Echolocation calls of eight microchiroptera from Papua New Guinea

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ABSTRACT

The bat fauna of Papua New Guinea (PNG) is more diverse than that of Australia, yet knowledge of the distribution and ecology of PNG's 57 microchiropteran species is particularly poor, almost a third being known from five or less localities. The lack of knowledge is partly due to problems with use of both mist nets and harp traps in PNG. Bat detectors may help overcome some of these problems, however, they have not been widely used in PNG primarily due to the lack of a body of reference calls to aid species identification. Using the Anabat system, we recorded 744 reference echolocation call sequences from eight microchiropteran species captured in PNG. Calls were analysed using Analook software and described. The characteristic frequency of the predominant harmonics were: *Aselliscus tricuspidatus* 112–113 kHz; *Hipposideros cervinus* 136.5–138 kHz; *H. diadema* 54–59 kHz; *H. maggietaylorae* 121–123 kHz; *Mormopterus* cf. *beccarii* 44–50 kHz; *Mosia nigrescens* 45–60 kHz; *Rhinolophus arcuatus* 70–72 kHz; and *Rhinolophus euryotis* 52–56 kHz. Comparison with published calls of some of these species from Australia, south-east Asia and elsewhere in PNG suggest regional variations occur within PNG and abroad and/or that there are taxonomic issues such as cryptic species. This emphasises the need for far greater collection of reference echolocation calls, the development of regional PNG call libraries with vouchered specimens and cautions against using reference libraries developed in Australia or elsewhere.

Key words: echolocation, Papua New Guinea, *Aselliscus tricuspidatus, Hipposideros cervinus, Hipposideros diadema, Hipposideros maggietaylorae, Rhinolophus arcuatus, Rhinolophus euryotis, Mormopterus* cf. *beccarii, Mosia nigrescens,* Anabat, intraspecific regional variation, tree hollow roost

Introduction

The bat fauna of Papua New Guinea as currently known is more diverse than that of Australia. Ninety-two bat species have been recorded from Papua New Guinea (PNG) compared with 76 extant species from Australia (Bonaccorso 1998; Churchill 1998; Leary and Mamu 2004; Helgen 2005; Van Dyck and Strahan 2008). The taxonomic uncertainty of several genera is likely to increase the number of bat species for both PNG and Australia. Additional new species are likely to be discovered from poorly surveyed parts of PNG and it is also possible that further Australian species may yet be recorded in PNG (e.g. Filewood 1983). Twenty-eight percent of the PNG bat fauna (26 species) is endemic to PNG or the island of New Guinea (Bonaccorso 1998).

The PNG bat fauna comprises 57 species (including 73 sub-species) of microchiroptera and 35 species (including 48 sub-species) of megachiroptera (Bonaccorso 1998; Helgen 2005). Fifteen microchiropteran species are endemic to PNG or the island of New Guinea (Bonaccorso 1998), 22 species are shared with Australia (although some of these are represented by different subspecies in PNG), and the remainder are either shared with Solomon Islands or Indonesia or have wider cosmopolitan distribution (Van Dyck and Strahan 2008; Bonaccorso 1998; Churchill 1998).

Knowledge of the distribution and ecology of many bat species is poor, but it is particularly poor for PNG microchiropteran species. Only 13 species (23%) of microchiropteran are known from 30 or more localities with 18 species (32%) having been recorded from five or less localities (Bonaccorso 1998). The poor state of knowledge of the distribution of microchiropterans in PNG is related to the difficulty in capturing many species with mist-nets, which have in the past been the most commonly used technique for surveying bats in PNG. Harp traps which are a standard survey technique for bats in Australia and other parts of the world have not been widely used in PNG for a number of reasons. Foremost of these reasons is that harp traps are heavy and difficult to transport to remote areas where there are no roads or water transport. Bat detectors, which have become one of the standard methods for surveying bats in Australia since the early 1990's (Pennay *et al.* 2004), have not been widely used in PNG. The main reason for this lack of use is that there has been no development of a reference library of calls for each species.

The use of bat detectors to survey for bats has the benefit of being able to record free flying bats in the wild without having to capture them. The use of bat detectors in PNG would undoubtedly increase the known distribution of many microchiropteran species. In Australia, there has been considerable debate on the reliability of identifications, which has in part stemmed from the underestimation of variation within bat calls across a species geographic range, and the lack of recognition of overlapping call characteristics between some species in certain regions (Reinhold *et al.* 2001; Law *et al.* 2002;

Reardon 2003; Pennay *et al.* 2004). For Papua New Guinea, this means that the use of Australian echolocation reference libraries, even for the 22 species that are shared, are likely to be unreliable without validation with PNG reference calls. This paper is written in the hope of stimulating researchers to begin collecting reference echolocation calls of PNG bats.

Methods

Study sites

The bats whose echolocation calls are reported here were incidentally recorded from captured microbats during broader mammal surveys commissioned by the World Wide Fund for Nature (WWF) Kikori Integrated Conservation and Development Project and the WWF Transfly Project. The echolocation recordings were made on bats collected from four different sites (Libano Sok, Darai Plateau, Keboi Kerowa and Akwam) in three different provinces (Southern Highlands, Gulf and Western Province). The location of captures is given in Table 1 and shown in Figure 1. The following sections provide a description of the habitat at each site. We have provided relatively detailed information on habitat at each site because even information on habitats utilised by

most New Guinea bat species is poorly known (eg. see Bonaccorso 1998), and because although some of the sites were classified as the same vegetation community after Paijmans (1976) the structure and species compositions of the forest were quite different.

Libano Sok, Southern Highlands Province

Libano Sok is the local name given to the junction of the Libano and Hegigio Rivers. Nets were set on both sides of the Libano River (Photo 1). The forest had an open structure with four distinct tree layers with emergents to 45 m and the upper canopy reaching to 30–35 m (Gebia and Balun 2004). Dominant species in the upper and sub-canopy and emergents included: *Octomeles sumatrana, Pometia pinnata, Cryptocarya* spp., *Celtis philippensis, Sterculia schumanniana, Haplolobus floribundus,* and *Erythrospermum candidum* (Gebia and Balun 2004). The understorey was open but epiphytic climbers, lianas / vines and climbing ferns were common.

Darai Plateau, Gulf Province

The site was at the southern end of the Darai Plateau in lowland hill forests on polygonal karst geology. The forest had four distinct tree layers with emergents to 40–45 m and the upper canopy reaching to 30–35 m (Gebia and Balun 2004) (Photo 2). The forest was floristically very

Table 1: Location and description of survey sites.

| Site	Province	Survey Period	Latitude in decimal degrees	Longitude in decimal degrees	Altitude (m)	Vegetation type (after Paijmans 1976)
Darai Plateau	Gulf	23/7/03–30/7/03	7.13028°S	143.61124°E	380	Lowland Hill Forest
Libano Sok	Southern Highlands	05/8/03–13/8/03	6.40018°S	142.97412°E	270	Lowland Alluvial and Lowland Hill Forest
Akwam	Western	31/3/04–04/4/04	9.09794°S	141.43425°E	5	Swamp Forest and Monsoon Forest
Keboi Kerowa	Gulf	15/7/03–22/7/03 15/8/03–22/8/03 2/12/03–8/12/03	7.52803°S	144.26260°E	0	Swamp Forest and Mangroves
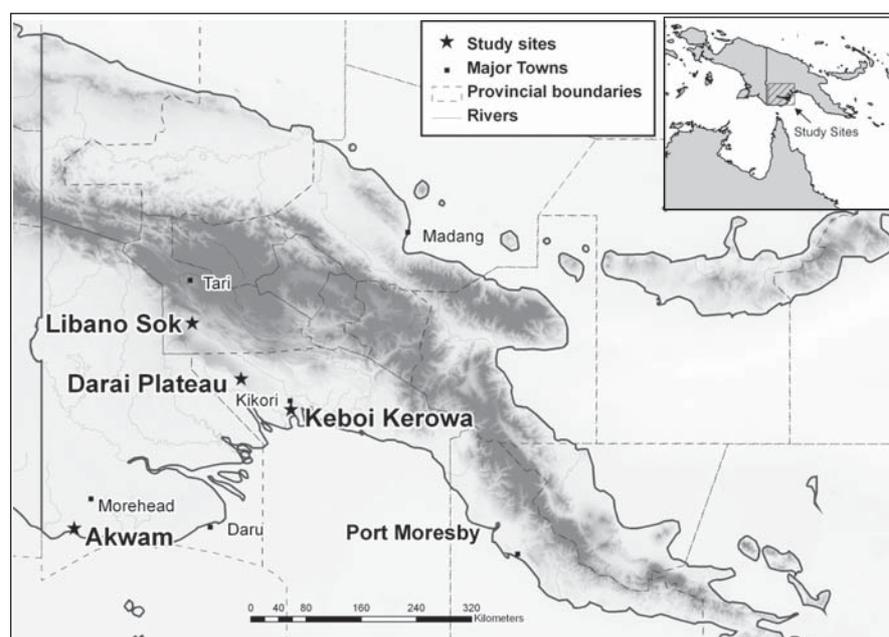
Figure 1: Location of study sites. Shading indicates increasing altitude.

diverse and common species in the upper canopy included *Elaeocarpus nouhuysii*, *Dysoxylum* spp., *Cryptocarya* spp. and *Chisocheton* spp. (Gebia and Balun 2004).

Keboi Kerowa, Gulf Province

Keboi Kerowa lies in the Kikori River delta approximately 18 km south-east of Kikori station in the transitional zone between mangrove forest and swamp lowland forest (Paijmans 1976) (Photo 3). The forest had a relatively open canopy with three distinct tree layers with emergents to 45 m and the canopy reaching to 30 m (O. Gebia pers. comm.). Dominant species in the canopy and sub-canopy included: *Calophyllum suberosum, Gonystylus macrophyllus, Polyalthia forbesii, Gluta papuana, Horsfieldia polyantha, Nothaphoebe archboldiana, Semecarpus forstenii,* and *Vatica papuana.*

Akwam, Western Province

Akwam is approximately 13 km north-east of Bula on the Moorehead River. The site was in monsoon / littoral rainforest although this area is classified as Swamp Forest / Grassland in the mapping of Paijmans (1976). The closed canopy consisted of large old trees 30–35 m high with some emergents exceeding this height. The diameter of some trees was in excess of 2.5 m. This forest had a very poorly developed shrub layer and the understorey was almost non-existent (Photo 4). Little recruitment of canopy tree species was apparent, which may have been because of the high levels of seedling grazing by Rusa deer *Rusa timoriensis* in the area.

Capture methods

All bats, except the *Hipposideros cervinus* from the Darai Plateau, and the *Mormopterus* cf. *beccarii* from Akwam were captured in mist nets (2 ply polyester with a mesh size of 31 mm x 70 denier). Mist nets were either suspended from ropes and pulleys just below the canopy or across water or set on poles. Mist nets used were either 2 m high by 18 m long or 2 m high by 12 m. The *H. cervinus* was captured in a harp trap. Three *M.* cf. *beccarii* (two males and one female) were taken from a tree hollow roost of an unidentified rainforest tree at Akwam. The entry to the roost had a diameter of approximately 10 cm, was approximately 1.7 m above ground in a tree with a diameter at breast height of approximately 40 cm. The animals in the roost were making audible sounds which led to their detection by the first author. There were at least a further five individuals in this hollow which escaped capture.

Echolocation calls

Echolocation calls were recorded using an Anabat II detector connected to an Anabat CF storage Zcaim or a Sony TCM465V audio cassette recorder. Recorded calls were loaded into AnalookW version 3.2 for analysis, with the exception of batch parameters (mean figures), which were obtained using the 'ctrl q' function in measure mode in Analook v4.8f, and exported into spreadsheet tables for analysis.

Calls were recorded from wild caught bats when both flying and perched inside a mosquito net enclosure approximately 2.5 m long, 1 m wide, and 1.5 m high. Distance between the bat and recording microphone ranged from between 30 cm and 2.8 m depending on the bat's position within the enclosure. Given the taxonomic uncertainty of New Guinean bats and the paucity of museum specimens from the study areas, recorded bats were not released, but retained as voucher specimens for the reference calls recorded, and hence release calls were not recorded.

Enclosures and stationary bats are routinely used to record the calls of Hipposiderid and Rhinolophid bats to minimise the impact of Doppler compensation of the constant frequency component of the calls (Matsumura 1979; Aldridge *et al.* 1990; Surlykke *et al.*1993; Kingston *et al.* 2000; Kingston *et al.* 2001; Macias and Mora 2003; Chen *et al.* 2004; Kingston and Rossiter 2004; Fukui *et al.* 2004; Siemers and Ivanova 2004; Smotherman and Metzner 2004; Li *et al.* 2007). There is evidence that calling behaviour of bats in enclosures differs from free flying bats in natural conditions (Parsons 1998). However, the degree and types of differences are variable depending on the species with some showing significant difference and others little (see discussion for more detail).

Measurements were taken of all animals captured, and voucher specimens were lodged in the University of Papua New Guinea Biology Department Museum in Port Moresby, PNG. Registration numbers are given in Table 2.

Approximately 20 h of recordings were made of unidentified free flying bats in natural conditions at Darai and Libano Sok for comparison with the reference calls.

Call descriptions

Terminology

Terminology used for describing call characteristics follows standard terms used by other authors describing bat calls in general, but it does include some terms specific to calls recorded using the Anabat system (see Corben and O'Farrell 1999, and Pennay *et al.* 2004 for a detailed description of these terms). Bat calls are vocalisations emitted as sound pulses, the terms call and pulse are used interchangeably or together to represent a single vocalisation made by a bat. Vocalised call pulses are usually repeated in rapid succession when echolocating, a series of repeated calls from a single echolocating bat is referred to here as a call sequence. Call shape descriptions refer to standard terms used to define the components of a call pulse when viewed in a frequency versus time graph (see Pennay *et al.* 2004 for examples).

Results

Bats captured

Table 3 lists bat species captured at each site. Table 2 provides morphometric data on each individual recorded and its museum registration number.

Trident Leaf-nosed Bat *Aselliscus tricuspidatus* – Photo 5
Call sequences n=74, calls analysed n=1640.

A narrow band constant frequency tone sometimes preceded and always terminated by a frequency modulated sweep. The call sequences display two harmonics. The pulse shape is convex or flat, with a long down-sweeping tail (mean 8 kHz) and sometimes a very short upsweeping initial. Characteristic frequency of the

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Table 2: Morphometric data of voucher specimens from which calls were recorded. All specimens (except UP4268 – sub-adult) are adults and are lodged at the University of Papua New Guinea, Biology Department Museum. (All measurements in millimetres and weights in grams).

Museum Registration Number	Species	Sex	Date Recorded	Locality	Forearm Length	Head + Body Length	Tail Length	Hind Leg Length	Ear Length	Hindfoot Length	Weight
UP4197	Mosia nigrescens	F	06/08/03	Libano Sok	33.3	35.4	19.5	11.4	11.2	5.5	3.25
UP4271	Aselliscus tricuspidatus	M	18/7/03	Keboi Kerowa	40.7	37.4	23.8	14.9	13.5	7.3	3.5
UP4270	A. tricuspidatus	M	19/8/03	Keboi Kerowa	41.1	38.1	19.2	14.3	13.2	6	3
UP4181	Hipposideros cervinus	M	28/7/03	Darai Plateau	45.5	48.7	14.7	16.1	–	8.6	6.75
UP4268	H. diadema	M	6/8/03	Libano Sok	73.9	86.1	47.0	30.2	30.4	14.6	34
UP4183	H. maggietaylorae	F	25/7/03	Darai Plateau	55.8	65.7	36.1	25.5	22.8	11.9	15.5
UP4182	H. maggietaylorae	F	25/7/03	Darai Plateau	58.8	62.8	38.1	26.8	20.2	–	16.5
UP4191	Rhinolophus arcuatus	M	6/8/03	Libano Sok	48.3	50.6	21	21.6	21.2	10.2	11
UP4190	R. arcuatus	F	6/8/03	Libano Sok	47.5	51	17.6	22.3	20.5	8	9
UP4187	R. euryotis	F	30/07/03	Darai Plateau	57.7	56	25.5	27.5	23.4	12.7	14.5
UP4374	Mormopterus cf. beccarii	M	3/4/03	Akwam	34.1	57.3	33.5	12.1	15.9	7.5	10.75
UP4198	M. cf. beccarii	F	7/12/03	Keboi Kerowa	35	58.9	36.4	12.8	12.3	8.4	15

predominant harmonic was 112–113 kHz (mean 112.55 kHz) or of the fundamental harmonic was 56–56.5 kHz (Figure 2). A relatively short call, with a short interval between pulses. Mean pulse duration was 2.26 ms and mean time between pulses was 47.53 ms. Pulses are often repeated in pairs (doublets) 14–19 ms apart with a 70–90 ms pause between doublets (Figure 3).

Fawn Horseshoe Bat *Hipposideros cervinus* – Photo 6

Call sequences n=15, calls analysed n=143.

Calls have both constant frequency and frequency modulated components. The characteristic section is usually a constant frequency tone, the tail modulates in frequency, and most call sequences display two harmonics. The pulse shape is convex or flat, with a long down-sweeping tail dropping 10–20 kHz (mean 13.83 kHz). Characteristic frequency of the two predominant harmonics are between 136.5–138 kHz (mean 137.53 kHz) (Figure 4) and 66.5–69.5 khz (mean 68.12 kHz) (Figure 5). Mean pulse duration is 3.67 ms, and the mean time between pulses is 55.71 ms, but pulses are usually repeated in multiplets (groups of three or four pulses) timed 21–31 ms (mean 26.98 ms) apart, with a 60–120 ms (mean 82.07 ms) pause between multiplet pulse groups (Figure 6).

Figure 7 and 8 show a 67.6 kHz recording of an unidentified bat in free-flight at Libano Sok. The call characteristics are comparable to those recorded for *H. cervinus* at Darai Plateau in the lower harmonic, suggesting that the recordings made in the small flight enclosure do not differ greatly from free-flying bats.

Diadem Horseshoe Bat *Hipposideros diadema* – Photo 7

Call sequences n=49, calls analysed n=2464.

Calls either comprise of a predominantly narrow band constant frequency tone with frequency modulated components (Figure 9), or predominantly frequency modulated with the characteristic section only moderately constant (Figure 10), both the tail and initial sections modulating. Call sequences display multiple harmonics. The pulse shape is flat or convex, with a down-sweeping tail dropping about 10 kHz (mean 7.9 kHz). The characteristic frequency of the predominant harmonic is between 54 and 59 kHz (mean 56.94 kHz). A few pulses (n=12) were recorded in a lower harmonic 28.1–29.2 kHz (mean 28.58 kHz), but the great majority (99.5%) of pulses were in the 56.94 kHz harmonic. Mean pulse duration was 8.95 ms and the mean time between pulses was 61.55 ms. Pulses are often repeated in doublets 28–30 ms apart with a 160–240 ms pause between doublets.

An unidentified bat in free-flight was recorded at Libano Sok on the 11/8/03, and it had a comparable pulse shape and frequency (Figure 11). The call sequence was also comparable (Figure 12).

Table 3: Bat species captured at each site.

| Common name	Scientific name	Libano Sok	Darai Plateau	Akwam	Keboi Kerowa
	PTEROPIDAE				
Big-eared Flying-fox	*Pteropus macrotis*				X
Greater Flying-fox	*Pteropus neohibernicus*	X	X		X
Lesser Bare-backed Fruit Bat	*Dobsonia minor*				X
Greater Bare-backed Fruit Bat	*Dobsonia moluccensis*		X		X
Common Blossom Bat	*Syconycteris australis*	X	X	X	X
Least Blossom Bat	*Macroglossus minimus*	X	X	X	X
Greater Tube-nosed Bat	*Nyctimene aello*	X			X
Common Tube-nosed Bat	*Nyctimene albiventer*		X	X	X
Pallas' Tube-nosed Bat	*Nyctimene cephalotes* (cf. *N. robinsoni*)			X	
Unstriped Tube-nosed Bat	*Paranyctimene raptor*	X	X		
	EMBALLONURIDAE				
Lesser Sheathtail Bat	*Mosia nigrescens*	X			
	HIPPOSIDERIDAE				
Trident Leaf-nosed Bat	*Aselliscus tricuspidatus*				X
Spurred Horseshoe Bat	*Hipposideros calcaratus*		X		
Fawn Horseshoe Bat	*Hipposideros cervinus*		X		
Diadem Bat	*Hipposideros diadema*	X			X
Maggie Taylor's Bat	*Hipposideros maggietaylorae*		X		
Wollaston's Horseshoe Bat	*Hipposideros wollastoni*		X		
	RHINOLOPHIDAE				
Western Horseshoe Bat	*Rhinolophus arcuatus*	X			
New Guinea Horseshoe Bat	*Rhinolophus euryotis*		X		X
	MOLOSSIDAE				
Beccari's Mastiff Bat	*Mormopterus* cf. *beccarii*			X	X
Total number of species		8	11	5	12
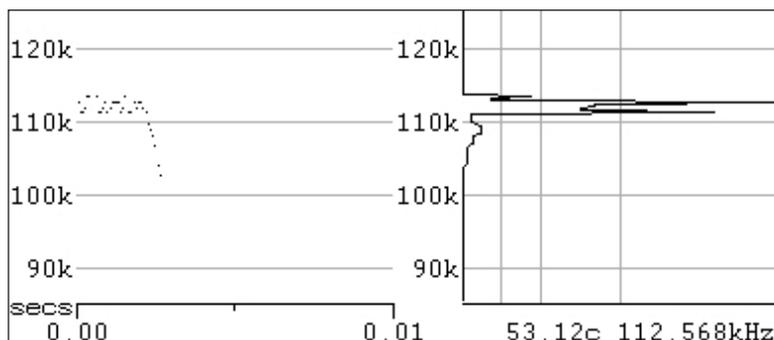
Figure 2: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse from *A. tricuspidatus* recorded in the flight enclosure at Keboi Kerowa 19/8/03. Scale: real time, 5 ms per tick (F8 and TBC uncompressed in Analook).
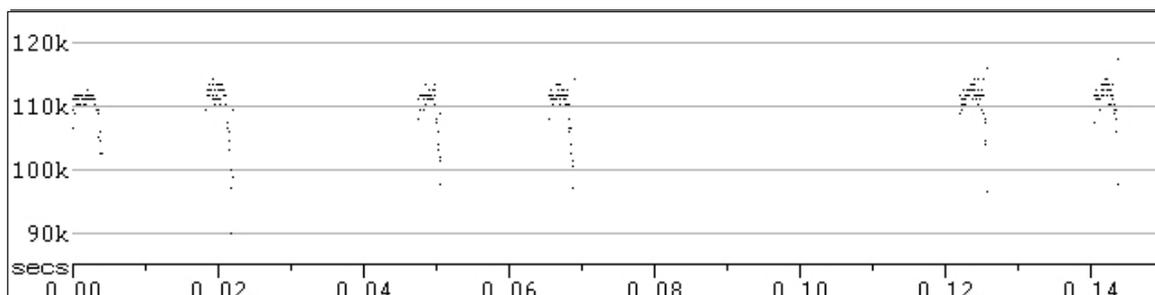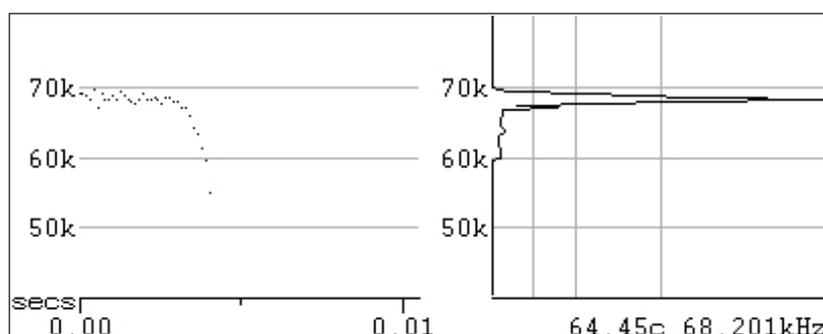

Figure 3: Frequency versus time graph of a call sequence of *A. tricuspidatus* recorded in the flight enclosure at Keboi Kerowa 19/8/03, pattern of doublets (repeated pairs of pulses) visible. Scale: real time 10 ms per tick (F7 and TBC uncompressed in Analook)
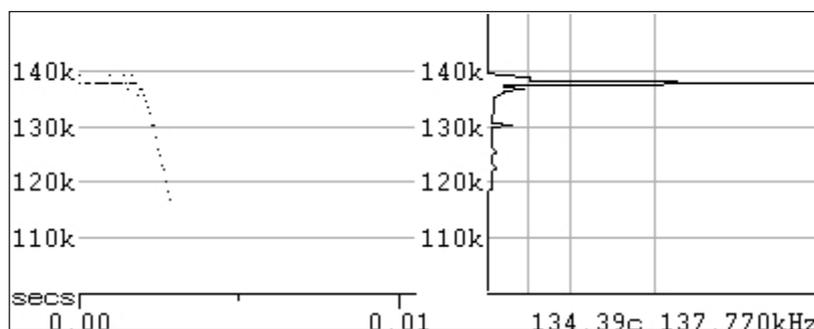
Figure 4: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse in the 137 kHz harmonic from *H. cervinus* recorded in the flight enclosure at Darai Plateau 29/7/03. Scale: real time, 5 ms per tick (F8 and TBC uncompressed in Analook).

Figure 5: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse in the 68 kHz (fundamental) harmonic from *H. cervinus* recorded in the flight enclosure at Darai Plateau 29/7/03 recorded on audio tape. Scale: real time, 5 ms per tick (F8 and TBC uncompressed in Analook).

Maggie Taylor's Bat *Hipposideros maggietaylorae* – Photo 8

Call sequences n=2, calls analysed n=24.

Particular caution should be taken when interpreting the data from this species as analysis is based on a limited number of brief pulses and fragmented sequences.

Calls have both constant frequency and frequency modulated components. The characteristic section is usually a narrow band constant frequency tone, whilst the tail and sometimes initial sections modulate in frequency. Call sequences display multiple harmonics. The pulse shape is flat or convex, with long down-sweeping tail dropping 30–50 kHz with echoes or other non-harmonic tones often visible joining the tail (Figure 13). The characteristic frequency is difficult to calculate as many tones are visible. The highest harmonic with peak cycles is the 121–123 kHz range (mean 121.67 kHz), but there are trace fragments of tones at many other frequencies below this frequency. The mean pulse duration is 1.38 ms, and the mean time between pulses is 30.5 ms. Pulses appeared to be repeated relatively regularly with no obvious pattern (Figure 14).

Beccari's Mastiff Bat *Mormopterus* cf. *beccarii* – Photo 9

Call sequences n=179, calls analysed n=211.

A broadband frequency modulated call with two visible harmonic ranges. The pulse shape is concave or sloped, sometimes with a down-sweeping initial and up-sweeping tail. The characteristic frequency of the predominant harmonic is between 44 and 50 kHz (mean 47.17 kHz) (Figure 15), but also many consecutive pulses in some sequences (n=32) recorded in the fundamental harmonic 22–27 kHz (mean 24.25 kHz) (Figure 16). However, the majority (75.5%) of pulses are in the secondary 47 kHz harmonic. Pulses are of relatively long duration (mean 7.35 ms), and the time between pulses is also relatively long (mean 96.5 ms). Pulses appeared to be repeated relatively regularly with no obvious pattern.

Figure 17 shows a call sequence from an unidentified bat in free-flight at Libano Sok recorded on the 11/8/03. The call characteristics are comparable with *M.* cf. *beccarii* recorded at Keboi Kerowa and Akwam.
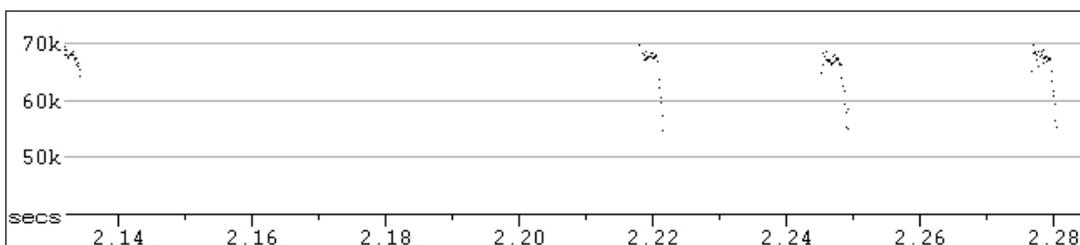

Figure 6: Frequency versus time graph of a typical call sequence in the 68 kHz harmonic from *H. cervinus* showing pulses approximately 20 ms apart with an 86 ms break between sequences. Recorded in the flight enclosure on audio tape at Darai Plateau 29/7/03. Scale: real time, 10ms per tick (F7 and TBC uncompressed in Analook).
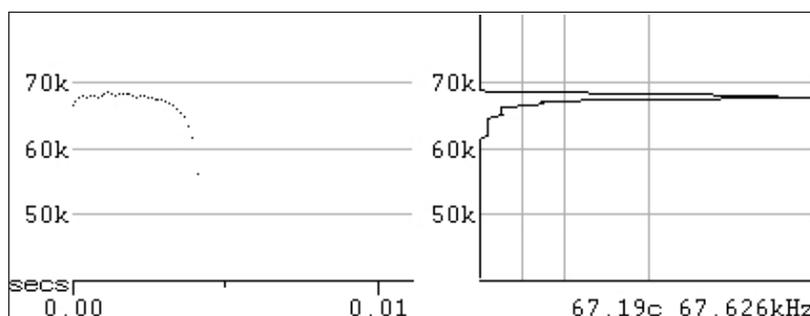

Figure 7: Frequency versus time graph (left) and duty cycle (right) of an unidentified bat in free flight at Libano Sok 10/8/03. 67.6 kHz – frequency, call shape and duration comparable with *H. cervinus* recorded at Darai Plateau in the 68 kHz harmonic. Scale: real time, 5 ms per tick (F8 and TBC uncompressed in Analook).
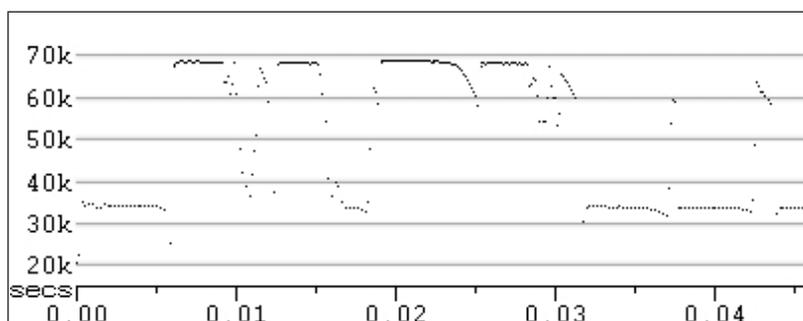

Figure 8: Frequency versus time graph of an unidentified bat in free-flight at Libano Sok 10/8/03. Call characteristics comparable to the lower harmonic (67 and 33 kHz) recordings of *H. cervinus* at Darai Plateau. Scale: real time, 5 ms per tick (F8 and TBC compressed in Analook).

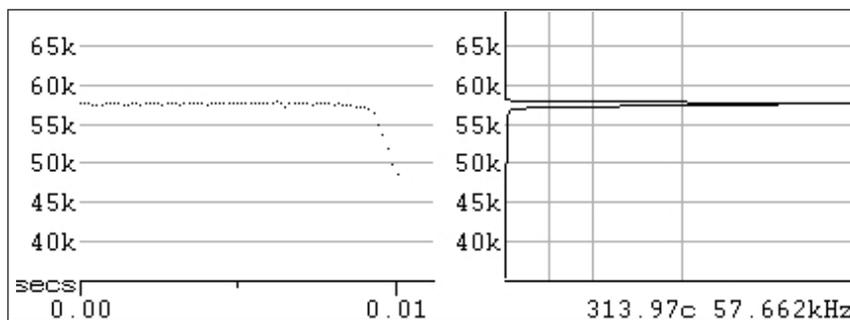   *The Biology and Conservation of Australasian Bats*

Figure 9: Frequency versus time graph (left) and duty cycle (right) showing a typical (predominantly CF) flat pulse from *H. diadema* recorded in the flight enclosure at Libano Sok 6/8/03. Scale: real time, 5 ms per tick (F9 and TBC uncompressed in Analook).
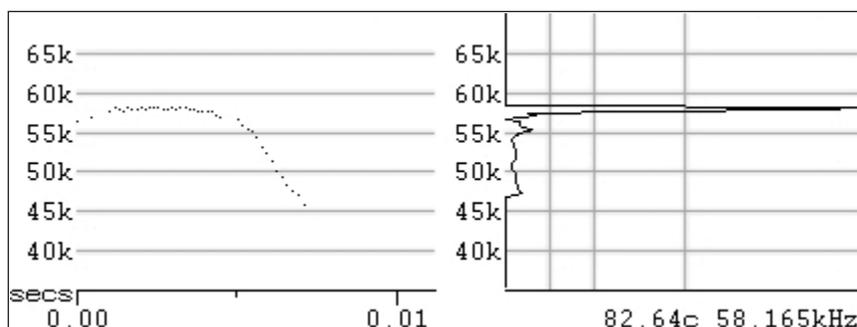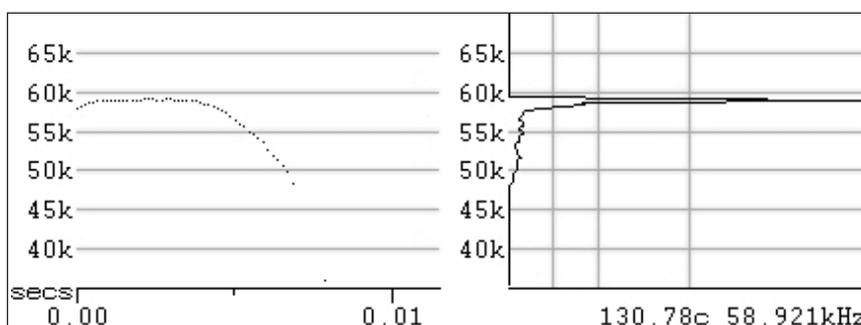

Figure 10: Frequency versus time graph (left) and duty cycle (right) of a typical (predominantly FM) call pulse from *H. diadema* recorded in the flight enclosure at Libano Sok 6/8/03. Scale: real time, 5 ms per tick (F9 and TBC uncompressed in Analook).

Figure 11: Frequency versus time graph (left) and duty cycle (right) showing a typical (predominantly FM) 58.9 kHz pulse of an unidentified bat in free flight at Libano Sok 11/8/03. The call shape and duration is comparable with reference calls recorded from *H. diadema* at the same location. Scale: real time, 5 ms per tick (F9 and TBC uncompressed in Analook).
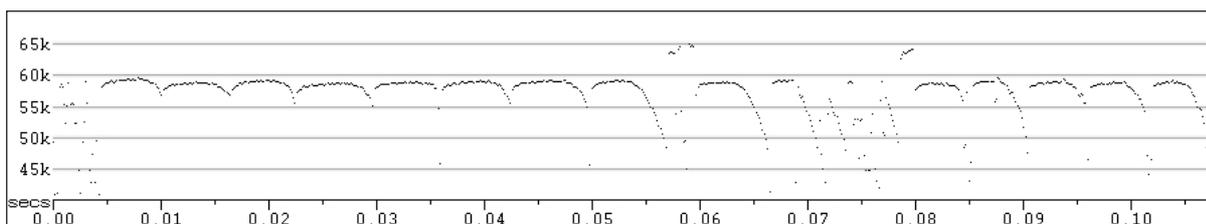

Figure 12: Frequency versus time graph of a call sequence of an unidentified bat in free-flight at Libano Sok on the 11/8/03. The call sequence is comparable with that of *H. diadema* reference calls recorded from the same location. Scale: real time, 5 ms per tick (F8 and TBC compressed in Analook).
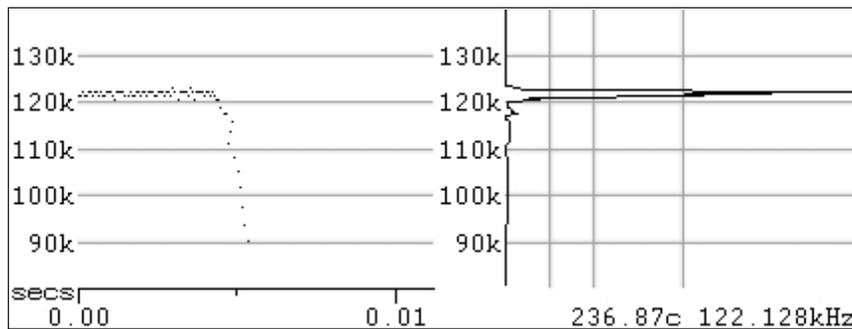
Figure 13: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse from *H. maggietaylorae* recorded in the flight enclosure at Darai 25/7/03. Scale: real time, 5 ms per tick (F9 and TBC uncompressed in Analook).
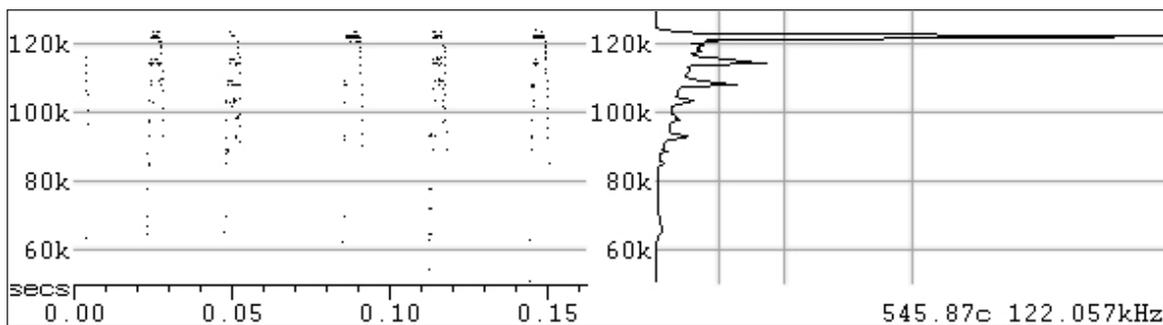

Figure 14: Frequency versus time graph (left) and duty cycle (right) of a sequence of call pulses from *H. maggietaylorae* illustrating multiple trace fragments of tones at lower frequencies. Recorded in the flight enclosure at Darai 25/7/03. Scale: real time, 25 ms per tick (F6 and TBC uncompressed in Analook).
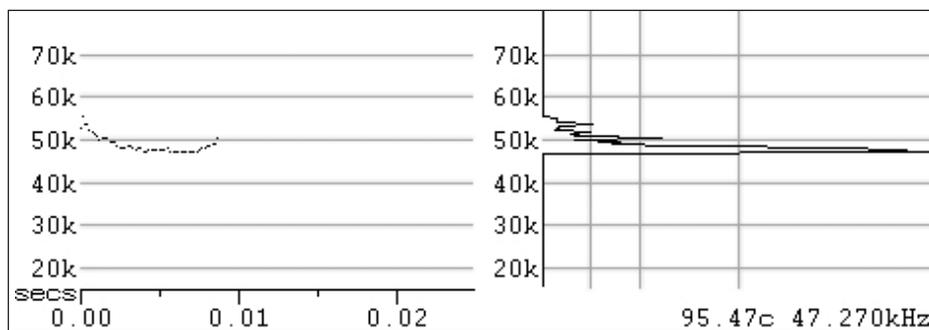

Figure 15: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse from *Mormopterus* cf. *beccarii* in the 44–50 kHz harmonic recorded in the flight enclosure at Akwam 3/4/03. Scale: real time, 5 ms per tick (F8 and TBC uncompressed in Analook).
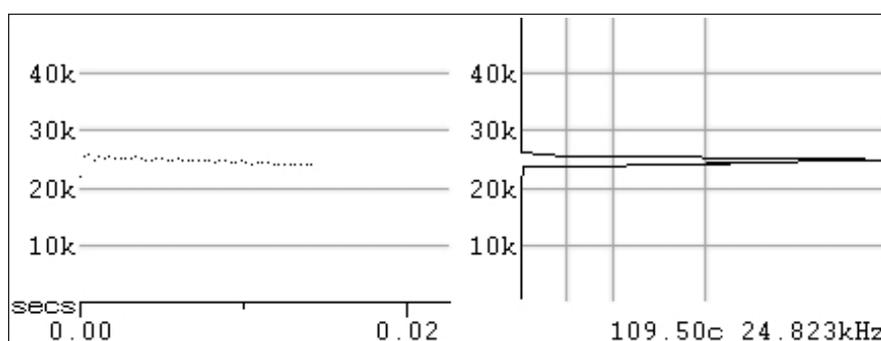

Figure 16: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse from *Mormopterus* cf. *beccarii* in the 22–27 kHz harmonic recorded in the flight enclosure at Keboi Kerowa 7/12/03. Scale: real time, 10 ms per tick (F8 and TBC uncompressed in Analook).

Western Horseshoe Bat *Rhinolophus arcuatus* – Photo 10

Call sequences n=143, calls analysed n= 9128.

A narrow band constant frequency call with minor frequency modulated components (initial and tail) in multiple harmonic ranges. The pulse shape is long and flat usually with both a short up-sweeping initial and a down-sweeping tail (mean 13.6 kHz) (Figure 18). The characteristic frequency of the predominant harmonic is between 70 and 72 kHz (mean 71.30 kHz). Some pulses show traces of harmonics at lower frequencies, irregular entire pulses in a lower harmonic with characteristic frequency of 35–36 kHz (mean 35.52 kHz, n= 80), but the 71 kHz harmonic is clearly dominant. The pulse duration is very long 20–69 ms (mean 36.33 ms), as is the time between pulses (mean 82.47 ms). Pulses appear to be repeated relatively regularly with no obvious pattern.

Figure 19 shows the call sequence of an unidentified bat in free-flight at Libano Sok, recorded on the 10/8/03. The call characteristics are comparable with the reference calls recorded within the flight enclosure for *R. arcuatus* at the same location.

New Guinea Horseshoe Bat *Rhinolophus euryotis* – Photo 11

Call sequences n=235, calls analysed n=5328.

A narrow band constant frequency call with minor frequency modulated components (initial and tail) in multiple harmonic ranges. The pulse shape is long and flat, usually with both a short up-sweeping initial and a down-sweeping tail (mean 9.3 kHz) (Figure 20). The characteristic frequency of the predominant harmonic is between 52 and 56 kHz (mean 54.07 kHz). Some pulses show traces of harmonics at lower frequencies. The pulse is of very long duration, usually 20–60 ms (mean 48.78 ms) and the time between pulses is also long (mean 85.28 ms). Pulses appear to be repeated relatively regularly with no obvious pattern.

Lesser Sheathtail Bat *Mosia nigrescens*

Call sequences n=47, calls analysed n=234.

The call consists almost entirely of a broadband frequency sweep starting between 59 and 54 kHz (mean 56.94) and dropping to between 30 to 20 kHz, although it is sometimes lower (Figure 21). The pulse shape is steep, near vertical, with the frequency dropping rapidly and increasing in slope following a brief (c. 0.5 ms) initial section. The characteristic frequency is absent due to the near vertical call shape. The pulse is of very short duration (mean 1.90 ms) and the time between pulses is rapid and irregular (usually between 20–80 ms) with no obvious pattern.
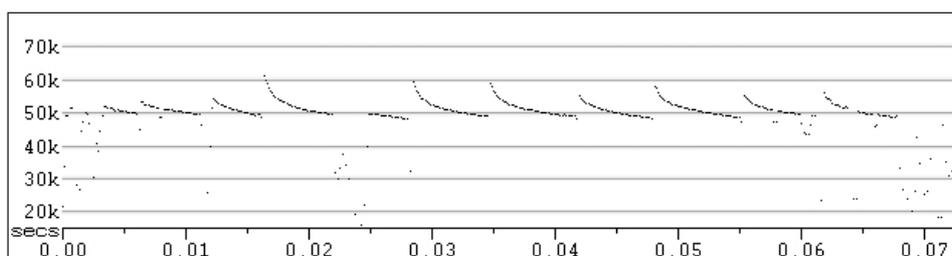

Figure 17: Frequency versus time graph of a call sequence of an unidentified bat in free-flight at Libano Sok on the 11/8/03. The call sequence is comparable with that of *M.* cf. *beccarii* reference calls recorded at Keboi Kerowa and Akwam. Scale: real time, 5 ms per tick (F8 and TBC compressed).
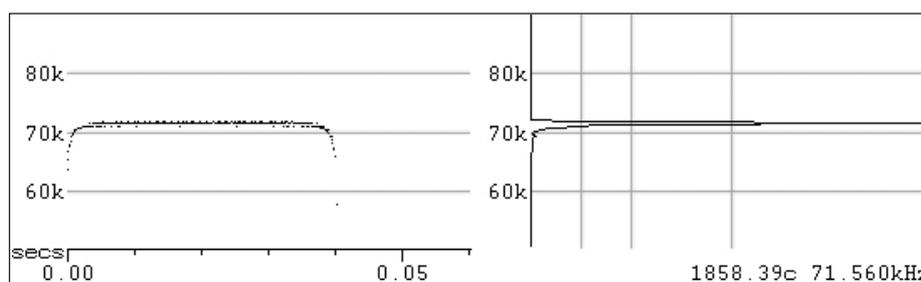

Figure 18: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse from *Rhinolophus arcuatus* recorded in the flight enclosure at Libano Sok 6/8/03. Scale: real time, 10 ms per tick (F7 and TBC uncompressed in Analook).
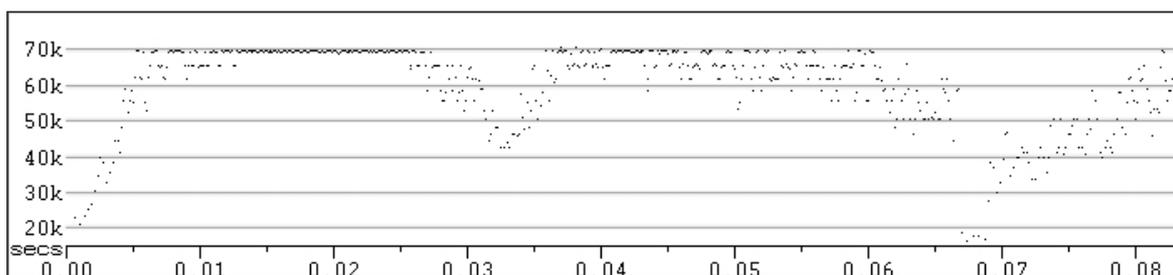

Figure 19: Frequency versus time graph of a call sequence of an unidentified bat in free-flight at Libano Sok on the 10/8/03. The call sequence is comparable with that of *R. arcuatus* reference calls recorded at the same location. Scale: real time, 5 ms per tick (F8 and TBC uncompressed in Analook).

Discussion

Interpreting the results

Caution should be applied in interpreting these calls as they were all recorded in a small net enclosure. Confined space recordings of echolocation calls of bats (such as in a net enclosure) may not resemble the natural calls made by bats when foraging. Ideally recordings for identification should be made of free flying bats in active search phase (Parsons 1998; Pennay *et al.* 2004). The taxonomic uncertainty of many New Guinea bats determined our need to lodge voucher specimens of the animals from which our call sequences were recorded. It was also necessary to record the calls of species with very high frequency calls (*Aselliscus tricuspidatus*, *Hipposiderus cervinus* and *H.maggietaylorae*), all of which call above 110 kHz. At these frequencies atmospheric attenuation is extreme and normal release calls are not possible.

Flight enclosures have been regularly used in numerous studies to record echolocation calls from bats (Matsumura 1979; Obrist *et al.*1989; Aldridge *et al.* 1990; Surlykke *et al.* 1993; Parsons 1998; O'Farrell and Miller 1999; O'Farrell 1999; Kazial *et al.* 2001; Macias and Mora 2003; Surlykke *et al.* 2003; Fukui *et al.* 2004; Ratcliffe *et al.* 2005; Siemers and Ivanova 2004; Macias *et al.* 2005). Generally, when they have been recorded in an enclosure, bats that use high duty cycle frequency modulated (FM) calls produce calls that resemble calls made by free flying bats in cluttered environments or during approach phase. These calls are structurally similar, but are shorter in duration, have greater frequency sweep and higher

repetition rates than free flying bats in search phase (Obrist *et al.* 1989: Parsons 1998; Macias and Mora 2003; Macias *et al.* 2005). The calling response of high duty cycle FM bats in enclosures relates to their sensitivity to overlap interference. Unlike constant frequency (CF) calling bats, high duty cycle FM calling bats adjust their calling design to separate echoes from calls in the time domain to avoid overlap. CF calling bats are able to rely on Doppler shifts in the returning frequency to separate echoes (Fenton *et al.* 1995: Schnitzler and Kalko 2001; Holderied *et al.* 2005; Jones and Holderied 2007). When approaching objects (vegetation and other clutter such as the side of an enclosure), the 'overlap free window' needed by FM calling bats is adjusted accordingly by reducing call duration and interpulse intervals (Schnitzler and Kalko 2001). Bandwidth is also broadened to ensonify many reflecting surfaces simultaneously (Jones and Holderied 2007).

The degree of difference between the calls of FM calling species recorded in confined spaces and calls recorded in free flight differs greatly between species. For example, Surlykke *et al.* (1993) found the Bumblebee Bat *Craseonycterus thonglongyai* gave similar calls in a net cage to those recorded from free flying bats, whereas others such as Parsons (1998) and Macias *et al.* (2005) have found significant differences between the calls of bats recorded in enclosures and those recorded in free flight. Recently developed stereo videogrammetry, laser scanning and acoustic tracking have shown that high duty cycle FM calling bats adjust call design in a range dependent manner to accurately ensonify obstacles (Jones and
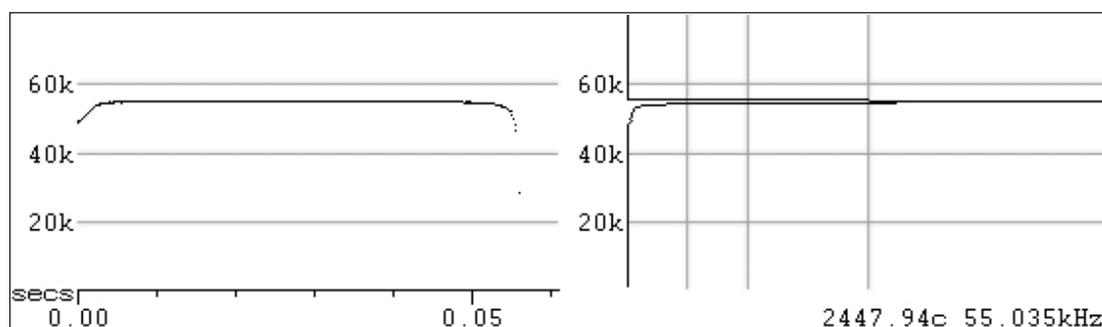

Figure 20: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse from *R. euryotis* recorded in the flight enclosure at Darai Plateau on the 30/7/03. Scale: real time, 10 ms per tick (F7 and TBC uncompressed in Analook).
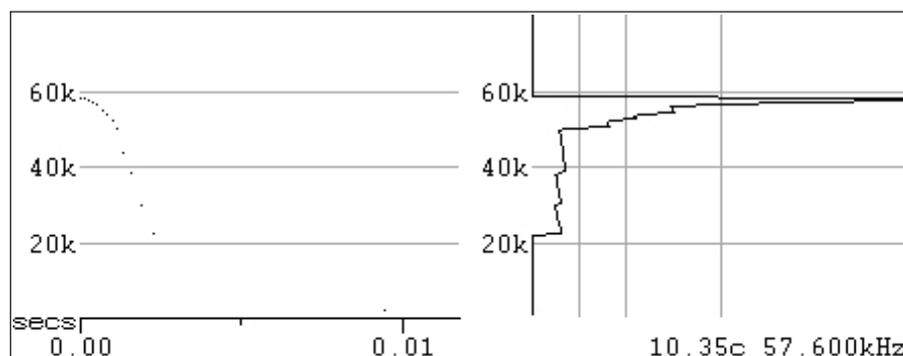

Figure 21: Frequency versus time graph (left) and duty cycle (right) of a typical call pulse from *Mosia nigrescens* recorded in the flight enclosure at Libano Sok on the 7/8/03. Scale: real time, 5 ms per tick (F9 and TBC uncompressed in Analook).

Holderied 2007). Thus, the degree of variation between free flight and calls from enclosures is likely to be related to the degree of clutter in the normal foraging behaviour of the species (Broders *et al.* 2004). Species that normally forage in highly cluttered environments are likely to use calling strategies where the overlap free window is adjusted (focussed) to short distances during natural foraging (Broders *et al.* 2004; Jones and Holderied 2007). These calls will more closely resemble the calls given in a confined space where the bat is utilising the same strategy. Species that forage in open spaces, where there is little clutter, are likely to exhibit the greatest degree of difference between natural foraging calls, and calls recorded in small enclosures / cluttered environments. This is because typically they employ (and hence, are recorded using) long range focused call strategies, ie. the call pulse is long, interpulse interval is long and frequency sweep is shallow (Aldridge and Rautenbach 1987; Schnitzler and Kalko 2001; Jones and Holderied 2007). In confined spaces they would be required to adjust their calls to focus in the short range, a strategy only employed naturally when approaching prey or other objects.

In terms of interpreting the calls recorded in this study only *Mormopterus* cf. *beccarii* and *Mosia nigrescens* utilise low duty cycle, frequency modulated calling strategies. Particular caution should be applied in viewing the parameters known to be affected by clutter (call duration, time between calls and frequency sweep) from these species. Call duration and time between calls will almost certainly be shorter and frequency sweep broader than free flying bats.

The calls of *M.* cf. *beccarii* are likely to be more affected by the use of a small enclosure than those of *M. nigrescens* because it normally flies in open spaces (Bonaccorso 1998; Bullen and McKenzie 2002). In this study *M.* cf. *beccarii* were able to fly within the enclosure but were unable to maintain sustained flight due to low manoeverability. Most low duty cycle FM bats emit a call pulse per wing beat when in normal 'search phase', this rate increases significantly when bats are in approach phase or navigating clutter (Jones 1994; Holderied and Von Hilversen 2003; Holderied *et al.* 2005; Jones and Holderied 2007). Only calls that resembled search phase calls were used for analysis in this study, which when compared against frequency data from a similar bat *Mormopterus planiceps* (Bullen and McKenzie 2002), the *M.* cf. *beccarii* calls had a comparable rate (9.6 calls per second) to the normal wingbeat (and hence call) rate 9.34 ± 1.38 per second of *M. planiceps*. *Mormopterus* cf. *beccarii* is a slightly larger bat and the call rate is slightly higher, but this comparison suggests that whilst perhaps not true search phase calls, the calls used for analysis in this study resemble those of search phase calls in timing and duration. The mean pulse length and interval recorded equate to a forward overlap zone of 1.25 metres and an 'overlap free window' of 16.4 metres. This depth of focus is appropriate for a bat that utilises an intercept attack strategy in open spaces (Bullen and McKenzie 2002), and hence also suggests that the calls recorded approximate calls used naturally by this species.

The calls of *Mosia nigrescens* recorded in the enclosure are less likely to differ from natural calls as it would employ similar 'overlap free window' adjustments as it forages naturally in highly cluttered environments from the canopy to ground level and gleans prey from foliage (Bonaccorso 1998). *Mosia nigrescens* is a small and agile bat and was able to fly well within the net enclosure. The data recorded in this study indicates *M. nigrescens* had a forward overlap zone of about 32 cm and an 'overlap free window' (distance of focus) of between 3.4 and 13.6 m. In addition, the calls we recorded are almost identical to those recorded by Grinnell and Hagiwara (1972) and are consistent with other bats that utilise a broad frequency sweep call for hawking and gleaning in cluttered environments (Schnitzler and Kalko 2001; Jones and Holderied 2007).

The majority of species in this study (six out of eight), utilise high duty cycle, narrow band call strategies. Species with narrow band, predominantly constant frequency (CF) calls have limited plasticity in their calls due to the presence of an 'acoustic fovea' that constrains both production and reception of sound. Their hearing is narrowly 'tuned' to the specific call frequency due to an over representation in the cochlea and inferior colliculus (Kingston *et al.* 2000; Kingston *et al.* 2001; Schnitzler and Kalko 2001; Hopkins 2004; Kingston and Rossiter 2004; Siemers and Ivanova 2004; Smotherman and Metzner 2004; Li *et al.* 2007).

Like FM calling bats, bats with predominantly narrow band CF calls alter the duration of call pulses and inter-call period when in enclosures, however the frequency of CF component changes little. This behaviour is important because the frequency of the CF component is one of the main characteristics used in species identification (eg. Kingston *et al.* 2000; Kingston *et al.* 2001; Kingston and Rossiter 2004; Siemers and Ivanova 2004; Papadatou *et al.* 2008). Due to the limited ability to alter the constant frequency component of calls, echolocation studies of CF bats routinely record restrained bats (often held in the hand). This minimises the impact of 'Doppler compensation' where the bats adjust their call slightly to ensure the returning echo reaches the bat within the limited auditory fovea (Kingston *et al.* 2000; Kingston *et al.* 2001; Kingston and Rossiter 2004; Li *et al.* 2007).

In terms of interpreting calls from this study the constant frequency components of calls should be the same as the calls made by the same species in free flight due to the physiological and perceptive constraints in CF calling bats. The constant frequency component of calls equates to the "characteristic frequency" in Analook. Characteristic frequency should be able to be used reliably to identify species where there is no other species with overlapping frequencies. All six CF calling species were adept slow, manoevourable flyers able to sustain prolonged flight in the small flight enclosure that we used, and they were recorded in the enclosure both in flight and resting. Some pulses recorded when the bats were in flight will be Doppler compensated, thus the frequency range of the CF component will be slightly larger than stationary bats recorded in some studies, but more realistically reflect frequencies used naturally in free flight.

Harmonics and harmonic traces were frequently detected from calls of the Hipposiderid and Rhinolophid bats. The Anabat system uses zero crossings analysis to record call characteristics, so it is only capable of recording the

dominant harmonic at any single time, ie. the harmonic with the greatest amplitude received by the detector (Parsons *et al.* 2000; Corben and Fellers 2001). Other harmonics are seen occasionally in calls or series of calls that fit within a sequence, have the same structural and temporal characteristics but are precisely double or half of the frequency of the dominant harmonic (Corben and Fellers 2001). There are a number of factors that may affect which harmonic is recorded such as distance of the microphone, atmospheric attenuation and behaviour of the bat (Corben and Fellers 2001). All sub-dominant harmonic traces detected in this study were lower (fundamental) harmonics suggesting that the second harmonic was most frequently the dominant harmonic. This is consistent with observations of CF calling bats in other studies that have used a range of detection and recording devices (O'Farrell and Miller 1999: Macias and Mora 2003; Chen *et al.* 2004; Kingston and Rossiter 2004; Macias *et al.* 2005; Li *et al.* 2007).

Pulse duration, interpulse duration and frequency modulated components of CF calls are constantly adjusted by the bats depending on the situation. The response of CF bats to calling in enclosures is much like that of other bats; call duration decreases, interpulse duration shortens, and there is a greater sweep in frequency modulated components, resembling those of bats navigating clutter (Siemers and Ivanova 2004; Smotherman and Metzner 2004). The temporal sequence of calls also changes, CF bats switch to doublets or multiplets (repeated calls in short duration spaced by longer pauses) when echoes return above the call frequency (Smotherman and Metzner 2004).

The flexible call components recorded in this study should be interpreted with caution, as they may not be diagnostic or represent calls from free flying bats because they will have been influenced by the recording method. The FM components (ie. 'initial' and 'tail') are likely to be exaggerated, pulse duration and interpulse interval may also be shorter than those in free flying bats, but the degree of difference is difficult to determine, as these temporal and phase changes in calls are also natural responses to navigation in cluttered environments, which all of these species forage in naturally.

Call variation

A number of researchers (e.g. Novick 1977; Heller and Von Helversen 1989) have demonstrated that for *Rhinolophus* and *Hipposideros* body size and call frequency are inversely correlated (although the regression lines are separate), and this correlation appears to hold good for the three *Hipposideros* and two *Rhinolophus* recorded by us.

Table 4 shows the dominant frequency of echolocation calls recorded during this study and calls published for the same species elsewhere and illustrates that the predominant frequency for at least some species varies between geographical areas. Our study demonstrated that for at least four of the eight species (actually 67% of the species for which we could find published calls) there appear to be regional differences both within PNG and between calls recorded in Australia and south-east Asia. There appear to be major differences in *Hipposideros cervinus* calls over the species range, including between northern and southern PNG (Grinnell and Hagiwara

1972 and this study). There are also variations in the calls of *Mormopterus* cf. *beccarii, H. diadema* and *R. arcuatus* between those recorded in this study and some of those recorded in Australia and south-east Asia (Fenton 1982; Brown and Berry 1983; Crome and Richards 1988; Heller and Von Helversen 1989; Pavey and Burwell 1995; Kingston *et al.* 2000; Reinholdt *et al.* 2001; McKenzie *et al.* 2002; Milne 2002; McKenzie and Bullen 2008; Pavey and Burwell 2008; Pavey *et al.* 2008).

It is possible that the variation in calls is the result of the enclosure method used to record bats, however as discussed previously, this is unlikely to explain the variation in the characteristic frequencies used. There are at least three other possible reasons for the observed regional variation in calls. Firstly, some of these differences may be the result of incorrect identification of morphologically similar sibling species, which we believe emphasises the need to lodge voucher specimens (as we have done) for each reference call made from a region. Some sibling species such as *Hipposideros maggietaylorae* and *Hipposiderus calcaratus* are extremely difficult to separate in the field. The taxonomic uncertainty of some groups further adds to identification issues. For example, the taxonomic uncertainty of *Mormopterus* species in general (T. Reardon – SA Museum, pers. comm. 2007) may result in the bats identified by us from the keys and description in Bonaccorso (1998) as *Mormopterus* cf. *beccarii* being assigned to a different species than the northern Australia form. There is certainly potential for confusion as the echolocation calls recorded by us fall both within the frequency range shown by Crome and Richards (1988) (in their Figure 1) for *Mormopterus loriae*, (42–50 kHz), but also a series of pulses within some of the same call sequences were emitted in a lower harmonic, approximately half this frequency (22–27 kHz), which is in the typical characteristic frequency range of *Mormopterus beccarii* in Northern Australia (Reinhold *et al.* 2001; McKenzie *et al.* 2002; Milne *et al.* 2002). We note, however, that the figure in Crome and Richards (1988) is different from that recorded by Milne (2002) who records the characteristic frequency of *M. loriae* to be 31.7 kHz, reportedly from bats recorded in northern Queensland. The bats at both Akwam and Keboi Kerowa appeared larger and more solidly built than typical *M. loriae,* further highlighting the need for collection of voucher specimens. It may be that the bats we recorded were either or neither of these species, and that accurate identification cannot be based on echolocation calls alone.

The systematics of many PNG mammals is still relatively fluid with many recent revisions of genera and the need for further revisions of a number of genera (Leary and Mamu 2004; Helgen 2006). These systematic revisions will add further difficulties to surveying with bat detectors unless voucher specimens are lodged. For example, since Grinnell and Hagiwara (1972) recorded *Hipposideros calcaratus* and *H. cupidus* calls, there has been a revision by Smith and Hill (1981), which now means it is not possible, without examination of voucher specimens, to correctly assign these calls to *H. calcaratus cupidus* or *H. maggietaylorae* (see Table 4).

A second potential reason for the geographical differences in calls apparent in Table 4 is the presence of morphologically indistinguishable cryptic species with

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Table 4: Predominant harmonic frequencies of echolocation calls of PNG bats from this study and published literature.

Species	Location	Predominant Frequency (KHz)	Reference	Forearm Range[1]
Aselliscus tricuspidatus novaeguinea	Keboi Kerowa, Gulf Province, PNG	112–113	This study	39.4–44.7
A. t. novaeguinea	Madang, Madang Province, PNG	110–112	Grinnell and Hagiwara 1972	
Hipposideros cervinus cervinus	Darai Plateau, Gulf Province, PNG	136.5–138	This study	44.3–50.7
H. galeritus[2]= H. c. cervinus	Madang, Madang Province, PNG	140–145	Grinnell and Hagiwara 1972	
H. c. cervinus	Cape York, Qld, Australia	144–145	Pavey and Burwell 2008; Bonaccorso 1998[3]	
H. c. labuanensis	Krau Wildlife Reserve, Pahang, Malaysia	125.5	Kingston et al. 2000	
H. c. labuanensis	Kuala Lumpur, Malaysia	126	Heller and Von Helversen 1989	
H. diadema griseus	Libano Sok, Southern Highlands Province, PNG	54–59	This study	72.4–83.4
H. d. griseus	Madang, Madang Province, PNG	58	Grinnell and Hagiwara 1972	
H. d. inornatus	Top End, Northern Territory, Australia	69.1	Milne 2002	
H. diadema masoni	Kuala Lumpur, Malaysia	55	Heller and Von Helversen 1989	
H. d. masoni	Krau Wildlife Reserve, Malaysia	60.4	Kingston et al. 2000	
H. diadema reginae	Chillagoe, Qld, Australia	50.9–54.9	Fenton 1982	
H. d. reginae	Chillagoe, Qld	55	Brown and Berry 1983	
H. d. reginae	Windsor Tablelands, Qld, Australia, and NE Qld	58	Crome and Richards 1988; Pavey et al. 2008	
H. d. reginae	NE Qld, Australia	55–58	Pavey and Burwell 1998	
H. maggietaylorae erroris	Darai Plateau, Gulf Province, PNG	121–123	This study	50.4–58.5
H. cupidus[5]	Madang, Madang Province, PNG	123–124	Grinnell and Hagiwara 1972	
H. calcaratus[5]	Madang, Madang Province, PNG	125 –130	Grinnell and Hagiwara 1972	48.3–55.8[6]
Mormopterus cf. beccarii astrolobiensis	Akwam, Western Province and Keboi Kerowa, Gulf Province, PNG	44–50 and 22–27	This study	33.0–37.0
M. cf. beccarii beccarii	Windsor Tablelands, Qld, Australia	28–30	Crome and Richards 1988 [4]	
M. cf. beccarii beccarii	SE Qld, NE NSW, Australia	22–24	Reinhold et al. 2001	
M. cf. beccarii beccarii	Qld, Australia	24.3	Milne 2002	
M. cf. beccarii beccarii	Listed for PNG but refers to Australian species	23.5	Bonaccorso 1998[7]	
M. cf. beccarii beccarii	Little Sandy Desert, Western Australia	26.3	McKenzie et al. 2002	
Mosia nigrescens papuana	Libano Sok, Southern Highlands Province, PNG	45–60	This study	30.1–35.6
Emballonura nigrescens[8]	Madang, Madang Province, PNG	61	Grinnell and Hagiwara 1972	
Rhinolophus arcuatus mcintyrei	Libano, Southern Highlands Province, PNG	70–72	This study	48.0–54.0
Rhinolophus a. exiguus	Philippines	66.5	Novick 1958 in Heller and Von Helversen 1989	
R. euryotis timidus	Darai, Gulf Province, PNG	52–56	This study	50.0–58.5

1 From Bonaccorso 1998.
2 H. galeritus cervinus is synonymous with H. cervinus cervinus see Jenkins and Hill 1981.
3 Frequency stated in Bonaccorso 1998 does not come from PNG bats but is taken directly from Pavey and Burwell 1995 – F. Bonaccorso (pers. comm. 2007).
4 Frequency is an approximation only – estimated from Figure 1 in Crome and Richards 1988.
5 The taxonomy of this group was previously confused and these could refer to animals of either H. calcaratus cupidus or H. maggietaylorae – see Smith and Hill 1981.
6 Fore-arm range for Hipposideros calcaratus cupidus.
7 Frequency stated in Bonaccorso 1998 does not come from PNG bats but is taken directly from McKenzie 1995 – F. Bonaccorso (pers. comm. 2007) which is in fact the lowest frequency so is not directly comparable.
8 Species removed from Emballonura by Griffiths et al. 1991 and placed in Mosia.

different echolocation calls. The presence of morphologically indistinguishable cryptic species that have been first detected by their different echolocation calls have been suggested for *H. commersoni* in Kenya (Pye 1972), *Pipistrellus pipistrellus* in Europe (Barratt *et al.* 1997), *H. bicolour* in Malaysia (Kingston *et al.* 2001), *Myotis alcathoe* in Europe (von Helversen *et al.* 2001), *Scotophilus dinganii* in Africa (Jacobs *et al.* 2006) and *H. larvatus* in India (Thabah *et al.* 2006). Some of these differences have been supported by molecular genetic evidence (e.g. Barratt *et al.* 1987; Kingston *et al.* 2001; von Helversen *et al.* 2001; Jacobs *et al.* 2006; Thabah *et al.* 2006). Molecular work on *H. cervinus, H. diadema, R. arcuatus* and *Mormopterus* cf. *beccari* across their geographic ranges is needed to rule out the possibility of cryptic species.

Lastly, an alternative argument for which there is growing acknowledgement within Australia is that there is, in general, an underestimation of variation within bat calls across a species geographic range, and that there are real regional variations in calls (e.g. Reinhold *et al.* 2001; Law *et al.* 2002; Reardon 2003; Pennay *et al.* 2004). Various reasons for intraspecific variation in echolocation calls across a species geographic range have been proposed including: adaptation to different habitats (e.g. Obrist 1995; Wund 2006); other environmental factors such as prey encounter rates (Barclay *et al.* 1999) or humidity (e.g. Guillen *et al.* 2000); morphological differences such as overall body size (e.g. as represented by forearm length – Heller and Von Helversen 1989; Kingston and Rossiter 2004), body condition (Guillen *et al.* 2000) or nasal chamber volume (Armstrong and Coles 2007); sexual selection and simple drift (Guillen *et al.* 2000; Jones and Barlow 2004).

Our study suggest that at least for *H. cervinus, H. diadema, Mormopterus* cf. *beccarii* and *R. arcuatus* that there are regional differences both within PNG and between calls recorded in Australia and south-east Asia. This further emphasises the need for the development of regional call libraries for PNG, and cautions against the use of Australian call libraries for the identification of free-flying bats. Regional call libraries for PNG should be developed for at least the northern and southern lowlands, the Transfly, the central highlands, and the PNG islands. Voucher specimens should be lodged for reference call sequences recorded to ensure that the identity of the species can be determined even if there are subsequent taxonomic revisions. Where possible, this should be further supported by recordings of unvouchered released individuals in free-flight.

We hope this research will stimulate researchers to begin collecting reference echolocation calls of PNG bats, as the use of bat detectors in PNG would undoubtedly increase the known distribution of many species.

References

Aldridge, H.D.J., Obrist, N.M., Merriam, H.G. and Fenton, M.B. 1990. Roosting, vocalizations, and foraging by the African bat, *Nycteris thebaica. Journal of Mammalogy* 71 (2): 242–246.

Aldridge, H. D. J., Rautenbach, I.L. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *The Journal of Animal Ecology* 56 (3): 763–778.

Armstrong, K.N. and Coles, R.B. 2007. Echolocation differences between geographic isolates of *Rhinonicteris aurantia* (Chiroptera: Hipposideridae): implications of nasal chamber size. *Journal of Mammalogy* 88: 94–104.

Barclay, R.M.R., Fullard, J.H., and Jacobs, D.S. 1999. Variation in the calls of the hoary bat (*Lasiurus cinereus*): influence of body size, habitat structure and geographic location. *Canadian Journal of Zoology* 77: 530–534.

Barratt, E.M., Deaville, R., Burland, T.M. and Bruford, M.W. 1997. DNA answers the call of the pipisterelle bat species. *Nature* **387**: 138–139.

Bonaccorso, F. 1998. *Bats of Papua New Guinea*. Conservation International Tropical Field Guide Series, Washington, DC.

Broders, H.G., Findlay, S.F., and Zhang, L. 2004. Effects of clutter on echolocation call structure of *Myotis septentrionalis* and *M. lucifugus*. *Journal of Mammalogy* **85** (2): 273–281.

Brown, P. E. and Berry, R. D. 1983. Echolocation behaviour of a "Flycatcher" bat *Hipposideros diadema*. *The Journal of the Acoustical Society of America* **74**(S1), S32.

Bullen, R.D. and McKenzie, N. L. 2002. Scaling bat wingbeat frequency and amplitude. *The Journal of Experimental Biology* **205**: 2615–2626.

Chen, M., Feng, J., Liu, Y., Zhang, X., Li, Z., Zhou, J. and Zhang, S. 2004. Relationship between echolocation calls and age in the bat species of *Rhinolophus pearsoni*. *Zoological Research* **25** (1): 15–19.

Churchill, S. 1998. *Australian Bats*. Reed New Holland Publishing, Sydney.

Corben, C. and Fellers, G.M. 2001. Choosing the 'correct' bat detector — a reply. *Acta Chiropterologica* **3** (2): 245–256.

Corben, C. and O'Farrell, M.J. 1999. Techniques for the effective use of Anabat in identifying free-flying bat species. Anabat system manual.

Crome, F.H.J. and Richards, G.C. 1988. Bats and gaps: Microchiropteran community structure in a Queensland rainforest. *Ecology* **69** (6): 1960–1969.

Fenton, M.B. 1982. Echolocation calls and patterns of hunting and habitat use of bats (Microchiroptera) from Chillagoe, north Queensland. *Australian Journal of Zoology* **30**: 417–425.

Fenton, M.B., Audet, D., Obrist, M.K., and Rydell, J. 1995. Signal strength, timing, and self-deafening: The evolution of echolocation in bats. *Paleobiology* **21** (2): 229–242.

Filewood, L.W. 1983. The possible occurrence in New Guinea of the ghost bat (*Macroderma gigas*: Chiroptera: Megadermatidae). *Australian Mammalogy* **6**: 35–36.

Fukui, D., Agtsuma, N., and Hill, D.A. 2004. Acoustic identification of eight species of bat (Mammalia: Chiroptera) inhabiting forests of southern Hokkaido, Japan: Potential for conservation monitoring. *Zoological Science* **21**: 947–955.

Gebia, O. and Balun, L. 2004. Species diversity and composition in the Darai limestone karst and Libano alluvial forest in Gulf and Southern Highlands Provinces. KICDP Scientific Report: SR-04-01. Unpublished report to WWF.

Griffiths, T.A., Koopman, K.F. and Starrett, A. 1991. The systematic relationship of *Emballonura nigrescens* to other species of *Emballonura* and to *Coleura* (Chiroptera: Emballonuridae). *American Museum Novitates* **2996**: 1–16.

Grinnell, A.D. and Hagiwara, S. 1972. Adaptations of the auditory nervous system for echolocation. Studies of New Guinea bats. *Zeitscrift fur vergleichende Physiologie* **76**: 41–81.

Guillen, A., Juste, B., and Ibanez, C. 2000. Variation in the frequency of the echolocation calls of *Hipposideros ruber* in the Gulf of Guinea: an exploration of the adaptive meaning of the constant frequency value in rhinolophid CF bats. *Journal of Evolutionary Biology* **13**: 70–80.

Hall, L.S. and Richards, G. 1995. Diadem Leafnosed-bat *Hipposideros diadema*. Pp. 459–460 in *The Mammals of Australia, Second Edition*, edited by R. Strahan. Reed Books, Chatswood, NSW.

Helgen, K. 2005. Systematics of the Pacific monkey-faced bats (Chiroptera: Pteropidae) with a new species of *Pteralopex* and a new Fijian genus. *Systematics and Biodiversity* **3** (4): 433–453.

Helgen, K. 2006. A taxonomic and geographic overview of mammals of Papua. Pp. 689–749 in *The Ecology of Papua* edited by A.J. Marshall and B. M. Beehler. Periplus editions, Singapore.

Heller, K.G. and Von Helversen, O. 1989. Resources partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia* **80**: 178–186.

Holderied, M.W. and von Helversen, O. 2003. Echolocation range and wingbeat period match in aerial-hawking bats. *Proceedings of the Royal Society Biological Sciences* **270**(1530): 2293–2299.

Holderied, M.W., Korine, C., Fenton, M.B., Parsons, S., Robson, S. and Jones, G. 2005. Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. *Journal of Experimental Biology* **208**: 1321–1327.

Jacobs, D.S., Eick, G.N., Schoeman, M.C. and Matthee, C.A. 2006. Cryptic species in an insectivorous bat *Scotophilus dinganii*. *Journal of Mammalogy* **87**: 161–170.

Jenkins, P.D. and Hill, J.E. 1981. The status of *Hipposideros galeritus* (Cantor, 1846) and *Hipposideros cervinus* (Gould 1854) (Chiroptera: Hipposideridae). *Bulletin of the British Museum of Natural History, Zoology* **41**: 279–294.

Jones, G. 1994. Scaling of wingbeat and echolocation pulse emission rates in bats: Why are aerial insectivorous bats so small? *Functional Ecology* **8**(4): 450–457.

Jones, G. and Barlow, K.E. 2004. Cryptic species of echolocating bats. Pp. 345–349 in *Echolocation in bats and dolphins*, edited by J.A. Thomas, C.F. Moss, and M. Vater. University of Chicago Press, Chicago, Illinois.

Jones, G. and Holderied, M.W. 2007. Bat echolocation calls: adaptation and convergent evolution. *Proceedings of the Royal Society Biological Sciences* **274**(1612): 905–912.

Kazial, K.A., Burnett, S.C. and Masters, W.M. 2001. Individual and group variation in echolocation calls of big brown bats, *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *Journal of Mammalogy* **82**(2): 339–351.

Kingston, T. and Rossiter, S.J. 2004. Harmonic hopping in Wallace's bat. *Nature* **429**: 654–657.

Kingston, T., Jones, G., Zubaid, A. and Kunz, T.A. 2000. Resource partitioning in rhinolophoid bats revisited. *Oecologia* **124**: 332–342.

Kingston, T., Lara, M.C., Jones, G., Zubaid, A., Kunz, T.H. and Schneider, C.J. 2001. Acoustic divergence in two cryptic *Hipposideros* species: a role for social selection? *Proceedings of the Royal Society of London, Series B Biological Sciences* **268**: 1381–1386.

Law, B.S., Reinhold, L. and Pennay, M. 2002. Geographic variation in the echolocation calls of *Vespadelus* spp. (Vespertilionidae) from New South Wales and Queensland, Australia. *Acta Chiroptologica* **4** (2): 201–215.

Leary, T. and Mamu, T. 2004. Conserving Papua New Guinea's forest fauna through community planning. Pp. 186–207 in *Conservation of Australia's Forest Fauna* (Second Edition), edited by D. Lunney. Royal Zoological Society of New South Wales, Mosman, NSW.

Li, G., Liang, B., Wang, Y., Zhao, H., Helgen, K.M., Liangkong, L., Jones, G. and Zhang, S. 2007. Echlocation calls, diet and phylogenetic relationships of Stoliczka's trident bat *Aselliscus stoliczkanus* (Hipposideridae). *Journal of Mammalogy* 88(3):736–744.

Macias, S. and Mora, E.C. 2003. Variation of echolocation calls of *Pteronotus quadridens* (Chiroptera:Mormoopidae) in Cuba. *Journal of Mammalogy* 84(4):1428–1436.

Macias, S., Mora, E.C., Koch, C. and Von Helversen, O. 2005. Echolocation behaviour of *Phyllops falcatus* (Chiroptera: Phyllostomidae): unusual frequency range of the first harmonic. *Acta Chiropterologica* 7(2): 275–283.

Matsumura, S. 1979. Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): development of vocalization. *Journal of Mammalogy* 60(1): 76–84.

McKenzie, N.L. 1995. Beccari's Freetail-Bat *Mormopterus beccarii*. Pp. 480–481 in *The Mammals of Australia* (Second Edition) edited by R. Strahan. Reed Books, Chatswood, NSW.

McKenzie, N.L. and Bullen, R.D. 2008. Beccari's Free-tailed Bat *Mormopterus beccarii*. Pp. 486–487 in *The Mammals of Australia* (Third Edition) edited by S. Van Dyck and R. Strahan. Reed New Holland Books, Chatswood, NSW.

McKenzie, N.L., Start, A.N. and Bullen, R.D. 2002. Foraging ecology and organisation of a desert bat fauna. *Australian Journal of Zoology* 50 (5): 529–545.

Milne, D.J. 2002. *Key to the Bat Calls of the Top End of the Northern Territory*. Parks and Wildlife Commission of the Northern Territory. Technical Report 71.

Novick, A. 1958. Orientation in palaeotropical bats. I. Microchiroptera. *Journal of Experimental Biology* 138: 81–153.

Novick, A. 1977. Acoustic orientation. Pp. 74–289 in *Biology of Bats– Volume III* edited by W.A. Wimsatt. Academic Press, New York.

O'Farrell, M.J. and Miller, B.W. 1999. Use of vocal signatures for the inventory of free-flying Neotropical bats. *Biotropica.* 31(3): 507–516.

O'Farrell, M., Miller, B.W. and Gannon, W.L. 1999. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy* 80(1): 11–23.

Obrist, M., Aldridge, H.D.J.N. and Fenton, M.B. 1989. Roosting and echolocation behavior of the African bat, *Chalinolobus variegatus*. *Journal of Mammalogy* 70(4): 828–833.

Obrist, M.K. 1995. Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behavioral Ecology and Sociobiology* 36: 207–219.

Paijmans, K. 1976. *New Guinea Vegetation*. Australian National University Press, Canberra.

Papadatou, E., Butlin, R.K. and Altringham, J.D. 2008. Identification of bat species in Greece from their echolocation calls. *Acta Chiropterologica* 10(1): 127–143.

Parsons, S. 1998. The effect of recording situation on the echolocation calls of the New Zealand lesser short-tailed bat (*Mystacina tuberculata* Gray). *New Zealand Journal of Zoology* 25: 147–156.

Parsons, S., Boonman, A.J. and Obrist, M.K. 2000. Advantages and disadvantages of techniques for transforming and analyzing chiropteran echolocation calls. *Journal of Mammalogy* 81(4): 927–938.

Pavey, C.R. and Burwell, C.J. 1995. Fawn Leafnosed Bat *Hipposideros cervinus*. Pp. 457–458 in *The Mammals of Australia* (Second Edition) edited by R. Strahan. Reed Books, Chatswood, NSW.

Pavey, C.R. and Burwell, C.J. 1998. Bat predation on eared moths: a test of allotonic frequency hypothesis. *Oikos* 81:143–151.

Pavey, C.R. and Burwell, C.J. 2000. Foraging ecology of three species of hipposiderid bats in tropical rainforest in north-east Australia. *Wildlife Research* 27: 283–287.

Pavey, C.R. and Burwell, C.J. 2008. Fawn Leafnosed Bat *Hipposideros cervinus*. Pp. 459–461 in *The Mammals of Australia* (Third Edition) edited by S. Van Dyck and R. Strahan. Reed New Holland Books, Chatswood, NSW.

Pavey, C.R., Hall, L.S. and Richards, G. 2008. Diadem Leafnosed-bat *Hipposideros diadema reginae*. Pp. 463–464 in *The Mammals of Australia* (Third Edition) edited by S. Van Dyck and R. Strahan. Reed New Holland Books, Chatswood, NSW.

Pennay, M., Law, B., and Reinhold, L. 2004. *Bat calls of New South Wales: Region based guide to the echolocation calls of Microchiropteran bats*. NSW Department of Environment and Conservation, Hurstville.

Pye, J.D. 1972. Bimodal distribution of constant frequencies in some Hipposiderid bats (Mammalia: Hipposideridae). *Journal of Zoology, London* 166: 328–335.

Ratcliffe, J.M., Raghuram, H., Marimuthu, G., Gullard, J.H. and Fenton, M.B. 2005. Hunting in unfamiliar space: echolocation in the Indian false vampire bat, *Megaderma lyra*, when gleaning prey. *Behavioral Ecology and Sociobiology* 58: 157–164.

Reardon, T. 2003. Standards in bat detector based surveys. *The Australian Bat Society Newsletter* 20: 41–43.

Reinhold, L., Law, B., Ford, G. and Pennay, M. 2001. *Key to the bat calls of south-east Queensland and north-east New South Wales*. Forest Ecosystem Research and Assessment Technical paper 2001–7, Department of Natural Resources and Mines, Queensland.

Schnitzler, H. and Kalko, E.K.V. 2001. Echolocation by insect-eating bats. *BioScience* 51: 557–569.

Siemers, B.M. and Ivanova, T. 2004. Ground gleaning in horseshoe bats: comparative evidence from *Rhinolophus blasii*, *R. euryale* and *R. mehelyi*. *Behavioural Ecology and Sociobiology* 56:464–471.

Smith, J.D. and Hill, J.E. 1981. A new species and subspecies of bat of the *Hipposideros bicolor* group from Papua New Guinea, and the systematic status of *Hipposideros calcaratus* and *Hipposideros cupidus* (Mammalia: Chiroptera: Hipposideridae). *Contributions in Science, Natural History Museum of Los Angeles County* 331: 1–19.

Smotherman, M. and Metzner, W. 2005. Auditory-feedback control of temporal call patterns in echolocating horseshoe bats. *Journal of Neurophysiology* 93: 1295–1303.

Strahan, R. (ed.) 1995. *The Mammals of Australia* (Second Edition). Reed Books, Chatswood, NSW.

Surlykke, A., Futtrup, V. and Tougaard, J. 2003. Prey-capture success revealed by echolocation signals in pipistrelle bats (*Pipistrellus pygmaeus*). *The Journal of Experimental Biology* 206: 93–104.

Surlykke, A., Miller, L.A., Møhl, B., Andersen, B.B, Christiensen-Dalsgaard, J., and Jørgensen, M.B. 1993.

Echolocation in two very small bats from Thailand *Craseonycteris thonglongyai* and *Myotis siligorensis. Behavioral Ecology and Sociobiology* **33**(1): 1–12.

Thabah, A., Rossiter, S.J., Kingston, T., Zhang, S., Parsons, S., Mya Mya K., Zubaid, A. and Jones, G. 2006. Genetic divergence and echolocation call frequency in cryptic species of *Hipposideros larvatus s.l.* (Chiroptera: Hipposideridae) from the Indo-Malayan region. *Biological Journal of the Linnean Society* **88**: 119–130.

Van Dyck, S., and Strahan, R. (eds.) 2008. *The Mammals of Australia* (Third Edition). Reed New Holland, Sydney.

Von Helversen, O., Hellet, K.G., Mayer, F., Nemeth, A., Volleth, M. and Gombkto, P. 2001. Cryptic mammalian species: a new species of whiskered bat (*Myotis alcathoe* n. sp.) in Europe. *Naturwissenschaften* **88**: 217–223.

Wund, M.A. 2006. Variation in the echolocation calls of Little Brown Bats (*Myotis lucifugus*) in response to different habitats. *American Midland Naturalist* **156**: 99–108.

Appendix

Photo 1: Crossing the river at Libano Sok photographed by Michael Pennay.

Photo 2: Tanya setting a net at the Darai Plateau site photographed by Michael Pennay.

Photo 3: Ara and Topina setting nets on ropes and pulleys across a creek at Keboi Kerowa site photographed by Tanya Leary.

Photo 4: Habitat at Akwam showing little understorey development photographed by Tanya Leary.

Photo 5: *Aselliscus tricuspidatus* photographed by Tanya Leary.

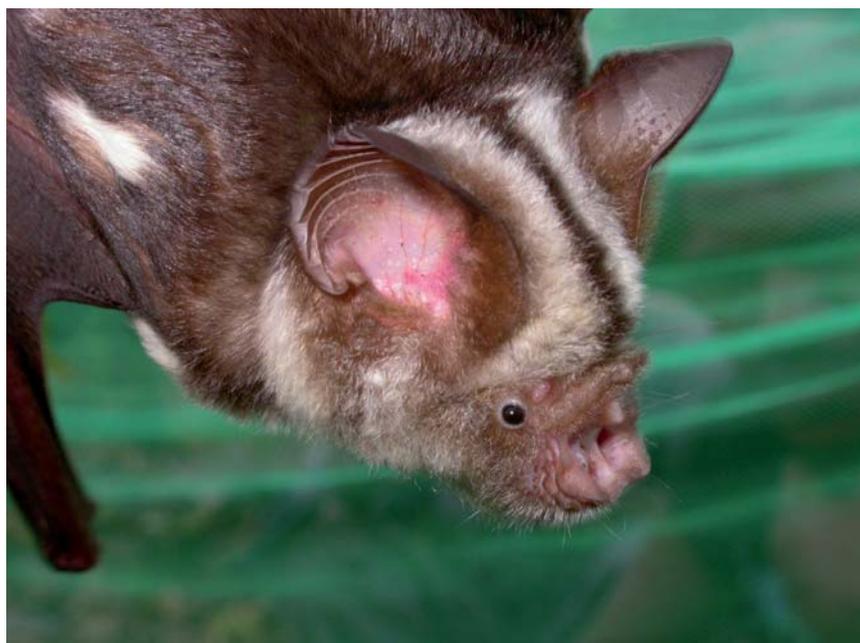

Photo 6: *Hipposideros cervinus* photographed by Tanya Leary.

Photo 7: *Hipposideros diadema* photographed by Michael Pennay.

Photo 8: *Hipposideros maggietaylorae* photographed by Michael Pennay.

Photo 9: *Mormopterus* cf *beccarii* from Keboi Kerowa photographed by Tanya Leary.

Photo 10: *Rhinolophus arcuatus* photographed by Michael Pennay.

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Photo 11: *Rhinolophus euryotis* photographed by Michael Pennay.

Photo 12: *Mosia nigrescens* photographed by Allen Allison.