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Chapter 19

Bats of the Muller Range, Papua New Guinea

Kyle N. Armstrong and Ken P. Aplin

SUMMARY

The bat fauna of Papua New Guinea (PNG) is incompletely known, and further field collections are required for a better understanding of taxonomic relationships, distributions and conservation status.

A survey of the bat fauna at three altitudinally separated habitats (c. 500, 1,600, 2,900 m) was undertaken in the remote Muller Range, which contains a largely undocumented and intact mammal fauna. Capture rates were relatively low, producing a total of 37 individuals of five species in two families. Most captures were of small Pteropodidae, with one capture of a hipposiderid bat. At least two of the captured pteropodid species are currently unnamed (in the genera *Nyctimene*, *Syconycteris*), though each is known from other localities in PNG. Genetic analysis was used to confirm the identity of the pteropodid *Paranyctimene raptor*. AnaBat recordings of bat echolocation calls documented 16 different call types, representing at least 12 species of insectivorous bats. Of these, four could be allocated a species name based on available information. Most bat call sequences were recorded at the edge of artificial clearings (helicopter pads) rather than on natural corridors along watercourses. The greatest diversity of insectivorous bats (13 call types, possibly nine species) was recorded at an elevation of 1,600 m, with seven call types/species at 500 m, and four call types from at least three species at 2,900 m. The richness at 2,900 m is a notable observation, since only two insectivorous bats have been captured at similarly high elevations elsewhere in New Guinea. The results highlight the general need for further collecting to help with taxonomic and distributional studies, and the particular need to acquire reference echolocation calls so that bats can be surveyed with greater confidence using acoustic recordings.

INTRODUCTION

Despite its relatively small geographical area, Papua New Guinea contains a diverse bat fauna (Flannery 1995, Bonaccorso 1998, Helgen 2007), with a species richness that currently exceeds that of continental Australia if taxa from major satellite islands are included (Churchill 2008). In the most recent and comprehensive treatment, Bonaccorso (1998) listed 91 bat species, which comprised 21 pteropodids (flying foxes, fruit and blossom bats) and 70 insectivorous bats. This represents around 8% of the world's recognised bat richness. In the last decade, there have been several new descriptions and taxonomic reorganisations (e.g. Bergmans 2001, Helgen 2005, Simmons 2005, Parnaby 2009), and while there is work in progress on some major groups (e.g. Nyctimeninae; N. Irwin, unpublished), there are many other groups that probably warrant revision. An incomplete taxonomy may conceal losses in diversity if extinction occurs before species discovery or resolution, and lead potentially to misdirected efforts and resources for conservation (Mace 2004).

Few parts of PNG have been surveyed well for bats, and distributional limits for many species are based on relatively few records – less than five localities in the case of 18 species

(Bonaccorso 1998). Field surveys can contribute to knowledge of bat diversity in PNG in three main ways: 1) by providing whole morphological specimens, genetic material and acoustic recordings to contribute to comprehensive taxonomic comparisons and descriptions; 2) through entirely new discoveries in new or poorly surveyed areas; and 3) by contributing to a better understanding of distribution limits, habitat associations and general ecology.

The Muller Range is located in Western and Southern Highlands Provinces, north of the Trans Fly region, and its remoteness from large human settlements suggested the possibility of encountering an unexploited and intact mammal fauna. The range contains a variety of habitats that change along an altitudinal gradient from lowland tropical rainforest through lower and upper montane forests to subalpine woodland, shrubland and grassland. The Muller Range is one of the few large ranges in PNG that has had no significant prior historical mammal collecting or systematic surveys. For bats, the only prior modern records derive from mist netting during the Atea 1978 cave survey expedition (James and Dyson 1980), with vouchers of at least three species of bats lodged in the Australian Museum, Sydney (identified by prefix 'AM M'). A few species of bats were also reported by Worthy and Flannery (1998) for bone assemblages derived from owl pellets from caves at c. 2,200 m elevation on the Muller Plateau. While some of this material is probably quite recent, much of it is of unknown age and perhaps better regarded as prehistoric.

While bats are more likely to be able to disperse longer distances than non-volant mammals, the combination of the intactness of the vegetation communities, the range of habitats, and the lack of systematic prior survey pointed to the possibility that new forms could be encountered for the first time. This area was targeted by Conservation International as part of its Rapid Assessment Program (RAP) survey series, with the aim of documenting a poorly-known fauna and discovering and documenting the maximum number of species new to science in a range of target groups, within the short time available for the field survey.

Surveys for bats in remote areas of PNG face considerable logistical constraints in terms of access and equipment transport, in addition to the regular challenge of capturing individuals. These days, well-designed surveys incorporate a range of techniques to maximise the detection rate of species. In the last few years, significant developments in technology that allows the ultrasonic echolocation calls of insectivorous bats to be recorded and analysed has resulted in a growing reliance on recognising bat species through the use of electronic bat detectors (e.g. Parsons et al. 2000, Parsons and Obrist 2004, Parsons and Szcwczak 2009). Many bat species can be distinguished readily from the shape and characteristic frequencies of their echolocation pulses. Acoustic surveys can produce a more complete inventory of species for a site compared to capture-based methods because some species can be difficult to capture in the open and above treetops, or because bats can detect the nets; and there is a greater chance

of encountering the brief appearance of a species (e.g. Kalko et al. 1996). However, the approach does not detect all species equally, namely non-echolocating fruit bats, those that produce low amplitude calls (e.g. *Nyctophilus*; O'Farrell and Gannon 1999, Duffy et al. 2000), and species that cannot be distinguished reliably from others that produce similar calls (e.g. McKenzie and Muir 2000, Milne 2002). The most important consideration in acoustic surveys is whether 'anonymously' recorded (i.e. without a voucher specimen) calls can be identified based on a comparison with a reference set collected from vouchered bat species.

The use of bat detectors presents excellent opportunities for surveys and monitoring programmes, and some environmental assessments undertaken for development proposals in PNG have relied greatly on acoustic recordings to document regional bat faunas (Richards 2005, 2008). However, a reference echolocation library is not available currently for PNG bats. While reference information is available from limited captures (eight species: Leary and Pennay in press; a further six species: K.N. Armstrong and K.P. Aplin unpublished data), or from conspecifics in Australia (e.g. Reinhold et al. 2001, Milne 2002), it is mostly incomplete, and the variation within each species derived from functional, geographic or other ecologically related factors needs to be documented in detail to allow a better understanding of the extent to which acoustic signatures overlap. It is only through field captures that an echolocation library can be developed, and such an effort will complement taxonomic, distributional and ecological work.

The primary aim of our bat survey in the Muller Range was to document the richness of the bat fauna, based on captures and collection of specimens, thus making a contribution to future conservation and management decisions, taxonomic work, and knowledge of species distributions and habitat associations. The majority of the anticipated capture was small blossom bats, tube-nosed fruit bats, and insectivorous bats. A secondary, but important, aim was to assist with the development of a reference collection of insectivorous bat echolocation calls that could be used for acoustic surveys.

MATERIALS AND METHODS

Study sites

Three camps were established in pristine habitats along a major altitudinal gradient. The major habitat types were lowland primary rainforest at 515 m (05°43.751S, 142°15.797E; 2-11 September 2009; Camp 1, 'Gugusu'), transitional lower to upper montane forest at 1,587 m (05°39.397S, 142°18.277E; 11-18 September 2009; Camp 2, 'Sawetau'), and upper montane forest/fernland mosaic with *Pandanus* at 2,875 m (05°29.174S, 142°18.117E; 18-26 September 2009; Camp 3, 'Apalu Reke'). Access was by helicopter because of the rough terrain, and survey activities generally were restricted to an area within a few hundred metres of helipads.

Kyle Armstrong conducted fieldwork at Gugusu and Sawetau; Ken Aplin at Sawetau and Apalu Reke; and the late Paul Igag assisted by setting shared mist nets at all three camps.

Survey methods

Three approaches were used to capture and detect bats: trapping in harp traps, netting with mist nets, and recording ultrasonic echolocation calls with AnaBat (Titley Scientific, Brisbane) electronic bat detectors. Survey effort is summarised in Table 19.1. Trapping equipment was placed in positions most likely to capture bats, typically across small streams, at the rim of limestone sinkholes, and at the edges of clearings. Advantage was also taken of the long line of mist nets ($n = 10\text{--}15$) used for capturing birds, which were kept open overnight throughout the period spent at each locality. Deep caves were notably absent from most of the immediate survey areas but small cave entrances, fissures and overhangs were investigated whenever located. Specimens have been lodged with the CSIRO Australian National Wildlife Collection (identified by prefix 'ANWC M') in Canberra. In addition to the guides of Flannery (1995) and Bonaccorso (1998), identifications were aided by examination of other specimens in the ANWC, and genetic work will benefit from the liver samples taken. Captured specimens of *Nyctimene* and *Paranyctimene* were identified following amplification of partial fragments of the mitochondrial genetic markers cytochrome-*b* and 12S, respectively, and subsequent comparison with an unpublished extensive multigene dataset of the Nyctimeninae (held by N. Irwin).

AnaBat units were left overnight at each sampling site. Recorded echolocation signals were downloaded and then examined in AnalookW 3.7u software. To assist with descriptions and identifications, four call variables were measured on good quality search phase pulses in representative call sequences: pulse duration (milliseconds), maximum frequency (kHz), characteristic frequency (the point of minimum frequency in a downwards-sweeping call, before any terminal secondary frequency sweep; kHz), and minimum frequency (kHz).

Classification of echolocation call types

Identifications were attempted based on available information (Leary and Pennay, in press; K.N. Armstrong and K.P. Aplin, unpublished data), but relatively few calls could be identified to a species, especially because of the lack of

captures on the survey. Calls were therefore grouped into categories thought to represent search phase pulses from a single species. These categories are taken from the scheme of Armstrong and Aplin (in prep.), as modified from de Oliveira (1998a,b) and Corben and O'Farrell (1999) (Table 19.2). Echolocation pulses generally consist of three main sections: an initial frequency sweep (IFS), followed by the main body (BST: Body Sub Type), and ending in a terminal frequency sweep (TFS). Each call type is named according to the shape of the pulse, which is represented by codes in the form '# # IFS.BST.TFS', prefixed by a value (#) representing the mean characteristic frequency in kHz. The name is allocated if the majority of search phase pulses in a sequence fall within a particular category, though in some cases there may be more than one main type that can be observed commonly.

RESULTS

Captures and sightings

Bat captures totalled 37 individuals and five species (Table 19.3). All captures were made in mist nets and capture rates were uniformly low. No bats were captured at Apalu Reke, though some were observed hawking above the camp over the *Pandanus*–fernland community. No bats were located during cave searches around Sawetau and Apalu Reke, even though some caves presented with passages of sufficient size and depth to support roosting colonies. Their absence might be attributed to the excessive water flow down cave walls, which might vary on a seasonal basis. No larger pteropodid bats were seen or heard at any site during evening patrols. The identity of the Nyctimeninae was provided based on genetic sequence and comparison with unpublished datasets (*Nyctimene* sp.: partial cytochrome-*b*; *Paranyctimene raptor* Tate, 1942; partial 12S; N. Irwin unpublished DNA sequences and manuscripts in preparation).

AnaBat echolocation recordings

A total of 21 AnaBat recording nights was made during the survey at all three localities (Table 19.4). From these recordings, 16 echolocation call types were recognized (Tables 19.4, 19.5; Figure 19.1). With four exceptions (Emballonuridae: *Mosia nigrescens* Gray, 1843; Hipposideridae: *Hipposideros wollastoni* Thomas, 1913; Molossididae: *Mormopterus beccarii* Peters, 1881, *Tadarida kuboriensis* McKean and Calaby, 1968) they could not be attributed unambiguously to a particular species because of the lack of an available reference call library, and the paucity of captures on the survey. Some of these types might originate from the one species, so the most conservative estimate of the total number of species detected is 12. Such considerations are noted in Table 19.6 along with other remarks relating to species identification.

Based on these call types, the greatest diversity of echolocating insectivorous bats was recorded at an elevation of 1,600 m, with a total of 13 call types from at least nine species (cf. seven call types / spp. at 500 m, and four call

Table 19.1. Summary of survey effort for bats.

| Locality | Harp trap nights (No. sites) | Mist net nights (No. sites) | Anabat nights (No. sites) |
|----------------------|------------------------------|-----------------------------|---------------------------|
| Gugusu (500 m) | 12 (6) | 90 (4) | 13 (6) |
| Sawetau (1,600 m) | 4 (2) | 96 (6) | 6 (4) |
| Apalu Reke (2,900 m) | 0 | 80 (3) | 2 (2) |

Table 19.2. Echolocation call categories based on the morphology of the dominant type or types of single search-phase pulses in high quality sequences (adapted from Armstrong and Aplin, in prep.; examples are not scaled equally; only call types observed in echolocation sequences recorded at Muller Range are presented).

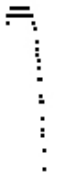

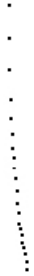





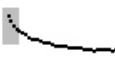



| Code | Description | Example |
|-------------|--|---|
| CF | Constant Frequency main Body Sub Type | |
| <i>sCF</i> | Short duration (<15 ms) |  |
| <i>mCF</i> | Medium duration (15 – 30 ms) |  |
| FM | Frequency Modulated main Body Sub Type |  |
| <i>bFM</i> | Broadband, slightest degree of curvature only, no significant development of serpentine component (<i>sFM</i>, not illustrated) |  |
| <i>cFM</i> | Curved, simple or curvilinear trace |  |
| <i>cvFM</i> | Convex curved, essentially <i>cFM</i> rotated 180° |  |
| <i>fFM</i> | Flat or with a very slight curve, narrowband, not <i>CF</i> |  |
| | Initial Frequency Sweep | |
| <i>i.</i> | Inclined, a narrowband increasing frequency sweep |  |
| <i>sb.</i> | Short, shallow or narrowband frequency sweep |  |
| <i>st.</i> | Steeply decreasing, broadband frequency sweep |  |
| | Terminal Frequency Sweep | |
| <i>.d</i> | Drooped, decreasing frequency sweep following the characteristic frequency in the main body of the call |  |
| <i>.h</i> | Hooked, increasing in frequency |  |

Table 19.3. Bat captures made at each site, with richness based on captures only.

| Species | Gugusu | Sawetau | Apalu Reke |
|---------------------------------|-----------|-----------|------------|
| Pteropodidae | | | |
| <i>Nyctimene</i> sp. unnamed | 1 | - | - |
| <i>Paranyctimene raptor</i> | 1 | - | - |
| <i>Syconycteris australis</i> | 16 | 1 | - |
| <i>Syconycteris</i> sp. unnamed | - | 17 | - |
| Hipposideridae | | | |
| <i>Hipposideros wollastoni</i> | - | 1 | - |
| Total individuals | 18 | 19 | 0 |
| Total species richness | 3 | 3 | 0 |

types from at least three spp. at 2,900 m). In addition, most bat call sequences were recorded within clearings rather than natural corridors along watercourses (Table 19.4).

DISCUSSION

The survey produced records of four pteropodids and at least 12 species of insectivorous bats. Given the brevity of the survey, and its limitation to three relatively small areas, the number of bat species inhabiting the wider area is likely to be much greater. Indeed, one additional species – a *Nyctophilus* species close to *N. microdon* Laurie and Hill, 1954 (H. Parnaby pers. comm.) – is represented in the small collection derived from a caving expedition in 1978 (AM M12634 and M12635, collected at 'Atea Gana Anda' by G. Smith and R. Wilson).

Two of the captured bats are almost certainly undescribed (*Nyctimene* sp., *Syconycteris* sp.), though known from other localities, and two others require further taxonomic work to separate them from closely related species (*Paranyctimene raptor*) or to examine the possibility of subspecific or species status (*Hipposideros wollastoni*). The data collected from echolocation recordings highlighted that there is an almost undocumented ultrasonic realm in PNG, and that this is a significant knowledge gap.

Notable records

Nyctimene

The tube-nosed bat *Nyctimene* sp., captured at Gugusu (ANWC M35456), is a distinctive species in the 'albiventer' size range. It is probably unnamed but based on size, pelage characteristics and cranio-dental morphology, the same taxon is probably represented in previous collections from the Astrolabe Range, and possibly also on the northern side of the central ranges of PNG at hill forest elevations (Aplin, pers. obs.). It is widespread according to N. Irwin (pers. comm. to K.N. Armstrong, 14 April 2010).

Paranyctimene

The Green Tube-nosed Bat genus *Paranyctimene* is poorly understood. The Muller Range *Paranyctimene* (ANWC M35467), captured at Gugusu, has a forearm length of 50.1 mm, which is at the lower end of the range given for *P. raptor* (Bonaccorso 1998) and just slightly smaller than that measured from the types of *P. tenax* Bergmans 2001. While *P. tenax* has not been recorded formally south of the central cordillera, the full extent of its distribution is not known. Bergmans (2001) raised the possibility of sympatry with *P. raptor*, highlighting that specimens might have been wrongly attributed to this species because of the lack of critical assessment. The specimen from Gugusu was identified as *Paranyctimene raptor* based on a partial fragment of the ribosomal 12S DNA marker after comparison with an unpublished dataset (N. Irwin unpublished data).

Syconycteris

The blossom bat genus *Syconycteris* is a complex group with a number of distinct morphological forms currently grouped as *S. australis* (Peters, 1867). What appears to be true *S. australis* was common around Gugusu at 500 m altitude, and one specimen (ANWC M35472) was also captured at below Sawetau Camp. Between 1,600 m and a few hundreds of elevational metres above Sawetau, a second presently unnamed species of *Syconycteris* was captured (e.g. ANWC M35500). This form is widespread in montane New Guinea (K.M. Helgen pers. comm.). Despite considerable mist-netting effort, no *Syconycteris* were captured at Apalu Reke and on this basis it seems likely that the patchily distributed montane species *S. hobbit* Ziegler, 1982 is absent from Muller Range.

Hipposideros wollastoni

This is a morphologically and genetically diverse species of leaf-nosed bat that is poorly known outside of the Telefomin area (Flannery and Colgan 1993). The single individual captured at Sawetau (ANWC M35464) seems distinct from the subspecies found at Telefomin in fur colouration and nose-leaf structure but is similar in external appearance to examples collected recently from Mt Bosavi (K.M. Helgen pers. comm.). The Muller Range and Mt Bosavi groups may represent typical *wollastoni* (described in 1913 from Utakwa River, West Papua) or alternatively, an unnamed form. Echolocation calls recorded in flight at the helipad of Sawetau Camp and identified as *H. wollastoni* (on the basis of reference material from elsewhere; K.N. Armstrong and K.P. Aplin unpublished data) had a characteristic frequency of c. 82 kHz, but unfortunately comparative acoustic material is unavailable from Telefomin. Genetic studies have begun, but are also limited by comparative material.

Call categories

Given that the echolocation calls of PNG bats are mostly undocumented, and that many species identifications made from anonymously recorded calls will therefore be tenuous,

Table 19.4. Summary of echolocation call types recorded at all sites. AnaBat nights with no calls are excluded. Adjacent shaded columns represent call types from the same putative species.

| Locality | Date | AnaBat serial / site | GPS (WGS84) | Habitat | 13 sh.cFM T. kuboriensis | 16 sh.cFM | 20 sh.cFM | 22 st.bFM | 26 sh.cFM M. beccarii | 32 i.fFM.d | 33 st.cFM.h | 35 st.cFM | 35 st.cFM.h | 44 st.cFM | 43 i.fFM.d / sCF | 45 cvFM / i.fFM.d | 53 st.cFM.d | 57 mCF | 61 sCF M. nigrescens | 82 mCF H. wollastoni | |
|--|-----------|----------------------|---------------------------|---|--------------------------|-----------|-----------|---------------------------|---|------------|-------------|-----------|-------------|-----------|------------------|-------------------|-------------|--------|----------------------|----------------------|---|
| Gugusu (Camp 1) | 4/9/2009 | 3186 AN02 | 05°43.7652S, 142°15.8592E | Artificial clearing on ridgetop in primary rainforest | — | — | ✓ | — | ✓ | — | — | ✓ | — | — | ✓ | — | ✓ | — | ✓ | — | |
| | | | | | 500 m | 5/9/2009 | 3230 AN03 | 05°43.7900S, 142°15.6856E | First order stream in primary rainforest ('creek 4') | — | — | — | — | — | — | — | — | — | — | ✓ | — |
| | 6/9/2009 | 5181 AN02 | 05°43.7652S, 142°15.8592E | Artificial clearing on ridgetop in primary rainforest | — | — | — | — | ✓ | — | — | ✓ | — | — | ✓ | — | — | — | ✓ | — | |
| | | | | | | 8/9/2009 | 3186 AN02 | 05°43.7652S, 142°15.8592E | Artificial clearing on ridgetop in primary rainforest | — | — | — | — | — | ✓ | — | — | — | — | — | ✓ |
| | 8/9/2009 | 5181 AN06 | 05°43.7996S, 142°15.6618E | First order stream in primary rainforest ('creek 5') | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | |
| | | | | | Sawetau (Camp 2) | 11/9/2009 | 3230 AN07 | 05°39.3970S, 142°18.2770E | Artificial clearing in moss forest on gentle slope, limestone | — | ✓ | — | — | — | ✓ | — | — | — | ✓ | — | — |
| 1,600 m | 12/9/2009 | 3230 AN08 | 05°39.3774S, 142°18.2568E | First order stream in moss forest | — | — | — | — | — | — | — | ✓ | — | ✓ | — | — | ✓ | — | ✓ | — | |
| | | | | | | 16/9/2009 | 3186 AN07 | 05°39.3970S, 142°18.2770E | Artificial clearing in moss forest on gentle slope, limestone | — | ✓ | — | — | — | ✓ | — | — | — | ✓ | — | — |
| Apalu Reke (Camp 3) | 18/9/2009 | 3186 AN11 | 05°29.1740S, 142°18.1170E | Low hill overlooking Blechnum fern community | — | — | — | — | — | — | — | ✓ | — | — | — | — | ✓ | — | — | — | |
| | | | | | 2,900 m | 19/9/2009 | 3186 AN12 | 05°29.1740S, 142°18.1170E | Low hill overlooking Blechnum fern community | ✓ | — | — | — | ✓ | — | — | — | — | ✓ | — | — |
| Gugusu total richness = 7 call types, 7 putative species | | | | | — | — | ✓ | — | ✓ | — | — | ✓ | — | — | — | — | ✓ | — | — | — | |
| Sawetau total richness = 13 call types, 9 putative species | | | | | — | ✓ | ✓ | ✓ | — | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Apalu Reke total richness = 4 call types, 3 putative species | | | | | ✓ | — | — | — | — | — | ✓ | — | — | — | — | — | ✓ | — | — | — | — |

it was necessary to refer to ‘call types’. The scheme used here (Table 19.2; K.N. Armstrong and K.P. Aplin, in prep.) is modified from de Oliveira (1998a,b) and Corben and O’Farrell (1999), which required some additions and modifications to allow classification of bats in PNG with greater accuracy. While only four species could be identified with confidence based on echolocation recordings, the gradual compilation of reference calls in the future should allow retroactive identification of those species recorded from the Muller Range RAP. The development of an echolocation

call library for PNG is essential because species identifications are required in order to match survey inventories with species listed in Threatened categories under national environmental legislation and by the IUCN. In addition, anonymously recorded calls are useful for understanding the richness of feeding guilds in particular habitats based on echolocation call characteristics (see next section).

Most call types recorded at Muller Range are likely to correspond to a single species, but it is possible that more than one species might contribute to a single defined call

Table 19.5. Summary of variables from representative call sequences. ¹ s,p: number of sequences measured, combined total number of pulses measured; ² Mean \pm SD; range.

| Call category | s,p ¹ | Duration (msec) ² | Max Frequency (kHz) ² | Char frequency (kHz) ² | Min frequency (kHz) ² |
|--------------------------------|------------------|------------------------------|----------------------------------|-----------------------------------|----------------------------------|
| <i>13 sh.cFM</i> | 3,5 | 10.0 \pm 4.2 | 14.6 \pm 1.8 | 13.2 \pm 1.2 | 13.0 \pm 1.2 |
| <i>Tadarida kuboriensis</i> | | 5.6 – 16.4 | 12.7 – 16.5 | 11.7 – 14.5 | 11.5 – 14.1 |
| <i>16 sh.cFM</i> | 3,2 | 5.9 \pm 0.5 | 18.0 \pm 1.5 | 16.4 \pm 0.2 | 16.3 \pm 0 |
| | | 5.6 – 6.2 | 17.0 – 19.1 | 16.2 – 16.5 | 16.2 – 16.3 |
| <i>20 sh.cFM</i> | 3,5 | 7.5 \pm 1.5 | 21.5 \pm 0.8 | 20.1 \pm 0.3 | 19.3 \pm 0.2 |
| | | 5.1 – 9.0 | 20.6 – 22.7 | 19.7 – 20.5 | 19.1 – 19.7 |
| <i>22 st.bFM</i> | 3,22 | 2.4 \pm 0.5 | 33.7 \pm 4.3 | 24.6 \pm 2.5 | 21.4 \pm 1.1 |
| | | 1.5 – 3.2 | 27.6 – 43.0 | 22.1 – 30.2 | 19.1 – 22.8 |
| <i>26 sh.cFM</i> | 3,7 | 9.6 \pm 2.8 | 28.1 \pm 1.3 | 26.3 \pm 0.8 | 26.1 \pm 0.7 |
| <i>Mormopterus beccarii</i> | | 5.1 – 13.8 | 26.8 – 30.2 | 25.5 – 27.6 | 25.4 – 27.0 |
| <i>32 i.fFM.d</i> | 3,5 | 8.7 \pm 1.2 | 32.9 \pm 0.7 | 32.3 \pm 0.6 | 31.1 \pm 1.0 |
| <i>Emballonura</i> sp. | | 6.7 – 9.6 | 31.9 – 33.5 | 31.4 – 32.9 | 30.3 – 32.5 |
| <i>33 st.cFM.h</i> | 3,13 | 6.6 \pm 1.9 | 41.1 \pm 3.3 | 33.1 \pm 0.7 | 32.7 \pm 0.5 |
| | | 4.3 – 9.6 | 36.5 – 50.0 | 32.0 – 34.3 | 31.9 – 33.5 |
| <i>35 st.cFM</i> | 3,36 | 6.2 \pm 1.7 | 41.8 \pm 5.5 | 34.5 \pm 1.8 | 34.1 \pm 2.1 |
| | | 4.4 – 10.1 | 32.0 – 48.8 | 31.1 – 36.2 | 29.4 – 36.0 |
| <i>35 st.cFM.h</i> | 3,46 | 9.5 \pm 1.3 | 42.0 \pm 2.2 | 35.9 \pm 0.6 | 35.7 \pm 0.6 |
| | | 6.5 – 12.3 | 38.5 – 49.1 | 34.8 – 37.2 | 34.3 – 36.9 |
| <i>43 i.fFM.d / sCF</i> | 3,54 | 8.3 \pm 1.2 | 43.7 \pm 0.3 | 43.1 \pm 0.6 | 40.2 \pm 2.6 |
| <i>Emballonura</i> sp. | | 3.9 – 11.0 | 43.0 – 44.7 | 40.8 – 44.0 | 32.1 – 43.2 |
| <i>44 st.cFM</i> | 3,5 | 7.7 \pm 2.0 | 54.3 \pm 5.9 | 44.0 \pm 0.8 | 43.2 \pm 0.4 |
| | | 5.7 – 11.0 | 46.2 – 60.6 | 43.0 – 45.2 | 42.8 – 43.7 |
| <i>45 cvFM / i.fFM.d</i> | 3,12 | 7.8 \pm 1.6 | 47.2 \pm 0.7 | 45.5 \pm 0.6 | 41.2 \pm 1.4 |
| <i>Emballonura</i> sp. | | 5.6 – 11.3 | 46.2 – 48.8 | 44.4 – 46.5 | 39.0 – 43.5 |
| <i>53 st.cFM.d</i> | 3,15 | 3.6 \pm 1.2 | 61.4 \pm 6.3 | 52.9 \pm 1.4 | 50.9 \pm 1.2 |
| | | 2.0 – 5.2 | 54.1 – 80.8 | 51.0 – 55.2 | 48.5 – 52.3 |
| <i>57 mCF</i> | 1,3 | 11.2 \pm 1.3 | — | 57.2 \pm 0 | |
| | | 9.7 – 12.2 | | — | |
| <i>61 sCF</i> | 3,48 | 4.4 \pm 0.7 | 62.0 \pm 0.5 | 61.5 \pm 0.6 | 54.7 \pm 2.7 |
| <i>Mosia nigrescens</i> | | 2.2 – 5.3 | 61.1 – 63.0 | 60.2 – 63.0 | 50.3 – 60.6 |
| <i>82 mCF</i> | 3,25 | 21.9 \pm 3.5 | 84.1 \pm 0.7 | 82.4 \pm 3.0 | 71.6 \pm 2.6 |
| <i>Hipposideros wollastoni</i> | | 16.4 – 29.6 | 83.3 – 85.1 | 72.7 – 85.1 | 66.7 – 79.2 |

Table 19.6. Comments on defined call types and identifications made on the Muller Range RAP survey.

| | |
|---|---|
| 13 sb.cFM | Relatively narrowband, frequency modulated, long duration calls below 15 kHz are typical of <i>Tadarida australis</i> in Australia (Churchill 2008). The most likely candidate for the similar calls recorded at Apalu Reke is <i>Tadarida kuboriensis</i> . |
| 16 sb.cFM | Narrowband, relatively flat frequency modulated sequences with a low characteristic frequency might be attributed to a species of <i>Saccolaimus</i> . Sequences of regularly shaped pulses with a shallow curvilinear shape are typical in this genus, and characteristic call frequency is also typically around 20 kHz or less (Milne 2002; Milne et al. 2009). However, only one sequence was recorded, so it is also possible that this was the fundamental frequency of a species of <i>Emballonura</i> (call type 33 i.fFM.d), which was recorded at the same site around the same time. |
| 20 sb.cFM | Attributable to several candidates based on pulse structure and characteristic frequency, including: one of the three <i>Saccolaimus</i> species (examples in Milne 2002; Milne et al. 2009), <i>Chaerephon jobensis</i> , or either of the <i>Otomops</i> species. |
| 22 st.cFM | Generally, short duration broadband calls such as this are attributable to nyctophiline bats, but the minimum frequency is much lower than any species recorded from Australia (e.g. Bullen and McKenzie 2002), as well as <i>Myotis moluccarum</i> , which makes similarly shaped calls with a minimum frequency at least 10 kHz higher (K.N. Armstrong and K.P. Aplin, unpublished data). Such calls also resemble approach phase calls of larger species such as <i>Saccolaimus</i> spp. that fly above treetops, however the associated high amplitude search phase calls were not present in each recorded sequence. The mean time between pulses was 206 ms (n=4, 32 sequences, pulses), which is similar to that measured from sequences of 20 sb.cFM at a mean of 226 (n=2, 14 sequences, pulses), and much greater than search phase calls of <i>Nyctophilus</i> spp. that typically have a mean time between pulses of c. <100 ms (K. N. Armstrong unpubl. data). Thus, both call types can probably be attributed to the same species. |
| 26 sb.cFM <i>Mormopterus beccarii</i> | Pulses in the example sequence for this call type had a frequency, pulse shape and sequence pattern similar to <i>Mormopterus beccarii</i> in Australia (e.g. Milne 2002). |
| 32 i.fFM.d <i>Emballonura</i> sp. | Call shape (with terminal droops) typical of <i>Emballonura</i> , based on similar morphology from elsewhere (e.g. Pottie et al. 2005; other unpublished sources). |
| 33 st.cFM.b, 35 st.cFM and 35 st.cFM.b | These call types may be attributable to two or more vespertilionid species, or alternatively represent the variation within a single species. Candidates are likely to be relatively large vespertilionids or <i>Miniopterus</i> , such as <i>M. magnater</i> (based on unpublished data of K.N. Armstrong and K.P. Aplin) or <i>M. macrocneme</i> . |
| 43 i.fFM.d <i>Emballonura</i> sp. and 45 cvFM / i.fFM.d <i>Emballonura</i> sp. | Call shape (with terminal droops) typical of <i>Emballonura</i> , based on similar morphology from elsewhere (e.g. Pottie et al. 2005; other unpublished sources). There appears to be some variation in characteristic frequency across PNG for call types with the pulse shape i.fFM.d, with mean characteristic frequencies at c. 43 kHz, 47 kHz and 54 kHz (K. N. Armstrong and K. P. Aplin, unpublished data). This suggests much variation within a single species (e.g. phonic types or sexual dimorphism), or several similar species. |
| 44 st.cFM | Pulses with curvilinear, frequency modulated pulses might be attributable to one of several vespertilionid or <i>Miniopterus</i> species. A candidate species is <i>Pipistrellus angulatus</i> , based on reference calls collected elsewhere (K. N. Armstrong and K. P. Aplin, unpublished data). |
| 53 st.cFM.d | Pulses with steep curvilinear frequency modulated pulses containing a terminating 'droop' are most likely to have come from a species of <i>Miniopterus</i> , but some vespertilionids also produce such pulse shapes. |
| 57 mCF | Only two example sequences of this call type were recorded. The terminal sections of each pulse were degraded, so pulse duration cannot be estimated accurately. Despite this, the pulses appeared relatively short, and were within the characteristic frequency range of <i>Hipposideros diadema</i> (Leary and Pennay in press, K. N. Armstrong and K. P. Aplin, unpublished data). |
| 61 sCF <i>Mosia nigrescens</i> | Attributable with high confidence based on reference calls collected elsewhere (Leary and Pennay in press, K. N. Armstrong and K. P. Aplin, unpublished data). |
| 82 mCF <i>Hipposideros wollastoni</i> | Attributable to this species based on reference sequences collected elsewhere in PNG (K. N. Armstrong and K. P. Aplin, unpublished data). Sequences containing some pulses with a dominant fundamental frequency component at half of the typical first harmonic were also observed (Figure 19.1). |

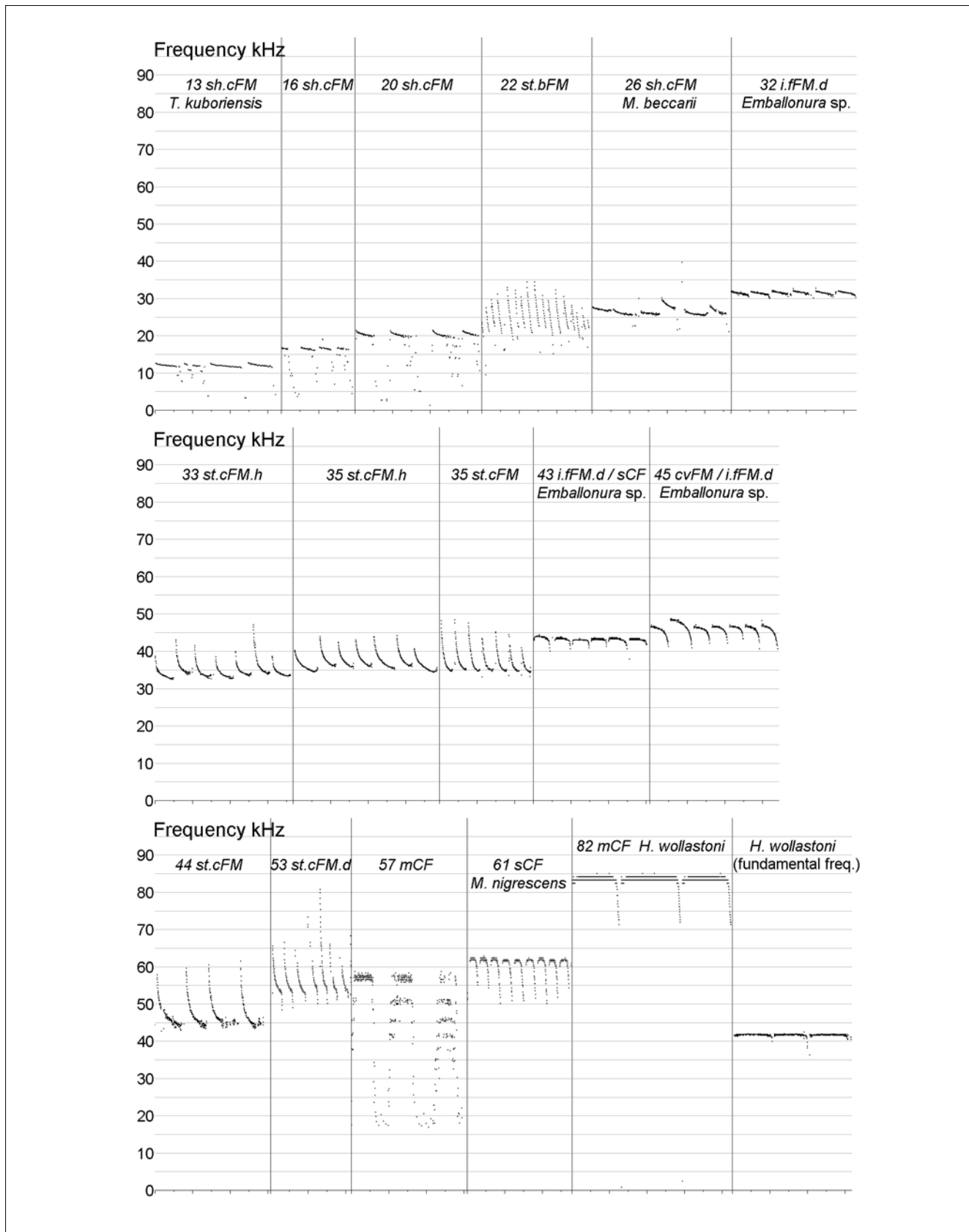


Figure 19.1. Representative sequences of call types and species identified on the survey (following Zero Crossings Analysis). The time between individual pulses has been compressed, and tick marks are 10 ms apart.

type, and conversely that one species may have produced more than recognised one call type (highlighted in Table 19.4). Some of the call types were not lumped on precautionary grounds. For example, while type *45 cvFM / i.fFM.d* appeared less common than *43 i.fFM.d*, both may represent natural variation correlated with sex, body size or foraging activity within a single species of *Emballonura*. However, both call types have been recorded elsewhere in PNG (K.N. Armstrong and K.P. Aplin, unpublished data) where a third phonic type around 5 kHz higher was also encountered. Thus, it was prudent to distinguish two types at Muller Range so that future resolution of echolocation signatures in *Emballonura* can provide a determination of how many may be represented there.

In the case of types *33 st.cFM*, *35 st.cFM* and *35 st.cFM.d*, which are relatively similar, these are more likely to represent variation with a single species because of body size variation, sex or functional differences. However, there are some well known examples in Australia of vespertilionids that cannot be separated reliably based on standard measurements of AnaBat calls (e.g. species of *Chalinolobus* and *Scotorepens*; Milne 2002). In PNG, calls from *Chalinolobus nigrogriseus* Gould, 1856, *Philetor brachypterus* Thomas, 1902, *Miniopterus* spp., *Pipistrellus* spp. and *Scotorepens sanborni* (Troughton, 1937), which together produce calls with a characteristic frequency spanning the range of c. 33 – 55 kHz, need to be characterised with greater detail to allow a better appreciation of their variation and overlap.

Observations of echolocation relevant for identifications

Several observations were made during the analysis of AnaBat recordings that could confound identification work at other sites. Occasional expressions of the fundamental frequency were noted in some species, most importantly in calls by *H. wollastoni* (example in Figure 19.1), but also *M. nigrescens* and possibly call type *43 i.fFM.d / sCF* from a species of *Emballonura*. Bat echolocation calls comprise multiple harmonics, and AnaBat equipment records preferentially that part of the signal with the greatest amplitude. This usually corresponds to the dominant second harmonic in hipposiderids because they filter their fundamental frequency in the vocal tract (Hartley and Suthers 1988), but which can be expressed if the animal simply opens its mouth (Neuweiler 2000:151). At Sawetau, several sequences of *H. wollastoni* contained a subset of pulses with half the characteristic frequency of the remainder, and one sequence was composed entirely of pulses where the fundamental dominated Figure 19.1). It is unknown whether there is a functional significance for the expression of the lower frequency fundamentals, but the implication is that it could result in a misidentification. For example, the characteristic frequency of *H. wollastoni* fundamentals was almost identical to that of *Rhinolophus philippinensis* Waterhouse, 1843 recorded elsewhere (K.N. Armstrong and K.P. Aplin, unpublished data). Pulse duration, repetition rate and the presence of other pulse fragments might give a clue to the

correct species in this case. In the case of *M. nigrescens*, fundamentals were sometimes observed, but could be distinguished from call type *32 i.fFM.d* based on pulse duration, the constant frequency portion of the call and fragments of the terminal frequency sweep of the second harmonic. In a third example, it is quite possible that call type *16 sh.cFM* was the fundamental frequency of a species of *Emballonura* (call type *33 i.fFM.d*), and further examples are needed to confirm this.

Patterns of diversity with habitat and altitude

There were too few sites and species to make a comprehensive association of species assemblages with habitats at each locality. In this situation, a coarser type of analysis can be used where different call types are associated with a foraging habitat based on their characteristic frequency and pulse structure. Echolocation calls can be categorised as: those used for foraging in open spaces away from the influence of echoes derived from clutter ('Open'); those used in the smaller open spaces at the edge of vegetation or in large gaps around the canopy where prey echoes follow closely but do not overlap with clutter echoes ('Edge and Gap'); and those used in the highly cluttered space within stands of vegetation where the target echoes are buried in those from background clutter ('Narrow Space') (review in Denzinger et al. 2004). At Muller Range, call types associated with Open habitats would be narrow band calls with characteristic frequencies below 26 kHz (representing at least four species). Call types *57 mCF* and *82 mCF* can be associated with both Edge and Gap and Narrow Space habitats, and the remainder can be associated with Edge and Gap.

Echolocation calls were present on ten out of 21 AnaBat night recordings. Seven of these were made either alongside artificial clearings made for helipads or from low hills overlooking a *Blechnum* fern community. These may be defined as Open habitats, and they had the greatest diversity, with all 16 call types recorded. In comparison, only six call types were recorded from first order streams in primary forest. The higher richness of Open habitats derives from the simple fact that placement of an AnaBat unit in a clearing has the potential to sample bats in all three main foraging groups, because there is no clutter to limit detection of calls from species flying high over treetops, the edges of the clearing are favoured by species that forage in smaller open spaces and close to vegetation, and the clearings were small enough that Narrow Space foragers occasionally flew across them. The placement of an AnaBat detector on a track or stream bank within the forest is likely to encounter only those species foraging beneath the canopy in natural corridors. The two call types recorded from streams at Gugusu, *53 st.cFM.d* and *57 mCF*, are suitable for foraging close to vegetation and the latter is clutter resistant. Call type *53 st.cFM.d* is similar to that of *Chalinolobus morio* (Gray, 1841) in Australia, which has a similar call frequency and also produces terminal droops after the characteristic frequency, which might give extra information on texture and range at short distances.

C. morio forages against vegetation predominantly (Bullen and McKenzie 2001), and the Muller Range species is likely to forage in a similar way. The call type *57 mCF* is likely to originate from *Hipposideros diadema* (Geoffroy, 1813), which forages in and around stands of vegetation. At Sawetau, the space over the stream where the AnaBat was placed was relatively open (Site AN08; Table 19.4), and therefore suitable for species that foraged in gaps beneath or amongst the canopy (*Miniopterus* spp., small vespertilionids including *53 st.cFM.d* and *Mosia nigrescens*). A greater survey effort would probably result in the detection of species of *Murina*, *Phoniscus* and *Kerivoula*.

The presence of at least three different insectivorous bat species at 2,800 m based on echolocation call types may represent the entire insectivorous bat assemblage at Apalu Reke because very few species have been recorded at an equivalent elevation before. Bonaccorso (1998) notes only two (*Tadarida kuboriensis* and *Miniopterus macrocneme* Revilliod, 1913), and Helgen (2007) also mentions that *Pipistrellus collinus* occurs in montane habitats up to 3,000 m on the basis of specimens available in museums. The molossid *T. kuboriensis* was identified based on the similarity of the call type *13 sh.cFM* to the Australian *T. australis* (Gray, 1838) (Churchill 2008), and its foraging habitat also seems to correspond with the Australian species, which is apparently limited to relatively cool, dry atmospheres where it can dissipate physiological heat built up during high speed flight (Bullen and McKenzie 2005). The other two call types are typical of vespertilionid bats but they cannot be identified unambiguously at present. The call types *33 st.cFM.h* and *35 st.cFM* might derive from one of the larger *Miniopterus* species such as *M. macrocneme*, given the relatively low characteristic frequency and similarity to unpublished reference calls from elsewhere of the similarly-sized *M. magnater* Sanborn, 1913 (K.N. Armstrong and K.P. Aplin, unpublished data). The higher frequency call type *53 st.cFM.d* could very well derive from the small sized *P. collinus* Thomas, 1920.

Capture

The relatively low capture rate of insectivorous bats on this survey was disappointing. Similarly low capture rates in New Guinea were made by Richards (2005, 2008), Leary and Pennay (in press) and Boeadi and Widodo (2000), with biases towards small fruit bats (*Nyctimene* spp., *Syconycteris australis*) that are captured relatively easily in mist nets set for birds. Other studies have recorded greater numbers of insectivorous bat captures, especially on islands and in lowland habitats where the bat fauna is relatively diverse and where mist nets might be set more easily in open spaces (Wright et al. 1998, Emmons and Kinbag 2001). In the present study, a greater species richness and greater number of recorded echolocation sequences were obtained in open habitats than along corridors such as watercourses. Though sample size and site replication was somewhat limited, it was clear that relatively few bats commuted or foraged along streams. It is

clear that a good capture return of insectivorous bats requires significant effort in hill forest habitats.

There are compelling studies from outside PNG that demonstrate the effectiveness of harp traps in closed forests (Duffy et al. 2000, Kingston et al. 2003, Armstrong unpublished). However no bats were captured in harps on the Muller Range RAP despite being set carefully in open flight paths along streams and tracks, and ensuring that mist nets were set to funnel bats towards the traps. In a study in Timor-Leste, harp traps were particularly effective when placed across streams and forest tracks, and even at the edges of larger watercourses where the flight corridors could not be obstructed entirely with netting (Armstrong unpublished). Kingston et al. (2003) used quadruple bank harp traps along well established tracks in rainforest in Malaysia, and these have been noted as more effective than the double bank traps that were available for the Muller Range RAP. However, since relatively few echolocation calls were recorded by AnaBats along streams, especially at Gugusu, low harp capture rates might derive simply from the relative absence of bats. To maximise the possibility of success with harps in PNG, it would be preferable to use quadruple bank traps and ensure attention to detail when setting nets and cloth baffles to ensure bats did not simply fly around the traps.

Some species will always be difficult to capture because they either detect then avoid traps and nets readily, or else it will never be practicable to use capture apparatus in the canopy where some species forage exclusively. In such cases, targeted efforts at points of concentration such as isolated watering places, caves and tree hollows will be more effective, though some species will always be challenging to capture. Some specialist design features may aid setup or bat retrieval in difficult terrain or at heights. If an entire bat assemblage is to be fully sampled, then it will require the full-time attention of bat specialists in such challenging country, and an approach comprising multiple techniques.

CONSERVATION RECOMMENDATIONS

The conservation value of intact forest habitats for bats is high, especially when the diversity of community assemblages is enhanced by altitudinal gradients and significant areas of karst. The Muller Range contains an intact mammal fauna in just such a setting, and the bat assemblage recorded on the relatively brief RAP survey represents only a portion of that present. The area is known to have remarkably extensive areas of karst, which doubtless contain much greater bat diversity than was recorded in cave bone accumulations collected by Worthy and Flannery (1982). Areas of karst have high conservation value in South East Asia (Clements et al. 2006), and additionally, large underground structures in PNG have the potential to contain colonies of the Threatened (IUCN Red-list) Bulmer's Fruit Bat *Aproteles bulmerae*. Furthermore, while the detectability of certain bat species might be enhanced following vegetation clearing, as was

apparent from the higher diversity recorded around helipads on the present survey, diversity is likely to decrease overall. Species with a limited geographic range and low wing aspect ratio that forage in forest clutter have a particularly high extinction risk (Jones et al. 2003, Kingston et al. 2003), and removal of vegetation will result in a net loss of foraging habitats. Listing the Muller Range as a World Heritage Area will ensure that diverse, intact faunal assemblages in a complex biome are preserved for the long term.

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REFERENCES

- Armstrong, K. N. unpublished. Survey for bats on the proposed Ira Lalaro hydropower scheme, Timor-Leste. Field survey and impact assessment. Unpublished report by Molhar Pty Ltd for EPANZ Services Pty Ltd (New Zealand) and the Norwegian Water Resources and Energy Directorate, 10 December 2006.
- Armstrong, K. N. and K. P. Aplin. in prep. Echolocation call categories based on the morphology of single search-phase pulses, for classifying anonymous calls in Australasia and South East Asia.
- Bergmans, W. 2001. Notes on distribution and taxonomy of Australasian bats. I. Pteropodinae and Nyctimeninae (Mammalia, Megachiroptera, Pteropodidae). *Beaufortia* 51: 119–152.
- Boeadi and W. Widodo. 2000. Mammals of the Wapoga River Area, Irian Jaya, Indonesia In: Mack, A. L. and L. E. Alonso (eds.). *A Biological Assessment of the Wapoga River Area of Northwestern Irian Jaya, Indonesia*. RAP Bulletin of Biological Assessment 14. Conservation International. Washington, D.C. Pp. 60.
- Bonaccorso, F. J. 1998. Bats of Papua New Guinea. Conservation International Tropical Field Guide Series. Conservation International. Washington, D.C.
- Bullen, R. D. and N. L. McKenzie. 2005. Seasonal range variation of *Tadarida australis* (Chiroptera: Molossidae) in Western Australia: the impact of enthalpy. *Aust. J. Zool.* 53: 145-156.
- Bullen, R. D. and N. L. McKenzie. 2001. Bat airframe design: flight performance, stability and control in relation to foraging ecology. *Aust. J. Zool.* 49: 235-261.
- Bullen, R. D. and N. L. McKenzie. 2002. Differentiating Western Australian *Nyctophilus* (Chiroptera: Vespertilionidae) echolocation calls. *Aust. Mammal.* 23: 89-93.
- Churchill, S. K. 2008. *Australian bats*. 2nd ed. Allen and Unwin, Crows Nest, New South Wales.
- Clements, R., N. S. Sodhi, M. Schilthuizen, and P. K. L. Ng. 2006. Limestone karst of Southeast Asia: imperiled arks of biodiversity. *Bioscience* 56: 733-742.
- Corben, C. and M. J. O'Farrell. 1999. *Anabat system user's guide*. Anabat system manual, 2nd ed., published by the authors.
- de Oliveira, M. C. 1998a. Towards standardized descriptions of the echolocation calls of microchiropteran bats: pulse design terminology for seventeen species from Queensland. *Aust. Zool.* 30: 405-411.
- de Oliveira, M. C. 1998b. *Anabat system practical guide*. Department of Natural Resources, Queensland.
- Denzinger, A., E. K. V. Kalko and G. Jones. 2004. Ecological and evolutionary aspects of echolocation in bats. *In: Thomas, J. A., C. F. Moss and M. Vater (eds). Echolocation in bats and dolphins*. University of Chicago Press. Chicago. Pp. 311-326.
- Duffy, A. M., L. F. Lumsden, C. R. Caddle, R. R. Chick and G.R. Newell. 2000. The efficacy of Anabat ultrasonic detectors and harp traps for surveying microchiropterans in south-eastern Australia. *Acta Chiropt.* 2: 127–144.
- Emmons, L. H. and F. Kinbag. 2001. Survey of mammals of Southern New Ireland. In: B. M. Beehler and L. E. Alonso, (eds). *Southern New Ireland, Papua New Guinea: A biodiversity assessment*. RAP Bulletin of Biological Assessment 21. Conservation International. Washington, D.C. Pp. 67-69.
- Flannery, T. F. 1995. *Mammals of New Guinea*. Revised and updated edition. Reed Books. Chatswood, New South Wales.
- Flannery, T. F. and D. J. Colgan. 1993. A new species and two new subspecies of *Hipposideros* (Chiroptera) from western Papua New Guinea. *Rec. Aust. Mus.* 45: 43-57.
- Hartley, D. J. and R. A. Suthers. 1988. The acoustics of the vocal tract in the horseshoe bat *Rhinolophus hildebrandii*. *J. Acoust. Soc. Amer.* 84: 1201-1213.
- Helgen, K. M. 2005. Systematics of the Pacific monkey-faced bats (Chiroptera: Pteropodidae), with a new species of *Pteralopex* and a new Fijian genus. *System. Biodiv.* 3: 433-453.
- Helgen, K. M. 2007. A taxonomic and geographic overview of the mammals of Papua. *In: Marshall, A. J. and B. M. Beehler (eds.). The Ecology of Papua*. Ecology of Indonesia series Volume VI, Part One. Periplus Editions.
- James J. M. and H. J. Dyson. (eds). 1980. *Caves and karst of the Muller Range: report of the 1978 Speleological*

- Expedition to the Atea Kananda, Southern Highlands, Papua New Guinea. Area. Newtown, N.S.W.
- Jones, K. E., A. Purvis and J. L. Gittleman. 2003. Biological correlates of extinction risk in bats. *Am. Nat.* 161: 601-614.
- Kalko, E. K. V., C. O. Handley, Jr and D. Handley. 1996. Organization, diversity and long-term dynamics of a Neotropical bat community. *In: Cody, M. and J. Smallwood (eds.)*. Long term studies of vertebrate communities. Academic Press, New York. Pp. 503-553.
- Kingston, T., C. M. Francis, Z. Akbar and T. H. Kunz. 2003. Species richness in an insectivorous bat assemblage from Malaysia. *J. Trop. Ecol.* 19: 67-79.
- Leary, T. and M. Pennay. In press. Echolocation calls of eight Microchiroptera from Papua New Guinea. *Aust. Zool.*
- Mace, G. 2004. The role of taxonomy in species conservation. *Phil. Trans. Roy. Soc., Lond. B* 359: 711-719.
- McKenzie, N. L. and W. P. Muir. 2000. Bats of the southern Carnarvon Basin, Western Australia. *Rec. W. Aust. Mus. Suppl.* 61: 465-477.
- 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 No. 71.
- Milne, D. J., F. C. Jackling, M. Sidhu and B. R. Appleton. 2009. Shedding new light on old species identifications: morphological and genetic evidence suggest a need for conservation status review of the critically endangered bat, *Saccolaimus saccolaimus*. *Wildl. Res.* 36: 496-508.
- Neuweiler, G. 2000. The biology of bats. Oxford University Press. New York and Oxford.
- O'Farrell, M. J. and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *J. Mammal.* 80: 24-30.
- Parnaby, H. E. 2009. A taxonomic review of Australian Greater Long-eared Bats previously known as *Nyctophilus timoriensis* (Chiroptera: Vespertilionidae) and some associated taxa. *Aust. Zool.* 35: 39-81.
- Parsons, S. and M. K. Obrist. 2004. Recent methodological advances in the recording and analysis of chiropteran biosonar signals in the field. *In: Thomas, J. A., C. F. Moss and M. Vater (eds.)*. Echolocation in bats and dolphins. University of Chicago Press, Chicago. Pp. 468-477.
- Parsons, S. and J. M. Szewczak. 2009. Detecting, recording, and analysing the vocalizations of bats., *In: Kunz, T. H. and S. Parsons (eds.)*. Ecological and behavioural methods for the study of bats. 2nd revised edition. Johns Hopkins University Press, Baltimore. Maryland, USA. Pp. 91-111.
- Parsons, S., A. M. Boonman and M. K. Obrist. 2000. Advantages and disadvantages of techniques for transforming and analysing chiropteran echolocation calls. *J. Mammal.* 81: 927-938.
- Pottie, S. A., D. J. W. Lane, T. Kingston and B. P. Y.-H. Lee. 2005. The microchiropteran bat fauna of Singapore. *Acta Chiropt.* 7: 237-247.
- Reinhold, L., B. Law, G. Ford and M. Pennay. 2001. Key to the bat calls of south-east Queensland and north-east New South Wales. Forest Ecosystem Research and Assessment Technical Paper 2001-07, Department of Natural Resources and Mines, Queensland.
- Richards, G. C. 2005. The Papua New Guinea gas project: a study of bat faunal biodiversity and an assessment of potential impacts. Prepared by Greg Richards and Associates Pty Ltd for Enesar Consulting Pty Ltd, July 2005. Included as 'Annex 05. Biodiversity survey results: Bats at Hides, Nogoli and Benaria in 2005.' in the PNG LNG Project Environmental Impact Statement Part II. Existing Environment, prepared by Coffey Natural Systems Pty Ltd for Esso Highlands Ltd, January 2009.
- Richards, G. C. 2008. The Papua New Guinea liquefied natural gas project: a study of bat faunal biodiversity and an assessment of potential impacts. Prepared by Greg Richards and Associates Pty Ltd for Coffey Natural Systems Pty Ltd, July 2008. Included as 'Annex 06. Biodiversity survey results: Bats at Juha North, Juha South, Baia River, South Karius and Deviation Camp in 2008.' in the PNG LNG Project Environmental Impact Statement Part II. Existing Environment, prepared by Coffey Natural Systems Pty Ltd for Esso Highlands Ltd, January 2009.
- Simmons N. B. 2005. Order Chiroptera. *In: D. E. Wilson and D. M. Reeder (eds.)*. Mammal species of the world: a taxonomic and geographic reference. 3rd edition. Johns Hopkins University Press. Baltimore. Pp. 312-529.
- Worthy, T. H. and T. F. Flannery. 1998. Fossil bones from Mamo Kananda, Southern Highlands, Papua New Guinea. *Helictite* 34: 49-54.
- Wright, D. D., S. Balagawi, T. T. Raga and R. T. Ipu. 1998. Mammals. *In: A. L. Mack (ed.)*. A Biological Assessment of the Lakekamu Basin, Papua New Guinea. RAP Bulletin of Biological Assessment 9. Conservation International, Washington, D.C. Pp. 67-71.