Habitat Relationships, Activity Patterns and Feeding Ecology of Insectivorous Bats of the Top End of Australia.

Thesis submitted by

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Abstract

The wet-dry tropics of the Northern Territory (the Top End) has a diverse microbat fauna. It supports 28 of Australia's 65 species, including one endemic species (*Taphozous kapalgensis*), both of Australia's monotypic genera (*Rhinonicteris* and *Macroderma*) and two species considered to be rare or endangered (*Saccolaimus saccolaimus* and *Hipposideros diadema*). However, most aspects of the ecology of this fauna are poorly known. The aim of this study was to investigate the composition of microbat assemblages; describe the habitat relationships of the microbat fauna at both the community and species levels; assess microbat activity patterns at several temporal scales; and to conduct a dietary analysis of the microbats of the Top End.

Robust methods for sampling bats are still being developed and tested. Based on recordings derived from the Anabat II detector, I compared the results of surveys where I changed the orientation of the detector, the type of recording media, and static versus active hand-held recording. Detector orientation did not significantly affect any survey results, more call passes were identified from digital recordings and more species were detected using hand-held recordings. I also derived species-accumulation curves for the Top End microbats and provide guidelines for minimum sampling effort in future studies.

Patterns in the composition of assemblages of microbat species sampled during the late dry season (the 'build-up') in the Top End were assessed against a range of environmental factors as well as four *a priori* defined habitat types (riparian, escarpments, coastal and woodlands). In general, species assemblages were not clearly defined and the number of significant environmental associations was relatively few. The most distinct species assemblages were strongly associated with topographic and climatic variables. There were also limited associations with vegetation structure, fire and local roost potential but no associations with insects or water availability. Total species diversity at sample sites was associated with distance to rivers and rainfall.

Generalised linear modelling (GLM) was used to develop habitat models for 25 of the 28 microbat species of the Top End. Based on these models, a geographic information

system (GIS) was used to derive probability of occurrence maps for each species. Almost all of the models identified a unique combination of environmental variables, and the resulting probability of occurrence maps revealed a variety of patterns of predicted distribution. Annual rainfall and habitat complexity were identified as significant variables in the majority of the models. All of the spatial models were combined to derive a probability map of species richness of microchiropteran bats in the Top End. This map shows greatest species richness in the north-west and north-central parts of the study area.

Temporal patterns of microbat activity and species richness were assessed at four scales: hourly, nightly, monthly and yearly, in relation to biotic (insect availability) and abiotic features in the environment. At the hourly scale, bat activity was highest in the first hour after dusk and declined throughout the night. Hourly bat activity was most closely associated with temperature. At the nightly scale there were significant associations between bat activity, moon light and temperature as well as a complex association with both moon phase and time of night. At the monthly scale bat activity increased dramatically in October which was possibly triggered by a combination of changing climatic factors that occur at this time of year in the Top End. At the yearly scale there was no overall difference in bat activity between years (n = 4) and no associations with climatic variables.

The dietary composition for 23 of the 28 Top End microbat species was described by identifying the prey remains collected from stomachs and faecal pellets to the lowest possible taxonomic level (usually order or lower). Dietary analysis revealed that most species consumed a variety of orders indicating that Top End microbats have generalist dietary requirements and/or opportunistic foraging habits. However, the dietary compositions for *H. diadema*, *H. stenotis*, *Mormopterus loriae*, *Nyctophilus geoffroyi*, *N. bifax* and *T. kapalgensis* contained only one or two insect orders suggesting these species may have more specialised diets. Microbats in the 'Uncluttered' foraging guild consumed proportionally more insects belonging to the orders Orthoptera and Coleoptera whereas the 'Background clutter' and 'Highly cluttered' foraging guilds consumed proportionally more Lepidoptera.

This study has greatly increased our understanding of some aspects of the ecology of microbats in the Australian wet-dry tropics. I make a number of recommendations for the conservation management and future research of Top End microbat fauna, most notably to investigate the association between microbat diversity and riparian areas, conduct further microbat surveys throughout the region to redress the still meagre number of records, and initiate targeted monitoring programs for microbats.

Preamble

This thesis is structured into eleven sections that includes seven chapters, a bibliography and three appendices. Chapter 1 is the introduction and is presented in a 'standard' thesis format (Times New Roman 12 font, 1.5 line spacing). The following five chapters are the main body of work for this study. Four of these (Chapters 2-5) have been published and are presented in their original published formats. The remaining chapter (Chapter 6) is unpublished and presented in standard thesis format as well as Chapter 7 (the conclusion). The appendices have also been published and are also presented in their original published formats.

The Bibliography presents references for the unpublished chapters only (Chapters 1, 5 and 7). The remaining published chapters and appendices have not been edited so references for these sections are included within each. The placement and formatting of these references is dependant on which journal they were published in.

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Chapter 1.
Introduction

Introduction

Bats are an important component of the environment. They are diverse (currently 1116 recognised species internationally, Smithsonian Institution 2006) and abundant, occurring from the tropics to sub-artic and sub-antarctic regions of the world. There are many indications they have a significant ecological role in environments where they occur. Despite their importance however, bats are regularly neglected in biological studies in terms of both their ecology and distribution. This study aims to address this issue for one major tropical region.

Mammal species diversity is greatest in the tropics, between approximately 20° north and south of the equator (e.g. Ruggiero 1994; Rosenzweig 1995; Kaufman and Willing 1998; Willig 2001). This region is also significant for supporting a disproportionally high number of endemic mammal species. The processes that drive this diversity include long periods of relative stability, high energy availability and higher rates of speciation that occur as result of high temperatures causing shorter generation times, higher mutation rates, and accelerated selection pressures (Willig *et al.* 2003 and references therein).

There are several threats to conserving this rich and diverse fauna. The terrestrial environments of the tropics are affected by habitat loss and fragmentation predominantly from deforestation (Brooks *et al.* 2002; Kinnaird *et al.* 2003; Rankmore submitted), pressures from hunting (Fa *et al.* 2002; Peres and Lake 2003; Brashares *et al.* 2004) and global climate change (Meyneeke 2004). In many parts of the tropics, the ecological patterns and processes that underpin mammal communities are poorly understood because of a lack of research in the tropics relative to other regions of the world (Amori 2000).

Compared to all other mammalian orders (combined or singly), bats (Chiroptera) have an even greater concentration of species in the tropical zone (Willig *et al.* 2003). In some tropical countries over 100 species have been recorded (e.g. Peru, 152 species; Venezuela, 154 species; Colombia 170 species, Mickleburgh *et al.* 2002). At the family level, some groups have undergone extensive radiations in the tropics, for example, 30

species of horseshoe bats (Rhinolophidae) occur in the rainforest of south-east Asia (Csorba *et al.* 2003).

The two suborders of bats, megachiroptera (megabats) and microchiroptera (microbats), both occur at their peak richness in the tropics. Megabats include fruit and blossom bats and are generally characterised by the use of vision and smell to locate food and play an important role in the dispersal of seeds and the pollination of flowers (Patterson *et al.* 2003). Microbats are termed 'insectivorous bats' and are characterised by generally using echolocation to detect prey items (Simmons and Conway 2003). The ecological role that microbats play in the environment is less clear than megabats. It is likely that foraging activity of microbats, in general, have a regulatory effect on insect populations. As well as influencing natural environmental processes, this may also have direct economic implications for insect pest control in agricultural areas (e.g. McCracken 2004). Microbats can also serve as indicators of environmental health in the tropics (Medellín *et al.* 2000; Ochoa 2000) and have several attributes that make them useful as indicators of environmental change: they are diverse and abundant, occupy virtually every trophic level, and many have specialised diets and select specific habitats for roosting and foraging (Medellín *et al.* 2000 and references therein). It is likely that changes within the environment will be reflected in one or more of these attributes.

This study focused on the microbat fauna of the Top End of Australia. This area is centred on the wet-dry tropics of the Northern Territory, north of 18°S (see Chapter 2, Figure 1) and is dominated by a tropical savanna that cover almost the entire northern half of Australia (for a description of this region see Tropical Savannas CRC 2005). There are several features of the Top End that distinguish it from all other regions of Australia (for further description of the area refer Chapter 2). Eucalypt woodlands and forests with a grassy understorey dominate 78% of the landscape and, unlike many other tropical regions, monsoon rainforests are largely absent occupying just 0.5% of the Top End (based on mapping by Fox *et al.* 2001). Topographic relief is relatively low (the maximum elevation is Kub-o-wer Hill in western Arnhem land at 570 m) with the main areas of relief being the Kakadu escarpment and the eastern edge of the Kimberley region. Temperature variation is relatively small across the study area with the highest average annual maximum temperature ranging between 32° C and 39° C. The north-south rainfall gradient is uniform but steep ranging from 1720 mm to 360 mm (based on

Houlder 2000) and rainfall is highly seasonal with almost all precipitation occurring from November to April. Therefore, the Top End environment is relatively simple and predictable and varies little across its entire area with the major exception of the Kakadu escarpment (Woinarski *et al.* 2005). The other major feature of the Top End environment is fire. On average, fire burns over half (52%) of the Top End every year (A. Edwards, pers. comm.).

These factors drive the species composition and characteristics of the mammals of the Top End. Given the homogeneity of the Top End landscape (see Woinarski *et al.* 2005) the majority of mammal species have extensive distributions, however those mammal species that are restricted in distribution are commonly associated with rocky environments (Freeland *et al.* 1988; Woinarski *et al.* 1992; Strahan 1995; Woinarski 2000). There are also few arboreal folivores (Common Brushtail Possum *Trichosurus vulpecula*) or small macropod species (Spectacled Hare-wallaby *Lagorchestes conspicillatus*, Nabarlek *Peradorcas concinna*) in the Top End, possibly due to the high frequency of fire or lack of moisture over the extended dry season months (Woinarski *et al.* 1992). There have been no detailed assessments of the effects of climate on the Top End mammal fauna, particularly of the extensive rainfall gradient, and the results of studies that provide general assessments are equivocal (see Menkhorst and Woinarski 1992; Woinarski *et al.* 1992; Woinarski *et al.* 1999). The effects of fire on mammals in the Top End are poorly understood, but given that fire has a major influence in shaping vegetation communities (e.g. Bowman and Minchin 1987; Russell-Smith *et al.* 1998; Williams *et al.* 2003) its effects on mammal assemblages are likely to be significant. The limited research that has been conducted on fire and mammals indicate that fire frequency and intensity significantly influence the distribution and abundance of at least some species of mammals (Begg *et al.* 1981; Kerle and Burgman 1984; Corbett *et al.* 2003; Woinarski *et al.* 2004).

Knowledge of the ecology and distribution of bats in the Top End is poorer than for other mammal orders. Recent studies have assessed the ecology and distribution of two of the three Top End megabat species (*Pteropus alecto* and *P. scapulatus*: Palmer and Woinarski 1999; Vardon and Tidemann 1999; Palmer *et al.* 2000; Vardon *et al.* 2001) but the ecology of only one Top End microbat species has been assessed in any detail (*Rhinonicteris aurantius*: Churchill 1991; Churchill 1994; Churchill 1995). Bats

represent almost one third (28%) of all mammal species recorded in this region, but in the Northern Territory Department of Natural Resources, Environment and the Arts fauna atlas (a spatial database of all known records for vertebrate species in the Northern Territory), bats represented only 12% of all Top End terrestrial mammal species records (prior to this study). There are also very few reports and publications that assess microbat species or populations in the Top End (either directly or indirectly). This paucity of knowledge about microbats has major implications for conservation planning and management. The assessment of existing and proposed conservation reserves as well as other land management proposals (e.g. land clearing) are routinely based on available data for wildlife in the area, typically the distribution of species derived from fauna surveys (e.g. Griffiths *et al.* 1997; Woinarski 1998; Price *et al.* 2003; Woinarski *et al.* 2003). In most cases, information for microbats is scant and unreliable. Until this situation is improved, the effective conservation and management of microbats and inclusion of microbats in a meaningful way in conservation planning in the Top End will not be possible.

The Top End supports a rich microbat fauna comprising 28 of Australia's 65 species (16 of Australia's 20 genera). Two species are considered to be rare vagrants (*Tadarida australis* and *Scotorepens balstoni*) whereas the remaining 26 species have varying distributions throughout the Top End (Chapter 3). Compared to other regions of Australia, the microbat diversity of the Top End is surpassed only by Cape York Peninsula and south-east Queensland that each support approximately 35 species. The Top End is also notable for the presence of one endemic species (*Taphozous kapalgensis*) and both of Australia's monotypic genera (*Rhinonicteris* and *Macroderma*). Two species that occur in the Top End, *Saccolaimus saccolaimus* and *Hipposideros diadema,* are regarded as threatened by various authorities (i.e. the *Commonwealth Environment Protection and Biodiversity Conservation Act 1999*, the Northern Territory *Territory Parks and Wildlife Conservation Act 2000* or the Action Plan for Australian Bats (Duncan *et al.* 1995)).

The aim of this study is to describe the habitat relationships of microbats at both the community and species levels; assess microbat activity patterns; and to conduct a dietary analysis of the microbats of the Top End of Australia. To achieve this I use a multi-scale approach by assessing factors at both the landscape (from GIS) and local

(field data) scales. This study encompasses all Top End microbat species and is the first comprehensive ecological assessment of any tropical mammal group at a regional scale in Australia.

In Chapter 2 I critically assess the Anabat system (Titley Electronics, Ballina, NSW) which is one of the main sampling methods used throughout this study. The Anabat detector records ultrasonic echolocation pulses that microbats use for foraging and navigation. Some of the methods and justifications that have been used to identify bats based on echolocation calls have been criticised (e.g. Barclay 1999; Sherwin *et al.* 2000). Therefore, this chapter aims to answer four main questions: (i) what is the importance of detector placement; (ii) what is the best type of sampling media; (iii) which is better, static or active recording; and (iv) what is an appropriate sampling period. As well as the key to the bat calls of the Top End of the Northern Territory (Appendix 1), Chapter 2 aims to demonstrate how the Anabat system is an accurate and robust survey technique for sampling the microbats of the study region.

In the next two chapters I analyse the habitat relationships of microbats at the community (Chapter 3) and species (Chapter 4) levels. Chapter 3 assesses patterns in the structure and composition of microbat assemblages and analyses the relationship of these assemblages to various environmental variables. Chapter 4 then uses generalised linear modelling to model habitat associations and derive probability maps of the spatial distribution of each microbat species that occurs in the Top End. Five questions are addressed in these chapters: (i) what is the structure and composition of microbat assemblages; (ii) what features in the environment are microbats associated with; (iii) can the distribution of microbat species be successfully modelled; (iv) if so what are the likely distributions of each species; and (v) what are the main drivers of species richness.

Having assessed aspects of the spatial ecology of Top End microbats, I then move onto assess the temporal patterns of bats (Chapter 5), specifically at four scales: hourly, nightly, monthly and yearly scales. The temporal patterns are related to biotic and abiotic features in the environment. To achieve this I aim to answer the following: (i) what are the patterns in bat activity at different temporal scales; (ii) what are the patterns in species composition at different temporal scales; (iii) what influence do

climatic, lunar and food (insect) availability have those patterns; and (iv) what are the implications for surveying and monitoring microbats. Temporal patterns are driven by both regular (seasonal and lunar cycles) and unpredictable (rainfall and disturbance regimes). Therefore a knowledge of the temporal patterns of bats is an important factor when assessing the habitat associations and is an aspect often overlooked in most ecological studies of microbats (Sherwin *et al.* 2000).

Chapter 6 describes the dietary composition of Top End microbats. Knowledge of food habits is one of the fundamental pieces of information that is required to understand the overall ecology of any faunal species or group but, like temporal patterns, is often neglected. Therefore I pose three basic questions: (i) what do microbats eat; (ii) what conclusions about their ecology can be drawn from their diets; and (iii) how does this compare with findings elsewhere. Using this information I assess aspects of their foraging ecology and use this information to interpret some of the patterns presented in chapters 3, 4, and 5.

Finally, the concluding chapter synthesises the results presented in previous chapters and describes some of the major threats to Top End microbat species and populations. This information provides the framework for understanding the management requirements of this diverse faunal group and identifies key priorities for the conservation management of, and further research on, microbat communities in the Top End.

Chapter 2.

A comparison of three survey methods for collecting bat echolocation calls and species accumulation rates from nightly Anabat recordings

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A comparison of three survey methods for collecting bat echolocation calls and species accumulation rates from nightly Anabat recordings.

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Abstract. Bat surveys are frequently undertaken using ultrasonic detectors to determine the species present in an area based on the identity of echolocation calls. We compared three techniques for using the Anabat II detector: the detector pointed along tracks (flyways) versus the detector pointed across tracks (non-flyways); recording output to audio cassette (analogue) versus direct recording to computer (digital); and active hand-held recording versus static automatic recording. In addition, we derived a species-accumulation curve from all-night Anabat recordings in the Top End of the Northern Territory. We found no significant difference between flyway and non-flyway recordings; significantly more calls were identified from digital recordings; and significantly more species were detected using hand-held than static recordings. Species-accumulation analysis suggests that the minimum time required to achieve a satisfactory (80%) inventory of bat species at a site is during the three-hour period

immediately after sunset. We use our findings to make recommendations for the design of bat surveys using the Anabat II detector.

Running Head: Anabat recording methods and species accumulation rates

Introduction

Numerous field survey techniques are available to assess vertebrate assemblages. Each technique has advantages, disadvantages and biases. It is important to assess the relative strengths and weaknesses of survey techniques to identify deficiencies and develop consistency in survey protocols thus improving future surveys, particularly as new technologies become available. One of these technologies that has recently been adopted as an efficient and reliable survey tool is the ultrasonic recorder used for detecting and identifying echolocating bats (Fenton, 2000 and references therein).

Ultrasonic bat detection has been evaluated in a number of ways: by comparing between echolocation recordings and bat trapping techniques (Mills *et al.* 1996; Kuenzi and Morrison 1998; Murray *et al.* 1999; O'Farrell and Gannon 1999; Duffy *et al.* 2000); by comparing different types of bat detectors and methods of signal transformation (O'Farrell *et al.* 1999; Fenton 2000; Parsons *et al.* 2000; Fenton *et al.* 2001); and by analysis and identification of echolocation signals (Barclay 1999; O'Farrell *et al.* 1999; Murray *et al.* 2001). The Anabat detector (Titley Electronics, Ballina, N.S.W.) is one of a number of devices available to record echolocating bats. It uses frequency division to transform echolocation calls into audible signals and zero-crossing analysis to view the spectral content (Parsons *et al.* 2000). Anabat is widely used for bat surveys and to identify microchiropteran bat species. Therefore, studies are required to demonstrate the

most reliable and efficient methods for using this system. The purpose of our study was to compare three different approaches to using the Anabat II bat detector. We compared the results of bat surveys where we changed the location of the detector (detector pointed along tracks (flyways) versus the detector pointed perpendicular to tracks (non-flyways)); type of recording media (recording the Anabat detector signals to audio-cassette (analogue) versus computer direct recording (digital)); and degree of movement of the detector (active hand-held detector versus static automatic-recording).

The aim of most bat surveys is to record a comprehensive inventory of species in a minimal time using minimal effort. However, very few studies have reported the accumulation rate of bat species over time using Anabat recordings. We derive a relationship between sampling time and sampling adequacy based on data collected over 44 sample nights undertaken in the Top End of the Northern Territory.

Methods and Analysis

Fieldwork was conducted between 22 September and 1 November 2000 and 26 September and 1 November 2001; sampling was conducted in the same period of each year to minimise effects of seasonal variation on bat activity. Data were obtained from 39 sites in a variety of environments and throughout the Northern Territory north of 18°S (the 'Top End') using four Anabat detectors in various combinations described below. Differences in the bat fauna between environments are not considered here; rather we used a paired-sample approach to minimise the effects of habitat variation.

Protocol comparisons:

Flyway vs. non-flyway

19 sites were sampled over two consecutive nights using an Anabat II detector recording via an Anabat V Zcaim to computer (Toshiba Portégé 3440CT or Toshiba Tecra 700CT) running Anabat6 software (version 6.3f) in monitor mode. We used the two methods of positioning the Anabat detector described by Law *et al*. (1998). One detector was placed on the ground (static) during both treatments. For the duration of the first night of recording, the detector pointed along a track (flyway), whereas for the duration of the second night the detector was turned 90˚ to point across the track into surrounding bushland (non-flyway). Flyways were chosen in areas where an unobstructed path could be clearly observed through areas of vegetation - usually tracks or roads. In each case the detector was elevated to approximately 40° above horizontal and placed on the edge of the track. We measured the width of the flyway corridor (the distance between the trees on either side of the track or road) at each site to evaluate the importance of this factor. All detectors used in this study had sensitivity set to seven and the division ratio set to 16.

Analogue vs. digital

We utilised the Anabat detector recording to computer described in the comparison above (digital), placed a second Anabat detector (analogue) beside it pointing in the same direction and operated both detectors concurrently for one night at a total of 18 sites. The analogue detector was connected to an Anabat II Delay Switch with output recorded to Sony Chrome UX 90-minute cassette tape via an Optimus CTR-115 tape recorder. On most nights, the tape was checked after approximately 2.5 h and changed if required.

Hand-held vs. static

We utilised the Anabat detector recording to tape recorder described in the comparison above (static), and operated a second detector which was held in the hand, manually activated on the detection of a call, and actively pointed in the direction achieving the best reception. The hand-held detector was operated for a three-hour period after dusk concurrently with the static detector. Calls were recorded to the same model of tape recorder as used in the static treatment. The hand-held Anabat unit was generally operated 50-100 m from the static recorder, but within the same habitat, so as not to disturb bats from normal flight habits in the vicinity of the static recorder. The operator moved no more than 10 m in any direction during the recording period.

Anabat call files recorded from these three comparisons were analysed using Analook software (version 4.8f). Calls were identified according to Milne (2002), based on measurable call parameters provided in Analook, and clearly defined call characteristics derived from a library of reference calls collected across the Top End. We defined each call as a "call pass" *sensu* Law *et al.* (1998) with the exception that constant frequency type calls (refer de Oliveira, 1998) were attributed to species based on one or more clearly recorded echolocation call pulses (as opposed to three pulses). A single observer (DM) identified all the calls to avoid variation resulting from inter-observer bias. Calls that could not be confidently attributed to any species were classified as 'unknown'. These calls were normally mixes of feeding buzzes and other 'excited' type calls that included a range of frequencies and, therefore, probably were produced by a number of species.

All identified calls were used in analysis of total call counts, however, calls classified as 'unknown' were excluded from analysis of total species richness. We made no attempt

to distinguish between calls of *Scotorepens greyii, S. sanborni* and *Chalinolobus nigrogriseus*; *Nyctophilus arnhemensis, N. bifax* and *N. geoffroyi*; or *Miniopterus schreibersii* and *Pipistrellus westralis* given their calls are so similar (Milne 2002). For analysis purposes we treated each of these combinations as a single species. Some species calls could not consistently be separated (e.g. *Chaerephon jobensis* and *Saccolaimus flaviventris*). In these instances, calls were excluded from analysis involving species counts, but were included in analysis for foraging guilds if both species occurred within the same guild.

We adopted the foraging guild classification of Schnitzler and Kalko (1998) which recognises three guilds based on habitat type: uncluttered (open) space bats; background cluttered (edge and gap) space bats and; highly cluttered (narrow) space bats. The majority of bat species were assigned to guilds following McKenzie and Rolfe (1986). Species that occur in the Top End that were not classified by McKenzie and Rolfe were assigned to guilds based on information about flight and foraging behaviours in Strahan (1995) and our own observations (Table 1). Not all species are restricted to a single foraging guild. In these instances, species occupying more than one guild were excluded from analysis.

Following call identification, the number of calls for each species were tallied for each site. Data were not normally distributed, therefore we used non-parametric Wilcoxon matched pairs tests to test the difference between tallies within each of the comparisons. These tests were undertaken for the following variables: total number of calls; total number of species; total number of calls in each foraging guild; and total number of calls for each species occurring at four or more sites.

Sensitivity between Anabat detectors can vary (Larson and Hayes 2000) and was a potential source of variation in our dataset. To assess this possibility, the four Anabat detectors used in this study were tested following field sampling. Using the calibration method described by Larson and Hayes (2000), we used an Arlec FVR1 'Ultrasonic Pest and Rodent Repeller' set to High as an ultrasonic signal source. Anabat sensitivity adjustment was within one unit of sensitivity between all four Anabat detectors. As a consequence, variability in sensitivities was an unlikely source of variation in our dataset.

Species-accumulation curves

The time at which the Anabat detector records a bat call in the field is associated with the resulting Anabat call file. The rate of species accumulation was analysed for data collected for the entire night from the static analogue and digital Anabat recordings. This analysis was carried out using data from 44 sampling nights at 29 sites (total 506 recording hours, average 11.5 hours/night). At these sites, recordings were made over one (13 sites), two (14 sites) or three (one site) nights. We excluded sites with less than three species from the analysis because these sites were generally associated with a high number of calls classified as 'unknown'. The time at sunset was used as a reference point for starting time and was calculated for each site using the sunrise/sunset calculator provided by the National Mapping Division (2003). To obtain a consistent and accurate time reference for each recorded call sequence, delay switches and the computer clocks were regularly calibrated to the time display of an active GPS unit (Magellan 2000 XL). For each night at each site, the percentage of the total nightly

species tally was calculated for each ½-hour interval, and a mean accumulation curve derived.

Results and Discussion

We recorded a total of 17 828 calls during 660 detector hours over 51 nights at 39 sites in this study. Of these, 26% were attributed to a single species, 58% to a species 'combination' (two or three species) and 16% were classified as 'unknown'.

Flyway vs. non-flyway

There was no significant difference between the two methods in the total number of calls, total number of species, foraging guilds or individual species (Table 2). This is similar to the results of Law *et al*. (1998) for south-eastern Australia. Although the median number of calls detected on flyways was much higher than non-flyways, the very high variability for total number of calls between sites accounted for the non-significant result. When sites were classified according to corridor width, species richness on those greater than 9 m (maximum 20 m) in width (n = 6), was significantly higher on flyways than non-flyways ($Z = 2.023$, $p = 0.043$). By comparison, we found no significant difference in species richness ($p = 0.27$, $n = 13$) between flyways and non-flyways for sites less than 9 m (minimum 3 m) in width. There were also no significant differences between any of the foraging guilds for either of the corridor widths. This pattern suggests that (in the Top End) bats prefer to use wide flyways over narrow flyways, however, because of the limited sample size, we recommend further investigation into the effect of corridor width on bat activity.

In our study, the non-flyway treatment was perpendicular, but nevertheless adjacent, to flyways. Law and Chidel (2002) found significantly lower levels of bat activity detected by paired Anabat detectors placed 15-20m away from forest tracks and pointed in the opposite direction, as compared to bats recorded along forest tracks. It is important to note that their study was undertaken in moist forests with a mainly rainforest understorey. Fewer bats are detected when the vegetation in front of the detector is dense (Weller and Zabel 2002). The Top End is predominantly open woodlands with a sparse understorey, therefore bat detection rates are less likely to be affected by vegetation density. The exception may be dense monsoon rainforest patches, particularly for bats with a relatively low call frequency (Patriquin *et al.* 2003).

Analogue vs. digital

Significantly more identifiable calls were recorded directly onto a computer than to the tape recorder (Table 2). In addition, two foraging guilds (uncluttered and background clutter) and five species/species combinations (*Chae. jobensis, Chal. nigrogriseus / Sc. greyii* / *Sc. Sanborni, M. schreibersii* / *P. westralis, Mormopterus loriae and Taphozous georgianus)* were detected more frequently using the digital recordings. We attribute this result to the higher quality of the digital recording which enabled us to more readily identify calls. Digital recording also provided considerable savings in processing time, as transferring calls from cassette-tape to computer after completion of a survey required a similar amount of time to identifying the calls themselves. We therefore estimate this time saving to be approximately 50%.

Several studies have used statistical techniques based on measurable call parameters to reduce the degree of subjectivity involved in identifying call sequences (e.g. Herr *et al.*

1997; Murray *et al.* 1999; McKenzie and Muir 2000; Milne 2002). Higher quality call recordings result in more consistent and accurate measurements derived from call parameters. Our study supports the value of recording calls directly to computer. Johnson *et al.* (2002) also detected significantly more calls and species using digital rather than analogue recording techniques, although White and Gehrt (2001) found no significant difference in the number of calls, passes or identifiable passes when recording to audio cassette versus computer.

A number of studies have recommended that Anabat sampling should be conducted throughout the night (Law *et al.* 1998; Duffy *et al.* 2000). This study was part of a larger research project that involved sampling over 57 nights using static Anabat detectors recording to tape recorder. On 28 nights the tape recorder failed to achieve a full night of recording; on three of these occasions recording was not achieved because of insect noise, whereas the other 25 nights were a result of almost continuous bat activity. As a result, on 16 occasions one side of a 90 minute cassette tape was filled and on the other 12 occasions the tape was changed and both sides were filled. Therefore, at least during September to November in the Top End, it can be difficult to achieve a full night of Anabat sampling using analogue recording techniques. This situation is comparable to that experienced in other parts of tropical and sub-tropical Australia (pers. obs.). Using digital recording media, the size of each Anabat file is small (usually < 5 KB) and the number of digital call files that can be saved is limited only by the capacity of the computer storage space. We therefore recommend that Anabat surveys be carried out using digital recording methods whenever it is logistically possible to do so. The recently released Anabat Compact Flash Storage Zero Crossing Analysis Interface Module (CF-Zcaim, Titley Electronics, Ballina, N.S.W.) also records

echolocation calls directly onto digital media. The new Zcaim is more convenient (pers. obs.) and, in our opinion, equally as effective as the computer recording method described here.

This method of digital recording does have some drawbacks. For example, Bullen and McKenzie (2002) note that portions of a signal can be lost when using an Anabat Zcaim to transfer Anabat detector output to a digital file. By analysing calls stored on audiocassette using sound analysis software (without transforming the signal with the Zcaim), they were able to distinguish between the six species of *Nyctophilus* that occur in Western Australia. This separation would not have been possible had recordings been made directly to computer using the method described here.

Hand-held vs. static

Significantly more species were detected using a hand held detector than a static detector, although the total number of calls recorded did not differ between the two methods (Table 2). This difference is probably the result of the operator's ability to actively track a calling bat with the hand held Anabat unit, resulting in relatively longer call sequences which are easier to identify than the shorter sequences obtained from static recording techniques.

Although there was no significant difference between the overall total number of calls recorded by hand-held and static detectors, hand-held detectors recorded significantly more calls for the 'uncluttered space' guild, and for four species (*Chae. jobensis, P. adamsi, Sa. flaviventris* and *T. georgianus)*. With the exception of *P. adamsi*, these bats are predominantly high flying. The hand-held detector could be pointed vertically, and

was therefore more likely to detect these bats than the static recorder set at a 40° angle. In addition, the hand-held detector was held at an approximate height of 1 m. Weller and Zabel (2002) detected significantly more calls from detectors set on stands (1.4 m high) than detectors placed on the ground. However, they made no assessment of the species detected. Nevertheless, holding the Anabat detector above the ground may also have contributed to the significant result.

Three of the four leaf-nosed bats that occur in the Top End of the Northern Territory, *Hipposideros ater, H. stenotis* and *Rhinonicteris aurantius,* produce low intensity echolocation calls (Milne 2002). Of these, *H. ater* was not detected during the study, *H. stenotis* was identified from one call sequence containing only a single call pulse, and *R. aurantius* was detected from 13 call sequences. None were detected using the hand-held detector technique. These species produce very brief call sequences when detected by Anabat (usually < 0.5 seconds) and are nearly always missed because of the time delay from when the operator hears the bat through the bat detector speaker to when the recording switch is activated. This situation is overcome using the static method as all signals are stored in the internal memory of the Anabat II Delay Switch and subsequently dumped to tape. As a consequence, the static method may be preferable in areas with large numbers of leaf-nosed bats such as Cape York Peninsula, Papua New Guinea and south-east Asia.

Inexperienced users of Anabat were often slow in activating the unit on detection of bat calls and would often miss the first few pulses of a call sequence. This response delay can be critical in some studies which attempt to accurately measure levels of bat activity and where identifications are based on as few as three call pulses.

Our results suggest that in general hand-held detectors are preferable to static detectors because more species are detected per sampling period. However, this needs to be balanced against the increased likelihood of missing certain species, the greater time investment required by the operator, the importance of an experienced operator, and the fact only one site can be sampled by an operator at any one time. Researchers may also have the choice of using either the digital static recording technique or the analogue hand-held recording technique. How do these two methods compare? As with previous hand-held analysis, there were significantly more species detected using the hand-held detector ($p = 0.049$, $n = 15$), however, unlike the comparison with an analogue static recorder, there were significantly more calls detected using the digital static detector ($p = 0.041$, $n = 15$). Therefore, in this instance, the choice of recording method will depend on the aim(s) of the research being conducted.

One feature noted during analysis was a very high variation in the total number of calls detected at each site from the flyway vs. non-flyway and hand-held vs. static comparisons. This variation is possibly a result of nightly variation in bat activity (Hayes 1997) during the flyway vs non-flyway comparison which was conducted over two separate (consecutive) nights, or smaller scale spatial variation affecting the hand-held vs. static comparison. In light of this variation, the power of the analysis may have been improved by sampling each site for more than one night or, in the case of the flyway vs. non-flyway comparison, through paired-sampling during the same night.

Species-time analysis

The species-time accumulation curve for Top End bats (for September to November) revealed that the greatest increase in the cumulative number of species detected occurred in the first three hours after sunset, during which time 80% of species were detected (Fig. 1). After this period, there was a slow increase in the number of species detected throughout the remainder of the night. 25 recording nights using the analogue recording method were excluded from the analysis because they failed to record throughout the night as a result of relatively continuous bat activity. Had it been possible to record bats throughout the night on those occasions, the average time taken to record 100% of species would have likely been lower. While the seasonal activity patterns of bats in northern Australia remain unknown, it is likely that activity levels would be relatively high during our sampling period which was just prior to the northern tropical wet season. During this period, temperature and humidity levels rise and flying insects are abundant. During periods of lower bat activity, the time required for an adequate sample may be longer.

We are aware of only two studies (i.e. Duffy *et al.* 2000; Richards 2001) that have presented species-time relationships derived from Anabat recordings. This is surprising given the relative ease of deriving these data. Our study and that of Duffy *et al*. (carried out in Victoria) used a similar definition of a call sequence, thereby allowing a broad comparison between the two datasets. Between 55% and 70% of species were detected after 3 hours in Victoria compared with 80% in the Top End, and between 75% and 90% were detected after 6 hours in Victoria compared to 97% in the Top End. This comparison suggests that a shorter sampling period may be employed for species inventories using an Anabat detector in northern Australia than would be appropriate in south-eastern Australia. However, our results indicate that brief sampling periods (e.g.

1-2 hours) may provide an inadequate inventory. An important difference to note in this comparison is that Duffy *et al.* analysed only those calls that could be identified to the level of species (at best, 35% of all recorded calls) whereas our analysis included calls that could be attributed to a species or species combination (84% of all recorded calls). Identifying more calls would tend to increase the species accumulation rate.

Conclusion

Each of the methods for applying Anabat technology has inherent advantages and disadvantages. The methods used in any given study depend largely on the researcher's aims and the resources that are available. Based on our results we make the following recommendations:

- calls should be collected using digital recording methods;
- the minimum sampling time required to achieve a satisfactory (80%) inventory of bat species at a site in the Top End of the Northern Territory is three hours;
- when Anabat recordings are conducted over short periods for the purpose of general species inventory, hand-held detectors should be used as opposed to static recording techniques; and
- Anabat sensitivity should be set at eight or greater, in particular in areas occupied by particularly quiet calling bat species such as *H. ater*. When using the digital recording technique described here, the monitor mode option in the Anabat6 program excludes the majority of insect noises from being saved to file. Therefore increasing sensitivity increases the likelihood of detecting these species without increasing the resulting number of call files requiring analysis.

The focus of additional research on Anabat survey techniques should include:

- determining the efficacy of walk and drive transects using a hand-held Anabat detector as opposed to a stationary observer;
- comparing the output of the Anabat detector placed at various angles up to and including 90° above horizontal;
- clarifying the effect of flyway size on bat activity; and
- investigating small scale variation in bat activity that may account for variation in the total number of calls observed between samples.

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Uncluttered space	Background cluttered space	Highly cluttered space
Chaerephon jobensis	*Chalinolobus gouldii*	*H. ater**†
Mormopterus beccarii	*Chal. nigrogriseus / Scotorepens greyii / Sc. sanborni*	*Nyctophilus arnhemensis / N. bifax / N. geoffroyi*
*Mo. loriae**	*Hipposideros ater**†	*N. walkeri*
Saccolaimus flaviventris	*H. diadema*	*R. aurantius**
Sa. saccolaimus†	*H. stenotis*	
Taphozous georgianus	*Miniopterus schreibersii / Pipistrellus westralis*	
T. kapalgensis	*Macroderma gigas*†	
	*Mo. loriae**	
	Myotis macropus	
	P. adamsi	
	*Rhinonicteris aurantius**	
	Vespadelus caurinus	
	V. finlaysoni	

Table 1. Classification of species into the foraging guilds used in this study. Species separated by '/ 'represent species combinations that could not be distinguished based on Anabat calls. (* species occupies more than one foraging guild, † species known to occur in the Top End of the Northern Territory but not recorded by Anabat in this study.)

	Flyway vs Non-flyway			Analogue vs Digital			Hand-held vs Static		
	n	median (F / N)	Z	n	median (A / D)	Z	n	median (H / S)	Z
Totals									
call sequences	19	(117 / 60)	1.308 ns	18	(81 / 123)	3.408 ***	26	(59.5 / 52)	0.317 ns
species	19	(5 / 4)	1.672 ns	18	(4 / 4)	0.829 ns	26	(5 / 3.5)	3.229 **
Foraging guilds (total no. call sequences)									
uncluttered	19	(12 / 11)	0.443 ns	16	(8 / 17)	2.983 **	25	(9 / 3)	2.700 **
background clutter	19	(65 / 34)	1.328 ns	18	(59.5 / 105)	3.157 **	26	(24.5 / 26.5)	0.038 ns
highly cluttered	7	(4 / 3)	1.183 ns	5	(30 / 37)	1.753 ns	6	(2 / 3)	0.943 ns
Species (total no. call sequences)									
Chae. jobensis	14	(2.5 / 7)	1.067 ns	12	(1.5 / 6)	2.863 **	16	(2.5 / 0.5)	2.527 *
Chal. gouldii	6	(1 / 1)	0.0 ns	-	-	-	9	(1 / 0)	0.355 ns
Chal. nigrogriseus / Sc. greyii / Sc. sanborni	16	(41 / 40)	0.362 ns	18	(14.5 / 16)	2.550 *	26	(15 / 16)	0.920 ns
Mi. schreibersii / P. westralis	10	(5.5 / 4)	0.357 ns	8	(34 / 58)	2.521 *	13	(3 / 1)	0.612 ns
Mo. loriae	4	(3 / 0.5)	1.095 ns	6	(17.5 / 19.5)	1.993 *	10	(9 / 5.5)	0.889 ns
Nyctophilus spp.	7	(4 / 3)	0.0 ns	4	(4 / 7)	1.461 ns	6	(1 / 5.5)	0.943 ns
P. adamsi	4	(7.5 / 6.5)	1.095 ns	4	(8.5 / 6)	1.604 ns	6	(5.5 / 1)	2.023 *
Sa. flaviventris	16	(5 / 1.5)	0.738 ns	10	(1 / 1)	1.099 ns	21	(7 / 1)	2.274 *
T. georgianus	7	(1 / 1)	0.507 ns	5	(0 / 2)	2.023 *	11	(2 / 0)	2.934 **
V. caurinus	7	(9 / 3)	1.859 ns	6	(6.5 / 8)	1.826 ns	13	(1 / 2)	1.599 ns

Table 2. Results of comparisons of Anabat detector survey techniques. The median number of calls or species (derived from concurrent recording periods at each site) for each method are shown, however statistical analysis is based on differences between paired sites. Z-values refer to Wilcoxon matched-pair tests. Only species recorded from four or more sites are shown (ns, not significant; * P<0.05; ** P<0.01; *** P<0.001).

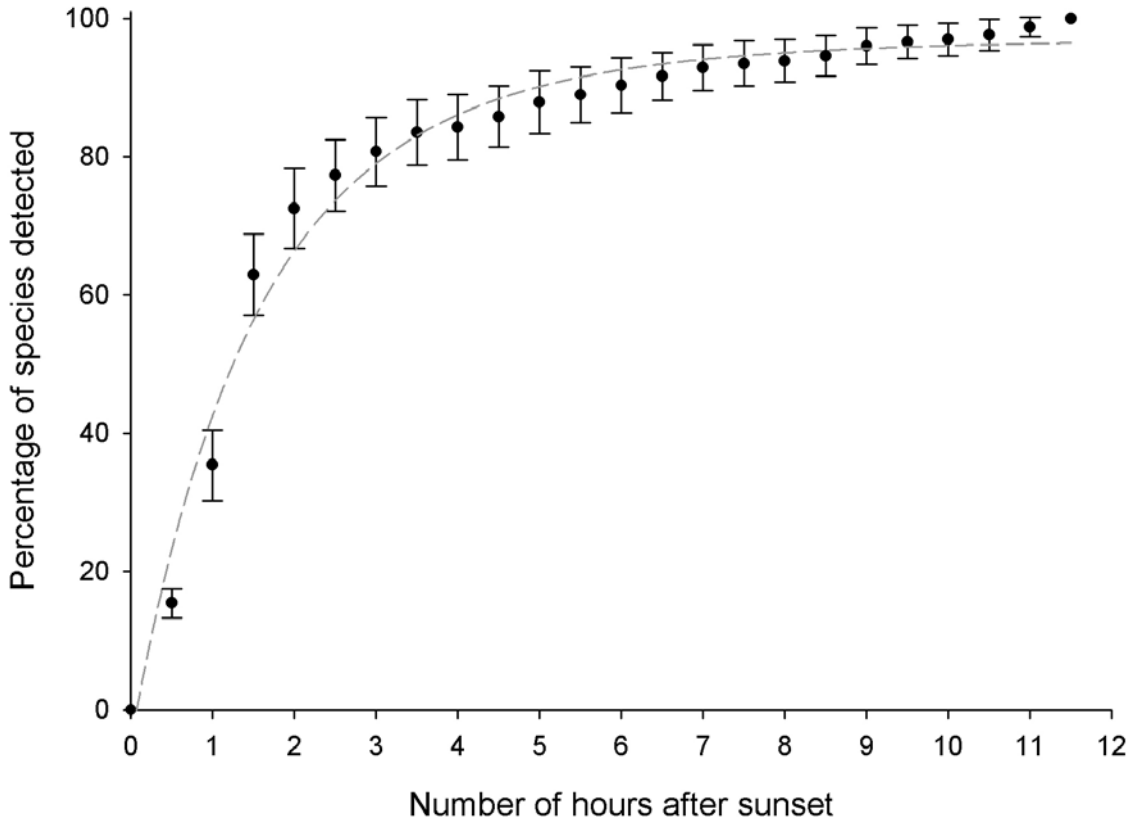

Fig. 1. Species accumulation curve derived from all-night Anabat recordings (for September - November in the Top End of the Northern Territory), averaged over all sites and shown in half-hourly increments. Bars represent one standard error and the dashed line is a fitted logarithmic curve.

Chapter 3.

Structure and environmental relationships of insectivorous bat assemblages in tropical Australian savannas

D.J. Milne, M. Armstrong, A. Fisher, T. Flores and C.R. Pavey. *Austral Ecology* (2005) 30, 906-919.

Structure and environmental relationships of insectivorous bat assemblages in tropical Australian savannas.

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Running Title: Insectivorous bat assemblages in Australian savannas

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Abstract Patterns in the composition of assemblages of microbat species sampled during the late dry season (the 'build-up') in north Australian savannas were assessed against a range of environmental factors as well as four *a priori* defined habitat types (riparian, escarpments, coastal and woodlands). Distinct species assemblages were most strongly associated with topographic and climatic variables. There were also limited associations with vegetation structure, fire and local roost potential but no associations with insects or water availability. Total species diversity at sample sites was associated with distance to rivers and rainfall. In general, species assemblages were not clearly defined and the number of significant environmental associations was relatively few. We compare these associations with those reported for bat assemblages elsewhere in Australia.

INTRODUCTION

Understanding of the diversity and evolutionary ecology of Australia's mammal fauna has not been uniform across orders. In particular, most detailed tests of evolutionary hypotheses (e.g. Johnson 1998; Fisher *et al.* 2001) omit bats (Order Chiroptera). Assessments of population trends and extinction proneness have also excluded Chiroptera (e.g. Woinarski *et al.* 1992; Johnson 2002). This is a significant shortcoming as bats represent over 30% of Australia's mammal species, many of which are endemic.

Although Australian mammal diversity peaks in the tropical forests of eastern Queensland including Cape York Peninsula, significant diversity also occurs in the savannas of north-western Australia where 94 species are known (Woinarski *et al.* 1992). An assessment of the response of mammals within this region to 23 environmental variables revealed that a single environmental gradient (of substrate and disturbance) described the distribution of all species, excluding bats (Woinarski *et al.* 1992). Rock-inhabiting mammals are a significant component of this fauna, however, diversity of this assemblage decreases with decreasing outcrop size and increasing isolation. Woinarski *et al.* (1992) identified three other trends. First, that the mammal fauna of eucalypt open forest/woodland habitats of north-western Australia is characterised by extensive distributions of its component species. Second, that monsoon forests support a depauperate mammal fauna. Last, that the mammal fauna of this region undergoes substantial latitudinal change associated with a steep north-south rainfall gradient.

Woinarski *et al*. (1992) did not include systematic sampling of bats, preventing a rigorous examination of the response of the bat fauna to environmental

measures. However, data from captures (mist netting, harp trapping, roost searches) indicated that most bat species were present across the environmental range sampled (Woinarski *et al.* 1992). Here we revisit the issue of the response of bats to environmental variables in the tropical savanna of the Northern Territory and north-west Queensland using a more rigorous dataset. Our data collection incorporated the use of ultrasonic detectors to sample bats and GIS derived variables to represent environmental conditions. The study region supports a rich microbat fauna (26 of Australia's 65 species, 15 of Australia's 20 genera), including one endemic species (*Taphozous kapalgensis*), and both of Australia's monotypic genera (*Rhinonicteris*, *Macroderma*).

We assessed environmental factors at two levels, first at the landscape scale, using data available from a geographic information system (GIS), and second at a local scale where information was collected on the physical environment and food resource availability (insects) at individual sampling sites. We predicted that the high vagility of bats would result in species responding broadly to environmental variables. However, specific responses to a number of environmental variables were expected. In particular, we predicted that the distribution, composition and segregation of bat assemblages would respond to geographic patterns in annual rainfall, presence of rocky escarpments, water bodies, and canopy cover. Although a relationship with insect abundance and composition was examined, we predicted that this relationship would not be significant given the generalist feeding ecology of most insect-eating bats (Fenton 1990).

The bat assemblages of tropical Australian savannas are also compared with assemblages elsewhere in Australia. Specifically, we compared our results with

community composition and environmental association studies in north Queensland rainforest (Crome & Richards 1988), mangroves in north-western Western Australia (McKenzie & Muir 2000), and open forest/woodland in Victoria (Kutt 1995; Lumsden & Bennett 1995; Herr 1998), south-east New South Wales (Law *et al.* 1999) and Tasmania (Taylor & O'Neill 1988).

METHODS

Study area

The study area, called the Top End of Australia, included the tropical savanna of the Northern Territory and north-west Queensland, north of 18°S, but excluding offshore islands (Figure 1). Across this area, maximum mean weekly temperature ranges between 32° C and 39° C and mean annual rainfall between 360 mm and 1720 mm (Houlder 2000, Figure 1). Rainfall is highly seasonal with almost all precipitation occurring from November to April. Topographic relief is relatively low. The maximum elevation is 553 m on the Arnhem Land plateau, with the main areas of topographic relief being the Kakadu escarpment and the eastern edge of the Kimberley region in the south-west of the study area. Eucalypt woodlands and forests dominate 78% of the study area (Fox *et al.* 2001). Other notable environments include monsoon rainforests and floodplains dominated by sedgelands and grasslands. On average, over half (52%) of the Top End is burnt every year (A. Edwards, pers. comm.).

Study sites

A total of 39 sampling sites were located across the Top End (Figure 1). Fieldwork was conducted from 22 September - 1 November 2000 (18 sites), 26 September – 1

November 2001 (19 sites) and 23 - 25 October 2002 (two sites). Sampling was conducted at similar times of year to reduce possible effects of seasonal variation on species composition. Each site was a circular plot of 100 m radius. Plots were primarily selected to cover a large geographic area and to sample four broad habitat types:

(a) Riparian – adjacent to perennial rivers, creeks or permanent waterholes (10 sites);
(b) Escarpments – sandstone cliffs (11 sites);
(c) Coastal – coastal and near coastal environments (excluding estuaries and mangroves) (8 sites);
(d) Woodlands – continuous areas of eucalypt woodlands or open forests not associated with the other habitats types (10 sites).

Habitat types were chosen *a priori* and were based on information gleaned from species' distribution maps and descriptions of microbat habitat preferences (Strahan 1995; Churchill 1998) that suggested these habitats may contain distinctive species assemblages. Two sites were usually sampled at a time on the same nights. With one exception, no two sites within a sampling pair sampled the same habitat type. Distances between sampling pairs ranged between 2 km and 30 km (mean 10 km).

Bat sampling

At each site we used a range of sampling techniques to maximise the likelihood of obtaining a full inventory of bat species (Kuenzi & Morrison 1998; Murray *et al.* 1999; O'Farrell & Gannon 1999). Bats were sampled using two (18 sites) or three (21 sites) harp traps over two consecutive nights as well as one night of shot sampling for

a three hour period after dusk. Harp traps were usually placed across “flyways” (tracks, streams or other gaps within the vegetation where bats are more likely to be trapped) and were either positioned side by side or spaced between 20 and 30 meters apart. We also conducted active searches of caves, road culverts and any other features potentially used as diurnal roosts by bats within 400 m of the centre of the sampling site. In addition, bat calls were recorded at every site with ultrasonic bat-detectors (Anabat II, Titley Electronics) using two methods. The first method involved placing a detector on the ground, elevated to approximately 40°, and operated from dusk for a cumulative total of at least six recording hours over two consecutive nights (maximum 22 hrs, mean 20 hrs). This time period has been shown to sample 90% of species calls at a given site (Milne *et al.* 2004). Detectors were connected to either an Anabat II Delay Switch with output recorded to 90-minute cassette tape (Sony Chrome UX) via tape recorder (Optimus CTR-115) (18 sites) or an Anabat V Zcaim and computer (Toshiba Portégé 3440CT or Toshiba Tecra 700CT) running Anabat6 software in monitor mode (21 sites). There are no differences in the species detected between these two recording techniques (Milne *et al.* 2004). For the second method, an Anabat detector was held in the hand and manually activated on detection of a bat-call and actively pointed in the direction of the call. Calls were recorded via tape-recorder and cassette-tape, for three hours after dusk for one night. All recorded calls were identified according to Milne (2002). At several sites (14), shot sampling was not permitted. Instead we trapped bats using mist-nets at these sites. It is likely therefore, that some ‘high-flying’ bat species that are readily detected using shot sampling, may not have been trapped at these sites. However, we expect this will have a negligible effect on our results as shot sampling at all other sites, used in conjunction with Anabat detectors, enabled us to collect an extensive reference call library for ‘high-flying’ bat species for the entire study area

(Milne 2002). Anabat detectors were systematically used at all sites and will normally detect 'high-flying' species that are not readily trapped (O'Farrell & Gannon 1999).

Environmental data

We collated environmental data for each site from field habitat measurements, analysis of spatial data, and insect sampling.

Habitat measurements At the centre of each site we measured tree basal area, canopy cover and stem count, 10 m either side of a 100 m transect (0.2 ha) in an area of undisturbed vegetation usually adjacent and parallel to flyways where harp traps were set. On escarpment sites, the transects either traversed the escarpment or were situated at the base of the escarpment. Basal area and stem counts were derived by measuring diameter at breast height (DBH) of every tree along the transect, whereas canopy cover was measured using a spherical densiometer at 0 m, 50 m and 100 m along the transect. For the entire site (3.1 ha), we measured slope, maximum canopy height, crown cover, rock cover, distance to water and local roost potential. Crown cover in three height classes (1-3 m, 3-10 m and >10 m) was estimated using crown separation ratios (McDonald *et al.* 1998). Local roost potential for each site was visually assessed according to the following scale:

0 – no trees or rock outcrops

1 – only small trees (<5 cm DBH and <5 m tall)

2 – mostly intermediate sized trees (5-20 cm DBH and 5-15 m tall) OR small trees and rock outcrop showing small (hand size) cracks and holes

3 – mostly large trees (>20 cm DBH and > 15 m tall) OR small – intermediate trees and rock outcrop with large (body size) cracks and holes

4 – mostly large trees AND rock outcrop with large cracks and holes

We chose to assess whole trees and rock outcrops rather than count individual hollows because small microbats (< 10 g) can roost in hollows equivalent to their own body diameter (pers. obs.). Entrances to these hollows are very small and would regularly be overlooked if we attempted to count hollows directly. Large trees have been shown to contain more tree hollows than smaller trees (Whitford 2002) and are preferred roost sites for many bat species (Lunney *et al.* 1988; Herr & Klomp 1999; Law & Anderson 2000; Lumsden *et al.* 2002).

Spatial data Several variables were derived using GIS from a 3 second (c. 100 m) digital elevation model (DEM, provided by the Department of Defence) including elevation, ruggedness index (the range in cell values of the DEM within a 3 x 3 cell neighborhood), and distance to 25 and 100 metre "escarpments" (defined here as any adjacent DEM cells having an altitude difference of 25 or 100 metres). Climate variables (annual mean temperature, minimum monthly temperature and annual rainfall) were derived using BIOCLIM (Houlder 2000). Other GIS data included fire frequency (number of years in which the site was burnt over the preceding 7 years) and years since last fire (datasets provided by the Bushfires Council of the Northern Territory), distance to perennial rivers, and NDVI (normalised difference vegetation index, which is a measure of vegetation 'greenness' derived from satellite imagery) and projective foliage cover (Meakin *et al.* 2001).

Insects At each site we trapped flying nocturnal insects for one night concurrently with bat sampling. The insect trap was constructed from a white cotton sheet (1.5 m x 2.5 m), suspended off the ground by strings tied to the corners to form a funnel,

one end higher than the other. At the bottom of the funnel a hole was cut in the sheet and a plastic jar (65 mm diameter x 130 mm depth) partially filled with 70 % ethanol was attached to hang underneath. A 12 V fluorescent light ("Col-Light" brand) was hung from the higher end of the sheet to attract insects. The trap was positioned approximately 100 m from the Anabat detector so as not to disturb bats from natural flight habits in the vicinity of the detector, and left unattended for the entire night. Insects that fell into the jar were collected the following morning. In the laboratory, insect samples were filtered through a 2 mm sieve to remove the smallest insects (mostly <3 mm in length) and then identified to order and assigned to four size (head-body length) classes: <5 mm, 5-10 mm, 10-15 mm and >15 mm. The choice of size classes was based on the range of body sizes found to be prey items of bats in Tasmania (O'Neill & Taylor 1989).

Analysis

Analysis of bat communities was based on species presence-absence at each site derived from the combination of all sampling methods. Anabat calls for the following combinations cannot be reliably separated in the Top End: (1) *Chalinolobus nigrogriseus*, *Scotorepens greyii* and *S. sanborni*; (2) *Miniopterus schreibersii* and *Pipistrellus westralis*; and (3) *Nyctophilus arnhemensis*, *N. bifax,* and *N. geoffroyi* (Milne 2002). Anabat call sequences that were attributed to these species combinations were therefore excluded from the analysis, although species within these combinations were included if identified using one of the physical sampling methods. The one exception was *S. greyii* and *S. sanborni* which cannot be readily separated in the field (Churchill 1998) and were treated here as a single species although in some areas their distributions are allopatric (McKenzie & Muir 2000).

Species assemblages were assessed using PATN software (Belbin 1994). Similarities in species composition between sites were calculated using the Bray-Curtis association measure. Cluster analysis (unweighted pair group mean) was used to define assemblages (groups of sites) following visual inspection of the dendrogram. ANOSIM (Clarke & Green 1988) was used to test whether bat species composition differed significantly between the defined assemblages as well as the four *a priori* habitat types. The relationship between sites was also portrayed by ordination (multi-dimensional scaling) of sites by their bat species composition. In both analyses, only sites with at least three species were included.

All environmental variables (Table 1) were continuous or rank ordered. Variables were initially compared using the Spearman rank correlation test. Where pairs of variables had a correlation coefficient greater than 0.8, one of the pair was excluded from further analysis. The mean of each environmental variable was calculated for each group of sites derived from the cluster analysis and the significance of differences between bat assemblage groups was tested using Kruskal-Wallis ANOVA. The relationship between environmental variables and the arrangement of sites in the ordination space was also tested using vector fitting (Kantvilas & Minchin 1989). Finally, generalized linear modelling (GLM; Crawley 1993) was used to develop a predictive habitat model for total site species richness. A Poisson error distribution and log link function was used and a backward stepwise procedure was adopted to generate the minimum adequate model with only those variables having a significant correlation in the vector fitting included in the model development.

RESULTS

Species assemblages

A total of 23 microbat species were identified from the 39 sites, representing over 80% of the species recorded from north-western Australia (Woinarski *et al.* 1992). Two species known to occur in the Top End, *Macroderma gigas* (Ghost bat) and *Saccolaimus saccolaimus* were not detected in this study. We identified five groups from the classification of all sites by their species composition (Figure 2). The initial classification divided the sites into four groups. We subdivided the largest of these groups into two and assigned two outlying sites to Group 1 based on the relative position of these sites in the ordination. ANOSIM analysis confirmed that the groups differed significantly in composition ($R = 0.70$, $P < 0.001$) and that there was a significant difference between each pair of groups ($P < 0.01$ or better).

The occurrence of bat species within the derived groups and habitat types is summarised in Table 2 and the geographic distribution of sites (classified according to group) is shown in Figure 1. Four species were ubiquitous throughout the groups and habitats (*Chaerephon jobensis*, *Pipistrellus adamsi, Mormopterus loriae* and *Saccolaimus flaviventris*) while three species were each detected at single sites only (*Hipposideros diadema*, *H. stenotis* and *Miniopterus schreibersii*). The distribution of sites in ordination space and the relationship with environmental vectors is shown in Figure 3. A total of 14 environmental variables were significantly correlated with variation in species composition between sites (Table 3). A summary of mean values for these variables for each group is provided in Table 4. A description of species composition and the environmental characteristics for each group is provided below.

Group 1 Species that were detected most often in this group include *Chalinolobus gouldii* (present in all sites), *Chaerephon jobensis, Saccolaimus flaviventris*, *Scotorepens greyii* / *Scotorepens sanborni* and *P. adamsi*. *Chalinolobus gouldii* was strongly associated with this group (i.e. tended to occur in Group 1 more than the other four groups). Group 1 had the highest total species richness and mean site species richness of all groups. Sites were characterised by high percentage canopy cover, frequent burning, and high annual rainfall and were located in the north and west of the Top End.

Group 2 The greatest number of sites occurred in this group (14). Species that were detected most often include *Vespadelus caurinus* (present at all sites), *Saccolaimus flaviventris*, *Taphozous georgianus* and *Chaerephon jobensis*. *V. caurinus* was strongly associated with this group. Sites were characterised by rugged, steep rocky slopes, high elevations and short distances to escarpments and rivers. Minimum temperatures were cool and annual rainfall low. Sites were widely distributed across the Top End, except the coastal zone.

Group 3 Species detected most often in this group include *Saccolaimus flaviventris*, *N. arnhemensis, Myotis macropus* and *Scotorepens greyii / Scotorepens sanborni*. *N. arnhemensis* was strongly associated with this group. Group 3 was not clearly associated with any of the environmental variables measured and occupied an intermediate value on most environmental gradients. However, this group displayed the highest mean values for minimum temperature.

Group 4 This group had equal fewest sites (5) and had the lowest total and mean site species richness. Species detected most often include *Chaerephon jobensis* (present

at all sites) *Saccolaimus flaviventris*, *Mormopterus loriae* and *Chalinolobus nigrogriseus*. There were no strong species associations, although *Chalinolobus nigrogriseus* occurred at proportionately more sites in this group than any other. Sites were characterised by lower mean annual temperatures, long distances to rivers and no rock cover.

Group 5 Species detected most often include *Saccolaimus flaviventris*, *P. westralis* (both present at all sites), *P. adamsi*, *Mormopterus loriae*, and *T. kapalgensis*. *P. westralis* and *T. kapalgensis* were strongly associated with this group. Group 5 also had relatively few sites and low species richness, but was associated with the minima or maxima of several environmental variables including long distances to escarpments, flat terrain at low elevations with no rock, low local roost potential, high annual temperatures and low fire frequency. All five sites were located near the coast (Figure 1).

Relationships with habitat types

There was a significant difference in species composition between habitat types (ANOSIM, $R = 0.35$, $P < 0.001$) as well as between all pairwise combinations of habitats except between "Woodland" and "Riverine" ($R = 0.037$, $P = 0.27$). *V. caurinus* and *T. georgianus* were detected most often in "Escarpment" habitat. Both of these species, as well as *Rhinonicteris aurantius* and *Chalinolobus nigrogriseus*, were absent from "Coastal" habitat. *P. westralis* was strongly associated with "Coastal" habitat and absent from both "Escarpment" and "Riparian" habitat. *N. arnhemensis* was also absent from "Escarpment" habitat. All habitats had similar total and site species richness, with slightly lower species richness in the "Coastal" habitat.

The relationship between groups and habitats is summarised in Table 5. The habitat type of each site was not independent of group classification ($\chi^2 = 32.54$, $P < 0.01$). Most of the "Escarpment" sites occurred in Group 2 (steep, rocky, rugged sites) with two further sites in Group 1. "Coastal" sites mainly occurred in Group 3 (few environmental correlates) and Group 5 (flat, low elevation), whereas "Riparian" sites occurred across four of the groups and "Woodland" sites were evenly represented across all five groups.

Relationships with insects

We found no significant associations between bat species assemblages and various measures of insect availability including total number of insects, total number of insect orders, total number of insects in various size classes, proportion of insects in various size classes or total number of insects in each order.

Species richness model

Habitat modelling identified distance to perennial rivers and annual rainfall as the major predictors for site species richness (Table 6). The minimum adequate model was only moderately robust with 40% of the deviance captured. This suggests that there was considerable 'noise' in the data or that some important explanatory variables were not quantified.

DISCUSSION

As predicted, the insectivorous bat fauna of north-western Australia responded broadly to most environmental variables. The main environmental feature associated

with the distribution of microbat assemblages in the study area was topography (variation in elevation, slope, topographic ruggedness and distance to escarpments). Not surprisingly therefore, species considered to be obligate cave roosters (*H. ater*, *H. diadema*, *H. stenotis, Myotis macropus*, *Miniopterus schreibersii, R. aurantius, T. georgianus, V. caurinus*, *V. finlaysoni*), mainly occurred in (but were not restricted to) Groups 1 and 2 which were associated with high values for the topographic variables. Although we expected a relationship between microbat assemblages and distance to escarpments, the significant effect of elevation was not predicted. Elevation generally increased away from the coast and was autocorrelated with 'distance to coastlines', making it unclear which of these features was most important in influencing bat composition.

The second factor influencing bat composition was climate, specifically annual rainfall (≈ maximum temperature and latitude), mean temperature and minimum temperature (≈ temperature range; refer Table 1). The influence of annual rainfall was expected given the relationship between rainfall and species composition exhibited by the entire mammal fauna of north-western Australia (Woinarski *et al.* 1992). A similar pattern was shown by the vegetation (Bowman *et al.* 1988) and birds (Whitehead *et al.* 1992) of north-western Australia

In contrast to the significant relationship identified between bat assemblages and mean climatic variables, there was no significant relationship between ambient temperature (measured at 10 pm each sampling night) at each site and species composition. At the time of year that we sampled, temperature was unlikely to limit the number of bat species that were active. However, during the dry season, low inland temperatures may reduce insect activity, restrict bat activity to the earlier,

warmer times of the night and /or induce some species to enter torpor. Therefore, restricting our sampling to one period of the year may have affected our results but sampling at different times of the year would have required a much greater sampling effort. Between years, there was no observable difference in general weather patterns during each sampling period, therefore inter-year variations were unlikely to have affected our results.

There were significant associations between bat species assemblages and fire frequency (≈ time since fire). The effects of fire on landscapes in northern Australia can depend on the number of times an area is burnt and on the time since last fire (assessed here), fire intensity, seasonal timing of fires and spatial extent of burning (Dyer *et al.* 2001; Andersen *et al.* 2003). The link between fire and bat species composition is likely to be an indirect one. It is also possible that characteristics of the landscape such as fuel loads, geography and habitat type are actually the primary influence for species assemblages and fire frequency is a secondary consequence of these landscape characteristics. Therefore, our results should be viewed with caution and further investigation into the effects of fire on bat species assemblages is required before conclusions can be drawn.

We assessed several variables involving insect availability at each site. None of the variables showed any significant relationship with microbat assemblages. This suggests that, in the Top End at least, available food resources do not influence the composition of bat communities. This conclusion was consistent with previous research on insect-eating bats that indicated most species capture prey opportunistically (Fenton 1990). Specific research on Tasmanian bats also concluded that bat assemblages were generally opportunistic foragers (O'Neill & Taylor 1989).

Four aspects of our sampling strategy may have influenced our analysis. First, we did not sample non-volant insects and other arthropods that are eaten by some bat species in the Top End (e.g. spiders, CP unpublished data). Second, high flying insects that are preyed on by bats such as *Taphozous* spp. were probably not attracted to our light trap. Third, bats may only show a response to insects at certain times of the year. It is likely that at the time of sampling (late dry season), insects were abundant and food resources did not affect the activity of bats. Fourth, insect sampling was limited to one night per site, which may not have been sufficient to provide an adequate representation of overall insect availability. Therefore, we suggest that a combination of insect sampling methods should be used in future assessments of prey availability and bat assemblages, particularly when the diversity of bats is high. These methods should aim to sample volant and non-volant invertebrates.

Did our study adequately sample a cross section of the major environmental gradients in the Top End? Compared with much of Australia, the environment of the Top End is relatively uniform. Landscape relief is low, woodlands dominate most of the landscape, temperature varies little throughout the year and the climatic gradients are gradual. Therefore, environmental variation is relatively small, and fewer sampling sites should be required compared to areas with greater topographic, climatic and vegetative variation. However, there may have been two significant deficiencies in our sampling. First, the highly seasonal rainfall in the monsoon tropics results in starkly contrasting ‘wet’ and ‘dry’ seasons. From our study, we were unable to say how bat composition may vary seasonally and there are no data available to assess seasonal patterns. Second, the chosen study area was huge (530 000 km^2) and most of the north-east of the Top End (Arnhem Land) was unsampled.

Therefore, clearer patterns of bat assemblages may have emerged if we had sampled more comprehensively, both spatially and temporally.

Most sites (34) were sampled in pairs and the minimum distance between any two sites was 2 km (mean 10 km). Bats can travel long distances during the night. Foraging distances for a selection of species range between 1 km and 10 km (Herr & Klomp 1999; Law & Anderson 2000; Lumsden *et al.* 2002), therefore some of our results were potentially autocorrelated due to the same bats being sampled at both sites within a pair. Therefore, we assessed the similarity in site species composition using the Bray-Curtis index. This index was calculated by dividing the number of shared species between pairs of sites by the total number of species of both sites. The resulting value was plotted against the distance between each pair of sites (Figure 4). The scatter of points was highly variable, however, the slope of the regression line was shallow. This pattern indicated that the relative change in species composition as a result of geographic separation was small.

One of the environments largely neglected during sampling was monsoon rainforest, although "Riverine" sites did sample components of monsoon rainforest environments. We considered this had little effect on our results because monsoon rainforests occupy just 0.5 % of the landscape (based on mapping by Fox *et al.* 2001) and usually occur in patches less than 5 ha (Russell-Smith 1991). In addition, Menkhorst and Woinarski (1992) found no bat species that were tightly associated with monsoon rainforests in the Top End and these forests support a depauperate mammal fauna in general (Woinarski *et al.* 1992).

Comparisons with other studies in Australia

Some of the environmental variables that we found to be significantly correlated with bat assemblages in the Top End differed from those related to bat community variation in other areas of Australia. Waterbodies have been found to support high species diversity and some species are strictly associated with them (Law *et al.* 1998, south-west slopes of N.S.W.; Young & Ford 2000, central western Queensland). In the Top End, GLM analysis suggested bat species richness increases with decreasing distance to perennial rivers. However, species richness was not exceptionally high at our "Riparian" sites. Further, Group 2, which was on average closest to rivers, did not have the highest species diversity. Also, we found no significant difference in species assemblages between "Riverine" and "Woodland" habitats and there was no relationship with distance to available surface water. Given that sampling was carried out during the driest time of the year (late dry season September – November) the likelihood of detecting significant associations with waterbodies was maximised.

A relationship between vegetation structural complexity and microbat diversity has been established in studies in Western Australia (McKenzie & Muir 2000) and New South Wales (Law *et al.* 1998). By contrast, we found significant correlations of bat species diversity with canopy cover but no associations with structural complexity. Compared to the vegetation in the areas sampled by McKenzie and Muir (2000)and Law *et al*. (1998), the vegetation of the Top End is usually shorter and contains fewer understorey layers (D. Lewis pers. comm.). This limits the degree of vegetation structural complexity in the Top End that likely accounts for the lack of correlation between structural complexity and bat communities.

Although we identified significant differences between the species assemblages within classification groups and habitat types, the assemblages were not clearly

defined. Most species occurred in more than one group and some were present in all groups. In addition, there were no associations between insect variables and bat assemblages and relatively few associations with environmental variables. This pattern is not restricted to microbats. Birds, reptiles and non-volant mammals also exhibit 'loose' patterns of species composition (Woinarski & Fisher 1995; Woinarski *et al.* 2000) and limited associations with particular environments and environmental gradients (Menkhorst & Woinarski 1992; Woinarski *et al.* 1999) in the Top End. Woinarski *et al.* (1999) suggested this trend was a consequence of the homogeneity of eucalypt woodlands and forests that dominate the Top End landscape. This relatively uniform environment militates against highly specialised and habitat-specific faunas. However, there were exceptions. Specifically, some microbat species had a clear association with rugged rocky areas, particularly escarpments and adjacent areas. These areas provided a complex mix of habitats that contained foraging and roosting sites suitable for both cave and tree roosting species. This pattern extended to other vertebrate species as well. Rocky escarpment regions in the Top End support high species diversity as well as a number of endemic or habitat restricted species (Woinarski *et al.* 1992; Woinarski & Gambold 1992).

Vegetation corridors beside rivers and surrounding areas (but not the waterbodies themselves) appeared to be important environments as they supported high bat species richness. Bats are regularly characterised by the foraging strategy they employ within their immediate environment (McKenzie & Rolfe 1986; Neuweiler 1989; Schnitzler & Kalko 1998). Rivers are often associated with environments with tall dense vegetation. These areas do not appear to be of conservation significance because we did not observe high species richness at our "Riparian" sample sites. However, riverine environments usually have a distinct

outer ‘edge’ and vegetation surrounding these areas is usually shorter and relatively open. We propose that these areas had greater species richness as they provide a diversity of environments for bats that employ different foraging strategies. We recommend that further research be conducted to examine the relationship between rivers and bats in the Top End.

Our study did not take into account longer term bat population dynamics. Bats in the Top End are poorly surveyed and, with few exceptions, surveys have been unstructured and unsystematic. Therefore, attempting to identify and compare historical trends in bat populations is very difficult. Given the Top End environment is (currently) relatively unmodified, it could be assumed that mammal populations will remain stable and secure over the short to medium term. Unfortunately, this is not the case. Woinarski *et al.* (2001) described a case of decline in terrestrial small mammals in a conservation reserve in the Top End that could not be confidently attributed to any clear environmental factor(s). Further cases have also emerged (e.g. Pardon *et al.* 2003; Watson & Woinarski 2003). Therefore, we recommend establishing long-term monitoring programs to track changes in bat populations so that changes may be quickly identified, assessed and appropriately managed. This is a highly challenging task that can only be achieved through a considerable commitment of time and resources.

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Table 1. Environmental variables used in the analysis and other variables that were excluded due to high correlation (i.e. Spearman rank correlation test resulted in a correlation coefficient > 0.8). Variables in *italics* were derived from GIS, field measurements are in plain text.

Variable type	Variables	Highly correlated variables
Climate	*Annual rainfall*	Latitude, *maximum temperature*
	Mean temperature	
	Minimum temperature	*Temperature range*
	Temperature at 10 p.m.	
Topography	*Distance to 25 m escarpments*	*Distance to 50 m escarpments*
	Distance to 100 m escarpments	*Distance to 75 m escarpments*
	Elevation	*Distance to coast*
	Longitude	
	Ruggedness index	
	Slope	
Vegetation	Canopy cover	
	Canopy height	
	Crown cover 1-3 m	
	Crown cover 3-10 m	
	Crown cover >10 m	Basal area / hectare
	NDVI cover	
	Number of stems	
	Projective foliage cover	
Water	Distance to water	
	Distance to perennial rivers	
Other	*Fire frequency*	*Time since last fire*
	Rock cover	
	Local roost potential	
Insects	Total number of insects	Total insects < 5 mm, <10 mm and < 15 mm
	Total number of insect Orders	
	Total number > 5 mm	
	Total number > 10 mm	
	Total number > 15 mm	
	Proportion < 5 mm	
	Proportion < 10 mm	
	Proportion < 15 mm	
	Proportion > 5 mm	
	Proportion > 10 mm	
	Proportion > 15 mm	
	Total number of Blattodea	
	Total number of Coleoptera	
	Total number of Dermaptera	
	Total number of Diptera	
	Total number of Hemiptera	
	Total number of Isoptera	
	Total number of Lepidoptera	
	Total number of Orthoptera	

Table 2. Comparison of species composition within (a) bat groups and (b) habitats. Figures represent percentage of sites within each group or habitat in which each species was detected. Differences in proportions were tested using χ^2 statistic and differences in mean species richness were tested using Kruskal-Wallis ANOVA (ns, not significant; * P<0.05; ** P<0.01; ***P<0.001).

(a)

Species	No. Sites	Groups					
		1	2	3	4	5	χ^2
Chaerephon jobensis	30	88	71	43	100	100	8.32 ns
Saccolaimus flaviventris	30	75	86	100	60	40	7.37 ns
Vespadelus caurinus	19	63	100				31.50***
Taphozous georgianus	16	38	86		20		20.86***
Chalinolobus gouldii	15	100	43	14			20.89***
Scotorepens greyii / S. sanborni	15	75	29	71			14.56**
Pipistrellus adamsi	13	75	7	29	20	60	12.64*
Mormopterus loriae	12	13	21	29	60	60	5.85 ns
Nyctophilus arnhemensis	11	13	14	86		40	16.05 **
Rhinonicteris aurantius	11	38	43		40		6.86 ns
Myotis macropus	10	38		86		20	20.47***
Chalinolobus nigrogriseus	8	25	14	14	60		6.67 ns
Mormopterus beccarii	8	50		29	40		10.61*
Nyctophilus walkeri	7	38	7	43			8.32 ns
Pipistrellus westralis	7			29		100	29.30***
Hipposideros ater	6	25	29				5.53 ns
Taphozous kapalgensis	4			14		60	16.65**
Vespadelus finlaysoni	3	13	14				2.53 ns
Nyctophilus bifax	2	25					8.17 ns
Nyctophilus geoffroyi	2	13				20	4.57 ns
Hipposideros diadema	1		7				1.83 ns
Hipposideros stenotis	1	13					3.98 ns
Miniopterus schreibersii	1	13					3.98 ns
Total species richness		20	15	13	8	9	
Mean no. species per site		8.3	5.7	5.9	4.0	5.0	H = 11.19*
Number of sites		8	14	7	5	5	

(b)

Species	No. Sites	Habitats				
		Riparian	Escarpments	Coastal	Woodlands	χ^2
Chaerephon jobensis	30	90	82	63	70	2.32 ns
Saccolaimus flaviventris	30	80	82	50	90	4.43 ns
Vespadelus caurinus	19	50	100		30	20.59***
Taphozous georgianus	16	30	91		30	17.88***
Chalinolobus gouldii	15	50	55	13	30	4.34 ns
Scotorepens greyii / S. sanborni	15	60	18	25	50	5.05 ns
Pipistrellus adamsi	13	40	18	25	50	2.84 ns
Mormopterus loriae	12	40	9	63	20	7.15 ns
Nyctophilus arnhemensis	11	50		63	10	12.95**
Rhinonicteris aurantius	11	20	55		30	7.26 ns
Myotis macropus	10	30	9	50	20	4.34 ns
Chalinolobus nigrogriseus	8	10	27		40	5.38 ns
Mormopterus beccarii	8	40	18	25		5.05 ns
Nyctophilus walkeri	7	40	9	13	10	4.48 ns
Pipistrellus westralis	7			63	20	15.40**
Hipposideros ater	6		45		10	11.14*
Taphozous kapalgensis	4			38	10	8.85*
Vespadelus finlaysoni	3	10	9		10	< 1 ns
Nyctophilus bifax	2	10	9			1.82 ns
Nyctophilus geoffroyi	2		9	13		2.33 ns
Hipposideros diadema	1		9			2.61 ns
Hipposideros stenotis	1		9			2.61 ns
Miniopterus schreibersii	1	10				2.98 ns
Total species richness		17	19	13	17	
Mean no. species per site		6.6	6.6	5.0	5.3	H = 4.45 ns
Number of sites		10	11	8	10	

Table 3. Environmental variables with a significant correlation with the ordination of sites by species composition (*P<0.05; **P<0.01; ***P<0.001). See also Figure 3.

Variable	r
Distance to 25 m escarpments	0.79***
Distance to 100 m escarpments	0.78***
Elevation	0.71***
Canopy cover	0.68***
Rock cover	0.66***
Minimum temperature	0.65**
Local roost potential	0.63**
Slope	0.59***
Ruggedness	0.54**
Fire history	0.52**
Longitude	0.52**
Annual rainfall	0.50*
Distance to rivers	0.49*
Mean temperature	0.48*

Table 4. Comparison between bat groups for the environmental variables listed in Table 3. Values are the mean for sites in each group, H values refer to the Kruskal-Wallis statistic (ns; not significant; *P<0.05; **P<0.01; ***P<0.001).

Variable	Group					H
	1	2	3	4	5	
Distance to 25 m escarpments (km)	4.7	1.3	19.3	18.2	28.1	24.16***
Distance to 100 m escarpments (km)	38.9	28.9	119.6	60.6	128.3	24.52***
Elevation (m)	82.8	106.0	30.9	39.2	3.6	16.99**
Canopy cover (%)	53.5	48.5	21.1	28.6	6.7	12.06*
Rock cover (%)	8.7	37	0.7	0.0	0.0	14.86**
Minimum temperature (^{o}C)	14.6	12.4	16.5	13.1	15.9	18.91***
Local roost potential	2.1	2.5	2.1	1.6	0.6	17.45**
Slope (%)	6.4	29.7	4.4	5.0	0.2	20.41***
Ruggedness (m)	2.7	10.8	1.2	0.7	0.3	9.03 ns
Fire history (no. times burnt over preceding 7 years)	2.9	1.2	1.0	2.6	0.8	7.71 ns
Longitude (decimal ^{o} E)	131.2	132.9	132.6	135.0	133.1	4.92 ns
Annual rainfall (mm)	1210	848	1157	991	1149	12.72*
Distance to rivers (km)	2.7	1.6	6.6	8.5	7.6	8.84 ns
Mean temperature (^{o}C)	26.7	26.5	26.9	26.2	27.0	14.13**

Table 5. Comparison of the number of sites that occurred in each bat group according to habitat.

Group	Habitat			
	Riparian	Escarpments	Coastal	Woodland
1	4	2		2
2	3	9		2
3	2		3	2
4	1		1	3
5			4	1

Table 6. Summary of results from generalized linear modelling (GLM) for site species richness. Minimum adequate models and explanatory power (percent of deviance captured) are shown. Probability levels * P < 0.05, ** P < 0.01.

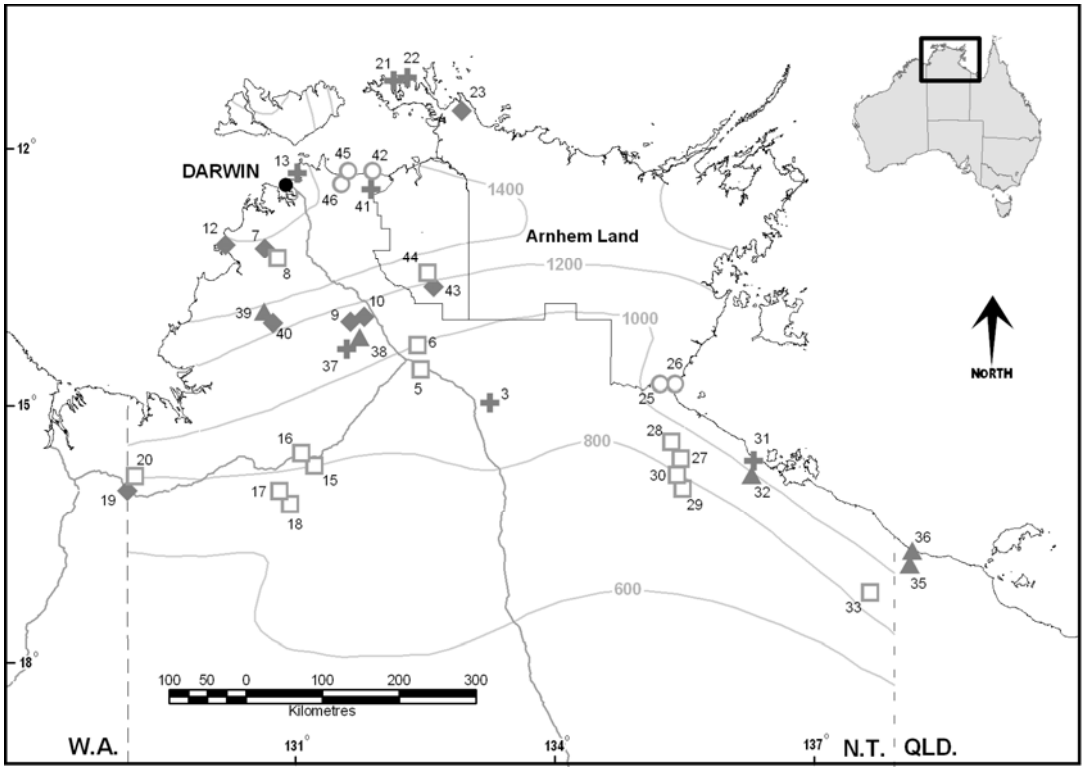
Variable	Estimate	SE	P
SPECIES RICHNESS (Deviance = 18.607; deviance captured = 40.0%; n = 39)			
Constant	1.3902	0.2578	
Distance to rivers (km)	-0.0403	0.0130	**
Annual rainfall (mm)	0.0005	4.6617	*

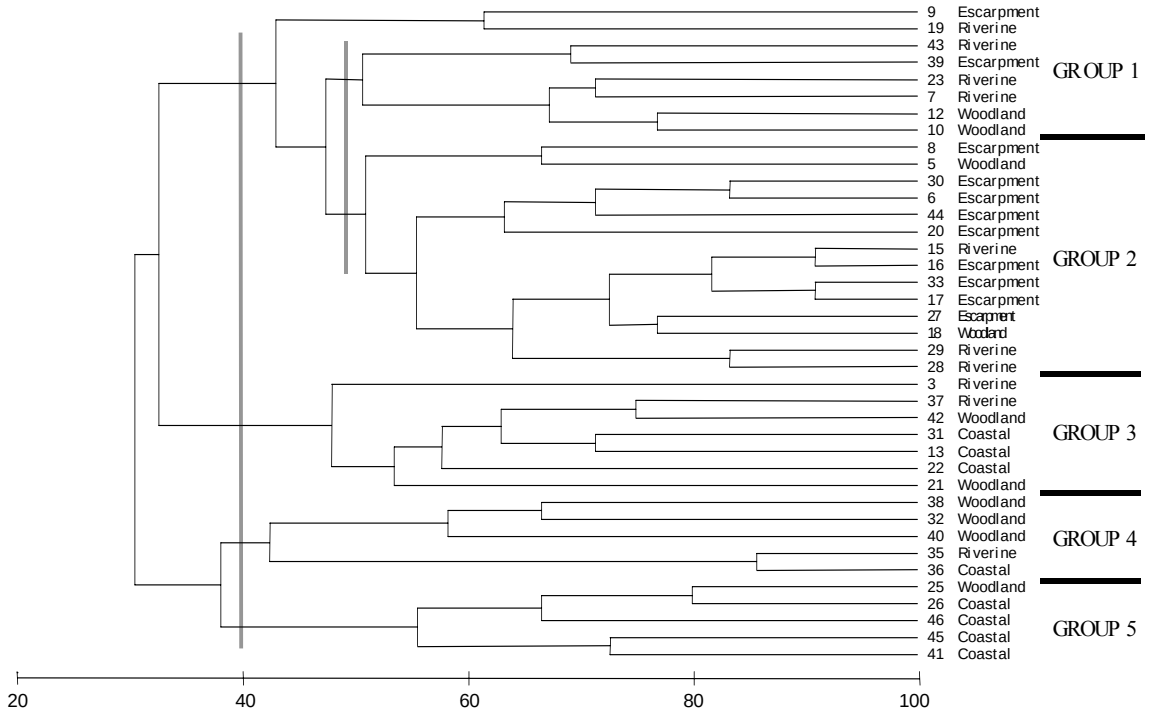
Fig. 1. Map of the study area showing the location of sampling sites and site labels as well as average annual rainfall isohyets (in millimetres). Sites are symbolised according to bat assemblage (diamond = Group 1, square = Group 2, cross = Group 3, triangle = Group 4, circle = Group 5).

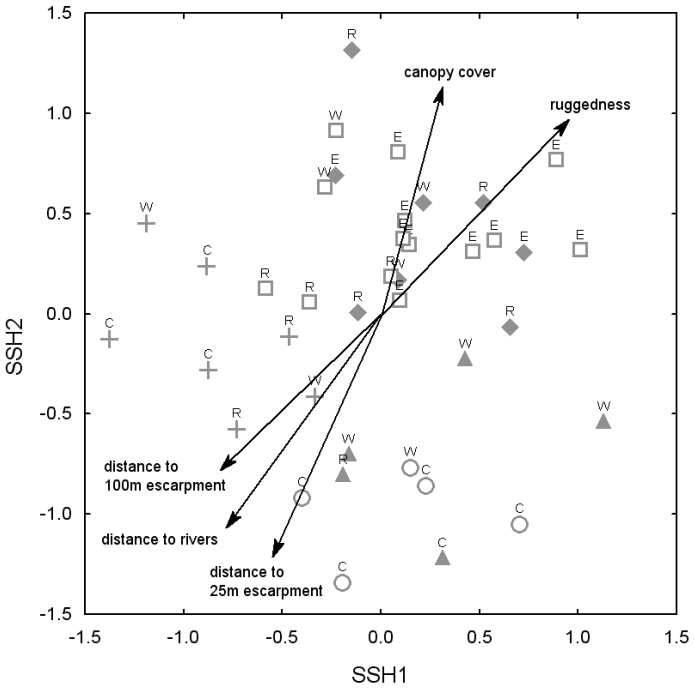
Fig. 2. Dendrogram showing classification of the 39 sites to form 5 groups. Grey lines indicate levels at which groups were delineated. Habitat types are shown adjacent to the site numbers.

Fig. 3. Ordination of sites by species composition. The ordination is displayed in two dimensions in graphs (a), (b) and (c) and three dimensions in (d). Significant environmental variables are plotted as vectors on the graphs. The two longest dimensions of the vectors were used to determine on which of the graphs vectors were plotted. Symbols represent groups (refer Figure 1) and letters represent habitats (R = Riparian, E = Escarpment, C = Coastal, W = Woodland). 3-dimensional stress value = 0.16.

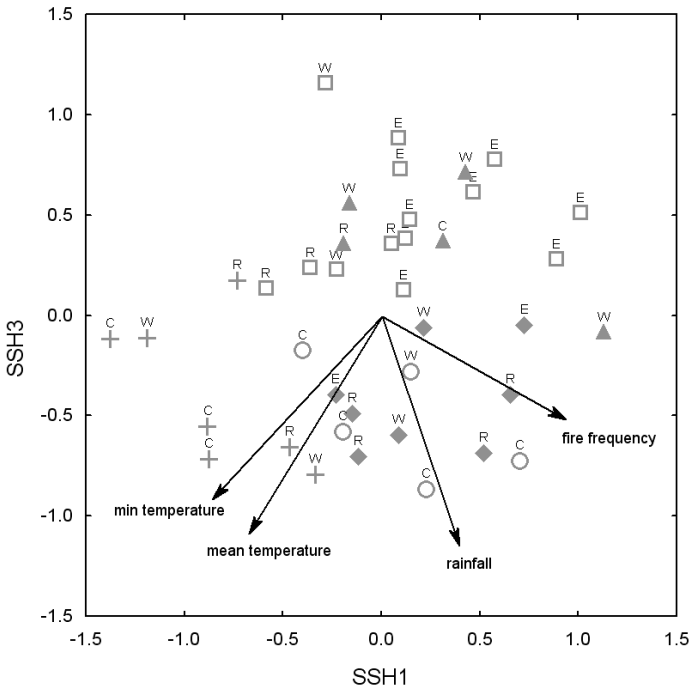
Fig. 4. Similarity in bat species composition between pairs of sites (using the Bray Curtis similaity index, refer text) plotted against the distance between each pair. Graph also displays the fitted linear regression line.


DARWIN
Arnhem Land
1400
1200
1000
800
600
NORTH
12°
15°
18°
100 50 0 100 200 300
Kilometres
W.A.
131°
134°
137°
N.T.
QLD.

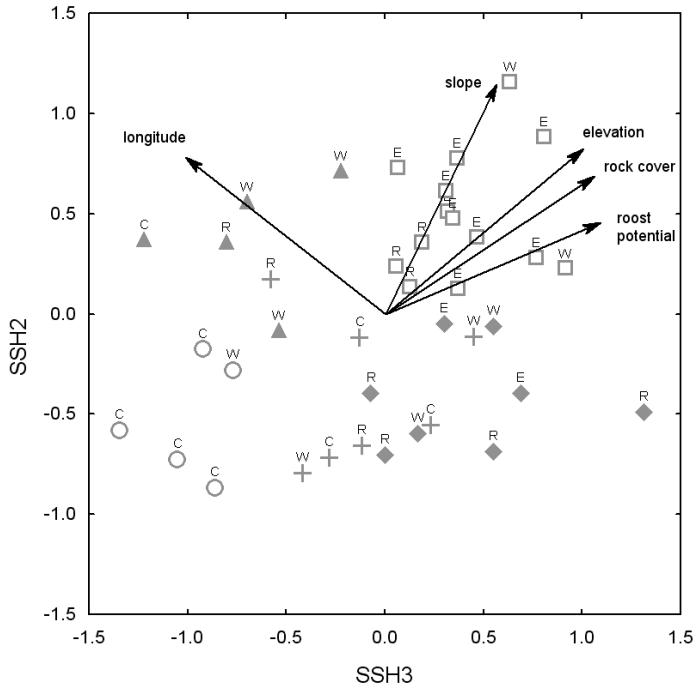

9 Escarpment
19 Riverine
43 Riverine
39 Escarpment
23 Riverine
7 Riverine
12 Woodland
10 Woodland
8 Escarpment
5 Woodland
30 Escarpment
6 Escarpment
44 Escarpment
20 Escarpment
15 Riverine
16 Escarpment
33 Escarpment
17 Escarpment
27 Escarpment
18 Woodland
29 Riverine
28 Riverine
3 Riverine
37 Riverine
42 Woodland
31 Coastal
13 Coastal
22 Coastal
21 Woodland
38 Woodland
32 Woodland
40 Woodland
35 Riverine
36 Coastal
25 Woodland
26 Coastal
46 Coastal
45 Coastal
41 Coastal
GROUP 1
GROUP 2
GROUP 3
GROUP 4
GROUP 5
20
40
60
80
100


canopy cover
ruggedness
distance to
100m escarpment
distance to rivers
distance to
25m escarpment
SSH2
SSH1
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5

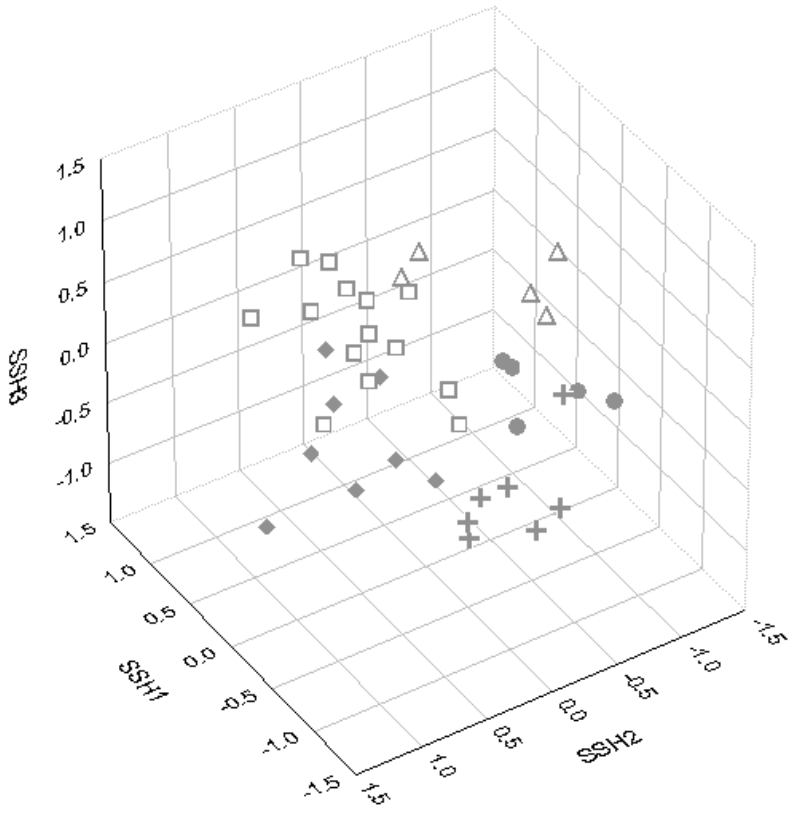
(a)


fire frequency
min temperature
mean temperature
rainfall
SSH3
SSH1
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5

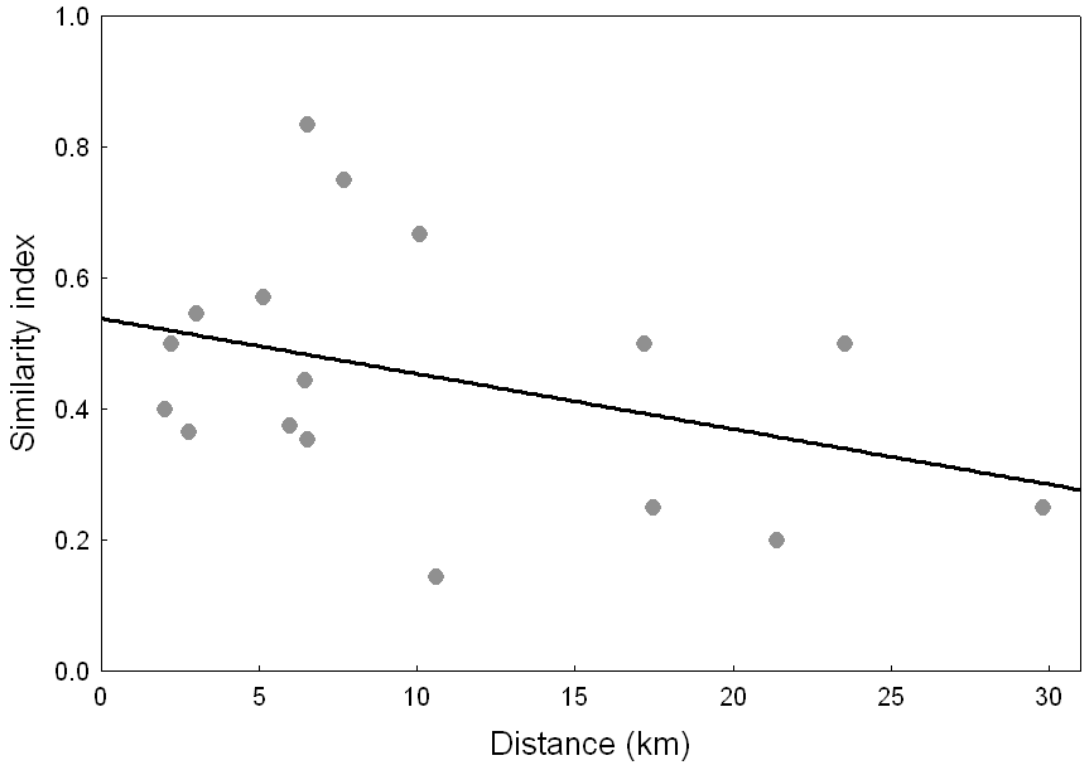
(b)


slope
elevation
rock cover
roost potential
longitude
SSH2
SSH3

(c)


SSH3
SSH1
SSH2

(d)


1.0
0.8
0.6
0.4
0.2
0.0
Similarity index
0
5
10
15
20
25
30
Distance (km)

Chapter 4.

Models of the habitat associations and distributions of insectivorous bats of the Top End of the Northern Territory, Australia.

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Models of the habitat associations and distributions of insectivorous bats of the Top End of the Northern Territory, Australia

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ABSTRACT

Generalised linear modelling (GLM) was used to develop habitat models for 25 of the 28 microchiropteran bat species that occur in the wet–dry tropics of the Northern Territory (the 'Top End'). Based on these models, a geographic information system (GIS) was used to derive probability of occurrence maps for each species. Almost all of the models identified a unique combination of environmental variables, and the resulting probability of occurrence maps revealed contrasting predicted distributions. The reliability of the models was variable. Based on model variances, 11 of the species models were considered to be weak (<30% of the deviance captured) whereas seven models were robust (>40% of the deviance captured). ROC plot analysis suggested all models were at least moderately robust (area under the ROC curve >0.7). Annual rainfall and habitat complexity were identified as significant variables in the majority of the models. All of the spatial models were combined to derive a probability map of species richness of microchiropteran bats in the Top End. This map shows greatest species richness in the north–west and north-central parts of the study area.

1. Introduction

Distributional modelling can be an important management tool if output is correctly interpreted and the limitations of the method employed are understood. Potential uses of distributional modeling include: identify features in the environment that may be important for a species survival so that appropriate conservation practices may be implemented; predict the likely effects of disturbance on species (logging, climate change); and identify likely areas of occurrence, particularly for areas that are logistically challenging to sample. In Australia, models of habitat associations and spatial distributions of mammals have been constructed mostly for small to medium sized terrestrial and arboreal mammals (Claridge and Barry, 2000; Vernes, 2003; Gibson et al., 2004; Kutt et al., 2004). In general, these models are based on the assumption that species distributions are determined by one or more biophysical factors. There are two potential limitations with this approach. First, the determining factors may operate at a scale that is different to available predictors (Lindenmayer et al., 1999; Catling et al., 2002). For example, attempts to model environmental associations of arboreal mammals in southern Australia were hampered by an inability to map fine scale habitat parameters (Mackey and Lindenmayer, 2001). Second,

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available species records may not provide a good representation of the species' habitat associations and distribution.

Few studies have used modelling to assess and quantify habitat associations of Australian microchiropteran bats (microbats) (Law et al., 1999). Further, modelling the geographic distribution of microbat species has not been previously undertaken in Australia and has been attempted in only a handful of studies in other countries (Jaberg and Guisan, 2001; Wang et al., 2003). Unlike other mammals, microbats are less likely to be as affected by smaller scale environmental influences as a consequence of the high vagility and relatively large home ranges of most species. In the wet–dry tropics of the Northern Territory, the distribution and habitat associations of microbats is poorly known. This is regrettable given that the region supports a rich microbat fauna (28 of Australia's 65 species, 15 of Australia's 20 genera (Churchill, 1998)), one endemic species (*Taphozous kapalgensis*) and both of Australia's monotypic genera (*Rhinonicteris*, *Macroderma*). Only one previous study (Milne et al., 2005a) has assessed habitat associations of microbats in the Top End. Their study detailed associations of microbat communities (as opposed to individual microbat species assessed here) within four contrasting environments and a number of predictor variables.

Several techniques are available for habitat modelling including generalised additive modelling, classification and regression trees, principal component analysis and canonical correspondence analysis (Guisan and Zimmermann, 2000). Generalised linear modelling (GLM) is one of the more popular methods for modelling species distributions because the technique can be easily implemented into a geographic information system (GIS) (Guisan and Zimmermann, 2000) and was the method chosen here. The aim of this study was to use GLM to develop simple models of the habitat associations at a landscape scale for each species of microbat that occurs in the Top End of the Northern Territory. From those models, spatial distribution maps were derived that depicted the probability of occurrence for each species. To achieve this, a database of all known microbat records for the wet–dry tropics of the Northern Territory was collated, as well as key environmental variables that have been digitally mapped for the entire region using a GIS.

2. Methods

2.1. Study area

The study area is the Northern Territory, north of 18°S (the 'Top End', Fig. 1). This area is within the wet–dry tropics of northern Australia and forms part of the vast tropical savannas. Milne et al. (2005a) provides a detailed description of the area which is summarised here. Mean weekly temperature ranges between 32 °C and 39 °C and rainfall is highly seasonal with mean annual rainfall between 360 mm and 1720 mm. The maximum elevation is 553 m. Forests and woodlands, dominated by *Corymbia* and *Eucalyptus* sp., cover 78% of the study area. On average over half (52%) of this region is burnt every year.

2.2. Environmental data

With one exception (*Rhinonicteris aurantius*: Churchill, 1991, 1994, 1995) there is little detailed information about the ecology of microbat species of the Top End or for Top End

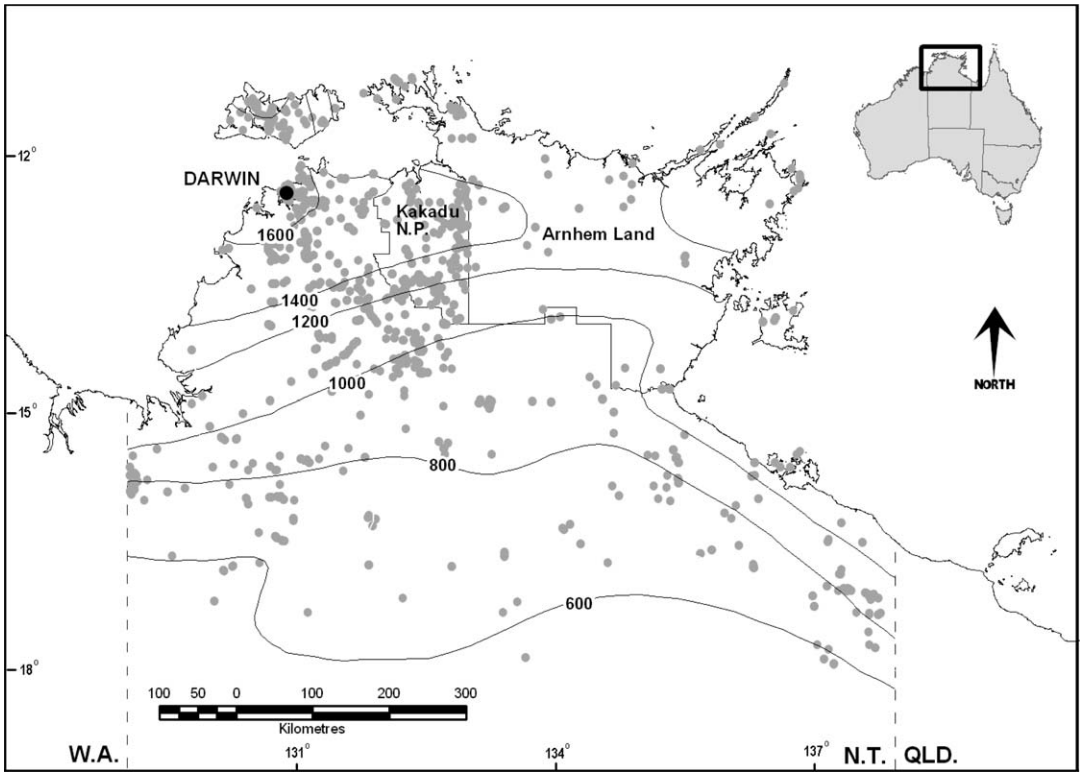

Fig. 1 – Map of the study area showing the distribution of all bat records used in this study and average annual rainfall isohyets (mm).

species that occur elsewhere across northern tropical Australia. It was therefore necessary to assess a diverse array of variables to identify potential useful predictors. However, given the small number of records for some species, only a subset of these variables could be used for modelling (Harrell, 2001). Consequently, variables were selected that a previous study of microbat assemblages in the Top End (Milne et al., 2005a and associated unpublished data) had shown to exhibit some statistical association with microbat distribution as well as four other environmental variables (soil texture, surface geology, vegetation communities, habitat complexity) that we considered might be important predictor variables at a landscape scale. Given the scope of this study, only those variables that had been consistently mapped, or could be derived, with GIS for the entire Top End were used.

Seventeen environmental variables were used (Table 1). Elevation, slope, aspect and topographic ruggedness (an index calculated from the range in cell values within a 3×3 cell neighborhood) were derived from a 3 s (c. 100 m × 100 m resolution) digital elevation model (DEM, provided by the Department of Defence). BIOCLIM (Houlder, 2000) was used to derive annual mean and maximum temperature, annual rainfall and rainfall seasonality (the standard deviation of weekly mean rainfall). Other variables included vegetation communities (Wilson et al., 1990) which were simplified into five broad categories (Table 1), surface geology (Bureau of Rural Sciences after Australian Geological Survey Organisation, 1991) and soil texture (Bureau of Rural Sciences after Commonwealth Scientific and Industrial Research Organisation, 1991). These three variables were also used to derive an additional composite variable, habitat complexity, which was an index calculated from the total number of different vegetation, geology and soil types within a 10 km × 10 km neighborhood. Locational variables included longitude, distance to coastline, distance to perennial watercourses and distance to 25 m and 100 m high "escarpments" (defined here as any adjacent DEM cells having an elevation difference of >25 m or >100 m). Latitude was not included because it was highly correlated with annual rainfall.

Table 1 – Environmental predictor variables used in the analysis

Variables	Units/values
Longitude	Decimal °E
Vegetation (5 classes)	Non-eucalypt forests ('nef'); eucalypt forests and woodlands ('ef–w'); low woodlands with tussock grass understorey ('lw–tg'); low woodlands with hummock grass understorey and grasslands ('lw–hg'); littoral and floodplain ('l–f')
Surface geology (6 classes)	Bedrock; quartz sand; sand, silt, clay and gravel; limestone; ferruginous, aluminous and siliceous ('fas') duricrust; clay, silt and minor sand
Soil texture (6 classes)	Uniform coarse; uniform medium; uniform fine; uniform cracking; gradational; duplex
Elevation	m
Slope	%
Ruggedness	m
Aspect (5 classes)	North, south, east, west, no aspect
Mean temperature	°C
Maximum temperature	°C
Annual rainfall	mm
Rainfall seasonality	mm
Habitat complexity	Index value (1–53)
Distance to water courses	km
Distance to coast	km
Distance to 25 m escarpments	km
Distance to 100 m escarpments	km

For predictive species habitat modelling, Austin (2002) recommends using a resolution equal to that of the species' home range. In the Top End, the home range of only one microbat species has been assessed (*Macroderma gigas*; Tidemann et al., 1985), therefore we chose to convert all variables to a resolution of 625 ha (2.5 km × 2.5 km). This area approximates the mean foraging and/or home ranges of several Australian microbat species (Dwyer, 1966; Tidemann et al., 1985; Jolly, 1990; Pavey, 1998; Herr and Klomp, 1999; Law and Anderson, 2000; Lumsden et al., 2002; Law and Chidel, 2004). Using GIS, each variable was converted to the larger resolution using bilinear interpolation.

2.3. *Microbat records*

Microbat records for the Top End were obtained from two primary sources. The first was the vertebrate fauna atlas that is maintained by the Northern Territory Department of Natural Resources, Environment and the Arts, which contains geolocated fauna records from a variety of sources including Museum records, biological surveys, the Northern Territory Biological Records Scheme, published literature and environmental literature. The second source was a series of microbat surveys conducted across the Top End as described in Milne et al. (2003, 2004, 2005a,b). Bats that were identified via echolocation recordings using Anabat detectors (Titley Electronics, Ballina, Australia), were only included if identified to the species level based on Milne (2002).

Both data sources were combined and approximately 2100 microbat records were rigorously assessed, particularly for locational accuracy. Several of the specimens held by the N.T. Museum were also checked where their provenance was doubtful. All spurious records were excluded from the analysis. In addition, two species that occur in the Top End, *Scotorepens greyii* and *S. sanborni*, can only be reliably separated using protein electrophoretic analysis (Churchill, 1998), so the likelihood of incorrect records due to misidentifications was high. Therefore records for these species were combined into one species 'group' and were treated as a single species in the analysis (even though in some areas their distributions are considered to be allopatric; McKenzie and Muir, 2000). Finally, to avoid autocorrelation errors and to match the resolution of the environmental data, microbat records were excluded so that there was only a single presence record per species in any 2.5 km cell used in the analysis.

GLM analysis requires both presence and absence data. The atlas contained presence-only data and could not be used

to indicate absences. Therefore, absence points for each species were derived by randomly selecting grid cells within the study area, excluding those cells that had presence records for the species. Because these are not 'true' absences, they are referred to as 'pseudo-absences'. An equal number of pseudo-absence points were chosen as presence records for each species. Three species (*Hipposideros diadema*, *H. stenotis* and *Taphozous kapalgensis*) were represented by ⩽20 presence records and in these cases, the number of pseudo-absence points was twice the number of absence points. Finally, the presence and pseudo-absence records for each species were incorporated into the GIS and values for all seventeen predictor variables were derived for each record.

2.4. *Modelling*

For each species, the correlation between predictor variables (using both presence and pseudo-absence records) was tested using Spearman rank correlation. Where pairs of variables had a correlation coefficient greater than 0.8, one of the pair was randomly excluded from further analysis. GLM (Crawley, 1993) was then used to develop predictive habitat models. A binomial error distribution and logit function was used with a backward stepwise process to derive the minimum adequate models. To evaluate the models, two methods were used. The first assessed the goodness of fit of the derived model by calculating the percent of the deviance captured (Crawley, 1993). The second method measured the association between the presence and pseudo-absence records by using receiver operating characteristic (ROC) plot analysis and calculating the area under the curve (Fielding and Bell, 1997). To assess for curvilinear relationships between dependant and predictor variables a squared term of each continuous variable was included for each model and the procedure described previously was repeated. Curvilinear relationships were deemed to exist if there was a significant improvement in the percentage of deviance captured. Finally, GIS was used to derive 'probability of occurrence' maps for each species using the logit transform

$$\text{probability} = \frac{e^{\text{model}}}{(1 + e^{\text{model}})}$$

The result is a digital spatial 'layer' for each species ranging in value from 0 (unlikely to occur) to 1 (highly likely to occur) across the Top End. Finally, again using GIS, each layer was added to derive a single map representing an index of predicted microbat species richness in the Top End.

3. Results

After the removal of spurious records and species data points within 2.5 km of each other, there was a total of 1591 records for 28 microbat species. Three species, *Scotorepens balstoni*, *Tadarida australis* (both considered to be rare vagrants) and *Saccolaimus saccolaimus* (a rare resident species), each had fewer than four records and modelling was not attempted for these species.

Records were distributed across the Top End; however, records were concentrated in the north–west of the study area and in Kakadu National Park, an extensive reserve in the north-central part of the study area. Relatively few records were obtained from the Arnhem Land region and across the south of the study area (Fig. 1).

Minimum adequate models were calculated using GLM for each of 23 species and one species group (*S. greyii*/*S. sanborni*) (Table 2). Fourteen of the 17 predictor variables occurred in one or more of the models whereas two variables, annual rainfall and habitat complexity, were the most commonly identified predictor variables occurring in 11 and 10 of the species models respectively. Overall, models were moderately robust with the area under the ROC curve for each model greater than 0.7, however the range in the percentage of deviance captured was large (12.2–80.2%). When tested for curvilinear relationships, the maximum improvement in the amount of deviance captured for any model was less than 4%, therefore there were unlikely to be significant curvilinear relationships between any microbat species and environmental variables. Maps of actual distribution and probability of occurrence plotted for each taxon display a variety of predicted distributions (Fig. 2). The 'species richness' map (Fig. 3) depicts a broad scale gradient in the predicted diversity of microbats in the Top End with high species richness in the northern and coastal areas and low species richness in the southern-central region of the study area. The areas with the highest likely species richness includes much of the Kakadu National Park and the north–west of the study area around Darwin (Fig. 3).

4. Discussion

GLM modelling identified unique habitat associations for almost all Top End bat species (i.e. each model contained a unique combination of environmental variables, Table 2) and the species probability maps (Fig. 2) display contrasting distributions of the predicted occurrence of each species. The exception was *Nyctophilus arnhemensis* and *Pipistrellus adamsi* that both had a positive association with annual rainfall. This result was not unexpected because, even though there has been little autecological research on microbats in the Top End, the microbat fauna contains a high number of genera (15) as well as an ecologically and morphologically diverse range of species. For example, body mass of the 25 species ranges from an average of 3 g for *P. westralis* to 100+ g for *M. gigas* (Churchill, 1998), which is close to the extremes of size found among the world's microbat species.

Based on the amount of explained deviance, 11 of the 24 GLM models were relatively weak (i.e. the models did not describe the occurrence of each species very well) with less than 30% of the deviance captured (Table 2). Five issues may explain the weaknesses in the models. (1) There was considerable 'noise' in the data, most likely resulting from locational inaccuracies of microbat species records. (2) The distribution of these species may be determined by environmental variables not quantified in the study (insect availability, roost hollow availability, vegetation species composition). (3) Five of the species (*Saccolaimus flaviventris*, *Taphozous georgianus*, *Chaerephon jobensis*, *Mormopterus beccarii* and *Miniopterus schreibersii*) are relatively large (>15 g), fast flying species (Strahan, 1995) that are capable of traveling long distances. Therefore,

Table 2 – Summary of results from generalized linear modelling (GLM) of habitat associations for microbats of the Top End

Species	Estimate	SE	P
Macroderma gigas (*n* = 87; *deviance* = 157.4; *deviance captured* = 34.7%; *area under ROC curve* = 0.86)			
Constant	−6.824		
Annual rainfall	0.006	0.001	***
Distance to coast	0.012	0.003	***
Distance to 25 m escarpments	−0.110	0.033	***
Hipposideros ater (*n* = 78; *deviance* = 142.6; *deviance captured* = 34.0%; *area under ROC curve* = 0.87)			
Constant	−5.347		
Annual rainfall	0.005	0.001	***
Distance to coast	0.011	0.003	**
Distance to 100 m escarpments	−0.016	0.004	***
Hipposideros diadema (*n* = 15; *deviance* = 11.6; *deviance captured* = 80.1%; *area under ROC curve* = 0.98)			
Constant	104.529		
Rainfall seasonality	−0.895	0.374	*
Distance to 100 m escarpments	−0.126	0.047	**
Hipposideros stenotis (*n* = 20; *deviance* = 47.0; *deviance captured* = 38.5%; *area under ROC curve* = 0.88)			
Constant	−1.423		
Habitat complexity	0.201	0.082	*
Distance to 25 m escarpments	−0.692	0.286	*
Rhinonicteris aurantius (*n* = 80; *deviance* = 161.8; *deviance captured* = 27.1%; *area under ROC curve* = 0.83)			
Constant	−28.843		
Maximum temperature	0.599	0.215	**
Annual rainfall	0.006	0.001	***
Habitat complexity	0.103	0.038	**
Saccolaimus flaviventris (*n* = 136; *deviance* = 307.5; *deviance captured* = 18.4%; *area under ROC curve* = 0.77)			
Constant	−3.454		
Annual rainfall	0.002	0.001	***
Habitat complexity	0.115	0.028	***
Soil texture (uniform coarse)	−0.128	0.280	ns
Soil texture (uniform medium)	0.586	0.526	ns
Soil texture (uniform fine)	−0.252	0.751	ns
Soil texture (uniform cracking)	−0.102	0.465	ns
Soil texture (gradational)	0.691	0.298	*
Soil texture (duplex)	aliased		
Taphozous georgianus (*n* = 127; *deviance* = 270.9; *deviance captured* = 23.1%; *area under ROC curve* = 0.81)			
Constant	−32.7851		
Longitude	0.247	0.075	**
Habitat complexity	0.120	0.028	***
Distance to 100 m escarpments	−0.015	0.003	***
Taphozous kapalgensis (*n* = 17; *deviance* = 14.5; *deviance captured* = 76.5%, *area under ROC curve* = 0.98)			
Constant	−111.944		
Rainfall seasonality	−0.355	0.185	ns
Mean temperature	5.685	2.262	*
Chaerephon jobensis (*n* = 117; *deviance* = 230.6; *deviance captured* = 28.0%, *area under ROC curve* = 0.81)			
Constant	1.188		
Vegetation (nef)	−0.267	0.739	ns
Vegetation (ef–w)	1.355	0.337	***
Vegetation (lw–tg)	−1.164	0.456	*
Vegetation (lw–hg)	0.487	0.381	ns
Vegetation (l–f)	aliased		
Soil texture (uniform coarse)	−4.047	549.873	ns
Soil texture (uniform medium)	−2.247	549.874	ns
Soil texture (uniform fine)	15.429	2749.367	ns
Soil texture (uniform cracking)	−3.757	549.874	ns
Soil texture (gradational)	−3.139	549.873	ns
Soil texture (duplex)	aliased		
Habitat complexity	0.194	0.038	***

Table 2 – *continued*

Species	Estimate	SE	*P*
Mormopterus beccarii (*n* = 25; *deviance* = 59.6; *deviance captured* = 12.2%, *area under ROC curve* = 0.75)			
Constant	−6.006		
Annual rainfall	0.004	0.002	**
Distance to coast	0.014	0.006	*
Mormopterus loriae (*n* = 24; *deviance* = 33.2; *deviance captured* = 50.6%, *area under ROC curve* = 0.90)			
Constant	1.934		
Distance to coast	−0.029	0.010	**
Miniopterus schreibersii (*n* = 67; *deviance* = 151.8; *deviance captured* = 18.3%, *area under ROC curve* = 0.78)			
Constant	−28.358		
Maximum temperature	0.620	0.228	**
Annual rainfall	0.006	0.001	***
Nyctophilus arnhemensis (*n* = 86; *deviance* = 164.6; *deviance captured* = 31.0%, *area under ROC curve* = 0.85)			
Constant	−5.110		
Annual rainfall	0.005	0.001	***
Nyctophilus bifax (*n* = 44; *deviance* = 88.6; *deviance captured* = 33.4%, *area under ROC curve* = 0.815)			
Constant	−72.492		
Longitude	0.513	0.156	**
Annual rainfall	0.004	0.001	***
Nyctophilus geoffroyi (*n* = 46; *deviance* = 104.4; *deviance captured* = 18.2%, *area under ROC curve* = 0.78)			
Constant	−3.298		
Habitat complexity	0.102	0.045	*
Annual rainfall	0.002	0.001	**
Nyctophilus walkeri (*n* = 75; *deviance* = 141.2; *deviance captured* = 32.1%, *area under ROC curve* = 0.86)			
Constant	−3.102		
Annual rainfall	0.004	0.001	***
Distance to 100 m escarpments	−0.013	0.003	***
Chalinolobus gouldii (*n* = 81; *deviance* = 201.4; *deviance captured* = 13.6%, *area under ROC curve* = 0.71)			
Constant	−0.561		
Elevation	−0.003	0.002	*
Habitat complexity	0.111	0.031	***
Chalinolobus nigrogriseus (*n* = 122; *deviance* = 290.5; *deviance captured* = 14.1%, *area under ROC curve* = 0.74)			
Constant	−3.608		
Vegetation (nef)	−1.036	0.719	ns
Vegetation (ef–w)	0.505	0.283	ns
Vegetation (lw–tg)	0.962	0.368	**
Vegetation (lw–hg)	0.701	0.382	ns
Vegetation (l–f)	aliased		
Annual rainfall	0.002	0.001	***
Habitat complexity	0.101	0.028	***
Myotis macropus (*n* = 37; *deviance* = 58.0; *deviance captured* = 49.47%, *area under ROC curve* = 0.91)			
Constant	5.200		
Soil texture (uniform coarse)	−7.750	972.268	ns
Soil texture (uniform medium)	−5.105	972.268	ns
Soil texture (uniform fine)	11.849	3511.683	ns
Soil texture (uniform cracking)	−7.919	972.268	ns
Soil texture (gradational)	−5.113	972.268	ns
Soil texture (duplex)	aliased		
Elevation	−0.009	0.004	*
Habitat complexity	0.236	0.085	**
Pipistrellus adamsi (*n* = 68; *deviance* = 109.0; *deviance captured* = 42.2%, *area under ROC curve* = 0.90)			
Constant	−7.438		
Annual rainfall	0.006	0.001	***
Pipistrellus westralis (*n* = 16; *deviance* = 11.7; *deviance captured* = 80.2%, *area under ROC curve* = 0.99)			
Constant	47.126		
Elevation	−0.210	0.107	*
Rainfall seasonality	−0.378	0.191	*

(*continued on next page*)

Table 2 – *continued*

Species	Estimate	SE	P
Scotorepens greyii/S. sanborni (*n = 118; deviance = 262.5; deviance captured = 19.8%, area under ROC curve = 0.71*)			
Constant	−4.915		
Soil texture (uniform coarse)	−0.061	0.318	
Soil texture (uniform medium)	0.982	0.494	*
Soil texture (uniform fine)	−1.242	0.690	ns
Soil texture (uniform cracking)	−1.174	0.543	*
Soil texture (gradational)	0.740	0.372	*
Soil texture (duplex)	aliased		
Surface geology (bedrock)	3.664	653.980	ns
Surface geology (quartz sand)	2.424	653.980	ns
Surface geology (sand, silt, clay and gravel)	4.846	653.980	ns
Surface geology (f, a and s duricrust)	3.191	653.980	ns
Surface geology (limestone)	0 (no presence records)		
Surface geology (clay, silt and minor sand)	aliased		
Habitat complexity	0.135	0.031	***
Vespadelus caurinus (*n = 68; deviance = 136.3; deviance captured = 27.7%, area under ROC curve = 0.82*)			
Constant	−2.119		
Vegetation (nef)	0.834	1.057	ns
Vegetation (ef–w)	−0.088	0.433	ns
Vegetation (lw–tg)	−0.6723	0.537	ns
Vegetation (lw–hg)	1.148	0.515	*
Vegetation (l–f)	aliased		
Habitat complexity	0.104	0.039	**
Ruggedness	0.028	0.009	**
Vespadelus finlaysoni (*n = 30; deviance = 42.6; deviance captured = 46.0%, area under ROC curve = 0.87*)			
Constant	−2.385		
Ruggedness	0.087	0.028	**

Parameter estimates and explanatory power (percent of deviance explained) of the minimum adequate model and the area under the ROC curve are shown for each species. For categorical variables, the estimate refers to the difference from the 'aliased' category. (ns, not significant).
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

it is possible the grid cell resolution of 2.5 km by 2.5 km was too small for modelling these species appropriately. (4) Errors were present in the data (an issue explored later in this discussion). (5) The species are habitat 'generalists' that are capable of using a wide range of environments. Caution should be used when using the term 'generalists'. In a study in Victoria, Australia, Lumsden et al. (2002) demonstrated that two species considered to be 'generalists' (that also occur in the Top End; *Chalinolobus gouldii* and *Nyctophilus geoffroyi*), do have specific roosting habitat preferences.

The modelling revealed two variables to be particularly important in determining microbat distributions. Annual rainfall and habitat complexity were identified as significant variables, either singularly or together, in 19 of the 24 species habitat models (Table 2). In all 19 models, both variables had positive coefficients so that the likelihood of species occurrences increased with both increasing habitat complexity and rainfall. The annual rainfall gradient for the Top End is pronounced, ranging from 360 mm in the south to 1720 mm in the north (based on Houlder, 2000, Fig. 1), and has an overriding influence on the broad distribution of Top End flora and fauna (Bowman et al., 1988; Whitehead et al., 1992; Woinarski et al., 1992, 2000). Therefore, it is likely that rainfall would also have a similar influence on the microbat fauna.

Habitat complexity was identified as a significant positive predictor variable in 11 of the models. Habitat complexity is an integrative index of the number of different 'habitat' types within the area (based on vegetation, soils and geology mapping). Areas of high complexity generally correspond to areas with riverine environments and variable relief (i.e. rocky areas, particularly escarpments). Although not assessed directly, the study mentioned previously by Milne et al. (2005a) identified habitat complexity as significant in terms of species richness, (highest in close proximity to rivers and adjacent areas) and one of the species assemblages (that was associated with escarpments and adjacent areas). Milne et al. argued that these areas provide a diversity of environments and thus support a range of species with different foraging strategies. This explanation accounts for the relationship between species assemblages and habitat complexity but it does not clarify an association at the species level.

The 11 species that showed an association with habitat complexity belonged to a range of genera and foraging guilds (as defined by Milne et al., 2004). One possible explanation for the association of individual species with habitat complexity is provided by the work of Woinarski et al. (2005). In terms of vegetation, soils and topography, the north Australian landscape is broadly homogeneous (i.e. flat, and relatively featureless), and rainfall is highly seasonal with almost all precipitation occurring from November to April, causing an enormous annual fluctuation in available resources.

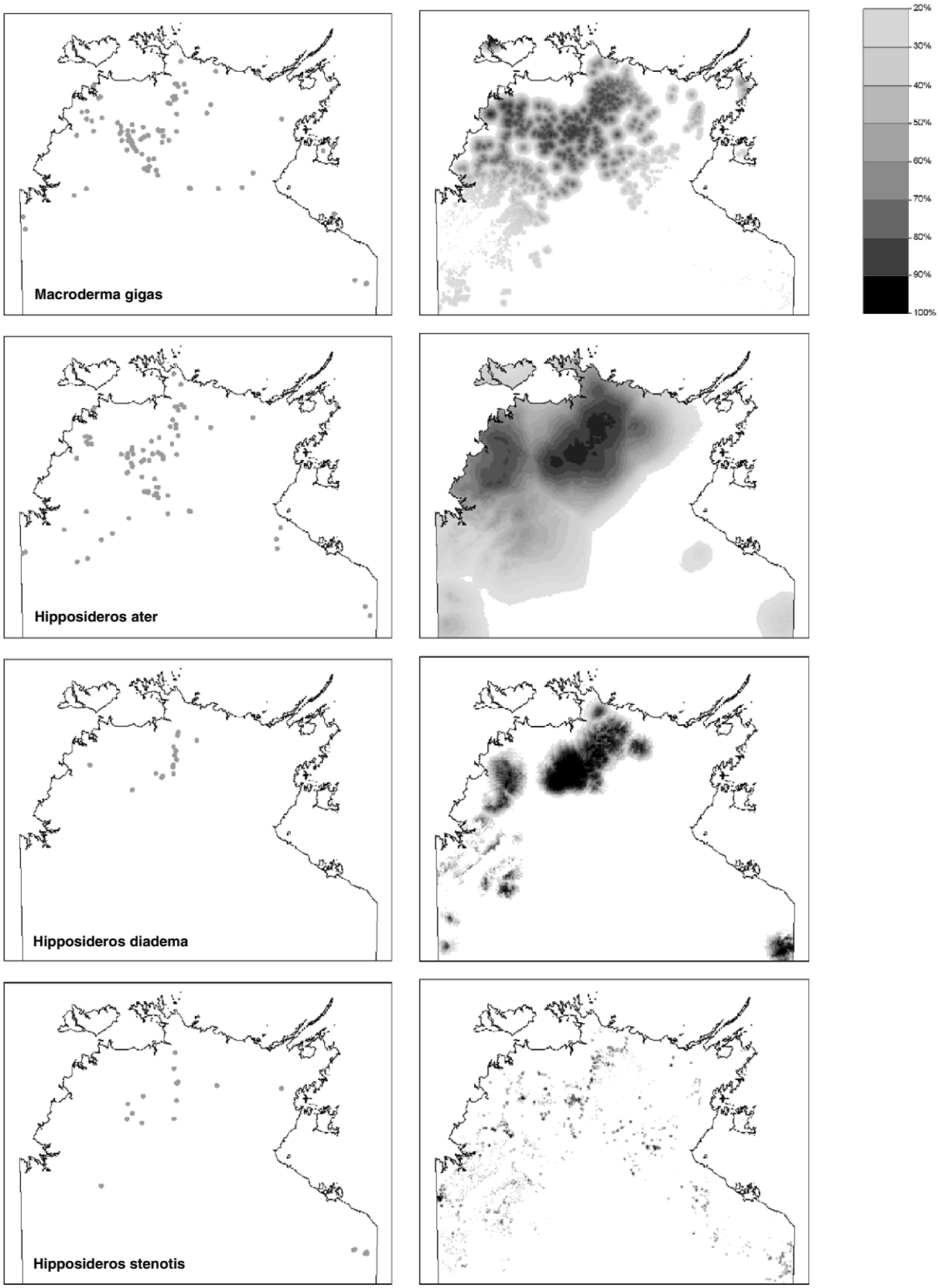

Fig. 2 – Maps of actual distributions (left) and probability of occurrence (right) of Top End bat species based on the minimum adequate model (Table 2). Only areas with a probability of occurrence of >20% are shaded. The shading scale is shown adjacent to the first map.

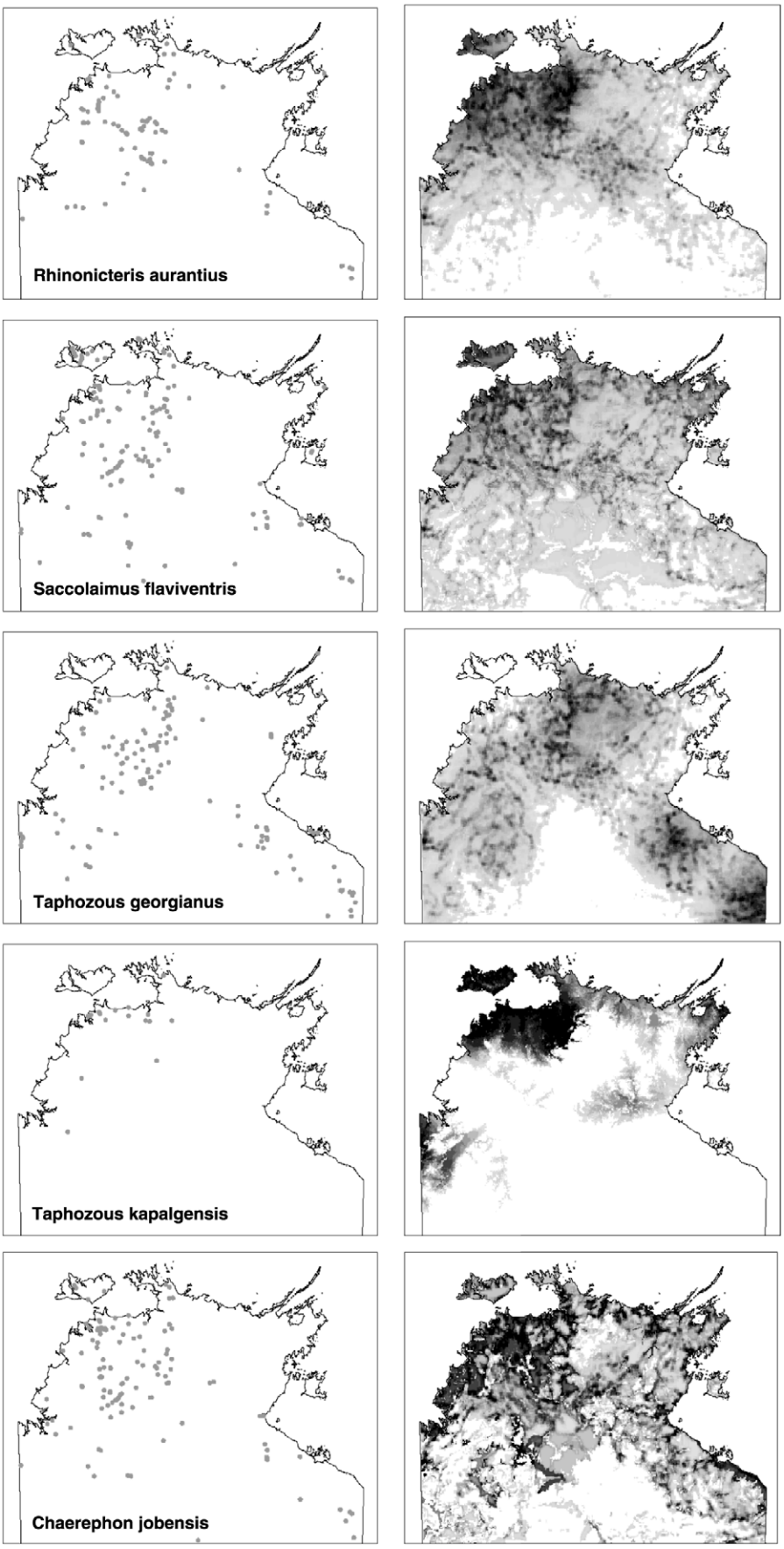

Fig 2 – ***continued***

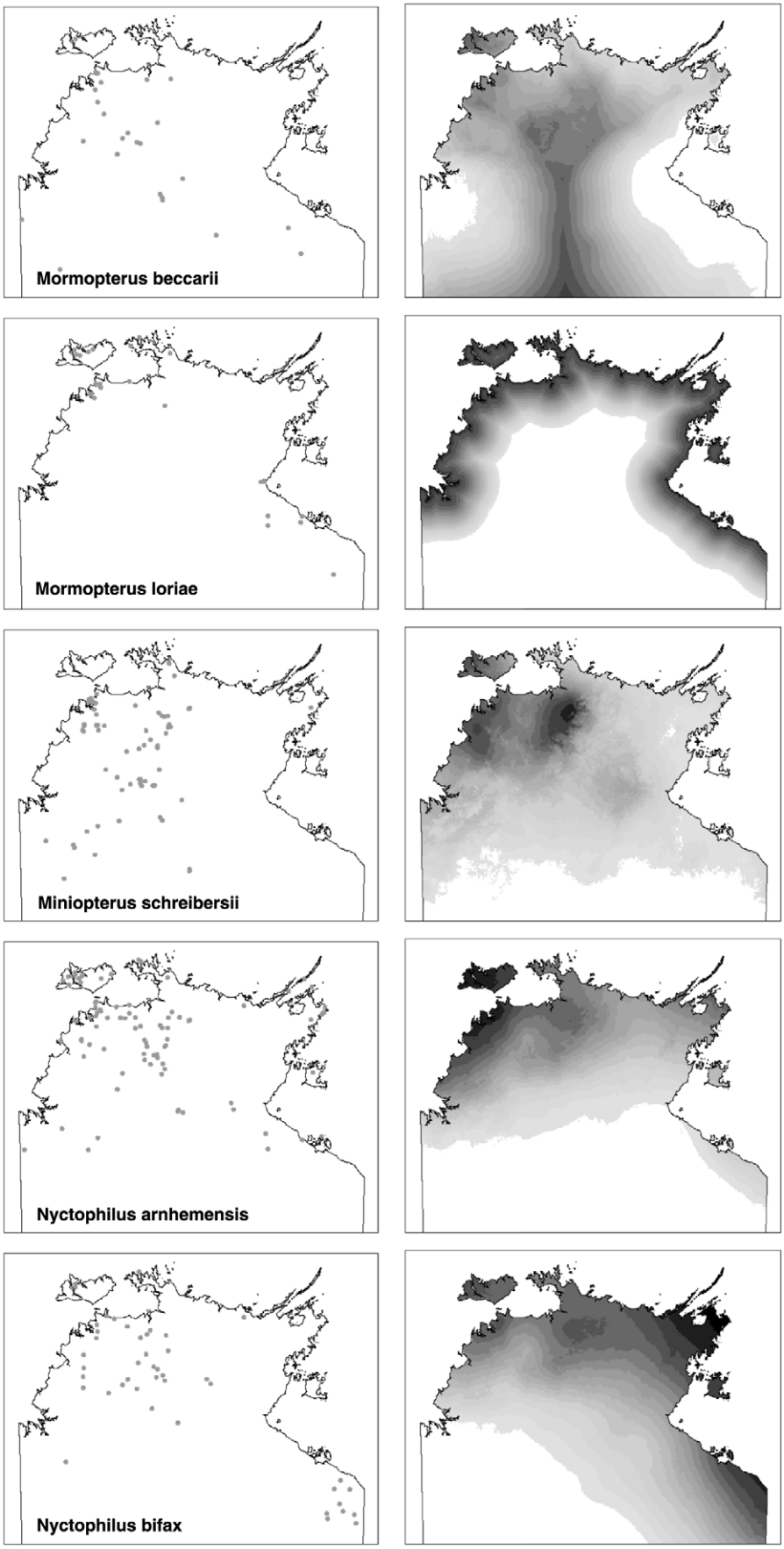

Fig 2 – *continued*

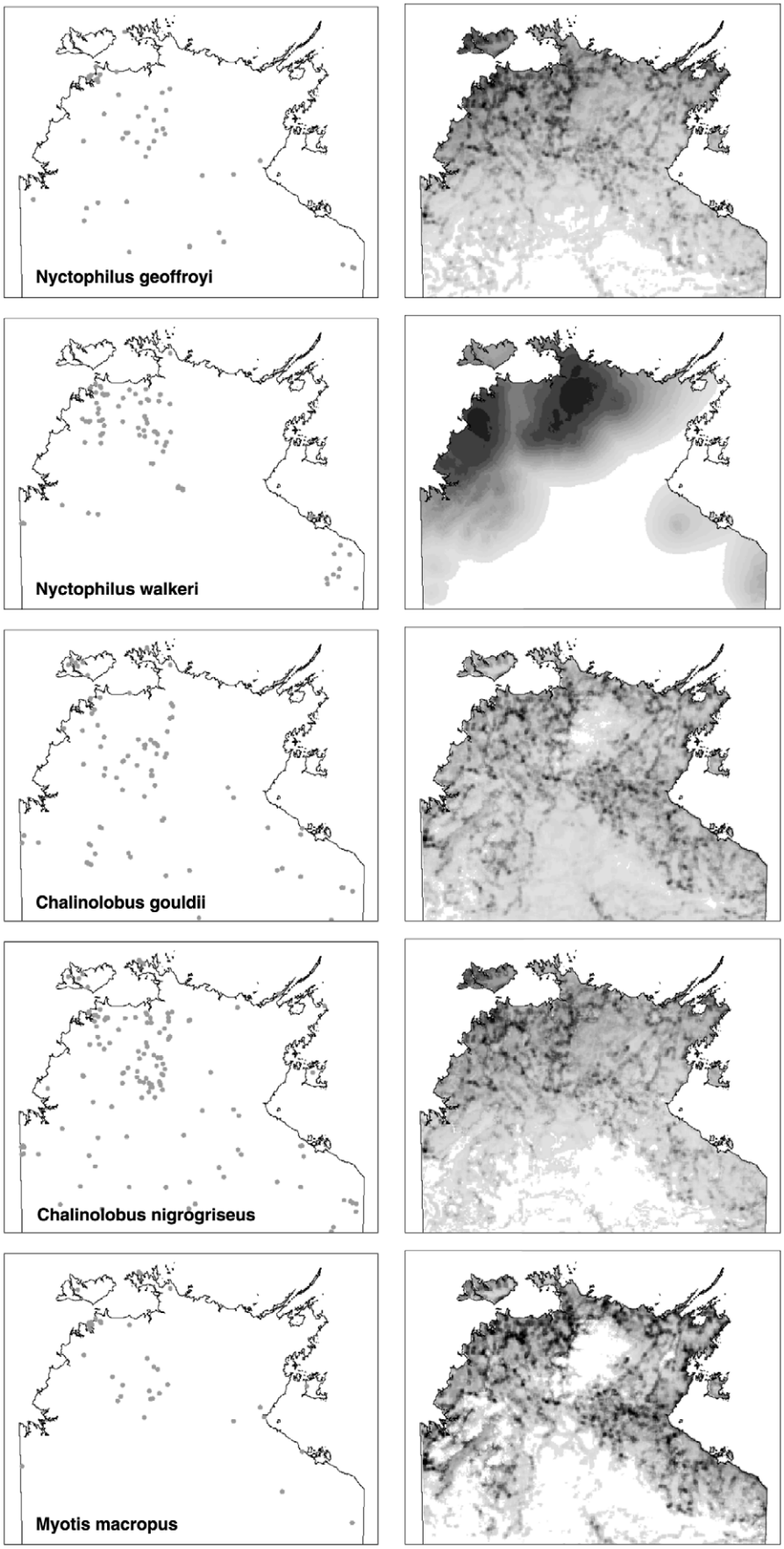

Fig 2 – *continued*

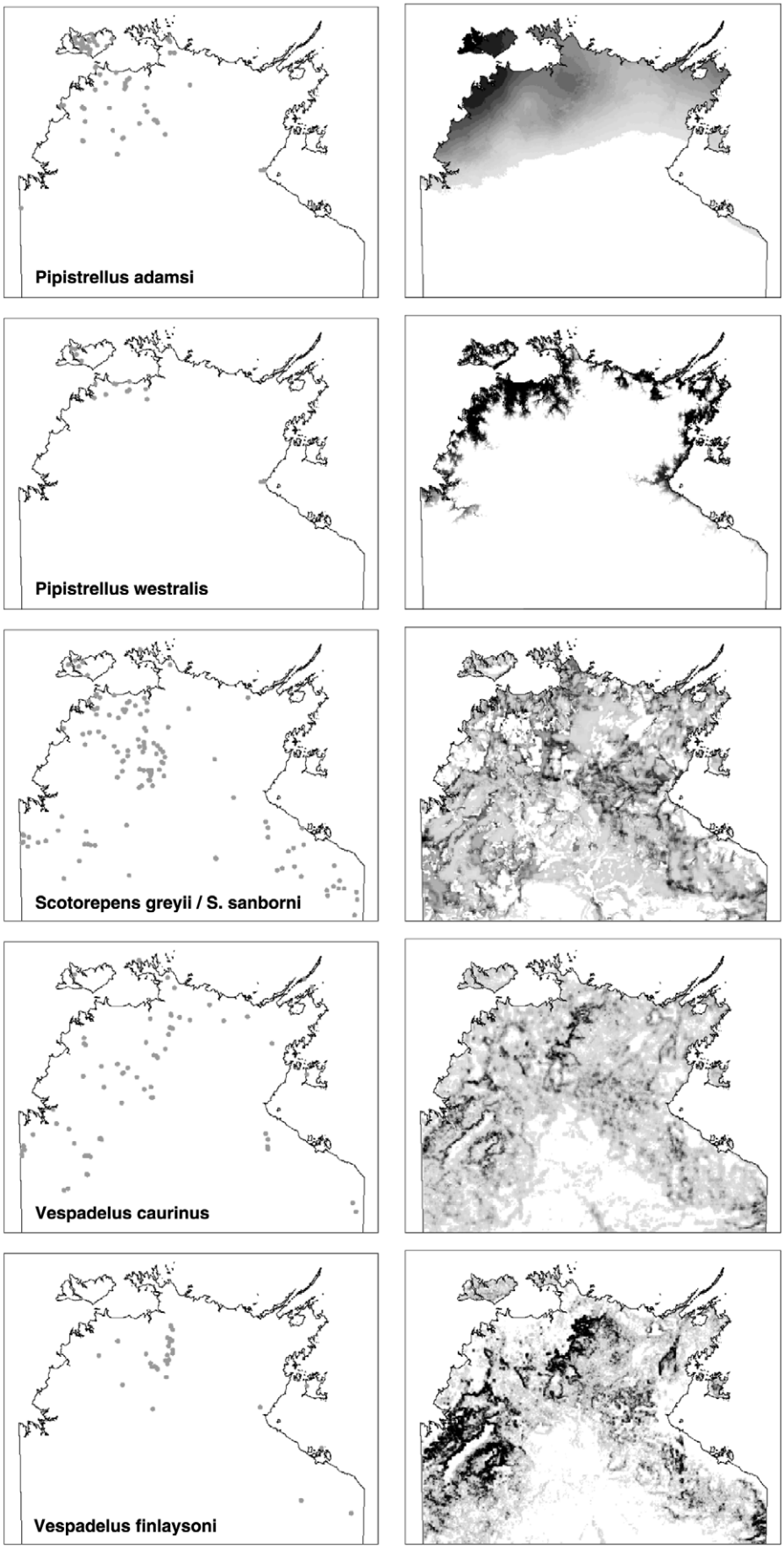

Fig 2 – *continued*

Therefore, when resource shortages occur, particularly during the northern tropical 'dry' season, these are likely to be repeated across entire land systems. Woinarski et al. argued that subtle differences in the landscape (in this case riverine environments and escarpment areas) may provide different resources, or resources that fluctuate slightly out of phase with the rest of the landscape. One other factor that may have produced the significant association with habitat complexity is that surveys are often conducted at areas with water, as microbats will usually drink after emergence at dusk. Therefore, the actual locations for microbat records may have been focused in and around riparian zones (areas identified with high habitat complexity). In addition, five of the 11 species that showed an association with habitat complexity are considered to be obligate cave-roosting species. Caves are typically found in areas associated with rocks and escarpments and therefore, areas with high index values for habitat complexity as well.

Modelling results for some species are of particular interest. The minimum adequate model for *Hipposideros stenotis* revealed strong associations with both short distances to 25 m escarpments and high habitat complexity although the model was only moderately robust (38.5% of deviance captured, Table 2). The resulting probability of occurrence map shows relatively small and isolated patches where this species is most likely to occur (Fig. 2). Almost nothing is known about the ecology of this species and there are only 28 known records (only five of which have been obtained in the last 10 years; Department of Natural Resources, Environment and the Arts vertebrate fauna atlas). The occurrence map identifies potential areas for further surveys and suggests that this species may be naturally rare and with a restricted distribution.

The model for *Taphozous kapalgensis* revealed an association with low rainfall seasonality and a strong association with high mean temperatures (Table 2). The model was also highly robust (76.5% of deviance captured). The resulting probability of occurrence map shows *T. kapalgensis* to have a substantially expanded range compared to its currently known distribution which is highly restricted. The probability map also identifies the Roper River region as an area where the species is likely to occur, although there are no confirmed records in this area. This is an interesting result as Aboriginal residents have stated that *T. kapalgensis* occurs there (McKean and Thomson, 1995) and echolocation calls suspected to be those of *T. kapalgensis* have also been recorded in the Roper River region (Milne et al., 2003).

Hipposideros diadema and *P. westralis* are noteworthy because models for both of these species were highly robust (80.1% and 80.2% of deviance captured respectively) and display interesting predicted distributions. *H. diadema* is known from just 22 records (Department of Natural Resources, Environment and the Arts vertebrate fauna atlas). The probability of occurrence map identifies two main areas in the northwest of the study area where this species is likely to occur. The most westerly of these areas has been largely unsurveyed (Fig. 1) and coincides with one locality record for *H. diadema* (McKean and Hertog, 1979, Fig. 2) in a now abandoned roosting site (Churchill, 1998). Given the conservation status of this species ('vulnerable'; *Territory Parks and Wildlife Conservation Act 2000*) this area should be targeted for future surveys. *P. westralis* has an association with areas of low rainfall seasonality and low elevation, particularly the latter (Table 2). This combination of variables suggests a likely distribution for *P. westralis* that is discontinuous around the Top End's northern coastline (Fig. 2). These areas of low elevation are typically associated with floodplains, mangroves and swamps.

The predicted total microbat species richness (Fig. 3) largely reflected the two variables that were identified as significant in the majority of the species models; rainfall and habitat complexity. However, two areas stand out as having the highest species richness: the Kakadu region and the north–west of the study area around Darwin. As stated previously, high index values for habitat complexity are usually associated with rivers and escarpments. The major topographic feature of Kakadu is an extensive sandstone escarpment system. It also has a number of major and minor river systems associated with a range of vegetation types. This combination provides roosting opportunities for both cave and tree roosting species and probably accounts for the high measure of species richness in this area. It is also propitious that most of this area is under a conservation reserve. However, we also suspect this result is partially attributed to the unusually large survey effort in these two areas (particularly in the north–west around Darwin; Fig. 1). Across the rest of the study area, microbat sampling is sparse and patchy. Further records are required in poorly sampled areas, mainly in the north–east and south of the study area, for this result to be verified.

4.1. *Potential sources of error*

Several potential sources for errors and weaknesses exist in the species models. It is important to consider these in order to verify the effectiveness of the methodology and the accuracy of any conclusions generated by this study.

For most records, the nature of the Department of Natural Resources, Environment and the Arts databasing system meant that the activity of the species at the time of detection was not recorded, so it is not known whether microbats were foraging or roosting when they were detected and recorded. This information could be important in interpreting the results because microbats can use different habitats for roosting and foraging (Lumsden et al., 2002; Law and Chidel, 2004). This partitioning of habitat is unlikely to affect tree-roosting species because roost trees are rarely observed (pers. obs.) therefore most records were probably obtained in foraging areas. However, records for cave-roosting species are regularly obtained at both roosting sites and foraging areas. If the roosting and foraging habitats for these species are different, the habitat models may be confounded and present a less clear picture than if foraging and roosting records were able to be assessed independently.

Why did we use pseudo-absences instead of true absences? Only a limited number of microbat surveys have been conducted in the Top End (Friend and Braithwaite, 1986; Menkhorst and Woinarski, 1992; Woinarski et al., 1992; Milne et al., 2005a) so that the total number of survey sites for which true presence–absence data could be derived was small and

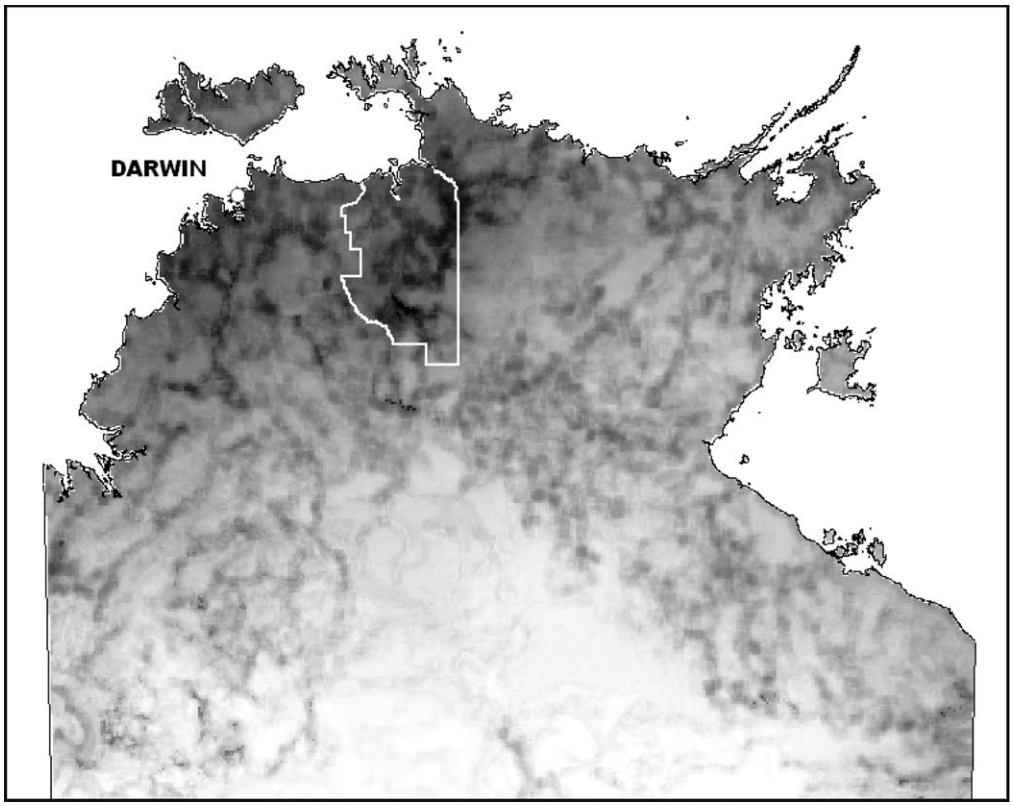

Fig. 3 – Map of the predicted relative microbat species richness in the Top End of the Northern Territory based on the combined probability of occurrence maps for all species (as shown in Fig. 2). Darker areas represent higher relative species richness. The white boundary line indicates Kakadu National Park.

the extent of the survey areas were not representative of the geographic range of the study area. Pseudo-absence data has been incorporated in other studies that used GLM modelling (Hirzel et al., 2001; Huettmann and Linke, 2003) and, for species distribution modelling such as ours, has been shown to be a more robust method of analysis than techniques that require presence-only data (such as ecological niche factor analysis, Engler et al., 2004).

Alternative approaches have been proposed to improve the quality of pseudo-absence data. In a study of ferns in New Zealand, Zaniewski et al. (2002) used GAM to firstly select areas that encompassed the environmental characteristics for all fern sampling sites combined. Pseudo-absence points were then randomly chosen but weighed towards these areas. This weighted pseudo-absence approach resulted in models that were more similar to models that used 'true' absence data than the models that incorporated randomly selected absences alone. This was attributed to sites being located in areas with similar environmental attributes as the 'true' absence data (Zaniewski et al., 2002). This approach was not used in this study for the following reasons. Unlike the study by Zaniewski that used one sampling method, microbat data were collected using a variety of methods (harp-traps, mist-nets, echolocation recordings, shot-sampling, cave searches and incidental observations). Each method has biases for detecting different microbat species (Francis, 1989; Kuenzi and Morrison, 1998; O'Farrell and Gannon, 1999). Data were also obtained from the literature and museum records that provide no indication of species absences. In addition, bat activity and detection rates are highly variable, both temporally and spatially (Bergallo et al., 2003; Patriquin et al., 2003; Milne et al., 2005b). Additionally, we are attempting to model species distributions at a relatively coarse scale, using many predictor variables that vary gradually across large areas. We therefore did not believe it was appropriate to limit the environmental envelope from which pseudo-absence points could be selected, or that we could do this reliably with the data available.

Several species of Top End bats have undergone taxonomic revision in recent years, namely *V. caurinus* and *V. finlaysoni* (Kitchener and Caputi, 1985); *P. adamsi* and *P. westralis* (Kitchener et al., 1986); and *S. greyii* and *S. sanborni* (Kitchener et al., 1987). For this study, the status of *S. greyii* and *S. sanborni* is not an issue because all records for these two species were combined and treated as a single species group (refer methods). For *Vespadelus* and *Pipistrellus*, most of the museum specimens obtained prior to the taxonomic revision of these genera have been gradually re-assessed and corresponding database records have been updated. However, records obtained prior to the publication of the revisions for these genera that cannot be verified by museum specimens (predominantly 'catch-and-release' observations) may have been misattributed and are unable to be substantiated.

The habitat association and distribution models developed here provide a measurable estimate of the likelihood of occurrence of species in areas that are difficult to access

and therefore are a useful and cost effective management tool at a scale suitable for broad scale planning and management (bioregional planning and assessment, reserve selection and design). However, this is the first step in what should be a two stage process. To examine the accuracy of these models (predictions), efforts should be directed to their validation by conducting targeted field surveys, particularly given the poor performance of the models for some of the species of Top End microbats Also, the models are based on records that have been collected predominantly over the past 50 years. The models do not take into account declines in mammal populations that have occurred during this period (e.g. Braithwaite and Griffiths, 1994; Woinarski et al., 2001; Pardon et al., 2003; Watson and Woinarski, in litt.). Therefore, we recommend that the models (and therefore the probability of occurrence maps) should be regarded as 'maximum-likelihood' models and should be viewed with some circumspection.

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Chapter 5.

Temporal patterns of bats in the Top End of the Northern Territory, Australia

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TEMPORAL PATTERNS OF BATS IN THE TOP END OF THE NORTHERN TERRITORY, AUSTRALIA

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Temporal activity patterns of microchiropteran bats were assessed at 4 scales (hourly, nightly, monthly, and yearly) in the Top End of the Northern Territory, Australia, in relation to biotic (insect availability) and abiotic features in the environment. At the hourly scale we found activity declined throughout the night and was most closely associated with temperature. At the nightly scale we found associations between bat activity, moonlight, and temperature as well as a complex association with both moon phase and time of night. At the monthly scale we found bat activity increased dramatically in October and provide evidence that this was triggered by a combination of changing climatic factors that occur at this time of year in the Southern Hemisphere tropics. At the yearly scale, no overall difference was found in bat activity between years ($n = 4$) and no associations were found with climatic variables. At all temporal scales we found no significant associations or differences in species richness and only weak or no associations with insect availability. There also was a high degree of variation in bat activity across all temporal scales that have significant implications for surveying and monitoring microbats.

Key words: activity patterns, AnaBat, bats, insects, lunar, Microchiroptera, northern Australia, temporal, Top End, weather

Understanding the spatial ecology of bats has been an important step to ensure effective conservation and management of this diverse and widespread mammalian group. Spatial information is available at species (distribution and abundance), landscape (location of key resources such as feeding, roosting, and maternity sites), and local (home-range size and habitat associations) scales (e.g., Aguirre et al. 2003; Law et al. 1999; Law and Dickman 1998; Lumsden et al. 1995; Milne et al., in press; Russ and Montgomery 2002). However, most research has not taken into account temporal variations associated with spatial data sets. Temporal variation is driven by both regular (seasonal and lunar cycles) and unpredictable (rainfall and disturbance regimes) factors that influence weather, availability of resources, or habitat condition. As a consequence, the suitability of environments as habitat for bats varies on a temporal scale. In addition, the effects of temporal variation will differ across bat species and assemblages as well as between habitats and regions. Therefore, researchers must have a clear understanding of the consequences of temporal variation when carrying out ecological studies on bats to ensure effective interpretation of results and the success of subsequent management and conservation outcomes.

Ultrasonic echolocation recording is a relatively new and effective method to detect and survey bats. Although use of this method is capable of generating large data sets that are ideal for statistical analysis, large variations in the data also can arise. Numerous studies have identified sources of variation associated with echolocation recordings that should be managed in order to reduce such variation (e.g., detector orientation and surrounding habitat structure [Weller and Zabel 2002], recording media [Milne et al. 2004], differences in sensitivities between multiple detectors [Larson and Hayes 2000], and interobserver variation in call identification). However, variations associated with temporal factors often are unrecognized and may be more difficult to control or account for.

Here we report the results of a study that used ultrasonic detectors and conventional trapping techniques to examine temporal patterns of microchiropteran bats (microbats) in the wet–dry tropics of the Northern Territory, Australia. Specific aims of the study were to assess bat detectability at 4 temporal scales (hourly, nightly, monthly, and yearly); to examine variations in bat activity and species compositions at different temporal scales; to explore the relationship between variation in bat activity, composition, or both and several predictor variables including climate, insect availability, and lunar influences; and, finally, to examine the implications of our results for microbat

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survey and management within the study region. Our study is the 1st temporal assessment of a regional microbat fauna, taking into account both biotic and abiotic features of the environment, to be conducted at 4 temporal scales.

Materials and Methods

Bat calls were recorded with AnaBat detectors (Titley Electronics, Ballina, Australia) and supplemented, where appropriate, with capture records made with harp traps, mist nets, and shot sampling. Animal sampling procedures were approved by the Northern Territory Animal Ethics Committee and were in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). AnaBat call sequences (call passes) were identified according to Milne (2002) by 1 observer (DJM) to avoid interobserver bias. To assess temporal variation at a range of scales, bats were sampled at 4 temporal scales: continuously for 2 nights at several sites (hourly); continuously for 3 lunar cycles at 2 sites (nightly); for 2 nights at 2 sites every month over an entire year (monthly); and for 2 nights at 4 sites each October for 4 years (yearly). Further details for each timescale are provided below. Some sites were used to assess more than 1 temporal scale.

Hourly sampling.—Sampling was conducted at 49 sites for either 1 (23 sites) or 2 consecutive (26 sites) nights (total of 75 sample nights) between September 2000 and June 2003. Sites were located across the wet–dry tropics of the Northern Territory, Australia, north of 18°S (the Top End). A description of this area is provided by Milne et al. (in press). Bats were recorded by using either static analogue or digital recording methods (i.e., AnaBat detectors connected to either a tape recorder or laptop computer—Milne et al. 2004) or with AnaBat II bat detectors connected to AnaBat CF Storage Zcaims. Recordings were made continuously throughout the night at each site.

Nightly sampling.—Bats were recorded at 2 sites by using AnaBat II bat detectors connected to AnaBat CF Storage Zcaims. Detectors were mounted 1.4 m above the ground and elevated to approximately 30° above horizontal. Site 1 was located approximately 22 km east of Darwin, Northern Territory (12°28′S, 131°04′E) on a low ridge in woodland dominated by species of *Eucalyptus*. Bats were recorded continuously from 10 August to 24 October 2002 (3 complete lunar cycles), except for 2 nights (10–11 September) when recording failed (total of 74 detector nights with recording). Site 2 was located approximately 36 km southeast of Darwin (12°38′S, 131°06′E) adjacent to an annual creekline in shrubby woodland dominated by *Melaleuca*. Bats were recorded continuously from 19 September to 22 October 2002 (1 complete lunar cycle), except for 5 nights (10–14 October) when recording failed (total of 29 detector nights with recording). Both sites were located on the margin of low-density rural housing. Detectors were positioned within a clearing (~1 ha) and pointed toward areas of undisturbed vegetation approximately 10 m distant. No rainfall was recorded during either sampling period.

Data for temperature, relative humidity, barometric air pressure, and cloud cover, recorded every 3 h at Darwin Airport, were obtained from the Australian Commonwealth Bureau of Meteorology (in litt.). Details for moon phase, moonrise, moonset, sunrise, and sunset were obtained from Geoscience Australia (http://www.ga.gov.au/nmd/geodesy/astro/). Data for flying nocturnal insects were collected at the same times and locations that bats were recorded at the hourly sampling sites. Insects were collected on 1 of the 2 sampling nights by using the methods described in Milne et al. (in press) and ambient temperate at 2200 h also was recorded at each site by using a digital thermometer (TempTec, Australian Geographic, Terry Hills, New South Wales, Australia).

Monthly sampling.—Sampling was conducted at 2 sites (4 km apart) in tall *Eucalyptus* woodland within the Howard Springs Hunting Reserve, approximately 30 km east of Darwin (12°23′S, 131°09′E). One site was located on a low ridge line, the other in an open drainage depression. Sites were sampled concurrently for 2 nights every month (midmonth) for 1 year from December 2001 to November 2002 (total 46 sample nights). In 1 month (January) both sites were sampled for 1 night only because of monsoonal rain. AnaBat II detectors were positioned in the same location and pointed in the same direction each time. Calls were recorded by using static digital methods (see Milne et al. 2004).

At both sites, an ultraviolet light trap (Australian Entomological Supplies, Bangalow, Australia) was used to attract insects for sampling. The light trap was positioned approximately 100 m from the AnaBat detector so as not to disturb bats from natural flight habits in the vicinity of the detector. The light trap was elevated approximately 1.4 m above the ground and located in the same position each time. Both sites were sampled for insects for 1 night (on alternate nights) every month from April to November 2002. For the purposes of both the monthly and hourly assessment, flying nocturnal insects were collected from the light trap every hour after dusk for the entire night (16 sample nights, 176 samples). Ambient temperature was recorded by using a digital thermometer (described previously) at the end of every hour when insects were collected.

Yearly sampling.—Sampling was conducted at 4 sites for 2 successive nights in October for 4 years between 2000 and 2003 (16 samples). Sites were located in coastal monsoon rainforests and mangroves near Darwin (12°18′S, 131°01′E and 12°33′S, 130°52′E), and a low open woodland (13°57′S, 131°44′E) and sandstone gorge (13°58′S, 131°42′E) within the Umbrawarra Gorge Nature Reserve, 195 km south of Darwin. We recorded bats at each site by using handheld and static (analogue or digital) AnaBat II detectors (see Milne et al. 2004). Handheld detectors were used for 3 h after dusk and static detectors were used for 6 h after dusk. Detectors were positioned in the same location and pointed in the same direction during each sampling period. In addition, we trapped bats with mist nets for 1 night and with harp traps for 2 consecutive nights by using 2 (2000) or 3 (2001–2003) harp traps. Insects were collected and temperature was recorded by using the same methods described in the nightly methods. Sampling was conducted only on nights unaffected by rainfall.

Analysis

Nonparametric tests were used throughout because all data sets were significantly nonnormal (Shapiro–Wilk *W*-test).

Hourly sampling.—For all sample sites combined, we calculated the mean number of call passes recorded each hour starting from civil sunset (refer to Geoscience Australia, http://www.ga.gov.au/nmd/geodesy/astro/). For each species, bat foraging guild (i.e., the type of habitat where a species will generally forage, including cluttered, uncluttered, or background clutter [Milne et al. 2004; Schnitzler and Kalko 1998]), and for all call passes combined, we assessed if activity was evenly distributed throughout the night by using the Kolmogorov–Smirnov 2-sample test. All call data also were graphed and examined visually. We also tested the association between the number of call passes in each hour and insect availability (i.e., the total number of insects sampled) and temperature by using the Spearman rank correlation coefficient.

Nightly sampling.—The AnaBat CF Zcaim records the time of each call pass. To examine the relationship between bat activity and moonlight, all recorded call passes were classified as occurring at either light (bright illumination from moonlight) or dark (little or no

illumination from moonlight) periods by only considering call passes recorded between evening and morning nautical twilight when "it is dark for normal practical purposes" (Geoscience Australia, http://www.ga.gov.au/nmd/geodesy/astro/). We defined dark as the time before moonrise and after moonset or when less than one-fourth of the moon's visible surface was illuminated. We defined light as the time after moonrise and before moonset when more than one-half of the moon's visible surface was illuminated. All call passes not meeting either of these criteria were excluded from the analysis. To take into account periods when moonlight may have been affected by cloud cover, we obtained detailed 3-h cloud observation data from the Bureau of Meteorology for the sampling period.

The following measures of cloud data were used to determine if clouds may have obscured moonlight (refer to Bureau of Meteorology 1984): cloud level (high, middle, and low), the amount of sky covered by cloud in eighths (ranging from 0 [no cloud] up to 8 [100% cloud cover]), and cloud type. On the advice of Bureau of Meteorology staff (R. Lawry, pers. comm.), we determined moonlight would not be affected if for all cloud levels, cloud amount = 0 or 1; or for high cloud present only and cloud amount >1, cloud type = 1, 7, or 8. If the cloud data did not meet these conditions during time periods defined as light, then call passes were excluded from the analysis for a period of 3 h before and after the time of the cloud observation (the time period between cloud observations). Taking the 6-h period of exclusion into account, we assumed cloud conditions at Darwin airport were the same as those at the sampling sites (22 km and 36 km away).

We then used chi-square analysis to test the association between bat activity and moonlight. Observed values were the total number of light and dark call passes recorded in each of eleven 1-h intervals throughout the night. To derive expected values we calculated the proportion of each hourly interval that was light or dark during the total period of sampling and multiplied the total number of call passes in each hourly interval by this proportion.

Bat activity and species richness were assessed against 3 moon-phase categories: full moon (greater than three-fourths illuminated), quarter moon (between one-fourth and three-fourths illuminated), and new moon (less than one-fourth illuminated). Activity was derived from the total number of call passes recorded for 1 entire night from each of the samples used for the hourly assessment of bats. At sites where sampling was conducted over 2 nights, 1 sampling night was randomly chosen. Species richness was obtained from AnaBat recordings that could be identified to the level of species and from capture data. A total of 44 sample nights was used. Dates for moon phase were obtained from Geoscience Australia (http://www.ga.gov.au/nmd/geodesy/astro/). The significance of the difference between moon phases for activity and species richness was tested by using Kruskal–Wallis analysis of variance (ANOVA).

Nightly weather observations of temperature, humidity, and air pressure were recorded at 2100, 0000, and 0300 h and the total number of call passes was calculated for each corresponding 3-h period (1.5 h either side of weather observations). The relationships among the number of call passes and each weather variable, as well as moon phase, were tested by using generalized linear modeling (GLM—Crawley 1993). A Poisson error distribution and log-link function were used and a backward stepwise procedure was adopted to generate the minimum adequate model.

The associations among insect availability, temperature, total bat activity, activity of each foraging guild (see Milne et al. 2004), and bat species richness were tested by using the Spearman rank correlation coefficient. Bat activity was derived from the total number of call passes recorded throughout 1 entire night. For bat activity and foraging guilds, only those sites where analogue recordings were made ($n = 21$) were used because the number of call passes recorded when using analogue and digital methods can differ significantly (Johnson et al. 2002; Milne et al. 2004). Insect sampling and AnaBat recording were conducted concurrently. Species richness was derived from both AnaBat recordings and capture records. AnaBat calls for several species in the Top End cannot be reliably separated (e.g., *Miniopterus schreibersi* and *Pipistrellus westralis*—Milne 2002), and in these cases, species were only included if identified through physical trapping techniques. Bat species inventories were derived from 2 consecutive sampling nights, whereas insect sampling was conducted on 1 of those 2 nights.

Monthly sampling.—For each sampling night at each site we derived several measures of bat activity, namely total number of call passes, number of call passes for each species, and number of call passes for 3 foraging guilds. For each sampling night, we derived mean values for temperature, humidity, and air pressure from the Bureau of Meteorology weather data (described previously) from the five 3-h observations between 1800 and 0600 h. GLM was used to assess the relationship between measures of bat activity and each of the weather variables and by using the same procedure described previously for moon phase and weather. Insects were not sampled for the entire year and therefore were not statistically analyzed, but the mean numbers of insects collected at both sample sites each month were graphed and visually compared with bat activity.

Yearly sampling.—Bat species richness and activity were analyzed for overall differences between years by using repeated-measures ANOVA controlling for differences between sites. Species richness was derived from AnaBat recordings and trapping data. Some species were only recorded if identified through physical capture techniques, as described previously. Bat activity for each sample was derived from the total number of call passes identified from the static and handheld AnaBat recorders. We used analogue static recorders in 2000 and digital recorders in 2001–2003. As described previously, analogue and digital AnaBat recordings cannot be directly compared. Therefore, we used data from the study by Milne et al. (2004) to calculate the mean percentage difference in the number of call passes derived from the 2 recording methods. This difference (42.9%) was added to the total number of call passes derived from analogue static recordings in 2000.

Associations between bat activity and insect activity were tested by using the Spearman rank correlation coefficient. Because of gross environmental differences between sites, we standardized all variables by expressing them as a percentage of the sum of the variable over 4 years.

RESULTS

From all sampling procedures combined, we identified a total of 24 microbat species, including *Chaerephon jobensis*, *Chalinolobus gouldii*, *C. nigrogriseus*, *Hipposideros ater*, *H. diadema*, *H. stenotis*, *Macroderma gigas*, *Miniopterus schreibersi*, *Mormopterus beccarii*, *M. loriae*, *Myotis macropus*, *Nyctophilus arnhemensis*, *N. bifax*, *N. geoffroyi*, *N. walkeri*, *Pipistrellus adamsi*, *P. westralis*, *Rhinonicteris aurantius*, *Saccolaimus flaviventris*, *Scotorepens* sp. (*greyii*, *sanborni*, or both), *Taphozous georgianus*, *T. kapalgensis*, *Vespadelus caurinus*, and *V. finlaysoni*. These species include representatives from all 3 foraging guilds (uncluttered, background clutter, and highly cluttered).

Hourly sampling.—For the 1st aspect of this study (bat activity only), 16,905 call passes were analyzed. The hourly distribution of activity was significantly nonuniform for all call

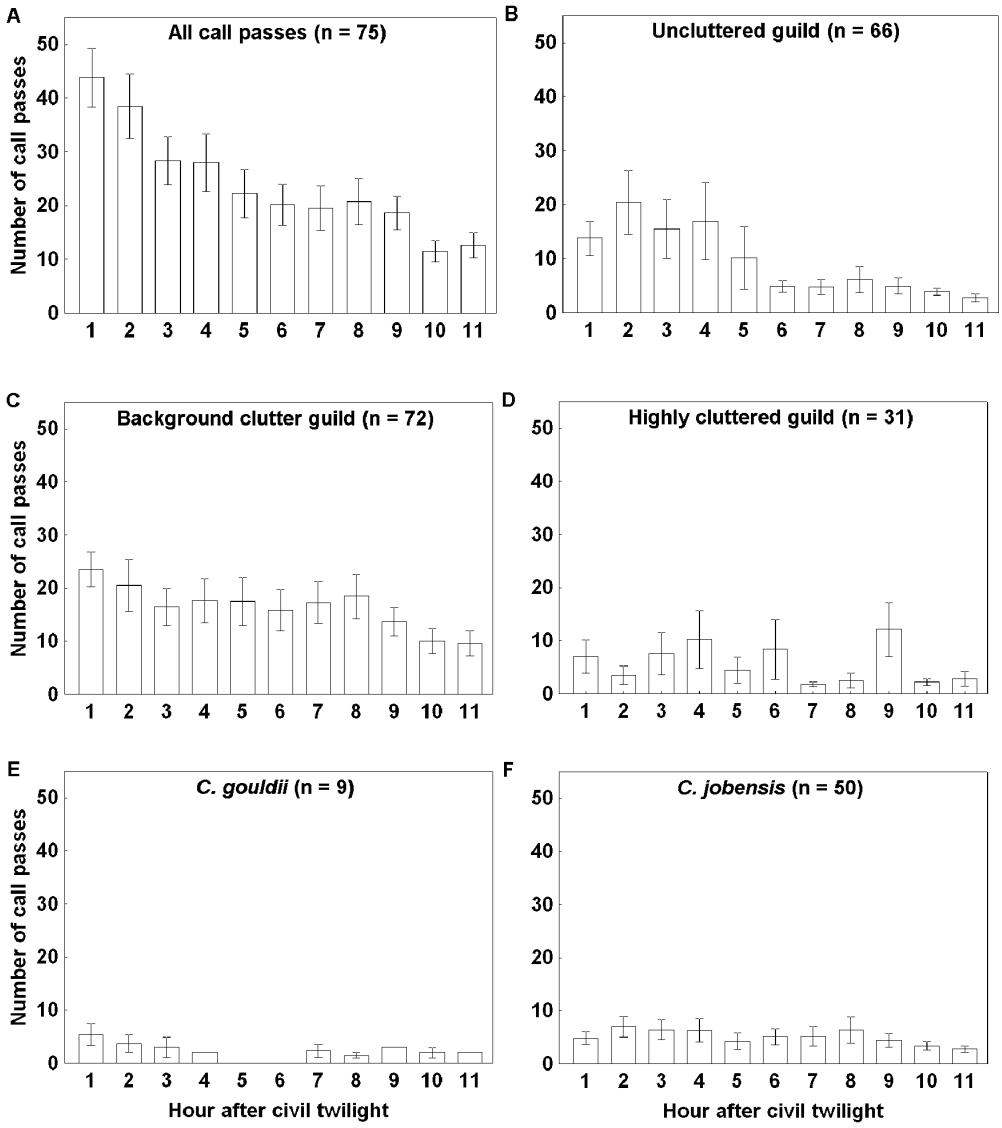

FIG. 1.—Mean number of call passes detected for each hour after civil twilight for A) all passes combined, B–D) foraging guilds, and E–Q) species or species groups in the Top End, Australia. Vertical lines are 95% confidence intervals; *n* is number of sample nights from which calls were identified. Only species that had >50 call passes are shown.

passes, foraging guilds, and species ($P < 0.05$). For all call passes, activity was highest in the 1st hour after dusk and declined gradually throughout the night (Fig. 1A). Most foraging guilds and species had either a slight peak in activity in the first 2 h after sunset or a relatively flat trend in activity throughout the night (Figs. 1B–1Q). There were 2 notable exceptions: *P. adamsi* exhibited a peak of activity in hours 6 and 7 (between 0200 and 0400 h; Fig. 1K) and *S. flaviventris* had high (although highly variable) activity in the first 5 h of the night and almost no activity thereafter (Fig. 1M). Activities of *N. walkeri* and *V. finlaysoni* apparently were erratic throughout the night (Figs. 1J and 1Q), although sample sizes were small ($n = 8$ and 7, respectively).

For the 2nd aspect of this study (comparison of bat activity with insect availability and temperature), we recorded 2,726 call passes from our monthly sampling sites (April–November only) and sampled 28,424 insects. Bat activity, the total number of insects, and temperature all declined throughout the night, although bat activity increased slightly in the 2 h before dawn (Fig. 2). Total bat activity was significantly correlated with temperature and insect availability and both temperature and insects also were correlated with activity of bat species in the uncluttered foraging guild as well as activity of *M. loriae* and *S. flaviventris* (Table 1). Temperature and total number of insects were autocorrelated ($r_s = 0.42$, $P < 0.001$).

This result may be misleading because temperature is generally highest early in the night, which coincides with the time when most bats emerge from diurnal roosting sites. It is difficult to attribute causality to this relationship. Therefore, to further explore this aspect, we looked at the relationship between temperature and bat activity in 2 time periods: the first 2 h after dusk (when bats are most active) and the remainder of

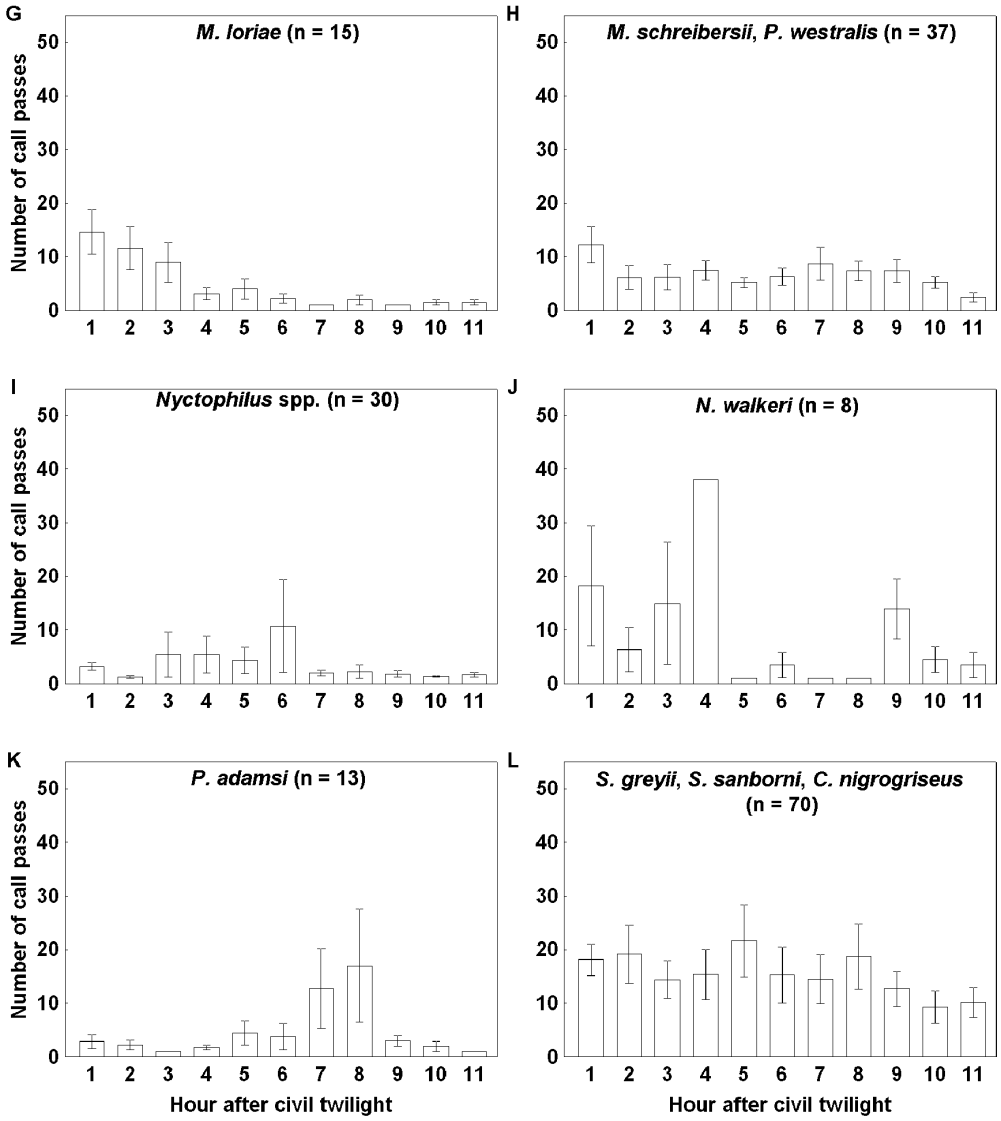

FIG. 1.—Continued.

the night. During field sampling for the monthly aspect of this study, we recorded temperature and bat activity for every hour throughout the night for 2 consecutive nights from April to November 2002 (16 sampling nights). We compared the activity of bats for each hour of the night with temperature, separately for the first 2 h after dark ($n = 28$) and the subsequent 9 h of the night ($n = 144$; Fig. 3). This analysis still demonstrated a positive relationship between temperature and bat activity during both time periods. Bat activity began to increase between 22°C and 24°C; however, a large proportion of samples showed little or no activity in this temperature range as well. Almost all samples displayed significantly elevated levels of activity above 25°C, suggesting that bats are more active above this temperature threshold regardless of time of night. More samples of bat activity on particularly warm nights are required to confirm this observation.

Nightly sampling.—A combined total of 25,193 call passes was identified from both nightly sample sites. The total bat activity throughout the sample period as well as overall trends for air pressure, humidity, and temperature are presented in Fig. 4. At both sites, no obvious trends were found in bat activity during the sampling period, and bat activity between nights also was highly variable, particularly at site 2. Only data from site 1 (8,615 call passes) were statistically analyzed because the sampling period for site 2 (29 nights) was considered inadequate for meaningful analysis.

At site 1, 8,615 call passes were used for the moonlight analysis, 9,089 call passes were used for the moon-phase and weather analysis, and 7,798 call passes (recorded during the hourly study) were used for the moon-phase analysis.

The total number of call passes recorded during dark periods of each sampling night was significantly higher than the total number of call passes recorded during light periods (Table 2). For each hour of the night, 8 of the 11 hours between dusk and dawn recorded significantly higher bat activity during dark periods compared to light periods; hours 2 and 7 did not differ

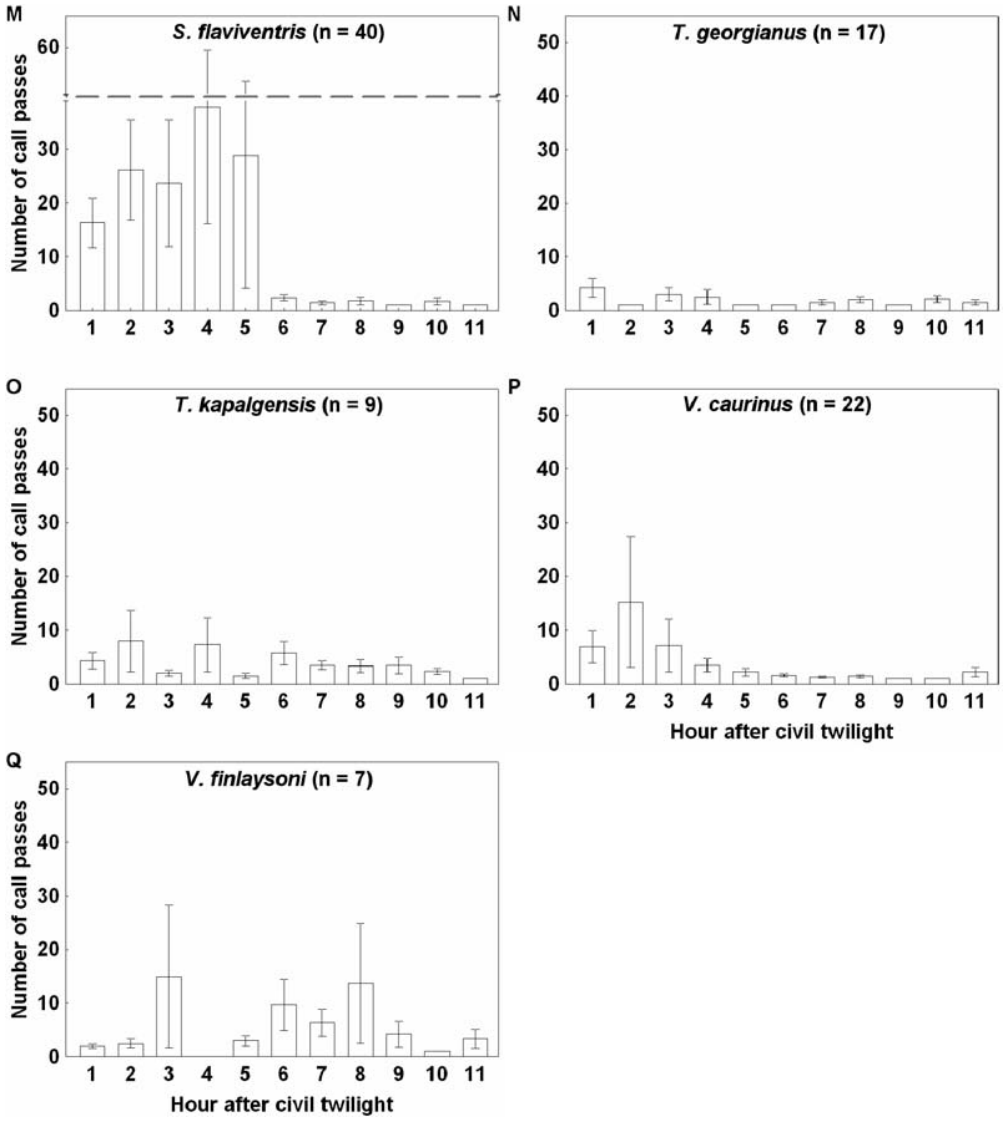

FIG. 1.—Continued.

significantly between dark and light periods, whereas hour 10 (between 0500 and 0600 h) recorded significantly more call passes during light periods than dark periods.

No significant difference was found between moon phases with respect to total bat activity ($H = 0.384$, $P = 0.825$) or species richness ($H = 3.011$, $P = 0.222$).

The GLM analysis identified temperature (positive association), time (highest activity in the 3 h around 2100 h and lowest activity in the 3 h around 0000 h), and moon phase (reduced activity during the new moon) as the main predictors of bat activity. However, an interaction was found between time and moon phase so that during the full moon bat activity was highest and lowest around 0300 h and midnight, respectively; during the quarter moon, activity was higher around 2100 h than around 0000 and 0300 h; and activity was independent of time during the new moon (Fig. 5).

No significant correlation occurred between insects or temperature and each of the 3 bat activity variables (species richness, total activity, and activity of each of the foraging guilds) for the nightly data.

Monthly sampling.—A total of 5,716 call passes was recorded over the 12 months. Total bat activity remained relatively static for most of the year but increased dramatically in October (Fig. 6A). For foraging guilds, bat activity peaked in October for the uncluttered foraging guild, remained relatively static (but declined slightly in March–April) for the background clutter foraging guild, and was slightly higher in January for the highly cluttered foraging guild (Fig. 6B–6D). However, the number of records in the latter guild was limited.

Models of bat activity with climatic variables were generally weak, with no more than 40% of the deviance captured in any of the models (Table 3). Temperature and air pressure (positive associations) were identified as the major predictors for total bat activity. Of those models that captured >15% of the deviance, temperature and air pressure were identified as the major predictors for the uncluttered foraging guild and

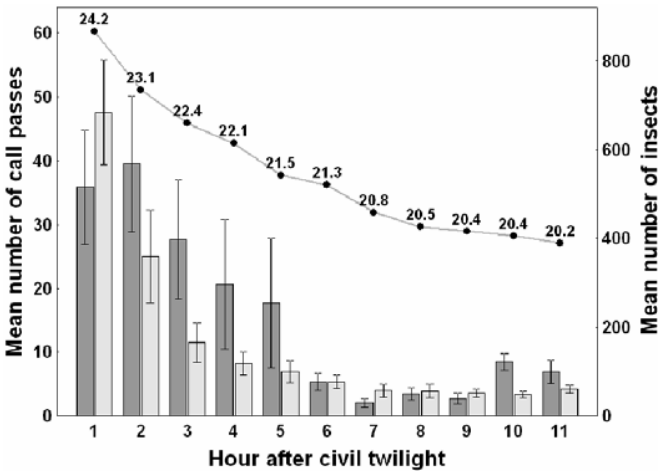

FIG. 2.—Comparison between mean number of call passes (dark bars) and insects (light bars) for each hour throughout the night near Darwin, Australia. Vertical lines are 95% confidence intervals. The line plot shows the mean temperature with actual values displayed above each point.

S. flaviventris (positive associations), whereas air pressure only was identified as the major predictor for the highly cluttered guild, *C. jobensis* (negative associations), and *M. schreibersi* and *P. westralis* (positive association). Humidity was not identified as a major predictor of bat activity in any of the more robust models. The total number of insects declined from a peak in April and remained relatively static from May to November (Fig. 6A).

Yearly sampling.—No significant difference was found between years for either bat activity ($F = 1.18$, $P = 0.57$) or species richness ($F = 7.33$, $P = 0.26$). The number of recorded call passes for each site also was highly variable between years (Fig. 7). No significant correlations were found between bat activity or species richness and temperature or insect abundance.

DISCUSSION

The overall hourly pattern of bat activity in the Top End, which featured a peak in bat activity in the 1–2 h immediately after dusk, is similar to that reported in previous studies (Kuenzi and Morrison 2003; Law et al. 1998; O'Donnell 2000; Taylor and O'Neill 1988;). However, Taylor and O'Neill (1988) and Hayes (1997) identified a 2nd peak in bat activity before dawn that was not clearly evident in our 1st study (analysis of bat activity based on sites from across the Top End). However, a small peak did appear in our 2nd study (analysis of bats and insects from sites nearer to Darwin). It is unclear what caused this difference; however, we speculate that it was due to the different sampling periods of each study and contrasting seasonal effects. Sampling for our 2nd study was conducted throughout the year. Temperatures were relatively cool in the dry season (May–August), and this may have reduced overall bat activity. It is likely that bats return to diurnal roosting sites at various times throughout the night; however, a slight peak is still expected just before dawn as bats that are still foraging at this time return to roost sites. Sampling for our 1st study was conducted predominantly in the buildup (September–November) just before the monsoon season, when temperatures were relatively warm throughout the night and bat activity was higher. Similar bimodal peaks in activity have been recorded in the dry season for other tropical bat species (e.g., Pavey 1998; Pavey et al. 2001). In addition, previous studies (Hayes 1997; Kuenzi and Morrison 2003; O'Donnell 2000) have noted a high degree of seasonal variation in the nightly activity patterns of bats. We were unable to test this variation with our data.

Two species, *P. adamsi* and *S. flaviventris*, exhibited patterns of hourly activity that contrasted with that of all other species. *P. adamsi* was the only species with a peak in activity during the later part of the night (Fig. 1K). This species may use gleaning as a foraging technique, therefore avoiding the need to capture insects in flight and instead capturing insects at rest on

TABLE 1.—Spearman rank correlation (r_s) of hourly bat activity with temperature and insects for foraging guilds and species and species groups near Darwin, Australia. Only species that had >50 call passes are shown.

Activity variable	Temperature	Insect availability
Total activity	0.18*	0.19**
Foraging guild		
Uncluttered	0.26***	0.33***
Background clutter	0.04	0.01
Highly cluttered	0.06	0.09
Chaerephon jobensis	−0.07	0.09
Mormopterus loriae	0.30***	0.21**
Miniopterus schreibersi and *Pipistrellus westralis*	−0.01	−0.01
Saccolaimus flaviventris	0.42***	0.39***
Chalinolobus nigrogriseus, *Scotorepens greyii* and *S. sanborni*	0.09	0.12

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

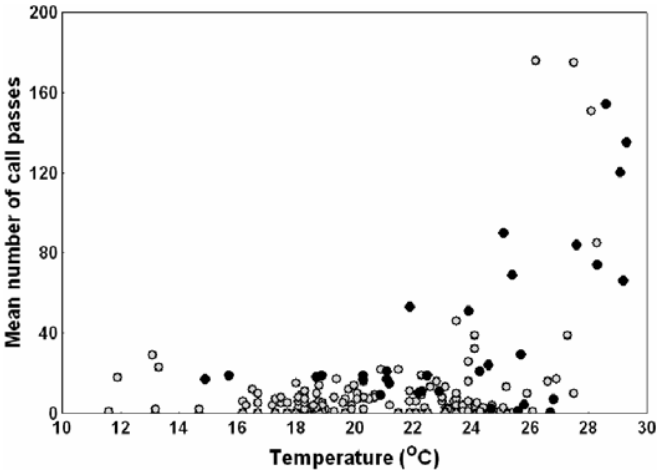

FIG. 3.—Total number of call passes recorded during each hour of the night plotted against temperature for bats in the Top End, Australia. Black dots represent samples recorded during the first 2 h after dusk; gray dots represent samples recorded during the rest of the night.

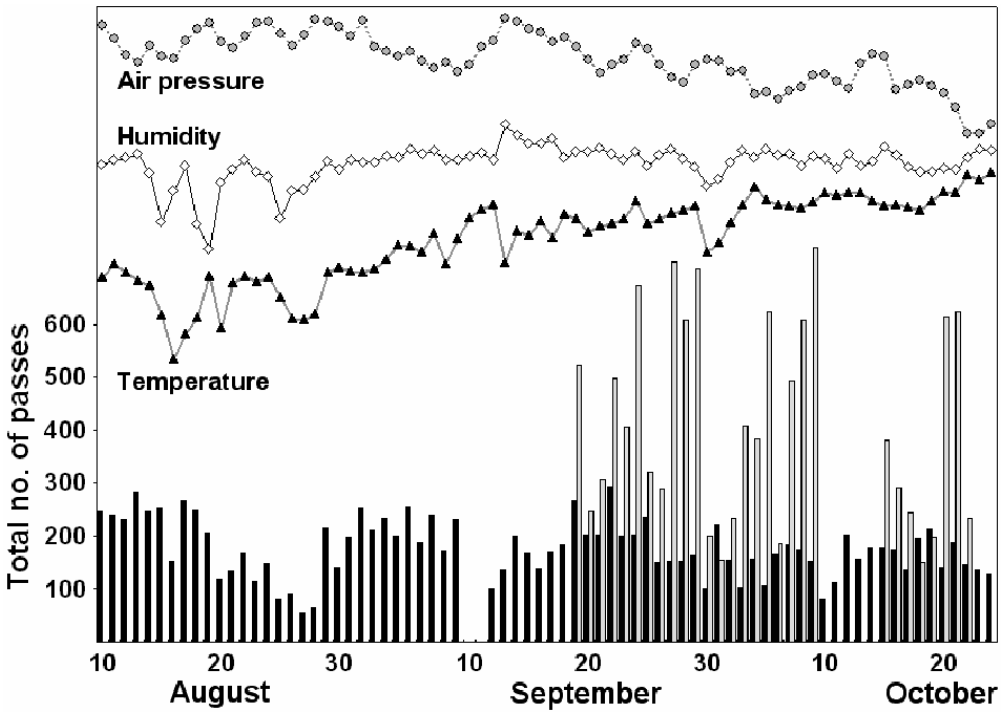

FIG. 4.—Total number of call passes recorded each night at site 1 (dark bars) and site 2 (light bars). Line graphs show the nightly average trend in air pressure, humidity, and temperature recorded at nearby Darwin Airport, Australia, from 10 August to 24 October 2002. Nights on which AnaBat recordings failed are represented by zero values.

vegetation during the cooler part of the night. This is consistent with observations by McKenzie and Rolfe (1986), who categorize the foraging zone of *P. tenuis* (now redescribed as *P. adamsi* and *P. westralis*) as close to surfaces of tree stands and canopies. *S. flaviventris* was active in the 1st half of the night and was almost inactive thereafter. Insect availability may have influenced this observed pattern because it is likely that *S. flaviventris* forages on high-flying insects (which were not sampled in this study). High-flying nocturnal insects are likely to be similar to other nocturnal insects in exhibiting the greatest peak of activity at twilight with activity dropping off during the remainder of the night until dawn (Jetz et al. 2003; Rautenbach et al. 1988). Therefore, we suggest that in the case of a large, relatively unmaneuverable species such as *S. flaviventris*, it eventually becomes energetically inefficient to continue

TABLE 2.—Bat activity levels (number of bat passes) during periods of little or no moonlight (dark) and bright moonlight (light) near Darwin, Australia. Probability level (*P*) indicates comparison of activity levels between dark and light periods (chi-square test). Expected values were calculated as described in the text.

	Dark		Light		
Hour	Observed	Expected	Observed	Expected	*P*
1	625	666	319	278	*
2	830	811	239	258	
3	950	875	126	201	***
4	712	668	68	112	***
5	657	634	47	70	*
6	562	548	17	31	*
7	532	540	20	12	
8	1,304	1,293	0	11	***
9	848	828	0	20	***
10	815	859	98	54	***
11	688	616	2	74	***
Total	8,523	8,338	936	1,058	**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

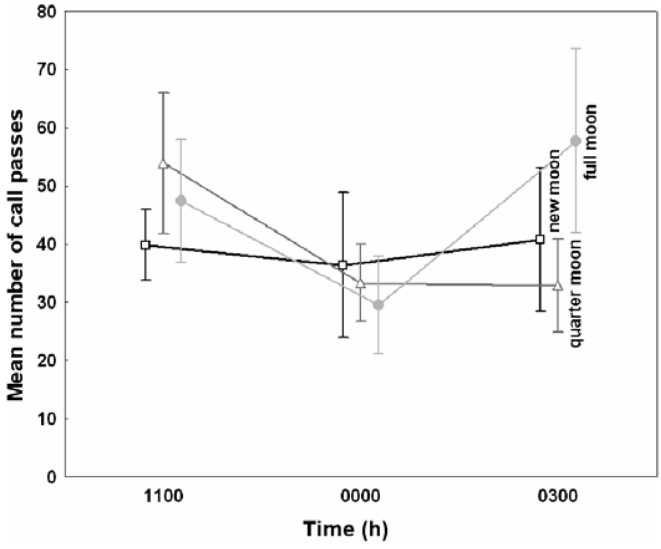

FIG. 5.—Mean number of call passes for 3 moon phases and 3 time periods; 2100 h (1930–2230 h), 0000 h (2230–0130 h), and 0300h (0130–0430 h) for bats of the Top End, Australia. The graph demonstrates the interaction between the 2 factors as indicators of bat activity. Error bars represent 95% confidence intervals.

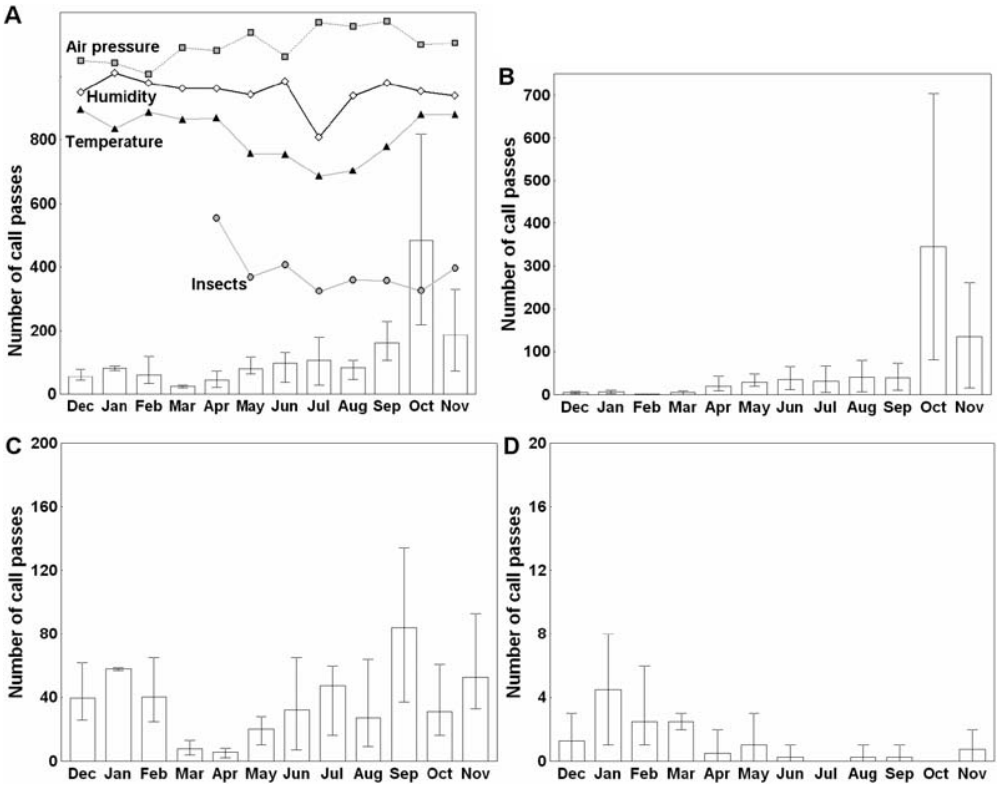

FIG. 6.—Monthly bat activity showing mean number of call passes recorded each night over 2 nights at 2 sites near Darwin, Australia, between December 2001 and November 2002 for A) all species; and call passes attributed to bat species within B) uncluttered, C) background clutter, and D) highly cluttered foraging guilds. Vertical lines represent range for number of call passes for each monthly sample. Line plots in A) represent relative values for air pressure, mean monthly temperature, humidity, and the total number of insects that were recorded during each monthly sample. Note that plots are not to equal scale.

foraging after the initial peak in insect abundance because of a decline in encounter probability.

Law et al. (1998) examined bat activity (for all species combined and for individual species) in southeastern Australia, and the similarity in sampling methods with our study allows for comparisons to be made between the 2 regional bat faunas. Overall, relative activity throughout the night in southeastern Australia was similar to that in the Top End, although Law et al. (1998) found bats were proportionately more active in the 1st hour after dusk. In both northern and southern areas, interspecific variation in activity patterns also was present, with a small number of species showing atypical activity rhythms.

The association between bat activity and lunar characteristics in the Top End is complex. When moon phase and moonlight were assessed independently of all other environmental and temporal factors, little or no association was found with microbat activity and moon phase, and a moderate association was found with moonlight. A similar conclusion has been drawn by several other studies that carried out univariate analyses of the relationship between lunar conditions and bat activity (Gaisler et al. 1998; Karlssön et al. 2002; Kuenzi and Morrison 2003; Negraeff and Brigham 1995). However, in our study, GLM analysis revealed an interaction between moon phase and time of night as the main determinants of bat activity (Fig. 5). This result is supported (in part) by the results of our moonlight analysis (Table 2), which showed that bat activity varies not with moonlight alone, but according to a combination of time of night and moonlight. Other studies also have shown that moonlight alone is not related to bat activity, but when assessed with multivariate analysis techniques, the authors found that bats were affected to some degree (Erickson and West 2002; Hayes 1997; Hecker and Brigham 1999).

Bats within each of the foraging guilds are exposed to different levels of moonlight as a consequence of the shading effects of vegetation; therefore, guilds might be expected to exhibit different responses to moonlight. To examine this aspect we used the same data from the moonlight analysis and classified call passes into foraging guilds (Milne et al. 2004) and applied the same chi-square analysis to each separate guild. The highly cluttered guild contained insufficient data for meaningful analysis and was not examined. For the uncluttered guild, the total number of call passes was significantly higher during dark periods compared with light periods ($\chi^2 = 12.3$, $P < 0.001$), whereas no significant difference was found for the background clutter guild ($\chi^2 = 0.0$, $P = 1.0$). Therefore, the shading effects of vegetation appear to influence responses of at least some microbats during periods of moonlight. However, sample sizes for light periods were relatively small for both the uncluttered (total number of call passes = 191) and background clutter (total number of call passes = 517) guilds and the

TABLE 3.—Summary of results from generalized linear modeling of monthly bat activity by using climate variables ($n = 46$) near Darwin, Australia. Minimum adequate models and explanatory power (percentage of deviance explained) are shown for total bat activity, activity of each foraging guild, and species (or species groups). Only species with >50 passes are shown. Where modeling identified a significant difference in activity between the 2 sampling sites, it is defined in the model summary as "site."

Variable	Estimate	*SE*	*P*
Total activity (deviance = 3,373; deviance captured = 23.2%)			
Constant	−231.95	8.07	
Temperature	0.29	0.01	***
Air pressure	0.23	0.01	***
Uncluttered foraging guild (deviance = 6,043; deviance captured = 27.9%)			
Constant	−439.14	14.21	
Temperature	0.62	0.02	***
Air pressure	0.424	0.01	***
Background clutter foraging guild (deviance = 944; deviance captured = 6.8%)			
Constant	−51.97	9.38	
Air pressure	0.06	0.01	***
Site	−0.13	0.02	***
Highly cluttered foraging guild (deviance = 95; deviance captured = 28.1%)			
Constant	264.10	60.26	
Air pressure	−0.26	0.06	***
Site	0.35	0.15	*
Chaerephon jobensis (deviance = 476; deviance captured = 37.3%)			
Constant	8.55	0.53	
Air pressure	−2.64	0.06	***
Site	0.37	0.02	***
Chalinolobus nigrogriseus, *Scotorepens greyi*, and *S. sanborni* (deviance = 685; deviance captured = 2.64%)			
Constant	3.46	0.44	
Temperature	−0.05	0.02	**
Humidity	0.01	0.004	*
Site	−0.11	0.04	**
Mormopterus loriae (deviance = 606; deviance captured = 15.0%)			
Constant	−9.19	1.58	
Temperature	0.522	0.07	***
Humidity	−0.05	0.01	***
Pipistrellus westralis and *Miniopterus schreibersi* (deviance = 514; deviance captured = 27.5%)			
Constant	−131	14.29	
Air pressure	0.13	0.01	***
Site	−0.26	0.04	***
Saccolaimus flaviventris (deviance = 6,789; deviance captured = 38.1%)			
Constant	−674.97	19.87	
Temperature	1.09	0.02	***
Air pressure	0.64	0.02	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

number of call passes for each foraging guild was highly variable throughout the night.

We express caution when interpreting our nightly results based on data recorded from just 1 site. Much more variation occurred in the activity of bats at site 2 than at site 1 (Fig. 4),

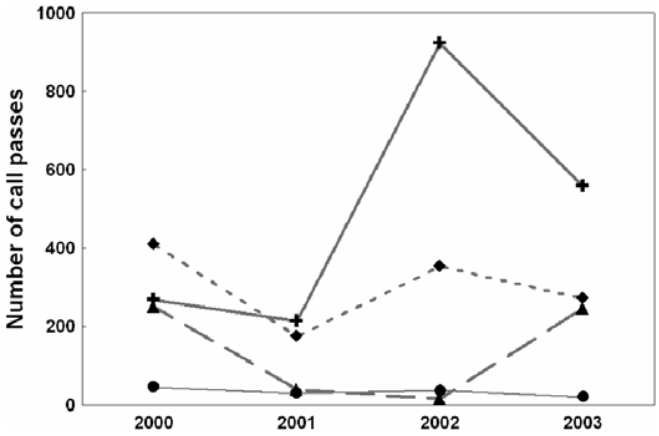

FIG. 7.—Total number of call passes recorded over 2 nights in October from 2000 to 2003 at 4 sites in the Top End, Australia. Line and point symbols differentiate the sites.

although we had inadequate data from site 2 for statistical analysis. In addition, the minimum adequate model (for the relationship between bat activity, moon phase, and weather) was moderately weak (15% of the deviance captured), suggesting either a high degree of variation in the data or that the model was dependent on other variables not quantified here.

One of the most striking results of this temporal study of microbats was the dramatic relative increase in bat activity recorded for October during the monthly assessment. This increase was solely a result of activity within the uncluttered foraging guild (Fig. 6). The increase in activity in October did not appear to be related to insect availability and can be only partially related to temperature, air pressure, or both. October is the peak of the buildup when temperature and humidity reach their highest annual levels and rainstorms begin, before the tropical wet season. It is possible that this relatively abrupt series of changes in weather conditions at this time of year triggers an increase in bat activity, possibly as a result of reproductive activity. Little information is available on the reproductive biology of microbats in the Top End; however, we noted that captured individual bats from several species (from across the Top End) were pregnant, lactating, or had suckling young at this time. Therefore, bats may have increased their foraging activity to compensate for the increased energy demands during this time (Barclay 1989; Kuenzi and Morrison 2003). Alternatively there may have been a sudden influx of volant young into the population.

We recorded an unexpected inverse relationship between monthly activity levels of species within the uncluttered and highly cluttered foraging guilds ($r_s = -0.449$). When activity for the uncluttered guild was highest in October, no bats from the highly cluttered guild were detected, and when activity for the highly cluttered guild was highest in December to March, bats from the uncluttered guild were almost absent. At our study sites, bats of the highly cluttered guild were all from the genus *Nyctophilus* and the overall activity of bats from the uncluttered guild was relatively low.

Assessments of bat activity elsewhere over the course of a year are limited. Brigham and Geiser (1998) found that

activity of bats from the genus *Nyctophilus* in northeastern New South Wales, Australia, was notably erratic for most of the year, but the lowest levels of activity were recorded during the coldest months. In Victoria, Australia, Lumsden and Bennett (1995) trapped relatively high numbers of bats during the warmest months (October–March) and very few bats during winter (although no trapping was conducted during July and August). The most detailed assessment is provided by Sanderson and Kirkley (1998), who used AnaBat detectors in South Australia. Like the Victorian study (also in temperate Australia), they found bat activity was highest in the warmest months (November–February) and reduced in the coldest months (May–July). In the Top End, we identified a single peak in activity in October and slightly elevated activity levels in September and November. We recorded bat activity across all months of the year, and bat activity was at moderate levels (mean = 70 call passes/night) even during the quietest period in December–August. We did not record high levels of bat activity persisting through the warmest months of the year, as observed in the studies in temperate Australia.

Studies of the effect of insect availability on bat activity have shown variable results (Hayes 1997; Kuenzi and Morrison 2003; O'Donnell 2000; Rydell et al. 1996). In our study, we identified only limited associations between bats and insect availability; however, insect activity can be influenced by several factors (e.g., temperature, humidity, wind velocity, barometric pressure, lunar influences, breeding cycles, and vegetation flowering and fruiting events). Therefore, we were unable to define a clear causal link between insect availability and bat activity. Further, carefully targeted studies are required that take into account all possible influences on bat and insect activity.

A high degree of variation was found in bat activity between samples across all temporal scales. For example, at our nightly sampling sites the total number of call passes recorded between consecutive nights varied up to 131% ($\bar{X}$ 29%) at site 1 and 252% ($\bar{X}$ 60%) at site 2. High levels of variation in bat activity also have been identified in previous studies (Hayes 1997; Kuenzi and Morrison 2003). This has significant implications for surveying bats using echolocation recording techniques. These implications are discussed in detail by Hayes (1997), who makes the following key points: Accurate and precise measures of bat activity will only be obtained by using intensive sampling efforts; sampling designs need to account for temporal variation; and statistical tests comparing activity between sites are likely to have poor statistical power to detect small differences in activity.

Our study shows that bat activity can be highly variable across a range of temporal scales and further detailed work is required to derive species–time curves, to determine the effects of spatial variation, and to conduct more detailed investigations into the interactions between prey availability and bat activity. Based on the information collected here we make the following recommendations for sampling bats within areas less than 1 ha in size: Sampling to inventory species should be conducted over at least 2 entire nights. Sampling to measure bat activity should be conducted over at least 5 entire nights. When establishing longer-term activity-monitoring programs, nightly variation at the particular site should be ascertained to determine the optimum sampling period. Caution must be taken when comparing samples collected during the buildup to the monsoon season (September–November) with samples collected at other times of the year. Temporal variation differs between species; therefore, when assessing individual species, sampling methods should take into account the temporal variation of the species concerned.

Time periods should be extended if sampling is affected by adverse weather conditions and provision also should be given for the physical nature of the sampling area (e.g., in areas of dense vegetation where echolocation call signals might be impeded, sampling periods also should be extended). We consider that these recommendations are broadly applicable to tropical savanna woodlands in the Old World, although similar studies assessing the temporal patterns of bats elsewhere in this region would be useful to confirm this suggestion.

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Chapter 6.
Dietary composition of insectivorous bats of the Top End of the Northern Territory, Australia.

Dietary composition of insectivorous bats of the Top End of Australia.

Introduction

In previous chapters, I assessed three important aspects of the ecology of Top End insectivorous bats (microbats): habitat associations and species composition at the community level; habitat associations and distributions at the species level; and temporal activity at four scales. Several of the explanations of observed patterns could be clarified with greater understanding of the diet and prey availability of the study species. In particular, associations of species with particular habitats and timing of activity could benefit from knowledge of foraging ecology. Here I examine the food habits of this faunal group in order to gain an understanding of this fundamental aspect of their ecology and to search for patterns that may explain some of the habitat associations documented in previous chapters. Other information that may also be obtained from analysis of microbat diets (but not examined here) include niche partitioning (i.e. how several species can co-exist at the same location and habitat, Pavey and Burwell 2000; Patterson *et al.* 2003), echolocation strategies and flight morphology (Fullard *et al.* 1991; Bogdanowicz *et al.* 1999), insect defence mechanisms (Appendix 3; Pavey and Burwell 1998; Bogdanowicz *et al.* 1999) as well as the impact of microbat foraging on insect herbivory in both natural and modified (e.g. agricultural) areas (McCracken 2004).

In Australia, little research has been done on microbat diets. The first comprehensive dietary assessment was carried out by Vestjens and Hall (1977) who assessed the food habits of 29 species. Since then, assessments have been carried out on various species groups (O'Neill and Taylor 1989; Pavey and Burwell 1998) or individual species (Churchill 1994; Pavey and Burwell 1997; Law and Urquhart 2000; Pavey and Burwell 2004), by analysing the composition of stomach, faecal pellets and/or discarded prey remains at roosts. In this chapter, I continue my regional assessment of this diverse tropical mammal group, by (1) describing the diets the microbat species that occur within the study area, (2) assessing aspects of their foraging ecology and (3) comparing dietary accounts of Top End microbat species with other studies conducted both locally and elsewhere in Australia.

Methods

Study area

The study area is the Northern Territory, north of 18˚S (the 'Top End', Chapter 3, Figure 1). This area is part of the wet-dry tropics of northern Australia and lies within the vast tropical savannas. A detailed description of this area is provided in Chapter 3.

Dietary samples

I used the bats captured during field sampling described in Chapters 2, 3 and 4 to obtain dietary samples for Top End species. Diets were assessed using stomach contents and faecal analysis. Stomachs were removed from voucher specimens and supplemented with stomachs removed from specimens held by the Museum and Arts Gallery of the Northern Territory. A small number of these stomachs (6) had no contents and were not used. Faecal samples (at least five faecal pellets from either individuals, a colony or group of captured bats) were collected from microbats using three methods: from individuals held in cloth bags for 1-2 hours after capture; from the bottom of harp-trap bags if there was only one species of bat present in the harp-trap; or under clusters of roosting bats.

Analysis

Microbat diets were analysed using the methods described in Appendix 3. In summary, stomach and scat samples were teased apart in alcohol and searched for identifiable fragments under a binocular microscope. Fragments were identified to the lowest possible taxonomic level and the percent volume of each order in each of the stomach samples and faecal pellets was visually estimated to the nearest 5% using methods similar to that described in Whitaker (1988) . Unidentifiable fragments were not included in the analysis. I then calculated the total mean percent volume of each order for each species of microbat, as well as for each foraging guild (refer Chapter 2). To assess prey availability I used the insect captures described in Chapter 3. I calculated the total mean percent count of insect orders that were collected at each site and compare it to the diet composition for each foraging guild.

To test overall sampling adequacy, as well as to assess the degree of dietary specialisation, I plotted the number of orders that were identified in the diets against the total sample size for each microbat species and fitted a logarithmic curve. To further examine dietary specialisation, I estimated dietary breadth of each microbat species using Levin's measure of standardized niche breadth (Krebs 1989) using the formula:

$$B_A = \frac{\left(1/\sum p_j^2\right) - 1}{n - 1}$$

where p_j = percentage composition of each order in the diet

n = number of samples

Results

I collected 100 stomach and 32 scat samples from 23 of the 28 species of microbat that occur in the Top End (Table 1) including three species that had never been previously assessed (*Taphozous kapalgensis*, *Nyctophilus arnhemensis* and *Pipistrellus adamsi*). Prey material was identified from two phyla (Arthropoda and Chordata). Three classes of arthropod were taken: Arachnida (spiders: Araenea), Myriapoda (centipedes: Chilopoda) and Insecta (insects). Insect orders captured were Blattodea (cockroaches), Coleoptera (beetles), Diptera (flies), Hemiptera (true bugs, hoppers and scale insects), Hymenoptera (sawflies, wasps, ants, bees), Isoptera (termites), Lepidoptera (moths and butterflies), Neuroptera (lacewings and antlions), Orthoptera (grasshoppers and crickets), and Trichoptera (caddisflies).

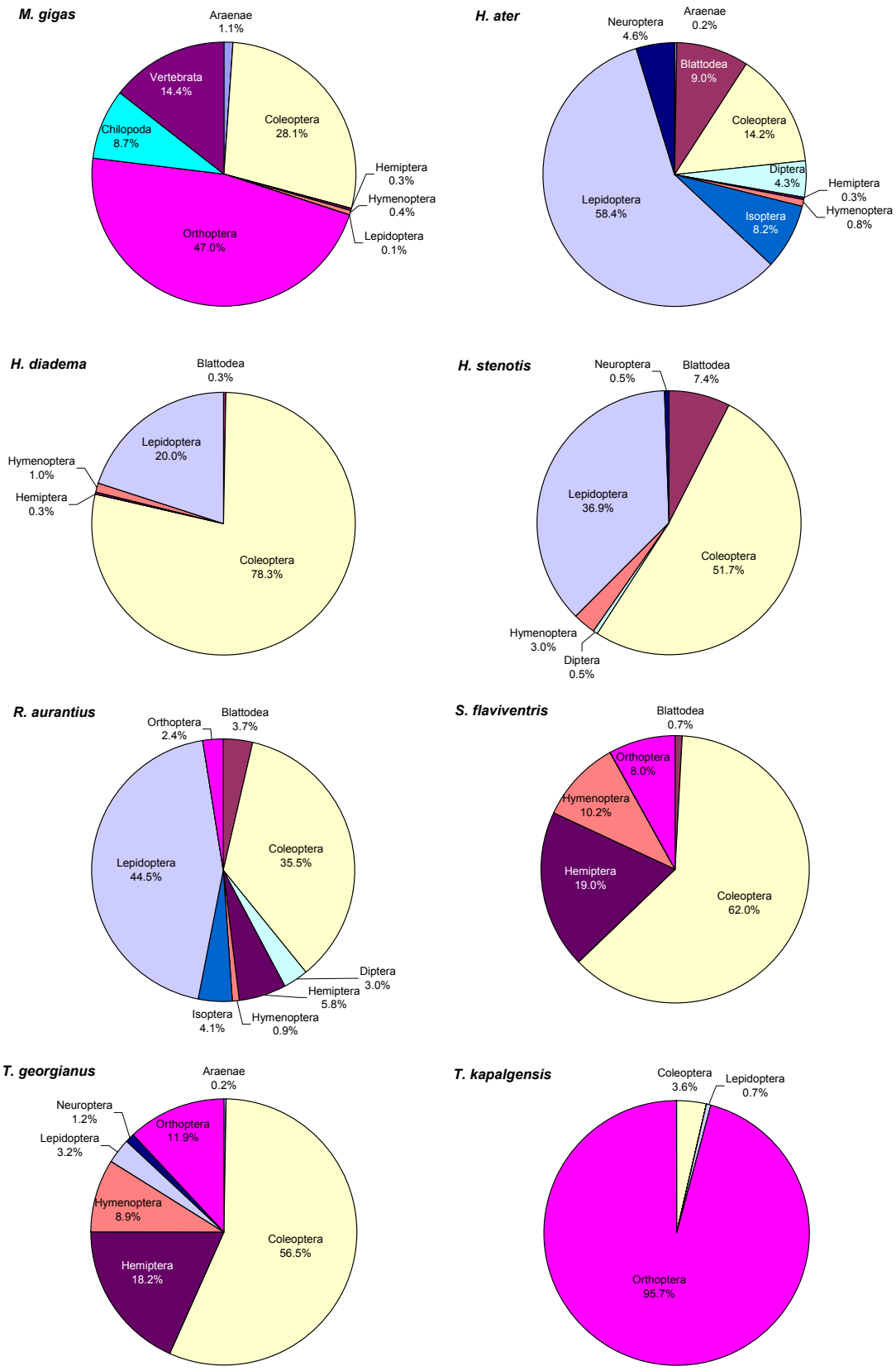
Description of microbat diets

The proportions of each of these prey items for each species of microbat is presented in Figure 1 and the proportions for each of the foraging guilds in Figure 2. As in previous chapters, *Scotorepens greyii* and *S. sanborni* are treated here as a single species group. The following section describes the dietary data that were found for each microbat species and I draw comparisons with other published studies. Common names follow Zborowski and Storey (2003).

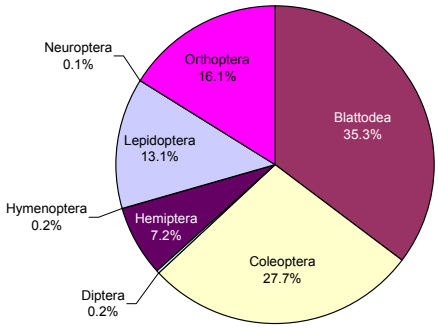
Table 1. Microbat species assessed in this study including the total number of stomachs and faecal pellets (with the number of individuals that faecal pellets were collected from shown in parentheses) used in the analysis. One faecal sample is equal to one individual producing five or more faecal pellets. For a colony or group of captured bats (indicated by *), one faecal sample is the total number of faecal pellets divided by five (rounded down to the nearest whole number). Total sample size (n) is the sum of stomach and faecal samples.

Species	No. of stomachs	No. of faecal pellets (no. of individuals)	Total sample size (n)
Macroderma gigas		20 (50+)*	4
Hipposideros ater	6	5 (1)	7
Hipposideros diadema	3		3
Hipposideros stenotis	2		2
Rhinonicteris aurantius	6	11 (2)	8
Saccolaimus flaviventris	10		10
Taphozous georgianus	5		5
Taphozous kapalgensis	3		3
Chaerephon jobensis	8		8
Mormopterus beccarii	2		2
Mormopterus loriae	4		4
Miniopterus schreibersii		22 (5)*	4
Nyctophilus arnhemensis	1	44 (6)	7
Nyctophilus bifax	2	7 (4)*	3
Nyctophilus geoffroyi	2		2
Nyctophilus walkeri	4	22 (2)	6
Chalinolobus gouldii	5		5
Chalinolobus nigrogriseus	7	31 (6)	13
Myotis macropus		20 (8)*	4
Pipistrellus adamsi	5		5
Pipistrellus westralis	5		5
Scotorepens greyii / S. sanborni	13	10 (2)	15
Vespadelus caurinus	7		7

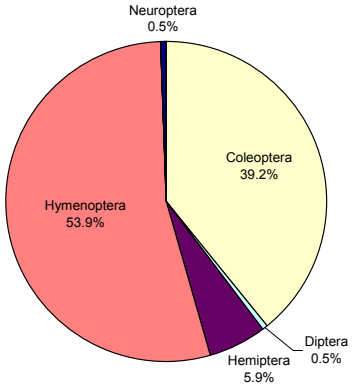
Figure 1. Dietary composition of 23 species of Top End microbats. Pie charts show the mean percentage composition of orders identified in the scats and stomach contents.



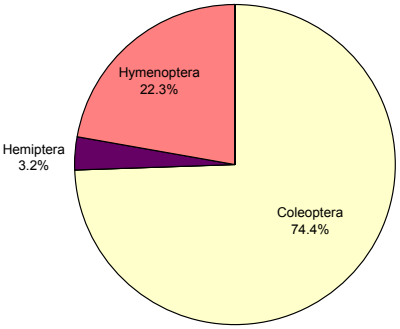
C. jobensis



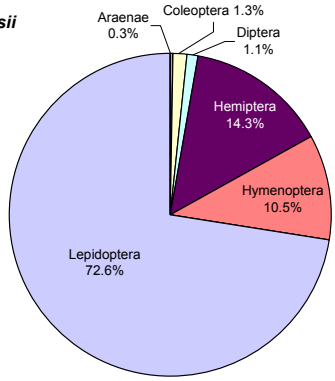
M. beccarii



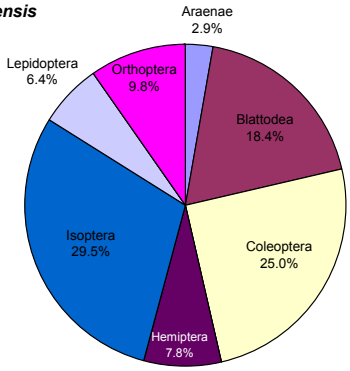
M. loriae



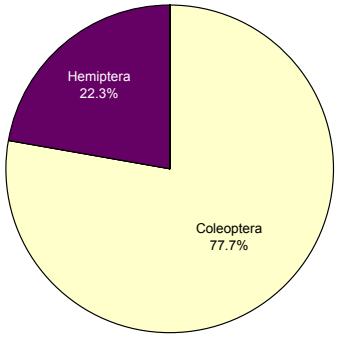
M. schreibersii



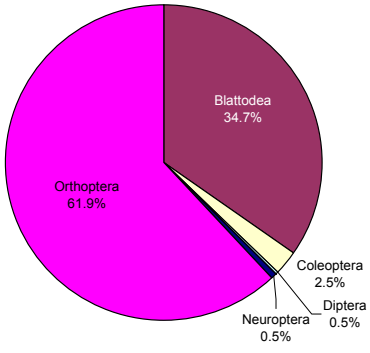
N. arnhemensis



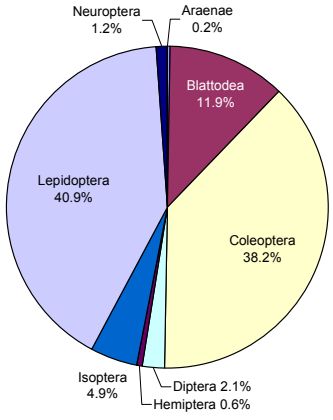
N. bifax



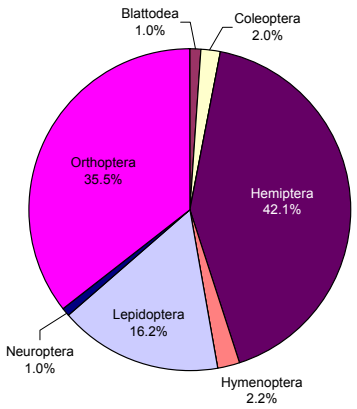
N. geoffroyi



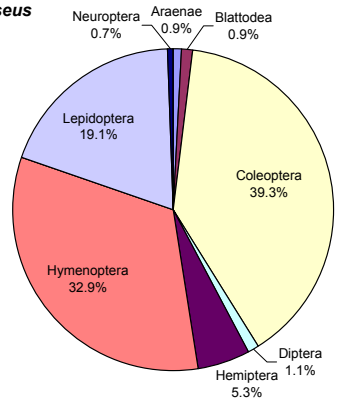
N. walkeri



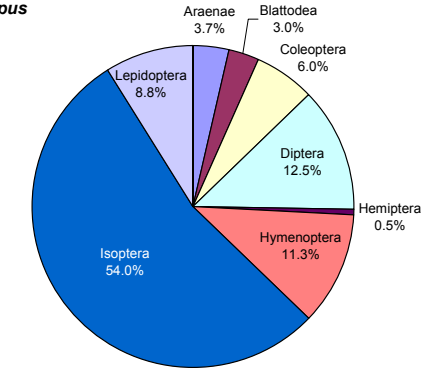
C. gouldii



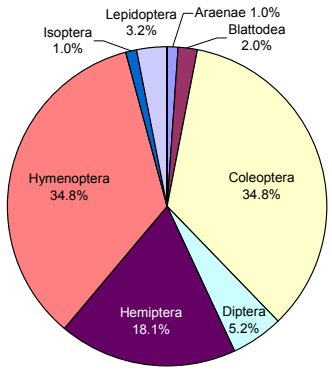
C. nigrogreseus



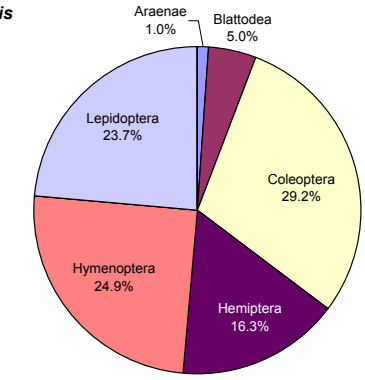
M. macropus



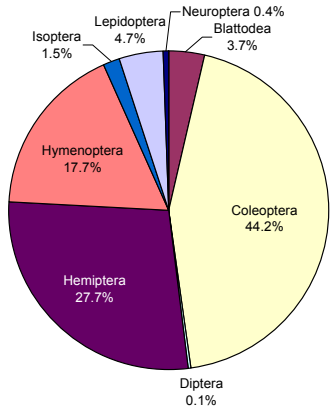
P.adamsi



P. westralis



S. greyii / S. sanborni



V. caurinus

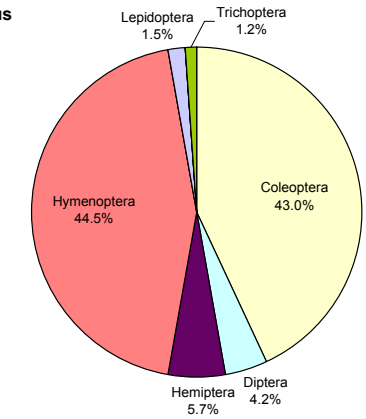
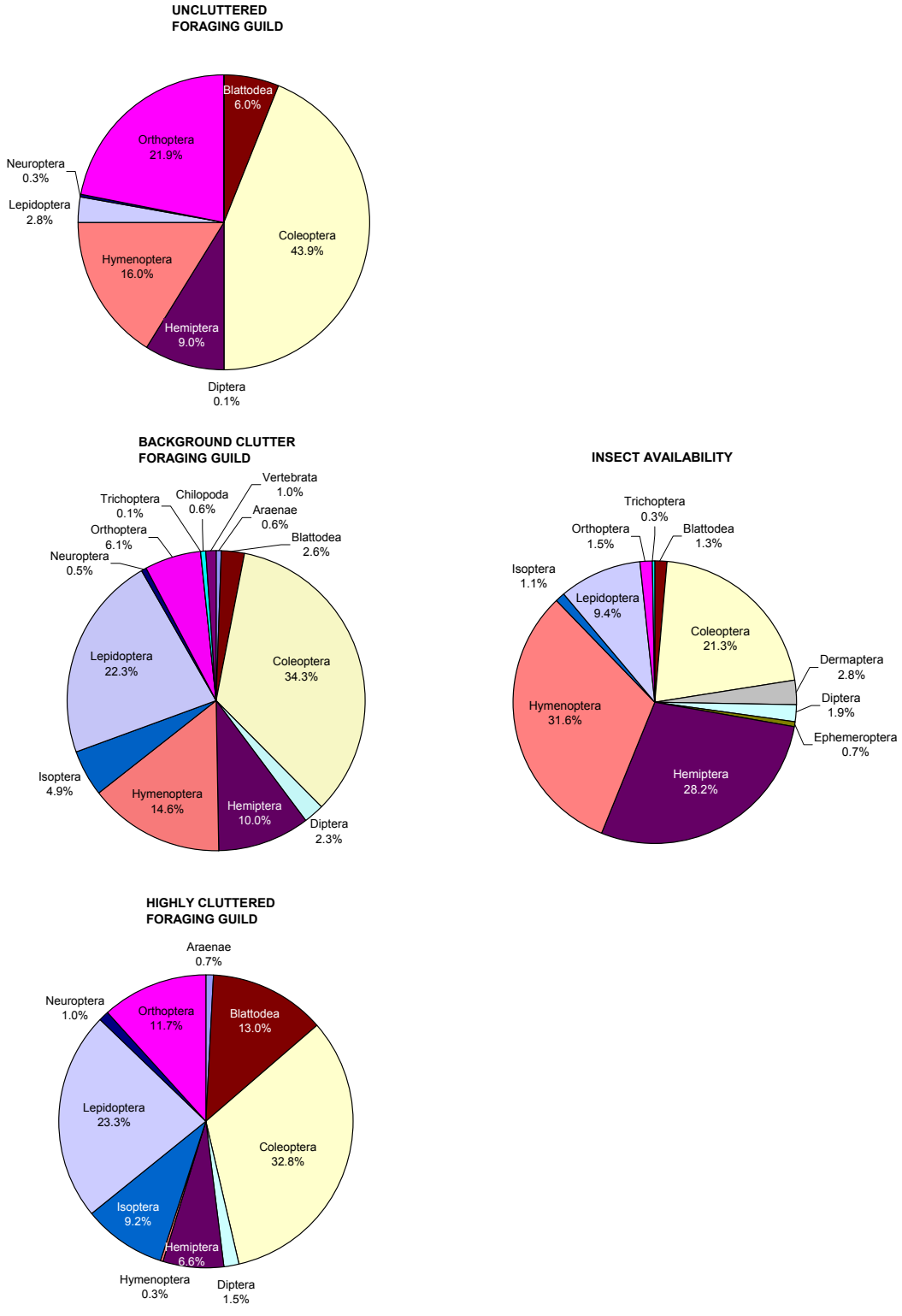


Figure 2. Dietary composition of microbat foraging guilds (left) and comparison with insect availability (right). Dietary composition is the percentage composition of orders identified in the scats and stomach contents of microbats belonging to each foraging guilds. Insect availability is the percentage count of orders identified at sampling sites described in Chapter 3. Only orders with counts >50 are shown.



Macroderma gigas. Scats were all collected from one roost site and consisted primarily of Orthoptera and Coleoptera. Mammal, bird and reptile (lizard) remains were also identified. At the family level, Formicidae (*Iridomyrmex*, *Pheidole* and *Rhytidoponera*) and Cicadidae (cicadas) were found. Of the bats assessed here, *M. gigas* was the only species to record Vertebrata or Chilopoda in the diet. These results are largely consistent with the findings of Pettigrew *et al.* (1986) and Vestjens and Hall (1977), the latter also identified frog remains in the stomachs of bats from the same location. As well as vertebrates, it is generally assumed that *M. gigas* only consumes "large" insects (Richards and Hand 1995; Churchill 1998), but my results and those of Vestjens and Hall identified the remains of termites and ants, which are not regarded as "large".

Hipposideros ater. The highest number of insect orders (nine) were identified in the scats and stomach samples of *H. ater*. Over half (58%) of the average percentage volume consisted of Lepidoptera. This compares to >90% for a dietary study of *H. ater* in North Queensland (Pavey and Burwell 2000). Insects present in the samples that were identified to family level included Formicidae (ants), Fulgoroidea (leaf-hoppers), Mantispidae (mantis flies) and Nematocera.

Hipposideros diadema. The three stomach samples of *H. diadema* consisted almost entirely of Coleoptera (78%) and Lepidoptera (20%). Insect fragments identified to the family level included Fulgoroidea (leaf-hoppers) and Scarabaeidae.

Hipposideros stenotis. Coleoptera (52%) and Lepidoptera (37%) dominated the two stomach samples that were analysed for *H. stenotis*. Insects that were identified to the family level included Tipulidae (crane-flies) and Curculionidae (weevils).

Rhinonicteris aurantius. A high proportion of Lepidoptera (45%) and Coleoptera (36%) were identified in the scat and stomach samples collected for *R. aurantius*. These findings are similar to the dietary assessment of *Rhinonicteris* by Churchill (1994) who, in addition, identified traces of Neuroptera and Mantodea. In this study, those insect fragments that could be identified to the family level included Tipulidae (crane-flies) and Curculionidae (weevils).

Saccolaimus flaviventris. A high proportion of fragments in the stomach samples of *S. flaviventris* could be identified to sub-order or family levels. These included Caelifera (grasshoppers), Braconidae, Dytiscidae (diving-beetles), Elateridae, Fulgoroidea (leaf-hoppers), Gryllacrididae (crickets), Hydrophilidae (water-beetles), Ichneumonidae and Scarabaeidae. Like many other species, the stomachs predominantly contained Coleoptera.

Taphozous georgianus. The composition of insect orders found in the stomachs of *T. georgianus* was similar to that of *S. flaviventris* with Coleoptera dominating the overall volume. Insect families recorded among stomach fragments included: Belostomatidae (*Diplonychus* - fish-killer bugs), Curculionidae (weevils), Cydnidae (burrowing bugs), Dytiscidae (diving-beetles), Formicidae (ants), Fulgoroidea (leaf-hoppers), Hydrophilidae (water-beetles) and Noctuidae (Catocalinae). The sub-order Caelifera (grasshoppers) was also identified.

Taphozous kapalgensis. The three stomach samples examined were almost entirely comprised of the family Gryllidae (field crickets) within the order Orthoptera and contrast dramatically with the diets of all other bat species. No dietary assessment of *T. kapalgensis* has previously been made and further dietary samples from other areas need to be collected to confirm that these findings are typical for the species.

Chaerephon jobensis. Stomach samples of *C. jobensis* contained the highest percent volume of Blattodea of all Top End bat species assessed. Insect fragments within stomach samples included the Dipteran sub-orders Cyclorrapha and Nematocera and the families Tetrigidae (pygmy grasshoppers), Carabidae (ground beetles including *Harpalani*), Dytiscidae (diving-beetles), Fulgoroidea (leaf-hoppers), Hydrophiloidea (water-beetles), Culicidae (mosquitoes) and Formicidae (ants). Vestjens and Hall (1977) also identified the presence of Dermaptera in the stomachs of this bat.

Mormopterus beccarii. The two stomach samples that were analysed for this species contained the highest percentage content of Hymenoptera of any Top End bat in this study (54%) as well as a high proportion of Coleoptera (39%). All of the Hymenoptera remains were ants (Formicidae).

Mormopterus loriae. Only three insect orders were identified in the four stomach samples that were analysed; Coleoptera (74%), Hymenoptera (22%) and Hemiptera (3%). Insects that could be identified to family/superfamily levels included Formicidae (sub-family Formicinae), Hydrophiloidea (water-beetles) and Fulgoroidea (leaf-hoppers).

Miniopterus schreibersii. Almost three-quarters (73%) of the scat samples that were analysed consisted of Lepidoptera. Lepidoptera was also considered to be the primary food item of *M. schreibersii* by Vestjens and Hall (1977 and references therein). This result is somewhat unexpected based on dietary predictions using call frequency analysis (Appendix 3). Insect families/superfamilies that were identified in the diet included Formicidae (ants), Miridae and Fulgoroidea (leaf-hoppers).

Nyctophilus arnhemensis. Seven insect orders were identified in the scat and stomach samples, however no order clearly dominated the diet of this species. Insects that were identified to higher taxonomic levels included Coccoidea as well as Hydrophiloidea (water-beetles) and Gryllidae (field crickets). Although this species is relatively common (pers. obs.), this is the first examination of the dietary habits of this northern tropical bat.

Nyctophilus bifax. Just two insect orders were identified in the stomachs and scats of *N. bifax*; Coleoptera (78%) and Hemiptera (22%). All of the Hemiptera insect fragments were identified as belonging to the family Cicadidae (cicadas).

Nyctophilus geoffroyi. In contrast to *N. bifax*, the two stomach samples for *N. geoffroyi* mainly consisted of Orthoptera (62%) and Blattodea (35%).

For both *N. geoffroyi* and *N. bifax*, Vestjens and Hall (1977) identified a high proportion of Lepidoptera in stomachs samples. No traces of Lepidoptera were detected in samples for either of these species in this study. However, for *N. geoffroyi*, Vestjens and Hall assessed a much larger sample size (36 stomachs), predominantly from southern Australia. Therefore, the absence of Lepidoptera in the diets of *N. geoffroyi* and *N. bifax* from Northern Australia may be a result of geographic variation in diet with these species; however, additional sampling is needed to confirm this pattern.

Nyctophilus walkeri. Scat and stomach samples for *N. walkeri* identified eight insect orders dominated by Lepidoptera (41%) and Coleoptera (38%). At the sub-order level, Nematocera was identified, and at the family level, Culicidae (mosquitoes), Delphacidae, Elateridae (click beetles), Fulgoroidea (leaf-hoppers), Hydrophiloidea (water-beetles) and Scarabaeidae were present.

Chalinolobus gouldii. Insect orders that dominated the stomach contents of *C. gouldii* in the Top End included Hemiptera (42%) and Orthoptera (36%). Formicidae (ants), Cydnidae (burrowing bugs), Gryllidae (field crickets) and Fulgoroidea (leaf-hoppers) were identified at the family/superfamily levels. In southern Australia, Lepidoptera have been claimed to be an important component of the diet of *C. gouldii* based on the presence of Bogong moths in the stomachs of several specimens collected at one location (Vestjens and Hall 1977). I suggest this may have been due to an increase in the availability of the moth due to its seasonal migration patterns however no sampling dates are provided by the authors to confirm this. In contrast to our sample, Tasmanian *C. gouldii* captured a high proportion of 'caterpillars' (O'Neill and Taylor 1989)

Chalinolobus nigrogriseus. Eight insect orders were identified in the stomachs and scats of *C. nigrogriseus* that were dominated by Coleoptera (39%), Hymenoptera (35%) and Lepidoptera (19%).

Myotis macropus. Scats for this microbat contained the highest percentage volume of Isoptera (termites) than all other species, however analysis was based on just four samples (20 faecal pellets) collected from one location. The availability of flying termites as prey for bats is limited seasonally. Within the study area, mass emergences of winged alates generally occur early in the wet season after rain in November and December (Andersen *et al.* 2004). Because sampling of bat diets took place at this time, it appears likely that the bats were exploiting the temporary abundance of a highly profitable food source. Therefore, this dietary profile is unlikely to be representative of the rest of the year. In addition to termites, fragments of insects from the Dipteran sub-orders Nematocera and Cyclorrapha were identified as well as the family Formicidae (genus *Myrmicinae*) and superfamily Fulgoroidea (leaf-hoppers). Nycteribiidae (bat-flies) were also present in dietary samples, however, these flies are commensal on bats

and are therefore likely to have been ingested incidentally. When compared to a dietary assessment of *M. macropus* in north-east N.S.W. (Law and Urquhart 2000), Lepidoptera, Blattodea, Isoptera and Araenae were only present in Top End dietary samples, whereas Trichoptera, Vertebrata (fish scales) and 'aquatic insects' were only present in NSW.

Pipistrellus adamsi. Coleoptera and Hymenoptera (both 35% volume) were the main prey in stomach contents of *P. adamsi*. Identifications below the ordinal level revealed Nematocera (sub-order), Culicidae (mosquitoes), Curculionidae (weevils), Delphacidae, Formicidae (ants) and Fulgoroidea (leaf-hoppers). No dietary analysis previously existed for this species.

Pipistrellus westralis. Major prey in the diet of *P. westralis* included Lepidoptera, Coleoptera, Hymenoptera and Hemiptera. Few family level identifications were possible.

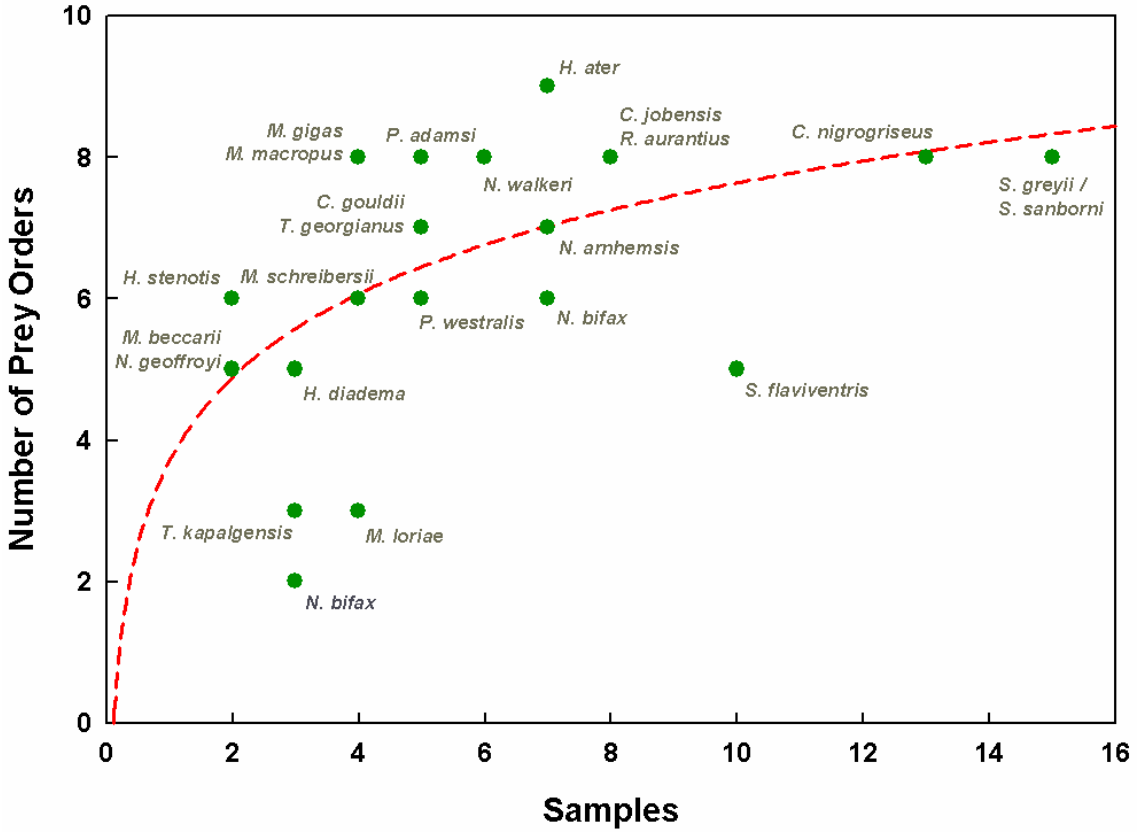
Scotorepens greyii and *S. sanborni*. Like many other bat species, Coleoptera was the main prey item identified (44%) as well as a high proportion of Hemiptera (28%).

Vespadelus caurinus. Scats and stomachs were dominated by Coleoptera (43%) and Hymenoptera (45%). *V. caurinus* was the only species to have Trichoptera detected in the diet. More specific taxonomic identifications included Nematocera, as well as Formicidae (ants), Fulgoroidea (leaf-hoppers), Hydrophiloidea (water-beetles) and Ephydridae.

Analysis of foraging guilds (Figure 2) showed that Coleoptera and Orthoptera were proportionally highest in the diets of bats attributed to the 'Uncluttered' foraging guild and Lepidoptera was greatest in the 'Highly cluttered' foraging guild. The highest number of orders occurred in the 'Background Clutter' foraging guild. For insect availability, Hymenoptera and Hemiptera were the most abundant insects for all sample sites.

The graph of sampling adequacy (Figure 3) revealed that the fitted logarithmic curve does not asymptote, therefore it is highly likely that sampling was inadequate

Figure 3. Graph of *sampling adequacy*. Total number of orders identified in the diets plotted against sample size for each microbat species. Dashed red line is a fitted logarithmic curve using the Marquardt-Levenberg algorithm (SigmaPlot Version 7, SPSS Inc., Illinois). The graph also indicates *dietary specialisation* (species below the line have relatively highly specialised diets whereas species above the line have relatively unspecialised diets).



particularly for species with smaller sample sizes. For dietary specialisation, those species that occur well above the fitted curve (and have relatively high sample sizes) suggests a relatively diverse diet (e.g. *H. ater*) whereas species that fall well below the line indicates a relatively specialised diet (e.g. *S. flaviventris*). Niche breadth analysis (Table 2) measured *M. gigas*, *M. macropus*, *P. adamsi* and *P. westralis* as having relatively wide dietary breadths ($B_A > 0.6$); conversely the dietary breadths of *S. flaviventris*, *N. arnhemensis* and *S. greyii* / *S. sanborni* were relatively narrow ($B_A < 0.2$).

Table 2. Dietary breadth of Top End Microbats. B_A is Levin's measure of standardized niche breadth whereas total sample size (n) is shown in brackets. Only those species with ≥ 4 samples are presented.

Species	B_A (n)
Macroderma gigas	0.65 (4)
Hipposideros ater	0.25 (7)
Rhinonicteris aurantius	0.27 (8)
Saccolaimus flaviventris	0.14 (10)
Taphozous georgianus	0.40 (5)
Chaerephon jobensis	0.42 (8)
Mormopterus loriae	0.21 (4)
Miniopterus schreibersii	0.22 (4)
Nyctophilus arnhemensis	0.18 (7)
Nyctophilus walkeri	0.32 (6)
Chalinolobus gouldii	0.50 (5)
Chalinolobus nigrogriseus	0.26 (13)
Myotis macropus	0.65 (4)
Pipistrellus adamsi	0.64 (5)
Pipistrellus westralis	0.81 (5)
Scotorepens greyii / S. sanborni	0.15 (15)
Vespadelus caurinus	0.24 (7)

Discussion

Overall, the prey remains in the scats and stomachs of each bat species analysed consisted of a variety of orders. This indicates that Top End microbats have generalist dietary requirements and/or opportunistic foraging habits. There were, however, several exceptions. The diets of *H. diadema*, *H. stenotis, M. loriae, N. geoffroyi, N. bifax* and *T. kapalgensis* were comprised almost entirely of one or two insect orders, although all six dietary accounts suffered from limited sample sizes (between 2 and 4 inclusive).

Apart from being slightly smaller, *T. kapalgensis* is morphologically similar to *T. georgianus,* however the diets differ dramatically (Figure 1). One of the main differences between the two species is echolocation call. Compared to *T. georgianus*, the Anabat call signature of *T. kapalgensis* is very short with a narrow frequency range (Appendix 1, 2) and is unique for Top End bats, or indeed bats recorded elsewhere (e.g. Pennay *et al.* 2004). This may be an adaptation to detecting and capturing crickets which made up almost the entire diet of this species in this sample. Further sampling is required to confirm this hypothesis. Currently, the known distributions of *H. diadema, H. stenotis, M. loriae* and *T. kapalgensis* are restricted (Chapter 5). If these species do have specialised diets, it may be one of the limiting factors that restrict their distribution to areas with suitable prey availability. Again further analysis of prey availability and prey selection is required to test this suggestion. The limited number of insect orders that were identified in the diets of *N. geoffroyi* and *N. bifax* cannot be readily explained and may be an anomaly resulting from the limited sample sizes.

For species with larger sample sizes, *S. flaviventris* was identified in the analysis of dietary specialisation (Figure 3) and dietary breadth (Table 2) as having a relatively specialised diet (primarily Coleoptera). Again, caution must be taken when interpreting these results because of the tremendous amount of variety that can occur within a given insect order. Microbats that were identified as foraging on a limited number of orders are not necessarily selectively foraging on a limited range of insect types. The two analyses also present contrasting results for *H. ater*. This was because of the two different units of measure that was used for each analysis. Dietary specialisation was based on the *number* of orders, whereas dietary breadth used *percent volume* of orders. The diet of *H. ater* consisted of several orders indicating low dietary specialisation (Figure 3). However, in terms of overall volume the diet was dominated by a single order, Lepidoptera, and therefore resulted in a low value for dietary breadth (Table 2).

Some of the prey remains identified from the diet samples were of non-volant taxa which indicate gleaning may be used as a foraging technique. *M. gigas* (Ghost bat) scats contained the remains of lizards and centipedes. Ghost bats are known to forage on terrestrial non-volant prey (Kulzer *et al.* 1984) and this result was not unexpected. Araenae (spiders) were identified in diets of several species including *H. ater*, *T. georgianus*, *M. schreibersii*, *N. walkeri*, *C. nigrogriseus*, *P. adamsi* and *P. westralis*. *H.*

ater and *N. walkeri* are both known to have a slow fluttery flight (Churchill 1984; Pavey and Burwell 1995) which may allow these species to glean spiders from surfaces. But gleaning was not identified as foraging technique (nor was Araenae identified in the diets) of *H. ater* in the study by Pavey and Burwell (2000) in north Queensland. *T. georgianus*, *M. schreibersii* and *C. nigrogriseus* each have relatively fast direct flight habits (pers. obs.) and are unlikely to use gleaning as a foraging technique. It is more likely bats are obtaining spiders by flying through their webs or foraging on ballooning spiders (Fenton 1990). It is unclear if *P. adamsi* and *P. westralis* might 'glean' when foraging. In Chapter 4, *P. adamsi* was shown to have atypical nightly temporal activity patterns compared to most other Top End microbat species. That activity indicated gleaning might be employed by this species as a foraging technique. Observations of foraging activity of these species using light-tagging is required to confirm this possibility.

I did not expect aquatic insects (Hydrophiloidea (water beetle) and Dytiscidae (diving-beetle)) to be identified in the diets of several microbat species (*S. flaviventris*, *T. georgianus*, *C. jobensis*, *M. loriae*, *N. arnhemensis*, *N. walkeri* and *C. nigrogriseus*). This result was probably related to the timing of sampling procedures. A large proportion of the dietary samples were obtained at the end of the northern tropical dry-season (October-November) when temporary waterholes dry up. Many aquatic insects fly in search of other water sources when this occurs (Zborowski and Storey 2003). No information is available on the volant activity of aquatic insects throughout the year, but it is possible that bats were exploiting a potentially seasonally abundant food source.

There were some notable differences between the diet compositions of each foraging guild (Figure 2). There was a higher proportion of Orthoptera and Coleoptera in the 'Uncluttered' foraging guild. Insects within these orders are generally larger and less maneuverable than insects in other orders. The flight of bats in this guild is generally fast and direct which is conducive to foraging on these types of insects. Conversely, the generally slow, fluttery insects of the order Lepidoptera were taken in much larger proportions by bats in the 'Background clutter' and 'Highly cluttered' foraging guilds and reflects the more maneuverable foraging habits of these groups of bats (Schnitzler and Kalko 1998). This observation is supported by the comparison with insect availability (Figure 2). For example Lepidoptera, that were represented by 9.4% (by

number) of flying insects captured, but made up just 2.8% (by volume) of the diet of bats in the 'Uncluttered' foraging guild but > 20% in both the 'Background clutter' and 'Highly cluttered' foraging guilds, indicating that these bats were selectively foraging on this insect group. Similar patterns can also be observed for the Orthoptera and Coleoptera orders. Hymenoptera occurred in relatively high proportions in the 'Uncluttered' and 'Background clutter' guild but was also virtually absent from the 'Highly cluttered' guild. This reason for this is unclear and may again be a product of limited sampling causing anomalies in some of my results. Generally however, there were few clear differences between foraging guilds in the proportions of other orders suggesting that there is considerable overlap between microbat diets irrespective of foraging strategy.

The overall conclusion that Top End microbats forage (more or less) opportunistically provides support for some of the findings in previous chapters. In Chapter 3, I showed there were no significant associations between Top End microbat communities and several measures of insect size, composition and taxonomy (orders). Similarly, Chapter 4 demonstrated only limited associations between the temporal activity of Top End microbats and insect activity. Both of these studies noted some shortcomings in the sampling methods, mainly a failure to sample non-volant and high-flying insects, therefore making conclusions tentative. This dietary analysis provides further evidence that any link between Top End microbats and insect availability is weak and strengthens the evidence of Chapters 3 and 4 for insects having little influence over bat community composition and temporal patterns.

Some caution must be used when interpreting these results as both microbat foraging behaviour (Barclay 1989; Rydell 1993; Churchill 1994, Chapter 4) and insect availability (Taylor 1963; Janzen and Scholener 1968; Bowden 1973, Chapter 4) can vary considerably. As previously mentioned, samples for several species were limited and may reflect the availability of prey at that time. Whitaker (1988) recommends at least 15 samples for this type of analysis. Nonetheless, this is the first complete dietary assessment of a regional bat fauna in northern Australia, as well as the first assessment of the diets for several microbat species. It provides a useful baseline for further research into dietary and foraging ecology as well as better informed management of Top End microbats in several ways. First, the data reveal previously unknown aspects of

Top End microbat ecology. Second, with respect to microbat conservation, given the generalist nature of microbat diets in the Top End, it is probably unnecessary for foraging assessments to be the primary focus of future research. However, this study has shown that dietary research is a potentially important to adequately manage several individual species.

Chapter 7.
Conclusion

Conclusion

I have described how the Top End of the Northern Territory supports a rich microbat fauna compared to other regions of Australia. However, microbat diversity is not as high in the Top End as in many other tropical regions (even though the processes that drive species diversity are the same, Chapter 1), nor are the habitat associations for microbat species and assemblages as distinct. For instance in Paraguay, López-González (2004) found bat species presence was strongly associated with vegetation patterns; similarly Aguirre (2002) attributed the high bat species diversity in Bolivia to vegetation structure; Kingston *et al.* (2003) identified that a significant proportion of microbat diversity in Malaysia specifically occurred within forest interiors; and Baker *et al.* (1994) describes five closely related species in the Genus *Chirodema* that occur in northern South America and identified allopatric distributions for three of those species. It appears that the relatively homogeneous landscape of the Top End, that is characterised by eucalypt grassy woodlands and relatively low topographic relief, has limited the evolution of a highly diverse microbat fauna and has also resulted in relatively broad distributions for the majority of species present. This is broadly similar to patterns observed for other mammals in the Top End (Woinarski *et al.* 2005).

Nevertheless, the microbat fauna of the Top End savannas contains a unique assemblage of species. This unique faunal community was relatively unknown at the outset of this study. As a consequence, each of the primary areas of research I addressed yielded novel information. Specifically, I described the habitat relationships of microbats at both the community and species levels; assessed microbat activity patterns; and conducted an assemblage-wide dietary analysis. The key results are summarized below.

- Within the relatively homogeneous landscape of the Top End, areas of high rainfall and high habitat complexity support a high diversity of microbat species (Chapters 3, 4). Areas of high habitat complexity include riparian zones *and* adjacent areas, (i.e. where the vegetation is influenced by riparian systems) and/or areas with high topographic variability (rugged hills and escarpments).

- Microbat activity is influenced by various combinations of moonlight, moonphase, temperature and time of night. Microbat activity also increases dramatically in October (Chapter 5).

- Microbat activity is highly variable across a range of temporal scales (hourly, nightly, monthly and yearly) which has significant implications for sampling. In general, sampling periods for microbats need to be relatively long to account for high temporal variation, and caution must be taken when comparing samples collected between different time periods or different species (Chapters 2, 5).

- There were generally weak associations between microbat species and assemblages and habitats (Chapters 3, 4). In addition, there were few microbat species that exhibited some degree of dietary specialisation (Chapter 6). This indicates that in the Top End, the majority of microbats are 'generalists' with respect to both habitat associations and foraging, a finding that was expected given the extensive geographic ranges of most species.

As a result of this study, an additional 279 microbat species presence records were added to the fauna atlas (Northern Territory Department of Natural Resources, Environment and the Arts) for the Top End. This represents a significant contribution to the atlas which is one of the main sources of information that is used for conservation planning and management of biodiversity in the Northern Territory (e.g. placement of Parks and Reserves and assessment of development proposals). However, records for bats represent only 16% of all Top End terrestrial mammal species records (12% prior to this study) and given that bats make up 28% of all Top End mammal species, this number is still highly unrepresentative and inadequate for the effective conservation and management of microbats in the Top End.

Implications for conservation

The Top End environment is often regarded as largely 'unmodified' and 'intact'. As a consequence, many of the major threatening processes faced by microbats at a national level (Hall 1990; Richards and Hall 1998 and references therein), including deforestation, insecticide poisoning, disturbance, and destruction of caves and mines, are not of major concern in the Top End. However, there are indications that this

situation may be changing. For instance, the rate of land clearing in the Top End is increasing with the area cleared of trees estimated to have increased six-fold in the period 1995-2000 compared to 1990-1995 (Hosking 2002). Invasive weed species are rapidly spreading in some areas (Braithwaite *et al.* 1989; Kean and Price 2003). Of particular concern are grassy weeds that can increase fuel loads and thereby cause intense, frequent fires that can kill trees and shrubs. In addition, there has been a trend away from traditional Aboriginal burning practices to a regime of extensive late dry season fires. The effects of these changes in the Top End, although largely unknown, are considered to be having a catastrophic effect on at least some aspects of the environment (Russell-Smith *et al.* 2000; Andersen *et al.* 2003). Therefore, it is important to enact appropriate management practices to ensure the long-term conservation of microbats in the Top End.

The identification of specific habitats and areas of high value to microbat biodiversity (Chapters 3 and 4) allows for explicit conservation recommendations to be made. Riparian and adjacent surrounding environments support high microbat diversity. These areas are particularly prone to disturbance because they usually have higher quality soils that are desirable for clearing for agriculture and are a focus for livestock that cause soil erosion. There are currently plans for major agricultural development on at least one major Top End river system, the Daly River (Price *et al.* 2003). It is unknown what affect disturbance to these areas will have on microbats, however given vegetation structure appears to be an important component (Chapter 3), management practices should aim to maintain riparian vegetation as well as the adjacent vegetation around these zones. Therefore, areas being cleared of native vegetation require adequate buffers that extend beyond the immediate vicinity of rivers and associated riparian environments. Currently, guidelines for clearing native vegetation in the Northern Territory have some provisions for buffer zones around waterways (Northern Territory Planning Scheme 2006). However, until a clear understanding of the association between microbat diversity and riparian areas is gained, the effectiveness of these guidelines as a surrogate for conserving Top End microbats is unknown.

Escarpments and areas of high topographic relief also support high microbat diversity, particularly for cave roosting species, and should be protected. However, hills and escarpments are not as prone to disturbance as riparian areas and are not under

significant pressure from agricultural or pastoral development. Moreover, large areas of escarpments and associated ranges occur within national parks and reserves including the vast western Arnhem Land escarpment that is protected within Kakadu and adjacent Nitmiluk National Parks. There are still potential threats to microbats in these areas, most notably changes in fire regimes that have had deleterious effects on fire-sensitive vegetation associated with sandstone plateaus (Russell-Smith *et al.* 2002). In addition, mining activities are generally concentrated in these areas and can physically damage or destroy caves and crevices that are used by roosting bats. Fortunately, areas impacted by mining are relatively small in extent.

Other environments should not be neglected. For instance one of the microbat assemblages identified in Chapter 3 contained species that were absent or poorly represented in assemblages containing high species diversity and associated with rivers and escarpments. This assemblage (Group 5) was associated with low elevations on flat terrain near the coast, typically floodplains. The extensive floodplains of the Top End are particularly subject to degradation, both from the immediate impacts of feral animals and weeds and long-term impacts of climate change and sea-level rise.

Five species of Top End microbats (*Hipposideros diadema*, *H. stenotis, Macroderma gigas*, *Taphozous kapalgensis* and *Saccolaimus saccolaimus*) are classified as 'threatened' or 'data deficient' in either the *Territory Parks and Wildlife Conservation Act* 2000, *Commonwealth Environment Protection and Biodiversity Conservation Act* 1999 or Action Plan for Australian Bats (Duncan *et al.* 1995). It is likely that *T. kapalgensis* has a much wider distribution than previously thought (Chapter 4) and of the five species mentioned is probably the least threatened, although further survey work is warranted (Appendix 2). *H. diadema* and *M. gigas* both have limited distributions (Chapter 4), but are probably reasonably secure within their known ranges. The status of *S. saccolaimus* in the Top End is unknown. There are just two known records of this species, collected in 1979 and 1980 (McKean *et al.* 1981). It is likely that *S. saccolaimus* flies high and readily avoids detection using conventional trapping techniques. Targeted surveys for this species should be conducted to determine its status in the Top End. The status of *H. stenotis* in the Top End appears to be more precarious. Areas of suitable habitat appear to be highly fragmented and it is known from just five records collected in the last 10 years (Chapter 4). During fieldwork for this study (that

included targeted surveys in escarpment areas, which is probably its preferred habitat) it was detected at just one location. Subsequently, a series of surveys targeting abandoned mines, adits and escarpment areas in Kakadu National Park, also detected it at just one location. In addition, it appears to be absent from at least two previously known roost sites (pers. obs.). There are however, vast areas of potentially suitable habitat (Chapter 4) that have not been surveyed. Targeted surveys of these areas as well as at previously known sites (preferably using non-invasive detection techniques such as the Anabat system) should be a focus of immediate action. The habitat modelling carried out in Chapter 4 has assisted in identifying suitable areas for future surveys.

Recommendations for future research

I have already made several proposals for further research on Top End microbats. In summary, these include: investigating various Anabat survey techniques (comparison of walk and drive transects, detector positioning, clarifying the effect of flyway size and small scale variations on bat activity; Chapter 2); carefully targeted studies into the effects of insect availability and insect activity (Chapter 5); conducting field surveys to examine the accuracy of species models and predictive distribution maps (Chapter 4); and additional sampling to confirm species dietary compositions (Chapter 6). Given the relatively meager number of microbat records for the Top End, I also recommend conducting further surveys, particularly in the Arnhem Land region and southern areas of the Top End where very few records exist (Chapter 4), to assist in wildlife assessments and conservation planning in the Top End in general.

A key recommendation for future research arising from this study is to further investigate the association between riparian areas and microbats, particularly as this environment is of significant conservation concern. I measured a significant relationship between microbat diversity and distance to rivers, but not with waterbodies themselves. I suggest that bats may be responding to structural components of the vegetation that change with distance from the river channel, therefore providing a diversity of environments for bats that employ different foraging strategies (Chapters 3, 4). This hypothesis should be tested and the area of influence around riparian areas explored so that specific conservation recommendations (e.g. buffer zone widths) can be developed.

As noted in Chapter 3, monitoring should be a key priority for the future management of microbats in the Top End. As is the case with most other vertebrate groups, limited time, funding, resources and planning usually prevent monitoring from being undertaken. However, the latest developments in echolocation equipment and software (e.g. the Anabat system) enable detectors to be set and left unattended for long periods of time and the resulting data can be quickly processed. These technological advances make microbat monitoring programs more achievable.

Finally, it is clear given the differences that have been described between the Top End microbat fauna and other regions of Australia, particularly southern areas, that my key findings are unlikely to be directly applicable to other regional bat faunas. However, it would be of interest to examine similarities with other tropical regions, particularly those with extensive areas of savanna vegetation.

This research redresses, to some degree, the disparity that existed between our knowledge of microbats and most other terrestrial faunal groups of the Top End. However deficiencies still exist in several areas such as their general biology, taxonomy, roosting preferences and locations, estimates of population sizes and structure and breeding characteristics. In the longer term, I hope that the information presented here will provide a platform for more informed research into the ecology of Top End microbats, in particular, local scale habitat assessments of species assemblages and autecological studies of selected bat species. This would lead to a better knowledge, public awareness and enhanced conservation of this ecologically significant and biologically unique group of animals.

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Appendix 1.

Key to the bat calls of the Top End of the Northern Territory

D.J. Milne (2002). Technical Report No. 71. Parks and Wildlife Commission of the Northern Territory.

KEY TO THE BAT CALLS OF THE TOP END OF THE NORTHERN TERRITORY

Damian J. Milne
Parks and Wildlife Commission of the Northern Territory

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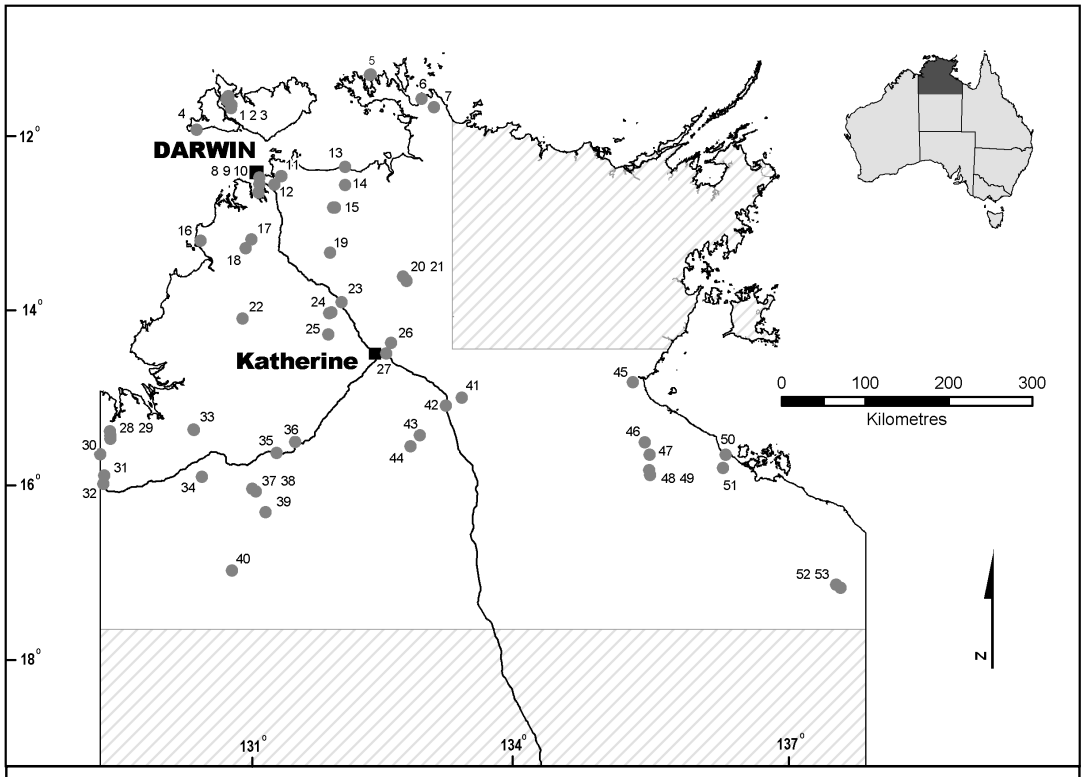
Contents

INTRODUCTION

Anabat detectors (Titley Electronic, Ballina, NSW) have been used with increasing popularity over recent years. Unfortunately, their use has resulted in species lists of bats being published based on Anabat calls without documentation of the characteristics used to separate species. The development of regional keys to bat calls, based on locally collected reference calls, defining the methods and parameters used to identify species is clearly required (Duffy *et al*. 2000). This guide provides such a key for the identification of the microchiropteran bat fauna that occurs in the Top End of the Northern Territory. These calls were obtained using Anabat detectors and analyzed using Analook software (Corben, 2000).

The area covered is north of the 18°S parallel in the monsoon tropics of the Northern Territory, excluding most of the Arnhem Land region where no reference calls have been collected (Figure 1). It is dominated by eucalypt savanna woodlands and encompasses an area of approximately 340 000 km^2 covering eleven bioregions. The area is generally referred to as the “Top End”.



Chaerephon jobensis (15 25 39 42 52), *Chalinolobus gouldii* (24 28 32 39 40 43), *C.nigrogriseus* (5 11 15 21 22 24 25 27 28 29 33 37 39 42 43 51 52), *Hipposideros diadema* (20), *H.ater* (24 27 31 48), *Macroderma gigas* (23) *Miniopterus schreibersii* (8 17 21 28 29 44) *Mormopterus loriae* (45), *Myotis macropus* (8 9) *Nyctophilus arnhemensis* (1 4 5 10 12 29 33 41), *N.bifax* (21 34), *N.geoffroyi* (14 22), *N.walkeri* (21 26 29 33 41), *Pipistrellus adamsi* (7 15 16 21), *P.westralis* (1 2 13 45), *Rhinonicteris aurantius* (18 25 47 52), *Saccolaimus flaviventris* (1 6 15 16 25 30 38 42 48 49 50 52 53), *Scotorepens greyii / S.sanborni* (1 2 5 11 14 16 21 24 32 33 36 40 46 47 50), *Taphozous georgianus* (21 47 53), *T.kapalgensis* (13), *Vespadelus caurinus* (17 21 24 30 35 48).

Figure 1. Locality map showing the area covered by the key (unshaded) and the locations of sites where reference calls were collected (gray dots). The attached text box lists the species that have been recorded and the sites where they were recorded from, according to the numbered sites on the map.

A reference collection of 205 call recordings, from hand identified bats from the Top End, was used to construct the key. The key is based primarily on call frequency, time and slope parameters of these reference calls. Only search phase call pulses of good quality that were unaffected by 'post-release stress' of hand released bats were used in the analysis.

For those species that could not be consistently identified from call frequency and shape of the call pulse, discriminant function analysis was used to test whether call parameters could mathematically differentiate between species. Discriminant function analysis is a powerful statistical tool, that can sometimes differentiate between the calls of two or more species that visually appear very similar. When parameters derived from ANALOOK (which will be described later) are analysed using discriminant function analysis it determines whether those parameters are able to form two or more naturally occurring groups (STATISTICA, 1999). These groups can then be described by a mathematical formula and the level of significance examined. The end result is a more robust and objective means for identifying bat calls.

A dichotomous key is provided to identify calls and includes illustrations to explain the terms used. A summary of characteristic frequency ranges for each species is shown in Figure 4. The range of all frequencies for each species are shaded depending on the method required to identify the call:

- white - the call can be identified based on frequency alone or distinctive call features;
- hatch - discriminant function analysis may be required for accurate identification of the call;
- black - identification to the level of species cannot be made with confidence.

The section on Species Call Descriptions then provides a summary of the average characteristic frequency and 95% confidence interval (= characteristic frequency range), the number and locations of reference calls used and other species that produce similar calls which can be confused with those of the target species. A brief description of the call for each species and one example of a reference call are also provided.

Earlier reference calls were collected using analog tape recorders and subsequently downloaded to computer. The majority of more recently collected reference calls have been digitally recorded from the Anabat detector to a laptop computer (via a ZCAIM unit). White and Gehrt (2001) found that calls recorded this way are of better quality and the parameters derived from ANALOOK can differ significantly between digital and analog recording methods. These parameters are critical in deriving reliable results from the discriminant function analysis. As more digitally recorded reference calls are collected, it is expected that using discriminant function analysis on species with similar calls will produce more reliable separation.

This key is designed to be used with the Analook software (Analook 4.8f - Corben, 2000), therefore a basic working knowledge of the software is required. Analook is a simple program that is easy to learn and freely available (http://www.titley.com.au/tdload.htm). Instructions are provided with the software or refer to "Anabat System Manual" (Corben and O'Farrell, 1999) for complete documentation.

The Anabat system is a non-intrusive means of detection and identification which avoids the need to handle and potentially cause injury to echolocating bats. However, the accuracy and reliability of the identification still depends, to some degree, on the experience and skill of the Anabat user. Inexperienced users should always err on the side of caution when identifying unknown calls. In some cases even expert users may identify to species level as few as 10% of Anabat call files collected during surveys (Duffy *et al.*, 2000). The bottom line…if in doubt, cross it out !

This guide follows many of the principles described in "Key to the bat calls of south-east Queensland and north-east New South Wales" (Reinhold *et al*., 2001). This publication should be referred to for more information on the technical aspects of identifying Anabat calls.

IDENTIFYING CALLS

TERMS USED IN THE KEY

The list below provides definitions of terms that are used in the key and are demonstrated in Figure 2. Definitions have been derived and/or modified from various sources in order to provide a simplified list of the characteristics of calls specific to the species of echolocating bats that occur in the Top End.

Call parameters [1]

Fc	Characteristic frequency, the frequency at the end or flattest portion of the call.
Fk	Frequency at the "knee" or the point at which the slope of the call abruptly changes from a downward slope to a more level slope.
Fmin	Minimum call frequency.
Fmax	Maximum call frequency.
DUR	Total duration of the call.
Tc	Time from the start of the call to Fc.
Tk	Time from the start of the call to Fk.
S1	Slope at the start of the call.
Sc	Slope of the call at Fc.

Sections of a call pulse [2]

Initial	Portion of call between the start of the call and Tk .
Body	Portion of call between Tk and Tc.
Tail	Portion of call between Fc and the end of the call.

Call Types [3]

Four different call types are recognised: flat, constant frequency, linear and curvilinear.

1 Definitions from Corben and O'Farrell (1999)
2 Definitions modified from Reinhold *et al.* (2001)
3 Modified from de Oliveira (1998a)

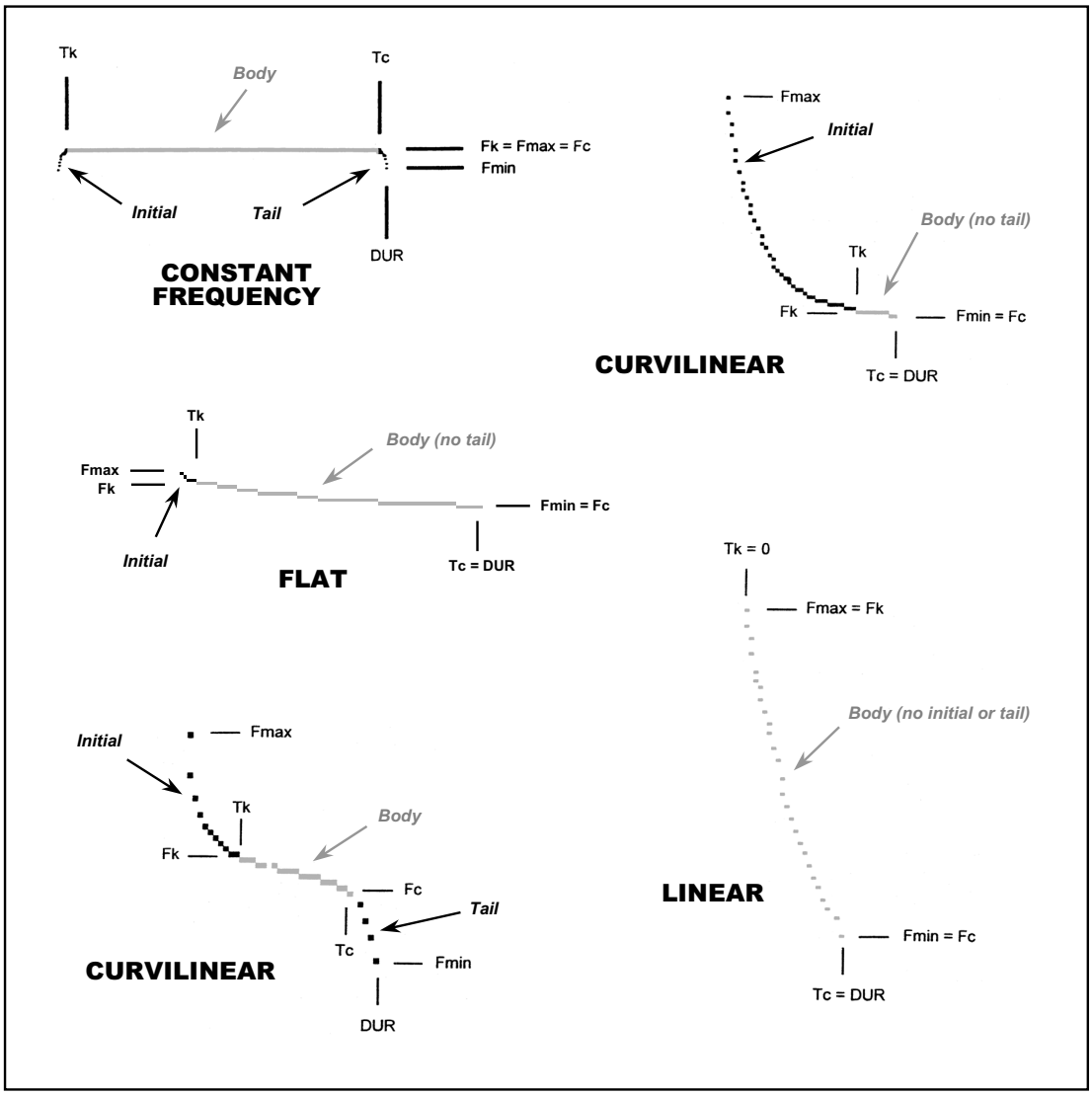


Figure 2. Various types of call pulses and their parameters. All images (except the “flat” call type) are modified from Corben and O’Farrell (1999)

CALL EDITING

To minimise subjectivity, the key is based primarily on measurable call parameters and clearly defined call characteristics of the search phase of calls. Therefore, some minor editing of call sequences is sometimes required to delete non-search phase calls before attempting identification. The following describes some of Analook's call editing techniques (editing the call does not change the original file and saving edits is not normally required).

Only calls based on search phase pulses should be used. Sections of calls containing attack phase pulses and feeding buzzes (Figure 3) should be deleted. Use the **MARK TO EXCLUDE** option to delete these pulses. A minimum of three consistent search phase pulses is required for call identification, but preferably longer call sequences should be used.

Fmin, Fmax and S1 will be affected by "noise" generated through the recording process above and below call pulses. Use the **MARK OFF POINTS** option to delete these points. Fc, Fk, Tc and Sc are affected by the position of the Body of the call. Analook automatically delineates this section (highlighted on screen by pressing "**m**"). However, it does not always do this consistently, particularly for poor quality and/or erratic call sequences. Use the **MODIFY BODIES** option to manually delineate this section of call pulse if required.

Parameters can be viewed at the bottom of the screen by pressing "**m**". They are the mean values for all pulses displayed on the screen, required for the discriminant function equations for the identification of some species. If the entire call sequence does not fit across the screen, reduce the horizontal resolution using the **F1-F10** keys. If the call sequence extends off the top of the screen, toggle the vertical resolution using the **+** and **–** keys.

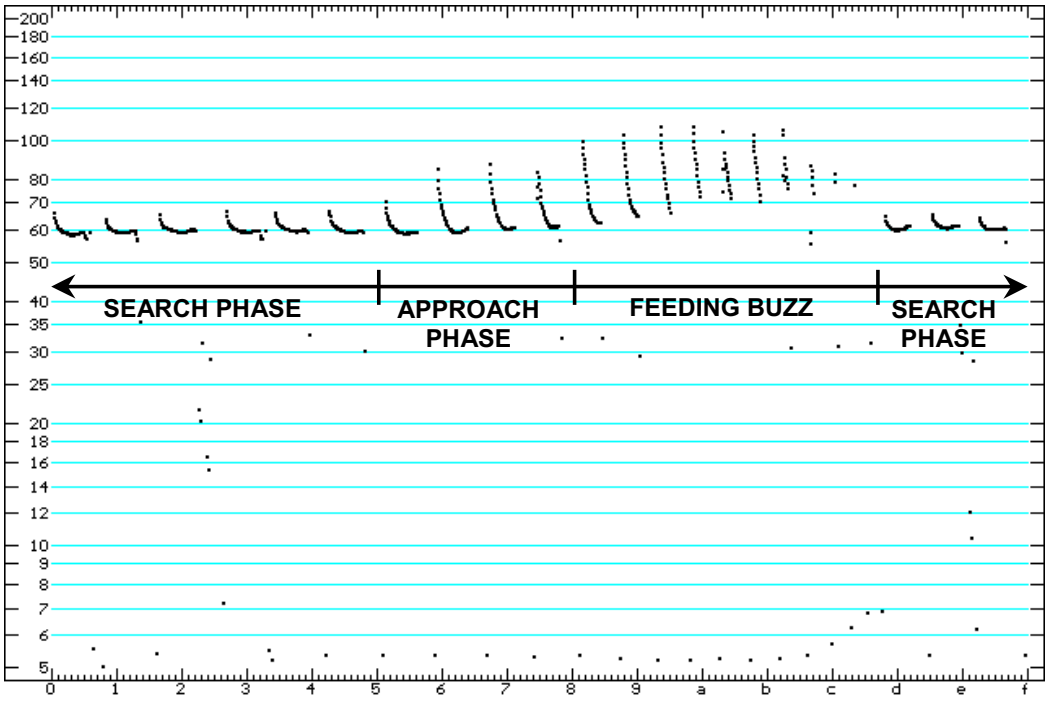
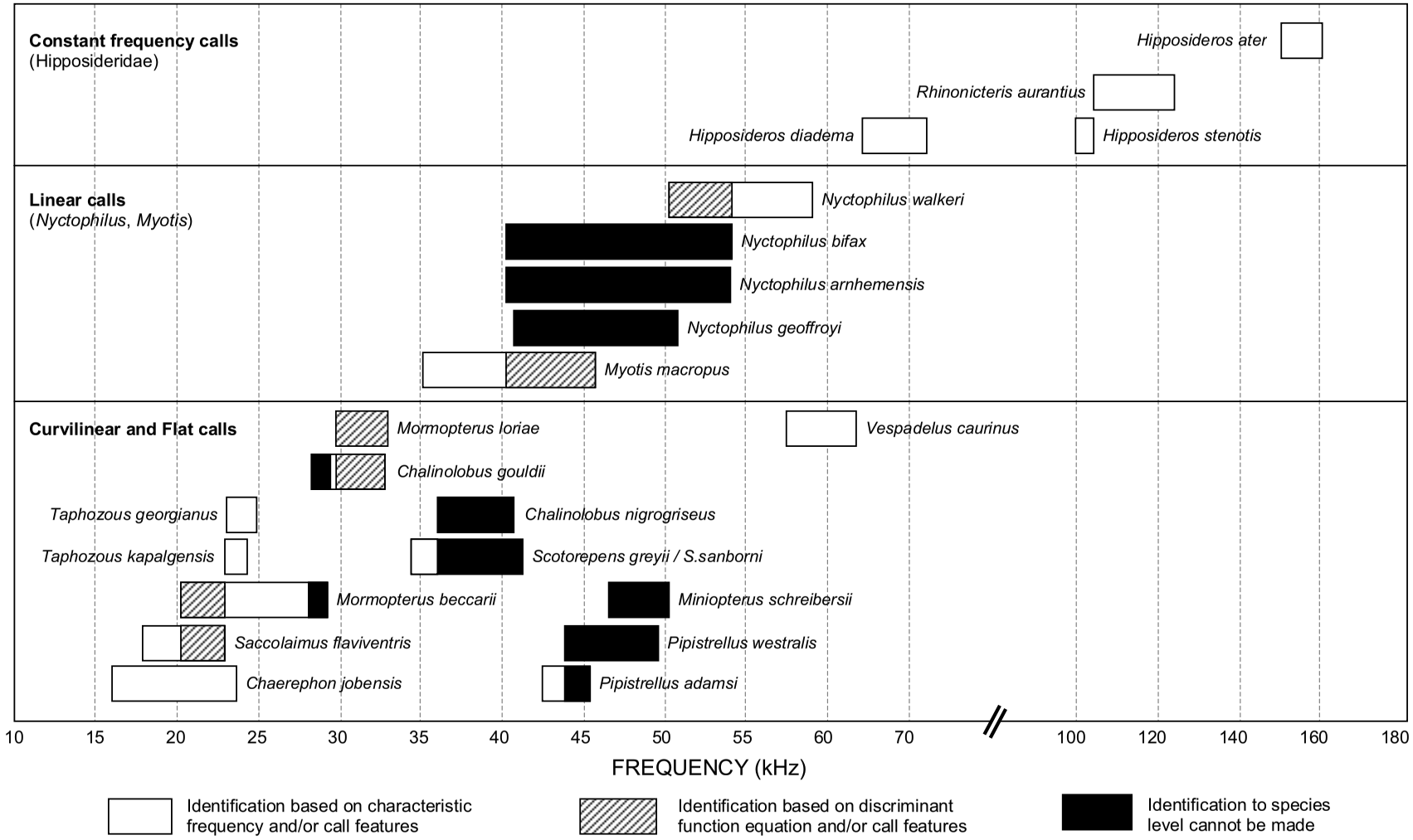


Figure 3. Different phases of a call sequence. Terminology of phases based on de Oliveira (1998b).

FIGURE 4. CHARACTERISTIC FREQUENCY RANGES



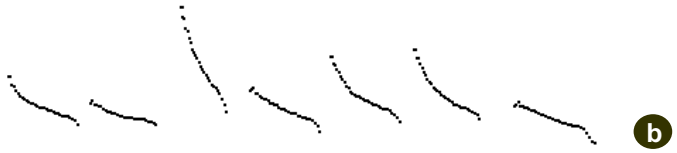
KEY TO BAT CALLS OF THE TOP END

1 a Characteristic frequency less than 33.1 kHz 2
b Characteristic frequency greater than 34.5 kHz 13

2 a Call harmonic (duel frequency) present (a) ..... ***Saccolaimus flaviventris*** (page 14)

b Call harmonic absent 3

3 a Call sequence "messy" i.e. pulse shape variable and inconsistent with abrupt changes in frequency (b), ... ***Chaerephon jobensis*** (page 13)



b Pulses even smooth and consistent, changes are gradual (a) 4

4 a Characteristic frequency less than 20.3 kHz ..... ***Saccolaimus flaviventris*** (page 14)
b Characteristic frequency greater than 20.2 kHz 5

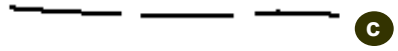
5 a Characteristic frequency less than 28.2 kHz 6
b Characteristic frequency greater than 28.1 kHz 10

6 a Call duration (DUR) of all pulses (minimum 8 pulses) less than 8ms .....
..... ***Taphozous kapalgensis*** (page 16)
b Call duration (DUR) of any pulse greater than 8ms 7

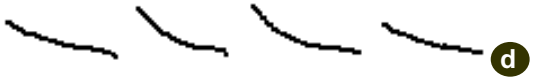
7 a Characteristic frequency less than 23.0 kHz 8
b Characteristic frequency greater than 22.9 kHz 9

8 a FK*7.101 + S1*0.0014 - 76.642 >
FK*8.658 + S1*0.026 - 114.431 ..... ***Saccolaimus flaviventris*** (page 14)
b FK*7.101 + S1*0.0014 - 76.642 <
FK*8.658 + S1*0.026 - 114.431 ..... ***Mormopterus beccarii*** (page 15)

9 a Pulse type flat (c) ..... ***Taphozous georgianus*** (page 17)



b Pulse type curvilinear (d) ..... ***Mormopterus beccarii*** (page 15)

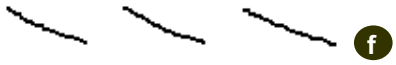


10 a Pulses alternate in characteristic frequency (e) ..... ***Chalinolobus gouldii*** (page 18)

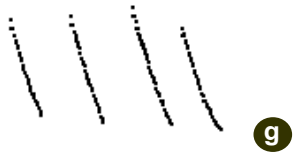
b Pulses do not alternate in frequency (a) 11

11 a Characteristic frequency less than 28.5 kHz .....
..... ***Mormopterus beccarii*** **or** ***Chalinolobus gouldii*** (pages 15,18)
b Characteristic frequency greater than 28.4 kHz 12

12 a Pulses predominantly curved (a)
FK*34.346 - FMAX*4.177 + TC*16.519 - 518.243 >
FK*37.662 - FMAX*5.178 + TC*17.791 - 597.869 ..... ***Chalinolobus gouldii*** (page 18)
b Pulses predominantly straight (f),
FK*34.346 - FMAX*4.177 + TC*16.519 - 518.243 <
FK*37.662 - FMAX*5.178 + TC*17.791 - 597.869 ..... ***Mormopterus loriae*** (page 19)



13 a Pulse type curvilinear (a) or linear (g), characteristic frequency less than 62 kHz 14



b Constant frequency pulse type (h), characteristic frequency greater than 66 kHz 25

14 a Pulse type curvilinear (a) 15
b Pulse type linear (g) 20

15 a Characteristic frequency less than 41.5 kHz 16
b Characteristic frequency greater than 42.4 kHz 17

16 a Characteristic frequency less than 36.1 kHz .....
..... ***Scotorepens greyii*** **or** ***S.sanborni*** (page 20)
b Characteristic frequency greater than 36.0 kHz .....
..... ***Scotorepens greyii*** **or** ***S. sanborni*** **or** ***Chalinolobus nigrogriseus*** (pages 20,21)

17 a Characteristic frequency less than 50.3 kHz 18
b Characteristic frequency greater than 57.4 kHz ..... ***Vespadelus caurinus*** (page 25)

18 a Characteristic frequency less than 44.0 kHz ..... ***Pipistrellus adamsi*** (page 22)
b Characteristic frequency greater than 43.9 kHz 19

19 a Characteristic frequency less than 46.7 kHz .....
.....***Pipistrellus adamsi*** **or** ***P.westralis*** (pages 22,23)
b Characteristic frequency greater than 46.6 kHz .....
.....***Pipistrellus westralis*** **or** ***Miniopterus schreibersii*** (pages 23,24)

20 a Characteristic frequency less than 40.1 kHz .....***Myotis macropus*** (page 26)
b Characteristic frequency greater than 40.0 kHz 21

21 a Characteristic frequency less than 50.2 kHz 22
b Characteristic frequency greater than 50.1 kHz 24

22 a Characteristic frequency less than 45.6 kHz 23
b Characteristic frequency greater than 45.5 kHz .....
..... ***Nyctophilus geoffroyi*** **or** ***N.arnhemensis*** **or** ***N.bifax*** (pages 27,28,29)

23 a FC*6.040 + DUR*17.033 + SC*0.034 - 150.114 >
FC*7.135 + DUR*19.373 + SC*0.023 - 202.991 .....***Myotis macropus*** (page 26)

b FC*6.040 + DUR*17.033 + SC*0.034 - 150.114 <
FC*7.135 + DUR*19.373 + SC*0.023 - 202.991 .....
..... ***Nyctophilus geoffroyi*** **or** ***N.arnhemensis*** **or** ***N.bifax*** (pages 27,28,29)

24 a Some indication of a bend at the end of most pulses (i) when viewed with log scale
FC*8.311 - SC*0.028 + DUR*15.670 - 219.761 <
FC*9.701 - SC*0.062 + DUR*17.632 - 292.275 ..... ***Nyctophilus walkeri*** (page 30)

b No indication of a bend at the end of most pulses (g) when viewed with log scale
FC*8.311 - SC*0.028 + DUR*15.670 - 219.761 >
FC*9.701 - SC*0.062 + DUR*17.632 - 292.275 .....
..... ***Nyctophilus geoffroyi*** **or** ***N.arnhemensis*** **or** ***N.bifax*** (pages 27,28,29)

25 a Characteristic frequency less than 72 kHz .....***Hipposideros diadema*** (page 31)
b Characteristic frequency greater than 101 kHz 26

26 a Characteristic frequency less than 107 kHz ..... ***Hipposideros stenotis*** (page 32)
b Characteristic frequency greater than 107 kHz 27

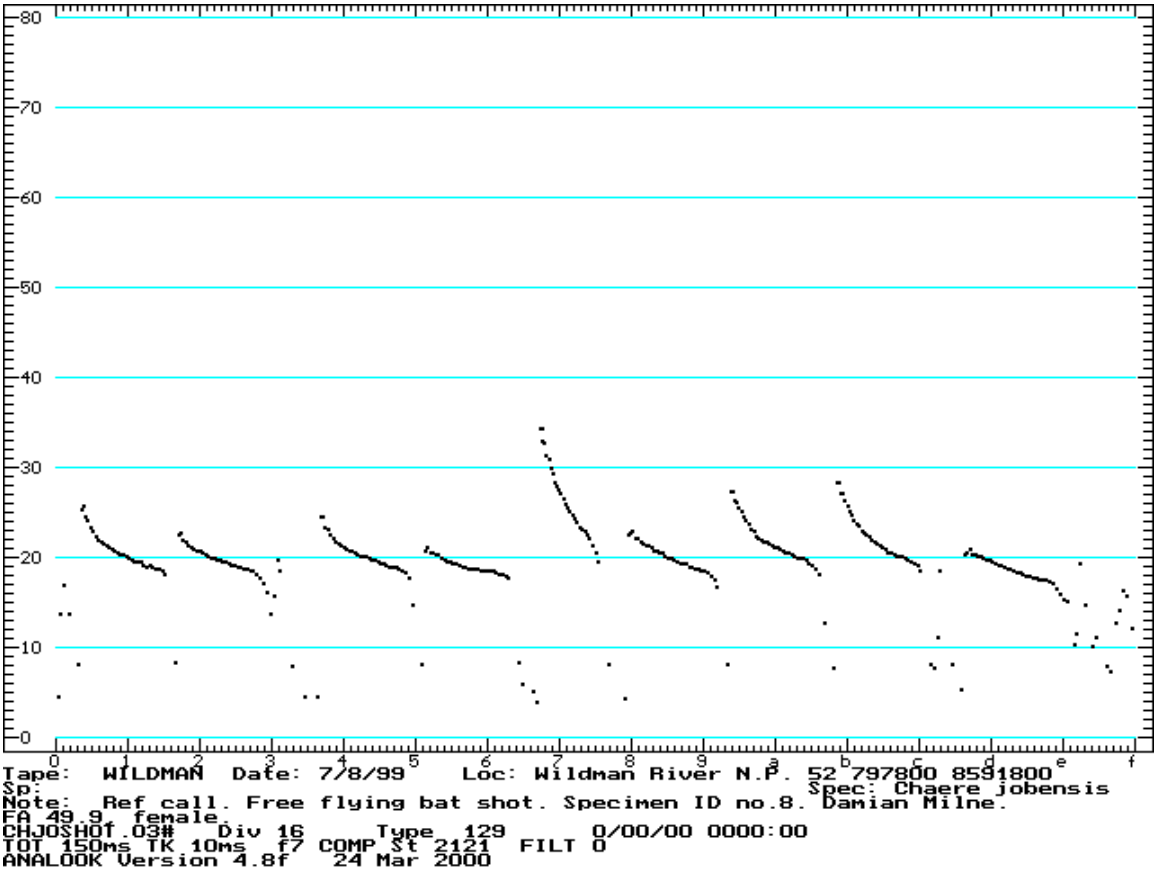
27 a Characteristic frequency less than 126 kHz .....***Rhinonicteris aurantius*** (page 33)
b Characteristic frequency greater than 150 kHz .....***Hipposideros ater*** (page 34)

SPECIES CALL DESCRIPTIONS

Chaerephon jobensis
Northern freetail bat

Characteristic frequency	19.8 kHz	(95% Confidence interval 16.1 - 23.6 kHz)
Number of reference calls	6	(Sites 15, 25, 39, 42, 52)
Similar calls	*Saccolaimus flaviventris*, *Mormopterus beccarii*	

C.jobensis often flies in pairs (T.Reardon pers. comm.). This behaviour tends to produce paired call pulses at alternating frequencies with intermittent, “excited”, linear pulses. This pattern is probably the result of bats interacting with each other. The calls of an individual *C.jobensis* are therefore likely to be difficult to identify from *S.flaviventris* or *M.beccarii*. So far all reference calls for *C.jobensis* have been produced by two individuals, whereas all reference calls collected for *S.flaviventris* (n = 18) have been of solitary animals. Reference calls from Queensland have shown this species to occasionally emit very flat low pulses just below 20 kHz.

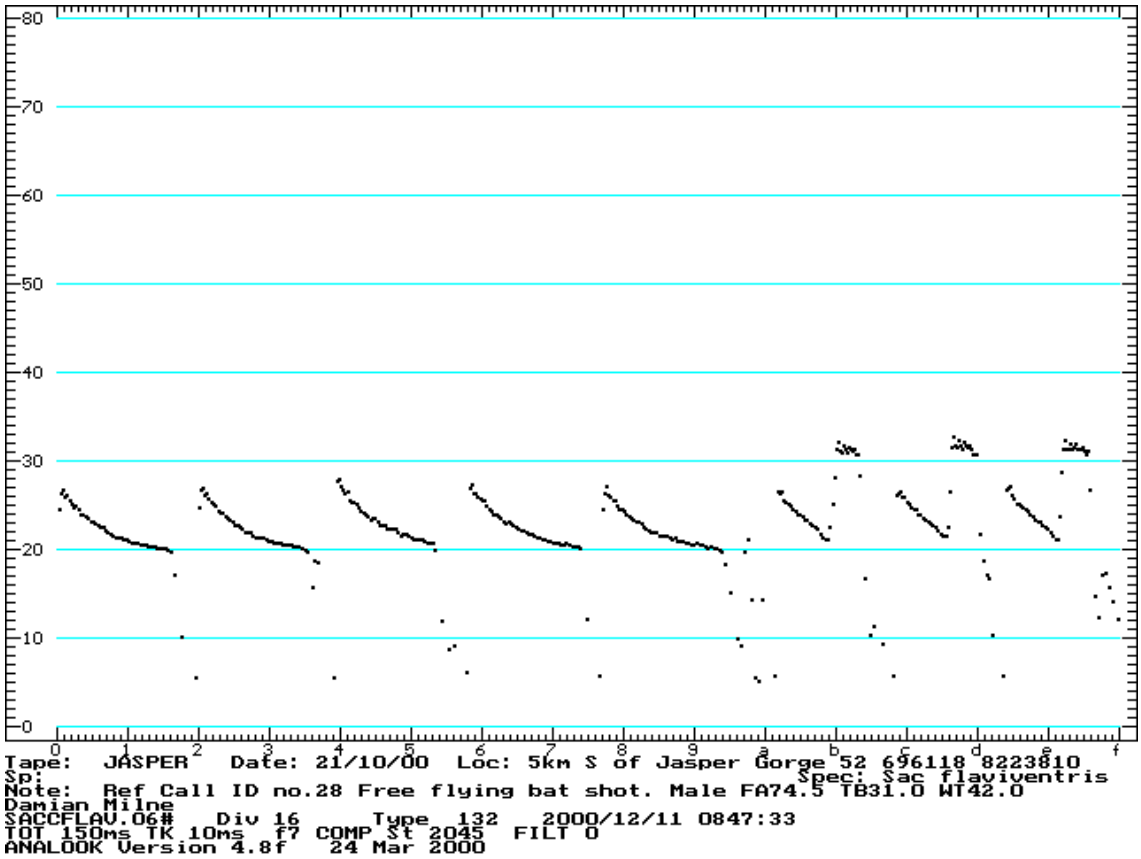


Saccolaimus flaviventris
Yellow-bellied sheathtail bat

Characteristic frequency	20.3 kHz	(95% Confidence interval 17.8 - 22.9 kHz)
Number of reference calls	18	(Sites 1,6,15,16,25,30,38,42,48,49,50,52,53)
Similar calls	*Chaerephon jobensis, Mormopterus beccarii*	

The search phase sonar pulses of *S.flaviventris* are always smooth, consistent and without abrupt changes in frequency between pulses. The curvilinear pulse shape is generally evenly curved, however it can sometimes be quite straight. In one reference call sequence, the pulse shape was flat and very long. *S.flaviventris* sometimes produces a harmonic call at around 30 kHz (shown below), which no other species around this frequency appears to produce. *S.flaviventris* overlaps with the characteristic frequency range of *Mormopterus beccarii* and can be identified if the following condition is satisfied:

FK*7.101 + S1*0.0014 - 76.642 > FK*8.658 + S1*0.026 - 114.431

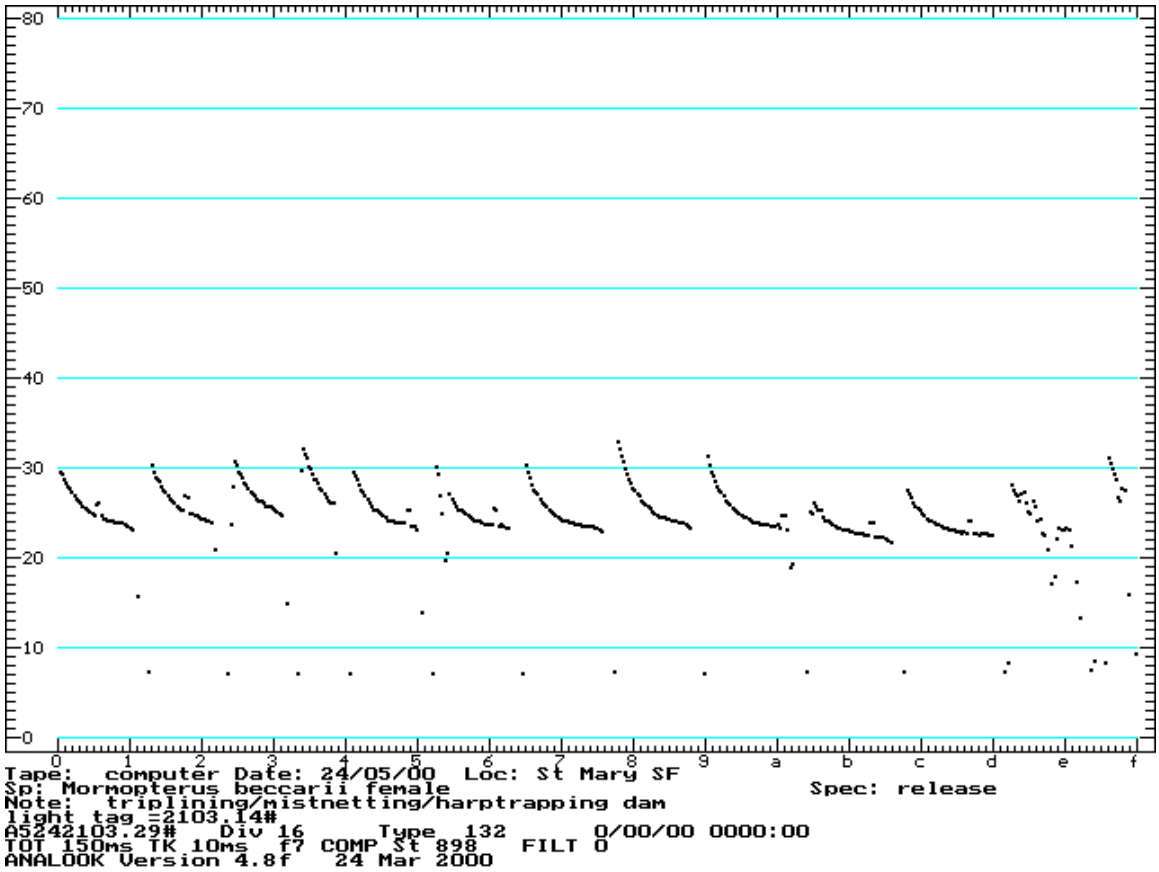


Mormopterus beccarii
Beccari's freetail bat

Characteristic frequency	24.3 kHz	(95% Confidence interval 20.3 - 28.4 kHz)
Number of reference calls	5	(all from Queensland)
Similar calls	*Saccolaimus flaviventris*	

Mormopterus beccarii produces curvilinear search phase call pulses. Where its characteristic frequency range coincides with *S.flaviventris*, and in the absence of call harmonics, it can only be confidently identified by satisfying the condition below. *M.beccarii* also just overlaps with the lower characteristic frequency range of *Chalinolobus gouldii* between 28.2 and 28.4 kHz. Reinhold *et al*. (2001) noted that the pulses of a feeding buzz of *Mormopterus* spp. go through a gradual change in pulse shape. This pattern is in contrast to the feeding buzzes for species such as *Saccolaimus flaviventris* where pulse change is very abrupt. No reference calls for this species have been collected for the Top End. Call parameters are based on reference calls provided by Terry Reardon and Linda Reinhold from bats recorded in Queensland.

FK*7.101 + S1*0.0014 - 76.642 < FK*8.658 + S1*0.026 - 114.431

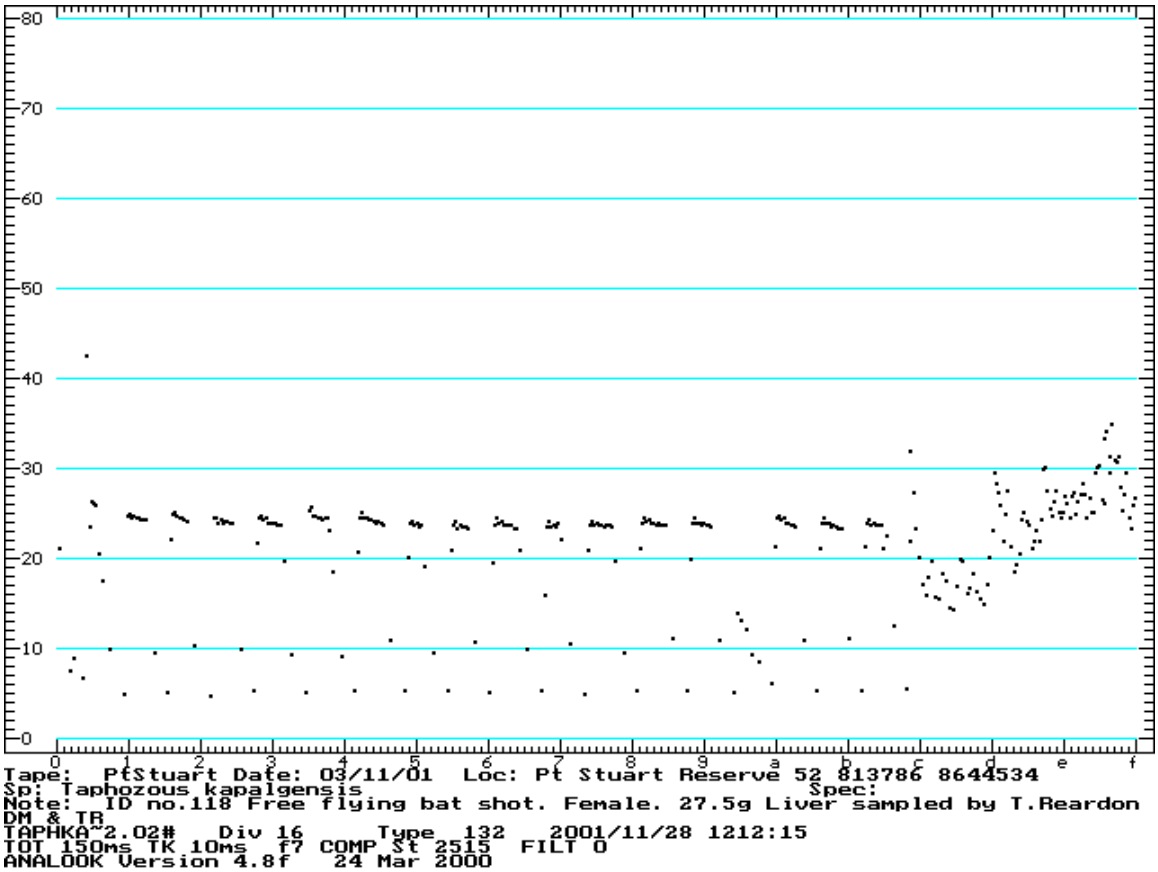


Taphozous kapalgensis
Arnhem sheathtail bat

Characteristic frequency	23.6 kHz	(95% Confidence interval 23.0 - 24.3 kHz)
Number of reference calls	2	(Site 13)
Similar calls	*Taphozous georgianus*, *Mormopterus beccarii*	

Only two reference calls have been obtained from this species, so a definitive description of its call cannot be made. However, one call sequence is of 20 seconds duration. Call pulses were consistent throughout the call sequence so it can be safely assumed to be a search phase call sequence for this species. This call is different to reference calls for other species. Therefore, even though the entire range of call characteristics may not have been obtained, calls detected of this type can be attributed to *T.kapalgensis*. The second reference call was recorded directly to computer and was consistent with the first.

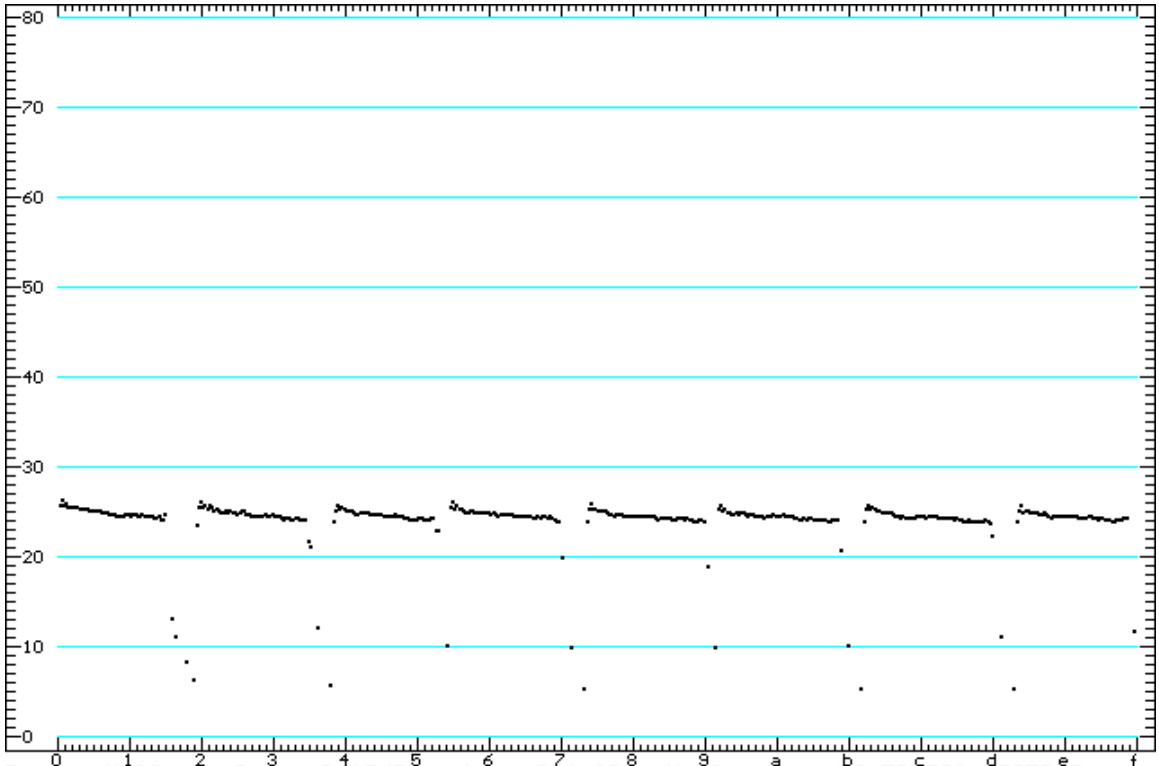
T.kapalgensis produces very short call pulses that are less than 8 ms in duration. This type of call could also be recorded for other “low frequency” bats but only if part of the pulse is recorded as a consequence of these bats flying at the limits of the distance at which the Anabat detector can detect their calls. However, it is unlikely that such pulses would remain consistent for more that three or four pulses as the distance of the bat from the detector will vary as the bat flies. In the key therefore, it is suggested that calls of this nature be attributed to *T.kapalgensis* only if the call sequence has at least 8 pulses.



Taphozous georgianus
Common sheathtail bat

Characteristic frequency	24.1 kHz	(95% Confidence interval 23.3 - 24.9 kHz)
Number of reference calls	6	(Sites 21, 47, 53)
Similar calls	*Taphozous kapalgensis*	

T.georgianus produces a flat type call pulse. It is typically long and straight or slightly curved and almost horizontal. These characteristics readily distinguishes this call from that of any other species. When recording reference calls from hand released individuals of this species, initially the pulse shape is curved, however this does not appear to be the typical pulse shape for this species when in normal “search mode” flight. *Taphozous*, *Chaerephon* and *Saccolaimus* all produce relatively low frequency echolocation calls that travel longer distances than higher frequency calls (Woodside and Taylor, 1985). This allows them to fly faster than most other species by having the capability to detect and avoid obstacles that are far ahead (Churchill, 1998). As a consequence of this signal system, these species tend to forage in open space.

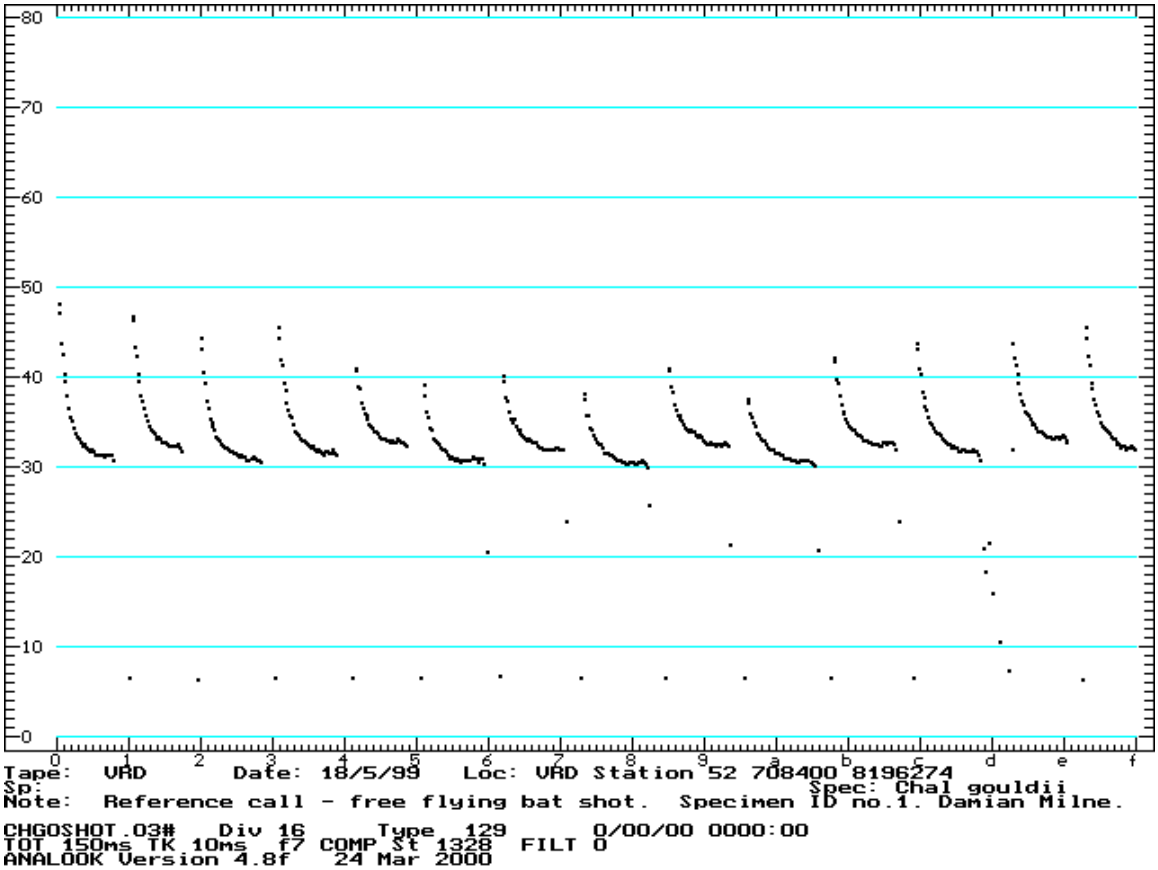


Chalinolobus gouldii
Gould's wattled bat

Characteristic frequency	30.5 kHz	(95% Confidence interval 28.2 - 32.8 kHz)
Number of reference calls	10	(Sites 24, 28, 32, 39, 40, 43)
Similar calls	*Mormopterus beccarii, M. loriae*	

C.gouldii produces a curvilinear pulse shape. In half of the reference call sequences collected, the calls show an alternating call pattern of higher and lower pulses. At the lower end of its characteristic frequency range, this species overlaps with *Mormopterus beccarii*. Above 30.4 kHz it coincides with *Mormopterus loriae* from which it can be distinguished by satisfying the condition set out below.

FK*34.346 - FMAX*4.177 + TC*16.519 - 518.243 > FK*37.662 - FMAX*5.178 + TC*17.791 - 597.869



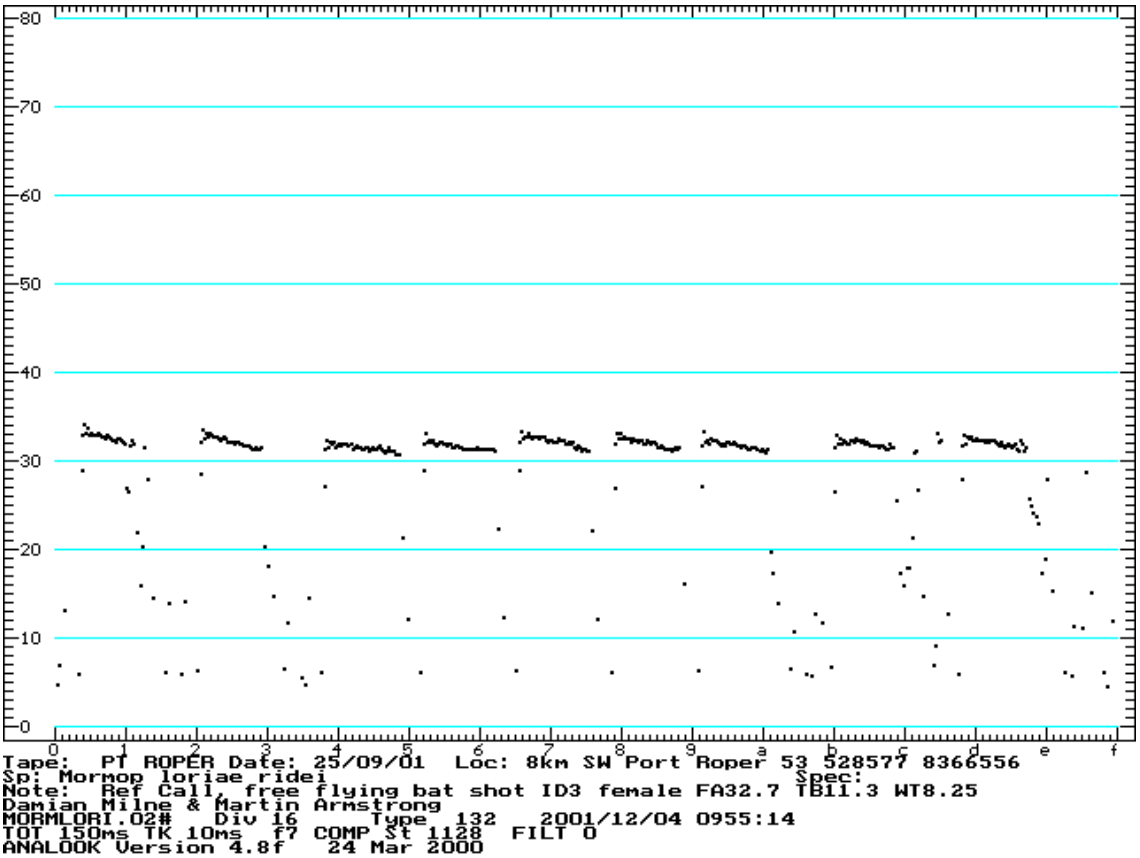
Mormopterus loriae ridei
Little north-eastern freetail bat

Characteristic frequency	31.7 kHz	(95% Confidence interval (29.5) 30.5 - 33.0 kHz)
Number of reference calls	2	(Site 45)
Similar calls	*Chalinolobus gouldii*	

The two reference call sequences collected for this species consist of relatively short, straight call pulses angled slightly above horizontal just above 30 kHz. Virtually its entire frequency range coincides with that of *Chalinolobus gouldii* from which it can be distinguished by having a straighter pulse shape. If there is any doubt over the identification, the discriminant function equation should be used. More reference calls need to be collected to assess the full range of call characteristics, however, calls from the Top End are consistent with those collected from Queensland (provided by Alex Kutt).

It is suspected that the characteristic frequency for this species may drop just below 30 kHz. This view is based on observations of several call sequences where the call pulses at the beginning of the sequence were identical to those described here but subsequent pulses gradually decreased in frequency to around 29.5 kHz by the end of the sequence.

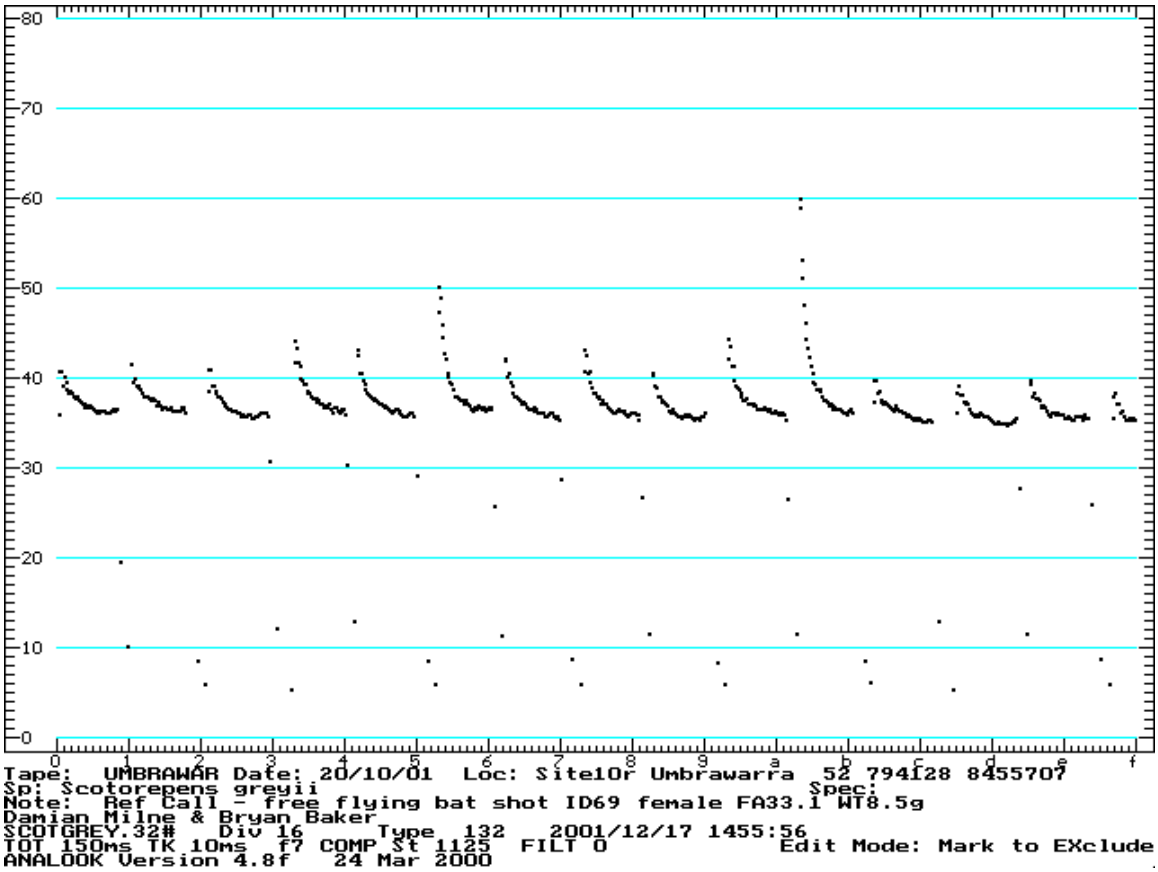
FK*34.346 - FMAX*4.177 + TC*16.519 - 518.243 < FK*37.662 - FMAX*5.178 + TC*17.791 - 597.869



Scotorepens greyii / S.sanborni
Little broad-nosed bat / Northern broad-nosed bat

Characteristic frequency	38.0 kHz	(95% Confidence interval 34.6 - 41.4 kHz)
Number of reference calls	30	(Sites 1,2,5,11,14,16,21,24,32,33,36,40,46,47,50)
Similar calls	*Chalinolobus nigrogriseus*	

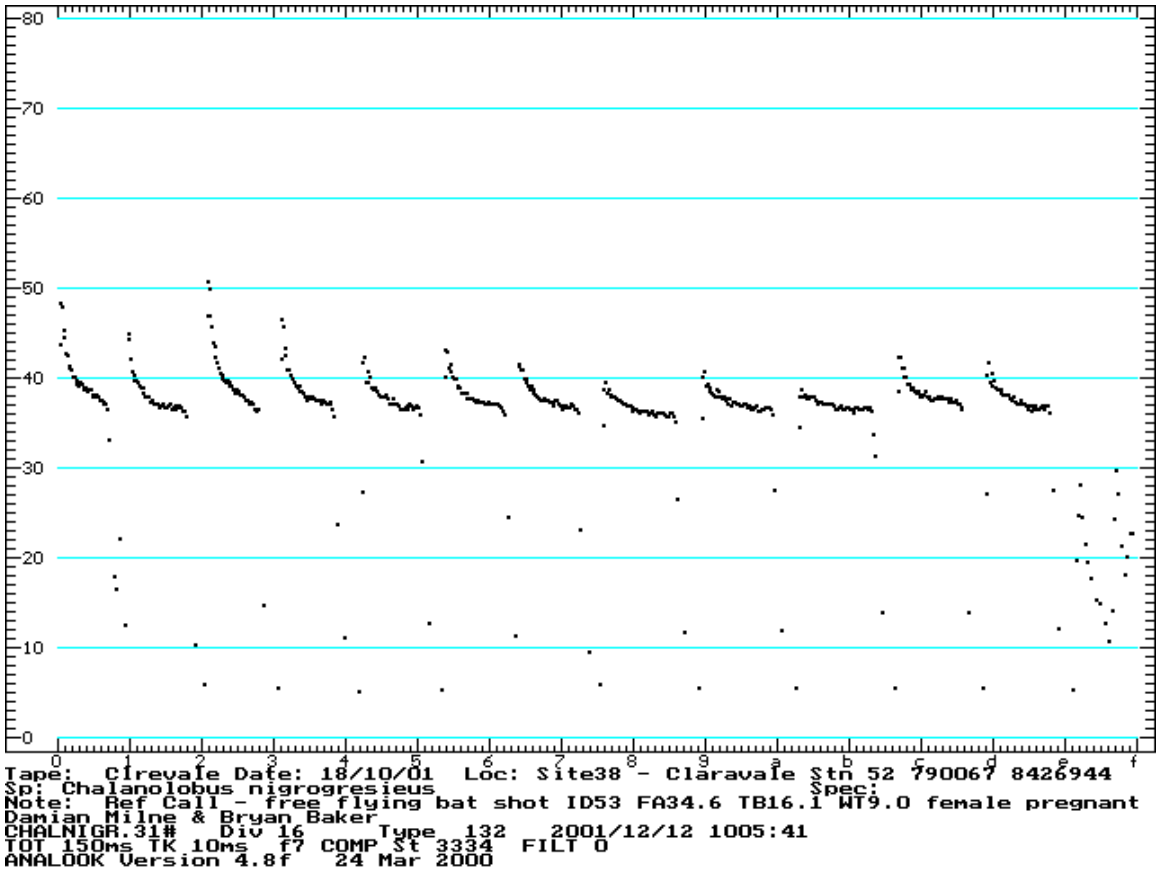
Because *Scotorepens greyii* and *S.sanborni* can only be accurately identified using protein electrophoresis (Churchill,1998) they were unable to be separated when collecting reference calls and are treated here as an amalgam. This probably accounts for the relatively broad characteristic frequency range. The call shape is curvilinear and the initial up sweeping portion of call pulses varies from distinct to non-existent. The call cannot be distinguished from that of *Chalinolobus nigrogriseus* except for a narrow frequency range below 36.1 kHz where the characteristic frequencies of the species do not overlap.



Chalinolobus nigrogriseus
Hoary wattled bat

Characteristic frequency	38.4 kHz	(95% Confidence interval 36.1 - 40.8 kHz)
Number of reference calls	33	(Sites 5, 11, 15, 21, 22, 24, 25, 27, 28, 29, 33, 37, 39, 42, 43, 51, 52)
Similar calls	*Scotorepens greyii / S.sanborni*	

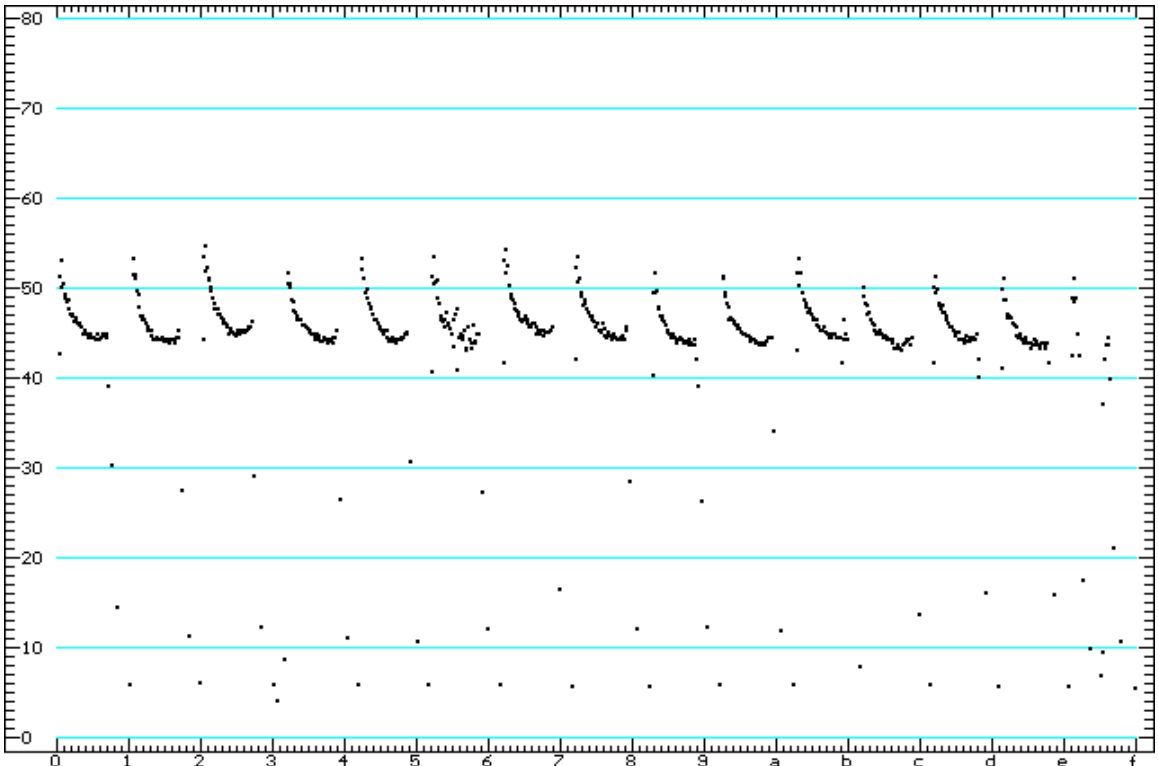
C.nigrogriseus has a call pulse shape that is curvilinear. Its characteristic frequency range falls entirely within the range of *S.greyii* / *S.sanborni*. As the Anabat call sequences for *C.nigrogriseus* are visually identical to *S.greyii* / *S.sanborni,* and discriminant function analysis of call parameters fails to discern between the two, these species cannot be reliably separated from each other.



Pipistrellus adamsi
Cape York pipistrelle

Characteristic frequency	43.9 kHz	(95% Confidence interval 42.5 - 45.3 kHz)
Number of reference calls	4	(Sites 7, 15, 16, 21)
Similar calls	*Pipistrellus westralis*	

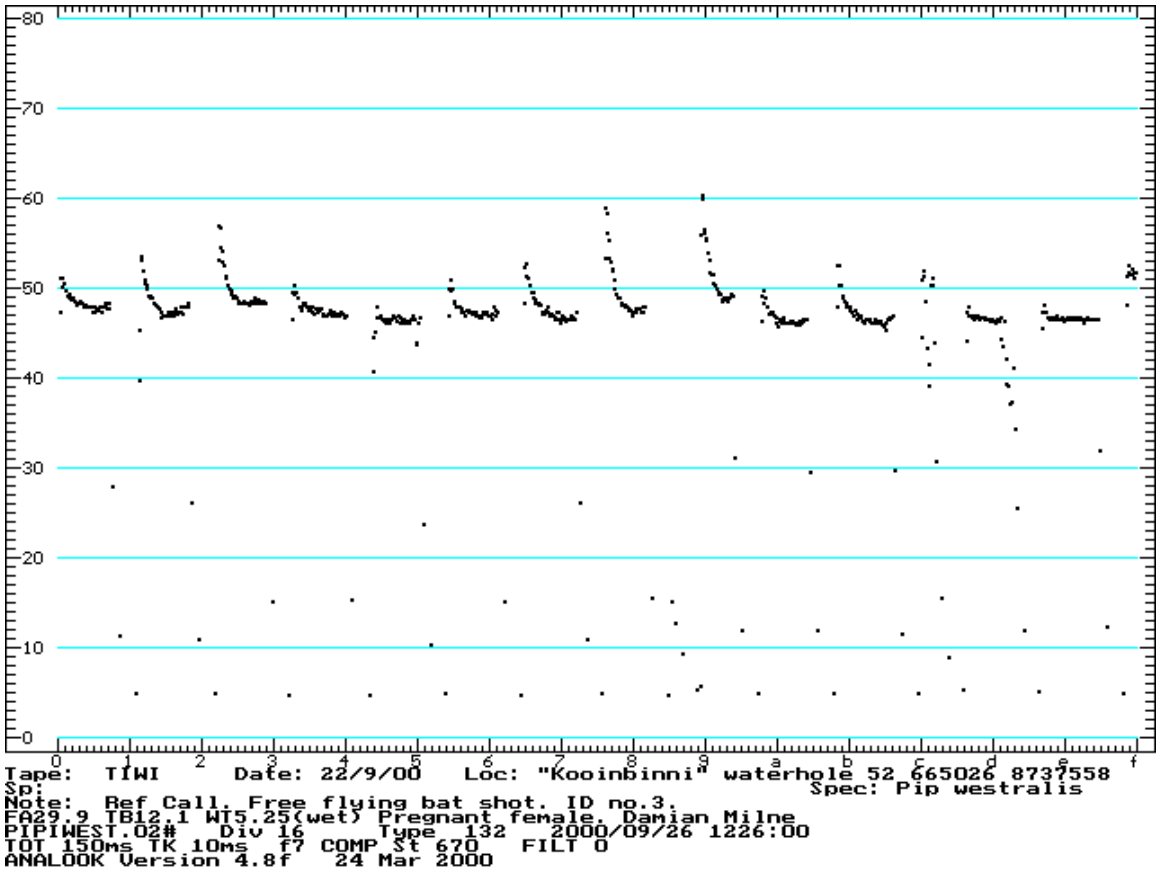
The pulse type of the calls of *P.adamsi* is curvilinear. Identification is based on its characteristic frequency, except above 43.9 kHz where its frequency range overlaps with *P.westralis*. Occasionally, the "feeding buzz" call pulses of *Scotorepens greyii* may creep up into the frequency range of *P.adamsi*, however, these pulses will appear very steep and erratic and can be readily distinguished from the consistent "search phase" call pulses of *P.adamsi*. Only four calls have been collected for this species, more calls are required to account for the full range of call characteristics.



Pipistrellus westralis
Northern pipistrelle

Characteristic frequency	46.6 kHz	(95% Confidence interval 44.0 - 49.3 kHz)
Number of reference calls	4	(Sites 1, 2, 13, 45)
Similar calls	*Pipistrellus adamsi, Miniopterus schreibersii*	

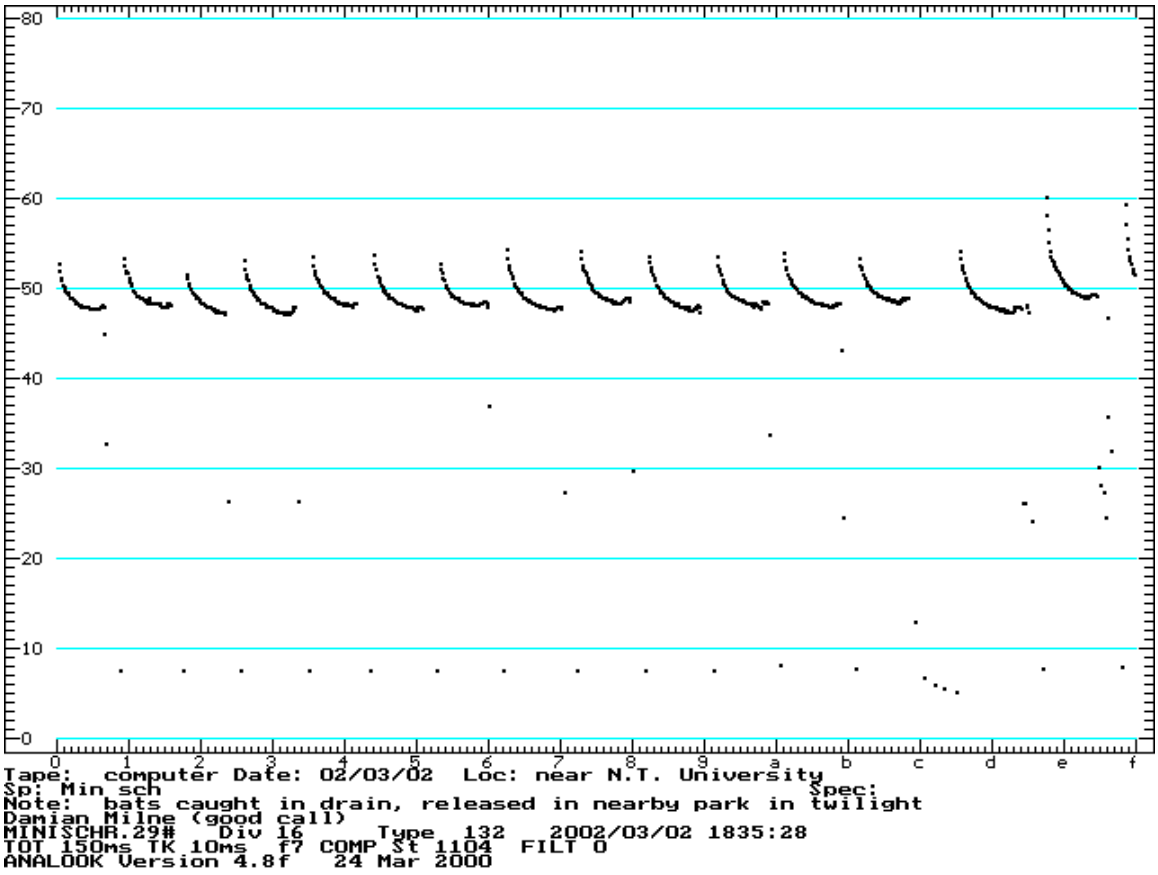
The Anabat call for *P.westralis* cannot be identified to the species level. Below 45.4 kHz it coincides with *P.adamsi* whereas above 46.6 kHz it occurs in the same frequency range as *Miniopterus schreibersii*. Calls detected between these two frequencies cannot be confidently attributed to *P.westralis* given the low number of reference calls collected for the two Pipistrelle species. The pulse type is curvilinear. The initial section is sometimes very short giving the call pulse a flat appearance. As more digitally recorded reference calls are collected for *P.westralis*, it may become possible to confidently identify this species from *P.adamsi* and *M.schreibersii*.



Miniopterus schreibersii orianae
Northern bent-wing bat

Characteristic frequency	48.5 kHz	(95% Confidence interval 46.7 - 50.2 kHz)
Number of reference calls	20	(Sites 8, 17, 21, 28, 29, 44)
Similar calls	*Pipistrellus westralis*	

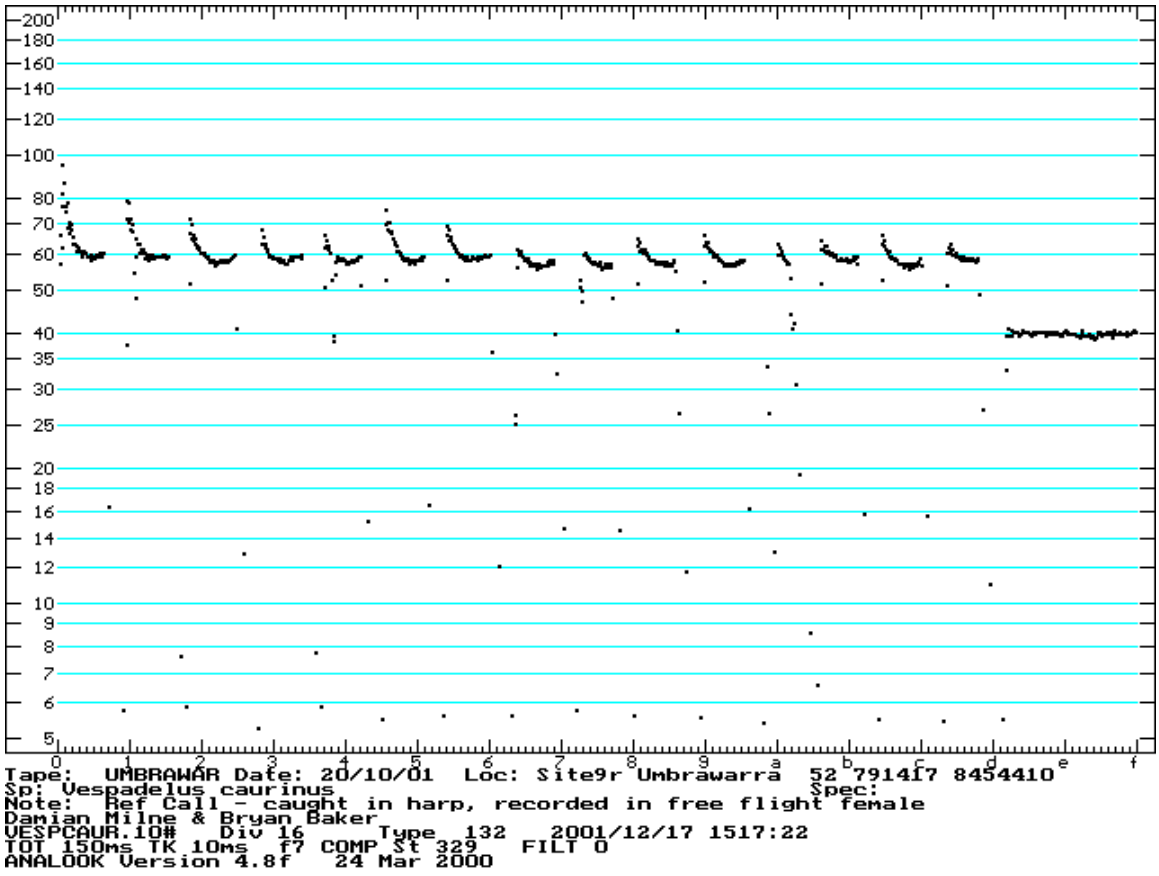
The pulse shape is curvilinear and has a relatively high initial section and usually no or at most a very short tail. Although the frequency range for *M.schreibersii* extends slightly higher than *Pipistrellus westralis*, it cannot be confidently separated given the limited number of reference calls collected for *P.westralis*



Vespadelus caurinus
Northern cave bat

Characteristic frequency	59.6 kHz	(95% Confidence interval 57.5 - 61.7 kHz)
Number of reference calls	29	(Sites 17, 21, 24, 30, 35, 48)

This tiny bat (less than 5 grams in weight) has the highest characteristic frequency of any of the vespertilonid bats in the Top End. It can be readily identified from its curvilinear pulse shape and a characteristic frequency above 57.4 kHz.

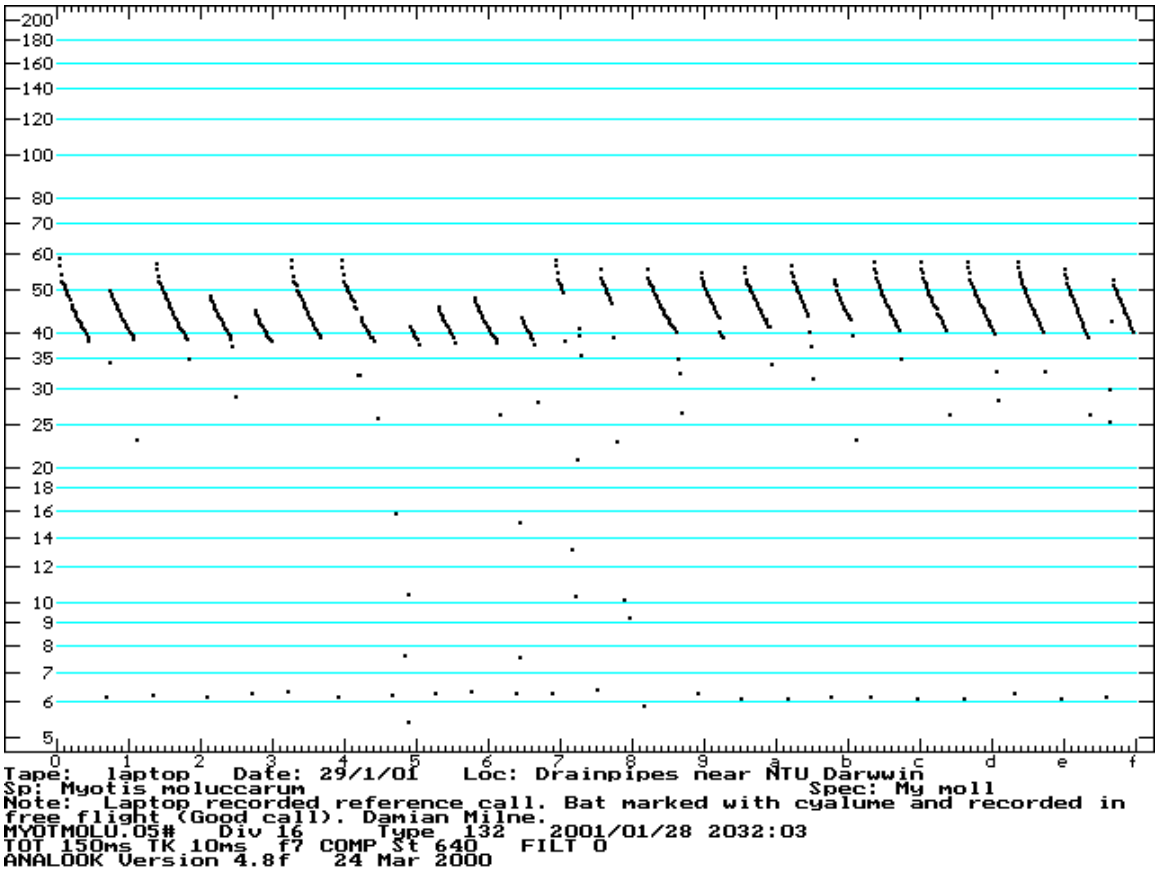


Myotis macropus
Northern myotis

Characteristic frequency	40.1 kHz	(95% Confidence interval 34.7 - 45.5 kHz)
Number of reference calls	6	(Sites 8, 9)
Similar calls	*Nyctophilus arnhemensis, N.bifax, N.geoffroyi*	

Myotis (like *Nyctophilus*) has a linear pulse shape. At frequencies of 40 kHz or lower, *Myotis* can be identified by its characteristic frequency. *Myotis* seems to maintain a relatively constant characteristic frequency when compared with *Nyctophilus*. Above a characteristic frequency of 40.0 kHz where it overlaps with the characteristic frequencies of *Nyctophilus*, *Myotis* can be identified by satisfying the condition:

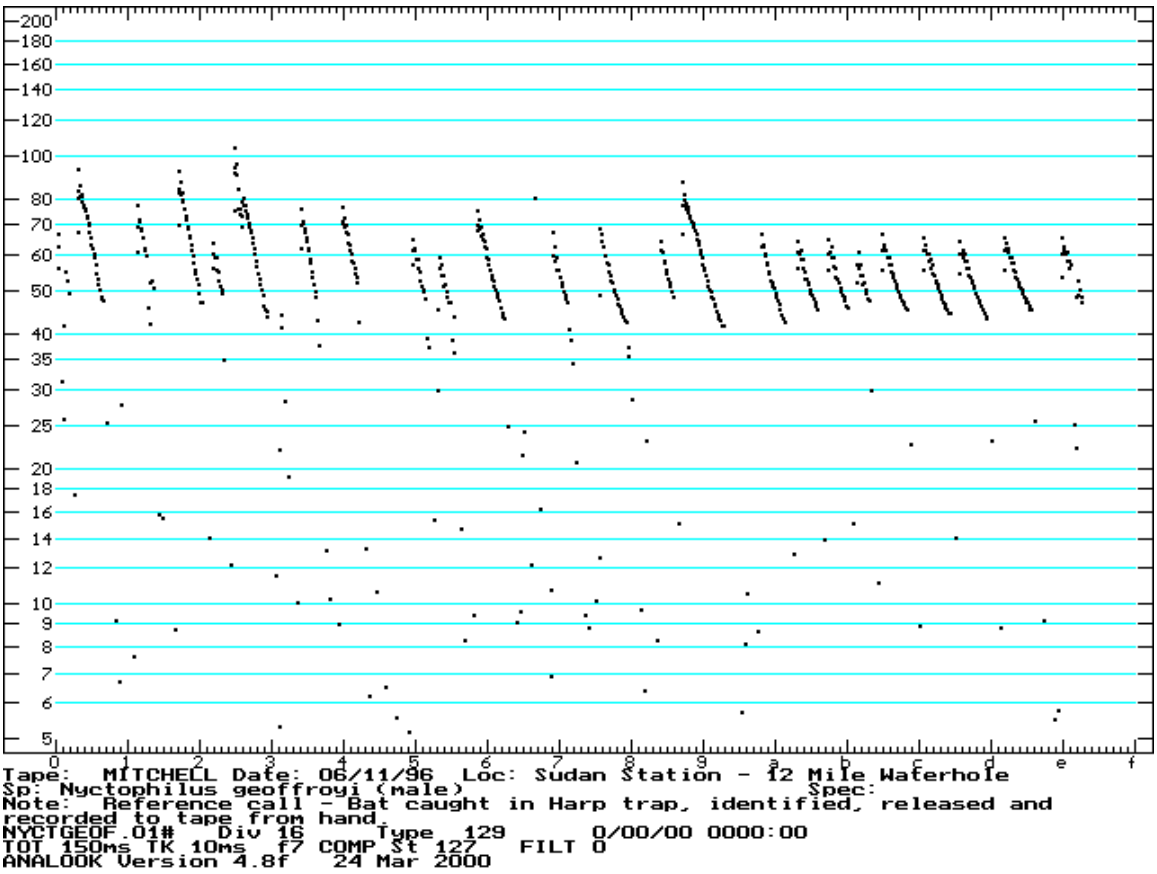
FC*6.040 + DUR*17.033 + SC*0.034 - 150.114 > FC*7.135 + DUR*19.373 + SC*0.023 - 202.991



Nyctophilus geoffroyi
Lesser long-eared bat

Characteristic frequency	45.8 kHz	(95% Confidence interval 40.7 - 50.8 kHz)
Number of reference calls	2	(14, 22)
Similar calls	*Myotis macropus, Nyctophilus arnhemensis, N.bifax, N.walkeri*	

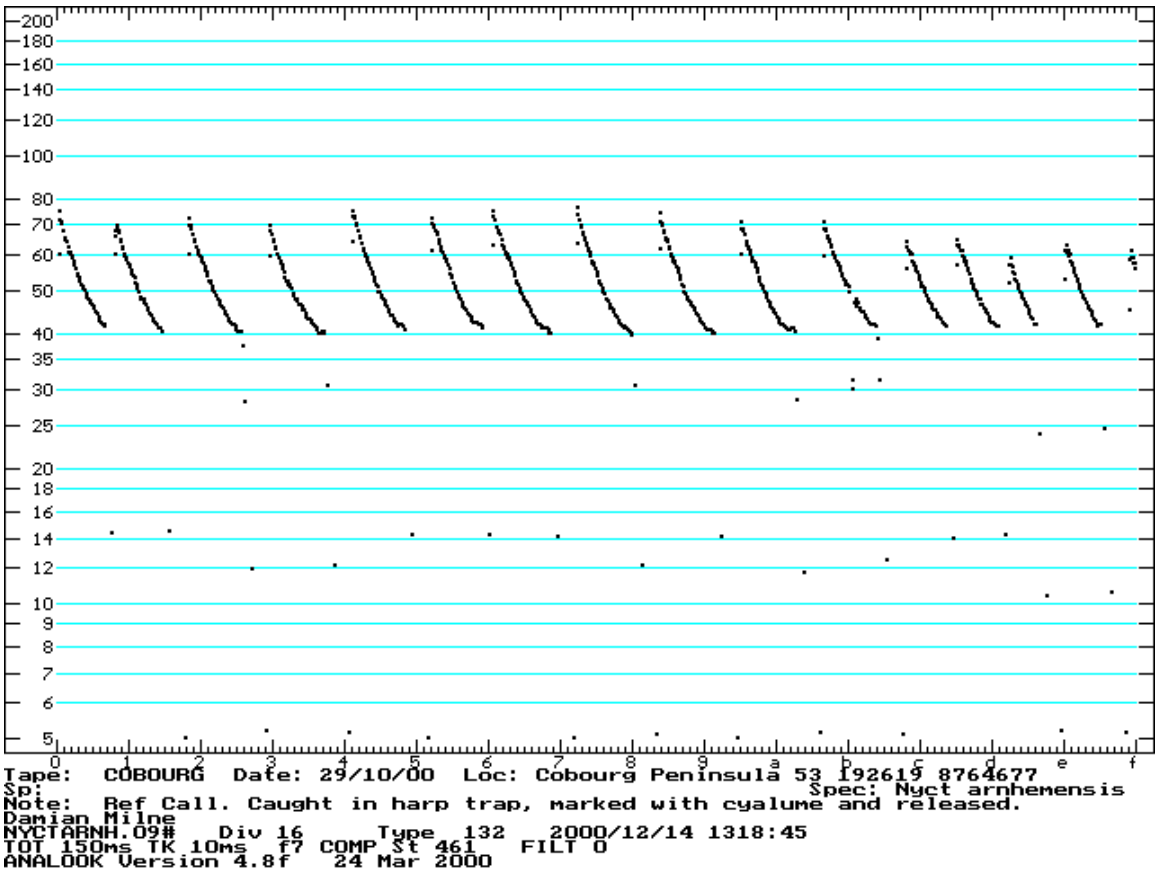
N.geoffroyi has linear call pulses. The characteristic frequency range appears to be much narrower than the other species of *Nyctophilus* species (refer Figure 2). However, as there have only been two reference calls collected for this species, it is doubtful the entire range of characteristic frequencies has been determined. Herr *et al*. (1997) report a characteristic frequency range (Fmin - Fmax) for *N.geoffroyi* from south-eastern Australia that extends much higher (39.5 kHz - 63.7 kHz, n = 11) than recorded for *N.geoffroyi* in the Top End. Therefore, based on the information available, *N.geoffroyi* cannot be confidently identified from *N.arnhemensis* or *N.bifax*.



Nyctophilus arnhemensis
Arnhem long-eared bat

Characteristic frequency	47.1 kHz	(95% Confidence interval 40.1 - 54.1 kHz)
Number of reference calls	8	(Sites 1, 4, 5, 10, 12, 29, 33, 41)
Similar calls	*Myotis macropus, Nyctophilus bifax, N.geoffroyi, N.walkeri*	

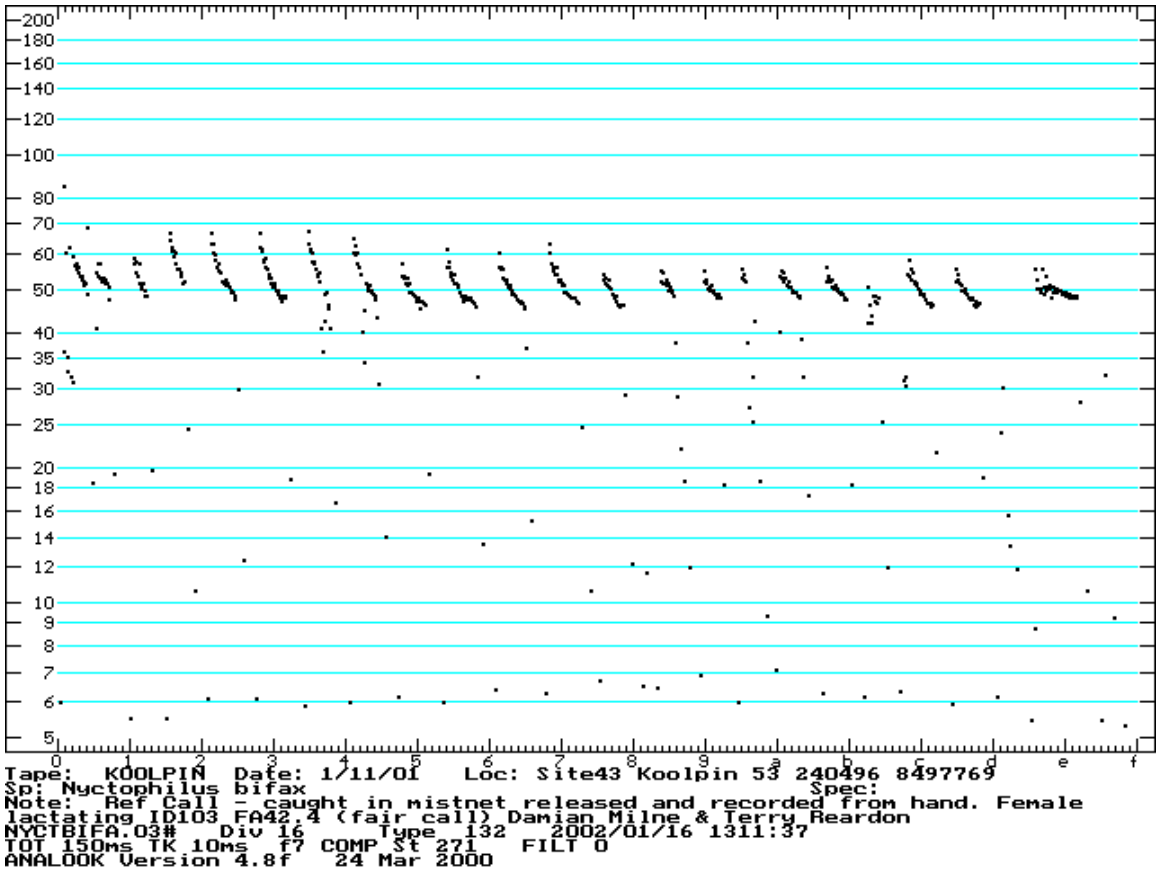
The pulse shape for *N.arnhemensis* is linear and, as with the other species of *Nyctophilus,* the frequency and length of each call pulse, within a sequence, can vary considerably. Being so variable and within the same frequency range of the calls of other *Nyctophilus*, it is impossible to identify *N.arnhemensis* to species level based on its Anabat call.



Nyctophilus bifax
Northern long-eared bat

Characteristic frequency	49.4 kHz	(95% Confidence interval 44.7 - 54.2 kHz)
Number of reference calls	3	(Sites 21,34)
Similar calls	*Myotis macropus, Nyctophilus arnhemensis, N.geoffroyi, N.walkeri*	

The same comments apply as presented for the previous two species of *Nyctophilus*. Based on three reference calls, it is unlikely that the entire range of call characteristics for this species has been sampled. The linear pulse shape of the *Nyctophilus* echolocation call allows these species to detect details of texture in their immediate environment such as a camouflaged moth perched on a leaf. It does not allow them to detect the speed and direction of flying insects. This echolocation technique is ideally suited for the gleaning mode of foraging used by long-eared bats (Woodside and Taylor, 1985).

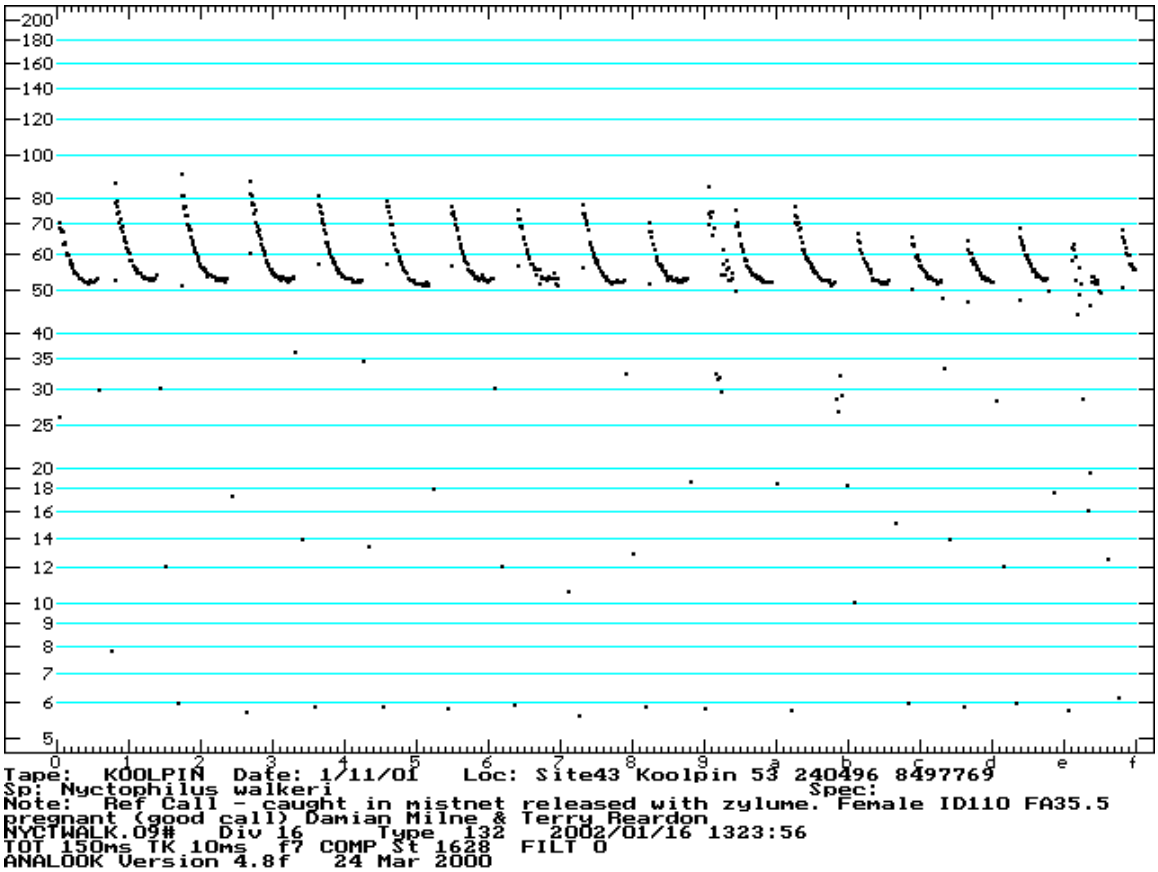


Nyctophilus walkeri
Pygmy long-eared bat

Characteristic frequency	54.7 kHz	(95% Confidence interval 50.2 - 59.1 kHz)
Number of reference calls	7	(Sites 21, 26, 29, 33, 41)
Similar calls	*Nyctophilus arnhemensis, N.bifax, N.geoffroyi*	

The call pulses for *N.walkeri* are linear, however when a call sequence for this species is viewed on a logarithmic scale with Analook, there is normally some indication of a "hook" at the bottom of each pulse. The hook varies from a small kink, to a complete 90° bend. If there is any doubt, the call sequence can be identified by satisfying the condition set out below.

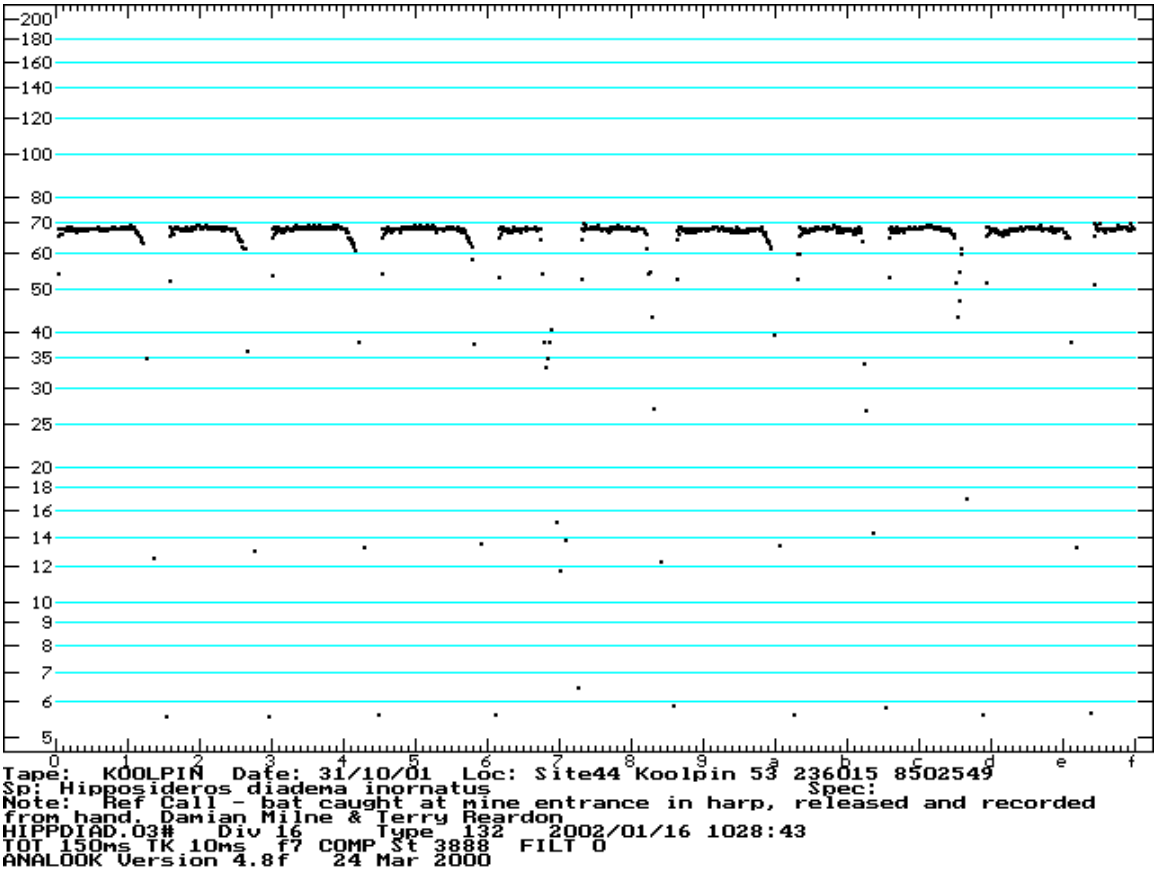
FC*8.311 - SC*0.028 + DUR*15.670 - 219.761 < FC*9.701 - SC*0.062 + DUR*17.632 - 292.275



Hipposideros diadema inornatus
Arnhem leaf-nosed bat

Characteristic frequency	69.1 kHz	(95% Confidence interval 67.1 - 71.2 kHz)
Number of reference calls	5	(Site 20)

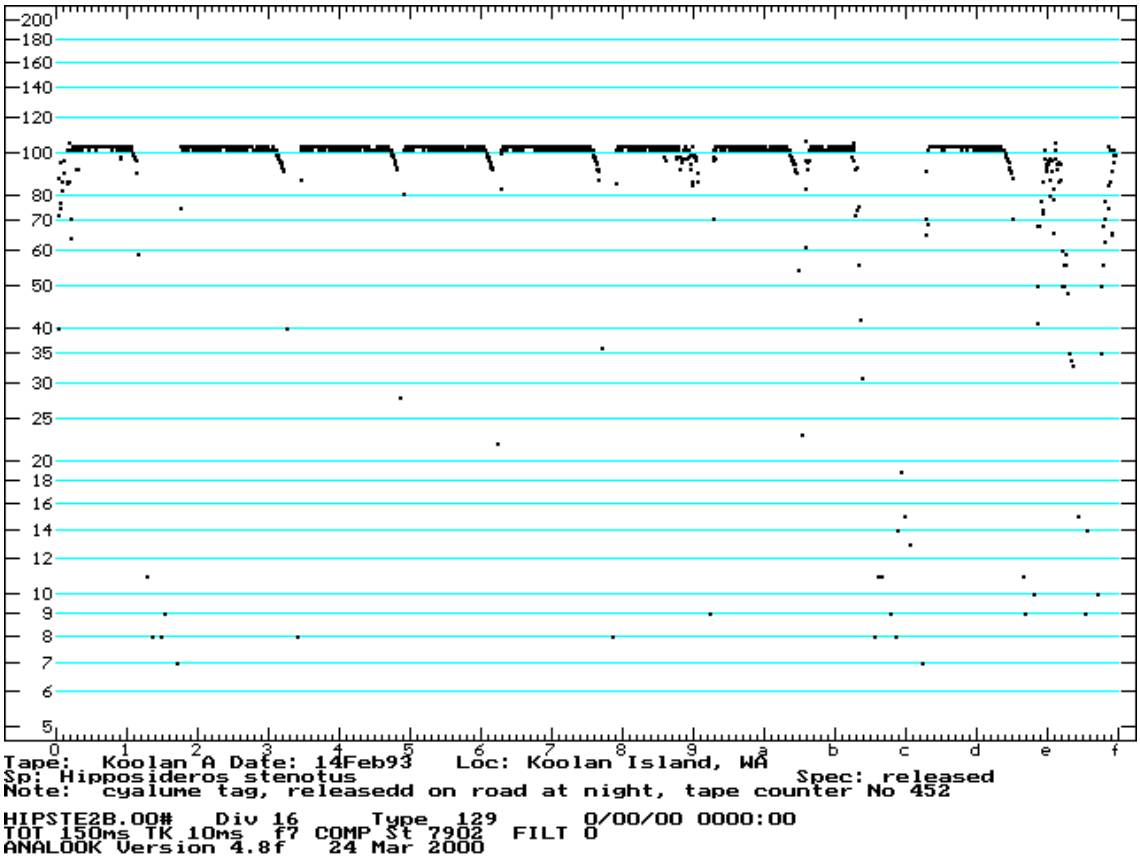
The largest of the four hipposiderid species that occur in the Top End, *H.diadema* has a much lower characteristic frequency than the other three species of leaf-nosed bats. The distance over which calls of this species can be detected by an Anabat detector is also greater than for other hipposiderid species, estimated at around 10 metres (with the detector sensitivity set between 7 and 8). Therefore, this species is likely to be detected using automatic Anabat detection techniques if there are individuals in the area.



Hipposideros stenotis
Northern leaf-nosed bat

Characteristic frequency	102-106 kHz
Number of reference calls	0

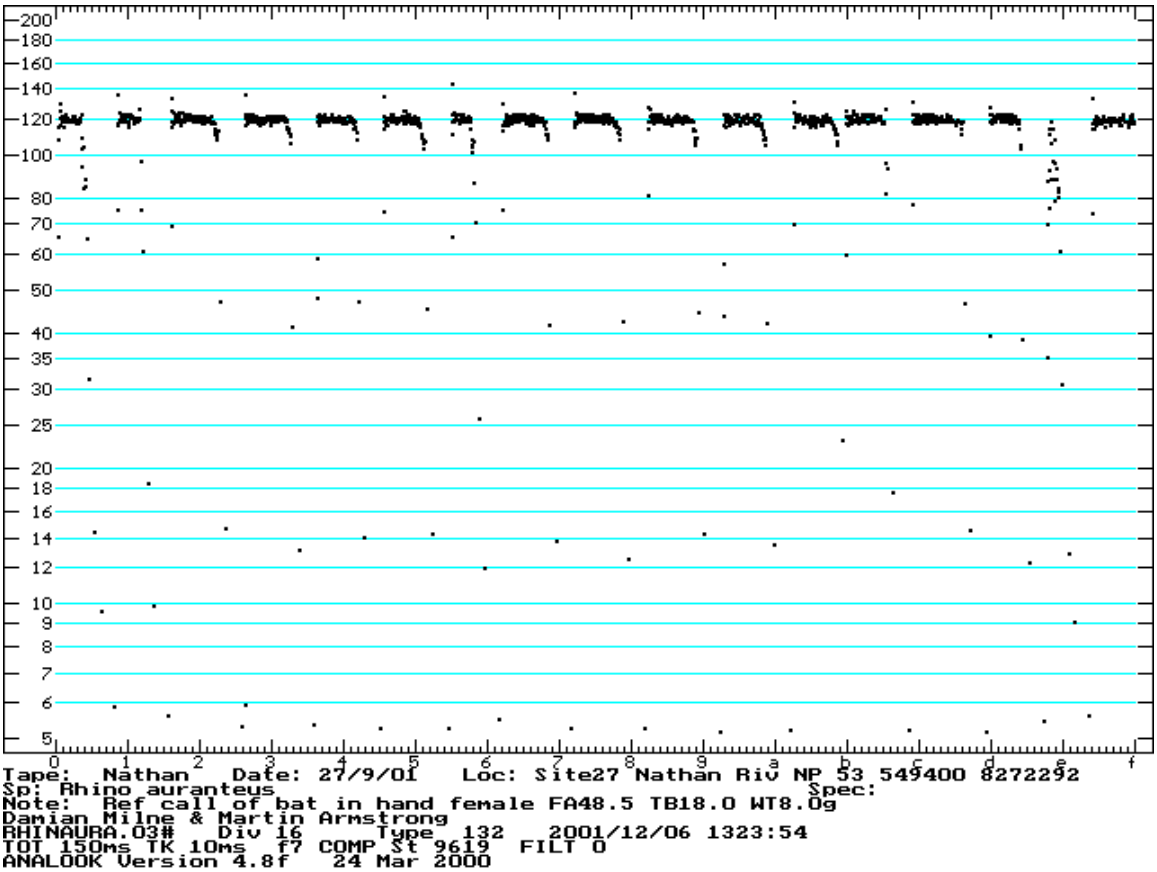
No Anabat recorded reference calls have been collected for this species in the Top End. Coles (1993) recorded *H.stenotis* at 106 kHz from the Top End using a U25 bat detector (Ultra Sound Advice, U.K.), whereas McKenzie *et al*. (1996) recorded this species at 102.5 kHz from northern W.A. using a D140 ultrasound detector (Petterson Elektronik, Sweden). Because these frequencies are very similar to those of *Rhinonicteris aurantius*, more reference calls need to be collected to confirm the characteristic frequency for this species in the Top End. The vertical resolution of Analook must be toggled to the logarithmic scale in order to see this call. The reference call shown was provided by Norm McKenzie.



Rhinonicteris aurantius
Orange leaf-nosed bat

Characteristic frequency	116 kHz	(95% Confidence interval 107 - 125 kHz)
Number of reference calls	6	(Sites 18, 25, 47, 52)

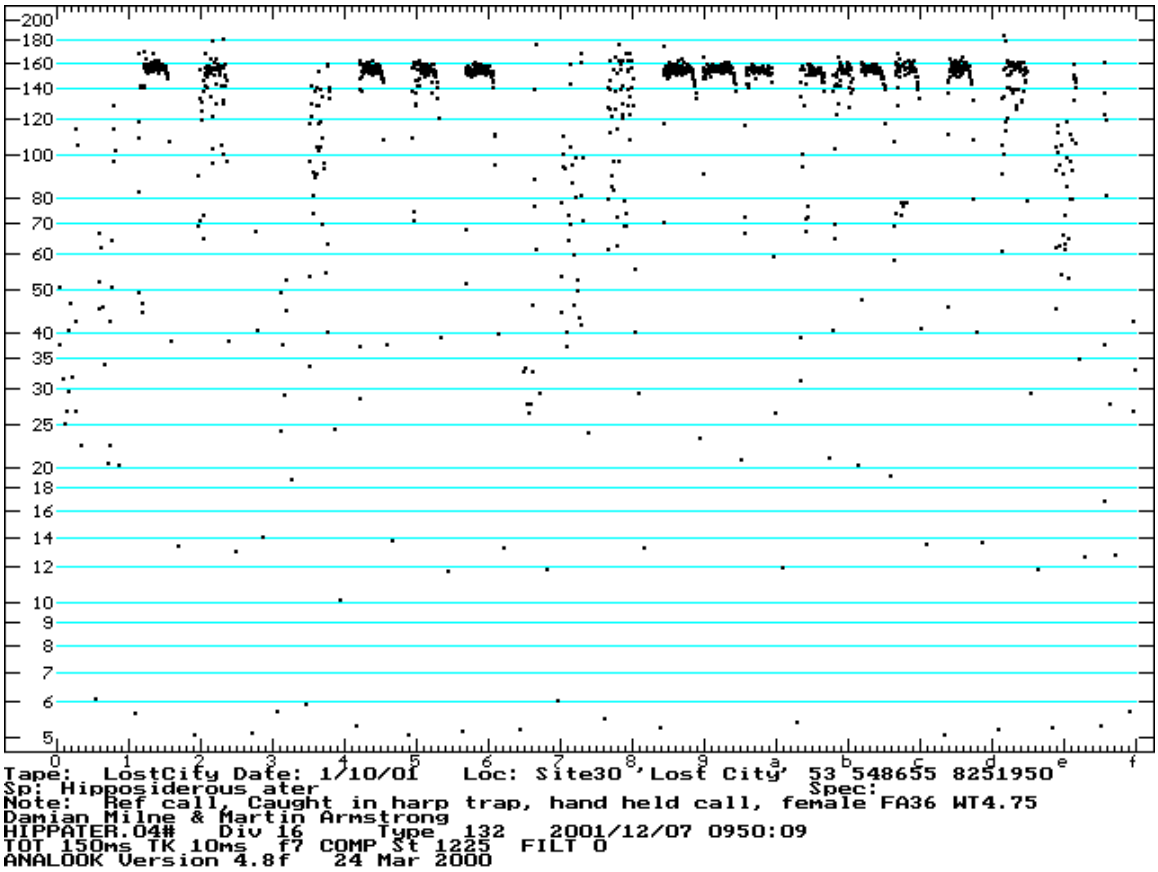
R.aurantius produces a constant frequency call type, with a slightly higher characteristic frequency than *H.stenotis*. Its characteristic frequency covers a relatively broad range. The detection range of calls of this species (as with the other small Hipposiderid bats) is very short (less than one metre) and free flying bats are only very occasionally recorded with the Anabat detector. When attempting to detect these species, the sensitivity of the Anabat detector should be set to at least 9. Even then, only one or two call pulses may result. The vertical resolution of Analook must be toggled to the logarithmic scale in order to see this call.



Hipposideros ater
Dusky leaf-nosed bat

Characteristic frequency	157 kHz	(95% Confidence interval 152 - 162 kHz)
Number of reference calls	4	(Sites 24, 27, 31, 48)

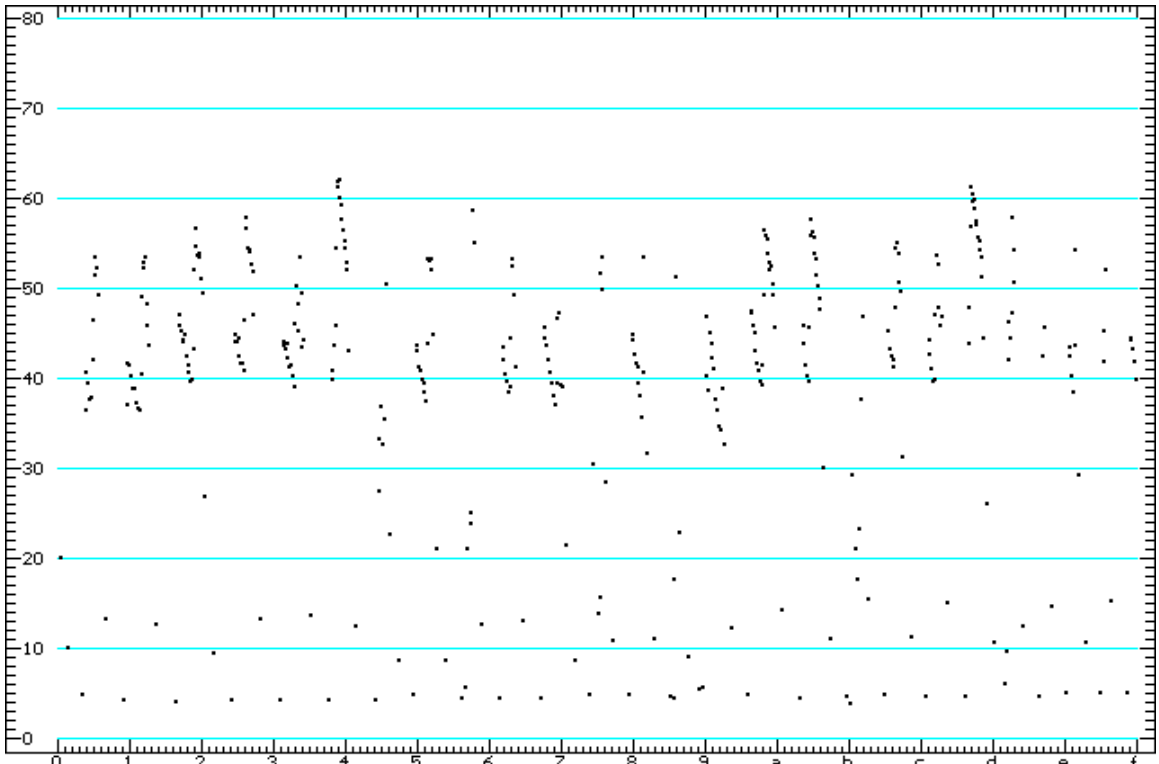
H.ater has a constant frequency search phase call type, much higher than any other bat. The vertical resolution of Analook must be toggled to the logarithmic scale in order to see this call. The constant frequency echolocation technique employed by the leaf-nosed bats allows them to detect the speed and direction of very small flying insects with great accuracy (Woodside and Taylor, 1985).



Macroderma gigas
Ghost bat

The calls of the ghost bat are so faint and poorly defined, the species would never be positively identified using Anabat during a general fauna survey. When in flight, this species regularly emits an audible “trill” from which it can be identified by a trained observer.

Identification of ultrasonic calls may be possible using better quality reference calls that are digitally recorded. However, this possibility has not been examined. The call sequence shown is the best quality call recorded (via tape recorder) from dozens of Anabat recordings of ghost bats flying near the exit of a mineshaft.



OTHER CALLS

The known geographic distributions of three other micro-bats come close to the Top End. The possibility of recording these species needs to be considered when examining the results of Anabat surveys close to the boundary of the area covered by this key.

- *Tadarida australis* occurs just to the south of the Top End. It has the lowest known characteristic frequency of any Australian bat species of around 10 - 13 kHz (Reinhold *et al*., 2001). Its call is therefore clearly audible to the human ear.

- *Scotorepens balstoni* also occurs just to the south of the Top End and has a characteristic frequency of 31-35 kHz (Reinhold *et al*., 2001).

- *Vespadelus finlaysoni* has a known distribution that extends into the south-east corner of the Top End (Churchill, 1998) and has a characteristic frequency of around 53 kHz (McKenzie and Muir, 2000).

LIMITATIONS

The call database on which this key is based has several limitations as detailed below. First, no reference calls were collected for *Saccolaimus saccolaimus* and therefore this species is not covered in this publication. Given that this species is the only bat recognised in Australia as critically endangered (Environment Australia, 2002) it may be a significant omission. Second, no reference calls were collected for either *Mormopterus beccarii* (call descriptions provided here are based on reference calls from Queensland) or *Hipposideros stenotis* (figures presented here were derived from frequencies reported in the scientific literature). Further, only two reference calls were collected from the region for *Taphozous kapalgensis, Mormopterus loriae* and *Nyctophilus geoffroyi*. Therefore, it is doubtful that the full variation of call parameters for each of these species is presented here. Third, although reference calls have been collected from across the Top End, reference calls for each species have not. Therefore, intraspecific geographic variation in echolocation calls, if it occurs, has not been fully described for all species.

Several factors also need to be considered when interpreting the results obtained from Anabat. The distance an ultrasonic call will travel varies considerable depending on the type of call produced by different species of bats (Woodside and Taylor, 1985). Therefore, some species will be detected by an Anabat unit more frequently than others. Furthermore, small Hipposiderid bats (e.g. *Hipposideros ater*) are rarely recorded by Anabat detectors but are more readily detected using harp traps. The environment in which bats are recorded can also impact on the results of Anabat surveys. Bats will be detected more readily in open areas that are free of obstructions as opposed to densely vegetated closed habitats. Tall forest environments may result in some species of bats flying higher and further away from an Anabat detector, when compared with a low woodland environment. This will also reduce the likelihood of calls being recorded (Law et al., 1999; Duffy et al., 2000). For these reasons, Anabat recordings cannot be used to directly measure bat abundances, nor can it be assumed that all echolocating bats will be detected using an Anabat detector during a survey.

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Appendix 2.

New records for the Arnhem sheathtail bat *Taphozous kapalgensis* (Chiroptera: Emballonuridae) from voucher specimens and Anabat recordings

D.J. Milne, T.B. Reardon and F. Watt (2002). *Australian Zoologist* 32, 439-445.

New records for the Arnhem sheathtail bat *Taphozous kapalgensis* (Chiroptera: Emballonuridae) from voucher specimens and Anabat recordings

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ABSTRACT

Taphozous kapalgensis was previously known from just nine records. In a recent survey we collected three individuals and identified two more from specimens held by the Northern Territory Museum. Two reference calls were also recorded for this species using the Anabat system. A review of fauna survey data containing an archive of 24400 digital Anabat call files recorded at 742 sites across the northern half of the Northern Territory identified 162 files from nine sites that matched the *T. kapalgensis* reference calls. We recommend, based on the information presented here, that *T. kapalgensis* be regarded as Near Threatened.

Key words: *Taphozous kapalgensis*, rare, bats, Anabat, echolocation

INTRODUCTION

Eight species of sheathtail bat (family Emballonuridae) occur in Australia, five of which are of conservation concern or poorly known. Sheathtail bats are difficult to survey. Surveys are usually conducted near or over fresh water bodies because most microbat species will drink or forage for insects that are attracted to water. However, sheathtail bats are generally high flying and some species do not appear to drink from open water bodies (pers. obs.). Survey methods used in the past for sheathtail bat species include searching for roosts, spotlighting and shooting, and less successfully, mist nets and harp traps. In recent years, new information on some species has been obtained using electronic bat detectors. However, identification of rarer species has not been possible because their calls are often unknown. The Arnhem sheathtail bat *Taphozous kapalgensis* was known from just nine records prior to those described here. Four individuals, from which the species was first described, were shot at Kapalga in 1978, in what is now Kakadu National Park; a fifth was collected nearby in 1979 (McKean and Friend 1979); McKean collected another specimen at Kapalga in 1980; that same year an individual was captured and released near Nourlangie camp, Kakadu National Park (D. Matthews pers. comm.); in 1982 a specimen was obtained near Ubirr Rock, Kakadu National Park; and in 1998 an injured *T. kapalgensis* (which subsequently died, NTM U.4852) was collected from the outskirts of Darwin (Figure 1).

Due to this paucity of records and our lack of knowledge of its ecology and distribution, it has been difficult to assess the conservation status and management requirements of this species. *T. kapalgensis* is not listed under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999*, was regarded as Data Deficient in the *Action Plan for Australian Bats* (Duncan *et al*. 1999), and is also listed as Data Deficient in the Territory *Parks and Wildlife Conservation Amendment Act 2000*. It is not known whether the paucity of records is a consequence of difficulties in detecting the species using traditional survey techniques, genuine rarity, or a combination of both. It is thought that *T. kapalgensis* generally flies high above the canopy, flying lower when foraging over open areas or unobstructed flyways (Churchill 1998). This type of flight behaviour is not conducive to trapping with mistnets or harp traps but may lend itself to echolocation recording and identification techniques (O'Farrell and Gannon 1999). Here we describe the echolocation call of *T. kapalgensis* that we recorded from free-flying individuals, which were subsequently shot and vouchered for positive identification. Using these calls, we conducted a retrospective analysis on an archive of Anabat call files collected from surveys in the Northern Territory over the last five years.

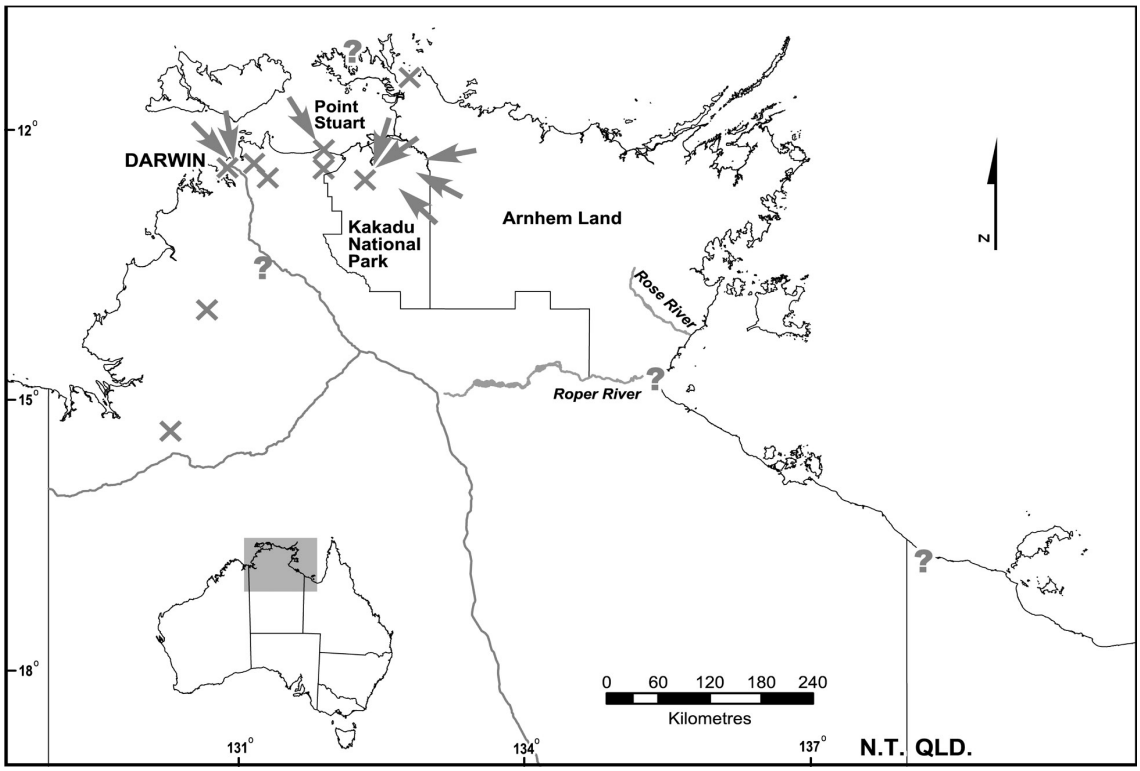


Figure 1. Location *T. kapalgensis* records. Crosses show sites where *T. kapalgensis* was identified from Anabat recordings. Sites at which Anabat call sequences were similar to the reference calls for *T. kapalgensis*, but could not be attributed with certainty to this species, are indicated by "?". Arrows indicate where *T. kapalgensis* has been physically caught or collected.

Collection of *T. Kapalgensis* and recording of reference calls

On the 23 October 2001, a large, free flying microbat was detected and recorded using an Anabat II bat detector (Titley Electronics, Ballina, NSW) and tape recorder (Optimus CTR-115 and Sony UX Chrome cassette-tape). During recording the bat was visually detected using a spotlight and then shot. The specimen was subsequently identified as *T. kapalgensis*. A 20-second call sequence was recorded and transferred to computer using an Anabat 6 ZCAIM and Anabat5 software. The Anabat detector was held in the hand, manually activated on detection of the call and pointed in a direction to obtain the best call reception. The adult male specimen was lodged in the Museum and Art Gallery of the Northern Territory (NTM U.5294, body mass at capture 29.5g). The location was on the Point Stuart Coastal Reserve, 116 Km ENE of Darwin (12°14'47"S, 131°53'02"E). The environment consisted of coastal floodplain adjacent to low woodland of *Pandanus spiralis* with small patches of monsoon forest nearby. The floodplain is subject to inundation during the wet season (November - April). The environment is similar to that described by McKean and Friend (1979) where the type specimen was collected, 63 km SE of our collection site.

Two more specimens were collected in the same manner during a follow-up survey at the same location: an adult female (NTM U.5227, body mass at capture 27.5g) on 3 November 2001; and a sub-adult male (NTM U.5295, body mass at capture 18.5g) prior to dawn on 4 November 2001. We successfully recorded the echolocation call of the first of these bats. A 6-second call sequence was recorded via a hand-held Anabat unit to the analog tape recorder, and a 3.5-second recording of the same call sequence was recorded via a hand-held Anabat unit to a lap-top computer (Toshiba Satellite T1910), running Anabat6 software. All three bats had distinctively coloured orange-brown dorsal fur (as opposed to red-brown fur described by Churchill 1998). However, only the two adult specimens had lateral white stripes of fur on the under-sides of the wings along the sides of the body. The juvenile specimen lacked these distinctive markings.

The collection of *T. georgianus* specimens held by the Northern Territory Museum and Arts Gallery was also checked for specimens of *T. kapalgensis* to investigate the

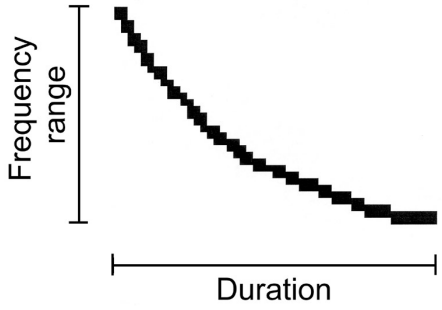


Figure 2. The frequency range and duration of a bat call pulse.

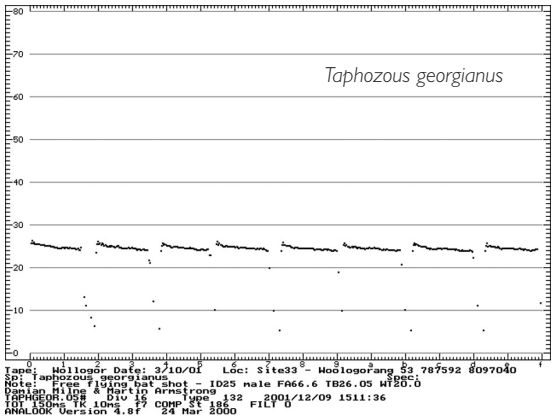
Table 1. Comparison of Anabat call attributes of *T. kapalgensis* with species with overlapping call frequencies. Data were obtained from reference calls collected from the Top End of the Northern Territory except for *M. beccarii* which were recorded in Queensland. Median frequency range and median pulse duration were compared between *T. kapalgensis* and the other four species using the Mann-Whitney U test: NS, not significant; ***P<0.001.

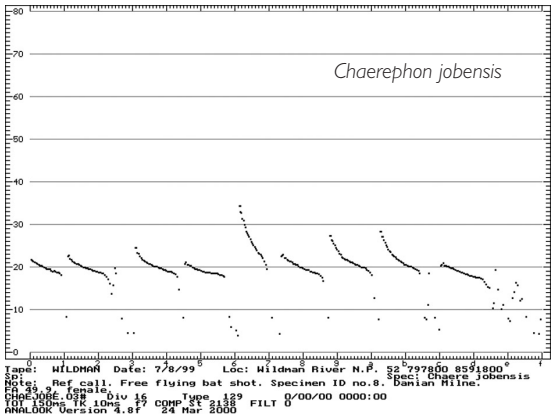
Species	n (pulses)	N (sequences)	Frequency (kHz)					Duration (ms)		
			Min	Max	Median frequency range	95th percentile range	Z	Median	95th percentile range	Z
T. kapalgensis	26	2	22.96	25.48	1.30	0.84-2.04		4.62	3.02-7.02	
T. georgianus	60	6	23.32	25.36	1.40	0.18-2.24	-0.263 NS	11.30	6.93-17.15	-7.316***
C. jobensis	143	6	16.11	24.35	4.65	1.59-14.39	-7.926***	10.15	5.70-16.48	-7.965***
M. beccarii	129	5	21.25	29.09	5.38	2.10-9.58	-7.813***	9.89	5.83-13.13	-7.854***
S. flaviventris	232	18	18.10	24.17	4.65	1.84-7.29	-8.231***	10.36	5.27-20.05	-8.165***

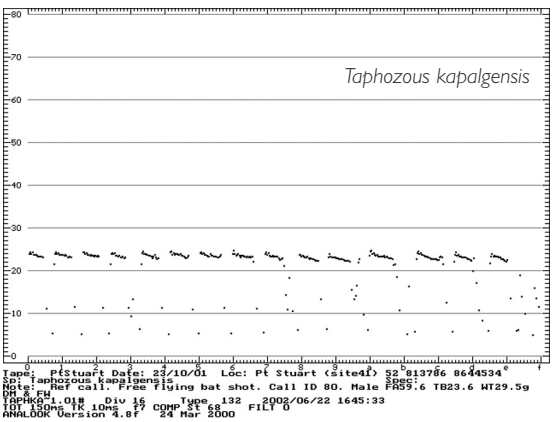
possibility that mis-identifications may have occurred given that the two species are physically similar. Two further individuals were discovered. The first of these specimens, a female (NTM U.4637), was collected in 1997 from the outskirts of Darwin (12°25'39"S, 130°56'03"E). The second specimen was collected in 1982 (NTM U.599) from Magela Creek in Kakadu National Park (precise locality unknown). This was a lactating female with a forearm length of 57.6 mm. Both specimens possessed the orange-brown fur and white fur stripes along the undersides of the wings, however, being soaked in preserving alcohol, their colour appeared much more drab than the *T. kapalgensis* individuals we collected before being preserved, and similar in appearance to many of the *T. georgianus* specimens.

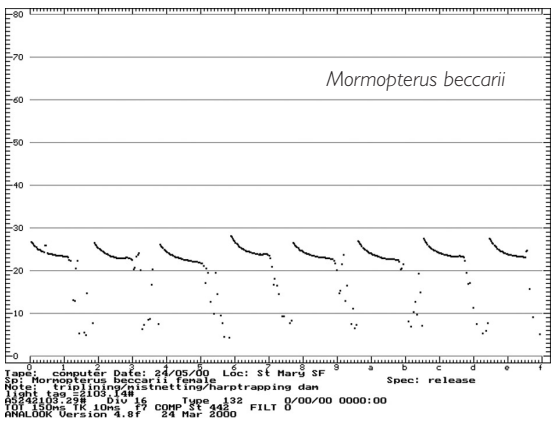
Description of anabat call for *T. kapalgensis*

Echolocation pulses for *T. kapalgensis* derived from an Anabat detector have a frequency band of 22.96 - 25.48 kHz and pulses are relatively short in duration (less than 8 ms). There are four other species in the Top End with call frequencies that are within the band of *T. kapalgensis*: *T. georgianus*, *Chaerephon jobensis, Mormopterus beccarii* and *Saccolaimus flaviventris*. These species can be distinguished from *T. kapalgensis* by the frequency range (i.e. maximum frequency minus minimum frequency) and/or duration of call pulses (Table 1, Figure 2). Both of these features are obvious from a visual comparison of reference calls of all species (Figure 3).









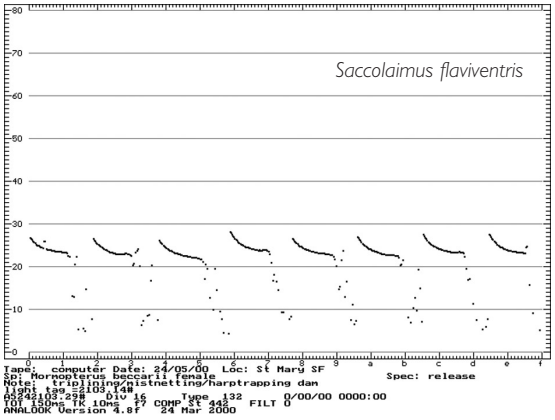


Figure 3. Reference call of *T. kapalgensis* and comparison with typical reference calls of other bat species with overlapping frequencies. Vertical axis represents frequency (kHz), horizontal axis represents time (major tick marks = 10 ms). Views are in the "compressed mode" of Analook to exclude gaps between call pulses.

It is possible that these four species could produce a similar call to *T. kapalgensis* should only part of their call pulses be recorded as a consequence of the bat flying at the limits of the distance at which the Anabat detector can detect their calls. These pulses are unlikely to remain consistent for more than three or four pulses, however, as the distance of the bat from the detector will vary as the bat flies. Therefore, in the review described below, unknown calls collected from Anabat surveys were only attributed to *T. kapalgensis* if at least eight consistent call pulses were observed that matched the *T. kapalgensis* reference calls.

Saccolaimus saccolaimus also overlaps in geographic range with *T. kapalgensis*, however, we have no reference call recordings for this species from the Northern Territory. Therefore, it is possible that calls we attributed to *T. kapalgensis* may have been confused with calls of *S. saccolaimus*. Call recordings of *S. saccolaimus* from Brunei in South-East Asia, have a frequency band of 24.5-26.1 kHz (R. Coles, pers. com.). This is coincident with the frequency band of *T. kapalgensis* (Table 1). However, the call pulse duration of *S. saccolaimus* ranges from 18-25 ms which is much longer than the call duration we measured for *T. kapalgensis* (3-7 ms) and therefore the calls of the two species are unlikely to be confused. One caveat to this statement is that the taxonomic status of Australian and Asian populations of *S. saccolaimus* populations is uncertain (Hall 1995). Calls need to be recorded from Australian populations of *S. saccolaimus* to determine if call characteristics are similar.

Review of anabat archives

DM reviewed an archive of Anabat call files collected since 1997 by the Parks and Wildlife Commission during the course of standard fauna surveys in the northern half of the Northern Territory and north-west Queensland. The archive contained 24400 Anabat call files, which were obtained over approximately 1420 hours of recording from 742 locations north of 22° latitude (Figure 4).

Two sampling methods were used in collecting these calls. At 691 sites, bat calls were recorded for a period of ten minutes during the first 3 hours after dusk within a 50m x 50m quadrat, using a hand-held Anabat II detector as described previously. The second method used static Anabat detectors set on the ground and elevated to an angle of approximately 45°, which recorded calls via either an Anabat II delay switch to an analog tape recorder or via ZCAIM to computer (Toshiba Portégé 3440CT or Toshiba Tecra 700CT) running Anabat5 software. Bats were sampled with this method for a period of either one (10 sites) or two (46 sites) consecutive nights. At sites that were sampled over two nights, bats were also sampled with a hand-held Anabat unit for a period of 3 hours immediately after dusk, concurrently with the static detector.

A total of 162 Anabat files that matched the *T. kapalgensis* reference calls were found from nine sites (Figure 1). A summary of location and environmental features at each site is provided in Table 2. There is a reasonable coverage of survey sites throughout the northern Northern Territory with the exception of eastern Arnhem Land and Tanami Desert. The major landforms and environments, except for arid environments, are also well represented in the sample.

Table 2. Location and environmental description for sites where *T. kapalgensis* was recorded during this study.

Location	Date	Detection method	No. of calls	Environment
15°20'50"S 130°16'35"E	15/3/02	Anabat (10 min.)	1	Extensively cleared area, otherwise open *Eucalyptus* woodland below sandstone escarpment, above major tidal river and floodplain
14°00'40"S 130°39'33"E	22/10/01	Anabat (2 nights)	1	*Eu. tectifica, Corymbia dichromophloia, Erythrophleum chlorostachys* low woodland near head of sandstone escarpment valley
12°26'42"S 130°52'28"E	15/6/00	Anabat (10 min.)	1	Mangroves dominated by *Ceriops* sp. and *Excoecaria ovalis*
12°23'50"S 131°09'14"E	15/12/01	Anabat (2 nights)	2	*Eu. tetrodonta, Eu. miniata* tall coastal woodland
12°33'23"S 131°17'47"E	9/11/01	Anabat (10 min.)	1	*Pandanus spiralis* mixed woodland adjacent to floodplain
12°27'32"S 131°52'55"E	23/10/01	Anabat (2 nights)	4	*Eu. tetrodonta, Eu. miniata* tall woodland adjacent to floodplain
12°14'47"S 131°53'02"E	23/10/01 23/10/01 3/11/01 4/11/01	Anabat (2 nights) individual shot individual shot individual shot	119	Coastal floodplain adjacent to *P. spiralis* woodland with nearby small patches of monsoon forests
12°34'46"S 132°18'59"E	11/10/99	Anabat (10 min.)	1	*Er. chlorostachys, Eu. tetrodonta, Eu. miniata* tall woodland adjacent to floodplain.
11°27'01"S 132°46'59"E	31/10/00	Anabat (2 nights)	32	Grassy coastal dunes with patchy monsoon forest and *Acacia sp.* regrowth

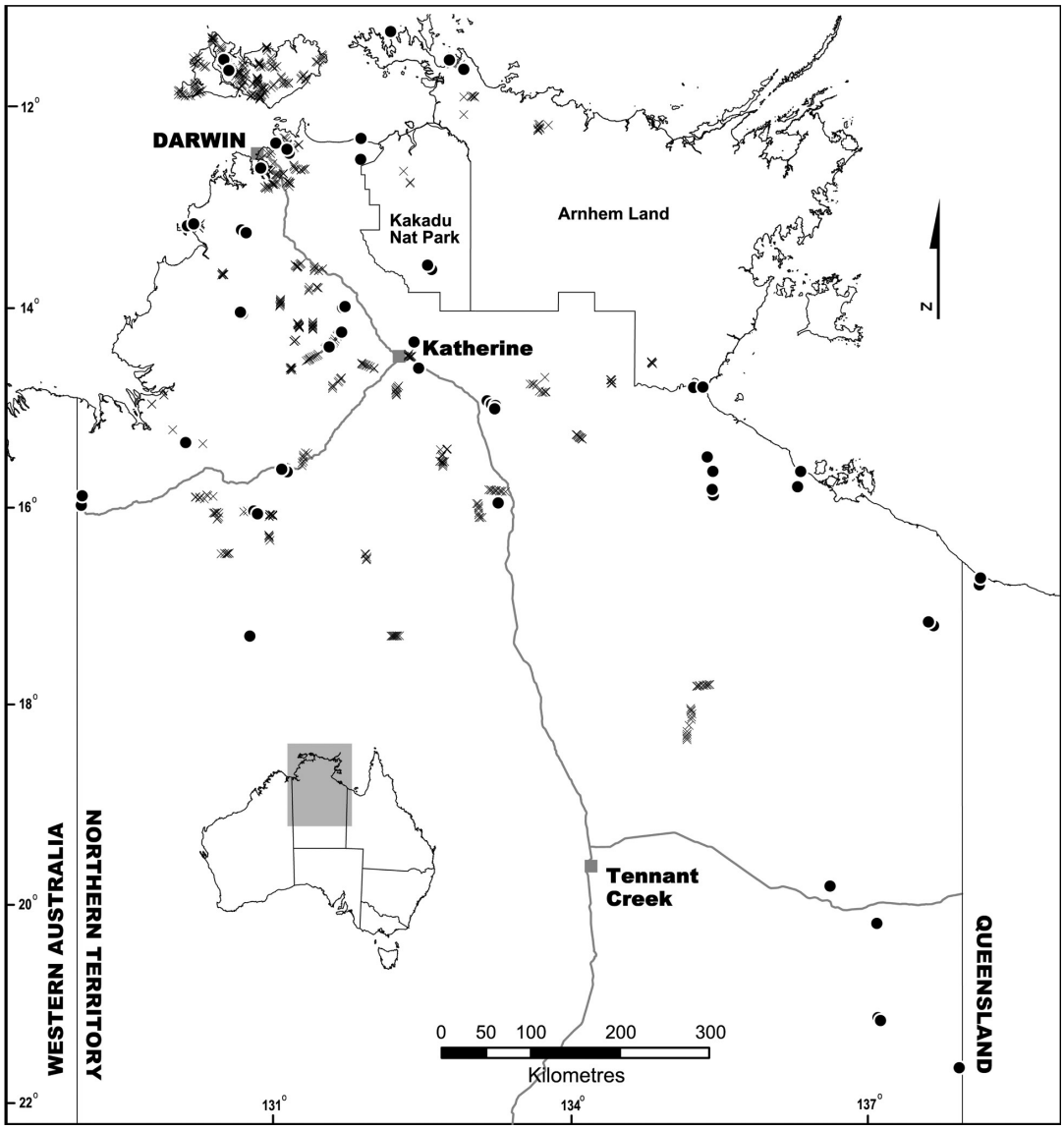


Figure 4. Location of 10 minute (crosses) and 1-2 night (circles) Anabat survey sites conducted since 1997.

Discussion

The collection of two validated reference calls for *T. kapalgensis* allowed us to identify nine new sites where we believe this species occurs based on an archive of Anabat recordings. This is a significant expansion of our knowledge of the distribution of the species. The reliability of these records depends on the accuracy of the reference calls collected and the completeness of reference calls for co-occurring species. A number of considerations which may limit this accuracy should be considered, as detailed below.

Sequences should be indicative of bats in natural flight (Duffy *et al*. 2000). The reference calls collected were almost certainly indicative of bats in natural flight. A long call sequence of 20 seconds was obtained from a free-flying bat before it was collected. The call was unaffected by "post-release stress" (a common problem for reference calls obtained from hand-released bats) and the pulses were consistent throughout the call sequence.

Calls should be recorded from bats flying in the habitats being studied (Barclay 1999). *T. kapalgensis* is generally considered to fly high above the canopy (Churchill 1998). The type of calls produced will be a consequence of the bat flying in unobstructed environments and will generally be unaffected by the habitat over which it is flying. The *T. kapalgensis* individuals that we recorded with the Anabat detector were flying approximately 10-20 m above the ground over a treeless floodplain, therefore we consider that the reference calls we collected fulfil this criterion.

Calls should be obtained from bats within the study area (Barclay 1999). Many of the acoustic surveys included in the review were conducted long distances away from where the reference call was collected. Therefore, there may be intraspecific geographic variation in echolocation calls which has not been accounted for. Nevertheless, calls considered to come from *T. kapalgensis* were a good match to the reference call, and did not match reference calls from any other species known from the study area.

The number of *T. kapalgensis* calls identified in the review of the call archive is likely to have been underestimated for three reasons. First, it is unlikely the entire range of call variation is covered by the two reference calls collected. Other call variants for this species are likely to have been recorded during Anabat surveys but not identified. Second, stringent conditions were placed on the attribution of calls to this species. Normally, the identification of an unknown Anabat recording is based on three or more consistent call pulses (e.g. Duffy *et al.* 2000; Law *et al.* 1998). In this instance, no call sequences were attributed to *T. kapalgensis* unless at least eight consistent call pulses were observed. Nonetheless, comparatively few call sequences matching the *T. kapalgensis* reference call that contained less than eight call pulses were observed. Third, the 10-minute sampling period at most sites is too short a time to gain an adequate representative sample of bats in a given area using echolocation-recording techniques. Law *et al*. (1998) recommend that sampling should take place throughout the night to allow for differences in activity levels during the night.

Nine sites from a total of over 700 had Anabat calls that were attributed to *T. kapalgensis*. Seven sites had recordings of four calls or less for this species, while two sites had more than 30 (Table 2). This observation suggests that the population of *T. kapalgensis* in the Northern Territory is relatively small and is sparsely distributed, but may be locally common. Alternatively, *T. kapalgensis* may be a very high-flying species that is usually out of the detection range of the Anabat detector. This possibility would also reduce the number of sites where *T. kapalgensis* was recorded compared to where it might have actually occurred.

Some caution needs to be exercised when interpreting results where more than one echolocation call sequence was detected at a site. If call sequences were separated by a period of at least 5 seconds, they were regarded as separate calls. Therefore, it is possible an individual bat may have been recorded several times.

Statements by Aborigines that *T. kapalgensis* occurs in the Roper and Rose River regions (McKean and Thomson 1995) were not confirmed by Anabat recordings from one of these areas. A total of 56 hours of recordings at two sites near the mouth of the Roper River did not result in any *T. kapalgensis* calls being observed. However, several of the calls collected (n=34) within the 20 to 30 kHz range could not be confidently attributed to any species (based on Milne 2002), and some of these calls may represent unrecorded variation in the call of *T. kapalgensis*. In particular, two call sequences very closely resembled the reference calls collected for *T. kapalgensis*, but could not be attributed to the species with absolute certainty because the duration of the call pulses was shorter than that measured from the reference calls. This was also the case for four other sites in the Top End of the Northern Territory and Queensland (Figure 1).

The only specific roost site recorded for *T. kapalgensis* is a mine in the Gunlom area of Kakadu National Park (Corbett and Richards 2002) based on Anabat calls recorded at the mine entrance. No *T. kapalgensis* individuals were physically caught and no reference calls for this species were available at the time. Corbett and Richards (2002) attributed Anabat sequences that were a "shallow frequency modulated call of long duration" at 25 kHz to *T. kapalgensis*, claiming that no other species in the Top End could be attributed to this call frequency. However, based on our experience this statement is inaccurate because the Anabat calls of *T. georgianus* are long and almost flat (relative to Anabat reference calls for other bat species) and have a frequency band of 23.3 - 25.4 kHz (Figure 3, Table 1). By contrast, the reference call pulses we collected for *T. kapalgensis* are relatively short. Corbett and Richards did not present Anabat graphs or details of pulse parameters of their *T. kapalgensis* calls and, in our view, the limited Anabat evidence presented by them appears equivocal. In addition, we set a harp trap across the mine adit for one night (leaving a second adit open for bats to freely enter and exit the same mine) eight days after the visit by Corbett and Richards. We failed to trap any *T. kapalgensis*, although three *T. georgianus* were captured. For these reasons, we regard the report of *T. kapalgensis* roosting in this mine with some reservation.

With the exception of four records, the majority of sites at which *T. kapalgensis* has been detected are considerable distances from areas containing rocky habitats that are considered to be potentially suitable for roosting. The distance of three sites from where *T. kapalgensis* specimens have been collected - Darwin, Kapalga and Point Stuart - to the nearest areas of known rocky habitats are 35 km (Daly Range), 60 km (Jabiluka), and 70 km (Mount Bundy), respectively. It is highly unlikely that a cave dependent species would travel so far in order to roost. Jolly (1990) found that the maximum distance that *T. georgianus* flew between roost sites in central Queensland was 12 km, although the author notes the actual foraging distance may have been greater. Furthermore, *Miniopterus schreibersii* has been shown to travel possibly as far as 40 miles (64 km) in one night (Dwyer 1966). There are two other possibilities that may present opportunities for cave roosting bats in these areas. First, there may be sea caves in these areas, which have been shown to support populations of *T. georgianus* on the Wessel Islands off the north-east coast of the Northern Territory (J. Woinarski pers. comm.) and *T. australis* off Queensland's east coast (Richards 1995). Second, road culverts, or disused concrete war bunkers, are also used by cave dwelling bats such as *M. schreibersii* and *T. australis* (Churchill 1998) and therefore may support populations of *T. kapalgensis* if it is a cave roosting species. However, given that the majority of specimens and Anabat recordings that we attributed to this species were from locations considerable distances from areas containing suitable rocky roosting sites, it is more likely that *T. kapalgensis* will roost in trees. This viewpoint is supported by some Aboriginal people who claim the species roosts in the base of pandanus leaves (McKean and Thomson 1995).

T. kapalgensis has been physically captured and ultrasonically detected from most coastal environments (floodplains, mangroves and patchy monsoon forests) and adjacent woodland areas with two notable records occurring in areas adjacent to sandstone escarpments, one of these located a considerable distance from the coast. It is unknown whether these habitats are used for foraging or roosting or whether they simply represent transient habitats for the species. It is possible that *T. kapalgensis* occurs in similar habitats of the Kimberly region in northern Western Australia. However, an extensive survey of bats in mangrove off the Kimberly coastline (McKenzie

and Rolfe 1986), which notably included the use of shot-sampling techniques, failed to detect its presence.

Threats to this species will most likely arise from gross habitat modification in the areas where we have shown it to occur. These threats include invasion of large areas of near-coastal floodplain by *Mimosa pigra* (e.g. Braithwaite *et al.* 1989); the replacement of natural floodplain vegetation with introduced pasture species; degradation of habitats by swamp buffalo *Bubalus bubalis*; and saltwater intrusion into coastal plains since the 1940s, possibly also resulting from swamp buffalo activities, and the subsequent death of large stands of *Melaleuca* trees (Mulrennan and Woodroffe 1998). There is currently no evidence that any of these factors pose an immediate threat to the persistence of *T. kapalgensis*, but some concern must arise due to the limited occurrence of the species in a few, possibly isolated populations.

We recommend that systematic Anabat surveys be undertaken in poorly sampled areas of the Top End, particularly the Arnhemland coastal regions, in order to better define the distribution and habitat of *T. kapalgensis*. Further reference calls for the species should be collected from across its suspected range to determine the degree of call variation, in order to increase the effectiveness of surveys using echolocation techniques. Reference calls for *S. saccolaimus* need to be collected from the Northern Territory to determine if its echolocation call can be clearly distinguished from *T. kapalgensis* calls. Clarifying the roosting preferences of the species using radio telemetry should also be a focus of future research.

Based on our study, *T. kapalgensis* is known to occur at no more than ten locations. This fulfils one of two criteria for a species to be regarded as Vulnerable under the IUCN (2001) criteria used to define conservation status. However, there is no evidence to indicate a decline in population size or available habitat, to meet the second criteria. We therefore recommend, based on the information presented here, that *T. kapalgensis* be regarded as Near Threatened (NT). However, this classification should be reviewed once more is known about the species.

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Appendix 3.

The relationship between echolocation-call frequency and moth predation of a tropical bat fauna

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The relationship between echolocation call frequency and moth predation of a tropical bat fauna

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Abstract.

The relationship between echolocation call frequency and moth predation of a tropical bat fauna

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The allotonic frequency hypothesis proposes that the proportion of eared moths in the diet should be highest in bats whose echolocation calls are dominated by frequencies outside the optimum hearing range of moths i.e. <20 kHz and >60 kHz. The hypothesis was tested on an ecologically diverse bat assemblage in northern tropical Australia that consisted of 23 species (5 families, 14 genera). Peak frequency of signals of bats within the echolocation assemblage ranged from 19.8 kHz to 157 kHz but was greatest between 20 and 50 kHz. A strong positive relationship existed between peak call frequency and percentage of moths in the diet for a sample of 16 bats from the assemblage representing 13 genera (R^2 = 0.54, P = 0.001). The relationship remained strong when the three species with low intensity calls were excluded. When the two species with high duty cycle constant frequency signals were removed, the relationship was weaker but still significant. In contrast to previous research, eared moths comprised only 54% of moth captures in light traps at bat foraging grounds and eared moths were significantly larger than non-eared individuals. These results show that the pattern of moth predation by tropical bats is similar to that already established for bat faunas in sub-tropical and temperate regions.

Introduction

Hearing has evolved in a range of insect groups including the Neuroptera, Orthoptera, Dictyoptera, Coleoptera, and Lepidoptera (Miller and Surlykke 2001). Among moths, ultrasonic hearing functions primarily as a defence against the echolocation calls of foraging bats (Spangler 1988; Fullard 1998; Miller and Surlykke 2001). Almost one half of the world's 200,000 species of moths belong to families that possess ears and can hear ultrasound (Scoble 1992; Fullard 1998). These 92,000 species of moths have been shown to be abundant at bat foraging grounds across the globe. Species from eared families contribute ≥ 85% of species richness of Macrolepidoptera in light trap catches at sites in Europe, North America, Africa and Australia, in environments ranging from temperate woodland to upland tropical rainforest (Fenton and Fullard 1979; Usher and Keiller 1998; Kitching et al. 2000; Schoeman and Jacobs 2003).

Hearing of eared moths is most sensitive to frequencies between 20 and 50 kHz, a range that coincides with the peak frequencies of most echolocating bats (Fullard 1987, 1998). Moths from regions with high bat diversity, which experience a greater bandwidth of echolocation frequencies, show increased sensitivity at high and low frequencies compared to moths from less diverse bat environments (Fullard 1982). However, although some moths can hear over a wider range of frequencies, sensitivity falls off gradually above 55 kHz (Fullard 1987). Although non-eared moths have evolved a suite of behavioural responses to reduce bat predation (Soutar and Fullard 2004 and references therein), the ability to hear combined with a variety of defensive flight

maneouvres enables eared moths to increase their chances of avoiding bat predation by up to 40% (Roeder 1967; Acharya and Fenton 1999).

Some echolocating bats are able to avoid detection by eared moths either by emitting low intensity calls that are almost imperceptible to moths or by calling at frequencies above and below the optimum hearing range of moths (Fullard 1998). Such frequencies are referred to as allotonic (i.e. frequency mis-matched between moths and bats). The allotonic frequency hypothesis proposes that the proportion of eared moths in the diet should be highest in bats whose echolocation calls are dominated by frequencies outside the optimum hearing range of moths i.e. <20 kHz and >60 kHz (Fenton and Fullard 1979).

The hypothesis is supported by research showing a high proportion of moths in the diet of bat species calling at allotonic frequencies (e.g. Rydell and Arlettaz 1994) and by a positive relationship between peak frequency of echolocation calls and incorporation of moths in the diet for bat assemblages with frequencies >20 kHz. The latter evidence is available for meta-analyses of bats with specific echolocation strategies (Jones 1992) and call frequencies (Bogdanowicz et al. 1999), and for foraging guilds (Pavey and Burwell 1998) and local bat communities in temperate and sub-tropical regions (Jacobs 2000; Schoeman and Jacobs 2003). Although some results must be treated with caution because data were collected in different ways at different times (Schoeman and Jacobs 2003), overall the findings suggest that the allotonic frequency hypothesis is valid for a wide range of bat assemblages. However,

the hypothesis has not been tested for bat faunas in the tropics, a major shortcoming given that bat diversity is concentrated in tropical regions (Findley 1993) and, consequently, the echolocation assemblages experienced by moths in the tropics are extremely diverse (e.g. Fullard 1998).

Here we report the results of a test of the allotonic frequency hypothesis in the tropics of the Northern Territory of Australia. The study had three aims: a) to describe the echolocation assemblage experienced by eared moths; b) to assess the level of moth predation by representative species in the bat assemblage; and c) to assess the relative proportions of eared and non-eared moths at bat foraging grounds. The bat fauna we examined is diverse, both taxonomically and ecologically, including five families, 14 genera (seven genera in the Vespertilionidae) and both of Australia's endemic genera; *Rhinonicteris* (Hipposideridae) and *Macroderma* (Megadermatidae) (Table 1). The study area is one of relatively few regions in the Old World tropics where horseshoe bats (Rhinolophidae) do not occur.

Materials and methods

Fieldwork was carried out during the late dry and early wet seasons (September to January) each year from 2000 to 2003 inclusive, with most sampling taking place from September to November (late dry season).

Study site

The study region is the tropics of the Northern Territory of Australia, north of the 18°S parallel. This area is dominated by eucalypt savanna woodland and encompasses approximately 340 000 km^2. Maximum mean weekly temperature ranges between 32° C and 39° C and mean annual rainfall between 360 mm and 1720 mm. Rainfall is highly seasonal with almost all precipitation occurring from November to April. Topographic relief is relatively low; maximum elevation is 553 m.

Echolocation frequency

Data on the structure and frequencies of search-phase echolocation signals of bats were obtained from 53 sites in a variety of environments throughout the study area. Voucher calls were taken from free-flying bats in the field.
We recorded calls of free-flying bats using a hand-held Anabat II bat-detector (Titley Electronics, Ballina, NSW) connected to an Optimus CTR-115 tape-recorder (Sony Chrome UX tapes). The person recording the calls usually sat on the roof of a stationary 4WD vehicle at this time. Upon hearing a bat through the Anabat speaker, the tape-recorder was manually switched on via the Anabat tape switch. A spotlight (12 Volt, 100 Watt) was switched on to locate the bat and better track its movements. On occasions the bat was then collected. Each specimen was identified and numbered. We also recorded calls of bats released after capture in mist-nets and harp-traps.

The Anabat system uses frequency division and zero-crossing analysis to construct frequency/time graphs from detected signals (de Oliveira 1998). The

frequency range of the microphone on the detector is 10 to 200 kHz with a peak frequency response at 50 kHz. The system responds to the dominant harmonic, regardless of which one it is. If another harmonic is strongly represented, the system will repeatedly jump between the two harmonics and neither one will be accurately represented. This situation rarely occurs (de Oliveira 1998). In this study, peak frequency for high duty cycle (i.e. constant frequency) bats is defined as the maximum frequency of the call, whereas for low duty cycle species it is defined as the frequency at the end or at the flattest portion of the call (refer Figure 2 of Milne 2002).

Dietary data

Dietary data were obtained by identifying prey in stomaches of specimens collected after recording of voucher calls, stomaches of specimens held in the Northern Territory Museum, and faecal pellets collected during field survey. Faecal pellets were obtained in three situations: a) from bats placed in cloth bags for 1-2 hrs after capture in mist-nets or harp-traps (all bats were captured before 2200 hrs); b) from the bottom of harp-trap bags in the morning if there was only one species of bat caught in the harp-trap during the entire night (bags were cleaned before use each evening); and c) under clusters of roosting bats.

Each pellet/stomach content was placed in a petri dish and teased apart using 10% KOH and 70% ethanol. We systematically searched the material for identifiable fragments under a low power (6.4-40×) binocular microscope. Prey items were identified at the lowest taxonomic level possible. We recorded

whether a taxon was present in each faecal pellet and counted the number of each body part present. The percent by volume of each order in each pellet/stomach was visually estimated to the nearest 5%.

Moth capture

We assessed the proportion of eared and non-eared moths by light trapping at 21 sites spread across the study area. Trapping was carried out for one night at 19 sites and for two nights at the remaining two sites. The light trap consisted of a 12 V fluorescent light hung from the higher end of a white cotton sheet (1.5 m x 2.5 m), suspended off the ground by strings tied to the corners to form a funnel, one end higher than the other. At the bottom of the funnel a hole was cut in the sheet and a plastic jar (65 mm diameter x 130 mm depth) partially filled with 70 % ethanol was attached to hang underneath. Insects that fell into the jar were collected the following morning. In the laboratory, we separated moths from all other insects after filtering the samples through a 2 mm sieve to remove the smallest insects (mostly <3 mm in body length). Each moth with a body length of 3 mm or greater was classified as either ‘eared’ or ‘non-eared’. Eared moths belonged to the Noctuidae, Arctiidae, Geometridae, Pyralidae, Notodontidae, and Lymantriidae. Moths belonging to all other families were classified as non-eared.

Data analysis

We regressed the arcsine of the mean percentage volume of moths in the bats’ diet against the log of their mean peak call frequency. For this analysis

we included bat species for which we obtained dietary data from a minimum of five individuals. If the sample included faecal pellets, we analysed at least five faecal pellets from each individual (Whitaker et al. 1996; Schoeman and Jacobs 2003). For some species, all dietary data came from faecal pellets collected under roosting bats. In this case a sample of at least 20 faecal pellets was analysed for each species (Whitaker et al. 1999; Arlettaz et al. 2000). Sixteen species were included in this analysis (Table 2) including representative species from each family, foraging guild and echolocation call type (Table 1). Thirteen of the 14 genera present in the study area were represented in this sample. A single representative was included from each genus, except *Nyctophilus*, *Chalinolobus* and *Pipistrellus* which had two representatives each.

We used standard t-tests to examine differences in abundance and wing length between eared and non-eared moths. Means are presented ± standard error.

Results

The insectivorous bat fauna of the study area consisted of 23 species with widespread distributions (Table 1) and a further five species that either occur only in the extreme south of the study area or are very rare. We cover the 23 widespread species here. All species are considered to be insectivorous or carnivorous; no partial frugivores are known from the assemblage.

Echolocation assemblage

We recorded echolocation signals of all 23 widespread species from the study area (Table 1). These species include three distinct approaches to echolocation. The four hipposiderid bats have high intensity, constant frequency calls produced at moderately high duty cycles. Five species produce signals of low intensity at low duty cycles. One of these species, *Macroderma gigas* (Dobson, 1880), is a facultative echolocator that on occasions hunts by passive sound localization using noise generated by its prey (Kulzer et al. 1984; Pettigrew et al. 1986). The majority of the bats of the study area produce high intensity, low duty cycle signals (Table 1).

The peak frequency of the signals of bats within the echolocation assemblage ranged from 19.8 kHz to 157 kHz (Table 1). However, the echolocation assemblage experienced by eared moths was greatest in the frequency range between 20 and 50 kHz (Fig. 1). Fifteen of the 23 species had peak frequencies within this range including 12 of the 14 species with high intensity low duty cycle signals i.e. typical aerial hawking species (Fig. 1). All species with peak frequencies greater than 60 kHz were high duty cycle echolocators. Although we lack standardized estimates of bat abundance, trapping with harp traps and mist-nets indicates that the most abundant species within the study area are those calling within the 20-50 kHz frequency band. In contrast, the high duty cycle echolocators especially *Hipposideros diadema* (Geoffroy, 1813) and *Hipposideros stenotis* Thomas, 1913 are comparatively rare (D.J. Milne unpublished data).

Diet

The 16 bat species included in the dietary sample had peak frequencies ranging from 19.8 to 157 kHz, thus including the extremes of frequency of the wider bat assemblage (Table 1). When data for the 16 species are combined, the list of prey captured includes 10 insect orders, two other arthropod classes (spiders: Class Arachnida, Order Araneae; centipedes: Class Chilopoda) and vertebrates. *Macroderma gigas* was the only species that captured centipedes and vertebrates. In contrast, eight species preyed on spiders, although spiders contributed >5% by volume to the diet of only one species, *Nyctophilus arnhemensis* Johnson, 1959 (Table 2).

Coleoptera was the only insect order recorded in the diet of all 16 bats (Table 2). Hemiptera were taken by all species except *Hipposideros ater* Templeton, 1848 and Lepidoptera by all species except *Saccolaimus flaviventris* (Peters, 1867) and *M. gigas*. The diet of only five species consisted of >50% by volume of a single insect order (Table 2).

Relationship between call frequency and diet

A strong positive relationship existed between peak call frequency of all bats and percentage of moths in the diet ($R^2 = 0.54$, $F_{1,14} = 16.15$, $p = 0.001$) (Fig. 2). The relationship remained strong when the three species with low intensity calls were excluded from the analysis ($R^2 = 0.52$, $F_{1,11} = 11.72$, $p = 0.006$). These species were *Nyctophilus walkeri* Thomas, 1892, *N. arnhemensis*, and *M. gigas*. The low intensity nature of the calls of these species suggested that

they may not have been readily detected by eared moths. When the two species with high duty cycle CF calls, *H. ater* and *Rhinonicteris aurantius* (Gray, 1845), were removed the relationship was weaker but still significant (R^2 = 0.31, $F_{1,12}$ = 5.32, p = 0.04). The three low intensity echolocators were included in this analysis.

The 10 vespertilionid bats included in the sample had peak frequencies ranging from 30.5 to 59.6 kHz i.e. within the range of best hearing of eared moths (Table 1). No significant relationship between peak call frequency and percentage of moths in the diet was present when only vespertilionids were assessed (R^2 = 0.12, $F_{1,8}$ = 1.08, p = 0.33).

Moth abundance

A total of 867 moths with body length ≥ 3 mm were captured during 23 nights of insect sampling. Moths belonging to eared families were more abundant than non-eared moths (eared moths, n = 469, 20.39 ± 7.23 captures/trap night; non-eared moths, n = 398, 17.30 ± 3.21 captures/trap night). However, the difference in mean abundance per trap night between eared and non-eared moths was not significant (t-test, p = 0.70).

The eared moths captured in the light trap samples were on average over 30% larger than non-eared moths when forewing length is used as a measure of body size (eared moths, 8.66 ± 0.16 mm vs non-eared moths, 6.64 ± 0.18 mm). This difference was highly significant (t-test, p <0.0001).

Discussion

Our study provides the first examination of the allotonic frequency hypothesis on a species-rich bat assemblage in the tropics. The assemblage examined is diverse both taxonomically and ecologically, containing five families and 14 genera (of which representative species from 13 genera were assessed). The assemblage includes species with a wide range of foraging strategies and echolocation call designs and representative species are close to the extremes of body size variation present in microchiropteran bats, ranging from 3.1 g to 104.6 g (Table 1). Previous research on the relationship between bat call frequency and moth predation has either compared bat diets across a wide range of studies without standard methods of diet assessment (e.g. Jones 1992) or investigated local communities/guilds with richness of up to 9 species from 7 genera (Schoeman and Jacobs 2003), but typically much less (e.g. Pavey and Burwell 1998).

The results of the study corroborate the allotonic frequency hypothesis. Specifically, a strong positive relationship existed when we regressed peak frequency against % moths in the diet for the 16 species in the assemblage with data for both variables available. This finding shows that the pattern of incorporation of moths into the diets of tropical bats is similar to that already established for bat faunas in sub-tropical and temperate regions (Jacobs 2000; Schoeman and Jacobs 2003).

Sampling for this study was carried out within an extensive area of the tropics of northern Australia and therefore represents a regional rather than a local bat assemblage. However, the bat fauna of the study area has a low β-diversity; species are widespread within the study area and there is little turnover of species across environments (Churchill 1998). The average local richness at sampling sites within the study area was six species with a maximum of 15 species.

A shortcoming of most studies of the relationship between bat call frequency and predation on moths is that presence of moths in the diet is determined only by identification of scales in faecal samples. This method does not enable identification of moths to family and, therefore, precludes an assessment of the proportions of eared and non-eared individuals in the diet. Moths present in faecal samples of bats are assumed to be mostly eared individuals because light trapping indicates that the majority of moths flying at night belong to eared families. In contrast to previous research, light trapping during our study indicated that eared individuals were not significantly more abundant than non-eared moths. This finding was unexpected given that light trap sampling in the tropics, sub-tropics and temperate regions of the Old World (Africa, Australia, Europe) indicates that a minimum of 80% and often >90% by number of moths captured are eared (Pavey and Burwell 1998; Usher and Keiller 1998; Kitching et al. 2000; Schoeman and Jacobs 2003). Further, the moth fauna of another site in eucalypt savanna woodland in northern Australia was dominated by eared individuals (Chillagoe site of Pavey and Burwell 1998).

We carried out 20 of the 23 nights of light trap sampling during the months of September and October. This temporal clumping of sampling may have resulted in the capture of large numbers of earless moths during mass emergences. Sampling during a wider range of seasons is needed to assess whether our results are representative of the moth fauna of the study region.

The lack of a significant difference in abundance between eared and non-eared moths in this study weakens our interpretation of the dietary data supporting the allotonic frequency hypothesis. However, the significantly larger size of eared moths in our light trap samples suggests that bats should actively select eared individuals when foraging because these are energetically more profitable and easier to detect. However, this expectation is countered by the likelihood that eared moths will be able to avoid bats more effectively.

The significantly greater forewing length of eared moths in our light trap samples contrasts with the results of a study in Scandinavia that found that species of non-eared moths had significantly greater wingspans and wing loadings that eared species (Rydell and Lancaster 2000). Our study was not structured to test this pattern, whereas Rydell and Lancaster (2000) sampled a wide range of eared and non-eared families and examined only one species per genus. Notwithstanding the differences in design between the two studies, the results from northern Australia suggest that the relationship between smaller body size and possession of ears may not hold for all moth faunas.

A factor that needs to be considered when interpreting moth predation and abundance data is that bats can capture large numbers of non-eared moths even if the nocturnal moth fauna is dominated by eared species. For example, non-eared moths were the major prey of *Rhinolophus megaphyllus* Gray, 1834 (peak call frequency 67-71 kHz) at three sites in eastern Australia despite eared moths comprising >80% of moth captures during light trapping at each site (Pavey and Burwell 1998). A linear index of food selection revealed that *R. megaphyllus* avoided all major families of eared moths and exhibited a strong preference for particular non-eared families including Anthelidae, Lasiocampidae and Hepialidae. This finding suggests that any assessment of the allotonic frequency hypothesis using faecal/stomach analysis to determine moth predation will be coarse, irrespective of the relative abundance of eared and non-eared moths. Further, the light trapping results from our study indicate that, despite the large body of previous work, it is not advisable to assume that eared moths are more abundant than non-eared individuals at all locations.

Only two species in the assemblage (*S. flaviventris*, *M. gigas*) did not consume any moths (Table 2). These species were the only two in the 23 species-strong regional pool to have a body mass >30 g (Table 1) and both fed on hard-bodied invertebrates (*S. flaviventris* – Coleoptera; *M. gigas* – Orthoptera, Coleoptera). Of the remaining species, 10 had >10% by volume of moths in the diet (Table 2). This pattern contrasts with dietary data from other

assemblages/species pools that include a high proportion of non-moth feeders (e.g. four of nine species, Schoeman and Jacobs 2003).

The peak frequencies of the 10 vespertilionid species included in the sample were confined to the 30-60 kHz band which corresponds to the optimal hearing abilities of all moth faunas assessed to date (Fullard 1998). As a consequence, the absence of a significant relationship between peak frequency and % volume of moths in the diet for vespertilionids was expected. However, of the four bats in the sample that captured >30% by volume of moths, two were vespertilionid species; *Miniopterus schreibersii* (Kuhl, 1817) and *N. walkeri*. Further, *M. schreibersii* had the highest % volume of moths in its diet of all species sampled. This result was unexpected as each of the local bat communities examined in southern Africa has had a high duty cycle echolocator capturing the highest percentage of moths (Jacobs 2000; Schoeman and Jacobs 2003). Lepidoptera have previously been recorded as a prominent component of the diet of *M. schreibersii* in Australia (Vestjens and Hall 1977).

It is often argued that bats with low intensity echolocation signals should be excluded from analyses that test the allotonic frequency hypothesis because moth ears are tuned to the frequencies of aerial-hawking bats that typically are obligate echolocators with high intensity signals (e.g. Rydell et al. 1995). In contrast, bats with low intensity signals are typically gleaners that fly close to surfaces and use prey generated sound, and often also vision, in combination with echolocation to hunt prey (Fullard 1998). As a consequence,

low intensity echolocation is considered an alternative approach to overcoming a moth's defenses because these bats are likely to be acoustically inconspicuous to moths.

One of the low intensity echolocators in our sample, *M. gigas*, is a facultative echolocator that uses passive hearing to localize prey when gleaning from the ground (Guppy and Coles 1983; Kulzer et al. 1984). However, capture of flying insects, which appears to be a common behaviour (Tidemann et al. 1985), involves the use of echolocation (Pettigrew et al. 1986). The other two low intensity echolocators studied were long-eared bats, genus *Nyctophilus*. Observations on two *Nyctophilus* species not included in our dietary sample, *N. geoffroyi* Leach, 1821 and *N. gouldi* Tomes, 1858, indicate that these species do use prey generated sound, vision, and echolocation to capture insects in the laboratory (Grant 1991; Hosken et al. 1994). However, gleaning appears to be rarely used by either species in the field, with aerial hawking being the dominant foraging strategy (O'Neill and Taylor 1986; Brigham et al. 1997). Despite the differences in call intensity between *M. gigas*, *N. arnhemensis* and *N. walkeri*, and the remaining 13 species sampled, the strength of the relationship between peak frequency and moth predation did not change when these three species were removed from the analysis.

Call frequency and intensity may not be the only factors that determine the level of moth predation by insectivorous bats. The long duration high duty cycle signals of *Rhinolophus* species may favour moth predation because the signals enable the classification of prey. Schoeman and Jacobs (2003)

suggested that large-winged insects such as moths may produce more prominent glints (amplitude modulations) in echoes than smaller-winged insects and this enables them to be detected more readily. As a consequence, high levels of moth predation by horseshoe bats may be the result of signal structure and duration not peak frequency. Conversely, the long duration signals of rhinolophid species may make them more apparent to tympanate moths (Waters and Jones 1996). As a consequence, detection distances of rhinolophid species by eared moths will be similar to those for FM bats calling at lower frequencies (Waters and Jones 1996). This situation would reduce the ability of rhinolophid bats to capture eared moths relative to FM bats calling at similar frequencies. If either interpretation is correct, it weakens the evidence in support of the allotonic frequency hypothesis because previous guild and community-level assessments have all included rhinolophid species (Pavey and Burwell 1998; Jacobs 2000; Schoeman and Jacobs 2003). In contrast, our study demonstrates a strong positive relationship between peak signal frequency and moth predation in a regional bat assemblage lacking horseshoe bats and, therefore, without concerns about conflation in patterns resulting from signal duration. Although hipposiderid bats also produce pure tone calls, the hipposiderid echolocation system differs from that of rhinolophid bats in consisting of shorter duration signals given at significantly lower duty cycles (Jones 1999). Further, the hipposiderid system does not appear to be adapted for prey selection (Pavey et al. 2001). The significant positive relationship between peak frequency and % moths in the diet of our sample of 16 species remained even after excluding the two hipposiderid species.

In summary, we consider that the dietary data presented here support the allotonic frequency hypothesis, despite the observation that a species calling at 48.5 kHz (*Miniopterus schreibersii*) captured the highest proportion of moths. The strong positive relationship between peak call frequency and percentage of moths in the diet for a sample of 16 species of bats from this tropical assemblage is similar to results obtained for bat faunas in sub-tropical and temperate regions. However, the absence of a significant difference in abundance between eared and non-eared moths in light trap samples during our study was unexpected and weakens the case in support of the allotonic frequency hypothesis which assumes that the majority of moths available to foraging bats are eared. An inability to separate eared and non-eared moths in dietary samples is a shortcoming of this study and most previous tests of the hypothesis.

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Table 1. Echolocation call characters, foraging guild and body mass of the 23 species of insectivorous bats from tropical northern Australia included in the study with species for which dietary data were collected marked in bold.

	Bat species	Call type*	Peak frequency (kHz)†	Intensity	Foraging guild‡	Body mass (g) §
Emballonuridae	***Saccolaimus flaviventris*** (Peters, 1867)	LDFM	20.3	High	US	51.4-54.8
	Taphozous kapalgensis McKean and Friend, 1979	LDFM	23.6	High	US	26.0
	Taphozous georgianus Thomas, 1915	LDFM	24.1	High	US	24.1
Molossidae	*Mormopterus loriae* (Thomas, 1897)	LDFM	31.7	High	US, BCS	7.4
	Mormopterus beccarii Peters, 1881	LDFM	24.3	High	US	14.8
	Chaerophon jobensis (Miller, 1902)	LDFM	**19.8**	High	US	20.4
Megadermatidae	***Macroderma gigas*** (Dobson, 1880)	LDFM	20.0-12.0‖	Low	BCS	104.6
Hipposideridae	***Rhinonicterus aurantius*** (Gray, 1845)	HDCF	**116.0**	High	BCS, HCS	8.4
	Hipposideros ater Templeton, 1848	HDCF	**157.0**	High	BCS, HCS	4.2

	Hipposideros diadema (Geoffroy, 1813)	HDCF	69.1	High	BCS	26.5
	Hipposideros stenotis Thomas, 1913	HDCF	106.0	High	BCS	5.5
Vespertilionidae	***Miniopterus schreibersii*** (Kuhl, 1817)	LDFM	**48.5**	High	BCS	11.3
	Pipistrellus westralis Koopman, 1984	LDFM	**46.6**	High	BCS	3.1
	Pipistrellus adamsi Kitchener, Caputi and Jones 1986	LDFM	**43.9**	High	BCS	4.2
	Chalinolobus nigrogriseus (Gould, 1856)	LDFM	**38.4**	High	BCS	6.0
	Chalinolobus gouldii (Gray, 1841)	LDFM	**30.5**	High	BCS	9.8
	Scotorepens greyii (Gray, 1843)	LDFM	**38.0**	High	BCS	6.6
	Myotis macropus Gould, 1855	LDFM	**40.1**	High	BCS	8.3
	Nyctophilus arnhemensis Johnson, 1959	LDFM	**47.1**	Low	HCS	6.6
	Nyctophilus walkeri Thomas, 1892	LDFM	**54.7**	Low	HCS	4.4
	Nyctophilus bifax Thomas, 1915	LDFM	49.4	Low	HCS	9.3
	Nyctophilus geoffroyi Leach, 1821	LDFM	45.8	Low	HCS	5.8
	Vespadelus caurinus (Thomas, 1914)	LDFM	**59.6**	High	BCS	3.1

* LDFM, low duty cycle frequency-modulated; HDCF, high duty cycle constant frequency.

† Data from Milne (2002) and Milne et al. (2003), except *Macroderma gigas* (Kulzer et al. 1984, Guppy et al. 1985).

‡ US, uncluttered space; BCS, background cluttered space; HCS, highly cluttered space. Guild assignments based on Milne et al. (2004, Table 1).

§ Body mass data from Churchill (1998), except *Saccolaimus flaviventris* (Rhodes and Hall 1997).

‖ frequency data for *M. gigas* are for the first harmonic; each pulse typically has 3 to 4 harmonics.

Table 2 . Percent volume of prey categories in the diets of 16 bat species from tropical northern Australia (abbreviations are: *Saccolaimus flaviventris* (*Sf*), *Taphozous georgianus* (*Tg*), *Chaerophon jobensis* (*Cj*), *Macroderma gigas* (*Mg*), *Rhinonicterus aurantius* (*Ra*), *Hipposideros ater* (Ha), *Miniopterus schreibersii* (*Ms*), *Pipistrellus westralis* (*Pw*), *Pipistrellus adamsi* (*Pa*), *Chalinolobus nigrogriseus* (*Cn*), *Chalinolobus gouldii* (*Cg*), *Scotorepens greyii* (*Sg*), *Myotis macropus* (*Mm*), *Nyctophilus arnhemensis* (*Na*), *Nyctophilus walkeri* (*Nw*), *Vespadelus caurinus* (*Vc*)).

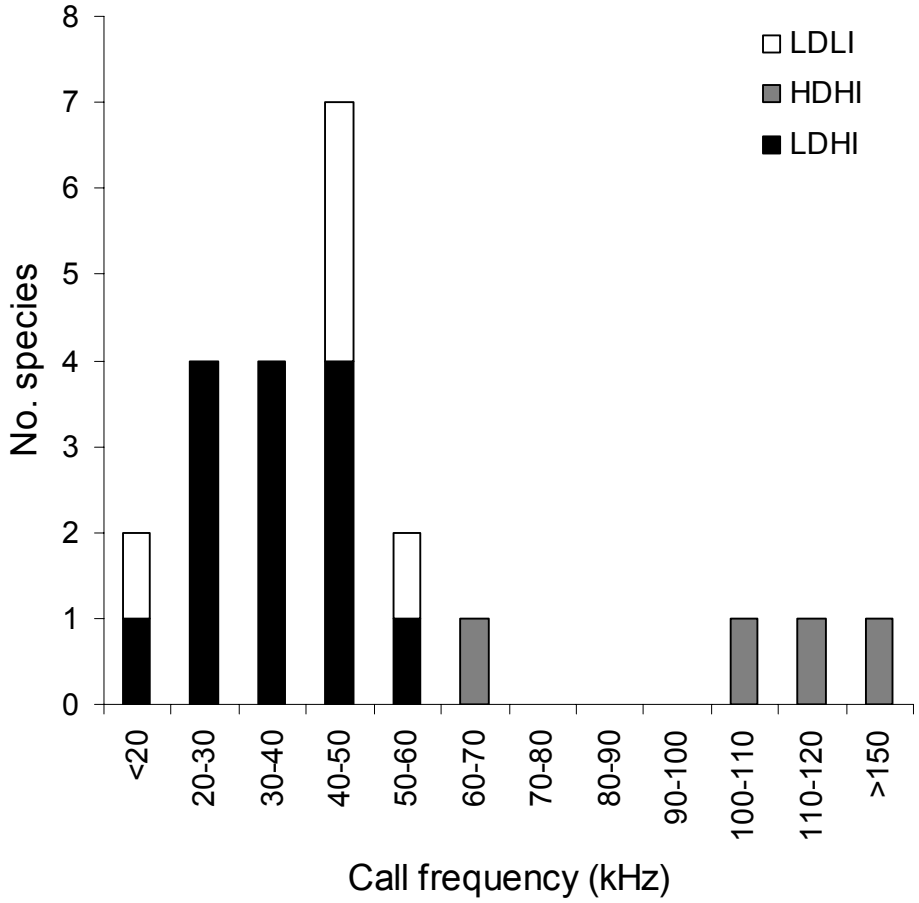
Bat species	*Sf*	*Tg*	*Cj*	*Mg*	*Ra*	*Ha*	*Ms*	*Mm*	*Pw*	*Pa*	*Cn*	*Cg*	*Sg*	*Na*	*Nw*	*Vc*
No. individuals	10	5	8	*	7	7	*	*	5	5	11	5	15	5	5	6
Prey category																
Blattodea	0.75		35.6		4.2	7.9		3.0	5.0	2.0	1.0	1.0	3.6	26.0	13.2	
Isoptera					3.6	7.1		54.25		1.0			1.3	9.0	1.05	15.8
Orthoptera	8.0	9.0	16.25	47.75			12.5					36.0		3.0		
Orthopteroid		3.0			2.1											
Hemiptera																
Heteroptera	16.25	16.0	5.6		2.1		9.3		16.0	4.0	2.0	32.0	26.6	12.9		0.8

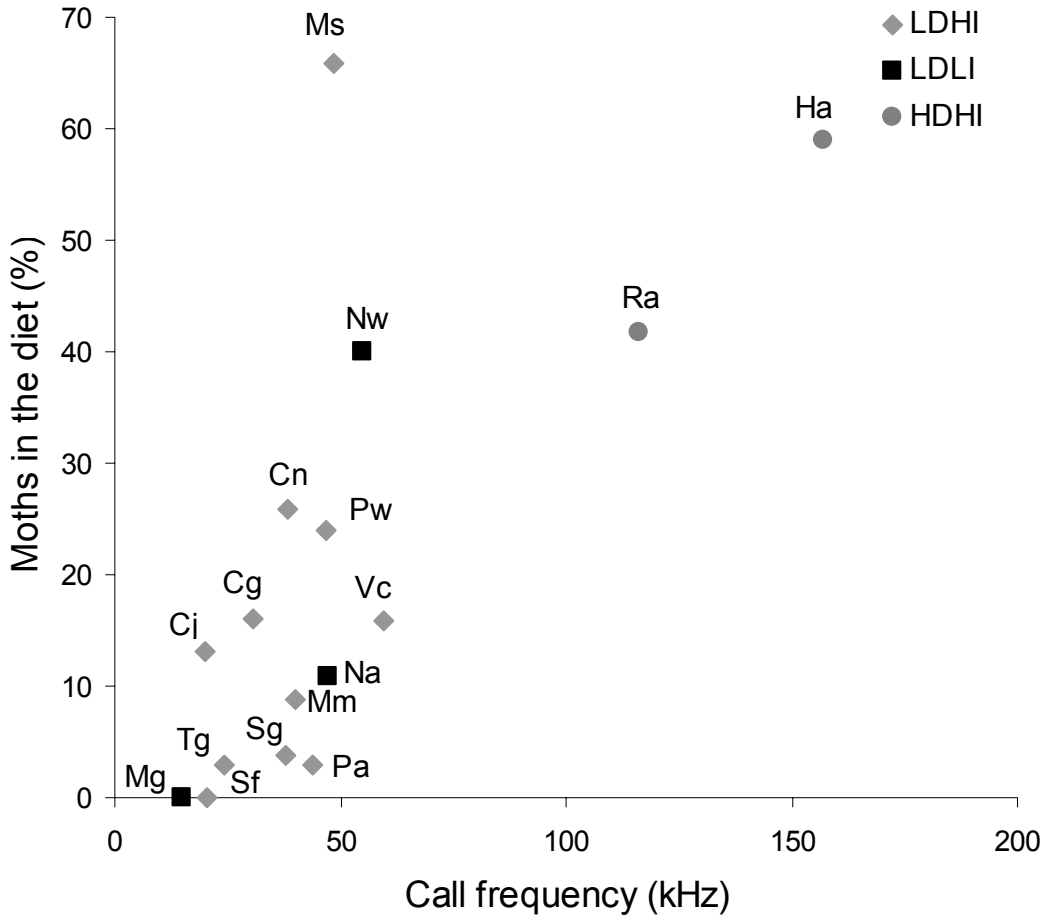
Auchenorrhyncha	2.5	2.0	1.25	0.25	3.6		0.7	0.5		14.0	1.8	10.0	0.1		0.1	2.5
Stenorrhyncha														0.05		
Neuroptera		1.0	1.0			3.1					0.6	1.0	0.3		1.0	
Coleoptera	62.5	57.0	28.1	28.5	39.2	16.7	1.1	6.0	29.0	35.0	36.0	2.0	45.9	32.2	42.7	30.0
Diptera					2.7	5.4	0.9	12.5		5.0	0.6				2.05	2.5
Trichoptera																0.8
Lepidoptera		3.0	13.1		41.7	59.0	65.9	8.75	24.0	3.0	25.8	16.0	3.8	10.8	39.95	15.8
Hymenoptera	10.0	9.0		0.25	0.8	0.7	9.3	11.25	25.0	35.0	31.3	2.0	18.3			30.0
Araenae				1.0			0.2	3.75	1.0	1.0	0.6			6.0		1.7
Chilopoda				8.75												
Vertebrate				13.5												

* faeces collected below a colony of at least 10 bats. Minimum of 20 pellets analysed.

Figure 1. Echolocation assemblage to which moths are exposed within the study area in tropical northern Australia, displayed as the number of bat species in three echolocation categories with peak frequencies in each 10 kHz frequency band. Abbreviations are: LDLI, low duty cycle low intensity; HDHI, high duty cycle high intensity; LDHI low duty cycle high intensity.

Figure 2. Relationship of the peak frequency of echolocation signals and mean percentage by volume of moths in the diets of 16 species of bats in tropical northern Australia represented according to their echolocation strategy (refer to Figure 1 for abbreviations). Species abbreviations as per Table 2.


LDLI
HDHI
LDHI
No. species
0
1
2
3
4
5
6
7
8
<20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
100-110
110-120
>150
Call frequency (kHz)


LDHI
LDLI
HDHI
Moths in the diet (%)
Call frequency (kHz)
0
10
20
30
40
50
60
70
0
50
100
150
200
Ms
Ha
Ra
Nw
Cn
Pw
Cg
Vc
Ci
Na
Mm
Sg
Tg
Pa
Mg
Sf