i.e., clades that have undergone increased rates of diversification). I ask whether these clades are up-shifted as a result of the echolocation call types used by the species they contain, and I explore the possible ecological models that might substantiate a link between echolocation call types and increased speciation rates.

I use a process of stepwise Akaike Information Criterion (AIC) to compare alternative placements of diversification rate shifts in the bat phylogeny, and find that the best model indicates two up-shifts in rate, one at the root of a clade of 80 species of Old World fruit bat (Pteropodidae), and the other at the root of the New World fruit bat sub-family Stenodermatinae (Phyllostomidae). I then use a whole-tree likelihood-based method to estimate the rates of speciation, extinction and transition between traits across the bat phylogeny based on (1) the whole tree and the 13 call types described in Chapter 4, and (2) the tree with the two up-shifted clades as partitions and the same 13 call types. This analysis suggests that call types 1 and 9 (no echolocation, and a multiharmonic, short duration, high bandwidth call) show increased rates of speciation compared with other call types. Analysis of speciation rates for all echolocation call types additionally highlights call types 3 (single harmonic, medium duration, narrowband), 7 (single harmonic, very short duration, high bandwidth), 8 (single harmonic, short duration, medium bandwidth), and 10 (multi-harmonic, short duration, high bandwidth) as being associated with increased speciation rates.

I put forward two mechanisms by which echolocation can influence speciation rate. The first, an allopatric model, sees echolocation calls altering niche use and expanded geographic range as a consequence, allowing greater opportunity for divergent selection and barriers to gene flow. The second, a sympatric model, suggests that through altered niche use, changes to echolocation calls also result in changes in communication calls which bring about reproductive isolation through sexual selection and assortative mating. I therefore suggest that certain echolocation call types (call types 1, 3, 7, 8, 9, and 10) can be considered key innovations, as (1) they are associated with increased rates of diversification; (2) there is a functional model explaining the link between the traits and increased speciation; and (3) an analogous trait (echolocation) in toothed whales shows a similar pattern of diversification.

6.2 Introduction

6.2.1 Background

The uneven distribution of species among higher taxa in many taxonomic groups has been of interest to biologists for nearly a century (Heard & Cox 2007; Willis & Yule 1922). Taxonomic groups typically show a 'hollow curve' distribution, with many species-poor groups and only a few species-rich groups (Dial & Marzluff 1989; Scotland & Sanderson 2004; Willis & Yule 1922). Whilst it is possible that hollow curve distributions (see Figure 6.1) are a consequence of random processes (Ricklefs 2003), it may also suggest that lineages differ in their probabilities of diversifying (Sanderson & Donoghue 1994), perhaps as a result of possessing different phenotypic traits (Freckleton, Phillimore, & Pagel 2008; but see Purvis *et al*. 2011; Venditti, Meade, & Pagel 2010). Several organismal traits have been linked to increased rates of diversification in many taxa (e.g., floral nectar spurs in orchids (Hodges & Arnold 1995); small adult body size in Carnivores (Isaac *et al.* 2005); sexual dichromatism in passerine birds (Barraclough, Harvey, & Nee 1995)).

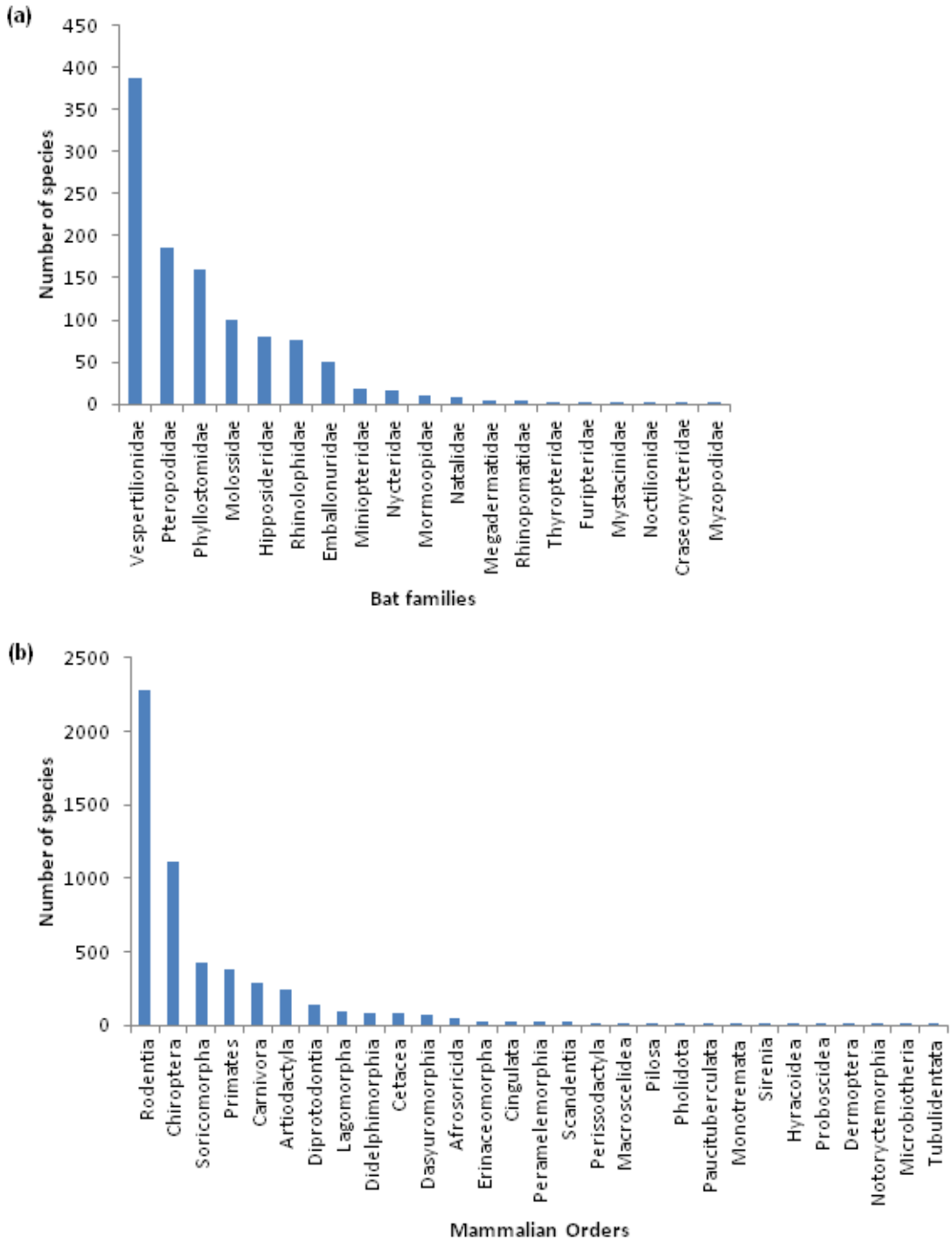


Figure 6.1: The hollow curve distributions for species in (a) bat families and (b) mammalian orders Taxonomy follows (Wilson & Reeder 2005) except with the sub-family Miniopterinae given family status (Miller-Butterworth et al. 2007).

Bats are a particularly speciose mammalian order, containing more than one fifth of recognised mammal species, and coming second only to the rodents in terms of species numbers (Wilson & Reeder 2005). The high species richness of bats is often said to be due to the twin key innovations of flight and echolocation, giving bats access to a niche previously unexploited by mammals: the night sky (Fenton et al. 1995; Schnitzler et al. 2003; Sears et al. 2006; Speakman 2001). This hypothesis has never been empirically tested. Traits pertaining to body size (adult body mass), life history (age at sexual maturity, gestation period, interbirth interval, litter size), abundance (population density, group size), and sexual dimorphism (mass dimorphism, length dimorphism) have been found *not* to correlate which bat species richness, although after removing one extreme outlier, the wing aspect ratio of micro-bats was found to correlate negatively with species richness (Isaac *et al.* 2005). This may indicate a role for small colony size and low rates of individual exchange between colonies in determining species richness, due to the bats' inefficiency at flying large distances (Isaac *et al.* 2005).

There have been two previous studies of diversification rates in bats, both on different permutations of the original bat supertree (Jones *et al.* 2002). The first of the two studies (Jones *et al.* 2005) used both the original supertree which splits the bats into suborders Megachiroptera and Microchiroptera (now thought to be erroneous), and a re-arrangement of the Jones *et al*. (2002) supertree based on the familial topology of Teeling *et al*. (2005), which sees the Megachiroptera absorbed into a newly defined suborder, the Pteropodiformes. The second study used the original bat supertree published by Jones *et al*. (2002) (Purvis *et al.* 2011). Both studies used the delta shift statistic (Chan & Moore 2005; Moore, Chan, & Donoghue 2004), a whole-tree likelihood-based test, and Jones, Bininda-Emonds, & Gittleman (2005) also used a sister-clade comparison technique, the Slowinski-Guyer test (Slowinski & Guyer 1993). Jones *et al*. (2005) identified a significant up-shift near the base of the Phyllostomidae (in the Teeling *et al*. (2005) topology), as well as a further shift near the base of the genus *Artibeus* (Stenodermatinae: Phyllostomidae) (in both topologies). Purvis *et al*. (2011), too, detect an up-shift in *Artibeus* (Stenodermatinae: Phyllostomidae). Jones *et al*. (2005) also detect three non-significant shifts within the Pteropodidae (in both topologies). Both Jones *et al*. (2005) and Purvis *et al*. (2011) detect

further significant up-shifts in clades within the Rhinolophoidea, Noctilionoidea, and Vespertilionoidea, as well as down-shifts in the Noctilionidae and Desmodontinae.

Bats are no exception to the hollow curve rule, with 10 out of 19 families possessing 10 species or fewer, and four families containing 100 or more species (see Figure 6.1) (Miller-Butterworth et al. 2007; Simmons 2005). Echolocation is often cited as being highly influential in the evolution of bats (Fenton et al. 1995; Schnitzler et al. 2003; Sears et al. 2006; Speakman 2001), and the variation in echolocation call types across the bat tree, along with the importance of echolocation in shaping the ecology of bats (Denzinger *et al.* 2004), suggests that echolocation call differences may be at least in part responsible for the unbalanced nature of the bat phylogeny. If echolocation is indeed a key innovation promoting increased rates of diversification, one might expect to see variation in the species richness of bat clades of the same age using different echolocation call structures. Observation suggests that certain echolocation call types, such as the flexible high bandwidth, short duration calls of the most speciose family of bats (Vespertilionidae), might be correlated with rapid diversification and increased species richness. In this chapter, I will test the hypothesis that certain echolocation call types have acted as key innovations and thereby enabled increased diversification rates in bats. Diversification rates can increase as a result of increased speciation rates, decreased extinction rates, or a combination of both.

The concept of a key innovation was first described by Simpson (1953) as a behavioural trait that opened new adaptive zones. Key innovations have since been defined in various ways (see Hunter (1998) and Cacho *et al.* (2010)), though all definitions are based on the concept that some novel traits can cause an increase in the diversification rate of a taxon (Cacho *et al.* 2010).

Cacho *et al.* (2010) suggest that the plausibility of a putative key innovation should be assessed using three kinds of evidence:

(1) The taxon having the trait has a higher rate of diversification than closely related taxa lacking the trait.
(2) There is a reasonable ecological or functional model to justify a causal link between the trait and increased diversity.
(3) Analogous traits are consistently associated with increased diversification rates.

Finding a 'reasonable ecological or functional model' that links the trait and increased diversity is the most challenging of the three conditions. Increased diversity (driven by an increase in speciation rate) can only come about as a result of an increase in the likelihood of reproductive isolation, as this is necessary for speciation (Dobzhansky 1937; Grant 1963; Mayr 1942; Yoder et al. 2010). It is generally accepted that reproductive isolation usually occurs as a by-product of allopatric divergence, leading to allopatric speciation (Coyne & Orr 2004; Mayr 1942). But since allopatrically-induced reproductive isolation occurs at a relatively slow rate, it is likely to limit the rate of speciation considerably (Coyne & Orr 2004). Therefore it seems likely that natural selection could be involved in bringing about reproductive isolation, through an ecological speciation model. As Yoder *et al*. (2010) report, a number of ecological mechanisms have been implicated in the process of ecological speciation including competition (Abrams 2006; Dieckmann & Doebeli 1999), mutualism (Kiester, Lande, & Schemske 1984), predation (Day, Abrams, & Chase 2002), host-parasite interactions (Nuismer 2006), sexual selection (Gavrilets & Waxman 2002), fluctuating environments (Abrams 2006), and environmental gradients (Doebeli & Dieckmann 2003; Slatkin 1973). In order for echolocation call type to bring about non-allopatric speciation, it is likely that one of these mechanisms could be responsible.

6.2.2 Hypotheses

If echolocation call types have acted as key innovations in the evolution of bats, then following Cacho *et al*.'s (2010) conditions I would expect to find that the bat tree has varying diversification rates showing a clear relationship between any clades with an up-shifted diversification rate and a particular echolocation call type, and that the call types associated with up-shifted clades are capable of enabling increased niche size, increased geographic range size and assortative mating (which could all lead to reproductive

isolation). I would expect call types 1, 3, 7, 8, 12, and 13 to enable these conditions to occur (see Figure 6.2 for call types).

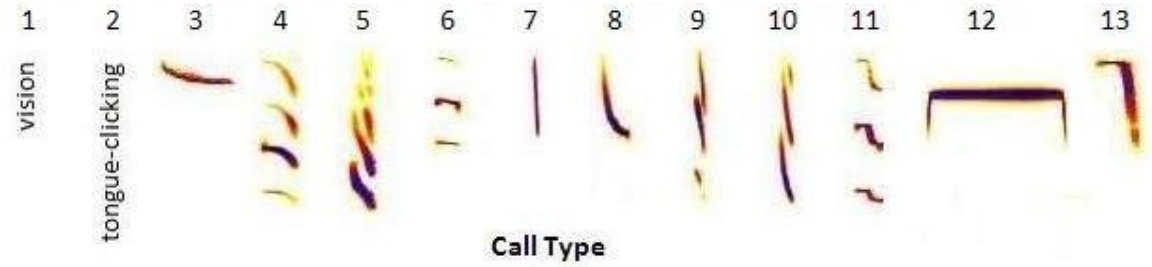


Figure 6.2: The 13 call types used by extant bats, as described in Chapter 4.

Call type 1, which is the use of vision and olfaction rather than echolocation, allows bats to break from the use of echolocation and increase in body size, giving them access to a new niche and a new geographic range. It is thought that echolocation constrains maximum body size because in order to be energy efficient, bats must breathe, flap their wings, and echolocate simultaneously (Speakman & Racey 1991). Larger body sizes result in wing beat frequencies that are too slow for echolocation to provide the necessary sensory input for orientation and food acquisition (Jones 1994). By losing echolocation and using vision as the primary sensory modality, bats are able to attain body sizes that allow food acquisition from a greater area, perhaps making frugivory from widely distributed foraging patches possible, as well as more diurnal behaviour, as larger body size lowers their predation risk.

Call types 3 and 8 allow bats to exploit niches outside of the forest environment (Kalko & Schnitzler 1993). Call type 3 (medium duration, narrowband and low frequency) enables the use of open spaces for commuting and foraging. Call type 8 (short duration, mid-bandwidth calls) is very flexible, and opens up edge-space, such as along forest waterways, tree fall clearings in forests, and forest margins. Consequently, both call types could open up new niche space.

Call types 7, 12 and 13 allow exploitation of extremely dense forest, each via a different mechanism (Kalko & Schnitzler 1993; Kingston *et al.* 1999; Schmieder *et al.* 2010). Call

type 7 is an extremely high bandwidth, short duration call which reveals detail about a range of size classes. Call type 12 is constant frequency and reveals the fluttering wings of insect prey against a still background. Call type 13 combines these two call features, and also allows the production of long duration calls without pulse-echo overlap as the pulse and echo are separated by frequency due to Doppler shift. All three could open new niche space.

All call types may promote assortative mating, as echolocation calls can be used in communication (Fenton 1986; Jones & Siemers 2011), and hence sexual selection based on calls may influence phenotypic and genotypic divergence and the initiation of reproductive isolation (see Kingston & Rossiter 2004).

A correlation between species richness and a phenotypic trait does not guarantee causation (Cracraft 1990). This may be especially true in bats, as aspects of echolocation call structure correlate strongly with wing morphology (Aldridge & Rautenbach 1987), which might confer varying abilities to disperse. The ability to disperse and colonise new geographical areas without an associated niche expansion may be responsible for a much greater degree of phylogenetic imbalance than we are currently aware (Heard & Cox 2007; Purvis *et al.* 2011).

In addition, echolocation may show correlations with diet (Aldridge & Rautenbach 1987), such that periods of increased diversification in lineages of flowering plants and insects may lead to increased diversification in bats with echolocation calls that are suited to such diets.

6.2.3 Chapter aims

The aims of this study are threefold: (1) To determine whether diversification rates are constant across the bat phylogeny, (2) to establish whether any shifts in diversification rate are correlated with echolocation call types, (3) to consider whether these echolocation call types cause increased diversification.

6.3 Methods

6.3.1 Data

6.3.1.1 Bat call data

I collated and measured the echolocation call data as described in Chapter 2: section 2.2. The echolocation data included data from species found in EchoBank that could be successfully measured, and data from species reported in the literature. I used the parameters chosen in section 2.2.8 in Chapter 2. The full list of species data is shown in Appendices A and E.

6.3.1.2 Supertree

I constructed the supertree as described in Chapter 2: section 2.3. I used a version of the supertree containing 1104 bat species, leaving out the 12 species that were placed polyphyletically to their families, as described in Chapter 3.

6.3.1.3 Imputed data sets

The bat call data contained between 291 and 408 data points for each of the eight continuous echolocation call parameters (Bandwidth, Call Duration, Characteristic Frequency, Dominant Slope, Maximum Frequency, Minimum Frequency, Peak Frequency, Total Slope) (see Appendix F). I used the programme PhyloPars (Bruggeman, Heringa, & Brandt 2009) to impute the remaining data points for each call parameter, as estimating diversification rates requires a full data set. Unevenly distributed missing date would skew the analysis, as species with missing data would be removed from the analysis. PhyloPars uses maximum likelihood estimation to estimate phylogenetic covariances and phenotypic variances. The model underlying the phylogeny is assumed to be one of Brownian Motion, which is often used as a null model in comparative methods. Although, analyses in Chapter 4 showed that echolocation calls in bats were most likely to have evolved under an Ornstein-Uhlenbeck model, unfortunately this imputation method does not incorporate OU. The covariances of the parameter distribution depend on the topology and branch lengths of the phylogeny, and on the rates and correlations of the observed parameters. The optimal

phylogenetic phenotypic covariances are initially combined with the phylogeny, and the covariances between the observations and the missing values are calculated. The covariances are then used to calculate each missing value as the product of all original observations and an estimate-specific set of associated weights (Bruggeman *et al.* 2009).

PhyloPars only imputes continuous data, and so to impute the missing echolocation call types, I inferred missing call types from phylogenetic relatives and from the imputed continuous call variables. In total, the call types of 333 species were known, and those of the remaining 772 species were assumed or imputed. Some families are known to only use a single echolocation call type, and, as such, assumed call types are extremely likely. Of the 772 assumed or imputed species, 308 were assumed, based on the single call type of the majority of their respective families (Hipposideridae (call type 13); Miniopteridae (call type 8); Phyllostomidae (call type 9); Pteropodidae (call type 1); Rhinolophidae (call type 12)). The call types of species in families which use more than one call type (the remaining 466 species) were imputed using the protocol below. Species without a known call type are referred to as 'missing species', and species with a known call type are referred to as 'observed species'.

(1) Assign all missing species with an observed sister species with that call type.
(2) For missing species without an observed sister species, assign the call type of the younger nearest neighbour, if it is an observed species.
(3) If not, assign the call type of the older nearest neighbour, if it is an observed species.
(4) Repeat, until all missing species have a call type.

6.3.2 Analysis

6.3.2.1 Location of diversification shifts

I used the function 'TurboMEDUSA' to locate diversification shifts within the bat supertree. This function is currently a self-contained and unreleased R package (Brown, J. 2011, pers. comm.) which will soon be integrated into the R package *Geiger*, alongside its predecessor, MEDUSA (Harmon *et al.* 2009). TurboMEDUSA uses stepwise AIC (Akaike

Information Criterion) to compare models of lineage diversification and quantify support for any shifts in speciation and extinction rates. Stepwise AIC compares 20 subsequent models, each with an additional diversification rate shift, and gives each an AICc score (small sample size-corrected AIC). The lowest AICc score that is larger than next lowest score by the necessary threshold calculated for the tree size (number of tips) is the best model. The advantage of TurboMEDUSA over similar methods like SymmeTREE (Chan & Moore 2005) is that it can be used with incompletely resolved phylogenies, and also allows adjustments to be made for incompletely sampled phylogenies. The adjustments I made are detailed below.

The bat supertree contains several polytomous clades which are likely to be artifacts of a lack of information about the phylogenetic position of a group of species in the supertree building process, rather than true associations between related species (see Alfaro *et al*. 2009). To avoid such polytomies influencing the rate shift identification process, I excised any polytomies of nine species or more and any monophyletically-placed species of the same genus, leaving a single species as a representative. I then compensated for the removal of these species by specifying a richness of 1 plus the number of excised species for the remaining representative species. Doing this resulted in the collapsing of the species within each of 14 clades containing between 10 and 103 species (with polytomies numbering between nine and 31 species), and a total of 440 species (103 *Myotis* spp., 19 *Kerivoula* spp., 18 *Pipistrellus* spp., 17 *Eptesicus* spp., 17 *Murina* spp., 16 *Hypsugo* spp., 12 *Glauconycteris* spp., 11 *Nyctophilus* spp. (Vespertilionidae); 77 *Rhinolophus* spp. Rhinolophidae); 64 *Pteropus* spp. (Pteropodidae); 64 *Hipposideros* spp. (Hipposideridae); 18 *Chaerephon* spp., 14 *Mops* spp., 10 *Mormopterus* spp. (Molossidae)).

In addition, to compensate for the 12 species I excised from the bat supertree due to their unlikely polytomous placement, I specified that *Tadarida insignis* had a richness of 2 (to accommodate excised *Tadarida teniotis*); that *Nycteris javanica* had a richness of 6 (to accommodate half the excised *Nycteris* species); and that *Nycteris arge* had a richness of 7 (to accommodate the other half of the excised *Nycteris* species). I chose these placements

for the excised species to place them with other members of the same genus. For the 16 *Nycteris* species, I split the richness between two species to balance the topology.

6.3.2.2 Diversification shifts and echolocation call types

To assess the relationships between echolocation call types and the clades that have experienced diversification shifts found by TurboMEDUSA, I used the function 'MuSSE' (Multi-State Speciation and Extinction) in the R package *diversitree* (FitzJohn 2011). MuSSE is a likelihood-based method that compares models with varying speciation, extinction and transition rates for a series of multi-state characters. It is an alternative to the extensively used sister clade comparison method. Sister clade analyses require that each clade has a single character state, and assume that states have remained the same throughout the evolutionary history of each lineage. MuSSE accepts variation in the character states seen across clades, as it uses the whole branching pattern of the phylogeny (FitzJohn 2010). Additionally, MuSSE allows speciation and extinction rates to be estimated independently, whereas more simple methods such as those developed by Paradis (2005) and Freckleton *et al*. (2008) (FitzJohn 2010) do not.

The combination of the speciation rate and the extinction rate gives the net diversification rate, and the transition rate indicates the likelihood of a state change (from one character to another). Initially I ran five models to establish the general pattern of speciation, extinction and transition rates, and to give a framework for comparison of the more complex models I ran later. The initial five models were:

1) One speciation rate, one extinction rate, one transition rate.
2) Speciation rates allowed to vary, one extinction rate, one transition rate.
3) One speciation rate, extinction rates allowed to vary, one transition rate.
4) One speciation rate, one extinction rate, transition rates allowed to vary.
5) Speciation and extinction rates allowed to vary, and one transition rate.

I then created a likelihood function based around the supertree with the 3 partitions indicated by the results of TurboMEDUSA, using the 'make.musse.split' function of MuSSE. I created 32 models in total, based on a combination of rate regimes for each of the

three model parameters: *lambda* (speciation), *mu* (extinction), and *q* (transitions between characters). In each model, I specified groups of allied rates for each character (echolocation call types 1 – 13, as outlined in Chapter 4) in each partition (partitions 1 – 3, found using TurboMEDUSA). For all three rate parameters, I first established two sets of rates, those that were possible, and those that were impossible. For example, speciation or extinction of lineages using call types 1-8 and 10-13 was deemed impossible in the partition containing species that use only call type 9, whereas speciation or extinction of lineages using call type 9 in a partition containing species that use call type 9 was deemed possible. In partition 1, which represented the rest of the tree, excluding clades found to have undergone up-shifts in diversification rate, all speciation and extinction events were considered possible (see Table 6.1 for a complete matrix). Impossible rates were coded as having a likelihood of 0.

		Call Type												
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Partition	**1**	p	p	p	p	p	p	p	p	p	p	p	p	p
	2	p	p	i	i	i	i	i	i	i	i	i	i	i
	3	i	i	i	i	i	i	i	i	p	i	i	i	i

Table 6.1: Speciation and extinction rates (*lambda* and *mu*) were designated as either possible (p) or impossible (i) for each call type in each partition of the tree.

Similarly for *q*, (the rate of transitions between characters (echolocation call types)), rates were split into two groups as shown in Table 6.2. The transitions marked as 'likely' are those which I perceive as likely based on the results of ancestral reconstruction analysis in Chapter 5. For example, a transition from call type 1 (no echolocation), to call type 12 ('sophisticated' Doppler Shift Compensation constant frequency calls) is unlikely, whereas a transition from call type 8 (medium bandwidth, medium duration calls) to call type 3 (low bandwidth, long duration calls) is considered likely. In contrast to the speciation and extinction rates, 'unlikely' transition rates were not coded as having a likelihood of 0, but were simply grouped together.

To Call Type \ From Call Type	1	2	3	4	5	6	7	8	9	10	11	12	13
1	**x**	l	l	l	l	l	l	l	l	l	l	l	l
2	l	**x**	u	u	u	u	u	u	u	u	u	u	u
3	u	u	**x**	u	u	u	u	l	u	u	u	u	u
4	u	u	u	**x**	u	u	u	u	l	u	u	u	u
5	u	u	u	l	**x**	u	u	u	l	l	u	u	u
6	u	u	u	l	l	**x**	u	u	u	u	u	u	u
7	u	u	u	u	u	u	**x**	l	u	l	u	u	l
8	u	u	l	u	u	u	l	**x**	u	l	l	u	u
9	l	l	u	u	u	u	u	u	**x**	u	u	u	u
10	u	u	u	u	u	u	u	u	l	**x**	u	u	u
11	u	u	u	l	l	l	u	u	l	u	**x**	u	u
12	u	u	u	u	l	l	u	u	u	u	l	**x**	l
13	u	u	u	l	l	l	u	u	l	u	l	u	**x**

Table 6.2: Transition rates (*q*) were designated as either likely (l) or unlikely (u) for each call type in all partitions of the tree.

I then split the possible rate parameters into groups to represent alternative evolutionary scenarios: four alternatives for each of *lambda* and *mu* and two for *q*, as shown below. Impossible parameters were constrained to zero for *lambda* and *mu*, and unlikely parameters were constrained to one another (as a single rate) for *q*. These models represent scenarios in which speciation and extinction are related to echolocation call type, as explained below.

- *lambda*/*mu*
    - **fully constrained (fc)** – all rates equal: echolocation call types do not differentially influence speciation/extinction rate
    - **fully relaxed (fr)** – all rates different: each echolocation call type influences speciation/extinction rate to a different degree
    - **half and half (hh)** – one rate for partition 1 (rest of the tree), and a second rate for all other partitions: the echolocation call types of up-shifted clades influence speciation/extinction rates differently than the echolocation call types of the rest of the tree

- **shift-based (sb)** – a different rate for each partition: the echolocation call type of each of the up-shifted clades, and of the rest of the tree, differently affects speciation/extinction rate

- *q*
  - **constrained (qc)** – all rates equal, plus one rate for unlikely transitions
  - **relaxed (qr)** – all rates different in each partition, plus one rate for unlikely transitions

Combining these alternatives produces 32 models with rate parameters numbering between four in the most constrained model (one *lambda*, one *mu*, and two *q*s) and 36 in the most relaxed (see Table 6.3).

qc

		lambda			
		fc	**fr**	**hh**	**sb**
mu	**fc**	4	19	5	6
	fr	19	34	20	21
	hh	5	20	6	7
	sb	6	21	7	8

qr

		lambda			
		fc	**fr**	**hh**	**sb**
mu	**fc**	6	21	7	8
	fr	21	36	22	23
	hh	7	22	8	9
	sb	8	23	9	10

Table 6.3: The 32 combinations of the four model sets for each of *lambda* and *mu*, and the two alternatives for *q*. The numbers indicate the number of parameters specified in each model.

The likelihood function based on the supertree and its partitions was then constrained to each of these 32 rate matrices, and 32 new likelihood functions were produced. Using maximum likelihood starting points for *lambda* and *mu* generated from the supertree (*lambda* = 0.0986015, *mu* = 0), and specifying that *q* should start at a value $1/5^{th}$ of *lambda* (*q* = 0.0197203), the maximum likelihood point of each model was found by nonlinear optimisation. Akaikie Information Criterion (AIC) values were extracted for each model and compared to choose the best performing models. Any model within 4 AIC points of the best performing model was also considered following Burnham & Anderson (2002). The speciation, extinction and transition rates from the best performing models were also extracted.

For comparison, the net speciation and extinction rates for the whole split-free tree were estimated using the 'birthdeath' function of the *Geiger* package (Harmon *et al.* 2009) in R (The R Core Development Team 2010).

6.4 Results

6.4.1 Location of diversification shifts

Three diversification shifts were identified in the bat supertree by TurboMEDUSA (see Figure 6.3, Table 6.4 and Table 6.5). The first (1) is a down-shift concerning the whole tree background rate, and is included for comparison only. The remaining two clade-specific diversification rate shifts, (2) and (3), are both up-shifts. The first is a clade of 80 species of the Pteropodidae family including nine of the 10 species in the genus *Rousettus*, at least three of which are known to use tongue-clicking echolocation in caves, although no other pteropodid genera use echolocation at all. This shift occurred ~24 million years ago (mya). The second up-shift is the whole Stenodermatinae (Phyllostomidae) sub-family of 67 species, at around ~13 mya. The clades that have undergone shifts in diversification rate, and the echolocation call types used by them, are shown in Figure 6.3. The net diversification rate for up-shifts ranges from 0.0399964 to 0.300013, and for down-shifts from 0.0018843 to 0.0070386. For comparison, a split-free tree with a single speciation rate and a single extinction rate had an estimated net diversification rate of 0.074215.

Model	log likelihood	AICc	AICc difference
1	-2042.28	4088.571	-
2	-2013.84	4037.729	-50.842
3	**-2005.35**	**4026.811**	**-10.918**
4	-1999.53	4021.264	-5.547
5	-1994.69	4017.711	-3.553
6	-1990.87	4016.229	-1.482
7	-1987.36	4015.402	-0.827
8	-1984.13	4015.156	-0.246
9	-1981.19	4015.511	0.355
10	-1977.38	4014.175	-1.336
11	-1974.53	4014.784	0.609
12	-1971.92	4015.893	1.109
13	-1969.36	4017.158	1.265
14	-1966.87	4018.566	1.408
15	-1964.77	4020.798	2.232
16	-1962.7	4023.119	2.321
17	-1960.61	4025.444	2.325
18	-1958.59	4027.926	2.482
19	-1956.53	4030.379	2.453
20	-1954.45	4032.8	2.421

Table 6.4: Alternative models for the location of up-shifted clades. The best performing model (shown in bold) was chosen based on the lowest AICc value with at least a 8.80625 difference from the next lowest – the appropriate AICc threshold for a tree with 664 tips, as calculated by TurboMEDUSA.

Partition	Clade	Net diversification rate (r)	Log(likelihood)	Shift direction
1	Rest of tree	0.075726	-1640.00	↓
2	80 spp. of Pteropodidae	0.133499	-210.96	↑
3	Stenodermatinae	0.252833	-154.38	↑

Table 6.5: The phylogenetic location and strength of the diversification rate shifts estimated by TurboMEDUSA. For comparison, a split-free tree with a single speciation rate and a single extinction rate had an estimated net diversification rate of 0.086482.

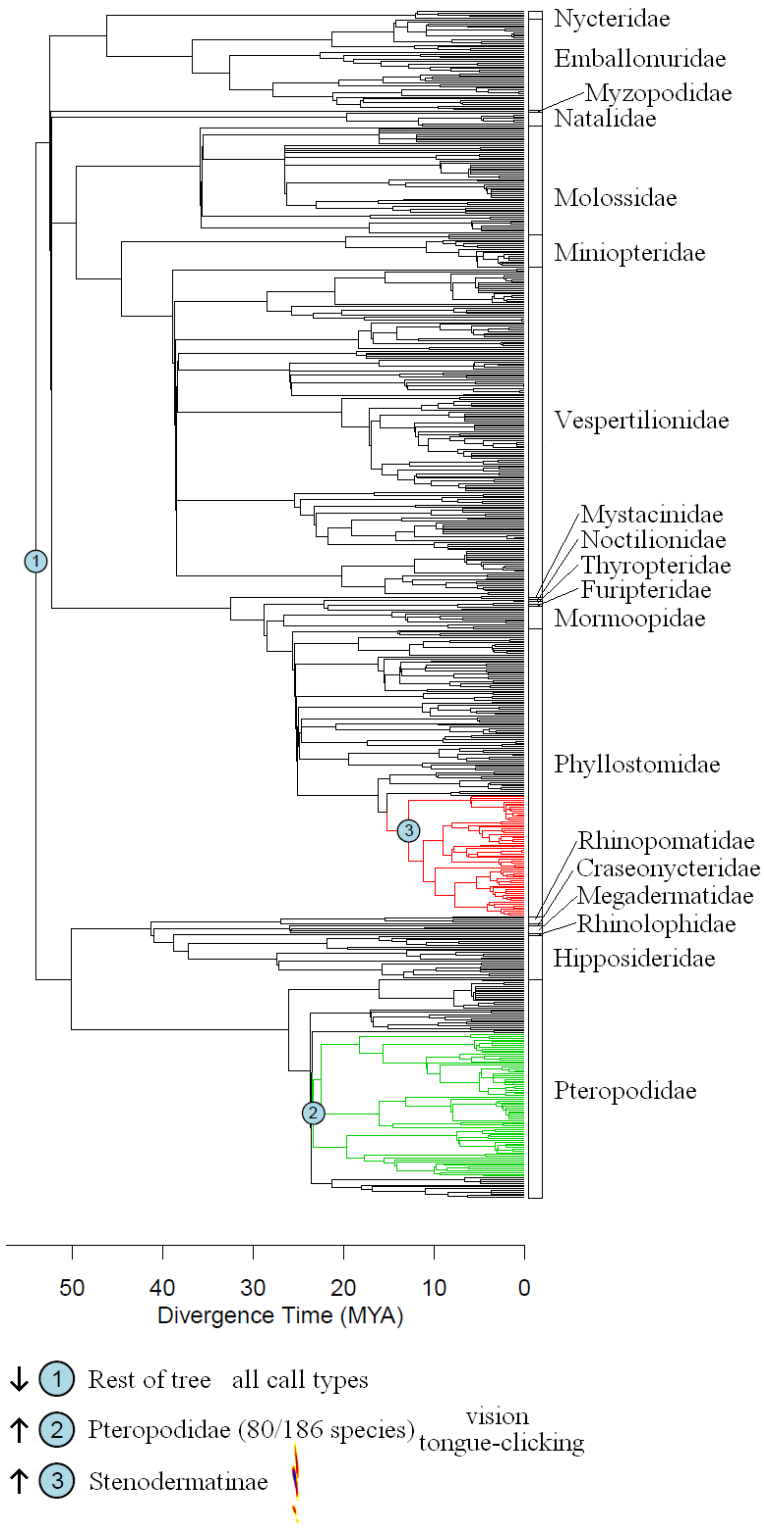


Figure 6.3: The bat supertree showing clades which have undergone shifts in diversification rates, as well as the echolocation call types used by these clades. Arrows indicate the direction of each shift.

6.4.2 Diversification shifts and echolocation call types

In the initial set of model tests on the whole tree without shifts, the model with a single extinction rate, a single transition rate and 13 speciation rates out-performed the other four models (by 18 - many more than the threshold 4 AIC units) (Burnham & Anderson 2002). See Table 6.6 for AIC scores.

Model			AIC score	Degrees of freedom
Speciation (lambda)	**Extinction (mu)**	**Transition (q)**		
fully relaxed	**fully constrained**	**fully constrained**	**8448.675**	**15**
fully relaxed	fully relaxed	fully constrained	8466.786	27
fully constrained	fully constrained	fully constrained	8476.559	3
fully constrained	fully relaxed	fully constrained	8490.586	15
fully constrained	fully constrained	fully relaxed	8584.763	158

Table 6.6: Comparison of diversification models based on the whole tree and echolocation call types using AIC scores. The best performing model (shown in bold) was chosen based on the lowest AIC value.

The favoured model in the split-free tree has negligible extinction and transition rates, and the speciation rates vary from negligible to 0.142 for call type 1 (no echolocation – vision and olfaction instead). See Table 6.7 for all rates. Call types 9, 8, 10, 3, 13 and 7 have particularly high speciation rates.

	Rate parameter	Rate for whole tree - lambda fully relaxed, mu fully constrained, q fully constrained
Speciation rates	Call type 1	0.14164
	Call type 2	0.00000
	Call type 3	0.09153
	Call type 4	0.07579
	Call type 5	0.05703
	Call type 6	0.02845
	Call type 7	0.08580
	Call type 8	0.10063
	Call type 9	0.11564
	Call type 10	0.09754
	Call type 11	0.05596
	Call type 12	0.07826
	Call type 13	0.09207
Extinction rate	One rate for whole tree	0.00001
Transition rate	One rate for whole tree	0.00072

Table 6.7: Rates estimated by the best model for the whole tree, shown to five decimal places.

Of the 32 partition-based models run, four models out-performed the others (by at least 4 AIC units from the smallest one) but were not significantly different from one another (Burnham & Anderson 2002) (see Table 6.8 for AIC scores).

Model			AIC score	Degrees of freedom
Speciation (lambda)	**Extinction (mu)**	**Transition (q)**		
fully relaxed	**fully constrained**	**constrained**	**8362.93**	**19**
fully relaxed	**half and half**	**constrained**	**8364.91**	**20**
fully relaxed	**fully constrained**	**relaxed**	**8365.14**	**21**
fully relaxed	**shift-based**	**constrained**	**8366.91**	**21**
fully relaxed	half and half	relaxed	8367.15	22
fully relaxed	shift-based	relaxed	8369.14	23
shift-based	fully constrained	constrained	8385.21	6

shift-based	half and half	constrained	8387.22	7
shift-based	fully constrained	relaxed	8387.61	8
shift-based	shift-based	constrained	8389.22	8
shift-based	half and half	relaxed	8389.45	9
fully relaxed	fully relaxed	constrained	8390.81	34
shift-based	shift-based	relaxed	8391.44	10
half and half	fully constrained	constrained	8393.48	5
fully relaxed	fully relaxed	relaxed	8394.61	36
half and half	half and half	constrained	8395.48	6
half and half	fully constrained	relaxed	8395.72	7
half and half	shift-based	constrained	8396.24	7
half and half	half and half	relaxed	8397.73	8
half and half	shift-based	relaxed	8398.28	9
half and half	fully relaxed	constrained	8408.31	20
shift-based	fully relaxed	relaxed	8409.89	23
shift-based	fully relaxed	constrained	8410.05	21
half and half	fully relaxed	relaxed	8412.88	22
fully constrained	fully constrained	constrained	8417.38	4
fully constrained	half and half	constrained	8419.39	5
fully constrained	fully constrained	relaxed	8419.63	6
fully constrained	shift-based	constrained	8421.38	6
fully constrained	half and half	relaxed	8421.65	7
fully constrained	shift-based	relaxed	8423.61	8
fully constrained	fully relaxed	constrained	8440.95	19
fully constrained	fully relaxed	relaxed	8442.31	21

Table 6.8: Comparison of diversification models based on tree partitions and echolocation call types using AIC scores. The four best performing models (shown in bold) were chosen based on the lowest AIC values, best any within 4 units of the lowest were considered.

The four best models have fully relaxed *lambda*s: 16 different speciation rates - one for each call type in the rest of the tree, one for each of the two call types in the Pteropodidae partition, and one for the single call type in the Stenodermatinae partition. The four models

estimate extremely similar speciation rates for each call type, except for call type 2 which is negligible in three models and 0.07679 in one model.

The best four models have either fully constrained *mus* (a single extinction rate), half and half *mus* (one extinction rate for the rest of the tree and one extinction rate for the two partitions), or shift-based *mus* (one extinction rate for the rest of the tree and two more extinction rates for each of the two partitions). However, all estimated extinction rates are less than 0.000008 and can be considered negligible.

The best four models have either relaxed or constrained *q*s: three models have two transition rates (likely and unlikely – as outlined in Table 6.2), and one model has four transition rates, in which the additional two parameters correspond to the rate of transition between call types in the partitions. Transition rates are largely negligible (below 0.002) except for the rate of transition from call type 1 (vision) to call type 2 (tongue-clicking) in the Pteropodidae partition, which was extremely high at 13207. See Table 6.9 for speciation, extinction and transition rates in the four models.

		Rate for each model			
	Rate parameter	**Speciation fully relaxed, extinction fully constrained, transition constrained**	**Speciation fully relaxed, extinction half and half, transition constrained**	**Speciation fully relaxed, extinction fully constrained, transition relaxed**	**Speciation fully relaxed, extinction shift-based, transition constrained**
Speciation rates	Rest of tree, call type 1	0.14626	0.14623	0.14624	0.14625
	Rest of tree, call type 2	0.07679	0.00000	0.00000	0.00000
	Rest of tree, call type 3	0.09153	0.09150	0.09151	0.09151
	Rest of tree, call type 4	0.07679	0.07681	0.07677	0.07678
	Rest of tree, call type 5	0.05619	0.05623	0.05623	0.05626
	Rest of tree, call type 6	0.02110	0.02108	0.02107	0.02109
	Rest of tree, call type 7	0.08589	0.08590	0.08589	0.08589
	Rest of tree, call type 8	0.10044	0.10042	0.10043	0.10043
	Rest of tree, call type 9	0.09558	0.09558	0.09558	0.09558
	Rest of tree, call type 10	0.09798	0.09798	0.09799	0.09798
	Rest of tree, call type 11	0.05610	0.05611	0.05609	0.05609
	Rest of tree, call type 12	0.07835	0.07832	0.07834	0.07834
	Rest of tree, call type 13	0.09200	0.09198	0.09200	0.09199
	Pteropodidae, call type 1	0.11906	0.11917	0.11905	0.11906
	Pteropodidae, call type 2	0.00003	0.00006	0.00000	0.00003
	Stenodermatinae, call type 9	0.25108	0.25103	0.25110	0.25109
Extinction rates	Rest of tree, all call types	0.00001	0.00000	0.00000	0.00000
	Partitions, all call types	N/A	0.00000	N/A	N/A
	Pteropodidae, call types 1 and 2	N/A	N/A	N/A	0.00000
	Stenodermatinae, call type 9	N/A	N/A	N/A	0.00000
Transition rates	Whole tree, all likely	0.00194	0.00194	N/A	0.00194
	Whole tree, all unlikely	0.00194	0.00032	N/A	0.00032
	Rest of tree, all likely	N/A	N/A	0.00197	N/A
	Rest of tree, all unlikely	N/A	N/A	0.00032	N/A
	Pteropodidae, all likely	N/A	N/A	13207.04000	N/A
	Stenodermatinae, all likely	N/A	N/A	0.00000	N/A

Table 6.9 (Previous page): The speciation, extinction, and transition rates estimated by the four best models, to five decimal places.

Speciation rates vary from negligible to 0.25110 (see Table 6.9 and Figure 6.4). The highest rate is found in lineages using call type 9 in the up-shifted clade of Stenodermatinae (67 species). This Phyllostomidae sub-family (and most other Phyllostomidae species) exclusively use call type 9 – a multiharmonic, high bandwidth, short duration call with the majority of the energy in the second or third harmonic. The speciation rate in this clade is more than twice the speciation rate for lineages using call type 9 in the rest of the tree, where an additional 111 species use this call type, or in the split-free tree.

In the other up-shifted clade of 80 species of Pteropodidae, two call types are used. Pteropodidae mainly use call type 1 – no echolocation; instead orienting and finding food using vision and olfaction, although some *Rousettus* species also use call type 2 (tongue clicking) in caves. The speciation rates show that it is call type 1 (vision) that causes the increased speciation rates in the up-shifted Pteropodidae clade, and call type 2 has a negligibly increased speciation rate. However, the effect of call type 1 on speciation rate in this clade is not as great as in the rest of the tree, where an additional 102 species use this call type, or in the split-free tree, as these have higher speciation rates than the up-shifted Pteropodidae clade.

The net diversification rate over the whole tree (without partitions) was estimated to be 0.086482 (with negligible extinction, so equivalent to speciation rate alone), and the average speciation rate for all call types over the tree excluding the accelerated clades is 0.07826. Comparison of the speciation rates for each call type in the split-free tree, the rest of the split tree (excluding the up-shifted clades), reveal the impact of call type on speciation rate. Behind the very fast speciation rates of call types 1 and 9, five other call types show speciation rates faster than the overall speciation rate for the split-free tree, and the average speciation rate for the rest of the tree. From fastest to slowest, these call types are 8, 10, 13, 3 and 7 (see Figure 6.4).

Six call types are slower than the overall speciation rate for the split-free tree, and the average speciation rate for the rest of the tree. From fastest to slowest, they are 12, 4, 5, 11, 6 and 2 (see Figure 6.4).

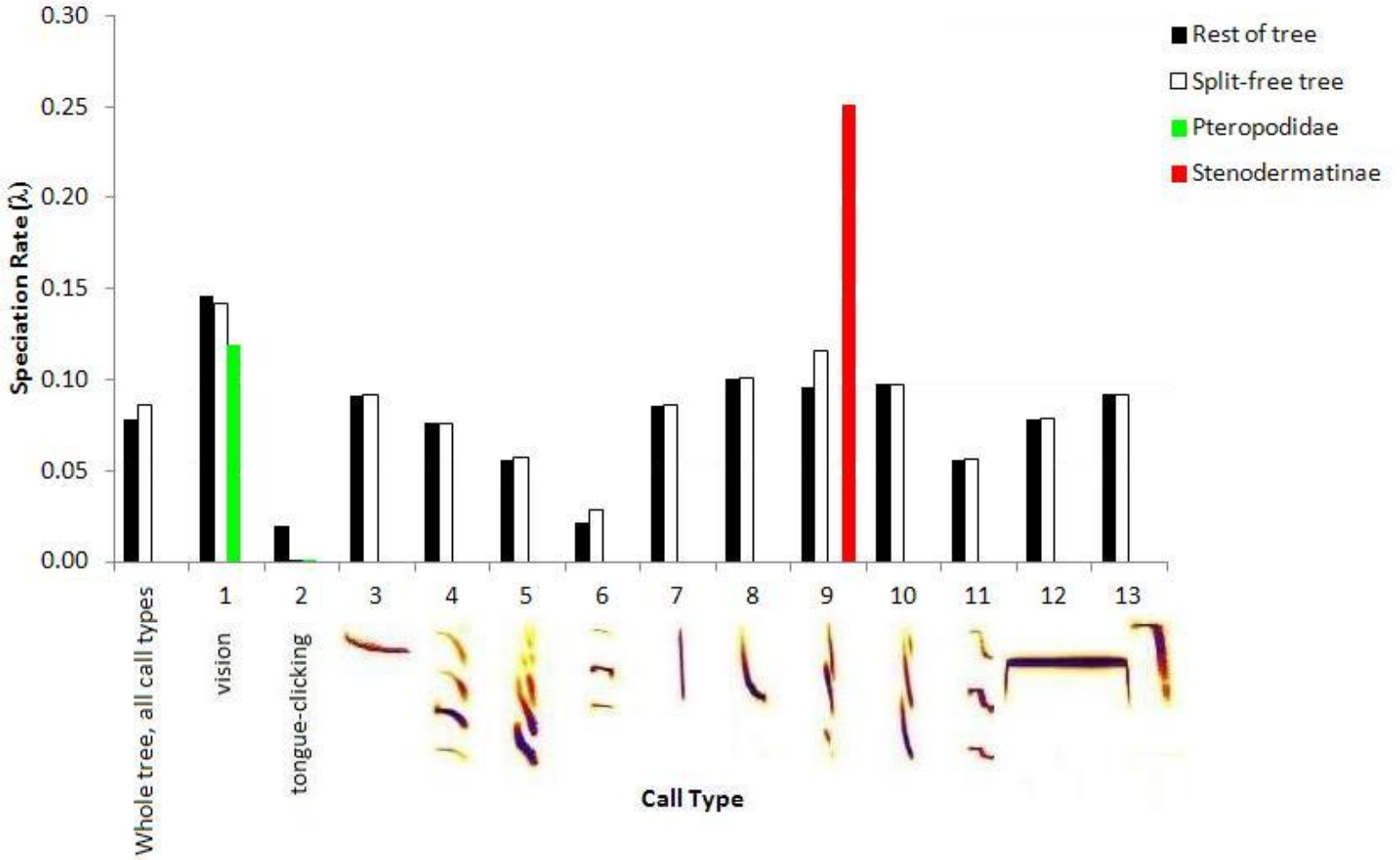


Figure 6.4: Average speciation rates for each call type (over the four best performing models), and speciation rates for all call types over the whole tree. Only call types used by each up-shifted clade have a speciation rate, as indicated by model selection.

6.5 Discussion

6.5.1 Location of diversification shifts

As expected, diversification rates across the bat tree have not been equal, with two clades showing a significant increase in diversification rate over the background rate. These up-shifted clades are the Phyllostomidae sub-family Stenodermatinae (67 species), and a clade of 80 species of Pteropodidae. In the two previous studies of diversification rates of bats, both Jones *et al*. (2005) and Purvis *et al*. (2011) identified a significant up-shift near the base of the genus *Artibeus* (Stenodermatinae: Phyllostomidae), and (Jones *et al.* 2005) also detect a significant up-shift near the base of the Phyllostomidae (in the Teeling *et al*. (2005) topology). These results compare favourably with my finding of an up-shift in the Stenodermatinae (Phyllostomidae) sub-family. Jones *et al*. (2005) also detect three non-significant shifts within the Pteropodidae (in both topologies) that correspond with the up-shifted Pteropodidae clade found in my analysis. However, both Jones *et al*. (2005) and Purvis *et al*. (2011) detect further significant up-shifts in clades within the Rhinolophoidea, Noctilionoidea, and Vespertilionoidea, as well as down-shifts in the Noctilionidae and Desmodontinae. My analyses did not replicate any of these shifts.

It is likely that the different topology and improved resolution of the new supertree used in this analysis compared to that used in the analyses of Jones *et al*. (2005) and Purvis *et al*. (2011) is responsible for the different findings, as well as the use of a different method, although still a whole-tree likelihood-based technique. Using TurboMEDUSA on the bat phylogeny tested in Purvis *et al*. (2011) does not replicate any of their findings either, instead detecting a single up-shift near the root of the Hipposideridae. Because of the supertree construction process, some unresolved clades are simply gatherings of species for which there are no topological data in the sources phylogenies. These unresolved clades may have unduly influenced the results all analyses carried out to date, but the improved resolution and accuracy of the new bat supertree should increase reliability.

The method used does not take in account extinct taxa not shown on the phylogeny. Without the inclusion of these taxa, the results may not accurately reflect the true locations

of diversification rate shifts. If extinctions had been included, some clades may not appear to have diversified as rapidly as is suggested in the results obtained here. However, Paradis (2005) showed no support for simulated random extinction inflating the Type I error rate of diversification rate analyses, although extinction has been shown many times to be non-random (e.g. Purvis *et al.* 2000).

6.5.2 Diversification shifts and echolocation call types

Estimating diversification rates for the lineages using each of the 13 call types reveals variation in the speciation rate across the bat phylogeny. The split-free tree shows variable speciation rates for different echolocation call types (see Table 6.7). Call type 2 (tongue-clicking) hardly increases the speciation rate at all, whereas call types 1, 3, 7, 8, 9, 10, and 13 have particularly high speciation rates. These call types each have clear functional roles. Call type 1 is the use of vision and olfaction instead of echolocation. Call type 3 is a long duration, low frequency, narrowband call that allows bats to search for obstacles and prey in open space as the bat can detect larger objects at a distance. Call type 7 is the opposite: a short duration, high frequency, broadband call that allows bats to orientate and find food in very cluttered forest habitats, as they are able to resolve different sized objects, including very small ones, at short distances. Call type 8 lies between call type 3 and 7. It is medium duration, bandwidth and frequency, and gives bats great flexibility in exploiting edge space habitats, where both long and short distance detection ability is necessary. Call types 9 and 10 are both short duration, multiharmonic, broadband calls. Call type 9 places the majority of the energy into the second harmonic and call type 10 places the majority of the energy into the fundamental harmonic. These calls are extremely flexible and are functionally similar to call type 7. Call type 13 is medium duration and contains a narrowband or constant frequency portion followed by a broadband down-sweep. Bats using this call type have partial Doppler Shift Compensation (DSC; the ability to separate pulse and echo in the brain using frequency) which enables them to detect the fluttering wings of their insect prey against a still background. The broadband component of their calls also allows these bats to operate in extremely cluttered habitats, where they can resolve a large range of size classes.

I hypothesised that clades using call types 1, 3, 7, 8, 12 and 13 would be subject to increased rates of diversification because of the clear functional role of these call types in aiding orientation and prey acquisition in the bats that use them. In the split-free tree, call types 1, 8, 13, 3, 7 and 12 had the 1st, 3rd, 5th, 6th, 7th, and 8th fastest speciation rates respectively, whereas in the shift-tree, they were the 1st, 2nd, 5th, 6th, 7th,and 8th fastest. All but call type 12 were faster than the average speciation rate across the tree, validating my hypotheses. However, call types 9 and 10 were used by lineages with the 2nd and 4th fastest speciation rates in the split-free tree and the 4th and 3rd fastest in the shift tree.

The call types which show much lower speciation rates (2, 4, 5, 6, 11, and 12) are less well understood functionally. Call type 2 is the broadband tongue-clicking echolocation used by some or all species of the genus *Rousettus* (Pteropodidae) in their dark cave roost sites. Although it had been thought that this call type was somewhat rudimentary (Griffin, Novick, & Kornfield 1958), recent experimental evidence suggests that these clicks may confer similar functionality to call type 7 (Waters & Vollrath 2003; Yovel, Geva-Sagiv, & Ulanovsky 2011). However, it does not appear to have promoted increased diversification in the lineages that use it (see Table 6.7), perhaps because its use is limited to orientation in caves, and is not employed in food acquisition. Call types 4, 5, 6 and 11 have complex structures and little work has been done to understand the functional benefits of these call structures. Recently, Lazure & Fenton (2011) found some evidence that *Pteronotus personatus* (which uses call type 11) partially compensated for Doppler shift, which may indicate that call type 11 is intermediate between the ancestral call type and call type 12. In terms of shape, call types 4, 5, and 6 may all be intermediate forms between the ancestral call type (see Chapter 5) and call types 13, 12 and 9, or 10 respectively. Further experimental work is essential to understand the functional significance of these call types. Call type 12 is a long duration, constant-frequency call that gives bats partial DSC abilities. This allows them to precisely distinguish their flying insect prey from an extremely cluttered background using the sound modulation caused by the fluttering of the insects' wings. Functionally, this call type is fairly well understood, and of the call types with slower rates of speciation than the average, call type 12 is the fastest. It is often said to be a particularly 'sophisticated' call type (Jones & Teeling 2006; Ma et al. 2008; Neuweiler

2003; Russo & Mucedda 2007; Schumm 1991) and either this assumption, or the connection between innovative traits and rapid diversification, should be called into question as a result of the surprisingly low speciation rate in lineages with call type 12. It is possible that the associated costs of using this call type may prevent any increase in diversification rate.

Interestingly, call type 1 has the highest speciation rate of all in the whole bat phylogeny. Call type 1 is 'no echolocation call'; instead, the Pteropodidae species in this group use excellent night-time vision and olfaction to orientate and forage during dusk and dawn. The phylogenetic position of this family has been much debated, and although they were once considered to be basal to the rest of the bats (as the sub-family 'Megachiroptera' Dobson (1875)), molecular phylogenetics now consistently places this family basal to the superfamily Rhinolophoidea, splitting the 'Microchiroptera' into two (Springer, Teeling, & Madsen 2001). This relocation means that either laryngeal echolocation had a single evolutionary origin in the ancestor of all bats, and was subsequently lost in the Pteropodidae, or that there were two (or more) origins of laryngeal echolocation in the lineages leading to the superfamily Rhinolophoidea and to the suborder Vespertilioniformes.

Many researchers consider it implausible that, once evolved, echolocation might be lost (see Speakman (2001)). However, it has been thought that although the initial single origin of echolocation in the proto-bat enabled exploitation of the night sky as a niche, it also limited the maximum body size of bats (Jones 1994). For echolocation to be energy efficient, calls must be coupled with wing beats and breathing (Speakman & Racey 1991). Bats with larger body sizes, and hence larger wings, flap less frequently than their smaller counterparts. Limiting the frequency of echolocation calls to time them with wing beats would reduce the sensory input to the bat to such an extent that echolocation would become functionless (Jones 1994).

I propose that the selective pressure to increase in body size, perhaps in order to travel greater distances in search of fruiting and flowering plants, was stronger than the selective

pressure to remain small enough to use echolocation. Using olfaction to locate roost sites and foraging grounds may have facilitated the transition from echolocation to sophisticated night vision. Along with the increase in body size in Pteropodidae, the risk of predation from diurnal raptors (thought to be responsible for nocturnality in bats (Rydell & Speakman 1995)) would have declined, leading to increasingly diurnal behavior in this family, and better vision. During the early stages, improved vision would have been useful on moonlit nights, and as body size increased and flying in lighter conditions became less dangerous, crepuscular, and even diurnal habits would have become possible. This idea is backed up by the much more diurnal activity cycle of many members of the Pteropodidae (especially those on predator-free islands (see Thomson, Brooke, & Speakman (1998)) when compared to other bat families (Speakman 1995), and the evolution of sophisticated vision as the primary sensory modality of pteropodids may have been responsible for the increased speciation rate seen in the up-shifted Pteropodidae clade. The question remains as to why the frugivorous Phyllostomidae have not also succumbed to this selective pressure, though their more mixed diets and frequent opportunism may be responsible for restricting them to the use of echolocation. The largely frugivorous Stenodermatinae subfamily (Phyllostomidae), which has also seen increased speciation rates, is known to use echolocation mainly for orientation, and vision and olfaction to locate food sources (Rieger & Jakob 1988). This may be indicative that a frugivorous diet means bats are less reliant on echolocation, and that vision and olfaction may be becoming increasingly important.

Strikingly, however, the up-shifted Phyllostomidae sub-family Stenodermatinae show the highest call type-specific speciation rate. Members of this large taxon use call type 9, which gives great flexibility in habitat use and foraging style. They typically consume fruit, though many species will also eat insects, pollen, and nectar found on flowers (Giannini & Kalko 2004). Of all the Phyllostomidae, the Stenodermatinae are the most heavily reliant on fruit. The association of both up-shifted clades with frugivory may be significant, though it is worth noting that *Mystacina tuberculata*, the sole extant species of the Mystacinidae family, very occasionally eats fruit within its mainly arthropod-based diet, and has not been subjected to rapid diversification. Tellingly, recent work on the Phyllostomidae phylogeny by Dumont *et al*. (2011) also finds a significant up-shift in the

Stenodermatinae sub-family. They attribute the increase in diversification rate to these bats' frugivorous diet and the skull morphology that enables this diet. They acknowledge the difficulty in labeling the skull morphology a key innovation without also looking at the skulls of the other major clade of frugivorous bats, the Pteropodidae. It seems a possibility that frugivory is the 'new niche' that both phyllostomids in the New World, and pteropodids in the Old World, have entered, but it is not clear whether the innovation that opened that niche is in common to the two. Of course, it is possible that several innovations in different areas combined to open the frugivory niche, such as skull and jaw morphology, sensory adaptations, and body size or wing morphology.

It is also interesting to note that call type 9 was found to be the nearest modern call type to the ancestral call type reconstructed in the analyses of Chapter 5. If call type 9 enables increased diversification, one might expect little modification to the call structure over evolutionary time. However, call type 9 may only be selectively advantageous in certain environments, leading to the evolution of other call types outside of those environments, albeit with a lower diversification rate. Additionally, if an ancestral version of call type 9 favoured a frugivorous diet, and frugivory was the key innovation promoting increased diversification, subsequent dispersal into geographic ranges which cannot support frugivory may have selected for alternative call structures, followed by decreases in diversification rate.

As there were missing data, I used imputation to predict the discrete call types for some species. The imputation method used may not have predicted all missing data accurately, particularly as the imputation methods, PhyloPars, used a Brownian Motion structure when the phylogeny is known to have evolved according to an Ornstein-Uhlenbeck model. However, the most striking results showed that call types 1 and 9 were most clearly associated with an increase in diversification rate. The species using these call types belong to families in which the vast majority of species use the same call type. This means the likelihood of the imputation, and hence the conclusion, being incorrect is very low. With regard to the other call types that showed higher diversification rates than average, these

also were often found to be used together by members of the same families, so any incorrect imputation may not have altered the results considerably.

6.5.3 Echolocation calls as key innovations

As acknowledged above, although there is a clear link between echolocation call types and increased rates of diversification in the bat tree, it is not necessarily the case that the call types themselves are key innovations (Cracraft 1990). Instead, the change in diversification rate may be due to a related trait, such as, in this case, wing morphology or diet (Aldridge & Rautenbach 1987; Norberg & Rayner 1987). The concept of a key innovation was first described by Simpson (1953) as a behavioural trait that opened new adaptive zones. Key innovations have since been defined in various ways (see Hunter (1998) and Cacho *et al.* (2010)), though all definitions are based on the concept that some traits cause an increase in the diversification rate of a taxon (Cacho *et al.* 2010).

To reiterate, Cacho *et al.* (2010) suggest that the plausibility of a putative key innovation should be assessed using three conditions:

(1) The taxon having the trait has a higher rate of diversification than closely related taxa lacking the trait.
(2) There is a reasonable ecological or functional model to justify a causal link between the trait and increased diversity.
(3) Analogous traits are consistently associated with increased diversification rates.

Taking each of these in turn, I consider the possibility that echolocation call types could have been key innovations in the evolutionary history of bats. As described above, condition 1 is clearly satisfied by the analyses of the changes in speciation rate associated with echolocation call types on the bat phylogeny (see Figure 6.3, Figure 6.4, Table 6.7 and Table 6.9). However, unusually, I am considering a series of traits that are not completely opposite. Some aspects of traits may be overlapping, such as the high bandwidth formed in different ways between call types 7 and 9, and hence lineages not possessing one particular call type cannot fully be considered to lack it, as they may have functional aspects of that

call type in their own echolocation behaviour. Despite this, a clear difference can be seen in the relative diversification rates of different echolocation call types, particularly those that have resulted in a significantly up-shifted clade.

Condition 2 is more complex, however, as increased diversity (driven by an increase in speciation rate) can only come about as a result of an increase in the likelihood of reproductive isolation, as this is necessary for speciation (Dobzhansky 1937; Grant 1963; Mayr 1942; Yoder et al. 2010). It is generally accepted that reproductive isolation usually occurs as a by-product of allopatric divergence, leading to allopatric speciation (Coyne & Orr 2004; Mayr 1942). Similarly to the mechanisms summarised in Purvis *et al*. (2011) as having been proposed to increase a clade's diversity, I consider there to be three key mechanisms leading to increased reproductive isolation in a lineage: the expansion of niche space, the expansion of the geographic range, and the promotion of assortative mating. The expansion of the geographic range of a lineage is the most likely of these to result in allopatric speciation, and in some cases, the expansion of niche space could form a first step in expanding the geographic range (Yoder *et al*. 2010). For example, if wing morphology and echolocation call changes allow the exploitation of a new 'open space' niche, this may give access to a new geographic range.

But since allopatrically-induced reproductive isolation occurs at a relatively slow rate, it is likely to considerably limit the rate of speciation (Coyne & Orr 2004). Therefore the role of natural selection in bringing about reproductive isolation should be considered, through an ecological speciation model. As Yoder *et al*. (2010) report, a number of ecological means have been implicated in the process of ecological speciation including competition (Abrams 2006; Dieckmann & Doebeli 1999), mutualism (Kiester *et al.* 1984), predation (Day *et al.* 2002), host-parasite interactions (Nuismer 2006), sexual selection (Gavrilets & Waxman 2002), fluctuating environments (Abrams 2006), and environmental gradients (Doebeli & Dieckmann 2003; Slatkin 1973). In order for echolocation call type to bring about non-allopatric speciation, it is possible that one of these means is responsible. In sympatrically occurring populations, assortative mating (sexual selection) as a result of echolocation call type or frequency may play a clear role in reinforcing reproductive isolation and bringing

about sympatric speciation, such as may have occurred in rhinolophid bats in the Wallacea region (Kingston & Rossiter 2004). In this study, it was found that having switched the peak echolocation call harmonic (which contains the most energy), three size morphs of the same species appear to have restricted communication between the morphs, inducing assortative mating and reproductive isolation, despite their sympatric distributions.

Several studies find that speciation in sympatry is unlikely to be responsible for more than a minority of speciation events when compared with allopatric speciation (e.g., Bolnick & Fitzpatrick (2007); Phillimore *et al.* (2008)). It is possible that the harmonic-hopping rhinolophids described above represent a special case, due to their specialised auditory foveae preventing the detection of morphs calling outside their finely-tuned frequency range. Nevertheless, with respect to the mechanisms listed above, I suggest two general 'reasonable functional or ecological models', both allopatric and sympatric, to explain the link between echolocation call type and increased rates of speciation.

First, an allopatric model. The evolution of a particular echolocation call type can open up new niche space to a lineage that in turn can alter or increase the available geographic range it occupies. In doing so, members of that lineage may become disparately distributed with much reduced gene flow, and due to forces of genetic drift, or divergent selection, reproductive isolation may occur. In addition, changes to echolocation call types are likely to be reflected in changes to communication call types (Jones & Siemers 2011; Kingston & Rossiter 2004) and reinforcement of population differences through sexual selection and assortative mating during any secondary contact will lead to allopatric speciation. This model is particularly easy to envisage in relation to call types 1 and 3. Call type 1, as discussed earlier, may have enabled the much larger body sizes of lineages using it, and consequently a change in niche and geographic range. The evolution of call type 3, concurrently with changes in wing morphology, enables the exploitation of open spaces, potentially resulting in an increased range as lineages become less dependent on forest environments.

In the sympatric model, I propose that differences in echolocation call types enable changes in niche use that lead to divergent selection. Any increase in niche space provides the opportunity for divergent/relaxed selection (Yoder *et al.* 2010). With the evolution of a new call type comes an opening of the frequency range as yet unoccupied by that call type. Calling at different frequencies allows the exploitation of different size classes of prey, and hence a range of new niches. Again, due to the link between echolocation calls and communication calls used to indicate con-specificity, small differences in echolocation call type could result in the differentiation of sympatric populations through sexual selection and assortative mating, as was observed in the rhinolophid morphs of the Wallacea region (Kingston & Rossiter 2004). Call types 7, 8, 9, 10 and 13 seems likely candidates for this model, as all have to potential to increase niche space within a forest habitat.

Though echolocation call types can be invoked as a causal factor in speciation, whether sympatric or allopatric, there are many other potential causes of increased speciation rates. In particular, climate changes and evolutionary events in species that bats depend on, such as flowering plants, may be involved. Currently, I am unaware of any significant events in the evolution of angiosperms, or in relation to the climate to may be responsible for the increases in speciation rates seen in the Stenodermatinae 13 mya or the Pteropodidae 24 mya.

Cacho *et al*.'s (2010) third condition is that analogous traits in other taxonomic groups are also associated with increased diversification rates. Whilst the analyses contained in this thesis chapter do not answer this question empirically, anecdotal consideration of the only other animal group known to use echolocation for orientation and to locate prey, the Cetacea, suggests that this condition is satisfied. There are 84 species in this order altogether, and members of the suborder Odontoceti have evolved the use of echolocation (Wilson & Reeder 2005). In species, they outnumber the other suborder, Mysticeti, which do not echolocate, 71 to 13. Although these two suborders differ in several morphological and behavioural traits, it is possible that echolocation has contributed to the more rapid diversification of the Odontoceti. Unfortunately, I do not have the necessary data to assess the impacts on diversification rate of different echolocation call types in cetaceans.

There are several limitations to the methods used here and to their interpretation. In particular, it may be difficult to identify clades that have undergone rapid rates of diversification if related clades have also done so. This is especially the case when looking at echolocation, as different echolocation call types may be key innovations in their own right, and could thereby obscure each other's evolutionary 'success'. In addition, the current diversity of bats is a snapshot in time, and does not allow us to see the consequences of potentially newly evolved call types. There may be some call types that have not yet had the opportunity to cause or influence increased rates of diversification in the clades that use them.

6.6 Conclusions

There have been two major up-shifts in the rate of diversification of the taxa in the bat phylogeny: one in a large clade of Old World fruit bats (Pteropodidae), and another in the New World fruit bat sub-family Stenodermatinae (Phyllostomidae). There is a strong association between these up-shifts and the sensory modality/echolocation call type used by the two clades (no echolocation, and a multiharmonic, short duration, high bandwidth call, respectively). Analysis of speciation rates for all echolocation call types also highlights call types 3 (single harmonic, medium duration, narrowband), 7 (single harmonic, very short duration, high bandwidth), 8 (single harmonic, short duration, medium bandwidth), 10 (multi-harmonic, short duration, high bandwidth), and 13 (partial Doppler Shift Compensating single harmonic call with a short duration constant frequency portion followed by a high bandwidth down-sweep) as causing increased speciation rates.

I suggest that these echolocation call types should be considered key innovations, as they satisfy Cacho *et al*.'s (2010) three conditions. They are associated with increased rates of diversification; there is an ecological model explaining the link between the traits and increased speciation; and an analogous trait in toothed whales shows a similar pattern of diversification. I put forward two mechanisms by which echolocation can influence speciation rate. The first, an allopatric model, sees echolocation calls altering niche use and

expanded geographic range as a consequence, allowing greater opportunity for divergent selection and barriers to gene flow. The second, a sympatric model, suggests that through altered niche use, changes to echolocation calls also result in changes in communication calls which bring about reproductive isolation through sexual selection and assortative mating.

7 Chapter 7: General Conclusions

7.1 The Evolution of Echolocation in Bats

The overall aim of my thesis was to understand how echolocation originated and evolved in bats. It has previously been difficult to understand the evolution of echolocation largely because there were not enough species-level data about their echolocation calls, and although we are now beginning to understand how echolocation calls work, our understanding of how they originated and evolved has been fairly basic. For example, how has evolutionary history influenced the variation in echolocation call structures? What kind of echolocation call structure did early bats use? And how has echolocation influenced the diversification of bats? To address these questions I compiled a large database of echolocation call recordings from bats, EchoBank, and constructed a new phylogenetic supertree of the bats. These tools enabled me to learn more about the evolutionary history of echolocation in bats using phylogenetic comparative methods.

Fundamental to understanding the evolution of echolocation is the question of why pre-bats lost vision and developed echolocation at all. Switching from one sensory modality to another presents some unique challenges, as evolution is unlikely to take a pathway that leaves individuals less fit than their ancestors. This question has already been addressed, and some likely selective pressures identified (Rydell & Speakman 1995). Viewing morphological and behavioural adaptations as a 'fitness landscape' where peaks represent trait values that increase fitness, and valleys represent trait values that reduce fitness helps us to imagine the difficulty in transitioning from a useful trait, such as vision, to another useful trait, such as echolocation, without crossing a valley where neither can be used (see Figure 7.1 (a)). Possessing high quality vision at the same time as high quality echolocation is unlikely, due to the necessary energy trade-offs and brain-space allocation to process the input from these two different sensory modalities (Aiello & Wheeler 1995; Speakman 2001).

To solve the problem of how bats switched from vision to echolocation, we needed to find out how the relative heights of the adaptive peaks and valleys might have changed over time. If the pre-bat was diurnal (as suggested by Rydell & Speakman (1995)), the use of vision would have served it well, and the adaptive peak representing vision would have stood proud from the surrounding adaptive landscape of sensory options. However, it is thought that bats became nocturnal due to predation by diurnal birds (Rydell & Speakman 1995). In a nocturnal niche, non-specialist daytime vision would have little selective power and the relative height of the 'vision' peak would have shrunk, i.e., if the selective pressure to become nocturnal (to avoid diurnal predation by birds) was strong enough, the adaptive peak for vision would be smaller. Thus, the transition to a new adaptive peak for echolocation could involve evolutionary steps that only increased fitness, with no decreases (see Figure 7.1 (b)). This way, the route from the adaptive peak for vision to the adaptive peak for echolocation is purely uphill in terms of fitness.

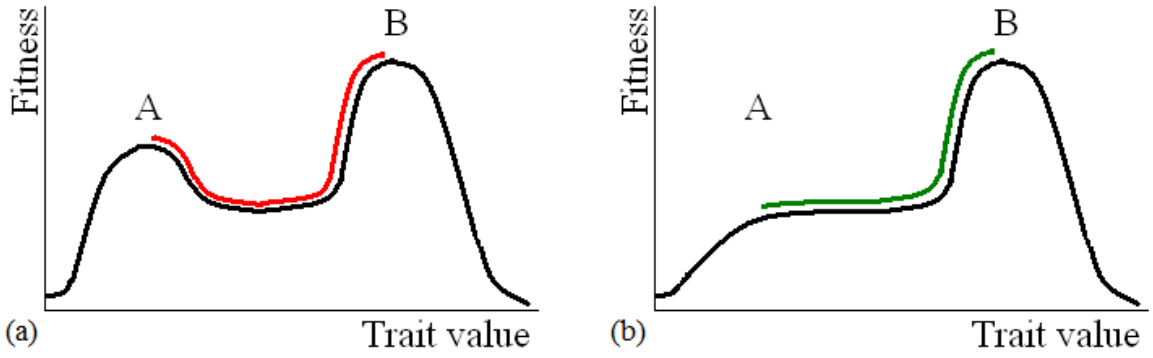


Figure 7.1: Two hypothetical adaptive landscapes. In (a) although trait B is fitter than trait A, populations with trait A cannot evolve to have trait B instead due to the adaptive valley between the traits. In (b) the fitness value from possessing trait A has decreased to such a level that evolving to trait B instead becomes possible.

Our current understanding is that echolocation evolved because predation by diurnal birds pushed bats into a nocturnal niche where vision was not good enough for orientation and prey acquisition (Rydell & Speakman 1995). Prior to the work contained in this thesis, our ideas of what the echolocation calls of the proto-bat would have been like were purely based on supposition (Fenton 1984; Fenton et al. 1995; Jones & Teeling 2006; Pye 1980; Schnitzler & Kalko 2001; Schnitzler et al. 2004; Simmons 1979; Simmons et al. 1984;

Simmons & Stein 1980; Simmons & Geisler 1998; Simmons et al. 2008; Springer, Teeling, & Madsen 2001). Since echolocation is not a morphological trait, it is very unlikely we will ever have fossil evidence that can tell us exactly what early bat calls sounded like. There is currently debate about whether all early bat fossil species were able to echolocate at all (Simmons *et al.* 2008; Veselka *et al.* 2010), and the cochleas of early bats reveal very little about echolocation call structures (Speakman 2001).

In the absence of further evidence regarding the origin of echolocation in bats, phylogenetic comparative methods offer our best means of predicting the structure of the proto-bat's echolocation call. My analyses in Chapter 5 used a number of different techniques to estimate the ancestral state of the echolocation call, using both continuous echolocation call parameters such as call duration and peak frequency, as well as discrete echolocation call types. I also considered evidence from ontogenetic sequences of newborn bats from several families, and the typical structure of mammalian communication calls in predicting the structure of the echolocation calls of early bats. My analyses and the further evidence consistently pointed to a multi-harmonic, short duration, narrowband ancestral call structure, which could have developed step-by-step from communication calls.

Over evolutionary time, selective pressures have formed various different echolocation call structures, through changes to the duration, bandwidth, and harmonic structure of the call, as well as its position on the frequency scale. My analyses showed that these different call structures were achieved through relatively simple adjustments to the ancestral call. For example, 'tilting' the call reduces its duration and increases its bandwidth, which gives the bat greater precision in target detection. Alternatively, increasing the duration of the call and suppressing the higher harmonics allows the bat to put more energy into a single frequency and therefore detect objects at greater distances. Figure 7.2 suggests how, through a process of step-by-step change, any of the echolocation calls used by modern bats can be produced. The initial call is a simple short duration, narrowband, multiharmonic call, which is the basic sound made by a mammalian larynx. In the first step, the call develops a 'peak' harmonic, which received more energy (and hence volume) than the

other harmonics. Next, the call develops curvature, and there are many variations of this, some of which are better understood than others.

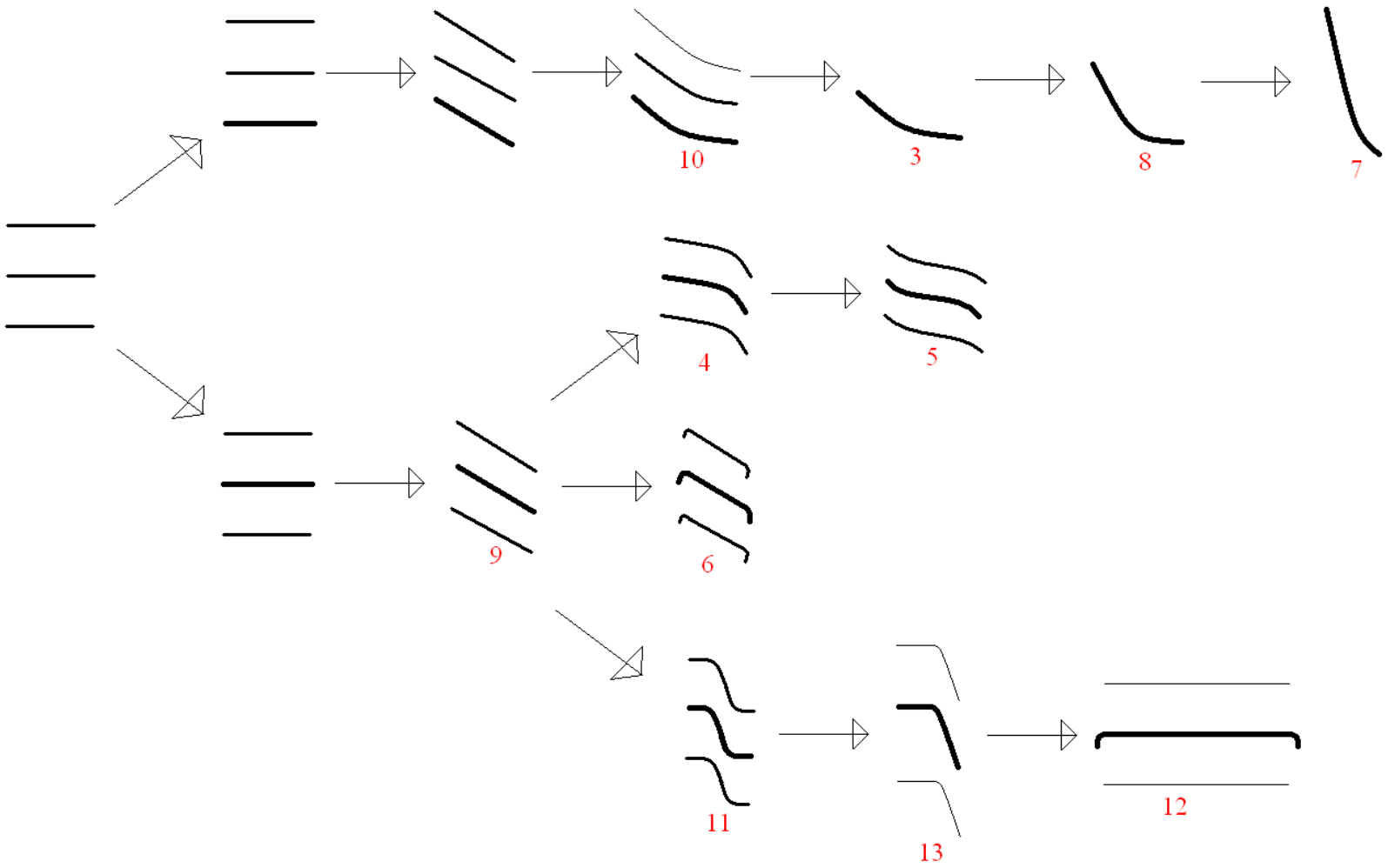


Figure 7.2: A suggested evolutionary pathway from the estimated ancestral echolocation call to each of the call types (numbered 3 – 13 in red) used by extant bats.

Work is underway to elucidate more about the evolution of the bat cochlea (Davies 2011, pers. comm.) and there are now sufficient data available about both echolocation call structures and cochlear morphology for an analysis of their relationships to be undertaken. In addition, work on the genetics of echolocation holds great potential for revealing the evolutionary history of echolocation. Already, two genes involved in echolocation have been identified. One, *Prestin*, codes for a motor protein in the cochlear outer hair cells which enables the high-frequency sensitivity and selectivity of the chiropteran auditory system (Li *et al.* 2008). The *Prestin* gene sequences of echolocating species converge, to the exclusion of the non-echolocating Pteropodidae family, indicating some involvement of *Prestin* in the high frequency hearing of echolocators. Another gene implicated in echolocation is *FoxP2*, known already for its involvement in human orofacial control and vocalisation. Its extreme diversity in echolocating bats, especially when contrasted with its relatively conserved status in non-human mammals, hints at its role in echolocation (Li, Wang, et al. 2007). It seems likely the genomics and transcriptomics can reveal further insights into the genetics of echolocation, and, potentially, its evolutionary history as well.

Much has been made of the influence of habitat on the structure of echolocation calls (Aldridge & Rautenbach 1987; Fenton 1995; Neuweiler 1990; Schnitzler & Kalko 1998, 2001), and little credit has been given to the constraints of evolution past in dictating modern call structures. In Chapter 4 I took a very broad of the variation in echolocation call structures across the 19 families of bats. It is clear from the recordings collected from 296 species in these 19 families that bats have evolved more than one way of tackling the different sensory challenges they face in orientating in landscapes, from traversing featureless deserts, through crossing mirror-like lakes, to negotiating dense rain-forest, and capturing prey, whether that is nectar hidden in a flower, an insect sitting on a leaf, or the blood in the ankle of a cow. But habitat or diet type alone is not enough to explain the variation in echolocation call types, and it is only in the context of evolutionary pathways that the reason for these alternative calls becomes clear. My analyses of phylogenetic and spatial signal, and of mode of evolution in Chapter 4 highlight the influence that evolutionary history has had on defining echolocation. Regardless of habitat, bats are most likely to have the echolocation call type of their phylogenetic neighbours, sharing not only

the structure, but also duration and position on the frequency scale. Some features of the call are more ecologically pliable and necessarily so for bats to have the required flexibility to detect, localise, and identify different objects. For example, the slope of the call shows much less phylogenetic signal, as this feature appears to dictate the bat's distance of focus (the point at which ranging errors are minimised) and Doppler tolerance (Jones & Holderied 2007). Similarly, the maximum and minimum frequencies of the call respond more flexibly to habitat, as they determine the range of size classes the bat can detect. But other features, such as harmonic structure, call duration, and bandwidth are determined largely by evolutionary history, and most bats are unable to use overall call structures radically different from than the ones they inherited.

Figure 7.2 suggests why this may be the case. Again using an adaptive landscape model, transitions between many echolocation call types seem unlikely, as any intermediate phase would be considerably less fit, or even totally functionless. Once a lineage has travelled down one evolutionary route, switching to another becomes impossible without a significant change in ecological circumstances. Alongside the evolution of echolocation call features comes the evolution of wing morphology and skull morphology, and with that, habitat and diet preferences. Echolocation can define niche, and once a new and fruitful niche has been entered, diversification follows, using the same echolocation template unless selection pressures change.

My final set of analyses, in Chapter 6, look at the impact of echolocation on the diversification of bat lineages. Surprisingly, it seems that both the lack of echolocation, and a very general echolocation call type, have promoted the highest diversification rates in bats. Although it remains extremely likely that the combination of flight and echolocation played a key role in allowing bats to become the second most speciose order of mammals (Wilson & Reeder 2005) the results of my diversification rates analysis in Chapter 6 suggest that subsequently, the loss of echolocation may have taken the Pteropodidae to another new niche, inaccessible except via an echolocating past. Having accessed the nocturnal niche through the use of echolocation, this frugivorous family of bats may have been constrained by the body size limitations that echolocation carries. Members of this

family are by far the largest of all bats, with the largest individuals measuring up to 1.7m in wingspan (Nowak 1999), which prevents them from using echolocation energy-efficiently (Jones 1994). My analyses suggest that the Pteropodidae may have lost echolocation in favour of larger body sizes, which enables them to re-enter the crepuscular and diurnal niches with a much reduced risk of predation by diurnal raptors.

Strikingly, the other clade to have experienced greatly increased diversification rates is the mainly frugivorous phyllostomid sub-family, the Stenodermatinae. Although still omnivorous to some extent, these 67 species are the most reliant of any phyllostomid group on fruit. That the two up-shifted clades of bats are the only two that rely on fruit is inescapable, and one recent study attributes the rapid speciation of the Stenodermatinae to their skull morphology, and hence their ability to eat predominantly fruit (Dumont *et al.* 2011). My analyses showed an extremely high speciation rate for bat lineages using the echolocation call type used by these bats (multi-harmonic, short duration and high bandwidth), indicating that their echolocation style has allowed them to diversify particularly quickly. As this call type is a very general one, giving great flexibility in foraging style and habitat use, it's also possible that the success of the Stenodermatinae is down to its echolocation behaviour. However, most other Phyllostomidae species, including those that do not eat fruit, use the same call type. Overall, increased diversification rates are probably the result of a suite of morphological and behavioural adaptations allowing access to new niches and geographic ranges, and promoting reproductive isolation between sub-groups. Echolocation is particularly likely to contribute to this, due to its connection with communication calls used to confer group membership.

The echolocation call data were split into continuous and discrete forms. The analyses in Chapter 4 used continuous data only, whereas Chapter 5 used both discrete and continuous data, and Chapter 6 used discrete data only. Each treatment of the data gives different information, as the discrete call type cannot be inferred from the continuous data alone, since it represents a call 'shape'. Similarly, not all continuous measures can be inferred from the discrete call type data, although it is possible to know something of the range the continuous measures might fall into by reviewing the information in Table 4.2. Chapter 4

aimed to understand the amount of phylogenetic and spatial signal shown by echolocation calls, and to assess the meachanisms of evolution acting on them. Using continuous data (measurements of different call parameters) for this allowed separation of different aspects of the echolocation calls, thereby giving detailed information about the gradual changes in echolocation call structures over evolutionary time. Had discrete call types been explored in Chapter 4, they would not have revealed which aspects of call structure are pliable, and which are not. Because it was not known how call structures evolve from one call type to another, looking in detail at the continuous measures of various call parameters gave a more subtle view of call structure change over time.

In Chapter 5, I carried out ancestral reconstruction analyses using both discrete call types and continuous measures of call parameters. Using both datasets meant that the different reconstructions could be compared. Chapter 6 contained a diversification analysis of discrete data only, as call shape is crucial in determining the ecological niche of a bat species. When looking for links between diversification rate and echolocation, taking the call type as a whole enables any differences in diversification rate to be assessed in the context of the bats' foraging strategy. It is possible to analyse the impact of continuous measures of echolocation calls on diversification rate, though it may be more difficult to draw biologically meaningful conclusions, as the parameters cannot operate in isolation.

The possibilities for further research into the evolutionary and ecological history of echolocation in bats are numerous, especially through combining the bat supertree and echolocation database with other data sets, such as those concerning wing morphology, cochlear morphology and genetics. In particular, there is potential for uncovering the relative timings of the evolution of flight and echolocation, the number of origins of echolocation in bats, and the genetic architecture behind high frequency vocalisations, hearing, and neural interpretation. New comparative techniques are constantly being developed and their reliability and limitations tested. Our understanding of the evolution of echolocation has really only just begun.

8 Appendices

8.1 Appendix A: Species list: EchoBank and literature

Sample sizes for the harmonics, calls, and files measured for each species from EchoBank and the literature.

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
All	All	Both		32356	20626	424	56	2	58940	3565
Craseonycteridae	*Craseonycteris thonglongyai*	EchoBank	2	87	**1239**	0	0	0	1326	31
Emballonuridae	*Balantiopteryx infusca*	Literature			**12**				12	
Emballonuridae	*Balantiopteryx io*	Literature			**46**				46	
Emballonuridae	*Balantiopteryx plicata*	EchoBank	2	0	**37**	0	0	0	37	1
Emballonuridae	*Centronycteris centralis*	EchoBank	2	0	**66**	0	0	0	66	3
Emballonuridae	*Centronycteris maximiliani*	EchoBank	2	0	**84**	0	0	0	84	10
Emballonuridae	*Coleura afra*	Literature								
Emballonuridae	*Cormura brevirostris*	EchoBank	2	0	**92**	13	0	0	105	9
Emballonuridae	*Cyttarops alecto*	Literature							123	
Emballonuridae	*Diclidurus albus*	Literature							36	
Emballonuridae	*Emballonura dianae*	EchoBank	2	0	**210**	1	0	0	211	15
Emballonuridae	*Emballonura furax*	EchoBank	2	8	**92**	0	0	0	100	6
Emballonuridae	*Emballonura monticola*	EchoBank	2	0	**1398**	0	0	0	1398	23
Emballonuridae	*Peropteryx kappleri*	Literature							140	
Emballonuridae	*Peropteryx macrotis*	EchoBank	2	0	**26**	0	0	0	26	3
Emballonuridae	*Rhynchonycteris naso*	EchoBank	2	0	**299**	0	0	0	299	27

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Emballonuridae	*Saccolaimus flaviventris*	Literature								
Emballonuridae	*Saccolaimus saccolaimus*	Literature							198	
Emballonuridae	*Saccopteryx bilineata*	EchoBank	2	27	**244**	0	0	0	271	17
Emballonuridae	*Saccopteryx leptura*	EchoBank	2	0	**111**	0	0	0	111	11
Emballonuridae	*Taphozous achates*	EchoBank	1	**5**	0	0	0	0	5	1
Emballonuridae	*Taphozous georgianus*	Literature							20	
Emballonuridae	*Taphozous hilli*	Literature								
Emballonuridae	*Taphozous kapalgensis*	Literature								
Emballonuridae	*Taphozous mauritianus*	EchoBank	2	0	**156**	0	0	0	156	18
Emballonuridae	*Taphozous melanopogon*	EchoBank	2	0	**32**	14	0	0	46	10
Emballonuridae	*Taphozous perforatus*	EchoBank	2	0	**43**	0	0	0	43	4
Emballonuridae	*Taphozous troughtoni*	Literature								
Furipteridae	*Furipterus horrens*	EchoBank	3	0	0	**23**	0	0	23	1
Hipposideridae	*Asellia tridens*	EchoBank	2	44	**275**	0	0	0	319	27
Hipposideridae	*Aselliscus stoliczkanus*	EchoBank	2	2	**711**	0	0	0	713	11
Hipposideridae	*Aselliscus tricuspidatus*	EchoBank	2	0	**177**	0	0	0	177	1
Hipposideridae	*Cloeotis percivali*	EchoBank	2	11	**35**	0	0	0	46	3
Hipposideridae	*Coelops frithii*	Literature								
Hipposideridae	*Hipposideros armiger*	EchoBank	2	0	**1302**	0	0	0	1302	30
Hipposideridae	*Hipposideros ater*	EchoBank	2	0	**17**	0	0	0	17	1
Hipposideridae	*Hipposideros bicolor*	EchoBank	2	0	**318**	0	0	0	318	7
Hipposideridae	*Hipposideros caffer*	EchoBank	2	0	**570**	0	0	0	570	20
Hipposideridae	*Hipposideros calcaratus*	EchoBank	2	0	**677**	0	0	0	677	12

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Hipposideridae	*Hipposideros cervinus*	EchoBank	2	2	**521**	0	0	0	523	9
Hipposideridae	*Hipposideros cineraceus*	EchoBank	2	0	**896**	0	0	0	896	20
Hipposideridae	*Hipposideros commersoni*	EchoBank	2	0	**25**	0	0	0	25	6
Hipposideridae	*Hipposideros diadema*	EchoBank	2	0	**153**	0	0	0	153	6
Hipposideridae	*Hipposideros fulvus*	EchoBank	2	0	**40**	0	0	0	40	7
Hipposideridae	*Hipposideros gigas*	EchoBank	2	0	**1**	0	0	0	1	1
Hipposideridae	*Hipposideros halophyllus*	EchoBank	2	7	**158**	0	0	0	165	2
Hipposideridae	*Hipposideros inornatus*	Literature								
Hipposideridae	*Hipposideros larvatus*	EchoBank	2	0	**1384**	0	0	0	1384	30
Hipposideridae	*Hipposideros lekaguli*	EchoBank	2	0	**258**	0	0	0	258	8
Hipposideridae	*Hipposideros lylei*	EchoBank	2	0	**172**	0	0	0	172	2
Hipposideridae	*Hipposideros maggietaylorae*	EchoBank	2	154	**213**	0	0	0	367	2
Hipposideridae	*Hipposideros pomona*	EchoBank	2	0	**1259**	0	0	0	1259	24
Hipposideridae	*Hipposideros pratti*	EchoBank	2	0	**34**	0	0	0	34	4
Hipposideridae	*Hipposideros ridleyi*	EchoBank	2	0	**50**	0	0	0	50	1
Hipposideridae	*Hipposideros ruber*	EchoBank	2	0	**61**	0	0	0	61	10
Hipposideridae	*Hipposideros semoni*	EchoBank	2	0	**15**	0	0	0	15	1
Hipposideridae	*Hipposideros speoris*	EchoBank	2	0	**243**	0	0	0	243	30
Hipposideridae	*Hipposideros stenotis*	Literature								
Hipposideridae	*Hipposideros turpis*	EchoBank	2	0	**110**	0	0	0	110	1
Hipposideridae	*Hipposideros vittatus*	Literature								
Hipposideridae	*Hipposideros wollastoni*	EchoBank	2	0	**171**	0	0	0	171	3
Hipposideridae	*Rhinonicteris aurantia*	Literature								

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	**2**	**3**	**4**	**5**		
Hipposideridae	*Triaenops furculus*	EchoBank	2	0	**2**	0	0	0	2	1
Hipposideridae	*Triaenops persicus*	Literature								
Hipposideridae	*Triaenops rufus*	EchoBank	1	**14**	8	0	0	0	22	4
Megadermatidae	*Lavia frons*	Literature								
Megadermatidae	*Macroderma gigas*	EchoBank	3	0	2	**4**	2	0	8	1
Megadermatidae	*Megaderma lyra*	EchoBank	3	0	29	**37**	0	0	66	9
Megadermatidae	*Megaderma spasma*	EchoBank	1	**36**	6	29	0	0	71	11
Miniopteridae	*Miniopterus australis*	EchoBank	1	**207**	0	0	0	0	207	10
Miniopteridae	*Miniopterus fraterculus*	EchoBank	1	**127**	0	0	0	0	127	20
Miniopteridae	*Miniopterus gleni*	EchoBank	1	**9**	0	0	0	0	9	2
Miniopteridae	*Miniopterus inflatus*	Literature								
Miniopteridae	*Miniopterus manavi*	EchoBank	1	**49**	0	0	0	0	49	9
Miniopteridae	*Miniopterus natalensis*	EchoBank	1	**513**	0	0	0	0	513	28
Miniopteridae	*Miniopterus pusillus*	EchoBank	1	**148**	0	0	0	0	148	3
Miniopteridae	*Miniopterus schreibersii*	EchoBank	1	**601**	0	0	0	0	601	31
Molossidae	*Chaerephon ansorgei*	Literature								
Molossidae	*Chaerephon bivittatus*	Literature								
Molossidae	*Chaerephon chapini*	Literature								
Molossidae	*Chaerephon jobensis*	Literature								
Molossidae	*Chaerephon johorensis*	EchoBank	1	**17**	4	0	0	0	21	3
Molossidae	*Chaerephon leucogaster*	EchoBank	1	**131**	0	0	0	0	131	6
Molossidae	*Chaerephon nigeriae*	Literature								
Molossidae	*Chaerephon pumilus*	EchoBank	1	**592**	0	0	0	0	592	29

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	**2**	**3**	**4**	**5**		
Molossidae	*Cheiromeles torquatus*	EchoBank	1	**7**	0	0	0	0	7	3
Molossidae	*Eumops glaucinus*	Literature							269	
Molossidae	*Molossops temminckii*	Literature								
Molossidae	*Molossus molossus*	EchoBank	1	**110**	0	0	0	0	110	14
Molossidae	*Molossus rufus*	EchoBank	1	**5**	0	0	0	0	5	1
Molossidae	*Mops condylurus*	EchoBank	1	**347**	0	0	0	0	347	21
Molossidae	*Mops midas*	Literature								
Molossidae	*Mops mops*	EchoBank	1	**2**	0	0	0	0	2	1
Molossidae	*Mops niveiventer*	EchoBank	1	**72**	0	0	0	0	72	4
Molossidae	*Mormopterus beccarii*	Literature								
Molossidae	*Mormopterus jugularis*	EchoBank	1	**10**	0	0	0	0	10	2
Molossidae	*Mormopterus loriae*	Literature								
Molossidae	*Mormopterus norfolkensis*	Literature								
Molossidae	*Nyctinomops macrotis*	Literature							370	
Molossidae	*Otomops madagascariensis*	EchoBank	1	**23**	1	0	0	0	24	6
Molossidae	*Otomops martiensseni*	Literature								
Molossidae	*Sauromys petrophilus*	EchoBank	1	**130**	0	0	0	0	130	21
Molossidae	*Tadarida aegyptiaca*	EchoBank	1	**411**	0	0	0	0	411	28
Molossidae	*Tadarida australis*	EchoBank	1	**166**	0	0	0	0	166	3
Molossidae	*Tadarida brasiliensis*	EchoBank	1	**9**	0	0	0	0	9	5
Molossidae	*Tadarida fulminans*	Literature								
Molossidae	*Tadarida insignis*	EchoBank	1	**32**	0	0	0	0	32	3
Molossidae	*Tadarida teniotis*	EchoBank	1	**386**	0	0	0	0	386	57

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Molossidae	*Tadarida ventralis*	Literature								
Mormoopidae	*Mormoops blainvillei*	Literature		?	**?**	?			181	10
Mormoopidae	*Pteronotus davyi*	EchoBank	2	9	**141**	3	0	0	153	16
Mormoopidae	*Pteronotus gymnonotus*	Literature							11	
Mormoopidae	*Pteronotus macleayii*	Literature		?	**?**	?			171	4
Mormoopidae	*Pteronotus parnellii*	EchoBank	2	0	**194**	0	0	0	194	18
Mormoopidae	*Pteronotus personatus*	EchoBank	2	0	**16**	0	0	0	16	1
Mormoopidae	*Pteronotus quadridens*	Literature		?	**?**	?			181	14
Mystacinidae	*Mystacina tuberculata*	EchoBank	2	63	**146**	6	0	0	215	28
Myzopodidae	*Myzopoda aurita*	EchoBank	1	**74**	0	0	0	0	74	10
Natalidae	*Natalus stramineus*	EchoBank	2	0	**115**	0	0	0	115	16
Natalidae	*Nyctiellus lepidus*	Literature								
Noctilioniade	*Noctilio leporinus*	EchoBank	1	**89**	0	0	0	0	89	7
Noctilionidae	*Noctilio albiventris*	Literature								
Nycteridae	*Nycteris gambiensis*	EchoBank	3	0	0	**56**	6	0	62	13
Nycteridae	*Nycteris grandis*	Literature								
Nycteridae	*Nycteris hispida*	Literature								
Nycteridae	*Nycteris macrotis*	EchoBank	2	0	**4**	0	0	0	4	2
Nycteridae	*Nycteris thebaica*	EchoBank	3	0	0	**15**	14	2	31	7
Nycteridae	*Nycteris tragata*	EchoBank	2	0	**2**	0	0	0	2	1
Nycteridae	*Nycteris woodi*	Literature								
Phyllostomidae	*Ametrida centurio*	EchoBank	2	0	**1**	0	0	0	1	1
Phyllostomidae	*Anoura geoffroyi*	EchoBank	2	2	**39**	0	0	0	41	8

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Phyllostomidae	*Ardops nichollsi*	EchoBank	1	**4**	0	0	0	0	4	2
Phyllostomidae	*Artibeus cinereus*	EchoBank	2	0	**1**	0	0	0	1	1
Phyllostomidae	*Artibeus concolor*	EchoBank	1	**3**	2	0	0	0	5	1
Phyllostomidae	*Artibeus gnomus*	EchoBank	2	0	**3**	0	0	0	3	1
Phyllostomidae	*Artibeus jamaicensis*	EchoBank	2	0	**67**	28	0	0	95	27
Phyllostomidae	*Artibeus lituratus*	EchoBank	2	0	**33**	2	0	0	35	7
Phyllostomidae	*Artibeus obscurus*	EchoBank	3	0	2	**5**	0	0	7	3
Phyllostomidae	*Artibeus phaeotis*	EchoBank	2	0	**2**	0	0	0	2	2
Phyllostomidae	*Artibeus toltecus*	EchoBank	2	0	**1**	0	0	0	1	1
Phyllostomidae	*Artibeus watsoni*	EchoBank	2	0	**2**	0	0	0	2	1
Phyllostomidae	*Brachyphylla cavernarum*	EchoBank	1	**52**	3	0	0	0	55	11
Phyllostomidae	*Brachyphylla nana*	Literature			**13**				13	
Phyllostomidae	*Carollia castanea*	EchoBank	2	0	**1**	0	0	0	1	1
Phyllostomidae	*Carollia perspicillata*	EchoBank	2	0	**21**	5	0	0	26	4
Phyllostomidae	*Carollia sowelli*	EchoBank	2	0	**2**	0	0	0	2	1
Phyllostomidae	*Chiroderma improvisum*	EchoBank	3	0	0	**17**	0	0	17	2
Phyllostomidae	*Chiroderma trinitatum*	EchoBank	3	0	0	**1**	0	0	1	1
Phyllostomidae	*Chiroderma villosum*	EchoBank	4	0	0	0	**2**	0	2	1
Phyllostomidae	*Choeronycteris mexicana*	EchoBank	2	0	**4**	0	0	0	4	1
Phyllostomidae	*Desmodus rotundus*	EchoBank	2	0	**50**	18	0	0	68	10
Phyllostomidae	*Diaemus youngi*	EchoBank	2	1	**22**	2	0	0	25	4
Phyllostomidae	*Ectophylla alba*	EchoBank	3	0	1	**23**	0	0	24	12
Phyllostomidae	*Erophylla bombifrons*	Literature							5	

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	**2**	**3**	**4**	**5**		
Phyllostomidae	*Erophylla sezekorni*	Literature								
Phyllostomidae	*Glossophaga longirostris*	Literature				**8**			8	
Phyllostomidae	*Glossophaga soricina*	EchoBank	2	0	**14**	3	0	0	17	6
Phyllostomidae	*Lampronycteris brachyotis*	EchoBank	3	0	0	**1**	0	0	1	1
Phyllostomidae	*Leptonycteris curasoae*	EchoBank	1	**9**	0	0	0	0	9	1
Phyllostomidae	*Lionycteris spurrelli*	EchoBank	2	0	**14**	0	0	0	14	4
Phyllostomidae	*Lonchophylla thomasi*	EchoBank	3	0	0	**6**	3	0	9	2
Phyllostomidae	*Lophostoma silvicolum*	EchoBank	2	0	**9**	1	0	0	10	5
Phyllostomidae	*Macrophyllum macrophyllum*	Literature							>156	
Phyllostomidae	*Macrotus waterhousii*	Literature								
Phyllostomidae	*Micronycteris hirsuta*	Literature								
Phyllostomidae	*Micronycteris megalotis*	Literature								
Phyllostomidae	*Micronycteris minuta*	EchoBank	2	1	**5**	0	0	0	6	2
Phyllostomidae	*Mimon crenulatum*	EchoBank	4	0	0	0	**6**	0	6	3
Phyllostomidae	*Monophyllus plethodon*	EchoBank	2	12	**17**	0	0	0	29	9
Phyllostomidae	*Phyllonycteris poeyi*	Literature		**88**					88	
Phyllostomidae	*Phyllops falcatus*	Literature							671	
Phyllostomidae	*Phyllostomus discolor*	EchoBank	3	0	6	**8**	0	0	14	3
Phyllostomidae	*Phyllostomus hastatus*	EchoBank	4	0	0	0	**5**	0	5	2
Phyllostomidae	*Platyrrhinus brachycephalus*	EchoBank	4	0	0	0	**2**	0	2	1
Phyllostomidae	*Platyrrhinus helleri*	EchoBank	2	0	**3**	0	0	0	3	1
Phyllostomidae	*Sturnira lilium*	EchoBank	3	0	13	**16**	0	0	29	9
Phyllostomidae	*Sturnira ludovici*	EchoBank	2	0	**1**	0	0	0	1	1

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	**2**	**3**	**4**	**5**		
Phyllostomidae	*Sturnira mordax*	EchoBank	4	0	0	0	**5**	0	5	3
Phyllostomidae	*Sturnira thomasi*	EchoBank	2	0	**6**	**6**	0	0	12	4
Phyllostomidae	*Sturnira tildae*	EchoBank	2	0	**1**	**1**	0	0	2	1
Phyllostomidae	*Tonatia bidens*	EchoBank	4	0	0	0	**1**	0	1	1
Phyllostomidae	*Tonatia saurophila*	Literature								
Phyllostomidae	*Trachops cirrhosus*	EchoBank	3	0	36	**66**	0	0	102	24
Phyllostomidae	*Trinycteris nicefori*	EchoBank	3	0	0	**2**	0	0	2	1
Phyllostomidae	*Uroderma bilobatum*	EchoBank	4	0	0	0	**4**	0	4	2
Phyllostomidae	*Vampyrodes caraccioli*	EchoBank	4	0	0	0	**6**	0	6	2
Phyllostomidae	*Vampyrum spectrum*	Literature								
Pteropodidae	*Rousettus aegyptiacus*	Literature							50	
Rhinolophidae	*Rhinolophus acuminatus*	EchoBank	2	0	**30**	0	0	0	30	3
Rhinolophidae	*Rhinolophus affinis*	EchoBank	2	0	**175**	0	0	0	175	15
Rhinolophidae	*Rhinolophus alcyone*	Literature								
Rhinolophidae	*Rhinolophus arcuatus*	Literature								
Rhinolophidae	*Rhinolophus blasii*	Literature								
Rhinolophidae	*Rhinolophus borneensis*	Literature								
Rhinolophidae	*Rhinolophus capensis*	EchoBank	2	0	**148**	0	0	0	148	24
Rhinolophidae	*Rhinolophus clivosus*	EchoBank	2	0	**166**	0	0	0	166	28
Rhinolophidae	*Rhinolophus coelophyllus*	EchoBank	2	0	**413**	0	0	0	413	19
Rhinolophidae	*Rhinolophus cornutus*	EchoBank	2	0	**10**	0	0	0	10	2
Rhinolophidae	*Rhinolophus creaghi*	Literature								
Rhinolophidae	*Rhinolophus darlingi*	EchoBank	2	0	**538**	0	0	0	538	21

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Rhinolophidae	*Rhinolophus deckenii*	Literature								
Rhinolophidae	*Rhinolophus denti*	EchoBank	2	0	**100**	0	0	0	100	19
Rhinolophidae	*Rhinolophus euryale*	EchoBank	2	0	**82**	0	0	0	82	12
Rhinolophidae	*Rhinolophus euryotis*	EchoBank	2	0	**656**	0	0	0	656	12
Rhinolophidae	*Rhinolophus ferrumequinum*	EchoBank	2	0	**279**	0	0	0	279	26
Rhinolophidae	*Rhinolophus fumigatus*	EchoBank	2	0	**11**	0	0	0	11	1
Rhinolophidae	*Rhinolophus hildebrandtii*	EchoBank	2	0	**163**	0	0	0	163	14
Rhinolophidae	*Rhinolophus hipposideros*	EchoBank	2	0	**682**	0	0	0	682	72
Rhinolophidae	*Rhinolophus landeri*	EchoBank	2	0	**2**	0	0	0	2	2
Rhinolophidae	*Rhinolophus lepidus*	EchoBank	2	0	**19**	0	0	0	19	2
Rhinolophidae	*Rhinolophus luctus*	EchoBank	2	0	**69**	0	0	0	69	2
Rhinolophidae	*Rhinolophus macrotis*	EchoBank	2	0	**24**	0	0	0	24	3
Rhinolophidae	*Rhinolophus malayanus*	EchoBank	2	0	**320**	0	0	0	320	13
Rhinolophidae	*Rhinolophus marshalli*	Literature								
Rhinolophidae	*Rhinolophus megaphyllus*	EchoBank	2	0	**177**	0	0	0	177	4
Rhinolophidae	*Rhinolophus mehelyi*	Literature								
Rhinolophidae	*Rhinolophus monoceros*	EchoBank	2	0	**35**	0	0	0	35	18
Rhinolophidae	*Rhinolophus paradoxolophus*	Literature							13	
Rhinolophidae	*Rhinolophus pearsonii*	EchoBank	2	0	**275**	0	0	0	275	8
Rhinolophidae	*Rhinolophus philippinensis*	EchoBank	2	0	**15**	0	0	0	15	1
Rhinolophidae	*Rhinolophus pusillus*	EchoBank	2	0	**58**	0	0	0	58	5
Rhinolophidae	*Rhinolophus rex*	EchoBank	2	0	**59**	0	0	0	59	4
Rhinolophidae	*Rhinolophus rouxii*	Literature							40	

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Rhinolophidae	*Rhinolophus sedulus*	EchoBank	2	0	**45**	0	0	0	45	3
Rhinolophidae	*Rhinolophus shameli*	EchoBank	2	0	**209**	0	0	0	209	5
Rhinolophidae	*Rhinolophus siamensis*	Literature								
Rhinolophidae	*Rhinolophus simulator*	EchoBank	2	0	**147**	0	0	0	147	7
Rhinolophidae	*Rhinolophus sinicus*	Literature								
Rhinolophidae	*Rhinolophus stheno*	EchoBank	2	0	**47**	0	0	0	47	7
Rhinolophidae	*Rhinolophus subrufus*	Literature								
Rhinolophidae	*Rhinolophus swinnyi*	EchoBank	2	0	**82**	0	0	0	82	30
Rhinolophidae	*Rhinolophus thomasi*	EchoBank	2	0	**178**	0	0	0	178	9
Rhinolophidae	*Rhinolophus trifoliatus*	EchoBank	2	0	**5**	0	0	0	5	1
Rhinolophidae	*Rhinolophus yunanensis*	EchoBank	2	0	**95**	0	0	0	95	4
Rhinopomatidae	*Rhinopoma hardwickii*	EchoBank	2	0	**42**	0	0	0	42	2
Rhinopomatidae	*Rhinopoma microphyllum*	EchoBank	2	2	**23**	0	0	0	25	1
Thyropteridae	*Thyroptera tricolor*	EchoBank	1	**15**	2	4	0	0	21	4
Vespertilionidae	*Antrozous pallidus*	EchoBank	1	**26**	3	0	0	0	29	3
Vespertilionidae	*Arielulus torquatus*	EchoBank	1	**62**	0	0	0	0	62	7
Vespertilionidae	*Barbastella barbastellus*	EchoBank	1	**355**	14	0	0	0	369	25
Vespertilionidae	*Barbastella leucomelas*	EchoBank	1	**294**	0	0	0	0	294	25
Vespertilionidae	*Chalinolobus dwyeri*	EchoBank	1	**4**	0	0	0	0	4	1
Vespertilionidae	*Chalinolobus gouldii*	EchoBank	1	**13**	0	0	0	0	13	11
Vespertilionidae	*Chalinolobus morio*	EchoBank	1	**131**	0	0	0	0	131	3
Vespertilionidae	*Chalinolobus nigrogriseus*	Literature							30	
Vespertilionidae	*Chalinolobus picatus*	Literature								

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Vespertilionidae	*Chalinolobus tuberculatus*	EchoBank	1	**314**	0	0	0	0	314	34
Vespertilionidae	*Cistugo lesueuri*	Literature								
Vespertilionidae	*Cistugo seabrae*	EchoBank	1	**65**	0	0	0	0	65	6
Vespertilionidae	*Corynorhinus townsendii*	EchoBank	1	**11**	0	0	0	0	11	1
Vespertilionidae	*Eptesicus bottae*	EchoBank	1	**130**	0	0	0	0	130	21
Vespertilionidae	*Eptesicus brasiliensis*	EchoBank	1	**59**	0	0	0	0	59	5
Vespertilionidae	*Eptesicus furinalis*	EchoBank	1	**169**	0	0	0	0	169	13
Vespertilionidae	*Eptesicus fuscus*	EchoBank	1	**468**	0	0	0	0	468	79
Vespertilionidae	*Eptesicus guadeloupensis*	EchoBank	1	**3**	0	0	0	0	3	1
Vespertilionidae	*Eptesicus hottentotus*	EchoBank	1	**127**	0	0	0	0	127	7
Vespertilionidae	*Eptesicus nilssonii*	EchoBank	1	**493**	0	0	0	0	493	28
Vespertilionidae	*Eptesicus serotinus*	EchoBank	1	**1347**	0	0	0	0	1347	74
Vespertilionidae	*Euderma maculatum*	Literature							>701	
Vespertilionidae	*Falsistrellus mackenziei*	Literature								
Vespertilionidae	*Falsistrellus tasmaniensis*	Literature								
Vespertilionidae	*Glauconycteris variegata*	EchoBank	1	**129**	0	0	0	0	129	7
Vespertilionidae	*Glischropus tylopus*	EchoBank	1	**30**	3	0	0	0	33	4
Vespertilionidae	*Hesperoptenus blanfordi*	Literature		**13**					13	
Vespertilionidae	*Hypsugo anchietae*	EchoBank	1	**157**	0	0	0	0	157	16
Vespertilionidae	*Hypsugo ariel*	EchoBank	1	**3**	0	0	0	0	3	1
Vespertilionidae	*Hypsugo bodenheimeri*	EchoBank	1	**767**	0	0	0	0	767	28
Vespertilionidae	*Hypsugo savii*	EchoBank	1	**647**	0	0	0	0	647	42
Vespertilionidae	*Ia io*	Literature		**4**					4	

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Vespertilionidae	*Idionycteris phyllotis*	EchoBank	1	**9**	6	0	0	0	15	2
Vespertilionidae	*Kerivoula argentata*	Literature								
Vespertilionidae	*Kerivoula hardwickii*	EchoBank	1	**11**	0	0	0	0	11	2
Vespertilionidae	*Kerivoula intermedia*	EchoBank	1	**23**	0	0	0	0	23	4
Vespertilionidae	*Kerivoula lanosa*	EchoBank	1	**174**	0	0	0	0	174	10
Vespertilionidae	*Kerivoula minuta*	EchoBank	1	**1**	0	0	0	0	1	1
Vespertilionidae	*Kerivoula papillosa*	EchoBank	1	**51**	0	0	0	0	51	8
Vespertilionidae	*Kerivoula pellucida*	EchoBank	1	**1**	0	0	0	0	1	1
Vespertilionidae	*Kerivoula picta*	Literature							74	
Vespertilionidae	*Laephotis botswanae*	Literature								
Vespertilionidae	*Laephotis namibensis*	Literature								
Vespertilionidae	*Laephotis wintoni*	EchoBank	1	**4**	0	0	0	0	4	1
Vespertilionidae	*Lasionycteris noctivagans*	EchoBank	1	**587**	0	0	0	0	587	64
Vespertilionidae	*Lasiurus borealis*	EchoBank	1	**60**	0	0	0	0	60	8
Vespertilionidae	*Lasiurus cinereus*	Literature							296	
Vespertilionidae	*Lasiurus ega*	Literature		**72**					72	5
Vespertilionidae	*Lasiurus intermedius*	EchoBank	1	**16**	0	0	0	0	16	1
Vespertilionidae	*Murina aenea*	Literature							12	
Vespertilionidae	*Murina cyclotis*	Literature							132	
Vespertilionidae	*Murina florium*	EchoBank	1	**2**	0	0	0	0	2	1
Vespertilionidae	*Murina hilgendorfi*	EchoBank	1	**57**	0	0	0	0	57	15
Vespertilionidae	*Murina leucogaster*	Literature		**>220**					>220	
Vespertilionidae	*Murina puta*	EchoBank	1	**41**	0	0	0	0	41	7

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Vespertilionidae	*Murina suilla*	EchoBank	1	**1**	0	0	0	0	1	1
Vespertilionidae	*Murina ussuriensis*	EchoBank	1	**153**	0	0	0	0	153	21
Vespertilionidae	*Myotis adversus*	Literature							243	
Vespertilionidae	*Myotis albescens*	EchoBank	1	**2**	0	0	0	0	2	1
Vespertilionidae	*Myotis alcathoe*	EchoBank	1	**247**	0	0	0	0	247	17
Vespertilionidae	*Myotis auriculus*	EchoBank	1	**35**	0	0	0	0	35	2
Vespertilionidae	*Myotis bechsteinii*	EchoBank	1	**254**	0	0	0	0	254	22
Vespertilionidae	*Myotis blythii*	EchoBank	1	**133**	0	0	0	0	133	17
Vespertilionidae	*Myotis bocagii*	EchoBank	1	**680**	0	0	0	0	680	26
Vespertilionidae	*Myotis brandtii*	EchoBank	1	**1009**	0	0	0	0	1009	45
Vespertilionidae	*Myotis californicus*	EchoBank	1	**17**	0	0	0	0	17	2
Vespertilionidae	*Myotis capaccinii*	EchoBank	1	**433**	0	0	0	0	433	30
Vespertilionidae	*Myotis chiloensis*	Literature								
Vespertilionidae	*Myotis chinensis*	EchoBank	1	**458**	0	0	0	0	458	20
Vespertilionidae	*Myotis dasycneme*	EchoBank	1	**124**	0	0	0	0	124	23
Vespertilionidae	*Myotis daubentonii*	EchoBank	1	**638**	0	0	0	0	638	40
Vespertilionidae	*Myotis dominicensis*	EchoBank	1	**20**	0	0	0	0	20	5
Vespertilionidae	*Myotis elegans*	EchoBank	1	**15**	0	0	0	0	15	1
Vespertilionidae	*Myotis emarginatus*	EchoBank	1	**318**	0	0	0	0	318	28
Vespertilionidae	*Myotis evotis*	Literature								
Vespertilionidae	*Myotis fimbriatus*	EchoBank	1	**19**	0	0	0	0	19	2
Vespertilionidae	*Myotis formosus*	EchoBank	1	**73**	0	0	0	0	73	9
Vespertilionidae	*Myotis frater*	Literature								

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Vespertilionidae	*Myotis goudoti*	EchoBank	1	**11**	0	0	0	0	11	5
Vespertilionidae	*Myotis hasseltii*	EchoBank	1	**112**	0	0	0	0	112	4
Vespertilionidae	*Myotis ikonnikovi*	EchoBank	1	**156**	0	0	0	0	156	14
Vespertilionidae	*Myotis keaysi*	EchoBank	1	**19**	0	0	0	0	19	2
Vespertilionidae	*Myotis keenii*	EchoBank	1	**135**	0	0	0	0	135	20
Vespertilionidae	*Myotis leibii*	EchoBank	1	**44**	0	0	0	0	44	12
Vespertilionidae	*Myotis longipes*	EchoBank	1	**102**	0	0	0	0	102	9
Vespertilionidae	*Myotis lucifugus*	EchoBank	1	**257**	0	0	0	0	257	30
Vespertilionidae	*Myotis macrodactylus*	EchoBank	1	**77**	0	0	0	0	77	12
Vespertilionidae	*Myotis macropus*	EchoBank	1	**18**	0	0	0	0	18	1
Vespertilionidae	*Myotis martiniquensis*	EchoBank	1	**79**	2	0	0	0	81	7
Vespertilionidae	*Myotis moluccarum*	EchoBank	1	**130**	0	0	0	0	130	11
Vespertilionidae	*Myotis muricola*	EchoBank	1	**130**	0	0	0	0	130	2
Vespertilionidae	*Myotis myotis*	EchoBank	1	**177**	0	0	0	0	177	20
Vespertilionidae	*Myotis mystacinus*	EchoBank	1	**806**	0	0	0	0	806	46
Vespertilionidae	*Myotis nattereri*	EchoBank	1	**1220**	0	0	0	0	1220	67
Vespertilionidae	*Myotis nigricans*	EchoBank	1	**122**	0	0	0	0	122	2
Vespertilionidae	*Myotis pequinius*	Literature							13	
Vespertilionidae	*Myotis punicus*	EchoBank	1	**41**	0	0	0	0	41	6
Vespertilionidae	*Myotis ricketti*	EchoBank	1	**104**	0	0	0	0	104	11
Vespertilionidae	*Myotis riparius*	EchoBank	1	**3**	0	0	0	0	3	1
Vespertilionidae	*Myotis septentrionalis*	EchoBank	1	**43**	0	0	0	0	43	9
Vespertilionidae	*Myotis siligorensis*	EchoBank	1	**27**	0	0	0	0	27	3

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Vespertilionidae	*Myotis thysanodes*	EchoBank	1	**13**	0	0	0	0	13	4
Vespertilionidae	*Myotis tricolor*	EchoBank	1	**308**	0	0	0	0	308	20
Vespertilionidae	*Myotis velifer*	EchoBank	1	**27**	0	0	0	0	27	3
Vespertilionidae	*Myotis volans*	EchoBank	1	**55**	0	0	0	0	55	8
Vespertilionidae	*Myotis welwitschii*	EchoBank	1	**6**	0	0	0	0	6	1
Vespertilionidae	*Neoromicia capensis*	EchoBank	1	**391**	0	0	0	0	391	25
Vespertilionidae	*Neoromicia nanus*	EchoBank	1	**189**	0	0	0	0	189	14
Vespertilionidae	*Neoromicia somalicus*	EchoBank	1	**173**	0	0	0	0	173	10
Vespertilionidae	*Neoromicia tenuipinnis*	Literature								
Vespertilionidae	*Neoromicia zuluensis*	EchoBank	1	**10**	0	0	0	0	10	2
Vespertilionidae	*Nyctalus aviator*	EchoBank	1	**5**	0	0	0	0	5	1
Vespertilionidae	*Nyctalus azoreum*	Literature								
Vespertilionidae	*Nyctalus lasiopterus*	EchoBank	1	**337**	0	0	0	0	337	24
Vespertilionidae	*Nyctalus leisleri*	EchoBank	1	**835**	0	0	0	0	835	77
Vespertilionidae	*Nyctalus noctula*	EchoBank	1	**460**	0	0	0	0	460	47
Vespertilionidae	*Nyctalus plancyi*	EchoBank	1	**80**	15	0	0	0	95	4
Vespertilionidae	*Nycticeinops schlieffeni*	EchoBank	1	**75**	0	0	0	0	75	3
Vespertilionidae	*Nycticeius cubanus*	Literature								
Vespertilionidae	*Nyctophilus arnhemensis*	Literature							229	
Vespertilionidae	*Nyctophilus bifax*	Literature								
Vespertilionidae	*Nyctophilus geoffroyi*	EchoBank	1	**85**	0	0	0	0	85	3
Vespertilionidae	*Nyctophilus timoriensis*	Literature							30	
Vespertilionidae	*Nyctophilus walkeri*	Literature								

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Vespertilionidae	*Otonycteris hemprichii*	EchoBank	1	**8**	0	0	0	0	8	1
Vespertilionidae	*Phoniscus atrox*	Literature								
Vespertilionidae	*Phoniscus jagorii*	Literature							>42	
Vespertilionidae	*Phoniscus papuensis*	Literature							18	
Vespertilionidae	*Pipistrellus abramus*	EchoBank	1	**72**	0	0	0	0	72	7
Vespertilionidae	*Pipistrellus adamsi*	EchoBank	1	**16**	0	0	0	0	16	1
Vespertilionidae	*Pipistrellus hesperidus*	EchoBank	1	**376**	0	0	0	0	376	30
Vespertilionidae	*Pipistrellus hesperus*	EchoBank	1	**14**	0	0	0	0	14	2
Vespertilionidae	*Pipistrellus kuhlii*	EchoBank	1	**2364**	0	0	0	0	2364	119
Vespertilionidae	*Pipistrellus maderensis*	EchoBank	1	**2**	0	0	0	0	2	1
Vespertilionidae	*Pipistrellus nathusii*	EchoBank	1	**258**	0	0	0	0	258	23
Vespertilionidae	*Pipistrellus pipistrellus*	EchoBank	1	**1296**	0	0	0	0	1296	99
Vespertilionidae	*Pipistrellus pygmaeus*	EchoBank	1	**2211**	0	0	0	0	2211	104
Vespertilionidae	*Pipistrellus rueppellii*	EchoBank	1	**12**	0	0	0	0	12	1
Vespertilionidae	*Pipistrellus rusticus*	EchoBank	1	**71**	0	0	0	0	71	10
Vespertilionidae	*Pipistrellus stenopterus*	EchoBank	1	**15**	0	0	0	0	15	2
Vespertilionidae	*Pipistrellus subflavus*	EchoBank	1	**199**	0	0	0	0	199	22
Vespertilionidae	*Pipistrellus tenuis*	Literature								
Vespertilionidae	*Pipistrellus westralis*	Literature								
Vespertilionidae	*Plecotus auritus*	EchoBank	1	**349**	45	0	0	0	394	48
Vespertilionidae	*Plecotus austriacus*	EchoBank	1	**345**	9	0	0	0	354	34
Vespertilionidae	*Plecotus kolombatovici*	EchoBank	1	**19**	0	0	0	0	19	1
Vespertilionidae	*Rhogeessa aeneus*	EchoBank	1	**48**	0	0	0	0	48	1

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	2	3	4	5		
Vespertilionidae	*Rhogeessa io*	Literature								
Vespertilionidae	*Rhogeessa tumida*	EchoBank	1	**104**	0	0	0	0	104	3
Vespertilionidae	*Scoteanax rueppellii*	Literature								
Vespertilionidae	*Scotoecus albofuscus*	EchoBank	1	**29**	0	0	0	0	29	1
Vespertilionidae	*Scotophilus dinganii*	EchoBank	1	**405**	0	0	0	0	405	23
Vespertilionidae	*Scotophilus leucogaster*	EchoBank	1	**11**	0	0	0	0	11	4
Vespertilionidae	*Scotophilus nigrita*	EchoBank	1	**77**	0	0	0	0	77	6
Vespertilionidae	*Scotophilus robustus*	EchoBank	1	**11**	0	0	0	0	11	2
Vespertilionidae	*Scotophilus viridis*	EchoBank	1	**27**	0	0	0	0	27	2
Vespertilionidae	*Scotorepens balstoni*	Literature								
Vespertilionidae	*Scotorepens greyii*	EchoBank	1	**9**	0	0	0	0	9	6
Vespertilionidae	*Scotorepens orion*	Literature								
Vespertilionidae	*Scotorepens sanborni*	EchoBank	1	**16**	0	0	0	0	16	1
Vespertilionidae	*Tylonycteris pachypus*	EchoBank	1	**93**	0	0	0	0	93	2
Vespertilionidae	*Tylonycteris robustula*	Literature								
Vespertilionidae	*Vespadelus baverstocki*	Literature							1920	
Vespertilionidae	*Vespadelus caurinus*	Literature								
Vespertilionidae	*Vespadelus darlingtoni*	EchoBank	1	**22**	0	0	0	0	22	1
Vespertilionidae	*Vespadelus douglasorum*	Literature								
Vespertilionidae	*Vespadelus finlaysoni*	Literature								
Vespertilionidae	*Vespadelus pumilus*	Literature								
Vespertilionidae	*Vespadelus regulus*	EchoBank	1	**61**	0	0	0	0	61	3
Vespertilionidae	*Vespadelus troughtoni*	Literature			**50**				50	

Family	Species	Source	Main harmonic	Calls of each harmonic (bold shows main harmonic for species)					Total calls measured	Total files measured
				1	**2**	**3**	**4**	**5**		
Vespertilionidae	*Vespadelus vulturnus*	EchoBank	1	**215**	0	0	0	0	215	9
Vespertilionidae	*Vespertilio murinus*	EchoBank	1	**245**	0	0	0	0	245	24
Vespertilionidae	*Vespertilio sinensis*	EchoBank	1	**10**	0	0	0	0	10	2

8.2 Appendix B: References for echolocation data from the literature

Echolocation call data for the following species were collected from the published literature. Only call parameters matching those collected from recordings in EchoBank were recorded.

Emballonuridae

Balantiopteryx infusca	Ibanez *et al*. 2002
Balantiopteryx io	Ibanez *et al*. 2002
Coleura afra	Monadjem *et al*. 2010
Cyttarops alecto	Jung, Kalko, & von Helversen 2007
Diclidurus albus	Jung *et al*. 2007
Peropteryx kappleri	Jung *et al*. 2007
Saccolaimus flaviventris	Churchill 2010
Saccolaimus saccolaimus	Pottie *et al*. 2005
Taphozous georgianus	Fenton 1982
Taphozous hilli	Churchill 2010
Taphozous kapalgensis	Churchill 2010
Taphozous troughtoni	Churchill 2010

Hipposideridae

Coelops frithii	Zhang *et al*. 2009
Hipposideros inornatus	Churchill 2010
Hipposideros stenotis	Churchill 2010
Hipposideros vittatus	Monadjem *et al*. 2010
Rhinonicteris aurantia	Churchill 2010
Triaenops persicus	Monadjem *et al*. 2010

Megadermatidae

Lavia frons	Monadjem *et al*. 2010

Miniopteridae

Miniopterus inflatus	Monadjem *et al*. 2010

Molossidae

Chaerephon ansorgei	Monadjem *et al*. 2010
Chaerephon bivittatus	Monadjem *et al*. 2010
Chaerephon chapini	Monadjem *et al*. 2010

Chaerephon jobensis	Churchill 2010
Chaerephon nigeriae	Monadjem *et al*. 2010
Eumops glaucinus	Mora & Torres 2008
Molossops temminckii	Guillén-Servent & Ibáñez 2007
Mops midas	Monadjem *et al*. 2010
Mormopterus beccarii	Churchill 2010
Mormopterus loriae	Churchill 2010
Mormopterus norfolkensis	Churchill 2010
Nyctinomops macrotis	Biscardi *et al*. 2004; Mora & Torres 2008
Otomops martiensseni	Monadjem *et al*. 2010
Tadarida fulminans	Monadjem *et al*. 2010
Tadarida ventralis	Monadjem *et al*. 2010

Mormoopidae

Mormoops blainvillei	Jennings & Parsons 2004; MacÍas, Mora, & Garcia 2006
Pteronotus gymnonotus	Ibáñez *et al*. 2000
Pteronotus macleayii	MacÍas *et al*. 2006
Pteronotus quadridens	Jennings & Parsons 2004; MacÍas *et al*. 2006; MacÍas, Mora, & Gannon 2003

Natalidae

Nyctiellus lepidus	Murray *et al*. 2009

Noctilionidae

Noctilio albiventris	Kalko *et al*. 1998

Nycteridae

Nycteris grandis	Monadjem *et al*. 2010

Phyllostomidae

Brachyphylla nana	Macias *et al*. 2006
Carollia castanea	Thies, Kalko, & Schnitzler 1998
Erophylla bombifrons	Jennings & Parsons 2004
Erophylla sezekorni	Murray *et al*. 2009
Glossophaga longirostris	Jennings & Parsons 2004
Lampronycteris brachyotis	Pio *et al*. 2010
Macrophyllum macrophyllum	Brinkløv 2009; Weinbeer & Kalko 2007
Macrotus waterhousii	Murray *et al*. 2009

Micronycteris hirsute	Pio *et al*. 2010
Micronycteris megalotis	Pio *et al*. 2010
Phyllonycteris poeyi	Mora & MacÍas 2007
Phyllops falcatus	MacÍas *et al*. 2005
Tonatia saurophila	Pio *et al*. 2010
Trinycteris nicefori	Pio *et al*. 2010
Vampyrum spectrum	Pio *et al*. 2010

Pteropodidae

Rousettus aegyptiacus	Holland, Waters, & Rayner 2004

Rhinolophidae

Rhinolophus alcyone	Monadjem *et al*. 2010
Rhinolophus arcuatus	Csorba *et al.* 2003
Rhinolophus blasii	Jacobs, Barclay, & Walker 2007; Papadatou, Butlin, & Altringham 2008
Rhinolophus borneensis	Csorba *et al*. 2003
Rhinolophus creaghi	Csorba *et al*. 2003
Rhinolophus deckenii	Monadjem *et al*. 2010
Rhinolophus marshalli	Zhang *et al*. 2009
Rhinolophus mehelyi	Papadatou *et al*. 2008
Rhinolophus paradoxolophus	Zhao, Zhang, *et al*. 2003; Zhao, Zuo, *et al*. 2003
Rhinolophus rouxii	Feng *et al*. 2002; Zhao, Zuo, *et al*. 2003
Rhinolophus siamensis	Zhang *et al*. 2009
Rhinolophus sinicus	Zhang *et al*. 2009
Rhinolophus subrufus	Csorba *et al*. 2003

Vespertilionidae

Chalinolobus nigrogriseus	Fenton 1982
Chalinolobus picatus	Churchill 2010
Cistugo lesueuri	Monadjem *et al*. 2010
Euderma maculatum	Fullard & Dawson 1997; Obrist 1995
Falsistrellus mackenziei	Churchill 2010
Falsistrellus tasmaniensis	Churchill 2010
Hesperoptenus blanfordi	Kingston *et al*. 2003
Ia io	Thabah *et al*. 2007
Kerivoula argentata	Monadjem *et al*. 2010
Kerivoula picta	Sripathi, Raghuram, & Nathan 2006
Laephotis botswanae	Monadjem *et al*. 2010
Laephotis namibensis	Monadjem *et al*. 2010
Lasiurus cinereus	Barclay, Fullard, & Jacobs 1999

Lasiurus ega	Rydell *et al*. 2002
Murina aenea	Kingston *et al*. 1999
Murina cyclotis	Kingston *et al*. 1999
Murina leucogaster	Fukui, Agetsuma, & Hill 2004
Myotis adversus	Pottie *et al*. 2005
Myotis chiloensis	Ossa *et al*. 2010
Myotis evotis	Faure & Barclay 1994
Myotis frater	Zhang *et al*. 2000
Myotis pequinius	Jones *et al*. 2006
Neoromicia tenuipinnis	Monadjem *et al*. 2010
Nyctalus azoreum	Dietz, von Helversen, & Nill 2009
Nycticeius cubanus	Mora & MacÍas 2007
Nyctophilus arnhemensis	Churchill 2010
Nyctophilus bifax	Fenton 1982
Nyctophilus timoriensis	Churchill 2010
Nyctophilus walker	Churchill 2010
Phoniscus atrox	Kingston *et al*. 1999; Thong *et al*. 2006
Phoniscus jagorii	Kingston *et al*. 1999
Phoniscus papuensis	Churchill 2010
Pipistrellus tenuis	Churchill 2010
Pipistrellus westralis	Churchill 2010
Rhogeessa io	Audet, Engstrom, & Fenton 1993
Scoteanax rueppellii	Churchill 2010
Scotorepens balstoni	Churchill 2010
Scotorepens orion	Churchill 2010
Tylonycteris robustula	Pottie *et al*. 2005; Zhang *et al*. 2007
Vespadelus baverstocki	Churchill 2010
Vespadelus caurinus	Churchill 2010
Vespadelus douglasorum	Churchill 2010
Vespadelus finlaysoni	Churchill 2010
Vespadelus pumilus	Fenton 1982
Vespadelus troughtoni	Churchill 2010

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8.4 Appendix D: Nodal support for bat supertree

Reduced Quantitative Support (rQS) index for Chiroptera supertree. Nodes are numbered from the base of the tree along the left-hand backbone of the tree until the first tip is reached then each clade is coded in the same way always starting at the most basal clade and going to the left first.

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
1	1116	novel	0	0	0	298
2	365		0.154	57	11	230
3	186	not contradicted	0.138	41	0	257
4	169		-0.003	22	23	253
5	157		-0.017	35	40	223
6	75		0.037	19	8	271
7	71		0.013	7	3	288
8	70		0	1	1	296
9	69		0.081	26	2	270
10	5	not contradicted	0.003	1	0	297
11	2	not contradicted	0.027	8	0	290
12	3	novel	0	0	0	298
13	64	not contradicted	0.003	1	0	297
14	36	not contradicted	0.027	8	0	290
15	35		0.027	9	1	288
16	33		0.077	25	2	271
17	32		0.094	30	2	266
18	18		0.034	15	5	278
19	11		0.007	5	3	290
20	9		0.03	11	2	285
21	8		-0.013	10	14	274
22	5		0.023	19	12	267
23	3		0.027	17	9	272
24	2		0.003	4	3	291
25	2		0.003	2	1	295
26	3		0.013	5	1	292
27	2		0.01	7	4	287
28	2		0.02	7	1	290
29	7		0.007	7	5	286
30	5	not contradicted	0.034	10	0	288

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
31	4		0.023	9	2	287
32	3	not contradicted	0.023	7	0	291
33	2	not contradicted	0.023	7	0	291
34	2		0	4	4	290
35	13	not contradicted	0.01	3	0	295
36	11		0.067	22	2	274
37	8		0	6	6	286
38	7		0.037	14	3	281
39	6	not contradicted	0.01	3	0	295
40	5	not contradicted	0.03	9	0	289
41	4	not contradicted	0.01	3	0	295
42	3	not contradicted	0.01	3	0	295
43	2	not contradicted	0.01	3	0	295
44	3		0.027	11	3	284
45	2	not contradicted	0.007	2	0	296
46	2	novel	0	0	0	298
47	2	not contradicted	0.01	3	0	295
48	28	novel	0	0	0	298
49	4	not contradicted	0.003	1	0	297
50	3	novel	0	0	0	298
51	82		-0.03	7	16	275
52	80		-0.05	22	37	239
53	27		0.054	23	7	268
54	13		0.01	5	2	291
55	11		0.01	5	2	291
56	10	not contradicted	0.01	3	0	295
57	9		0.03	13	4	281
58	8		0.03	16	7	275
59	3	not contradicted	0.03	9	0	289
60	2	not contradicted	0.003	1	0	297
61	5		0	2	2	294
62	3	not contradicted	0.013	4	0	294
63	2	not contradicted	0.013	4	0	294
64	2		0.007	4	2	292
65	2	not contradicted	0.003	1	0	297
66	14		0.06	19	1	278
67	11		0.05	19	4	275
68	8	not contradicted	0.003	1	0	297
69	7	not contradicted	0.06	18	0	280
70	6		0.003	5	4	289

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
71	5	not contradicted	0.003	1	0	297
72	2	not contradicted	0.007	2	0	296
73	3	novel	0	0	0	298
74	3		0.01	4	1	293
75	2	not contradicted	0.007	2	0	296
76	3	not contradicted	0.017	5	0	293
77	2	not contradicted	0.007	2	0	296
78	53		-0.084	12	37	249
79	18		0.081	29	5	264
80	4		-0.007	1	3	294
81	3		0	4	4	290
82	2	not contradicted	0.013	4	0	294
83	14	not contradicted	0.01	3	0	295
84	13	not contradicted	0.05	15	0	283
85	12	not contradicted	0.034	10	0	288
86	11	not contradicted	0.081	24	0	274
87	9	not contradicted	0.04	12	0	286
88	8	not contradicted	0.023	7	0	291
89	7	not contradicted	0.013	4	0	294
90	6	not contradicted	0.003	1	0	297
91	5	novel	0	0	0	298
92	2		0.03	10	1	287
93	35		0.07	31	10	257
94	32		0.044	27	14	257
95	24		0.097	32	3	263
96	19		0.003	2	1	295
97	18	not contradicted	0.01	3	0	295
98	17	not contradicted	0.087	26	0	272
99	6		0.003	2	1	295
100	3	not contradicted	0.01	3	0	295
101	2	not contradicted	0.003	1	0	297
102	3		0.013	5	1	292
103	2	not contradicted	0.003	1	0	297
104	11		0.003	2	1	295
105	7	not contradicted	0.003	1	0	297
106	4	novel	0	0	0	298
107	4	not contradicted	0.013	4	0	294
108	3	not contradicted	0.003	1	0	297
109	2	novel	0	0	0	298
110	5		0.067	26	6	266

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
111	4		0.01	6	3	289
112	3		0.007	4	2	292
113	2		0.02	7	1	290
114	8		0.013	7	3	288
115	7	not contradicted	0.06	18	0	280
116	3	not contradicted	0.027	8	0	290
117	2	not contradicted	0.02	6	0	292
118	4	not contradicted	0.003	1	0	297
119	3	novel	0	0	0	298
120	3	not contradicted	0.003	1	0	297
121	2	novel	0	0	0	298
122	2	not contradicted	0.017	5	0	293
123	12	not supported	-0.01	0	3	295
124	11		-0.013	10	14	274
125	9		-0.064	10	29	259
126	5		0.054	23	7	268
127	2	not contradicted	0.007	2	0	296
128	3	not contradicted	0.003	1	0	297
129	2	novel	0	0	0	298
130	4		0.003	2	1	295
131	3		0.05	18	3	277
132	2	not contradicted	0.007	2	0	296
133	2	not contradicted	0.003	1	0	297
134	17	not contradicted	0.007	2	0	296
135	15	not contradicted	0.087	26	0	272
136	4	not contradicted	0.007	2	0	296
137	3		0.067	21	1	276
138	2		0.013	6	2	290
139	11		0.013	6	2	290
140	9	not contradicted	0.003	1	0	297
141	8	novel	0	0	0	298
142	2		0.017	8	3	287
143	2	not contradicted	0.003	1	0	297
144	179		0.054	23	7	268
145	174		0.01	4	1	293
146	163		0.034	20	10	268
147	158		0.081	28	4	266
148	81		0.02	10	4	284
149	73		0.027	9	1	288
150	67		-0.003	2	3	293

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
151	9		0.003	2	1	295
152	7		0.003	2	1	295
153	6		0.003	2	1	295
154	2	not contradicted	0.01	3	0	295
155	4	not contradicted	0.003	1	0	297
156	2	novel	0	0	0	298
157	2	novel	0	0	0	298
158	2	novel	0	0	0	298
159	58		0.01	6	3	289
160	30		0.003	2	1	295
161	29		0.01	4	1	293
162	23		0.013	5	1	292
163	9	not contradicted	0.01	3	0	295
164	8	not contradicted	0.01	3	0	295
165	7	not contradicted	0.013	4	0	294
166	6	not contradicted	0.013	4	0	294
167	5	not contradicted	0.01	3	0	295
168	4	not contradicted	0.01	3	0	295
169	2	not contradicted	0.013	4	0	294
170	2	not contradicted	0.01	3	0	295
171	14	not contradicted	0.013	4	0	294
172	10		0.007	3	1	294
173	9	not contradicted	0.01	3	0	295
174	8		0.007	3	1	294
175	6	not contradicted	0.01	3	0	295
176	5	not contradicted	0.01	3	0	295
177	4		0.007	3	1	294
178	2	not contradicted	0.01	3	0	295
179	2	not contradicted	0.007	2	0	296
180	2	not contradicted	0.01	3	0	295
181	4	not contradicted	0.01	3	0	295
182	3	not contradicted	0.01	3	0	295
183	2	not contradicted	0.01	3	0	295
184	6	not contradicted	0.01	3	0	295
185	5	not contradicted	0.007	2	0	296
186	4	not contradicted	0.01	3	0	295
187	2	not contradicted	0.01	3	0	295
188	2	novel	0	0	0	298
189	28		0.02	8	2	288
190	27		0.01	5	2	291

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
191	21	not contradicted	0.003	1	0	297
192	20	novel	0	0	0	298
193	6	not contradicted	0.01	3	0	295
194	5	not contradicted	0.01	3	0	295
195	2	not contradicted	0.01	3	0	295
196	3	not contradicted	0.01	3	0	295
197	2	not contradicted	0.01	3	0	295
198	6		0.003	2	1	295
199	5	not contradicted	0.01	3	0	295
200	2	not contradicted	0.01	3	0	295
201	3	not contradicted	0.01	3	0	295
202	2	not contradicted	0.01	3	0	295
203	8		0.01	4	1	293
204	2	not contradicted	0.013	4	0	294
205	6		0.003	2	1	295
206	5	not supported	-0.003	0	1	297
207	4		0.003	2	1	295
208	3	not contradicted	0.01	3	0	295
209	2	not contradicted	0.01	3	0	295
210	77	not contradicted	0.034	10	0	288
211	73		0.057	18	1	279
212	29		0.034	11	1	286
213	17	not contradicted	0.01	3	0	295
214	2	novel	0	0	0	298
215	15	not contradicted	0.013	4	0	294
216	4		0.003	2	1	295
217	3	not contradicted	0.01	3	0	295
218	2	novel	0	0	0	298
219	11		0.013	6	2	290
220	6	not contradicted	0.01	3	0	295
221	5	not contradicted	0.01	3	0	295
222	4	not contradicted	0.01	3	0	295
223	3	not contradicted	0.027	8	0	290
224	2		0	2	2	294
225	5	not contradicted	0.01	3	0	295
226	4	not contradicted	0.013	4	0	294
227	2	not contradicted	0.01	3	0	295
228	2	not contradicted	0.01	3	0	295
229	12		0.013	7	3	288
230	11		-0.003	3	4	291

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
231	8	not contradicted	0.013	4	0	294
232	7	not contradicted	0.01	3	0	295
233	4	not contradicted	0.013	4	0	294
234	3	not contradicted	0.01	3	0	295
235	2	not contradicted	0.01	3	0	295
236	3	not contradicted	0.01	3	0	295
237	2	novel	0	0	0	298
238	3	not contradicted	0.013	4	0	294
239	2	not contradicted	0.003	1	0	297
240	26	novel	0	0	0	298
241	18	not contradicted	0.017	5	0	293
242	2	not contradicted	0.013	4	0	294
243	15	not contradicted	0.02	6	0	292
244	12		-0.007	2	4	292
245	11		0.007	5	3	290
246	9	not contradicted	0.007	2	0	296
247	8		-0.003	2	3	293
248	3	not contradicted	0.013	4	0	294
249	2	not contradicted	0.013	4	0	294
250	5		-0.003	1	2	295
251	4		0	1	1	296
252	3		-0.007	2	4	292
253	2		-0.007	1	3	294
254	2	not contradicted	0.013	4	0	294
255	3	not contradicted	0.007	2	0	296
256	2	not contradicted	0.007	2	0	296
257	4		0	4	4	290
258	3	not contradicted	0.013	4	0	294
259	2	not contradicted	0.01	3	0	295
260	5	not contradicted	0.02	6	0	292
261	4		0.007	3	1	294
262	3	not contradicted	0.007	2	0	296
263	2		0.003	2	1	295
264	11	not contradicted	0.003	1	0	297
265	10	novel	0	0	0	298
266	5		0	6	6	286
267	4	not contradicted	0.017	5	0	293
268	2	not contradicted	0.003	1	0	297
269	2	not contradicted	0.013	4	0	294
270	751		0.044	24	11	263

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
271	695		0.01	7	4	287
272	694		-0.02	16	22	260
273	179		0.044	18	5	275
274	177		-0.013	13	17	268
275	170		0.04	22	10	266
276	160		0.07	22	1	275
277	156		-0.013	9	13	276
278	145		0.013	14	10	274
279	125		-0.007	4	6	288
280	120		0.02	15	9	274
281	81		0.01	9	6	283
282	70		0.013	7	3	288
283	67		0.047	18	4	276
284	53		0.044	17	4	277
285	27		-0.023	5	12	281
286	26		0.01	11	8	279
287	8		0.03	10	1	287
288	4		0.017	8	3	287
289	3		0	5	5	288
290	2		0.003	5	4	289
291	4		-0.003	2	3	293
292	3		-0.02	2	8	288
293	2		0.02	8	2	288
294	18		0.081	26	2	270
295	9		0.007	8	6	284
296	8	not contradicted	0.013	4	0	294
297	7	not contradicted	0.037	11	0	287
298	4		0.047	15	1	282
299	3		0.007	7	5	286
300	2		0.007	5	3	290
301	3		0.013	7	3	288
302	2		0.01	4	1	293
303	9		0.013	5	1	292
304	4		0.013	5	1	292
305	3		0.007	3	1	294
306	2	not contradicted	0.017	5	0	293
307	5		0.003	3	2	293
308	4		0.003	3	2	293
309	3		0.007	3	1	294
310	2	not contradicted	0.003	1	0	297

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
311	26		-0.027	6	14	278
312	13		-0.017	4	9	285
313	5	not contradicted	0.027	8	0	290
314	4	not contradicted	0.02	6	0	292
315	2	not contradicted	0.01	3	0	295
316	2	not contradicted	0.007	2	0	296
317	8		-0.017	3	8	287
318	6		-0.007	2	4	292
319	5		-0.03	1	10	287
320	4		0.017	8	3	287
321	3	not contradicted	0.013	4	0	294
322	2	not contradicted	0.017	5	0	293
323	2		0.003	5	4	289
324	13		-0.003	8	9	281
325	11		0.037	12	1	285
326	10	not contradicted	0.013	4	0	294
327	9	not contradicted	0.023	7	0	291
328	6	not contradicted	0.007	2	0	296
329	5	not contradicted	0.01	3	0	295
330	4	not contradicted	0.017	5	0	293
331	2	not contradicted	0.01	3	0	295
332	2	not contradicted	0.007	2	0	296
333	3	not contradicted	0.007	2	0	296
334	2		0	3	3	292
335	2	not contradicted	0.017	5	0	293
336	14	not contradicted	0.01	3	0	295
337	12	not contradicted	0.003	1	0	297
338	11	not contradicted	0.01	3	0	295
339	10	not contradicted	0.023	7	0	291
340	5	not contradicted	0.013	4	0	294
341	2	not contradicted	0.01	3	0	295
342	3	not contradicted	0.01	3	0	295
343	2	not contradicted	0.007	2	0	296
344	5	not contradicted	0.013	4	0	294
345	3	not contradicted	0.007	2	0	296
346	2	not contradicted	0.01	3	0	295
347	2	not contradicted	0.007	2	0	296
348	3	not contradicted	0.01	3	0	295
349	2	not contradicted	0.013	4	0	294
350	11		0.003	4	3	291

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
351	6	not contradicted	0.01	3	0	295
352	5	not contradicted	0.01	3	0	295
353	2	not contradicted	0.003	1	0	297
354	3		0.007	3	1	294
355	2	not contradicted	0.003	1	0	297
356	5	not contradicted	0.023	7	0	291
357	3		0.007	4	2	292
358	2	not contradicted	0.003	1	0	297
359	2	not contradicted	0.007	2	0	296
360	39		0.017	11	6	281
361	30		0.003	11	10	277
362	13		0.017	10	5	283
363	5	not contradicted	0.007	2	0	296
364	4	not contradicted	0.013	4	0	294
365	2	not contradicted	0.003	1	0	297
366	2	not contradicted	0.01	3	0	295
367	8		0.023	10	3	285
368	5		0.037	12	1	285
369	3	not contradicted	0.01	3	0	295
370	2	not contradicted	0.01	3	0	295
371	2		0.027	10	2	286
372	3		0.007	3	1	294
373	2		0.007	4	2	292
374	17		-0.01	7	10	281
375	7		0.017	10	5	283
376	2	not contradicted	0.01	3	0	295
377	5	not contradicted	0.034	10	0	288
378	2	not contradicted	0.007	2	0	296
379	3	not contradicted	0.007	2	0	296
380	2	not contradicted	0.003	1	0	297
381	10		0.02	11	5	282
382	7		0.01	10	7	281
383	5	not contradicted	0.017	5	0	293
384	4		0.003	3	2	293
385	3		-0.007	1	3	294
386	2		0.003	3	2	293
387	2	not contradicted	0.013	4	0	294
388	3	not contradicted	0.007	2	0	296
389	2		0.003	2	1	295
390	9		0.027	9	1	288

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
391	7		0.01	10	7	281
392	6		0	5	5	288
393	5		0.003	4	3	291
394	3	not contradicted	0.01	3	0	295
395	2	not contradicted	0.01	3	0	295
396	2	not contradicted	0.02	6	0	292
397	2		-0.003	1	2	295
398	5	not contradicted	0.017	5	0	293
399	3	not contradicted	0.003	1	0	297
400	2	novel	0	0	0	298
401	2	not contradicted	0.003	1	0	297
402	20		0.023	10	3	285
403	19		-0.027	2	10	286
404	18		-0.013	4	8	286
405	2		0.034	11	1	286
406	16		0.01	9	6	283
407	5	not contradicted	0.02	6	0	292
408	3		0.013	5	1	292
409	2		0.007	3	1	294
410	2	not contradicted	0.02	6	0	292
411	11		0.007	6	4	288
412	9		0.023	9	2	287
413	4	not contradicted	0.007	2	0	296
414	2	not contradicted	0.003	1	0	297
415	2	not contradicted	0.003	1	0	297
416	5		-0.007	5	7	286
417	2		0	1	1	296
418	3	not contradicted	0.013	4	0	294
419	2	not contradicted	0.01	3	0	295
420	2	not contradicted	0.02	6	0	292
421	11		-0.023	3	10	285
422	10		0.017	8	3	287
423	9	not contradicted	0.023	7	0	291
424	6		0.013	5	1	292
425	4		0	1	1	296
426	3	not contradicted	0.003	1	0	297
427	2	novel	0	0	0	298
428	2	not contradicted	0.007	2	0	296
429	3		0.01	5	2	291
430	2	not contradicted	0.01	3	0	295

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
431	4		-0.01	1	4	293
432	3	not contradicted	0.04	12	0	286
433	2	not contradicted	0.037	11	0	287
434	10		0.06	23	5	270
435	3	not contradicted	0.003	1	0	297
436	2	not contradicted	0.057	17	0	281
437	7	not contradicted	0.077	23	0	275
438	6		0.03	13	4	281
439	5		0.03	13	4	281
440	2	not contradicted	0.044	13	0	285
441	3	not contradicted	0.003	1	0	297
442	2		0.054	17	1	280
443	7		-0.003	10	11	277
444	5		-0.027	3	11	284
445	2	not contradicted	0.01	3	0	295
446	3	not contradicted	0.027	8	0	290
447	2	not contradicted	0.017	5	0	293
448	2	not contradicted	0.101	30	0	268
449	2	not contradicted	0.01	3	0	295
450	515		0.02	11	5	282
451	507		0.081	35	11	252
452	408		0	1	1	296
453	407		0.044	17	4	277
454	388	not contradicted	0.067	20	0	278
455	386		0.154	49	3	246
456	205		0.02	14	8	276
457	189		-0.084	5	30	263
458	25		-0.003	2	3	293
459	12		0.054	17	1	280
460	2	not contradicted	0.023	7	0	291
461	10	not contradicted	0.003	1	0	297
462	8	not contradicted	0.04	12	0	286
463	6	not contradicted	0.04	12	0	286
464	4	not contradicted	0.03	9	0	289
465	3		0.013	7	3	288
466	2		0.017	8	3	287
467	2	not contradicted	0.023	7	0	291
468	2	not contradicted	0.02	6	0	292
469	2	novel	0	0	0	298
470	13		0	1	1	296

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
471	12	not contradicted	0.003	1	0	297
472	7	not contradicted	0.013	4	0	294
473	6	not contradicted	0.007	2	0	296
474	5	not contradicted	0.007	2	0	296
475	4	not contradicted	0.007	2	0	296
476	2	not contradicted	0.007	2	0	296
477	2	not contradicted	0.007	2	0	296
478	5	novel	0	0	0	298
479	164		0.04	25	13	260
480	60	not supported	-0.007	0	2	296
481	46		-0.003	2	3	293
482	42		0.01	4	1	293
483	40		0	1	1	296
484	35		0	1	1	296
485	5	not contradicted	0.003	1	0	297
486	4	novel	0	0	0	298
487	30		0.07	22	1	275
488	27		0.07	22	1	275
489	17	not contradicted	0.003	1	0	297
490	16	novel	0	0	0	298
491	10		0	1	1	296
492	3	not contradicted	0.007	2	0	296
493	2	not contradicted	0.007	2	0	296
494	7	not contradicted	0.003	1	0	297
495	6	novel	0	0	0	298
496	3	not contradicted	0.013	4	0	294
497	2	not contradicted	0.074	22	0	276
498	5	not contradicted	0.003	1	0	297
499	2	novel	0	0	0	298
500	3	novel	0	0	0	298
501	2		0.007	3	1	294
502	4	not contradicted	0.003	1	0	297
503	3	not contradicted	0.003	1	0	297
504	2	novel	0	0	0	298
505	14	not contradicted	0.003	1	0	297
506	2	novel	0	0	0	298
507	12	not contradicted	0.003	1	0	297
508	9	novel	0	0	0	298
509	3	not contradicted	0.007	2	0	296
510	2	novel	0	0	0	298

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
511	104		0.114	35	1	262
512	78		0.013	6	2	290
513	76		0.007	3	1	294
514	70		0.013	7	3	288
515	43		0.013	5	1	292
516	24		0	1	1	296
517	21		0.003	2	1	295
518	7	not contradicted	0.007	2	0	296
519	5	not contradicted	0.003	1	0	297
520	4	novel	0	0	0	298
521	2	not contradicted	0.007	2	0	296
522	14	not supported	-0.003	0	1	297
523	12	not contradicted	0.003	1	0	297
524	11	not contradicted	0.003	1	0	297
525	9	novel	0	0	0	298
526	2	not contradicted	0.007	2	0	296
527	2	not contradicted	0.007	2	0	296
528	3	not contradicted	0.007	2	0	296
529	2	novel	0	0	0	298
530	19		0.003	2	1	295
531	16	not contradicted	0.003	1	0	297
532	13	novel	0	0	0	298
533	2	novel	0	0	0	298
534	3	not contradicted	0.007	2	0	296
535	2	not contradicted	0.007	2	0	296
536	27		0	1	1	296
537	21		0.017	6	1	291
538	20	not supported	-0.003	0	1	297
539	16		0.01	5	2	291
540	13		0	1	1	296
541	6	not supported	-0.003	0	1	297
542	5	not contradicted	0.003	1	0	297
543	4	novel	0	0	0	298
544	7		0	1	1	296
545	6		0.007	3	1	294
546	5		0.007	3	1	294
547	4	not contradicted	0.003	1	0	297
548	3	not contradicted	0.003	1	0	297
549	2	not contradicted	0.007	2	0	296
550	2	not contradicted	0.007	2	0	296

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
551	4	novel	0	0	0	298
552	6	not contradicted	0.003	1	0	297
553	5	novel	0	0	0	298
554	6		0.003	2	1	295
555	5	not contradicted	0.003	1	0	297
556	4	not contradicted	0.003	1	0	297
557	3	novel	0	0	0	298
558	2	not contradicted	0.013	4	0	294
559	26		0	1	1	296
560	21		0.03	12	3	283
561	15		0.03	10	1	287
562	14		-0.01	4	7	287
563	10	not contradicted	0.007	2	0	296
564	2	not contradicted	0.003	1	0	297
565	8	not contradicted	0.02	6	0	292
566	7	not contradicted	0.003	1	0	297
567	5	not contradicted	0.02	6	0	292
568	3	not contradicted	0.01	3	0	295
569	2	not contradicted	0.007	2	0	296
570	2	not contradicted	0.007	2	0	296
571	2	novel	0	0	0	298
572	4		0.023	9	2	287
573	2	not contradicted	0.01	3	0	295
574	2	not contradicted	0.03	9	0	289
575	6		0	1	1	296
576	5	not contradicted	0.013	4	0	294
577	4	not contradicted	0.017	5	0	293
578	3	not contradicted	0.007	2	0	296
579	2	not contradicted	0.013	4	0	294
580	5	not contradicted	0.003	1	0	297
581	4	novel	0	0	0	298
582	16		0.02	8	2	288
583	2	not contradicted	0.023	7	0	291
584	14		-0.003	2	3	293
585	13		0.027	13	5	280
586	3		0.03	10	1	287
587	2		0.02	8	2	288
588	10		0.003	6	5	287
589	2	not contradicted	0.037	11	0	287
590	8	not contradicted	0.05	15	0	283

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
591	7		0.01	4	1	293
592	6	not contradicted	0.003	1	0	297
593	3	novel	0	0	0	298
594	3		0.003	2	1	295
595	2	not contradicted	0.01	3	0	295
596	181		-0.023	3	10	285
597	145		0.044	17	4	277
598	42	not contradicted	0.037	11	0	287
599	19	not contradicted	0.013	4	0	294
600	2	not contradicted	0.003	1	0	297
601	17	not contradicted	0.003	1	0	297
602	16	not contradicted	0.003	1	0	297
603	10	novel	0	0	0	298
604	6	not contradicted	0.013	4	0	294
605	2	not contradicted	0.013	4	0	294
606	4	not contradicted	0.013	4	0	294
607	2	not contradicted	0.013	4	0	294
608	2	not contradicted	0.013	4	0	294
609	23	not contradicted	0.003	1	0	297
610	19	not contradicted	0.003	1	0	297
611	18	not contradicted	0.003	1	0	297
612	15	novel	0	0	0	298
613	3	not contradicted	0.013	4	0	294
614	2	not contradicted	0.017	5	0	293
615	4	not contradicted	0.003	1	0	297
616	3	novel	0	0	0	298
617	103	not contradicted	0.124	37	0	261
618	31	novel	0	0	0	298
619	40		-0.02	15	21	262
620	25		-0.037	10	21	267
621	19		-0.047	10	24	264
622	6		-0.057	5	22	271
623	4		0.02	15	9	274
624	2		0.06	19	1	278
625	2	not contradicted	0.003	1	0	297
626	2	not contradicted	0.007	2	0	296
627	13		-0.077	6	29	263
628	4	not contradicted	0.023	7	0	291
629	3		0.064	28	9	261
630	2		-0.003	10	11	277

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
631	9		-0.044	3	16	279
632	8		0.101	31	1	266
633	3	not contradicted	0.01	3	0	295
634	2		0.097	30	1	267
635	5		0.03	15	6	277
636	4		0.027	21	13	264
637	3		0.003	2	1	295
638	2	novel	0	0	0	298
639	6	not contradicted	0.003	1	0	297
640	5		0.054	22	6	270
641	4		0.084	26	1	271
642	3		0.084	26	1	271
643	2	not contradicted	0.084	25	0	273
644	15		-0.034	9	19	270
645	11		-0.044	8	21	269
646	9		0.023	17	10	271
647	8		0.013	6	2	290
648	7	not contradicted	0.091	27	0	271
649	3		0.03	10	1	287
650	2		0.074	23	1	274
651	4	not contradicted	0.023	7	0	291
652	3		0.02	8	2	288
653	2		0.027	9	1	288
654	2		0.027	17	9	272
655	4	not contradicted	0.077	23	0	275
656	3	not contradicted	0.077	23	0	275
657	2	not contradicted	0.07	21	0	277
658	32		0.05	24	9	265
659	20		0.037	20	9	269
660	19	not contradicted	0.034	10	0	288
661	18		0.094	35	7	256
662	13	not contradicted	0.007	2	0	296
663	12		0.097	30	1	267
664	5		0.013	5	1	292
665	4		0.087	28	2	268
666	3		0.091	28	1	269
667	2		0.077	26	3	269
668	7		0.081	27	3	268
669	5		0.01	5	2	291
670	3		0.013	5	1	292

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
671	2	not contradicted	0.02	6	0	292
672	2	not contradicted	0.02	6	0	292
673	2		0.104	32	1	265
674	5	not contradicted	0.101	30	0	268
675	4	not contradicted	0.101	30	0	268
676	3	not contradicted	0.02	6	0	292
677	2	not contradicted	0.023	7	0	291
678	12	not contradicted	0.023	7	0	291
679	2	not contradicted	0.02	6	0	292
680	10		0.074	26	4	268
681	8		0.07	25	4	269
682	6		-0.007	3	5	290
683	3	not contradicted	0.02	6	0	292
684	2	not contradicted	0.02	6	0	292
685	3		0.013	6	2	290
686	2	not contradicted	0.02	6	0	292
687	2		-0.003	3	4	291
688	2	not contradicted	0.02	6	0	292
689	36		-0.02	1	7	290
690	35		-0.003	1	2	295
691	17	not contradicted	0.013	4	0	294
692	16		0.007	3	1	294
693	6	not contradicted	0.007	2	0	296
694	5	not contradicted	0.007	2	0	296
695	4	not contradicted	0.013	4	0	294
696	2		0	2	2	294
697	2	not contradicted	0.007	2	0	296
698	10	not contradicted	0.003	1	0	297
699	6	novel	0	0	0	298
700	4	not contradicted	0.013	4	0	294
701	3	not contradicted	0.007	2	0	296
702	2	not contradicted	0.01	3	0	295
703	18	not contradicted	0.003	1	0	297
704	17	novel	0	0	0	298
705	2	not contradicted	0.067	20	0	278
706	19	not contradicted	0.003	1	0	297
707	16	not contradicted	0.05	15	0	283
708	11		0.02	11	5	282
709	10	not contradicted	0.034	10	0	288
710	9	not contradicted	0.017	5	0	293

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
711	8	not contradicted	0.003	1	0	297
712	7		0.027	11	3	284
713	3		0.003	3	2	293
714	2		0.01	6	3	289
715	4	not contradicted	0.007	2	0	296
716	3	novel	0	0	0	298
717	5		0.007	5	3	290
718	4		-0.003	3	4	291
719	3		-0.01	2	5	291
720	2	not contradicted	0.007	2	0	296
721	3	novel	0	0	0	298
722	99		0.02	7	1	290
723	98		0.013	5	1	292
724	25	not contradicted	0.007	2	0	296
725	18	not contradicted	0.007	2	0	296
726	17	not contradicted	0.003	1	0	297
727	13	novel	0	0	0	298
728	4	not contradicted	0.007	2	0	296
729	3	not contradicted	0.007	2	0	296
730	2	not contradicted	0.007	2	0	296
731	7	not contradicted	0.007	2	0	296
732	6	not contradicted	0.003	1	0	297
733	4	novel	0	0	0	298
734	2	not contradicted	0.007	2	0	296
735	73		0.003	2	1	295
736	16	not supported	-0.003	0	1	297
737	2	novel	0	0	0	298
738	14	not contradicted	0.013	4	0	294
739	13	not contradicted	0.003	1	0	297
740	11	novel	0	0	0	298
741	2	not contradicted	0.013	4	0	294
742	57		0.044	15	2	281
743	48		0.003	6	5	287
744	20		0.01	8	5	285
745	9	not contradicted	0.007	2	0	296
746	5	not contradicted	0.007	2	0	296
747	4	not contradicted	0.007	2	0	296
748	2	not contradicted	0.007	2	0	296
749	2	not contradicted	0.007	2	0	296
750	4	not contradicted	0.003	1	0	297

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
751	2	not contradicted	0.013	4	0	294
752	2	not contradicted	0.003	1	0	297
753	11		0.02	8	2	288
754	9	not contradicted	0.003	1	0	297
755	8	not contradicted	0.017	5	0	293
756	7	not contradicted	0.007	2	0	296
757	6	not contradicted	0.003	1	0	297
758	5	novel	0	0	0	298
759	2	not contradicted	0.003	1	0	297
760	10		0.007	3	1	294
761	9	not contradicted	0.003	1	0	297
762	8	not contradicted	0.003	1	0	297
763	2	not contradicted	0.003	1	0	297
764	6	novel	0	0	0	298
765	4	not contradicted	0.003	1	0	297
766	2	novel	0	0	0	298
767	2	novel	0	0	0	298
768	10	not contradicted	0.003	1	0	297
769	9	novel	0	0	0	298
770	2	novel	0	0	0	298
771	9	not contradicted	0.01	3	0	295
772	5	novel	0	0	0	298
773	8	not contradicted	0.023	7	0	291
774	7	not contradicted	0.044	13	0	285
775	2	not contradicted	0.023	7	0	291
776	5	not contradicted	0.023	7	0	291
777	3	not contradicted	0.003	1	0	297
778	2	not contradicted	0.02	6	0	292
779	2		0.017	7	2	289
780	56		0	9	9	280
781	51		0.081	25	1	272
782	33		0.081	25	1	272
783	21		0.034	15	5	278
784	13		0.013	9	5	284
785	8		0	7	7	284
786	7		0.023	11	4	283
787	3	not contradicted	0.034	10	0	288
788	2	not contradicted	0.027	8	0	290
789	4		0.027	9	1	288
790	3	not contradicted	0.023	7	0	291

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
791	2		0.027	10	2	286
792	5	not contradicted	0.03	9	0	289
793	4	not contradicted	0.027	8	0	290
794	3	not contradicted	0.03	9	0	289
795	2	not contradicted	0.027	8	0	290
796	8		0.02	8	2	288
797	2	not contradicted	0.02	6	0	292
798	6		0.01	9	6	283
799	5	not contradicted	0.03	9	0	289
800	3	not contradicted	0.003	1	0	297
801	2	not contradicted	0.027	8	0	290
802	2		0.034	11	1	286
803	12		0.007	5	3	290
804	11		0.027	9	1	288
805	8		-0.01	2	5	291
806	7		-0.003	3	4	291
807	6		-0.007	4	6	288
808	4	not supported	-0.003	0	1	297
809	3		-0.003	2	3	293
810	2	not contradicted	0.003	1	0	297
811	2		0.017	6	1	291
812	3	not contradicted	0.013	4	0	294
813	2	not contradicted	0.01	3	0	295
814	18	not contradicted	0.017	5	0	293
815	4	not contradicted	0.01	3	0	295
816	3	not contradicted	0.01	3	0	295
817	2	novel	0	0	0	298
818	14	not contradicted	0.017	5	0	293
819	3	not contradicted	0.003	1	0	297
820	2	novel	0	0	0	298
821	11	not contradicted	0.01	3	0	295
822	10	not contradicted	0.01	3	0	295
823	9	not contradicted	0.013	4	0	294
824	4	not contradicted	0.01	3	0	295
825	2	not contradicted	0.01	3	0	295
826	2	novel	0	0	0	298
827	5	not contradicted	0.01	3	0	295
828	2		0.003	2	1	295
829	3		0.01	4	1	293
830	2		0.003	2	1	295

Node	Clade size	Status	rQS	Number of sources with matches	Number of sources with mismatches	Number of sources with equivocal trees
831	5	not contradicted	0.007	2	0	296
832	4	not contradicted	0.02	6	0	292
833	3	not contradicted	0.007	2	0	296
834	2	not contradicted	0.01	3	0	295

8.5 Appendix E: Fossil calibration dates for supertree

A compilation of the bat fossil genera used in to date the supertree, as recorded by Eiting (2009) with additional information from Eiting (Pers. Comm. 2010). Temporal records of bat genera were tabulated as present (1) or absent (0) in each discrete time interval. Sources record the first and last occurrences of each genus (excluding Recent), plus additional intervening occurrences when available (non-exhaustive). The midpoints of the oldest stage in which each fossil occurred were used in the supertree dating. Stratigraphic bin abbreviations as follows: Eo = Eocene, Oligo = Oligocene, Mio = Miocene, Plio = Pliocene; Ypr = Ypresian, Lut = Lutetian, Bart = Bartonian, Pria = Priabonian, Rup = Rupelian, Chat = Chattian, Aqui = Aquitanian, Burd = Burdigalian, Lang = Langhian, Serra = Serravallian, Tort = Tortonian, Mes = Messinian, Zan = Zanclean; E = Early, M = Middle, L = Late; Ma = Millions of Years Ago. Node is the node to which the fossil belongs, and Calibration node is the node to which the date was applied.

					Eo				**Oligo**		**Mio**						**Plio**
			Cali-		**E**	**M**		**L**	**E**	**L**	**E**		**M**		**L**		**E**
Family	**Genus**	**Node**	**bration**	**Date**	**Ypr**	**Lut**	**Bart**	**Pria**	**Rup**	**Chat**	**Aqui**	**Burd**	**Lang**	**Serra**	**Tort**	**Mes**	**Zan**
			node	Ma:	**55.8**	**48.6**	**40.4**	**37.2**	**33.9**	**28.4**	**23.0**	**20.4**	**16.0**	**13.8**	**11.6**	**7.2**	**5.3**
				Duration (my):	**7.2**	**8.2**	**3.2**	**3.3**	**5.5**	**5.4**	**2.6**	**4.4**	**2.2**	**2.2**	**4.4**	**1.9**	**1.7**
Emballonuridae	†Tachypteron	783	782	44.5	0	1	0	0	0	0	0	0	0	0	0	0	0
Emballonuridae	†Vespertiliavus	783	782	44.5	0	1	1	1	1	1	0	0	0	0	0	0	0
Emballonuridae	Diclidurus	795	794	12.714	0	0	0	0	0	0	0	0	0	1	1	1	1
Emballonuridae	Saccolaimus	817	816	18.2	0	0	0	0	0	0	0	1	1	1	1	1	1
Emballonuridae	Taphozous	820	816	18.2	0	0	0	0	0	0	0	1	1	1	1	1	1
Hipposideridae	†Palaeophyllophora	150	149	38.8	0	0	1	1	1	1	0	0	0	0	0	0	0
Hipposideridae	Asellia	160	153	18.2	0	0	0	0	0	0	0	1	1	1	1	1	1
Hipposideridae	Hipposideros	(151)	(150)	38.8	0	0	1	1	1	1	1	1	1	1	1	1	1

					Eo				Oligo		Mio						Plio
			Cali-		E	M		L	E	L	E		M		L		E
Family	**Genus**	**Node**	**bration**	**Date**	**Ypr**	**Lut**	**Bart**	**Pria**	**Rup**	**Chat**	**Aqui**	**Burd**	**Lang**	**Serra**	**Tort**	**Mes**	**Zan**
			node	Ma:	**55.8**	**48.6**	**40.4**	**37.2**	**33.9**	**28.4**	**23.0**	**20.4**	**16.0**	**13.8**	**11.6**	**7.2**	**5.3**
				Duration (my):	**7.2**	**8.2**	**3.2**	**3.3**	**5.5**	**5.4**	**2.6**	**4.4**	**2.2**	**2.2**	**4.4**	**1.9**	**1.7**
Megadermatidae	†Saharaderma	262	148	35.55	0	0	0	1	0	0	0	0	0	0	0	0	0
Megadermatidae	Megaderma	265	264	25.715	0	0	0	0	0	1	1	1	1	1	1	1	1
Molossidae	†Wallia	724	453	38.8	0	0	1	1	0	0	0	0	0	0	0	0	0
Molossidae	Eumops	762	745	12.714	0	0	0	0	0	0	0	0	0	1	1	1	1
Molossidae	Mormopterus	770	745	21.73	0	0	0	0	0	0	1	1	1	1	1	1	1
Molossidae	Tadarida	773	744	35.55	0	0	0	1	1	1	1	1	1	1	1	1	1
Mystacinidae	†Icarops	451	275	18.2	0	0	0	0	0	0	0	1	1	1	0	0	0
Natalidae	†Honrovits	775	452	52.2	1	0	0	0	0	0	0	0	0	0	0	0	0
Noctilionidae	Noctilio	450	445	9.427	0	0	0	0	0	0	0	0	0	0	1	1	1
Nycteridae	†Chibanycteris			31.15	0	0	0	0	1	0	0	0	0	0	0	0	0
Phyllostomidae	†Notonycteris	278	277	12.714	0	0	0	0	0	0	0	0	0	1	0	0	0
Pteropodidae	†Propotto	5	4	18.2	0	0	0	0	0	0	0	1	0	0	0	0	0
Rhinolophidae	Rhinolophus	212	149	35.55	0	0	0	1	1	1	1	1	1	1	1	1	1
Rhinopomatidae	Rhinopoma	269	268	9.427	0	0	0	0	0	0	0	0	0	0	1	1	1
Thyropteridae	Thyroptera	448	446	12.714	0	0	0	0	0	0	0	0	0	1	1	1	1
Vespertilionidae	†Stehlinia	455	454	44.5	0	1	1	1	1	1	0	0	0	0	0	0	0
Vespertilionidae	Antrozous	462	461	12.714	0	0	0	0	0	0	0	0	0	1	1	1	1
Vespertilionidae	Corynorhinus	588	587	6.289	0	0	0	0	0	0	0	0	0	0	0	1	1
Vespertilionidae	Eptesicus	(489)	(486)	18.2	0	0	0	0	0	0	0	1	1	1	1	1	1
Vespertilionidae	Lasionycteris	691	598	4.466	0	0	0	0	0	0	0	0	0	0	0	0	1
Vespertilionidae	Lasiurus	693	692	9.427	0	0	0	0	0	0	0	0	0	0	1	1	1
Vespertilionidae	Myotis	619	599	25.715	0	0	0	0	0	1	1	1	1	1	1	1	1
Vespertilionidae	Nyctalus	567	565	25.715	0	0	0	0	0	1	1	1	1	1	1	1	1

					Eo				Oligo		Mio						Plio
			Cali-		E	M		L	E	L	E		M		L		E
Family	**Genus**	**Node**	**bration**	**Date**	**Ypr**	**Lut**	**Bart**	**Pria**	**Rup**	**Chat**	**Aqui**	**Burd**	**Lang**	**Serra**	**Tort**	**Mes**	**Zan**
			node	Ma:	**55.8**	**48.6**	**40.4**	**37.2**	**33.9**	**28.4**	**23.0**	**20.4**	**16.0**	**13.8**	**11.6**	**7.2**	**5.3**
				Duration (my):	**7.2**	**8.2**	**3.2**	**3.3**	**5.5**	**5.4**	**2.6**	**4.4**	**2.2**	**2.2**	**4.4**	**1.9**	**1.7**
Vespertilionidae	Plecotus	592	590	12.714	0	0	0	0	0	0	0	0	0	1	1	1	1
Vespertilionidae	Scotophilus	473	472	12.714	0	0	0	0	0	0	0	0	0	1	1	1	1
Vespertilionidae	Vespertilio	560	514	12.714	0	0	0	0	0	0	0	0	0	1	1	1	1

8.6 Appendix F: Species list: Analyses

Sample sizes for each parameter used in the analyses shown in Chapters 4, 5, and 6.

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
	Measured	n = 333	n = 366	n = 376	n = 393	n = 408	n = 291	n = 354	n = 355	n = 408	n = 291
	Assumed	**n = 308**	**n = 0**	**n = 0**	**n = 0**	**n = 0**	**n = 0**	**n = 0**	**n = 0**	**n = 0**	**n = 0**
	Imputed	*n = 466*	*n = 552*	*n = 542*	*n = 525*	*n = 510*	*n = 627*	*n = 564*	*n = 563*	*n = 510*	*n = 627*
	Total	n = 1105	n = 918	n = 918	n = 918	n = 918	n = 918	n = 918	n = 918	n = 918	n = 918
Craseonycteridae	*Craseonycteris thonglongyai*	6	6.64	1.96	3.48	78.17	0.82	78.32	71.67	78.17	0.92
Emballonuridae	*Balantiopteryx infusca*	*4*	6	9.05	6.70	56.00	*0.02*	*57.73*	*51.16*	56.00	*0.35*
Emballonuridae	*Balantiopteryx io*	*4*	4.00	3.97	7.80	49.00	*0.72*	*50.18*	*46.02*	49.00	*0.41*
Emballonuridae	*Balantiopteryx plicata*	4	6.66	6.57	4.93	40.57	0.70	41.97	35.42	40.57	0.94
Emballonuridae	*Centronycteris centralis*	6	6.76	*14.20*	5.97	43.68	0.29	43.68	36.92	42.71	0.28
Emballonuridae	*Centronycteris maximiliani*	6	6.10	23	5.29	41.42	0.25	41.42	35.37	40.80	0.26
Emballonuridae	*Coleura afra*	*4*	2.40	10.68	7.70	32.90	*0.78*	*31.98*	*30.30*	32.90	*0.55*
Emballonuridae	*Coleura seychellensis*	*4*	*3.84*	*10.64*	*6.09*	*34.85*	*0.31*	*35.58*	*31.63*	*34.47*	*0.01*
Emballonuridae	*Cormura brevirostris*	6	2.96	9.26	10.80	29.38	0.21	30.09	27.33	29.38	0.15
Emballonuridae	*Cyttarops alecto*	*6*	*3.45*	5.30	9.80	36.00	*0.91*	*37.45*	*33.38*	36.00	*0.69*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Emballonuridae	*Diclidurus albus*	*4*	*1.44*	16.56	9.60	24.00	*0.89*	*21.21*	*22.09*	24.00	*0.79*
Emballonuridae	*Diclidurus ingens*	*4*	*1.56*	*12.30*	*9.78*	*24.51*	*0.88*	*22.01*	*22.60*	*24.73*	*0.77*
Emballonuridae	*Diclidurus isabellus*	*4*	*2.02*	*12.61*	*9.40*	*26.52*	*0.83*	*24.95*	*24.43*	*26.71*	*0.68*
Emballonuridae	*Diclidurus scutatus*	*4*	*1.82*	*13.62*	*9.59*	*25.61*	*0.85*	*23.62*	*23.59*	*25.82*	*0.72*
Emballonuridae	*Emballonura alecto*	*6*	*5.72*	*5.25*	*4.85*	*50.10*	*0.37*	*52.10*	*45.60*	*48.52*	*0.79*
Emballonuridae	*Emballonura atrata*	*6*	*8.86*	*4.55*	*4.20*	*51.57*	*1.51*	*58.55*	*46.81*	*51.16*	*2.09*
Emballonuridae	*Emballonura beccarii*	*4*	*12.75*	*4.31*	*3.45*	*54.65*	*3.36*	*66.98*	*49.70*	*55.76*	*4.03*
Emballonuridae	*Emballonura dianae*	4	8.38	13.21	3.13	35.78	2.46	35.78	27.50	32.36	2.50
Emballonuridae	*Emballonura furax*	4	13.09	15.94	3.08	35.36	3.91	48.70	35.36	41.90	4.13
Emballonuridae	*Emballonura monticola*	6	4.15	5.35	5.68	51.01	0.24	51.01	46.75	50.76	0.25
Emballonuridae	*Emballonura raffrayana*	*4*	*6.11*	*5.61*	*4.91*	*43.16*	*0.47*	*46.91*	*39.06*	*42.56*	*0.92*
Emballonuridae	*Emballonura semicaudata*	*6*	*8.80*	*6.29*	*4.41*	*47.18*	*1.57*	*54.80*	*42.86*	*47.32*	*2.09*
Emballonuridae	*Emballonura serii*	*4*	*11.15*	*7.09*	*3.82*	*47.13*	*2.85*	*58.25*	*42.86*	*48.42*	*3.38*
Emballonuridae	*Mosia nigrescens*	*4*	*11.69*	*3.33*	*3.82*	*60.58*	*2.35*	*70.22*	*55.15*	*60.22*	*3.10*
Emballonuridae	*Peropteryx kappleri*	*4*	*2.53*	9.85	9.60	32.00	*0.76*	*31.48*	*29.61*	32.00	*0.58*
Emballonuridae	*Peropteryx leucoptera*	*4*	*3.37*	*12.80*	*8.00*	*32.20*	*0.42*	*32.74*	*29.46*	*32.23*	*0.22*
Emballonuridae	*Peropteryx macrotis*	4	3.90	5.68	5.63	37.35	0.30	38.34	34.31	37.35	0.48
Emballonuridae	*Peropteryx trinitatis*	*4*	*4.71*	*4.19*	*6.46*	*42.18*	*0.04*	*44.60*	*38.82*	*41.55*	*0.30*
Emballonuridae	*Rhynchonycteris naso*	13	17.60	4.14	4.25	98.88	0.35	98.88	81.25	89.69	1.11
Emballonuridae	*Saccolaimus flaviventris*	*3*	6	45.25	19	19	*0.87*	25	19	19	*0.65*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Emballonuridae	*Saccolaimus mixtus*	*3*	*4.91*	*38.29*	*13.09*	*21.41*	*0.74*	*24.43*	*20.17*	*22.33*	*0.52*
Emballonuridae	*Saccolaimus peli*	*3*	*3.57*	*53.35*	*12.38*	*20.01*	*0.70*	*20.64*	*18.82*	*20.76*	*0.55*
Emballonuridae	*Saccolaimus saccolaimus*	*3*	*3.59*	43.00	12.2	23	*0.77*	24	22.00	23	*0.59*
Emballonuridae	*Saccopteryx antioquensis*	*5*	*6.96*	*6.27*	*5.89*	*56.83*	*0.29*	*59.69*	*51.32*	*54.98*	*0.68*
Emballonuridae	*Saccopteryx bilineata*	5	3.71	8.08	8.27	46.35	0.17	46.35	42.62	45.76	0.10
Emballonuridae	*Saccopteryx canescens*	*5*	*8.66*	*3.41*	*5.16*	*68.72*	*0.69*	*71.20*	*62.05*	*65.96*	*1.22*
Emballonuridae	*Saccopteryx gymnura*	*5*	*7.06*	*6.11*	*5.84*	*57.51*	*0.32*	*60.39*	*51.94*	*55.65*	*0.71*
Emballonuridae	*Saccopteryx leptura*	5	3.56	*7.20*	6.93	50.12	0.26	50.12	46.55	49.54	0.17
Emballonuridae	*Taphozous achates*	3	0.49	*28.93*	8.98	23.21	0.20	23.37	22.93	23.21	0.05
Emballonuridae	*Taphozous australis*	*3*	*1.72*	*33.15*	*11.62*	*21.05*	*0.92*	*20.45*	*20.07*	*21.59*	*0.86*
Emballonuridae	*Taphozous georgianus*	*3*	*1.28*	30.52	*12.97*	17	*0.97*	18	16	17	*0.95*
Emballonuridae	*Taphozous hamiltoni*	*4*	*2.92*	*39.15*	*8.89*	*22.42*	*0.08*	*22.96*	*21.18*	*23.01*	*0.08*
Emballonuridae	*Taphozous hildegardeae*	*3*	*2.90*	*29.37*	*9.07*	*25.15*	*0.10*	*26.00*	*23.86*	*25.36*	*0.06*
Emballonuridae	*Taphozous hilli*	*3*	1.00	21.99	10	27.50	*0.87*	28	27	27.50	*0.80*
Emballonuridae	*Taphozous kapalgensis*	*3*	1.5	26.45	5.00	24.00	*1.17*	25	23.5	24.00	*0.78*
Emballonuridae	*Taphozous longimanus*	*3*	*5.07*	*25.11*	*7.74*	*27.33*	*0.40*	*32.07*	*25.76*	*28.19*	*0.49*
Emballonuridae	*Taphozous mauritianus*	3	2.09	27.97	13.27	25.29	0.15	26.23	24.08	25.29	0.21
Emballonuridae	*Taphozous melanopogon*	4	8.05	25.99	4.06	29.11	0.84	32.08	24.19	29.11	1.21
Emballonuridae	*Taphozous nudiventris*	*3*	*2.15*	*32.49*	*7.77*	*23.41*	*0.30*	*22.99*	*22.38*	*23.67*	*0.16*
Emballonuridae	*Taphozous perforatus*	3	7.09	24.43	7.10	27.78	0.72	34.96	27.78	31.38	0.93

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Emballonuridae	*Taphozous theobaldi*	*4*	*3.15*	*36.83*	*8.81*	*22.99*	*0.06*	*24.02*	*21.69*	*23.62*	*0.05*
Emballonuridae	*Taphozous troughtoni*	*3*	2.00	53.52	13.00	22.00	*0.89*	23	21.00	22.00	*0.84*
Furipteridae	*Amorphochilus schnablii*	*7*	*44.19*	*7.20*	*2.85*	*111.39*	*10.19*	*138.53*	*93.41*	*117.68*	*12.55*
Furipteridae	*Furipterus horrens*	7	54.39	3.15	2.74	189.32	12.17	189.32	134.58	162.68	15.47
Hipposideridae	*Anthops ornatus*	**13**	*10.21*	*17.94*	*8.51*	*67.29*	*0.01*	*74.06*	*58.56*	*66.75*	*0.20*
Hipposideridae	*Asellia patrizii*	**13**	*18.81*	*8.72*	*6.48*	*111.16*	*0.65*	*114.06*	*94.92*	*109.84*	*1.29*
Hipposideridae	*Asellia tridens*	13	21.46	12.94	5.57	117.46	0.39	117.46	96.09	114.22	1.22
Hipposideridae	*Aselliscus stoliczkanus*	13	13.34	6.09	3.55	127.61	0.19	127.61	114.25	127.19	0.17
Hipposideridae	*Aselliscus tricuspidatus*	13	12.81	4.08	3.31	112.99	0.08	112.99	100.10	112.82	0.20
Hipposideridae	*Cloeotis percivali*	13	20.74	4.16	2.67	209.38	0.29	209.38	188.91	209.31	0.18
Hipposideridae	*Coelops frithii*	13	*17.40*	7.52	*5.51*	141.00	*0.59*	*137.12*	*122.98*	141.00	*0.23*
Hipposideridae	*Coelops robinsoni*	**13**	*18.22*	*6.50*	*5.33*	*145.04*	*0.51*	*141.13*	*127.61*	*147.23*	*0.11*
Hipposideridae	*Hipposideros abae*	**13**	*13.98*	*31.87*	*9.26*	*82.93*	*0.52*	*95.32*	*70.74*	*84.86*	*0.35*
Hipposideridae	*Hipposideros armiger*	13	8.24	49.99	8.87	67.16	0.06	67.16	58.89	67.07	0.08
Hipposideridae	*Hipposideros ater*	13	11.88	5.86	4.72	165.51	0.15	165.51	153.14	165.40	0.11
Hipposideridae	*Hipposideros beatus*	**13**	*20.65*	*6.70*	*6.46*	*139.07*	*0.31*	*136.89*	*118.99*	*139.21*	*0.78*
Hipposideridae	*Hipposideros bicolor*	13	20.06	8.39	5.51	143.48	0.07	143.48	123.31	142.18	0.04
Hipposideridae	*Hipposideros breviceps*	**13**	*10.85*	*13.21*	*7.82*	*96.45*	*0.35*	*94.09*	*85.29*	*93.41*	*0.09*
Hipposideridae	*Hipposideros caffer*	13	18.94	9.46	7.38	139.51	0.09	139.51	120.60	139.32	0.07
Hipposideridae	*Hipposideros calcaratus*	13	25.26	18.99	4.72	120.35	0.07	120.35	95.00	112.71	0.19

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Hipposideridae	*Hipposideros camerunensis*	**13**	*5.30*	*58.98*	*14.75*	*57.51*	*0.66*	*60.11*	*50.91*	*56.77*	*0.76*
Hipposideridae	*Hipposideros cervinus*	13	19.86	8.51	4.48	131.27	0.51	131.27	111.46	130.37	0.45
Hipposideridae	*Hipposideros cineraceus*	13	18.83	3.84	4.85	153.82	0.17	153.82	134.92	153.59	0.06
Hipposideridae	*Hipposideros commersoni*	13	11.57	89.99	9.94	66.94	0.06	66.94	55.32	66.43	0.05
Hipposideridae	*Hipposideros coronatus*	**13**	*10.46*	*15.00*	*8.03*	*92.85*	*0.40*	*91.36*	*82.11*	*90.11*	*0.16*
Hipposideridae	*Hipposideros corynophyllus*	**13**	*13.06*	*15.07*	*7.46*	*102.72*	*0.19*	*101.81*	*90.11*	*100.79*	*0.12*
Hipposideridae	*Hipposideros coxi*	**13**	*9.35*	*21.82*	*8.68*	*83.10*	*0.54*	*83.56*	*73.41*	*80.96*	*0.36*
Hipposideridae	*Hipposideros crumeniferus*	**13**	*9.35*	*21.82*	*8.68*	*83.10*	*0.54*	*83.56*	*73.41*	*80.96*	*0.36*
Hipposideridae	*Hipposideros curtus*	**13**	*11.49*	*13.21*	*7.64*	*77.17*	*0.26*	*82.96*	*67.29*	*75.94*	*0.56*
Hipposideridae	*Hipposideros cyclops*	**13**	*5.43*	*32.92*	*15.86*	*78.26*	*0.94*	*75.53*	*70.18*	*75.19*	*0.95*
Hipposideridae	*Hipposideros demissus*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros diadema*	13	8.89	46.90	11.12	60.19	0.09	60.19	51.27	59.98	0.04
Hipposideridae	*Hipposideros dinops*	**13**	*6.46*	*116.08*	*11.55*	*48.57*	*0.39*	*51.45*	*41.68*	*48.28*	*0.44*
Hipposideridae	*Hipposideros doriae*	**13**	*18.46*	*4.24*	*5.91*	*152.32*	*0.31*	*142.80*	*132.95*	*151.56*	*0.63*
Hipposideridae	*Hipposideros durgadasi*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros dyacorum*	**13**	*18.87*	*10.09*	*7.06*	*122.36*	*0.06*	*125.89*	*104.58*	*123.10*	*0.45*
Hipposideridae	*Hipposideros edwardshilli*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros fuliginosus*	**13**	*15.62*	*31.11*	*7.88*	*104.79*	*0.26*	*107.74*	*90.74*	*104.90*	*0.09*
Hipposideridae	*Hipposideros fulvus*	13	17.45	8.83	5.98	139.33	0.29	139.33	121.83	138.99	0.59
Hipposideridae	*Hipposideros galeritus*	**13**	*18.86*	*10.17*	*7.07*	*122.12*	*0.06*	*125.66*	*104.38*	*122.85*	*0.44*

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Hipposideridae	*Hipposideros gigas*	13	7.24	115.42	20.90	59.45	0.02	59.45	52.22	59.28	0.00
Hipposideridae	*Hipposideros grandis*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros halophyllus*	13	15.16	4	6.60	187.11	0.13	187.11	171.97	186.92	1.22
Hipposideridae	*Hipposideros hypophyllus*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros inexpectatus*	**13**	*6.32*	*136.34*	*11.75*	*47.56*	*0.38*	*50.24*	*40.81*	*47.32*	*0.44*
Hipposideridae	*Hipposideros inornatus*	13	5.00	25.90	12	69.20	*1.00*	64	69.00	69.20	*0.98*
Hipposideridae	*Hipposideros jonesi*	**13**	*13.47*	*5.49*	*6.75*	*92.30*	*0.63*	*95.55*	*80.48*	*90.11*	*1.04*
Hipposideridae	*Hipposideros lamottei*	**13**	*8.97*	*24.90*	*8.92*	*79.92*	*0.58*	*80.89*	*70.60*	*78.02*	*0.42*
Hipposideridae	*Hipposideros lankadiva*	**13**	*10.60*	*44.76*	*9.17*	*70.53*	*0.16*	*74.32*	*60.16*	*69.34*	*0.24*
Hipposideridae	*Hipposideros larvatus*	13	11.40	19.95	5.87	93.79	0.11	93.79	82.43	93.57	0.10
Hipposideridae	*Hipposideros lekaguli*	13	4.91	31.08	9.60	50.78	0.07	50.78	45.84	50.71	0.05
Hipposideridae	*Hipposideros lylei*	13	8.85	40	9.65	67.34	0.02	67.34	58.52	67.27	0.03
Hipposideridae	*Hipposideros macrobullatus*	**13**	*14.91*	*10.82*	*7.16*	*115.82*	*0.16*	*119.03*	*100.89*	*116.51*	*0.01*
Hipposideridae	*Hipposideros madurae*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros maggietaylorae*	13	38.09	16.1	5.37	122.00	0.16	122.00	84.03	114.26	0.04
Hipposideridae	*Hipposideros marisae*	**13**	*15.21*	*10.09*	*7.04*	*118.39*	*0.14*	*121*	*103.13*	*118.99*	*0.04*
Hipposideridae	*Hipposideros megalotis*	**13**	*17.75*	*7.20*	*6.40*	*139.49*	*0.13*	*137.12*	*121.51*	*140.75*	*0.16*
Hipposideridae	*Hipposideros muscinus*	**13**	*13.72*	*14.09*	*9.28*	*100.79*	*0.15*	*106.92*	*87.53*	*100.89*	*0.05*
Hipposideridae	*Hipposideros nequam*	**13**	*10.66*	*14.09*	*7.92*	*94.63*	*0.38*	*92.70*	*83.68*	*91.74*	*0.13*
Hipposideridae	*Hipposideros obscurus*	**13**	*14.49*	*9.60*	*6.69*	*114.32*	*0.09*	*110.46*	*100.18*	*111.94*	*0.46*

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Hipposideridae	*Hipposideros orbiculus*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros papua*	**13**	*12.43*	*18.99*	*7.24*	*97.61*	*0.10*	*98.05*	*85.63*	*96.06*	*0.16*
Hipposideridae	*Hipposideros pelingensis*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros pomona*	13	18.57	6.2	5.27	135.89	0.12	135.89	117.29	134.30	0.03
Hipposideridae	*Hipposideros pratti*	13	7.35	84.38	8.01	60.83	0.06	60.83	53.45	60.77	0.04
Hipposideridae	*Hipposideros pygmaeus*	**13**	*20.45*	*3.53*	*4.79*	*169.86*	*0.23*	*154.75*	*149.46*	*170.55*	*0.32*
Hipposideridae	*Hipposideros ridleyi*	13	8.26	9.59	7.06	62.51	0.09	62.51	54.27	62.36	0.08
Hipposideridae	*Hipposideros rotalis*	**13**	*16.56*	*7.26*	*6.57*	*130.58*	*0.00*	*129.73*	*113.86*	*130.97*	*0.24*
Hipposideridae	*Hipposideros ruber*	13	20.86	10.61	7.22	133.43	0.11	133.43	112.58	131.51	0.31
Hipposideridae	*Hipposideros scutinares*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros semoni*	12	7.13	14.00	51.43	67.50	0.00	67.50	60.39	67.46	0.00
Hipposideridae	*Hipposideros sorenseni*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros speoris*	13	21.77	10.39	6.29	139.16	0.31	139.16	117.47	135.74	0.32
Hipposideridae	*Hipposideros stenotis*	12	5.00	12	20.00	103	*1.00*	104.00	99.00	103	*0.99*
Hipposideridae	*Hipposideros sumbae*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros thomensis*	**13**	*9.39*	*21.52*	*8.65*	*83.43*	*0.54*	*83.83*	*73.70*	*81.29*	*0.35*
Hipposideridae	*Hipposideros turpis*	13	7.80	33.31	6.89	72.18	0.04	72.18	64.33	72.07	0.02
Hipposideridae	*Hipposideros vittatus*	13	*6.14*	*27.14*	12	61.00	*0.98*	*64.53*	*55.09*	61.00	*0.92*
Hipposideridae	*Hipposideros wollastoni*	13	3.88	6.93	18.39	92.08	0.01	92.08	88.12	92.03	0.03
Hipposideridae	*Paracoelops megalotis*	**13**	*14.84*	*11.20*	*6.46*	*111.05*	*0.72*	*117.07*	*97.61*	*113.18*	*0.44*

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Hipposideridae	*Rhinonicteris aurantia*	13	15	8.99	12	114	*0.94*	115.00	100	114	*0.98*
Hipposideridae	*Triaenops auritus*	**13**	*8.42*	*11.52*	*8.14*	*54.05*	*0.30*	*61.06*	*47.47*	*53.84*	*0.48*
Hipposideridae	*Triaenops furculus*	13	9.54	5.56	8.05	99.28	0.04	99.28	89.74	98.98	0.06
Hipposideridae	*Triaenops persicus*	13	*10.83*	13.18	8.50	83.00	*0.01*	*86.23*	*73.33*	83.00	*0.25*
Hipposideridae	*Triaenops rufus*	13	7.48	9.10	8.43	43.27	0.03	43.27	35.82	39.82	0.85
Megadermatidae	*Cardioderma cor*	*9*	*16.83*	*26.45*	*3.09*	*47.51*	*6.67*	*61.98*	*40.08*	*48.28*	*6.71*
Megadermatidae	*Lavia frons*	*9*	24	23.80	3.50	37.5	*8.48*	*57.20*	*29.93*	37.5	*8.78*
Megadermatidae	*Macroderma gigas*	9	18.61	124.37	1.13	43.48	11.99	62.10	43.48	51.07	13.45
Megadermatidae	*Megaderma lyra*	9	23.29	39.27	1.39	80.50	8.40	80.50	57.32	68.25	10.94
Megadermatidae	*Megaderma spasma*	10	8.88	24.71	1.69	24.74	5.90	24.74	15.76	20.10	5.68
Miniopteridae	*Miniopterus africanus*	**8**	*38.44*	*10.31*	*3.30*	*48.67*	*7.70*	*83.54*	*47.09*	*51.73*	*12.00*
Miniopteridae	*Miniopterus australis*	8	48.01	7.40	3.60	53.38	12.77	101.58	53.38	59.07	17.28
Miniopteridae	*Miniopterus fraterculus*	8	45.80	7.38	3.16	58.29	9.97	104.19	58.29	61.92	16.92
Miniopteridae	*Miniopterus fuscus*	**8**	*39.09*	*10.82*	*3.22*	*48.09*	*8.16*	*83.41*	*46.48*	*51.21*	*12.51*
Miniopteridae	*Miniopterus gleni*	8	25.94	*11.78*	2.42	37.71	6.22	64.25	37.71	41.43	11.28
Miniopteridae	*Miniopterus inflatus*	8	55.00	14.9	2.5	47.40	*13.26*	*89.23*	*43.21*	47.40	*18.11*
Miniopteridae	*Miniopterus macrocneme*	**8**	*38.16*	*7.53*	*2.99*	*47.09*	*8.67*	*81.27*	*45.70*	*49.90*	*13.06*
Miniopteridae	*Miniopterus magnater*	**8**	*36.87*	*14.14*	*3.70*	*46.62*	*7.19*	*80.35*	*45.02*	*49.85*	*11.13*
Miniopteridae	*Miniopterus majori*	**8**	*36.88*	*13.31*	*3.13*	*43.99*	*8.31*	*76.74*	*42.69*	*46.76*	*12.54*
Miniopteridae	*Miniopterus manavi*	8	44.49	7.81	2.96	54.97	7.27	96.22	51.36	54.97	15.87

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Miniopteridae	*Miniopterus medius*	**8**	*37.43*	*11.40*	*3.58*	*48.86*	*7.30*	*83.25*	*47.18*	*52.04*	*11.32*
Miniopteridae	*Miniopterus minor*	**8**	*42.23*	*10.01*	*2.92*	*49.11*	*9.79*	*87.12*	*47.37*	*52.67*	*14.39*
Miniopteridae	*Miniopterus natalensis*	8	36.29	10.43	3.48	46.32	6.13	82.75	46.32	52.07	11.77
Miniopteridae	*Miniopterus paululus*	**8**	*35.05*	*7.20*	*3.44*	*52.67*	*7.20*	*86.12*	*50.40*	*56.04*	*10.76*
Miniopteridae	*Miniopterus pusillus*	8	34.56	8.95	3.38	56.16	3.54	91.14	56.16	59.79	11.03
Miniopteridae	*Miniopterus robustior*	**8**	*33.13*	*10.46*	*3.71*	*47.32*	*6.68*	*78.85*	*45.24*	*50.60*	*10.03*
Miniopteridae	*Miniopterus schreibersii*	8	27.11	11.46	5.47	50.44	1.90	77.50	50.44	53.41	6.00
Miniopteridae	*Miniopterus shortridgei*	**8**	*33.82*	*9.14*	*3.61*	*49.16*	*6.87*	*81.43*	*47.04*	*52.51*	*10.29*
Miniopteridae	*Miniopterus tristis*	**8**	*35.14*	*15.17*	*3.84*	*44.35*	*6.65*	*76.35*	*42.78*	*47.37*	*10.43*
Molossidae	*Chaerephon aloysiisabaudiae*	*10*	*12.85*	*19.54*	*7.58*	*19.39*	*1.96*	*30.01*	*16.88*	*21.07*	*2.51*
Molossidae	*Chaerephon ansorgei*	*3*	12	14.53	15	17.80	*0.29*	*24.68*	*14.64*	17.80	*0.33*
Molossidae	*Chaerephon bemmeleni*	*10*	*13.55*	*12.39*	*7.27*	*20.61*	*2.14*	*32.57*	*17.94*	*22.35*	*2.74*
Molossidae	*Chaerephon bivittatus*	*10*	14	15.42	6.80	21.00	*2.29*	*31.56*	*17.43*	21.00	*2.86*
Molossidae	*Chaerephon bregullae*	*10*	*13.38*	*13.87*	*7.34*	*20.31*	*2.10*	*31.92*	*17.67*	*22.02*	*2.68*
Molossidae	*Chaerephon chapini*	*10*	8	7.49	10	20.00	*0.84*	*27.04*	*17.18*	20.00	*1.37*
Molossidae	*Chaerephon gallagheri*	*10*	*14.22*	*8.10*	*6.99*	*21.82*	*2.32*	*35.05*	*18.99*	*23.59*	*2.97*
Molossidae	*Chaerephon jobensis*	*10*	8	20.71	10	19.80	*0.57*	28	20.00	19.80	*1.08*
Molossidae	*Chaerephon johorensis*	10	9.94	15.69	5.76	14.93	1.68	24.79	14.93	19.59	1.88
Molossidae	*Chaerephon leucogaster*	10	25.41	*12.27*	5.59	31.46	4.24	43.52	18.11	31.46	4.53
Molossidae	*Chaerephon major*	*10*	*13.24*	*15.17*	*7.40*	*20.07*	*2.06*	*31.42*	*17.46*	*21.78*	*2.64*

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		Echolocation Call Type	Bandwidth (kHz)	Body Mass (g)	Call Duration (ms)	Characteristic Frequency (kHz)	Dominant Slope (kHz/ms)	Maximum Frequency (kHz)	Minimum Frequency (kHz)	Peak Frequency (kHz)	Total Slope (kHz/ms)
Molossidae	*Chaerephon nigeriae*	*10*	10.00	20.14	10	17	*2.88*	*29.86*	*16.84*	17	*3.31*
Molossidae	*Chaerephon plicatus*	*10*	*12.69*	*21.83*	*7.66*	*19.11*	*1.92*	*29.40*	*16.63*	*20.78*	*2.45*
Molossidae	*Chaerephon pumilus*	10	20.18	10.98	4.19	20.91	4.90	41.14	20.91	27.13	4.87
Molossidae	*Chaerephon russatus*	*10*	*13.07*	*16.98*	*7.49*	*19.77*	*2.02*	*30.78*	*17.20*	*21.46*	*2.58*
Molossidae	*Chaerephon shortridgei*	*10*	*13.38*	*13.87*	*7.34*	*20.31*	*2.10*	*31.92*	*17.67*	*22.02*	*2.68*
Molossidae	*Chaerephon solomonis*	*10*	*13.38*	*13.87*	*7.34*	*20.31*	*2.10*	*31.92*	*17.67*	*22.02*	*2.68*
Molossidae	*Chaerephon tomensis*	*10*	*14.34*	*7.48*	*6.93*	*22.07*	*2.35*	*35.52*	*19.20*	*23.83*	*3.01*
Molossidae	*Cheiromeles parvidens*	*3*	*9.39*	*70.39*	*10.65*	*26.36*	*0.54*	*35.00*	*24.51*	*27.58*	*0.86*
Molossidae	*Cheiromeles torquatus*	3	9.00	169.43	14.14	26.10	0.56	34.85	26.10	27.90	0.72
Molossidae	*Cynomops abrasus*	*3*	*7.05*	*35.39*	*10.67*	*18.84*	*0.45*	*23.03*	*16.68*	*20.31*	*0.11*
Molossidae	*Cynomops greenhalli*	*3*	*8.94*	*15.87*	*9.23*	*23.20*	*0.15*	*31.11*	*20.55*	*24.78*	*0.34*
Molossidae	*Cynomops mexicanus*	*3*	*9.31*	*15.96*	*8.99*	*24.09*	*0.09*	*32.73*	*21.35*	*25.71*	*0.43*
Molossidae	*Cynomops paranus*	*3*	*10.23*	*12.16*	*8.42*	*26.42*	*0.07*	*36.81*	*23.43*	*28.08*	*0.66*
Molossidae	*Cynomops planirostris*	*3*	*10.08*	*12.84*	*8.51*	*26.05*	*0.05*	*36.17*	*23.10*	*27.69*	*0.63*
Molossidae	*Eumops auripendulus*	*3*	*6.31*	*28.49*	*12.97*	*18.12*	*0.89*	*21.90*	*15.91*	*19.53*	*0.68*
Molossidae	*Eumops bonariensis*	*3*	*8.40*	*12.22*	*10.72*	*22.85*	*0.64*	*30.74*	*20.13*	*24.41*	*0.26*
Molossidae	*Eumops dabbenei*	*3*	*4.86*	*67.27*	*14.43*	*14.91*	*0.95*	*15.55*	*13.11*	*16.22*	*0.82*
Molossidae	*Eumops glaucinus*	*3*	5.00	36.20	14.20	18	*0.95*	23	15	18	*0.78*
Molossidae	*Eumops hansae*	*3*	*8.39*	*15.47*	*10.50*	*22.69*	*0.57*	*30.34*	*19.99*	*24.22*	*0.18*
Molossidae	*Eumops maurus*	*3*	*7.22*	*20.66*	*11.75*	*20.05*	*0.77*	*25.51*	*17.64*	*21.52*	*0.47*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	Bandwidth (kHz)	Body Mass (g)	Call Duration (ms)	Characteristic Frequency (kHz)	Dominant Slope (kHz/ms)	Maximum Frequency (kHz)	Minimum Frequency (kHz)	Peak Frequency (kHz)	Total Slope (kHz/ms)
Molossidae	*Eumops patagonicus*	3	6.44	29.81	12.52	18.28	0.84	22.16	16.09	19.71	0.60
Molossidae	*Eumops perotis*	3	5.41	50.97	13.41	15.94	0.88	17.53	14.03	17.29	0.70
Molossidae	*Eumops trumbulli*	3	6.44	29.81	12.52	18.28	0.84	22.16	16.09	19.71	0.60
Molossidae	*Eumops underwoodi*	3	5.11	58.67	14.08	15.43	0.93	16.57	13.56	16.76	0.79
Molossidae	*Molossops aequatorianus*	3	10.47	7.49	7.42	40.53	0.15	50.89	35.48	40.61	0.56
Molossidae	*Molossops mattogrossensis*	3	10.47	7.48	7.41	40.53	0.15	50.91	35.52	40.61	0.56
Molossidae	*Molossops neglectus*	3	10.08	6.91	7.46	43.82	0.32	53.00	38.24	43.25	0.36
Molossidae	*Molossops temminckii*	3	10.3	5.86	7.80	50.4	0.48	50.4	40.4	50.4	0.18
Molossidae	*Molossus aztecus*	13	9.23	14.86	6.66	33.62	1.16	41.28	29.11	34.33	1.52
Molossidae	*Molossus barnesi*	13	8.43	22.83	7.06	30.88	0.95	37.30	26.74	31.66	1.25
Molossidae	*Molossus coibensis*	13	8.43	22.83	7.06	30.88	0.95	37.30	26.74	31.66	1.25
Molossidae	*Molossus currentium*	13	8.89	17.79	6.83	32.43	1.07	39.59	28.08	33.18	1.40
Molossidae	*Molossus molossus*	4	4.62	13.7	9.29	33.41	0.47	38.09	33.41	37.66	0.50
Molossidae	*Molossus pretiosus*	4	5.95	98.00	8.63	23.17	0.32	25.31	20.05	24.07	0.46
Molossidae	*Molossus rufus*	13	12.94	21.07	5.59	41.91	1.60	41.91	26.69	38.41	2.84
Molossidae	*Molossus sinaloae*	13	8.77	21.09	6.92	31.66	1.04	38.60	27.41	32.46	1.36
Molossidae	*Mops brachypterus*	10	12.99	16.00	7.63	24.58	1.45	39.45	23.10	27.39	2.09
Molossidae	*Mops condylurus*	10	22.09	26.59	5.57	20.47	3.63	42.71	20.47	27.12	4.13
Molossidae	*Mops congicus*	10	9.71	42.84	9.46	18.07	0.69	26.28	16.96	20.39	1.09
Molossidae	*Mops demonstrator*	10	14.80	9.74	6.85	28.73	1.89	47.11	27.00	31.79	2.67

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Molossidae	*Mops leucostigma*	*10*	*17.60*	*26.79*	*7.20*	*21.48*	*2.79*	*39.82*	*19.95*	*25.36*	*3.45*
Molossidae	*Mops midas*	*3*	4.80	45.5	16.5	15	*0.93*	*14.91*	*13.44*	15	*0.74*
Molossidae	*Mops mops*	3	0.73	31.12	8.57	17.80	0.02	18.15	17.42	17.80	0.10
Molossidae	*Mops nanulus*	*10*	*18.46*	*3.88*	*5.60*	*38.32*	*2.79*	*63.09*	*36.09*	*41.85*	*3.87*
Molossidae	*Mops niangarae*	*10*	*12.88*	*16.49*	*7.68*	*24.36*	*1.43*	*39.00*	*22.90*	*27.14*	*2.06*
Molossidae	*Mops niveiventer*	11	20.78	21.82	8.82	17.06	1.75	38.15	17.06	22.11	2.31
Molossidae	*Mops petersoni*	*10*	*16.77*	*5.86*	*6.13*	*33.68*	*2.37*	*55.64*	*31.69*	*37.00*	*3.31*
Molossidae	*Mops sarasinorum*	*10*	*14.28*	*11.20*	*7.06*	*27.49*	*1.76*	*44.89*	*25.84*	*30.48*	*2.50*
Molossidae	*Mops spurrelli*	*10*	*15.51*	*8.08*	*6.57*	*30.45*	*2.06*	*50.17*	*28.65*	*33.62*	*2.90*
Molossidae	*Mops thersites*	*10*	*11.88*	*21.99*	*8.17*	*22.26*	*1.19*	*34.90*	*20.91*	*24.90*	*1.75*
Molossidae	*Mops trevori*	*10*	*8.83*	*21.23*	*8.98*	*22.90*	*0.02*	*30.26*	*20.29*	*24.43*	*0.50*
Molossidae	*Mormopterus acetabulosus*	*10*	*10.44*	*9.05*	*7.04*	*31.34*	*0.53*	*41.98*	*27.85*	*32.20*	*1.24*
Molossidae	*Mormopterus beccarii*	*3*	*5.29*	14.3	13.00	23.5	*0.97*	*26.27*	*20.80*	23.5	*0.72*
Molossidae	*Mormopterus doriae*	*10*	*10.70*	*8.41*	*6.91*	*32.14*	*0.58*	*43.20*	*28.56*	*32.98*	*1.32*
Molossidae	*Mormopterus jugularis*	10	28.42	11.56	3.98	32.04	8.97	51.45	23.19	32.04	7.62
Molossidae	*Mormopterus kalinowskii*	*10*	*11.19*	*7.49*	*6.73*	*33.45*	*0.67*	*45.33*	*29.76*	*34.33*	*1.45*
Molossidae	*Mormopterus loriae*	*10*	12	7	6.00	36.00	*1.18*	47.00	35.00	36.00	*2.07*
Molossidae	*Mormopterus minutus*	*10*	*13.23*	*4.27*	*5.88*	*40.53*	*1.12*	*55.41*	*36.09*	*41.22*	*2.09*
Molossidae	*Mormopterus norfolkensis*	*3*	1.5	8.00	8.00	31.00	*0.99*	31.5	30.00	31.00	*0.83*
Molossidae	*Mormopterus phrudus*	*10*	*11.86*	*6.11*	*6.40*	*35.84*	*0.83*	*48.78*	*31.88*	*36.63*	*1.67*

Family	Species	Species sets for each parameter									
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Molossidae	*Mormopterus planiceps*	*10*	*10.36*	*9.24*	*7.07*	*31.09*	*0.51*	*41.63*	*27.66*	*31.98*	*1.22*
Molossidae	*Myopterus daubentonii*	*3*	*9.67*	*18.45*	*8.46*	*24.98*	*0.18*	*33.94*	*22.13*	*26.55*	*0.72*
Molossidae	*Myopterus whitleyi*	*3*	*10.75*	*11.55*	*7.85*	*27.77*	*0.39*	*38.76*	*24.63*	*29.40*	*1.01*
Molossidae	*Nyctinomops aurispinosus*	*3*	*8.04*	*18.43*	*10.59*	*21.22*	*0.59*	*28.06*	*18.82*	*22.83*	*0.19*
Molossidae	*Nyctinomops femorosaccus*	*3*	*8.13*	*15.04*	*10.85*	*21.50*	*0.69*	*28.80*	*19.09*	*23.13*	*0.29*
Molossidae	*Nyctinomops laticaudatus*	*3*	*8.85*	*13.12*	*9.97*	*23.15*	*0.49*	*31.62*	*20.55*	*24.80*	*0.02*
Molossidae	*Nyctinomops macrotis*	*3*	5.00	16.38	15.70	17.5	*1.00*	24.5	15	17.5	*0.92*
Molossidae	*Otomops formosus*	*3*	*7.74*	*30.39*	*9.20*	*13.24*	*0.78*	*14.71*	*11.12*	*14.22*	*1.04*
Molossidae	*Otomops johnstonei*	*3*	*7.99*	*26.87*	*9.03*	*13.61*	*0.85*	*15.52*	*11.44*	*14.61*	*1.13*
Molossidae	*Otomops madagascariensis*	10	6.93	*27.66*	2.99	17.59	2.45	17.59	10.90	15.08	2.35
Molossidae	*Otomops martiensseni*	*3*	6.40	34.92	24.00	10.8	*0.24*	*8.76*	*8.78*	10.8	*0.01*
Molossidae	*Otomops papuensis*	*3*	*8.78*	*18.45*	*8.50*	*14.82*	*1.05*	*18.12*	*12.47*	*15.85*	*1.39*
Molossidae	*Otomops secundus*	*3*	*7.94*	*27.55*	*9.06*	*13.53*	*0.83*	*15.35*	*11.38*	*14.54*	*1.11*
Molossidae	*Otomops wroughtoni*	*3*	*7.14*	*39.15*	*9.67*	*12.37*	*0.62*	*12.82*	*10.40*	*13.34*	*0.84*
Molossidae	*Platymops setiger*	*3*	*14.37*	*5.37*	*6.26*	*38.47*	*1.13*	*55.44*	*34.16*	*40.13*	*2.06*
Molossidae	*Promops centralis*	*3*	*10.83*	*29.80*	*7.49*	*23.03*	*1.27*	*32.11*	*20.13*	*25.18*	*1.67*
Molossidae	*Promops nasutus*	*3*	*12.48*	*15.50*	*6.73*	*26.84*	*1.69*	*38.96*	*23.48*	*29.17*	*2.21*
Molossidae	*Sauromys petrophilus*	10	25.87	14.25	3.74	20.02	6.04	45.72	20.02	27.99	7.25
Molossidae	*Tadarida aegyptiaca*	8	17.44	17.63	4.93	18.79	3.63	36.23	18.79	23.57	4.18
Molossidae	*Tadarida australis*	3	7.36	36.40	15.52	11.00	0.38	18.21	11.00	12.77	0.54

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Molossidae	*Tadarida brasiliensis*	3	3.16	12.61	11.25	25.13	0.32	28.36	25.13	26.72	0.29
Molossidae	*Tadarida fulminans*	*3*	13	33.89	15	17	*0.11*	*24.26*	*14.17*	17	*0.64*
Molossidae	*Tadarida insignis*	5	14.22	*28.53*	3.19	10.17	3.52	24.15	10.17	16.32	4.54
Molossidae	*Tadarida kuboriensis*	*3*	*8.39*	*26.80*	*9.15*	*16.31*	*0.68*	*22.79*	*15.23*	*18.54*	*0.95*
Molossidae	*Tadarida latouchei*	*3*	*8.30*	*27.66*	*9.22*	*16.14*	*0.66*	*22.43*	*15.06*	*18.36*	*0.92*
Molossidae	*Tadarida lobata*	*3*	*8.02*	*30.39*	*9.41*	*15.66*	*0.59*	*21.37*	*14.61*	*17.85*	*0.84*
Molossidae	*Tadarida teniotis*										
Molossidae	*Tadarida ventralis*	*3*	4.00	37.43	9.00	19.3	*0.19*	*20.60*	*17.34*	19.3	*0.02*
Molossidae	*Tomopeas ravus*	*3*	*17.34*	*5.61*	*5.44*	*39.06*	*2.63*	*59.89*	*35.27*	*41.43*	*3.70*
Mormoopidae	*Mormoops blainvillei*	*11*	16	8.69	3.16	57.50	*5.71*	67	52.00	57.50	*6.57*
Mormoopidae	*Mormoops magna*	*11*	*17.43*	*12.29*	*3.29*	*56.20*	*6.29*	*68.74*	*50.00*	*57.28*	*7.10*
Mormoopidae	*Mormoops megalophylla*	*11*	*15.76*	*16.09*	*3.48*	*51.83*	*5.68*	*62.96*	*46.20*	*52.77*	*6.41*
Mormoopidae	*Pteronotus davyi*	11	13.03	9.52	4.76	71.22	1.23	71.22	58.16	66.22	4.51
Mormoopidae	*Pteronotus gymnonotus*	11	*10.46*	13.6	6.65	49.00	*1.04*	*54.64*	*44.70*	49.00	*1.87*
Mormoopidae	*Pteronotus macleayii*	11	12	12.39	4.03	69.00	*2.80*	71	59.00	69.00	*3.52*
Mormoopidae	*Pteronotus parnellii*	12	7.74	19.59	25.81	61.11	0.01	61.11	53.45	60.95	0.01
Mormoopidae	*Pteronotus personatus*	11	17.49	7.99	4.75	60.72	1.40	78.02	60.72	65.45	4.18
Mormoopidae	*Pteronotus pristinus*	*11*	*14.67*	*10.00*	*4.77*	*67.83*	*2.80*	*74.11*	*59.98*	*67.15*	*3.72*
Mormoopidae	*Pteronotus quadridens*	11	15.5	5.64	3.98	81.50	*3.36*	83.5	69.00	81.50	*4.35*
Mystacinidae	*Mystacina robusta*	*9*	*17.79*	*27.41*	*2.65*	*38.71*	*9.68*	*54.38*	*35.20*	*42.06*	*9.76*

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Mystacinidae	*Mystacina tuberculata*	9	19.97	13.14	1.94	41.37	10.72	61.35	41.37	48.38	11.24
Myzopodidae	*Myzopoda aurita*	11	6.72	9.10	5.32	33.40	1.16	37.37	29.83	33.40	1.33
Natalidae	*Chilonatalus micropus*	*9*	*43.88*	*5.86*	*1.92*	*101.80*	*23.10*	*127.24*	*84.44*	*99.29*	*23.56*
Natalidae	*Chilonatalus tumidifrons*	*9*	*47.01*	*3.62*	*1.73*	*118.39*	*24.40*	*140.42*	*98.30*	*114.78*	*25.11*
Natalidae	*Natalus jamaicensis*	*9*	*48.52*	*5.50*	*1.62*	*117.68*	*27.82*	*139.71*	*96.16*	*112.96*	*27.85*
Natalidae	*Natalus major*	*9*	*48.52*	*5.50*	*1.62*	*117.68*	*27.82*	*139.71*	*96.16*	*112.96*	*27.85*
Natalidae	*Natalus primus*	*9*	*48.52*	*5.50*	*1.62*	*117.68*	*27.82*	*139.71*	*96.16*	*112.96*	*27.85*
Natalidae	*Natalus stramineus*	9	49.56	5.68	1.58	150.94	29.74	150.94	101.01	116.48	32.05
Natalidae	*Natalus tumidirostris*	*9*	*50.41*	*6.30*	*1.52*	*123.47*	*30.18*	*144*	*100.18*	*117.68*	*29.90*
Natalidae	*Nyctiellus lepidus*	*9*	42.70	3.88	2.7	83.40	*17.26*	113.60	70.90	83.40	*18.79*
Noctilionidae	*Noctilio albiventris*	13	*27.40*	31.46	10.5	69.50	*4.16*	*85.08*	*52.35*	69.50	*5.57*
Noctilionidae	*Noctilio leporinus*	13	19.47	29.93	6.46	28.95	2.65	49.19	28.95	35.27	3.13
Nycteridae	*Nycteris arge*	*9*	*21.67*	*10.79*	*2.05*	*47.23*	*10.10*	*69.17*	*43.60*	*50.05*	*10.92*
Nycteridae	*Nycteris gambiensis*										
Nycteridae	*Nycteris grandis*	9	24	29.80	3.50	20.00	*9.15*	*33.50*	*16.98*	20.00	*9.78*
Nycteridae	*Nycteris hispida*										
Nycteridae	*Nycteris javanica*	*9*	*21.04*	*17.78*	*2.50*	*31.09*	*9.56*	*51.25*	*28.53*	*34.54*	*10.27*
Nycteridae	*Nycteris macrotis*	9	21.55	14.49	1.18	56.17	12.78	76.79	56.17	59.97	8.25
Nycteridae	*Nycteris thebaica*	9	20.43	9.20	1.41	61.75	10.36	82.30	61.75	71.32	14.69
Nycteridae	*Nycteris tragata*										

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Nycteridae	*Nycteris woodi*										
Phyllostomidae	*Ametrida centurio*	9	38.94	10.61	2.49	74.59	18.98	97.58	58.64	74.59	16.67
Phyllostomidae	*Anoura caudifer*	**9**	*37.40*	*10.81*	*1.79*	*74.00*	*18.99*	*105.27*	*65.10*	*81.29*	*19.33*
Phyllostomidae	*Anoura cultrata*	**9**	*36.82*	*17.39*	*1.88*	*67.02*	*19.19*	*98.82*	*59.15*	*74.22*	*19.35*
Phyllostomidae	*Anoura geoffroyi*	9	40.28	15.15	1.86	67.46	18.44	107.14	67.46	81.69	22.76
Phyllostomidae	*Anoura latidens*	**9**	*35.08*	*15.06*	*1.94*	*66.22*	*17.95*	*96.75*	*58.21*	*73.04*	*18.14*
Phyllostomidae	*Anoura luismanueli*	**9**	*36.64*	*12.81*	*1.84*	*71.09*	*18.68*	*102.21*	*62.55*	*78.18*	*18.96*
Phyllostomidae	*Ardops nichollsi*	9	59.79	19.23	2.39	36.93	14.65	99.42	36.93	72.59	22.09
Phyllostomidae	*Ariteus flavescens*	**9**	*51.48*	*10.09*	*2.31*	*50.70*	*18.05*	*100.60*	*42.91*	*63.43*	*19.58*
Phyllostomidae	*Artibeus amplus*	**9**	*24.50*	*61.04*	*2.26*	*52.20*	*12.32*	*70.61*	*45.33*	*54.76*	*12.62*
Phyllostomidae	*Artibeus anderseni*	**9**	*36.83*	*6.91*	*1.05*	*71.81*	*30.79*	*100.40*	*63.75*	*76.86*	*28.89*
Phyllostomidae	*Artibeus aztecus*	**9**	*30.44*	*20.81*	*1.25*	*59.20*	*25.53*	*82.99*	*52.51*	*62.87*	*24.02*
Phyllostomidae	*Artibeus cinereus*	9	41.02	12.70	1.11	60.46	56.27	98.95	57.93	60.46	36.57
Phyllostomidae	*Artibeus concolor*	9	14.73	19.65	2.92	37.21	5.23	49.32	34.74	37.21	3.66
Phyllostomidae	*Artibeus fimbriatus*	**9**	*22.80*	*63.89*	*2.36*	*45.20*	*12.40*	*63.03*	*39.57*	*48.09*	*12.45*
Phyllostomidae	*Artibeus fraterculus*	**9**	*25.84*	*25.54*	*2.07*	*55.26*	*13.53*	*75.43*	*48.38*	*58.26*	*13.85*
Phyllostomidae	*Artibeus glaucus*	**9**	*33.39*	*12.31*	*1.20*	*63.75*	*27.76*	*90.78*	*56.77*	*68.31*	*26.02*
Phyllostomidae	*Artibeus gnomus*	9	33.01	10.06	1.34	57.82	31.01	90.83	57.82	60.66	21.09
Phyllostomidae	*Artibeus hirsutus*	**9**	*24.89*	*40.42*	*2.16*	*51.94*	*13.13*	*71.45*	*45.47*	*54.93*	*13.36*
Phyllostomidae	*Artibeus incomitatus*	**9**	*27.53*	*14.88*	*1.42*	*59.80*	*20.46*	*80.84*	*53.30*	*62.74*	*19.87*

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Phyllostomidae	*Artibeus inopinatus*	**9**	*26.47*	*18.99*	*2.01*	*57.51*	*13.79*	*78.02*	*50.35*	*60.52*	*14.16*
Phyllostomidae	*Artibeus jamaicensis*	9	25.98	43.63	2.32	59.25	10.28	71.67	45.75	59.25	12.38
Phyllostomidae	*Artibeus lituratus*	9	24.89	59.3	1.66	76.89	13.22	76.89	52.22	62.06	15.35
Phyllostomidae	*Artibeus obscurus*	9	32.27	35.91	1.46	56.74	14.31	89.01	56.74	68.88	12.77
Phyllostomidae	*Artibeus phaeotis*	9	47.60	11.69	1.10	89.39	49.22	113.41	65.81	89.39	56.18
Phyllostomidae	*Artibeus toltecus*	9	34.38	15.47	0.81	67.15	39.79	93.96	59.58	67.15	41.42
Phyllostomidae	*Artibeus watsoni*	9	22.18	11.2	0.89	50.84	8.49	73.03	50.84	62.83	12.18
Phyllostomidae	*Brachyphylla cavernarum*	5	14.35	45.5	5.65	32.22	1.82	32.22	17.83	23.30	2.41
Phyllostomidae	*Brachyphylla nana*	9	54	37.25	2.38	59.00	*15.92*	89	34.00	59.00	*17.24*
Phyllostomidae	*Carollia brevicauda*	**9**	*29.70*	*14.85*	*1.38*	*59.44*	*18.32*	*84.95*	*53.09*	*66.75*	*18.17*
Phyllostomidae	*Carollia castanea*	9	26.14	13.1	0.81	95.40	*20.73*	98.02	71.88	95.40	*19.92*
Phyllostomidae	*Carollia colombiana*	**9**	*28.64*	*16.41*	*1.58*	*57.11*	*15.73*	*82.17*	*50.96*	*64.26*	*15.96*
Phyllostomidae	*Carollia perspicillata*	9	29.30	19.23	2.08	47.92	11.29	76.92	47.92	63.83	14.48
Phyllostomidae	*Carollia sowelli*	9	29.00	*16.02*	1.29	51.10	15.93	80.10	51.10	70.82	22.16
Phyllostomidae	*Carollia subrufa*	**9**	*29.02*	*15.84*	*1.46*	*59.26*	*17.08*	*84.14*	*52.83*	*66.29*	*17.08*
Phyllostomidae	*Centurio senex*	**9**	*36.68*	*23.09*	*2.42*	*54.00*	*14.98*	*87.46*	*46.34*	*61.56*	*15.86*
Phyllostomidae	*Chiroderma doriae*	**9**	*23.81*	*19.90*	*2.67*	*81.78*	*6.60*	*94.21*	*72.02*	*81.78*	*7.95*
Phyllostomidae	*Chiroderma improvisum*	9	24.50	35.39	3.67	76.79	7.69	76.79	52.20	59.65	7.89
Phyllostomidae	*Chiroderma salvini*	**9**	*23.81*	*26.30*	*2.48*	*72.53*	*8.38*	*87.68*	*63.88*	*73.55*	*9.41*
Phyllostomidae	*Chiroderma trinitatum*	9	23.58	13.91	3.68	86.92	5.72	101.10	77.53	86.92	6.39

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Phyllostomidae	*Chiroderma villosum*	9	23.66	23.81	0.95	78.34	11.36	102.00	78.34	83.29	10.41
Phyllostomidae	*Choeroniscus godmani*	**9**	*35.63*	*7.90*	*1.93*	*62.87*	*19.06*	*97.56*	*55.76*	*71.38*	*18.85*
Phyllostomidae	*Choeroniscus minor*	**9**	*35.22*	*8.63*	*1.96*	*61.50*	*18.89*	*95.90*	*54.49*	*69.83*	*18.64*
Phyllostomidae	*Choeroniscus periosus*	**9**	*34.51*	*10.46*	*2.02*	*59.15*	*18.59*	*93.06*	*52.40*	*67.29*	*18.30*
Phyllostomidae	*Choeronycteris mexicana*	9	35.44	17.26	2.36	41.82	25.45	76.93	41.82	50.96	14.60
Phyllostomidae	*Chrotopterus auritus*	**9**	*22.68*	*78.26*	*2.12*	*53.73*	*13.86*	*70.31*	*46.71*	*56.49*	*13.14*
Phyllostomidae	*Desmodus rotundus*	9	26.72	33.16	1.92	47.06	17.56	74.07	47.06	61.56	16.67
Phyllostomidae	*Diaemus youngi*	9	21.60	36.71	2.22	40.81	11.35	62.87	40.81	51.84	10.49
Phyllostomidae	*Diphylla ecaudata*	**9**	*24.70*	*28.11*	*2.27*	*50.86*	*13.45*	*73.07*	*45.06*	*56.26*	*13.15*
Phyllostomidae	*Ectophylla alba*	9	35.47	5.55	1.27	66.67	24.76	101.97	66.67	74.58	25.54
Phyllostomidae	*Enchisthenes hartii*	**9**	*31.08*	*16.99*	*1.77*	*62.74*	*17.32*	*88.57*	*55.20*	*67.76*	*17.40*
Phyllostomidae	*Erophylla bombifrons*	9	*21.76*	16.28	4.70	38.00	*6.65*	*53.66*	*30.30*	38.00	*7.75*
Phyllostomidae	*Erophylla sezekorni*	9	27	15.87	2.3	45.10	*9.13*	59.6	32.50	45.10	*10.17*
Phyllostomidae	*Glossophaga commissarisi*	**9**	*39.55*	*9.15*	*1.72*	*90.65*	*19.31*	*116.64*	*77.40*	*95.39*	*19.99*
Phyllostomidae	*Glossophaga leachii*	**9**	*39.11*	*10.24*	*1.72*	*89.21*	*19.38*	*115.13*	*76.10*	*93.78*	*19.97*
Phyllostomidae	*Glossophaga longirostris*	9	*38.61*	13.32	1.6	91.00	*19.68*	*113.64*	*75.19*	91.00	*20.14*
Phyllostomidae	*Glossophaga morenoi*	**9**	*39.84*	*8.54*	*1.69*	*92.30*	*19.55*	*117.94*	*78.81*	*97.03*	*20.22*
Phyllostomidae	*Glossophaga soricina*	9	40.68	9.97	2.28	86.48	17.66	111.24	70.49	86.48	19.58
Phyllostomidae	*Glyphonycteris behnii*	**9**	*27.79*	*14.53*	*1.09*	*66.75*	*22.67*	*88.57*	*59.92*	*71.81*	*21.28*
Phyllostomidae	*Glyphonycteris daviesi*	**9**	*26.29*	*18.61*	*1.16*	*60.76*	*21.89*	*82.07*	*54.49*	*65.63*	*20.39*

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Phyllostomidae	*Glyphonycteris sylvestris*	**9**	*29.61*	*8.91*	*1.01*	*74.51*	*23.60*	*96.53*	*66.95*	*79.84*	*22.36*
Phyllostomidae	*Hylonycteris underwoodi*	**9**	*35.83*	*7.50*	*1.90*	*65.69*	*18.88*	*99.78*	*58.09*	*74.00*	*18.79*
Phyllostomidae	*Lampronycteris brachyotis*	9	4.49	10.39	0.11	98.89	*35.13*	98.89	94.40	98.89	*27.04*
Phyllostomidae	*Leptonycteris curasoae*	9	58.31	25.27	5.39	41.47	9.99	98.40	41.47	73.50	12.15
Phyllostomidae	*Leptonycteris nivalis*	**9**	*47.86*	*24.26*	*3.89*	*49.75*	*10.64*	*98.43*	*42.18*	*63.62*	*12.45*
Phyllostomidae	*Leptonycteris yerbabuenae*	**9**	*48.06*	*22.24*	*3.82*	*50.86*	*10.78*	*99.74*	*43.08*	*64.85*	*12.62*
Phyllostomidae	*Lichonycteris obscura*	**9**	*36.41*	*6.50*	*1.86*	*67.76*	*19.12*	*102.21*	*59.98*	*76.25*	*19.08*
Phyllostomidae	*Lionycteris spurrelli*	9	43.12	8.85	2.99	131.72	13.31	131.72	87.93	111.54	15.68
Phyllostomidae	*Lonchophylla bokermanni*	**9**	*34.51*	*9.74*	*2.07*	*86.57*	*15.63*	*110.04*	*74.07*	*90.47*	*16.16*
Phyllostomidae	*Lonchophylla dekeyseri*	**9**	*35.51*	*7.20*	*1.96*	*92.76*	*16.38*	*115.35*	*79.52*	*96.54*	*16.90*
Phyllostomidae	*Lonchophylla handleyi*	**9**	*32.91*	*14.53*	*2.17*	*80.32*	*15.36*	*104.04*	*68.79*	*84.10*	*15.68*
Phyllostomidae	*Lonchophylla hesperia*	**9**	*35.29*	*8.72*	*1.98*	*91.65*	*16.30*	*114.28*	*78.57*	*95.49*	*16.80*
Phyllostomidae	*Lonchophylla mordax*	**9**	*31.96*	*21.56*	*2.26*	*76.02*	*14.98*	*99.86*	*65.10*	*79.84*	*15.23*
Phyllostomidae	*Lonchophylla robusta*	**9**	*33.08*	*13.72*	*2.16*	*81.04*	*15.43*	*104.65*	*69.48*	*84.86*	*15.76*
Phyllostomidae	*Lonchophylla thomasi*	9	32.36	7.09	1.56	88.77	21.93	120.90	88.77	97.35	18.89
Phyllostomidae	*Lonchorhina aurita*	**9**	*28.87*	*15.38*	*2.16*	*63.43*	*13.84*	*87.59*	*55.09*	*68.17*	*14.15*
Phyllostomidae	*Lonchorhina fernandezi*	**9**	*31.01*	*11.59*	*1.97*	*72.10*	*14.70*	*96.79*	*62.61*	*77.01*	*15.17*
Phyllostomidae	*Lonchorhina inusitata*	**9**	*28.72*	*15.53*	*2.17*	*62.93*	*13.78*	*86.99*	*54.60*	*67.63*	*14.08*
Phyllostomidae	*Lonchorhina marinkellei*	**9**	*28.31*	*17.67*	*2.21*	*61.37*	*13.62*	*85.27*	*53.25*	*66.02*	*13.88*
Phyllostomidae	*Lonchorhina orinocensis*	**9**	*31.83*	*9.04*	*1.91*	*75.64*	*15.02*	*100.40*	*65.69*	*80.56*	*15.56*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Phyllostomidae	*Lophostoma brasiliense*	**9**	*28.07*	*9.76*	*1.16*	*87.71*	*19.39*	*102.01*	*77.63*	*89.39*	*18.88*
Phyllostomidae	*Lophostoma carrikeri*	**9**	*25.43*	*22.35*	*1.30*	*74.29*	*18.12*	*89.78*	*65.69*	*76.25*	*17.41*
Phyllostomidae	*Lophostoma evotis*	**9**	*25.22*	*20.58*	*1.24*	*70.18*	*19.57*	*86.17*	*61.93*	*72.24*	*18.47*
Phyllostomidae	*Lophostoma schulzi*	**9**	*25.68*	*18.02*	*1.28*	*75.49*	*18.25*	*90.92*	*66.75*	*77.40*	*17.55*
Phyllostomidae	*Lophostoma silvicolum*	9	23.92	32.29	1.15	66.75	19.15	79.90	56.04	66.75	19.60
Phyllostomidae	*Macrophyllum macrophyllum*	9	20.5	8.02	2.00	55.00	*10.62*	61	44	55.00	*11.05*
Phyllostomidae	*Macrotus californicus*	**9**	*29.34*	*11.83*	*1.86*	*67.90*	*15.37*	*92.74*	*60.22*	*74.14*	*15.41*
Phyllostomidae	*Macrotus waterhousii*	9	28.5	16.27	1.30	69.20	*21.18*	84.20	55.7	69.20	*19.75*
Phyllostomidae	*Mesophylla macconnelli*	**9**	*33.87*	*6.86*	*1.42*	*85.88*	*19.13*	*108.78*	*76.32*	*89.93*	*19.48*
Phyllostomidae	*Micronycteris brosseti*	**9**	*34.51*	*8.48*	*1.19*	*81.29*	*24.63*	*104.45*	*66.89*	*84.35*	*23.22*
Phyllostomidae	*Micronycteris hirsuta*	9	28.8	12.89	1.40	80.80	*20.89*	97.9	69.10	80.80	*19.53*
Phyllostomidae	*Micronycteris homezi*	**9**	*34.49*	*8.50*	*1.19*	*81.21*	*24.62*	*104.45*	*66.82*	*84.27*	*23.21*
Phyllostomidae	*Micronycteris matses*	**9**	*34.51*	*8.48*	*1.19*	*81.29*	*24.63*	*104.45*	*66.89*	*84.35*	*23.22*
Phyllostomidae	*Micronycteris megalotis*	9	34.8	6.40	1.5	98.10	*21.83*	116.00	81.20	98.10	*21.01*
Phyllostomidae	*Micronycteris microtis*	**9**	*32.97*	*7.75*	*1.21*	*94.35*	*21.93*	*112.78*	*79.52*	*96.74*	*20.98*
Phyllostomidae	*Micronycteris minuta*	9	41.00	6.90	1.80	100.29	25.04	100.29	60.17	82.26	24.34
Phyllostomidae	*Micronycteris sanborni*	**9**	*34.82*	*8.48*	*1.20*	*80.88*	*24.67*	*104.45*	*66.42*	*84.02*	*23.29*
Phyllostomidae	*Micronycteris schmidtorum*	**9**	*34.81*	*7.73*	*1.18*	*82.68*	*24.78*	*105.88*	*68.03*	*85.71*	*23.39*
Phyllostomidae	*Mimon bennettii*	**9**	*23.73*	*12.90*	*1.30*	*73.41*	*17.00*	*87.67*	*65.83*	*75.11*	*16.46*
Phyllostomidae	*Mimon cozumelae*	**9**	*20.38*	*39.49*	*1.52*	*58.32*	*15.36*	*72.25*	*52.25*	*60.28*	*14.57*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Phyllostomidae	*Mimon crenulatum*	9	20.22	13.91	1.06	62.56	15.14	82.55	62.56	69.66	18.84
Phyllostomidae	*Mimon koepckeae*	**9**	*21.85*	*20.15*	*1.29*	*66.22*	*17.05*	*80.16*	*59.74*	*67.97*	*16.28*
Phyllostomidae	*Monophyllus plethodon*	9	47.43	15.33	2.62	71.70	19.76	119.23	71.70	96.62	20.38
Phyllostomidae	*Monophyllus redmani*	**9**	*43.26*	*8.79*	*1.91*	*87.71*	*18.82*	*122.10*	*75.94*	*97.51*	*19.58*
Phyllostomidae	*Musonycteris harrisoni*	**9**	*32.87*	*10.82*	*2.22*	*48.91*	*18.70*	*82.72*	*43.60*	*57.05*	*17.96*
Phyllostomidae	*Neonycteris pusilla*	**9**	*29.34*	*6.11*	*0.69*	*81.29*	*29.40*	*101.00*	*74.00*	*86.49*	*26.95*
Phyllostomidae	*Phylloderma stenops*	**9**	*16.68*	*55.82*	*2.08*	*46.43*	*11.22*	*57.96*	*41.22*	*48.47*	*10.59*
Phyllostomidae	*Phyllonycteris aphylla*	**9**	*20.92*	*14.15*	*3.38*	*45.20*	*6.37*	*61.23*	*37.49*	*46.90*	*7.47*
Phyllostomidae	*Phyllonycteris major*	**9**	*17.12*	*16.66*	*3.82*	*41.89*	*4.60*	*53.93*	*34.99*	*42.86*	*5.64*
Phyllostomidae	*Phyllonycteris poeyi*	9	11	15.59	4.69	39.00	*2.15*	46	34.00	39.00	*3.10*
Phyllostomidae	*Phyllops falcatus*	9	31.00	10.82	5.57	50.50	*7.92*	67	36.00	50.50	*9.48*
Phyllostomidae	*Phyllostomus discolor*	9	18.14	36.7	2.25	52.95	7.71	70.94	52.95	63.16	8.11
Phyllostomidae	*Phyllostomus elongatus*	**9**	*16.67*	*41.75*	*1.81*	*54.16*	*11.24*	*64.40*	*48.13*	*55.37*	*10.74*
Phyllostomidae	*Phyllostomus hastatus*	9	13.70	91.44	1.47	48.68	10.10	55.41	41.93	48.68	9.05
Phyllostomidae	*Phyllostomus latifolius*	**9**	*14.41*	*134.00*	*2.37*	*38.59*	*10.14*	*47.89*	*34.26*	*40.61*	*9.34*
Phyllostomidae	*Platalina genovensium*	**9**	*32.71*	*16.39*	*2.22*	*78.26*	*14.94*	*102.21*	*66.95*	*82.19*	*15.32*
Phyllostomidae	*Platyrrhinus aurarius*	**9**	*25.00*	*35.12*	*2.57*	*53.73*	*10.66*	*74.13*	*47.18*	*57.11*	*11.30*
Phyllostomidae	*Platyrrhinus brachycephalus*	9	40.20	14.26	4.50	91.38	6.13	115.36	75.17	91.38	8.59
Phyllostomidae	*Platyrrhinus chocoensis*	**9**	*26.57*	*23.93*	*2.40*	*59.38*	*11.26*	*80.77*	*52.20*	*62.87*	*12.02*
Phyllostomidae	*Platyrrhinus dorsalis*	**9**	*25.77*	*26.00*	*2.49*	*56.43*	*10.95*	*77.37*	*49.60*	*59.86*	*11.66*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Phyllostomidae	*Platyrrhinus helleri*	9	24.67	13.44	2.83	50.87	6.90	65.41	40.72	50.87	8.82
Phyllostomidae	*Platyrrhinus infuscus*	**9**	*23.91*	*50.76*	*2.70*	*50.05*	*10.24*	*69.61*	*43.95*	*53.36*	*10.80*
Phyllostomidae	*Platyrrhinus lineatus*	**9**	*26.83*	*24.34*	*2.30*	*60.89*	*11.85*	*82.21*	*53.57*	*64.33*	*12.55*
Phyllostomidae	*Platyrrhinus recifinus*	**9**	*30.28*	*10.82*	*2.60*	*69.90*	*9.11*	*93.92*	*61.07*	*74.00*	*10.76*
Phyllostomidae	*Platyrrhinus umbratus*	**9**	*25.82*	*25.17*	*2.48*	*56.66*	*10.97*	*77.58*	*49.75*	*60.04*	*11.68*
Phyllostomidae	*Platyrrhinus vittatus*	**9**	*24.38*	*37.01*	*2.65*	*51.57*	*10.42*	*71.55*	*45.33*	*54.93*	*11.02*
Phyllostomidae	*Pygoderma bilabiatum*	**9**	*37.28*	*18.50*	*2.39*	*54.87*	*15.10*	*89.02*	*47.13*	*62.68*	*16.04*
Phyllostomidae	*Rhinophylla alethina*	**9**	*34.57*	*6.91*	*1.28*	*87.71*	*20.35*	*111.30*	*77.87*	*93.22*	*20.48*
Phyllostomidae	*Rhinophylla fischerae*	**9**	*32.93*	*9.60*	*1.36*	*80.00*	*19.63*	*104.24*	*70.95*	*85.37*	*19.63*
Phyllostomidae	*Rhinophylla pumilio*	**9**	*32.94*	*9.58*	*1.36*	*80.08*	*19.63*	*104.24*	*71.02*	*85.46*	*19.63*
Phyllostomidae	*Scleronycteris ega*	**9**	*26.72*	*49.54*	*2.75*	*38.63*	*15.02*	*63.98*	*34.09*	*44.52*	*14.30*
Phyllostomidae	*Sphaeronycteris toxophyllum*	**9**	*37.80*	*16.06*	*2.28*	*59.26*	*15.60*	*93.26*	*50.86*	*67.02*	*16.54*
Phyllostomidae	*Stenoderma rufum*	**9**	*39.87*	*21.10*	*2.54*	*48.38*	*14.97*	*86.06*	*41.39*	*57.28*	*16.07*
Phyllostomidae	*Sturnira aratathomasi*	**9**	*27.12*	*49.67*	*1.81*	*53.68*	*19.35*	*77.53*	*49.01*	*58.67*	*18.27*
Phyllostomidae	*Sturnira bidens*	**9**	*30.89*	*18.05*	*1.61*	*65.76*	*19.94*	*91.64*	*59.32*	*71.24*	*19.38*
Phyllostomidae	*Sturnira bogotensis*	**9**	*30.64*	*19.94*	*1.61*	*62.61*	*21.37*	*89.04*	*57.00*	*68.24*	*20.35*
Phyllostomidae	*Sturnira erythromos*	**9**	*31.10*	*15.53*	*1.58*	*64.33*	*21.59*	*90.97*	*58.62*	*70.04*	*20.61*
Phyllostomidae	*Sturnira lilium*	9	38.94	20.19	1.93	73.27	20.56	112.45	73.27	88.06	20.02
Phyllostomidae	*Sturnira ludovici*	9	35.62	21.00	1.01	71.50	53.19	98.83	63.20	71.50	36.27
Phyllostomidae	*Sturnira luisi*	**9**	*33.98*	*11.99*	*1.85*	*71.09*	*17.76*	*100.40*	*64.39*	*78.02*	*17.93*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Phyllostomidae	*Sturnira magna*	**9**	*29.44*	*27.55*	*1.71*	*59.03*	*20.23*	*84.77*	*53.73*	*64.46*	*19.28*
Phyllostomidae	*Sturnira mistratensis*	**9**	*31.43*	*15.66*	*1.57*	*67.83*	*20.24*	*93.90*	*61.19*	*73.33*	*19.70*
Phyllostomidae	*Sturnira mordax*	9	29.93	11.79	1.65	64.75	17.13	94.68	64.75	72.07	18.34
Phyllostomidae	*Sturnira nana*	**9**	*35.24*	*6.64*	*1.35*	*84.18*	*21.92*	*110.25*	*76.02*	*90.20*	*21.70*
Phyllostomidae	*Sturnira oporaphilum*	**9**	*30.43*	*21.99*	*1.62*	*61.81*	*21.27*	*88.17*	*56.32*	*67.42*	*20.24*
Phyllostomidae	*Sturnira thomasi*	9	31.59	15.46	5.46	42.94	3.85	74.86	42.94	56.48	5.28
Phyllostomidae	*Sturnira tildae*	9	19.94	24.39	0.96	55.93	21.12	71.78	51.84	55.93	21.44
Phyllostomidae	*Tonatia bidens*	9	19.79	27.70	1.38	78.18	15.74	89.67	69.88	78.18	13.37
Phyllostomidae	*Tonatia saurophila*	9	19.5	*32.33*	1.40	56.50	*15.43*	71	51.50	56.50	*14.45*
Phyllostomidae	*Trachops cirrhosus*	9	24.11	36.9	1.02	59.68	23.11	83.71	59.68	64.87	20.80
Phyllostomidae	*Trinycteris nicefori*	9	25.09	8.25	0.39	68.50	*31.42*	93.59	68.50	82.96	*28.08*
Phyllostomidae	*Uroderma bilobatum*	9	28.57	16.28	1.20	92.35	28.63	109.51	80.94	92.35	24.23
Phyllostomidae	*Uroderma magnirostrum*	**9**	*30.48*	*17.30*	*1.31*	*82.68*	*22.68*	*101.00*	*73.26*	*84.94*	*21.47*
Phyllostomidae	*Vampyressa bidens*	**9**	*29.81*	*11.91*	*1.72*	*72.89*	*16.16*	*94.85*	*64.52*	*76.40*	*16.45*
Phyllostomidae	*Vampyressa brocki*	**9**	*24.70*	*48.00*	*2.14*	*53.04*	*13.96*	*73.07*	*46.90*	*56.37*	*13.85*
Phyllostomidae	*Vampyressa melissa*	**9**	*31.11*	*16.58*	*1.59*	*73.33*	*17.93*	*96.75*	*65.10*	*77.32*	*18.05*
Phyllostomidae	*Vampyressa nymphaea*	**9**	*23.80*	*69.00*	*2.18*	*47.04*	*14.55*	*66.60*	*41.64*	*50.50*	*14.14*
Phyllostomidae	*Vampyressa pusilla*	**9**	*33.64*	*8.77*	*1.44*	*84.77*	*19.03*	*107.74*	*75.34*	*88.77*	*19.36*
Phyllostomidae	*Vampyressa thyone*	**9**	*33.74*	*7.17*	*1.43*	*85.29*	*19.07*	*108.16*	*75.72*	*89.30*	*19.40*
Phyllostomidae	*Vampyrodes caraccioli*	9	20.86	35.89	1.03	64.50	18.22	85.38	64.50	71.74	20.18

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Phyllostomidae	*Vampyrum spectrum*	9	33	171.61	2.80	79.40	*16.00*	97	64.00	79.40	*15.51*
Pteropodidae	*Acerodon_celebensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Acerodon_humilis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Acerodon_jubatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Acerodon_leucotis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Acerodon_mackloti*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Aethalops_aequalis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Aethalops_alecto*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Alionycteris_paucidentata*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Aproteles_bulmerae*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Balionycteris_maculata*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Casinycteris_argynnis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Chironax_melanocephalus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Cynopterus_brachyotis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Cynopterus_horsfieldii*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Cynopterus_luzoniensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Cynopterus_minutus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Cynopterus_nusatenggara*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Cynopterus_sphinx*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Cynopterus_titthaecheilus*	**1**	-	-	-	-	-	-	-	-	-

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Pteropodidae	*Dobsonia_anderseni*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_beauforti*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_chapmani*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_crenulata*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_emersa*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_exoleta*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_inermis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_magna*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_minor*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_moluccensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_pannietensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_peronii*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_praedatrix*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dobsonia_viridis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dyacopterus_brooksi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Dyacopterus_spadiceus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Eidolon_dupreanum*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Eidolon_helvum*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Eonycteris_major*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Eonycteris_robusta*	**1**	-	-	-	-	-	-	-	-	-

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Pteropodidae	*Eonycteris_spelaea*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomophorus_angolensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomophorus_crypturus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomophorus_gambianus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomophorus_grandis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomophorus_labiatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomophorus_minimus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomophorus_minor*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomophorus_wahlbergi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomops_buettikoferi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomops_dobsonii*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Epomops_franqueti*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Haplonycteris_fischeri*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Harpyionycteris_celebensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Harpyionycteris_whiteheadi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Hypsignathus_monstrosus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Latidens_salimalii*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Lissonycteris_angolensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Macroglossus_minimus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Macroglossus_sobrinus*	**1**	-	-	-	-	-	-	-	-	-

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Pteropodidae	*Megaerops_ecaudatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Megaerops_kusnotoi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Megaerops_niphanae*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Megaerops_wetmorei*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Megaloglossus_woermanni*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Melonycteris_fardoulisi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Melonycteris_melanops*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Melonycteris_woodfordi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Micropteropus_intermedius*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Micropteropus_pusillus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Myonycteris_brachycephala*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Myonycteris_relicta*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Myonycteris_torquata*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nanonycteris_veldkampii*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Neopteryx_frosti*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Notopteris_macdonaldi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Notopteris_neocaledonica*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_aello*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_albiventer*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_cephalotes*	**1**	-	-	-	-	-	-	-	-	-

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Pteropodidae	*Nyctimene_certans*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_cyclotis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_draconilla*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_keasti*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_major*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_malaitensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_masalai*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_minutus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_rabori*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_robinsoni*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_sanctacrucis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Nyctimene_vizcaccia*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Otopteropus_cartilagonodus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Paranyctimene_raptor*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Paranyctimene_tenax*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Penthetor_lucasi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Plerotes_anchietae*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Ptenochirus_jagori*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Ptenochirus_minor*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteralopex_acrodonta*	**1**	-	-	-	-	-	-	-	-	-

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Pteropodidae	*Pteralopex_anceps*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteralopex_atrata*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteralopex_pulchra*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteralopex_taki*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_admiralitatum*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_aldabrensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_alecto*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_anetianus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_aruensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_banakrisi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_brunneus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_caniceps*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_capistratus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_chrysoproctus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_cognatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_conspicillatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_dasymallus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_faunulus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_fundatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_giganteus*	**1**	-	-	-	-	-	-	-	-	-

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Pteropodidae	*Pteropus_gilliardorum*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_griseus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_howensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_hypomelanus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_insularis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_intermedius*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_keyensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_leucopterus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_livingstonii*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_lombocensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_loochoensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_lylei*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_macrotis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_mahaganus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_mariannus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_melanopogon*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_melanotus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_molossinus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_neohibernicus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_niger*	**1**	-	-	-	-	-	-	-	-	-

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Pteropodidae	*Pteropus_nitendiensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_ocularis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_ornatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_pelewensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_personatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_pilosus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_pohlei*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_poliocephalus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_pselaphon*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_pumilus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_rayneri*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_rennelli*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_rodricensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_rufus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_samoensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_scapulatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_seychellensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_speciosus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_subniger*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_temminckii*	**1**	-	-	-	-	-	-	-	-	-

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Pteropodidae	*Pteropus_tokudae*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_tonganus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_tuberculatus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_ualanus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_vampyrus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_vetulus*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_voeltzkowi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_woodfordi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Pteropus_yapensis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_aegyptiacus*	2	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_amplexicaudatus*	2	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_bidens*	**2**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_celebensis*	**2**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_lanosus*	**2**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_leschenaultii*	**2**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_linduensis*	**2**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_madagascariensis*	**2**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_obliviosus*	**2**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Rousettus_spinalatus*	2	-	-	-	-	-	-	-	-	-
Pteropodidae	*Scotonycteris_ophiodon*	**1**	-	-	-	-	-	-	-	-	-

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Pteropodidae	*Scotonycteris_zenkeri*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Sphaerias_blanfordi*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Styloctenium_wallacei*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Syconycteris_australis*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Syconycteris_carolinae*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Syconycteris_hobbit*	**1**	-	-	-	-	-	-	-	-	-
Pteropodidae	*Thoopterus_nigrescens*	**1**	-	-	-	-	-	-	-	-	-
Rhinolophidae	*Rhinolophus acuminatus*	12	8.63	12.1	48.86	89.61	0.00	89.61	80.97	89.56	0.00
Rhinolophidae	*Rhinolophus adami*	**12**	*9.99*	*17.41*	*31.22*	*63.88*	*0.16*	*68.43*	*54.76*	*63.82*	*0.18*
Rhinolophidae	*Rhinolophus affinis*	12	15.78	13.7	27.88	80.65	0.01	80.65	64.87	80.55	0.01
Rhinolophidae	*Rhinolophus alcyone*	12	*15.39*	18.62	*35.41*	87.00	*0.21*	*91.45*	*72.53*	87.00	*0.07*
Rhinolophidae	*Rhinolophus arcuatus*	12	*10.00*	8.98	*35.34*	66.50	*0.20*	*69.76*	*57.28*	66.50	*0.10*
Rhinolophidae	*Rhinolophus beddomei*	**12**	*8.16*	*29.78*	*35.66*	*52.72*	*0.43*	*57.08*	*45.15*	*53.14*	*0.49*
Rhinolophidae	*Rhinolophus blasii*	12	4.00	10.29	44.10	60.5	*0.94*	*58.31*	*54.33*	60.5	*0.98*
Rhinolophidae	*Rhinolophus bocharicus*	**12**	*10.52*	*15.05*	*30.08*	*67.29*	*0.07*	*71.69*	*57.69*	*67.09*	*0.08*
Rhinolophidae	*Rhinolophus borneensis*	12	*12.81*	*12.80*	*31.94*	81.80	*1.30*	*83.80*	*69.97*	81.80	*1.02*
Rhinolophidae	*Rhinolophus canuti*	**12**	*9.88*	*17.94*	*31.44*	*63.18*	*0.17*	*67.77*	*54.16*	*63.18*	*0.20*
Rhinolophidae	*Rhinolophus capensis*	12	12.50	12.87	42.67	84.42	0.00	84.42	71.91	84.36	0.00
Rhinolophidae	*Rhinolophus celebensis*	**12**	*11.76*	*10.82*	*27.74*	*75.64*	*0.13*	*79.35*	*64.91*	*75.04*	*0.17*
Rhinolophidae	*Rhinolophus clivosus*	12	19.32	*15.21*	36.71	90.11	0.00	90.11	70.80	89.52	0.01

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Rhinolophidae	*Rhinolophus coelophyllus*	12	12.50	7.07	35.01	78.77	0.00	78.77	66.29	78.46	0.00
Rhinolophidae	*Rhinolophus cognatus*	**12**	*12.31*	*9.40*	*26.79*	*79.60*	*0.23*	*82.74*	*68.24*	*78.73*	*0.28*
Rhinolophidae	*Rhinolophus convexus*	**12**	*10.47*	*8.78*	*38.63*	*72.39*	*0.02*	*75.74*	*62.68*	*72.02*	*0.07*
Rhinolophidae	*Rhinolophus cornutus*	12	13.35	7.27	43.58	105.97	0.00	106.05	92.67	105.97	0.00
Rhinolophidae	*Rhinolophus creaghi*	12	*10.53*	16.92	*34.64*	68.00	*0.47*	*70.95*	*57.97*	68.00	*0.30*
Rhinolophidae	*Rhinolophus darlingi*	12	13.04	8.94	36.05	86.29	0.01	86.29	73.24	86.01	0.00
Rhinolophidae	*Rhinolophus deckenii*	12	*11.87*	20.09	*28.28*	72	*0.38*	*76.42*	*61.25*	72	*0.30*
Rhinolophidae	*Rhinolophus denti*	12	19.98	6.30	22.28	110.71	0.01	110.71	90.72	110.60	0.02
Rhinolophidae	*Rhinolophus eloquens*	**12**	*6.71*	*19.15*	*38.28*	*42.61*	*0.05*	*45.79*	*36.60*	*43.29*	*0.18*
Rhinolophidae	*Rhinolophus euryale*	12	15.58	9.25	21.82	106.91	0.01	106.91	91.24	105.67	0.01
Rhinolophidae	*Rhinolophus euryotis*	12	7.10	14.3	50.82	52.03	0.00	52.03	44.92	51.99	0.00
Rhinolophidae	*Rhinolophus ferrumequinum*	12	12.55	22.59	48.09	82.34	0.00	82.34	69.81	82.18	0.00
Rhinolophidae	*Rhinolophus formosae*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinolophidae	*Rhinolophus fumigatus*	12	6.64	13.09	41.27	53.28	0.01	53.28	46.57	53.24	0.00
Rhinolophidae	*Rhinolophus guineensis*	**12**	*10.53*	*15.00*	*30.08*	*67.36*	*0.07*	*71.77*	*57.74*	*67.15*	*0.07*
Rhinolophidae	*Rhinolophus hildebrandtii*	12	5.79	25.99	46.62	34.31	0.00	34.31	28.50	34.27	0.00
Rhinolophidae	*Rhinolophus hilli*	**12**	*10.90*	*13.60*	*29.34*	*69.76*	*0.01*	*73.99*	*59.80*	*69.41*	*0.01*
Rhinolophidae	*Rhinolophus hillorum*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinolophidae	*Rhinolophus hipposideros*	12	14.83	4.57	40.83	109.47	0.01	109.47	94.59	109.32	0.01
Rhinolophidae	*Rhinolophus imaizumii*	**12**	*11.76*	*10.82*	*27.74*	*75.64*	*0.13*	*79.35*	*64.91*	*75.04*	*0.17*

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Rhinolophidae	*Rhinolophus inops*	**12**	*10.88*	*13.65*	*29.37*	*69.69*	*0.02*	*73.93*	*59.74*	*69.34*	*0.01*
Rhinolophidae	*Rhinolophus keyensis*	**12**	*13.95*	*6.26*	*24.22*	*92.02*	*0.52*	*92.91*	*78.96*	*90.47*	*0.63*
Rhinolophidae	*Rhinolophus landeri*	12	19.20	9.39	41.85	105.46	0.01	105.46	86.25	105.41	0.00
Rhinolophidae	*Rhinolophus lepidus*	12	18.37	5.46	35.34	103.30	0.01	103.30	84.75	103.20	0.01
Rhinolophidae	*Rhinolophus luctus*	12	1.49	34.07	64.97	31.07	0.00	31.11	29.65	31.07	0.00
Rhinolophidae	*Rhinolophus maclaudi*	**12**	*6.34*	*35.84*	*42.52*	*44.43*	*0.53*	*46.85*	*37.98*	*44.93*	*0.64*
Rhinolophidae	*Rhinolophus macrotis*	12	6.44	6.18	28.47	47.00	0.01	47.00	40.58	46.95	0.00
Rhinolophidae	*Rhinolophus madurensis*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinolophidae	*Rhinolophus maendeleo*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinolophidae	*Rhinolophus malayanus*	12	13.95	6.73	32.04	85.62	0.00	85.62	71.68	85.55	0.00
Rhinolophidae	*Rhinolophus marshalli*	12	*4.82*	5.02	*49.45*	43.00	*0.89*	*45.55*	*38.36*	43.00	*0.88*
Rhinolophidae	*Rhinolophus megaphyllus*	12	7.56	10.17	56.06	68.80	0.00	68.85	61.29	68.80	0.00
Rhinolophidae	*Rhinolophus mehelyi*	12	5.00	14.03	35.90	110	*1.00*	*89.93*	*97.42*	110	*0.98*
Rhinolophidae	*Rhinolophus mitratus*	**12**	*8.98*	*27.55*	*37.49*	*57.11*	*0.51*	*61.64*	*48.62*	*57.45*	*0.53*
Rhinolophidae	*Rhinolophus monoceros*	12	16.27	7.49	40.39	106.45	0.01	107.29	90.99	106.45	0.01
Rhinolophidae	*Rhinolophus montanus*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinolophidae	*Rhinolophus nereis*	**12**	*10.88*	*13.65*	*29.37*	*69.69*	*0.02*	*73.93*	*59.74*	*69.34*	*0.01*
Rhinolophidae	*Rhinolophus osgoodi*	**2**	*11.24*	*12.39*	*28.67*	*72.10*	*0.04*	*76.16*	*61.87*	*71.66*	*0.06*
Rhinolophidae	*Rhinolophus paradoxolophus*	12	*5.07*	8.17	*48.76*	44	*0.83*	*46.23*	*38.71*	44	*0.84*
Rhinolophidae	*Rhinolophus pearsonii*	12	5.33	11.55	42.30	56.72	0.00	56.72	51.42	56.68	0.00

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Rhinolophidae	*Rhinolophus philippinensis*	12	4.71	10.91	81.84	39.78	0.00	39.85	35.10	39.78	0.00
Rhinolophidae	*Rhinolophus pusillus*	12	12.18	5.15	36.08	109.93	0.00	109.93	97.72	109.85	0.00
Rhinolophidae	*Rhinolophus rex*	12	3.99	32.62	43.52	26.01	0.00	26.04	22.06	26.01	0.00
Rhinolophidae	*Rhinolophus robinsoni*	**12**	*12.69*	*8.54*	*26.15*	*82.35*	*0.29*	*85.08*	*70.67*	*81.37*	*0.36*
Rhinolophidae	*Rhinolophus rouxii*	12	*12.85*	12.25	*33.52*	80.00	*0.27*	*83.39*	*68.31*	80.00	*0.27*
Rhinolophidae	*Rhinolophus rufus*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinolophidae	*Rhinolophus ruwenzorii*	**12**	*6.76*	*25.54*	*39.73*	*46.20*	*0.29*	*48.92*	*39.57*	*46.57*	*0.44*
Rhinolophidae	*Rhinolophus sakejiensis*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinolophidae	*Rhinolophus sedulus*	12	8.07	8.74	30.50	67.92	0.00	67.92	59.91	67.87	0.00
Rhinolophidae	*Rhinolophus shameli*	12	7.66	9.61	34.87	69.65	0.00	69.65	61.98	69.59	0.00
Rhinolophidae	*Rhinolophus shortridgei*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinolophidae	*Rhinolophus siamensis*	12	*10.09*	*14.11*	*30.85*	65.00	*0.20*	*69.69*	*55.92*	65.00	*0.19*
Rhinolophidae	*Rhinolophus silvestris*	**12**	*9.29*	*21.23*	*32.79*	*59.50*	*0.27*	*64.11*	*51.01*	*59.68*	*0.30*
Rhinolophidae	*Rhinolophus simulator*	12	14.59	8.13	29.37	80.76	0.00	80.76	66.20	80.71	0.01
Rhinolophidae	*Rhinolophus sinicus*	12	*13.46*	*10.12*	*32.33*	84.00	*0.39*	*86.84*	*71.74*	84.00	*0.40*
Rhinolophidae	*Rhinolophus stheno*	12	14.52	7.92	26.53	93.99	0.01	93.99	79.48	93.89	0.02
Rhinolophidae	*Rhinolophus subbadius*	**12**	*9.98*	*5.86*	*35.45*	*67.49*	*0.19*	*71.64*	*58.67*	*67.29*	*0.12*
Rhinolophidae	*Rhinolophus subrufus*	12	*7.27*	24.25	*42.73*	51.00	*0.36*	*54.08*	*44.08*	51.00	*0.47*
Rhinolophidae	*Rhinolophus swinnyi*	12	18.78	7.07	22.30	107.32	0.01	107.32	88.57	104.36	0.01
Rhinolophidae	*Rhinolophus thomasi*	12	14.80	8.26	33.89	89.61	0.00	89.61	74.82	89.53	0.00

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Rhinolophidae	*Rhinolophus trifoliatus*	12	8.21	15.16	19.51	52.56	0.01	52.56	44.24	52.41	0.01
Rhinolophidae	*Rhinolophus virgo*	**12**	*9.34*	*6.06*	*38.44*	*68.65*	*0.43*	*70.49*	*59.86*	*67.49*	*0.26*
Rhinolophidae	*Rhinolophus yunanensis*	12	4.74	19.33	49.34	49.77	0.00	49.77	45.03	49.70	0.00
Rhinolophidae	*Rhinolophus ziama*	**12**	*10.98*	*13.29*	*29.20*	*70.32*	*0*	*74.53*	*60.28*	*69.97*	*0.01*
Rhinopomatidae	*Rhinopoma hardwickii*	5	4.33	13.1	9.42	32.33	0.44	34.89	30.19	32.33	0.62
Rhinopomatidae	*Rhinopoma macinnesi*	*5*	*4.73*	*13.11*	*8.03*	*36.71*	*0.66*	*39.75*	*33.62*	*36.60*	*0.65*
Rhinopomatidae	*Rhinopoma microphyllum*	5	1.88	28.02	9.88	31.92	0.23	31.92	29.90	30.72	0.21
Rhinopomatidae	*Rhinopoma muscatellum*	*5*	*5.00*	*9.13*	*7.20*	*43.95*	*0.96*	*46.51*	*40.33*	*42.86*	*0.93*
Thyropteridae	*Thyroptera discifera*	*8*	*28.67*	*3.13*	*2.66*	*67.97*	*7.11*	*93.86*	*60.64*	*73.33*	*9.27*
Thyropteridae	*Thyroptera lavali*	*8*	*24.56*	*5.23*	*3.02*	*52.93*	*5.69*	*76.76*	*47.51*	*57.86*	*7.63*
Thyropteridae	*Thyroptera tricolor*	8	24.13	4.52	2.48	43.91	4.07	67.38	43.91	54.39	7.37
Vespertilionidae	*Antrozous pallidus*	10	34.36	22.24	2.59	27.22	11.34	61.55	27.22	44.76	13.22
Vespertilionidae	*Arielulus aureocollaris*	*10*	*36.09*	*9.49*	*3.55*	*32.36*	*10.36*	*68.06*	*31.25*	*38.36*	*13.04*
Vespertilionidae	*Arielulus circumdatus*	*10*	*34.51*	*10.40*	*3.75*	*31.69*	*9.52*	*65.64*	*30.60*	*37.37*	*12.16*
Vespertilionidae	*Arielulus cuprosus*	*10*	*37.79*	*6.91*	*3.33*	*35.48*	*10.89*	*73.82*	*34.26*	*41.85*	*13.75*
Vespertilionidae	*Arielulus societatis*	*10*	*36.54*	*8.72*	*3.49*	*33.18*	*10.50*	*69.57*	*32.01*	*39.25*	*13.23*
Vespertilionidae	*Arielulus torquatus*	10	41.64	*10.05*	2.71	28.55	14.09	70.26	28.55	35.82	16.85
Vespertilionidae	*Barbastella barbastellus*	5	17.77	8.31	3.52	28.82	3.52	46.49	28.82	35.33	4.47
Vespertilionidae	*Barbastella leucomelas*	10	11.33	15.05	2.52	28.55	3.48	39.82	28.55	34.49	3.55
Vespertilionidae	*Bauerus dubiaquercus*	*10*	*34.61*	*22.22*	*3.23*	*29.11*	*9.61*	*61.59*	*27.39*	*36.34*	*11.83*

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Vespertilionidae	*Chalinolobus dwyeri*	8	15.35	8.74	6.50	21.25	0.50	36.60	21.25	24.44	2.34
Vespertilionidae	*Chalinolobus gouldii*	8	18.27	14.24	9.19	29.39	0.65	44.89	26.62	29.39	2.05
Vespertilionidae	*Chalinolobus morio*	8	23.69	8.91	5.35	49.81	1.45	73.41	49.81	52.92	4.10
Vespertilionidae	*Chalinolobus neocaledonicus*	*8*	*17.66*	*8.14*	*6.30*	*35.45*	*0.77*	*51.84*	*34.57*	*37.26*	*2.82*
Vespertilionidae	*Chalinolobus nigrogriseus*	*8*	*13.51*	8.79	*6.90*	35.00	*0.10*	44	35.00	38.00	*1.53*
Vespertilionidae	*Chalinolobus picatus*	*8*	12	5.86	6.00	40	*0.12*	50	38.00	40	*1.53*
Vespertilionidae	*Chalinolobus tuberculatus*	8	22.90	10.46	6.54	36.41	1.22	59.35	36.41	40.47	3.35
Vespertilionidae	*Cistugo lesueuri*	7	45.80	6.38	2.9	46.50	*31.87*	*85.99*	*40.17*	46.50	*30.57*
Vespertilionidae	*Cistugo seabrae*	8	45.15	5.37	1.99	40.68	41.15	85.84	40.68	45.92	28.72
Vespertilionidae	*Corynorhinus mexicanus*	*10*	*21.35*	*10.28*	*3.40*	*24.98*	*4.78*	*44.64*	*21.85*	*30.88*	*6.04*
Vespertilionidae	*Corynorhinus rafinesquii*	*10*	*21.61*	*9.15*	*3.36*	*25.41*	*4.86*	*45.52*	*22.24*	*31.41*	*6.14*
Vespertilionidae	*Corynorhinus townsendii*	10	20.33	10.3	3.28	34.73	4.73	39.80	19.14	34.73	5.90
Vespertilionidae	*Eptesicus andinus*	*8*	*22.60*	*10.95*	*6.28*	*32.92*	*2.28*	*56.18*	*32.17*	*36.31*	*4.47*
Vespertilionidae	*Eptesicus bobrinskoi*	*8*	*24.44*	*7.54*	*5.77*	*37.23*	*2.67*	*63.30*	*36.42*	*40.81*	*5.07*
Vespertilionidae	*Eptesicus bottae*	3	14.99	15.66	7.76	30.47	0.92	45.56	30.47	33.56	2.00
Vespertilionidae	*Eptesicus brasiliensis*	8	20.06	9.20	9.45	32.64	0.80	52.48	32.64	34.86	2.32
Vespertilionidae	*Eptesicus chiriquinus*	*8*	*22.60*	*10.95*	*6.28*	*32.92*	*2.28*	*56.18*	*32.17*	*36.31*	*4.47*
Vespertilionidae	*Eptesicus diminutus*	*8*	*23.77*	*5.99*	*6.38*	*37.52*	*2.06*	*62.82*	*36.93*	*40.85*	*4.46*
Vespertilionidae	*Eptesicus dimissus*	*8*	*21.76*	*13.03*	*6.54*	*31.06*	*2.10*	*52.98*	*30.36*	*34.36*	*4.20*
Vespertilionidae	*Eptesicus floweri*	*8*	*24.68*	*7.20*	*5.71*	*37.79*	*2.72*	*64.21*	*36.97*	*41.43*	*5.15*

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Vespertilionidae	*Eptesicus furinalis*	3	26.97	7.70	5.35	38.15	3.36	65.32	38.15	42.84	6.18
Vespertilionidae	*Eptesicus fuscus*	8	31.56	17.49	7.93	27.28	2.11	58.81	27.28	32.55	4.10
Vespertilionidae	*Eptesicus gobiensis*	*8*	*22.60*	*10.95*	*6.28*	*32.92*	*2.28*	*56.18*	*32.17*	*36.31*	*4.47*
Vespertilionidae	*Eptesicus guadeloupensis*	8	13.82	18.99	6.73	26.98	1.02	38.26	25.52	26.98	1.92
Vespertilionidae	*Eptesicus hottentotus*	8	32.65	30.33	5.06	25.47	5.46	58.18	25.47	30.88	8.06
Vespertilionidae	*Eptesicus innoxius*	*8*	*24.48*	*7.49*	*5.76*	*37.30*	*2.68*	*63.43*	*36.49*	*40.89*	*5.08*
Vespertilionidae	*Eptesicus japonensis*	*8*	*22.60*	*10.95*	*6.28*	*32.92*	*2.28*	*56.18*	*32.17*	*36.31*	*4.47*
Vespertilionidae	*Eptesicus kobayashii*	*8*	*21.25*	*14.53*	*6.71*	*29.96*	*1.99*	*51.04*	*29.28*	*33.18*	*4.04*
Vespertilionidae	*Eptesicus matroka*	*8*	*25.14*	*6.57*	*5.59*	*38.94*	*2.83*	*66.03*	*38.09*	*42.65*	*5.30*
Vespertilionidae	*Eptesicus nasutus*	*8*	*24.21*	*7.91*	*5.84*	*36.63*	*2.62*	*62.35*	*35.84*	*40.21*	*4.99*
Vespertilionidae	*Eptesicus nilssonii*	8	9.53	10.72	11.72	26.50	0.60	35.95	26.50	28.55	1.07
Vespertilionidae	*Eptesicus pachyotis*	*8*	*24.09*	*8.10*	*5.86*	*36.34*	*2.59*	*61.89*	*35.55*	*39.92*	*4.95*
Vespertilionidae	*Eptesicus platyops*	*8*	*22.60*	*10.95*	*6.28*	*32.92*	*2.28*	*56.18*	*32.17*	*36.31*	*4.47*
Vespertilionidae	*Eptesicus serotinus*	7	25.60	23.09	6.39	26.42	3.20	52.15	26.42	31.17	5.24
Vespertilionidae	*Eptesicus tatei*	*8*	*21.54*	*13.65*	*6.61*	*30.60*	*2.06*	*52.14*	*29.90*	*33.85*	*4.13*
Vespertilionidae	*Euderma maculatum*	7	*21.92*	16.17	4.55	7.50	*5.67*	19	7.50	10.5	*6.70*
Vespertilionidae	*Eudiscopus denticulus*	*8*	*32.33*	*7.20*	*3.45*	*39.85*	*7.98*	*72.64*	*38.51*	*44.79*	*10.92*
Vespertilionidae	*Falsistrellus affinis*	*7*	*34.87*	*10.77*	*3.54*	*40.57*	*12.91*	*71.93*	*38.17*	*44.12*	*15.42*
Vespertilionidae	*Falsistrellus mackenziei*	*7*	35	23	5.00	40	*11.64*	68	33.00	40	*14.08*
Vespertilionidae	*Falsistrellus mordax*	*7*	*35*	*10.46*	*3.52*	*40.85*	*12.96*	*72.39*	*38.44*	*44.43*	*15.48*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	Bandwidth (kHz)	Body Mass (g)	Call Duration (ms)	Characteristic Frequency (kHz)	Dominant Slope (kHz/ms)	Maximum Frequency (kHz)	Minimum Frequency (kHz)	Peak Frequency (kHz)	Total Slope (kHz/ms)
Vespertilionidae	*Falsistrellus petersi*	*7*	*35.66*	*9.05*	*3.43*	*42.35*	*13.19*	*74.68*	*39.85*	*45.97*	*15.78*
Vespertilionidae	*Falsistrellus tasmaniensis*	*7*	35	22.54	6.00	36.00	*10.72*	70.00	35.00	36.00	*13.33*
Vespertilionidae	*Glauconycteris alboguttata*	*8*	*31.18*	*9.05*	*3.61*	*37.19*	*7.67*	*68.31*	*35.91*	*41.93*	*10.48*
Vespertilionidae	*Glauconycteris argentata*	*8*	*33.28*	*9.30*	*3.09*	*36.45*	*9.29*	*69.09*	*35.23*	*41.60*	*12.24*
Vespertilionidae	*Glauconycteris beatrix*	*8*	*34.89*	*7.50*	*2.84*	*38.32*	*10.10*	*72.83*	*37.08*	*43.77*	*13.18*
Vespertilionidae	*Glauconycteris curryae*	*8*	*31.19*	*9.03*	*3.60*	*37.19*	*7.67*	*68.34*	*35.95*	*41.97*	*10.48*
Vespertilionidae	*Glauconycteris egeria*	*8*	*31.62*	*8.41*	*3.54*	*38.13*	*7.79*	*69.87*	*36.86*	*42.95*	*10.65*
Vespertilionidae	*Glauconycteris gleni*	*8*	*30.15*	*10.81*	*3.76*	*34.99*	*7.36*	*64.59*	*33.78*	*39.57*	*10.06*
Vespertilionidae	*Glauconycteris humeralis*	*8*	*34.19*	*5.49*	*3.20*	*44.12*	*8.55*	*79.33*	*42.65*	*49.40*	*11.68*
Vespertilionidae	*Glauconycteris kenyacola*	*8*	*32.56*	*7.17*	*3.41*	*40.29*	*8.07*	*73.34*	*38.90*	*45.24*	*11.03*
Vespertilionidae	*Glauconycteris machadoi*	*8*	*31.19*	*9.03*	*3.60*	*37.19*	*7.67*	*68.34*	*35.95*	*41.97*	*10.48*
Vespertilionidae	*Glauconycteris poensis*	*8*	*32.79*	*6.91*	*3.38*	*40.77*	*8.14*	*74.17*	*39.41*	*45.79*	*11.12*
Vespertilionidae	*Glauconycteris superba*	*8*	*28.28*	*15.00*	*4.07*	*31.28*	*6.81*	*58.02*	*30.20*	*35.55*	*9.32*
Vespertilionidae	*Glauconycteris variegata*	8	34.16	11.25	2.26	33.64	8.49	68.12	33.64	40.63	14.94
Vespertilionidae	*Glischropus javanus*	*8*	*27.09*	*5.37*	*3.78*	*43.51*	*6.74*	*70.74*	*42.56*	*47.42*	*9.46*
Vespertilionidae	*Glischropus tylopus*	8	28.31	4.59	3.43	44.59	6.58	72.99	44.59	48.16	11.16
Vespertilionidae	*Harpiocephalus harpia*	*7*	*52.03*	*13.65*	*2.55*	*36.60*	*27.38*	*90.12*	*34.57*	*48.42*	*26.67*
Vespertilionidae	*Harpiocephalus mordax*	*7*	*51.79*	*20.09*	*2.57*	*36.23*	*27.28*	*89.38*	*34.23*	*47.94*	*26.55*
Vespertilionidae	*Hesperoptenus blanfordi*	*8*	*18.60*	6.91	8.30	36.00	*0.49*	*53.39*	*34.09*	36.00	*2.44*
Vespertilionidae	*Hesperoptenus doriae*	*8*	*19.40*	*9.74*	*7.09*	*33.25*	*1.01*	*52.30*	*32.39*	*35.41*	*3.05*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	Bandwidth (kHz)	Body Mass (g)	Call Duration (ms)	Characteristic Frequency (kHz)	Dominant Slope (kHz/ms)	Maximum Frequency (kHz)	Minimum Frequency (kHz)	Peak Frequency (kHz)	Total Slope (kHz/ms)
Vespertilionidae	*Hesperoptenus gaskelli*	*8*	*21.23*	*9.40*	*6.37*	*32.59*	*2.00*	*53.38*	*31.69*	*35.27*	*4.19*
Vespertilionidae	*Hesperoptenus tickelli*	*8*	*19.21*	*16.30*	*7.05*	*28.19*	*1.58*	*45.72*	*27.39*	*30.69*	*3.54*
Vespertilionidae	*Hesperoptenus tomesi*	*8*	*18.36*	*20.66*	*7.36*	*26.47*	*1.41*	*42.60*	*25.71*	*28.90*	*3.27*
Vespertilionidae	*Histiotus alienus*	*8*	*22.44*	*11.63*	*6.50*	*31.82*	*2.20*	*54.58*	*31.09*	*35.20*	*4.37*
Vespertilionidae	*Histiotus humboldti*	*8*	*22.44*	*11.63*	*6.50*	*31.82*	*2.20*	*54.58*	*31.09*	*35.20*	*4.37*
Vespertilionidae	*Histiotus laephotis*	*8*	*22.44*	*11.63*	*6.50*	*31.82*	*2.20*	*54.58*	*31.09*	*35.20*	*4.37*
Vespertilionidae	*Histiotus macrotus*	*8*	*22.72*	*11.00*	*6.41*	*32.43*	*2.25*	*55.65*	*31.72*	*35.84*	*4.46*
Vespertilionidae	*Histiotus magellanicus*	*8*	*22.44*	*11.63*	*6.50*	*31.82*	*2.20*	*54.58*	*31.09*	*35.20*	*4.37*
Vespertilionidae	*Histiotus montanus*	*8*	*21.10*	*15.94*	*6.93*	*28.99*	*1.92*	*49.59*	*28.36*	*32.20*	*3.94*
Vespertilionidae	*Histiotus velatus*	*8*	*22.55*	*11.32*	*6.46*	*32.07*	*2.22*	*55.03*	*31.34*	*35.45*	*4.41*
Vespertilionidae	*Hypsugo alaschanicus*	*7*	*21.66*	*5.60*	*4.41*	*40.33*	*4.00*	*61.56*	*39.41*	*42.52*	*6.48*
Vespertilionidae	*Hypsugo anchietae*	7	46.28	*8.74*	1.87	46.64	32.56	92.71	46.64	54.90	27.16
Vespertilionidae	*Hypsugo anthonyi*	*7*	*20.00*	*8.41*	*4.79*	*35.87*	*3.55*	*54.88*	*35.02*	*38.02*	*5.84*
Vespertilionidae	*Hypsugo arabicus*	*7*	*24.07*	*3.17*	*3.94*	*47.47*	*4.64*	*71.54*	*46.43*	*49.70*	*7.42*
Vespertilionidae	*Hypsugo ariel*	7	16.14	4.07	1.96	45.47	17.30	60.74	44.49	45.47	8.53
Vespertilionidae	*Hypsugo bodenheimeri*	8	18.09	2.73	3.97	44.26	1.13	62.43	44.26	46.91	4.57
Vespertilionidae	*Hypsugo cadornae*	*7*	*20.92*	*6.69*	*4.57*	*38.28*	*3.80*	*58.58*	*37.41*	*40.49*	*6.20*
Vespertilionidae	*Hypsugo crassulus*	*7*	*21.31*	*6.09*	*4.49*	*39.33*	*3.90*	*60.14*	*38.47*	*41.55*	*6.34*
Vespertilionidae	*Hypsugo eisentrauti*	*7*	*24.83*	*6.11*	*5.05*	*41.51*	*3.41*	*65.19*	*39.92*	*43.77*	*6.20*
Vespertilionidae	*Hypsugo imbricatus*	*7*	*21.17*	*6.29*	*4.52*	*38.98*	*3.87*	*59.60*	*38.09*	*41.18*	*6.30*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Vespertilionidae	*Hypsugo joffrei*	*7*	*19.71*	*9.05*	*4.86*	*35.13*	*3.48*	*53.71*	*34.30*	*37.26*	*5.73*
Vespertilionidae	*Hypsugo kitcheneri*	*7*	*20.62*	*7.20*	*4.64*	*37.49*	*3.72*	*57.38*	*36.63*	*39.69*	*6.09*
Vespertilionidae	*Hypsugo lophurus*	*7*	*20.96*	*6.64*	*4.57*	*38.40*	*3.80*	*58.71*	*37.52*	*40.57*	*6.21*
Vespertilionidae	*Hypsugo macrotis*	*7*	*22.01*	*5.14*	*4.34*	*41.31*	*4.09*	*63.01*	*40.37*	*43.51*	*6.62*
Vespertilionidae	*Hypsugo musciculus*	*7*	*26.13*	*1.99*	*3.59*	*54.27*	*5.20*	*80.26*	*53.09*	*56.49*	*8.22*
Vespertilionidae	*Hypsugo pulveratus*	*7*	*21.71*	*5.53*	*4.40*	*40.45*	*4.00*	*61.76*	*39.53*	*42.65*	*6.50*
Vespertilionidae	*Hypsugo savii*	8	16.70	6.30	7.08	33.59	1.96	50.32	33.59	36.15	3.74
Vespertilionidae	*Hypsugo vordermanni*	*7*	*21.66*	*5.60*	*4.41*	*40.33*	*4.00*	*61.56*	*39.41*	*42.52*	*6.48*
Vespertilionidae	*Ia io*	*8*	*18.86*	49.3	3.80	25	*6.90*	*37.20*	*22.87*	25	*8.33*
Vespertilionidae	*Idionycteris phyllotis*	10	15.83	12.13	2.92	13.69	4.82	29.67	13.69	20.37	5.25
Vespertilionidae	*Kerivoula africana*	*7*	*56.27*	*3.50*	*1.72*	*81.53*	*31.96*	*135.96*	*78.02*	*93.97*	*32.24*
Vespertilionidae	*Kerivoula agnella*	*7*	*50.74*	*7.20*	*2.04*	*63.62*	*29.56*	*115.13*	*60.89*	*74.22*	*29.39*
Vespertilionidae	*Kerivoula argentata*	*7*	36	10.11	2.3	92	*21.69*	*117.94*	*85.29*	92	*21.91*
Vespertilionidae	*Kerivoula cuprosa*	*7*	*52.63*	*5.61*	*1.92*	*69.34*	*30.37*	*122.32*	*66.35*	*80.56*	*30.36*
Vespertilionidae	*Kerivoula eriophora*	*7*	*56.27*	*3.50*	*1.72*	*81.53*	*31.96*	*135.96*	*78.02*	*93.97*	*32.24*
Vespertilionidae	*Kerivoula flora*	*7*	*52.10*	*6.01*	*1.95*	*67.69*	*30.15*	*120.34*	*64.78*	*78.73*	*30.09*
Vespertilionidae	*Kerivoula hardwickii*	7	95.09	4.55	1.99	92.97	39.78	188.17	92.97	148.17	39.87
Vespertilionidae	*Kerivoula intermedia*	7	69.35	3.68	2.74	77.55	39.52	147.15	77.55	83.82	38.91
Vespertilionidae	*Kerivoula lanosa*	7	43.33	6.66	2.13	36.88	27.63	79.77	36.88	45.57	24.06
Vespertilionidae	*Kerivoula lenis*	*7*	*53.45*	*5.03*	*1.87*	*71.95*	*30.73*	*125.22*	*68.85*	*83.43*	*30.79*

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Vespertilionidae	*Kerivoula minuta*	*7*	47.83	2.03	1.16	105.05	47.57	152.88	105.05	105.05	43.40
Vespertilionidae	*Kerivoula muscina*	*7*	*53.07*	*5.29*	*1.89*	*70.74*	*30.57*	*123.88*	*67.69*	*82.11*	*30.60*
Vespertilionidae	*Kerivoula myrella*	*7*	*50.74*	*7.20*	*2.04*	*63.62*	*29.56*	*115.13*	*60.89*	*74.22*	*29.39*
Vespertilionidae	*Kerivoula papillosa*	7	64.80	10.21	1.62	108.10	33.39	150.37	85.53	108.10	35.42
Vespertilionidae	*Kerivoula pellucida*	7	59.03	4.14	1.86	94.18	32.63	153.21	94.18	147.27	24.61
Vespertilionidae	*Kerivoula phalaena*	*7*	*57.42*	*3.03*	*1.66*	*85.71*	*32.44*	*140.42*	*82.02*	*98.59*	*32.81*
Vespertilionidae	*Kerivoula picta*	*7*	*66.93*	4.50	0.58	116	*51.04*	*160.28*	*101.09*	116	*48.86*
Vespertilionidae	*Kerivoula smithii*	*7*	*52.29*	*5.86*	*1.94*	*68.31*	*30.24*	*121*	*65.37*	*79.36*	*30.19*
Vespertilionidae	*Kerivoula whiteheadi*	*7*	*56.76*	*3.29*	*1.69*	*83.26*	*32.17*	*137.83*	*79.76*	*95.97*	*32.48*
Vespertilionidae	*Laephotis angolensis*	*3*	*22.03*	*6.11*	*4.54*	*31.19*	*4.79*	*50.94*	*29.93*	*33.52*	*7.28*
Vespertilionidae	*Laephotis botswanae*	*3*	22	7.28	5.00	33.00	*3.53*	*46.64*	*29.17*	33.00	*5.81*
Vespertilionidae	*Laephotis namibensis*	*3*	13.5	8.72	2.6	22.00	*2.06*	*31.47*	*21.78*	22.00	*3.90*
Vespertilionidae	*Laephotis wintoni*	3	5.85	6.10	10.95	21.05	0.53	26.90	21.05	23.08	0.58
Vespertilionidae	*Lasionycteris noctivagans*	8	24.76	11.02	9.21	26.33	0.83	51.04	26.33	30.19	2.51
Vespertilionidae	*Lasiurus atratus*	*3*	*17.49*	*12.09*	*7.11*	*34.47*	*0.95*	*52.39*	*34.23*	*37.90*	*2.69*
Vespertilionidae	*Lasiurus blossevillii*	*3*	*16.30*	*11.58*	*7.24*	*36.45*	*0.63*	*53.13*	*36.31*	*39.45*	*2.27*
Vespertilionidae	*Lasiurus borealis*	3	13.84	12.33	8.50	38.56	0.62	52.48	38.56	40.95	1.60
Vespertilionidae	*Lasiurus castaneus*	*3*	*22.86*	*12.51*	*6.30*	*30.72*	*2.60*	*53.54*	*30.20*	*35.41*	*4.72*
Vespertilionidae	*Lasiurus cinereus*	3	*16.96*	27.06	9.30	17	*0.78*	29	17	23.9	*2.21*
Vespertilionidae	*Lasiurus degelidus*	*3*	*17.35*	*12.01*	*7.12*	*34.71*	*0.92*	*52.49*	*34.47*	*38.09*	*2.64*

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		Echolocation Call Type	Bandwidth (kHz)	Body Mass (g)	Call Duration (ms)	Characteristic Frequency (kHz)	Dominant Slope (kHz/ms)	Maximum Frequency (kHz)	Minimum Frequency (kHz)	Peak Frequency (kHz)	Total Slope (kHz/ms)
Vespertilionidae	*Lasiurus ebenus*	*3*	*22.47*	*14.00*	*6.42*	*29.93*	*2.52*	*52.11*	*29.43*	*34.54*	*4.60*
Vespertilionidae	*Lasiurus ega*	*7*	*23.41*	12.2	9.10	28.8	*2.50*	*51.47*	28.8	32.20	*4.69*
Vespertilionidae	*Lasiurus egregius*	*3*	*21.74*	*17.41*	*6.65*	*28.45*	*2.35*	*49.41*	*27.97*	*32.92*	*4.35*
Vespertilionidae	*Lasiurus insularis*	*3*	*24.95*	*15.15*	*5.96*	*30.02*	*3.40*	*54.35*	*29.46*	*34.99*	*5.67*
Vespertilionidae	*Lasiurus intermedius*	7	30.41	22.96	3.18	31.04	4.22	60.89	31.04	36.18	8.32
Vespertilionidae	*Lasiurus minor*	*3*	*22.38*	*14.40*	*6.44*	*29.73*	*2.49*	*51.75*	*29.22*	*34.33*	*4.56*
Vespertilionidae	*Lasiurus pfeifferi*	*3*	*16.73*	*11.37*	*7.15*	*36.42*	*0.73*	*53.63*	*36.23*	*39.57*	*2.41*
Vespertilionidae	*Lasiurus salinae*	*3*	*22.38*	*14.40*	*6.44*	*29.73*	*2.49*	*51.75*	*29.22*	*34.33*	*4.56*
Vespertilionidae	*Lasiurus seminolus*	*3*	*16.92*	*9.88*	*7.08*	*36.97*	*0.76*	*54.43*	*36.78*	*40.13*	*2.46*
Vespertilionidae	*Lasiurus varius*	*3*	*22.38*	*14.40*	*6.44*	*29.73*	*2.49*	*51.75*	*29.22*	*34.33*	*4.56*
Vespertilionidae	*Lasiurus xanthinus*	*3*	*24.80*	*15.10*	*5.99*	*30.02*	*3.34*	*54.18*	*29.43*	*34.95*	*5.59*
Vespertilionidae	*Mimetillus moloneyi*	*8*	*31.51*	*8.89*	*3.56*	*38.05*	*7.74*	*69.69*	*36.74*	*42.86*	*10.59*
Vespertilionidae	*Murina aenea*	*7*	*56.61*	7.50	2.40	83.00	*28.75*	*131.10*	*69.34*	83.00	*28.99*
Vespertilionidae	*Murina aurata*	*7*	*66.67*	*4.27*	*1.60*	*67.83*	*36.91*	*137.59*	*63.75*	*85.88*	*36.37*
Vespertilionidae	*Murina cyclotis*	*7*	*56.34*	9.35	2.00	77.00	*31.22*	*125.66*	*64.14*	77.00	*30.85*
Vespertilionidae	*Murina florium*	7	44.82	4.41	1.01	60.51	23.81	99.58	54.76	60.51	21.75
Vespertilionidae	*Murina fusca*	*7*	*64.00*	*6.14*	*1.72*	*60.89*	*35.77*	*128.37*	*57.17*	*77.40*	*35.04*
Vespertilionidae	*Murina grisea*	*7*	*64.66*	*5.61*	*1.69*	*62.55*	*36.05*	*130.64*	*58.73*	*79.44*	*35.36*
Vespertilionidae	*Murina hilgendorfi*	7	75.22	*8.08*	1.37	40.96	48.02	116.47	40.96	58.22	46.26
Vespertilionidae	*Murina huttoni*	*7*	*62.31*	*7.56*	*1.92*	*49.35*	*33.49*	*116.64*	*46.62*	*65.83*	*32.65*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Vespertilionidae	*Murina leucogaster*	*7*	70	7.54	3.00	25	*44.05*	195.00	25	70	*39.95*
Vespertilionidae	*Murina puta*	7	70.19	6.91	1.49	54.90	40.87	125.03	54.90	65.99	43.39
Vespertilionidae	*Murina rozendaali*	*7*	*64.66*	*5.61*	*1.69*	*62.55*	*36.05*	*130.64*	*58.73*	*79.44*	*35.36*
Vespertilionidae	*Murina ryukyuana*	*7*	*67.54*	*5.89*	*1.73*	*48.42*	*38.21*	*120.78*	*45.83*	*66.35*	*36.88*
Vespertilionidae	*Murina silvatica*	*7*	*66.32*	*4.48*	*1.62*	*66.89*	*36.76*	*136.42*	*62.87*	*84.69*	*36.20*
Vespertilionidae	*Murina suilla*	7	92.50	4	1.25	60.56	50.56	153.06	60.56	124.14	60.07
Vespertilionidae	*Murina tenebrosa*	*7*	*63.72*	*6.38*	*1.74*	*60.16*	*35.65*	*127.46*	*56.54*	*76.55*	*34.90*
Vespertilionidae	*Murina tubinaris*	*7*	*64.87*	*5.45*	*1.68*	*63.05*	*36.15*	*131.33*	*59.26*	*80.08*	*35.47*
Vespertilionidae	*Murina ussuriensis*	7	71.59	4.69	1.84	43.35	40.56	115.90	43.35	67.14	40.94
Vespertilionidae	*Myotis abei*	*7*	*49.42*	*6.11*	*3.37*	*37.60*	*13.36*	*90.59*	*36.53*	*49.85*	*16.27*
Vespertilionidae	*Myotis adversus*	*7*	*47.68*	10.41	4.68	30.00	*10.12*	82	30.00	46.00	*13.04*
Vespertilionidae	*Myotis aelleni*	*7*	*46.27*	*9.40*	*3.74*	*32.39*	*12.40*	*80.26*	*31.44*	*43.21*	*15.03*
Vespertilionidae	*Myotis albescens*	7	44.23	5.69	1.49	73.02	32.33	102.98	58.75	73.02	30.09
Vespertilionidae	*Myotis alcathoe*	7	51.15	*8.17*	2.24	44.87	28.62	96.18	44.87	59.74	25.17
Vespertilionidae	*Myotis altarium*	*7*	*39.77*	*11.00*	*4.56*	*33.55*	*7.53*	*75.41*	*32.95*	*43.68*	*10.42*
Vespertilionidae	*Myotis anjouanensis*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis annamiticus*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis annectans*	*7*	*45.34*	*9.75*	*3.28*	*36.05*	*14.12*	*83.76*	*35.20*	*47.51*	*16.46*
Vespertilionidae	*Myotis atacamensis*	*7*	*37.46*	*7.37*	*2.73*	*39.57*	*13.37*	*77.21*	*38.63*	*47.32*	*15.97*
Vespertilionidae	*Myotis ater*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	Bandwidth (kHz)	Body Mass (g)	Call Duration (ms)	Characteristic Frequency (kHz)	Dominant Slope (kHz/ms)	Maximum Frequency (kHz)	Minimum Frequency (kHz)	Peak Frequency (kHz)	Total Slope (kHz/ms)
Vespertilionidae	*Myotis auriculus*	7	59.76	38.04	3.46	35.97	19.93	96.08	35.97	49.60	19.42
Vespertilionidae	*Myotis australis*	*7*	*47.64*	*7.79*	*3.57*	*34.57*	*12.81*	*84.68*	*33.55*	*46.02*	*15.56*
Vespertilionidae	*Myotis austroriparius*	*7*	*37.80*	*7.35*	*2.71*	*40.53*	*13.85*	*78.48*	*39.49*	*48.23*	*16.40*
Vespertilionidae	*Myotis bechsteinii*	7	48.09	9.47	3.51	32.47	17.05	81.20	32.47	46.11	16.98
Vespertilionidae	*Myotis blythii*	8	53.72	23.82	3.54	29.94	18.49	83.39	29.94	44.00	18.30
Vespertilionidae	*Myotis bocagii*	7	36.58	7.93	2.20	28.17	16.70	64.74	28.17	41.26	16.34
Vespertilionidae	*Myotis bombinus*	*7*	*66.90*	*9.74*	*4.12*	*24.00*	*16.06*	*87.12*	*22.94*	*38.71*	*18.78*
Vespertilionidae	*Myotis brandtii*	7	52.67	5.30	2.89	35.95	20.29	88.99	35.95	49.27	19.53
Vespertilionidae	*Myotis bucharensis*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis californicus*	7	48.61	4.39	3.29	37.55	14.52	86.01	37.55	51.44	14.83
Vespertilionidae	*Myotis capaccinii*	7	41.38	8.15	3.55	36.97	9.53	78.39	36.97	52.27	11.40
Vespertilionidae	*Myotis chiloensis*	*7*	*33.60*	8.41	2.10	43.4	*14.11*	*72.73*	*39.25*	43.4	*16.39*
Vespertilionidae	*Myotis chinensis*	7	33.68	41.99	4.56	25.30	7.02	59.10	25.30	34.47	8.55
Vespertilionidae	*Myotis ciliolabrum*	*7*	*49.52*	*4.89*	*3.23*	*39.37*	*12.34*	*92.43*	*37.86*	*52.35*	*15.55*
Vespertilionidae	*Myotis cobanensis*	*7*	*45.25*	*10.82*	*3.87*	*30.85*	*12.09*	*77.02*	*29.93*	*41.26*	*14.64*
Vespertilionidae	*Myotis csorbai*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis dasycneme*	7	32.90	15.16	4.45	28.15	5.38	60.86	28.15	39.43	6.46
Vespertilionidae	*Myotis daubentonii*	7	42.78	7.63	3.26	33.09	11.57	75.79	33.09	46.98	12.72
Vespertilionidae	*Myotis davidii*	*7*	*47.08*	*13.24*	*4.05*	*30.30*	*11.63*	*78.87*	*29.55*	*42.31*	*14.05*
Vespertilionidae	*Myotis dominicensis*	7	33.08	6.11	2.90	44.46	6.80	77.71	44.46	50.78	12.05

Family	Species	Species sets for each parameter									
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Vespertilionidae	*Myotis elegans*	7	45.92	4.21	2.61	66.28	9.25	101.16	55.92	66.28	17.90
Vespertilionidae	*Myotis emarginatus*	7	54.29	7.56	2.15	42.95	27.27	97.23	42.95	60.75	25.96
Vespertilionidae	*Myotis evotis*	*7*	40.00	6.91	2.72	52.00	*12.76*	80	40	52.00	*15.30*
Vespertilionidae	*Myotis fimbriatus*	7	58.95	*12.34*	2.80	15.45	20.77	74.56	15.45	26.34	23.03
Vespertilionidae	*Myotis findleyi*	*7*	*51.07*	*4.91*	*3.20*	*40.57*	*13.85*	*96.06*	*39.41*	*53.57*	*16.91*
Vespertilionidae	*Myotis formosus*	7	54.36	7.07	2.35	38.92	28.42	93.39	38.92	54.26	25.92
Vespertilionidae	*Myotis fortidens*	*7*	*42.56*	*4.37*	*2.47*	*51.99*	*14.91*	*95.49*	*50.55*	*60.89*	*17.91*
Vespertilionidae	*Myotis frater*	*7*	60.6	7.54	3.50	*51.01*	*15.56*	110.80	50.20	*68.17*	*18.76*
Vespertilionidae	*Myotis gomantongensis*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis goudoti*	7	58.34	5.56	3.01	45.62	15.50	103.93	45.62	64.37	19.65
Vespertilionidae	*Myotis grisescens*	*7*	*36.23*	*10.84*	*2.87*	*37.26*	*13.30*	*73.00*	*36.31*	*44.52*	*15.70*
Vespertilionidae	*Myotis hajastanicus*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis hasseltii*	7	42.67	8.70	5.63	37.26	6.53	79.95	37.26	47.72	7.88
Vespertilionidae	*Myotis hermani*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis horsfieldii*	*7*	*41.71*	*6.05*	*4.12*	*39.92*	*7.91*	*85.56*	*39.33*	*51.21*	*11.09*
Vespertilionidae	*Myotis hosonoi*	*7*	*48.80*	*6.64*	*3.44*	*36.53*	*13.17*	*88.55*	*35.48*	*48.47*	*16.02*
Vespertilionidae	*Myotis ikonnikovi*	7	59.03	5.86	2.18	40.02	32.42	98.73	40.02	48.34	28.24
Vespertilionidae	*Myotis insularum*	*7*	*49.42*	*6.11*	*3.37*	*37.60*	*13.36*	*90.59*	*36.53*	*49.85*	*16.27*
Vespertilionidae	*Myotis keaysi*	8	45.62	5.45	2.92	59.33	19.29	105.43	59.33	62.93	18.00
Vespertilionidae	*Myotis keenii*	7	67.77	6.51	1.14	39.84	40.05	107.53	39.84	59.67	38.87

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Vespertilionidae	*Myotis laniger*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis leibii*	8	52.90	5.22	3.77	38.88	9.21	91.73	38.88	55.78	13.31
Vespertilionidae	*Myotis levis*	*8*	*34.65*	*5.49*	*4.11*	*51.01*	*5.32*	*86.97*	*49.80*	*57.74*	*8.72*
Vespertilionidae	*Myotis longipes*	7	39.29	7.2	5.33	37.10	9.53	76.21	37.10	44.64	9.85
Vespertilionidae	*Myotis lucifugus*	8	41.15	7.80	2.52	36.55	12.39	77.15	36.55	47.39	14.87
Vespertilionidae	*Myotis macrodactylus*	7	41.09	7.48	4.68	43.84	2.93	85.54	43.84	51.29	8.64
Vespertilionidae	*Myotis macropus*	7	32.48	*8.32*	3.15	39.38	8.82	72.09	39.38	48.62	11.81
Vespertilionidae	*Myotis macrotarsus*	*7*	*37.28*	*12.64*	*4.69*	*33.28*	*6.88*	*72.45*	*32.79*	*42.82*	*9.67*
Vespertilionidae	*Myotis martiniquensis*	8	40.14	7.49	2.14	31.12	16.26	71.03	31.12	47.03	21.14
Vespertilionidae	*Myotis melanorhinus*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*
Vespertilionidae	*Myotis moluccarum*	10	46.60	*7.66*	4.84	32.10	5.11	78.70	32.10	41.94	8.08
Vespertilionidae	*Myotis montivagus*	*7*	*46.64*	*8.30*	*3.14*	*38.40*	*14.54*	*88.13*	*37.49*	*50.45*	*16.99*
Vespertilionidae	*Myotis morrisi*	*7*	*43.40*	*14.09*	*4.12*	*28.16*	*11.53*	*71.12*	*27.30*	*37.79*	*13.92*
Vespertilionidae	*Myotis muricola*	7	48.10	4.8	5.07	34.95	5.31	83.25	34.95	48.69	9.06
Vespertilionidae	*Myotis myotis*	8	38.52	25.59	5.24	26.24	7.91	64.95	26.24	35.45	8.50
Vespertilionidae	*Myotis mystacinus*	7	53.62	*7.61*	2.40	37.55	24.28	91.04	37.55	52.66	23.17
Vespertilionidae	*Myotis nattereri*	7	67.57	7.25	3.47	25.55	18.28	93.30	25.55	46.95	19.66
Vespertilionidae	*Myotis nesopolus*	*7*	*53.52*	*3.56*	*2.96*	*45.33*	*14.60*	*104.45*	*44.08*	*59.62*	*17.88*
Vespertilionidae	*Myotis nigricans*	8	34.18	*5.53*	5.18	51.68	1.78	86.13	51.68	56.20	6.33
Vespertilionidae	*Myotis nipalensis*	*7*	*47.75*	*7.66*	*3.56*	*34.78*	*12.85*	*85.08*	*33.75*	*46.25*	*15.61*

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Vespertilionidae	*Myotis occultus*	*8*	*45.31*	*8.79*	*2.98*	*34.92*	*14.13*	*81.65*	*33.68*	*46.02*	*16.64*
Vespertilionidae	*Myotis oreias*	*7*	*47.08*	*8.41*	*3.64*	*33.65*	*12.65*	*82.86*	*32.69*	*44.84*	*15.35*
Vespertilionidae	*Myotis oxygnathus*	*7*	*40.58*	*21.23*	*4.55*	*24.43*	*10.68*	*62.43*	*23.69*	*33.02*	*12.82*
Vespertilionidae	*Myotis oxyotus*	*7*	*35.88*	*5.65*	*3.72*	*50.25*	*6.98*	*87.31*	*48.96*	*57.34*	*10.36*
Vespertilionidae	*Myotis ozensis*	*7*	*49.74*	*5.86*	*3.34*	*38.13*	*13.45*	*91.62*	*37.04*	*50.55*	*16.39*
Vespertilionidae	*Myotis peninsularis*	*7*	*46.54*	*9.05*	*3.71*	*32.82*	*12.48*	*81.14*	*31.85*	*43.77*	*15.14*
Vespertilionidae	*Myotis pequinius*	*7*	*71.39*	17.41	5.72	17	*16.55*	84	17	33.00	*19.13*
Vespertilionidae	*Myotis planiceps*	*7*	*54.89*	*2.99*	*2.84*	*48.13*	*15.02*	*109.20*	*46.81*	*63.18*	*18.42*
Vespertilionidae	*Myotis pruinosus*	*7*	*50.14*	*4.91*	*2.80*	*45.29*	*15.68*	*100.20*	*44.26*	*59.09*	*18.43*
Vespertilionidae	*Myotis punicus*	7	32.61	*18.92*	3.91	27.16	7.43	60.30	27.16	35.43	8.51
Vespertilionidae	*Myotis ricketti*	7	39.36	26.19	3.65	30.62	10.01	70.10	30.62	40.52	10.83
Vespertilionidae	*Myotis ridleyi*	*7*	*45.32*	*4.06*	*3.90*	*48.86*	*7.18*	*99.04*	*48.18*	*61.50*	*10.96*
Vespertilionidae	*Myotis riparius*	10	34.33	4.57	3.19	55.35	6.94	90.28	55.35	57.68	11.87
Vespertilionidae	*Myotis rosseti*	*7*	*54.13*	*3.29*	*2.90*	*46.57*	*14.78*	*106.50*	*45.29*	*61.19*	*18.12*
Vespertilionidae	*Myotis ruber*	*8*	*41.04*	*4.99*	*2.84*	*55.09*	*11.75*	*95.75*	*53.41*	*62.49*	*15.28*
Vespertilionidae	*Myotis schaubi*	*7*	*62.15*	*11.99*	*4.10*	*24.98*	*15.10*	*84.81*	*24.00*	*39.17*	*17.70*
Vespertilionidae	*Myotis scotti*	*7*	*48.29*	*8.72*	*2.52*	*37.19*	*19.52*	*88.13*	*36.42*	*50.20*	*21.06*
Vespertilionidae	*Myotis septentrionalis*	*7*	68.39	*18.28*	2.95	38.37	20.18	106.94	38.37	49.93	27.28
Vespertilionidae	*Myotis sicarius*	*7*	*43.29*	*20.09*	*4.24*	*28.28*	*11.27*	*71.50*	*27.63*	*38.94*	*13.46*
Vespertilionidae	*Myotis siligorensis*	8	49.13	2.93	4.45	79.76	1.36	125.03	76.43	79.76	13.26

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Vespertilionidae	*Myotis simus*	*8*	*38.61*	*8.10*	*3.10*	*51.11*	*10.38*	*89.08*	*49.55*	*57.74*	*13.85*
Vespertilionidae	*Myotis sodalis*	*7*	*46.50*	*7.15*	*3.16*	*40.57*	*14.16*	*89.06*	*39.33*	*51.42*	*16.98*
Vespertilionidae	*Myotis stalkeri*	*7*	*42.34*	*16.43*	*4.28*	*26.68*	*11.21*	*67.80*	*25.89*	*35.91*	*13.50*
Vespertilionidae	*Myotis thysanodes*	7	66.97	8.49	4.01	17.87	17.07	84.71	17.87	36.52	18.38
Vespertilionidae	*Myotis tricolor*	7	56.91	13.67	2.16	34.64	28.59	90.97	34.64	49.12	27.29
Vespertilionidae	*Myotis velifer*	7	37.54	9.82	2.48	38.70	20.99	76.21	38.70	43.44	17.31
Vespertilionidae	*Myotis vivesi*	*7*	*34.31*	*25.63*	*3.71*	*29.81*	*11.58*	*61.45*	*28.88*	*36.34*	*13.67*
Vespertilionidae	*Myotis volans*	7	44.71	8.71	3.71	37.95	14.14	82.82	37.95	46.39	14.80
Vespertilionidae	*Myotis welwitschii*	7	28.30	15.88	2.47	23.06	10.19	51.54	23.06	32.66	11.96
Vespertilionidae	*Myotis yanbarensis*	*7*	*47.25*	*7.59*	*3.07*	*39.53*	*14.74*	*90.17*	*38.59*	*51.88*	*17.24*
Vespertilionidae	*Myotis yesoensis*	*7*	*49.42*	*6.11*	*3.37*	*37.60*	*13.36*	*90.59*	*36.53*	*49.85*	*16.27*
Vespertilionidae	*Myotis yumanensis*	*7*	*39.13*	*5.15*	*2.39*	*43.51*	*16.53*	*83.10*	*42.56*	*51.47*	*18.81*
Vespertilionidae	*Neoromicia brunneus*	*8*	*27.44*	*6.91*	*3.48*	*44.08*	*8.95*	*68.43*	*42.35*	*45.88*	*11.71*
Vespertilionidae	*Neoromicia capensis*	8	33.78	5.96	3.81	36.36	6.64	70.32	36.36	40.91	10.35
Vespertilionidae	*Neoromicia flavescens*	*8*	*25.98*	*10.50*	*3.75*	*41.06*	*8.14*	*63.89*	*39.45*	*42.86*	*10.77*
Vespertilionidae	*Neoromicia guineensis*	*8*	*30.30*	*3.50*	*3.12*	*53.52*	*9.57*	*80.73*	*51.47*	*55.20*	*12.69*
Vespertilionidae	*Neoromicia helios*	*8*	*30.23*	*3.56*	*3.13*	*53.30*	*9.54*	*80.46*	*51.21*	*54.98*	*12.66*
Vespertilionidae	*Neoromicia melckorum*	*8*	*27.43*	*7.20*	*3.52*	*44.97*	*8.62*	*69.46*	*43.21*	*46.71*	*11.42*
Vespertilionidae	*Neoromicia nanus*	8	22.58	3.88	4.63	68.34	5.23	90.87	68.34	69.41	6.90
Vespertilionidae	*Neoromicia rendalli*	*8*	*27.76*	*6.42*	*3.43*	*44.97*	*9.06*	*69.67*	*43.21*	*46.76*	*11.86*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	Bandwidth (kHz)	Body Mass (g)	Call Duration (ms)	Characteristic Frequency (kHz)	Dominant Slope (kHz/ms)	Maximum Frequency (kHz)	Minimum Frequency (kHz)	Peak Frequency (kHz)	Total Slope (kHz/ms)
Vespertilionidae	*Neoromicia somalicus*	8	43.30	3.53	2.15	36.99	28.92	80.00	36.99	44.98	25.51
Vespertilionidae	*Neoromicia tenuipinnis*	*8*	25	5.35	1.5	*56.66*	*12.41*	37	62	*49.25*	*15.05*
Vespertilionidae	*Neoromicia zuluensis*	7	41.14	4.14	3.06	44.89	12.40	75.71	33.82	44.89	14.56
Vespertilionidae	*Nyctalus aviator*	7	27.72	31.87	1.89	22.76	13.56	50.81	22.76	40.29	16.42
Vespertilionidae	*Nyctalus azoreum*	*8*	*20.34*	8.80	16	30.00	*1.50*	*47.35*	*26.44*	30.00	*3.21*
Vespertilionidae	*Nyctalus furvus*	*10*	*20.73*	*14.86*	*5.81*	*26.18*	*4.96*	*46.34*	*25.46*	*30.81*	*6.33*
Vespertilionidae	*Nyctalus lasiopterus*	8	5.03	45.98	22.03	14.20	0.15	19.29	14.20	15.23	0.23
Vespertilionidae	*Nyctalus leisleri*	8	21.30	12.47	7.97	26.52	1.33	48.02	26.52	30.67	3.61
Vespertilionidae	*Nyctalus montanus*	*10*	*20.73*	*14.86*	*5.81*	*26.18*	*4.96*	*46.34*	*25.46*	*30.81*	*6.33*
Vespertilionidae	*Nyctalus noctula*	3	10.01	28.48	13.13	21.33	0.44	31.44	21.33	22.86	1.00
Vespertilionidae	*Nyctalus plancyi*	10	29.27	*15.15*	1.85	23.37	16.26	52.75	23.37	34.96	17.63
Vespertilionidae	*Nycticeinops schlieffeni*	8	25.59	5.05	2.82	38.87	2.54	64.29	38.87	43.73	8.88
Vespertilionidae	*Nycticeius aenobarbus*	*8*	*24.15*	*14.11*	*5.39*	*34.71*	*4.07*	*56.88*	*33.65*	*37.11*	*6.58*
Vespertilionidae	*Nycticeius cubanus*	*8*	*19.56*	*14.66*	4.53	33.00	*3.30*	47.00	33.00	36.00	*5.55*
Vespertilionidae	*Nycticeius humeralis*	*8*	*28.83*	*9.12*	*4.98*	*39.69*	*5.01*	*67.55*	*38.24*	*42.82*	*7.88*
Vespertilionidae	*Nyctophilus arnhemensis*	*8*	35	6.83	3.00	51.00	*8.10*	80	45.00	51.00	*11.40*
Vespertilionidae	*Nyctophilus bifax*	*8*	*19.73*	9.89	*5.27*	46.00	*1.85*	59	46.00	55.00	*4.18*
Vespertilionidae	*Nyctophilus geoffroyi*	8	45.96	8.20	4.44	37.49	12.40	84.68	37.49	49.77	14.77
Vespertilionidae	*Nyctophilus gouldi*	*8*	*34.38*	*11.32*	*4.63*	*37.19*	*6.95*	*70.22*	*35.30*	*42.52*	*10.00*
Vespertilionidae	*Nyctophilus heran*	*8*	*26.00*	*7.61*	*4.79*	*45.29*	*3.65*	*69.69*	*43.38*	*47.80*	*6.50*

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Vespertilionidae	*Nyctophilus howensis*	*8*	*26.00*	*7.61*	*4.79*	*45.29*	*3.65*	*69.69*	*43.38*	*47.80*	*6.50*
Vespertilionidae	*Nyctophilus microdon*	*8*	*25.21*	*9.05*	*4.96*	*43.03*	*3.46*	*66.57*	*41.22*	*45.56*	*6.22*
Vespertilionidae	*Nyctophilus microtis*	*8*	*26.20*	*7.29*	*4.75*	*45.83*	*3.70*	*70.48*	*43.95*	*48.38*	*6.57*
Vespertilionidae	*Nyctophilus nebulosus*	*8*	*26.00*	*7.61*	*4.79*	*45.29*	*3.65*	*69.69*	*43.38*	*47.80*	*6.50*
Vespertilionidae	*Nyctophilus timoriensis*	*8*	*23.85*	11.02	*5.08*	44.40	*3.17*	*64.77*	*41.31*	44.40	*5.82*
Vespertilionidae	*Nyctophilus walkeri*	*8*	26	4.44	5.00	56.00	*3.01*	78.00	52.00	56.00	*5.97*
Vespertilionidae	*Otonycteris hemprichii*	10	28.94	21.98	4.28	20.43	3.76	49.63	20.43	37.46	6.91
Vespertilionidae	*Pharotis imogene*	*8*	*26.15*	*8.10*	*5.13*	*41.18*	*3.39*	*66.23*	*39.53*	*44.17*	*6.21*
Vespertilionidae	*Philetor brachypterus*	*8*	*39.09*	*12.00*	*4.57*	*37.34*	*6.08*	*74.32*	*35.52*	*42.86*	*9.93*
Vespertilionidae	*Phoniscus aerosa*	*7*	*70.45*	*7.79*	*2.52*	*69.90*	*29.22*	*135.96*	*63.24*	*82.19*	*31.58*
Vespertilionidae	*Phoniscus atrox*	*7*	*62.47*	4.81	2.89	82.00	*24.26*	*133.86*	*69.69*	82.00	*27.06*
Vespertilionidae	*Phoniscus jagorii*	*7*	*71.10*	4.70	2.20	94.00	*29.67*	*149.57*	*78.49*	94.00	*32.37*
Vespertilionidae	*Phoniscus papuensis*	*7*	95	6.32	3.00	80.00	*35.49*	160	65.00	80.00	*38.51*
Vespertilionidae	*Pipistrellus abramus*	8	8.83	5.87	8.33	43.33	0.56	52.19	43.33	44.60	1.36
Vespertilionidae	*Pipistrellus adamsi*	8	18.30	*4.93*	5.12	44.64	1.11	62.78	44.64	48.02	4.27
Vespertilionidae	*Pipistrellus aero*	*8*	*17.58*	*5.14*	*5.41*	*43.77*	*1.43*	*61.65*	*43.73*	*46.15*	*3.52*
Vespertilionidae	*Pipistrellus angulatus*	*8*	*18.34*	*3.35*	*5.20*	*46.34*	*1.59*	*65.08*	*46.34*	*48.76*	*3.78*
Vespertilionidae	*Pipistrellus ceylonicus*	*8*	*16.82*	*8.05*	*5.64*	*41.22*	*1.28*	*58.17*	*41.18*	*43.60*	*3.27*
Vespertilionidae	*Pipistrellus collinus*	*8*	*17.11*	*6.75*	*5.55*	*42.18*	*1.34*	*59.52*	*42.18*	*44.61*	*3.37*
Vespertilionidae	*Pipistrellus coromandra*	*8*	*20.37*	*4.59*	*6.64*	*46.39*	*1.50*	*67.11*	*44.97*	*48.33*	*3.61*

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Vespertilionidae	*Pipistrellus deserti*	*8*	*17.75*	*4.69*	*5.37*	*44.30*	*1.47*	*62.38*	*44.30*	*46.71*	*3.58*
Vespertilionidae	*Pipistrellus endoi*	*8*	*17.58*	*5.14*	*5.41*	*43.77*	*1.43*	*61.65*	*43.73*	*46.15*	*3.52*
Vespertilionidae	*Pipistrellus hesperidus*	10	41.64	*5.38*	2.67	45.19	9.74	86.90	45.19	52.32	17.48
Vespertilionidae	*Pipistrellus hesperus*	8	33.51	3.56	3.83	37.69	1.63	71.12	37.69	43.04	7.01
Vespertilionidae	*Pipistrellus inexspectatus*	*8*	*17.67*	*4.91*	*5.39*	*44.04*	*1.45*	*62.02*	*44.04*	*46.43*	*3.55*
Vespertilionidae	*Pipistrellus javanicus*	*8*	*18.95*	*4.92*	*6.65*	*45.97*	*1.36*	*65.00*	*44.70*	*47.51*	*3.38*
Vespertilionidae	*Pipistrellus kuhlii*	8	22.15	6.07	5.18	37.93	1.59	60.05	37.93	41.16	4.92
Vespertilionidae	*Pipistrellus maderensis*	8	15.35	4.91	4.53	42.66	2.06	58.01	42.66	46.44	3.33
Vespertilionidae	*Pipistrellus minahassae*	*8*	*17.00*	*7.20*	*5.58*	*41.85*	*1.32*	*59.03*	*41.80*	*44.21*	*3.33*
Vespertilionidae	*Pipistrellus nanulus*	*8*	*18.86*	*2.51*	*5.06*	*48.18*	*1.70*	*67.44*	*48.18*	*50.60*	*3.95*
Vespertilionidae	*Pipistrellus nathusii*	8	12.71	7.44	6.66	39.46	0.90	52.18	39.46	41.40	2.47
Vespertilionidae	*Pipistrellus papuanus*	*8*	*17.63*	*5.02*	*5.40*	*43.90*	*1.44*	*61.84*	*43.90*	*46.34*	*3.54*
Vespertilionidae	*Pipistrellus paterculus*	*8*	*17.67*	*4.91*	*5.39*	*44.04*	*1.45*	*62.02*	*44.04*	*46.43*	*3.55*
Vespertilionidae	*Pipistrellus permixtus*	*8*	*17.36*	*5.86*	*5.48*	*42.99*	*1.39*	*60.62*	*42.99*	*45.42*	*3.45*
Vespertilionidae	*Pipistrellus pipistrellus*	8	23.69	5.30	5.22	45.44	1.22	69.14	45.44	47.61	5.17
Vespertilionidae	*Pipistrellus pygmaeus*	8	28.55	*4.72*	5.08	53.04	1.25	81.71	53.04	54.55	6.29
Vespertilionidae	*Pipistrellus rueppellii*	8	43.09	7.07	6.71	50.49	1.60	94.33	50.49	56.01	7.90
Vespertilionidae	*Pipistrellus rusticus*	8	31.34	4.57	4.86	50.86	3.17	82.43	50.86	55.19	7.45
Vespertilionidae	*Pipistrellus stenopterus*	8	25.86	15.67	7.91	38.83	1.64	61.60	35.81	38.83	3.22
Vespertilionidae	*Pipistrellus sturdeei*	*8*	*17.91*	*4.27*	*5.32*	*44.88*	*1.50*	*63.12*	*44.84*	*47.28*	*3.64*

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		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Vespertilionidae	*Pipistrellus subflavus*	8	28.51	5.74	6.81	42.97	0.96	71.47	42.97	45.95	4.07
Vespertilionidae	*Pipistrellus tenuis*	*8*	23	3.48	7	48	*1.58*	68	45.00	48	*3.84*
Vespertilionidae	*Pipistrellus wattsi*	*8*	*17.63*	*5.02*	*5.40*	*43.90*	*1.44*	*61.84*	*43.90*	*46.34*	*3.54*
Vespertilionidae	*Pipistrellus westralis*	*8*	16	3.90	6.00	46.60	*1.00*	61	45.00	46.60	*3.00*
Vespertilionidae	*Plecotus alpinus*	*8*	*20.33*	*8.15*	*3.19*	*24.22*	*4.80*	*44.14*	*23.13*	*30.20*	*6.42*
Vespertilionidae	*Plecotus auritus*	10	25.51	8.19	2.51	25.57	7.38	51.18	25.57	36.39	10.77
Vespertilionidae	*Plecotus austriacus*	8	18.98	6.75	2.94	22.74	4.87	41.75	22.74	29.66	7.18
Vespertilionidae	*Plecotus balensis*	*8*	*20.01*	*7.93*	*3.25*	*24.88*	*4.39*	*44.74*	*23.81*	*30.81*	*6.06*
Vespertilionidae	*Plecotus kolombatovici*	10	19.76	*7.42*	3.57	26.22	2.66	46.02	26.22	31.25	5.56
Vespertilionidae	*Plecotus sardus*	*8*	*20.33*	*8.15*	*3.19*	*24.22*	*4.80*	*44.14*	*23.13*	*30.20*	*6.42*
Vespertilionidae	*Plecotus taivanus*	*8*	*20.33*	*8.15*	*3.19*	*24.22*	*4.80*	*44.14*	*23.13*	*30.20*	*6.42*
Vespertilionidae	*Plecotus teneriffae*	*10*	*19.58*	*7.64*	*3.34*	*25.89*	*3.83*	*45.62*	*24.80*	*31.72*	*5.57*
Vespertilionidae	*Rhogeessa aeneus*	8	39.16	*4.45*	3.25	46.80	4.27	85.11	46.80	52.82	10.13
Vespertilionidae	*Rhogeessa alleni*	*10*	*40.98*	*5.37*	*3.10*	*46.39*	*7.73*	*88.10*	*43.73*	*54.11*	*11.56*
Vespertilionidae	*Rhogeessa genowaysi*	*10*	*43.78*	*3.88*	*3.30*	*48.28*	*6.54*	*92.10*	*45.20*	*55.98*	*10.92*
Vespertilionidae	*Rhogeessa gracilis*	*10*	*41.16*	*5.14*	*3.08*	*46.81*	*7.77*	*88.76*	*44.12*	*54.60*	*11.62*
Vespertilionidae	*Rhogeessa hussoni*	*10*	*41.81*	*4.91*	*2.94*	*49.16*	*8.25*	*92.03*	*46.39*	*57.23*	*12.12*
Vespertilionidae	*Rhogeessa io*	*10*	60	*4.85*	2.80	52.40	*10.82*	99.6	39.60	52.40	*15.84*
Vespertilionidae	*Rhogeessa minutilla*	*10*	*42.93*	*3.75*	*2.83*	*51.99*	*8.54*	*96.12*	*49.06*	*60.34*	*12.54*
Vespertilionidae	*Rhogeessa mira*	*10*	*45.70*	*2.68*	*2.86*	*55.70*	*7.92*	*102.01*	*52.35*	*64.26*	*12.40*

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Vespertilionidae	*Rhogeessa parvula*	*10*	*43.34*	*4.37*	*3.10*	*49.60*	*7.33*	*93.49*	*46.62*	*57.57*	*11.56*
Vespertilionidae	*Rhogeessa tumida*	8	34.90	4.58	5.12	40.54	2.47	75.20	40.54	48.65	5.71
Vespertilionidae	*Scoteanax rueppellii*	*8*	40.00	26.41	9.00	35.00	*5.49*	72	32.00	35.00	*8.70*
Vespertilionidae	*Scotoecus albigula*	*8*	*24.44*	*10.08*	*3.90*	*30.23*	*5.56*	*53.45*	*29.14*	*34.43*	*7.90*
Vespertilionidae	*Scotoecus albofuscus*	10	26.16	4.50	2.68	33.63	4.23	60.58	33.63	39.08	9.72
Vespertilionidae	*Scotoecus hindei*	*8*	*24.27*	*10.41*	*3.93*	*29.90*	*5.51*	*52.84*	*28.82*	*34.09*	*7.84*
Vespertilionidae	*Scotoecus hirundo*	*8*	*25.51*	*8.45*	*3.75*	*32.43*	*5.89*	*57.37*	*31.25*	*36.86*	*8.33*
Vespertilionidae	*Scotoecus pallidus*	*8*	*26.27*	*7.20*	*3.59*	*34.02*	*6.09*	*60.11*	*32.82*	*38.55*	*8.63*
Vespertilionidae	*Scotomanes ornatus*	*8*	*22.17*	*22.24*	*4.69*	*27.49*	*5.80*	*46.50*	*26.52*	*30.30*	*7.73*
Vespertilionidae	*Scotophilus borbonicus*	*3*	*30.39*	*19.02*	*4.21*	*34.47*	*5.55*	*63.23*	*32.98*	*39.06*	*8.31*
Vespertilionidae	*Scotophilus celebensis*	*8*	*29.01*	*23.24*	*3.95*	*33.18*	*6.14*	*60.26*	*31.85*	*37.60*	*8.72*
Vespertilionidae	*Scotophilus collinus*	*8*	*29.01*	*23.24*	*3.95*	*33.18*	*6.14*	*60.26*	*31.85*	*37.60*	*8.72*
Vespertilionidae	*Scotophilus dinganii*	3	28.70	25.12	5.90	31.26	1.70	59.96	31.26	36.38	5.24
Vespertilionidae	*Scotophilus heathii*	*8*	*29.24*	*36.13*	*3.96*	*30.42*	*7.04*	*56.60*	*29.11*	*34.81*	*9.45*
Vespertilionidae	*Scotophilus kuhlii*	*8*	*29.92*	*20.31*	*3.82*	*34.36*	*6.51*	*62.60*	*32.98*	*38.94*	*9.16*
Vespertilionidae	*Scotophilus leucogaster*	7	47.83	20.24	1.73	46.27	38.45	87.86	39.09	46.27	31.89
Vespertilionidae	*Scotophilus nigrita*	8	31.21	27.34	3.92	27.59	8.96	58.59	27.59	32.85	9.28
Vespertilionidae	*Scotophilus nucella*	*8*	*29.01*	*23.24*	*3.95*	*33.18*	*6.14*	*60.26*	*31.85*	*37.60*	*8.72*
Vespertilionidae	*Scotophilus nux*	*8*	*29.72*	*30.00*	*3.88*	*31.60*	*7.09*	*58.64*	*30.27*	*36.09*	*9.58*
Vespertilionidae	*Scotophilus robustus*	8	19.38	60.10	4.24	34.13	2.04	52.98	34.13	36.54	4.41

Family	Species	Species sets for each parameter									
		Echolocation Call Type	**Bandwidth (kHz)**	**Body Mass (g)**	**Call Duration (ms)**	**Characteristic Frequency (kHz)**	**Dominant Slope (kHz/ms)**	**Maximum Frequency (kHz)**	**Minimum Frequency (kHz)**	**Peak Frequency (kHz)**	**Total Slope (kHz/ms)**
Vespertilionidae	*Scotophilus viridis*	8	28.94	19.81	3.67	33.94	3.58	62.58	33.94	40.10	8.08
Vespertilionidae	*Scotorepens balstoni*	*8*	31.00	11.92	8.00	34.00	*3.17*	61	30.00	34.00	*5.97*
Vespertilionidae	*Scotorepens greyii*	3	10.12	10	8.57	35.07	0.30	45.19	35.07	36.08	1.20
Vespertilionidae	*Scotorepens orion*	*8*	26	11.83	10	36.00	*1.42*	58	32.00	36.00	*3.91*
Vespertilionidae	*Scotorepens sanborni*	8	17.00	8.13	6.30	37.59	0.76	54.58	37.59	39.30	3.13
Vespertilionidae	*Scotozous dormeri*	*8*	*20.75*	*6.79*	*5.77*	*40.77*	*2.64*	*61.98*	*39.65*	*43.55*	*4.77*
Vespertilionidae	*Tylonycteris pachypus*	8	43.73	4.10	3.76	43.86	2.95	88.35	43.86	48.95	11.21
Vespertilionidae	*Tylonycteris robustula*	*8*	61	7.98	3.78	45.00	*10.98*	103.00	45.00	55.00	*16.03*
Vespertilionidae	*Vespadelus baverstocki*	*8*	18	4.30	4	47.00	*2.53*	62	44	47.00	*5.01*
Vespertilionidae	*Vespadelus caurinus*	*8*	23	3.10	5.00	59.6	*2.75*	82	59.00	59.6	*5.64*
Vespertilionidae	*Vespadelus darlingtoni*	8	18.60	6.06	5.02	45.71	0.95	61.74	43.41	45.71	3.44
Vespertilionidae	*Vespadelus douglasorum*	*8*	21	4.99	6.00	52.80	*1.99*	73.00	52.00	52.80	*4.61*
Vespertilionidae	*Vespadelus finlaysoni*	*8*	34	4.30	5.00	35.00	*5.59*	68	34.00	35.00	*8.87*
Vespertilionidae	*Vespadelus pumilus*	*8*	*16.89*	5.40	*5.37*	48	*1.44*	59	48	51.00	*3.70*
Vespertilionidae	*Vespadelus regulus*	3	19.45	5.05	6.40	44.62	1.00	64.11	44.62	48.62	3.03
Vespertilionidae	*Vespadelus troughtoni*	*8*	18	5.40	6.00	49.00	*1.46*	67	49.00	49.00	*3.84*
Vespertilionidae	*Vespadelus vulturnus*	3	31.28	3.77	4.61	48.89	2.02	80.33	48.89	51.38	7.60
Vespertilionidae	*Vespertilio murinus*	3	8.53	15.42	14.07	22.46	0.46	31.11	22.46	24.35	0.90
Vespertilionidae	*Vespertilio sinensis*	3	27.17	24.30	1.95	25.71	12.58	47.21	19.70	25.71	13.61

8.7 Appendix G: Species list and references for vocalisations in Chapter 5 Section 5.4.4 Figure 9

Order	Species	Reference
Monotremata	*Ornithorhynchus anatinus* (Platypus)	(OstrichesRuleMovies 2011)
Marsupialia	*Didelphis marsupialis* (Common Opossum)	ML Audio 29675 (Cornell Lab of Ornithology 2011)
Afrosoricida	Tenrecs and Golden Moles	(Eisenberg & Gould 1970)
Tubulidentata	*Orycteropus afer* (Aardvark)	(Ecotravel 2011)
Proboscidea	*Loxodonta africana* (African Elephant)	ML Audio 135445 (Cornell Lab of Ornithology 2011)
Hyracoidea	*Dendrohyrax arboreus* (Southern Tree Hyrax)	ML Audio 46536 (Cornell Lab of Ornithology 2011)
Sirenia	*Trichechus manatus* (Caribbean Manatee)	ML Audio 118184 (Cornell Lab of Ornithology 2011)
Xenarthra	*Tamandua mexicana* (Northern Tamandua)	ML Audio 165013 (Cornell Lab of Ornithology 2011)
Dermoptera	*Glaucomys volans* (Southern Flying Squirrel)	File 7 (Soundboard 2011)
Scandentia	*Urogale everetti* (Mindanao Tree Shrew)	ML Audio 38624 (Cornell Lab of Ornithology 2011)
Primates	*Pan troglodytes* (Chimpanzee)	ML Audio 53994 (Cornell Lab of Ornithology 2011)
Lagomorpha	*Sylvilagus floridanus* (Eastern Cottontail)	ML Audio 87152 (Cornell Lab of Ornithology 2011)
Rodentia	*Dicrostonyx groenlandicus* (Greenland Collared Lemming)	ML Audio 126500 (Cornell Lab of Ornithology 2011)
Eulipotyphla	*Blarina brevicauda* (Northern Short-tailed Shrew)	ML Audio 56707 (Cornell Lab of Ornithology 2011)
Carnivora	*Panthera leo* (Lion)	ML Audio 88116 (Cornell Lab of Ornithology 2011)
Pholidota	Pangolins	(The Hindu Newspaper 2011)
Perissodactyla	*Equus asinus* (Feral Ass)	ML Audio 63353 (Cornell Lab of Ornithology 2011)
Cetartiodactyla	*Tursiops truncatus* (Bottlenose Dolphin)	ML Audio 120779 (Cornell Lab of Ornithology 2011)
Cetartiodactyla	*Antilocapra americana* (Pronghorn)	ML Audio 102044 (Cornell Lab of Ornithology 2011)

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