A Biodiversity Survey of the Pilbara Region of Western Australia, 2002 – 2007

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The echolocation calls, habitat relationships, foraging niches and communities of Pilbara microbats

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Abstract – Between 2004 and 2007, we systematically surveyed microbats across the Pilbara region in Western Australia, and collected data on species' foraging ecology. Here we report the results of the echolocation survey of 69 sites dispersed among 24 survey areas covering the 179,000 km² region. Echolocation call sequences were identified using a library of known calls accumulated during field work. In combination, the frequency maintained for the greatest number of cycles (F_{peakC}) and the bandwidth ratio of this peak (Q) identified search-mode echolocation calls by 13 of the 17 species comprising the microbat fauna of the Pilbara bioregion. These variables did not separate *Taphozous georgianus* from *T. hilli* calls, *Chalinolobus gouldii* from *Mormopterus loriae*, and allopatric pairs of *Nyctophilus* species. Even so, the spectral characters provided an ecologically informative, viable and non-intrusive survey tool.

The survey revealed two compositionally distinct communities. One comprised 14 species and occupied landward environments, while the other comprised 9 species and occupied mangroves. Three members of the mangrove community were confined to mangroves (*M. loriae*, *Nyctophilus arnhemensis* and *N. geoffroyi pallescens*), being replaced by allopatric congenerics in the region's landward environments (*Mormopterus beccarii*, *Nyctophilus bifax daedalus* and *N. g. geoffroyi*). In both communities, the search-mode calls of syntopic species were dispersed in spectral space, showed only peripheral overlap in their spectral variables (Q and F_{peakC}) and were arrayed according to differences in foraging niche determined from empirical data on species' flight capabilities and foraging behaviours. These observations imply a niche-assembly model of metacommunity structure.

However, on its own, this model was insufficient to explain the composition of the Pilbara microbat assemblages. Nestedness was observed in assemblage composition that could be explained by environmental factors, implying the influence of environmental controls. The richest microbat assemblages were recorded in well-developed riparian environments with complex vegetation structures and permanent pools that were set in cavernous landscapes. Two species (*Nyctophilus bifax* and *Chalinolobus morio*) were restricted to these productive riparian environments, while two others (*Macroderma gigas* and *Rhinonicteris aurantia*) were found to be more common than previously supposed despite detectability constraints caused by their cryptic calls. The widespread occurrence of *M. gigas* and *R. aurantia* is reasonable because caves and mines are common in the ranges of the Pilbara region, and offer physiologically favourable day-roosts to these otherwise mesic tropical species. Proximity of cavernous landscapes also explained the presence or absence of other obligate cave/rock-crevice roosting species in assemblages (*Taphozous* spp., and *Vespadelus finlaysoni*).

Comparison with surrounding regions revealed a diversity-productivity model of faunal structure, with an organisation that conforms to the specialisation hypothesis in which co-occurring species occupy different foraging niches. Three riparian sites (Turee Creek, Cattle Gorge and Weeli Wolli) and four mangrove stands are identified for reservation.

Key Words: bat, echolocation, F_{peakC}, *Q6dB*, metacommunity, species composition, habitat relationships

INTRODUCTION

A conservation reserve system that 'captures' each species once is not enough to ensure the persistence of ecosystem complexity. Given the dynamic nature of ecosystem processes and landscape disturbance regimes, an understanding of the factors structuring communities, especially those that determine differences in species composition point-to-point across landscapes, is fundamental to reserve system design. It also contributes to effective off-reserve conservation.

Foraging method has proved to be an important mechanism of resource allocation in communities (e.g. Hespenheide 1975; McKenzie and Rolfe 1986; Simberloff and Dyan 1991). In bats, foraging method is tightly coupled to aspects of their flight morphology and echolocation call structure. In these terms, niche-assembly models of metacommunity structure related to resource partitioning have been documented previously for microbat communities of north-western Australia, including the Little Sandy Desert community (McKenzie et al. 2002) and those of mangrove stands along the Kimberley and Pilbara coasts (McKenzie and Rolfe 1986; McKenzie and Start 1989), but there has been no investigation of factors influencing differences in assemblage composition within these microbat communities from place to place.

The echolocation calls that microbats emit are reasonably stereotyped, but vary across species according to the characteristics of their different foraging niches (Neuweiler 1990). Within a species, apparent variation in sonar design can be related to differences between individuals and between populations (e.g. Parsons 1997; Barclay et al. 1999; Murray et al. 2001), to Doppler effects (e.g. Guppy and Coles 1988), to signal recording and analysis techniques (Parsons et al. 2000), to habitat differences and presence of conspecifics (Obrist 1995), and to the foraging context in which a bat is emitting calls including the 'search', 'approach' and 'interception' phases in call sequences (e.g. Griffin et al. 1960; Schnitzler et al. 1987; Kalko and Schnitzler 1993). Search-mode calls are useful for acoustic identification of species (e.g. O'Farrell et al. 1999; Murray et al. 2001; Bullen and McKenzie 2002a). They are prominent above background noise levels and, by measuring call repetition rates, can be uniquely discriminated from other phases of call sequences, thereby reducing the variability problem.

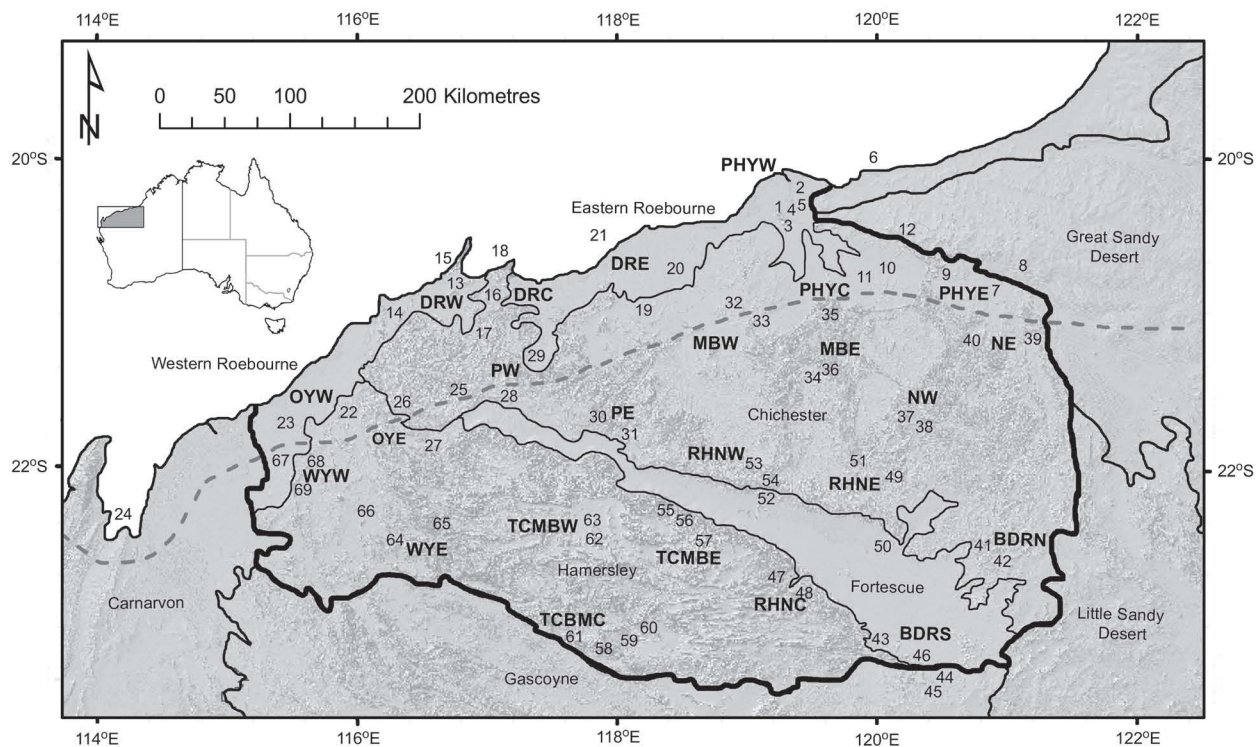In this paper we use spectral analysis in

Figure 1 The Pilbara biogeographic region (outlined in bold) showing the boundaries of its four IBRA sub-regions (Environment Australia 2000), the surrounding regions, the 69 sites sampled for microbats during the survey (numbered 1 to 69), the codes for the 24 survey areas (e.g. PHNW), and the boundary between its two biocli-matic zones (dashed line). These are superimposed on a digital elevation model (after Geoscience Australia GEODATA 3 second DEM version 2).

frequency domain (Bullen and McKenzie 2002a; McKenzie and Bullen 2003) to characterise and differentiate the search-mode echolocation calls of microbat species from the Pilbara Bioregion of Western Australia, and develop a call dictionary. Using this dictionary, we identify bat call sequences recorded during an echolocation survey of the region, display the composition of the Pilbara microbat fauna in terms of species co-occurrence patterns, then explore compositional patterns in terms of environmental factors.

To provide a context on metacommunity structure, we also document the foraging niches of Pilbara microbats in terms of differences in their flight capabilities, foraging microhabitats and foraging strategies. Since observations on species foraging niche are scarce for most Australian bats, our field program focused on collecting these data, and we report them in detail.

METHODS

Study area and fauna

The Pilbara biogeographic region has an area of 179,000 km² (Figure 1), and corresponds closely with the Pilbara Craton. It straddles two bioclimatic zones (Beard, 1990). The broad near-coastal band has a semidesert tropical climate with 9 to 11 months of dry weather, and summer rainfall. The rest of the region has a desert climate with summer rain, characterised by up to 12 months of dry weather and generally higher temperatures. Average annual rainfall is 290 mm, but locally unreliable, while average maximum temperatures range from 25.3°C in July to 37.8°C in January, and minimum night time temperatures range from 11.8°C in July to 25.2 °C in January.

The region is divided into four geomorphically distinctive IBRA subregions – Chichester, Fortescue, Hamersley and Roebourne (Figure 1). All are drained by seasonally active river systems that are fringed by large gum trees with frequent hollow branches and, in some areas, by tall riparian forests that have developed around permanent pools behind rock-bars or are associated with springs. The north and central parts of the region comprise low open woodlands and grasslands with scattered trees on broad plains that, in places, are interrupted by ranges covered by tree steppe and in which caverns and old underground mines are common. The region's south comprises ranges and plateaux with low woodlands over grasses, and is dissected by gorges. Caves are common along the scarps. Coastal and sub-coastal plains support grasslands with scattered trees, dwarf shrub steppes and low mangrove forests.

The region's microbat fauna includes arid zone populations of four molossids, three emballonurids, eight vespertilionids including four nyctophilinids, one hipposiderid and one megadermatid (Table 1). Nomenclature follows van Dyck and Strahan (2008), although we treat two subspecies of *Nyctophilus geoffroyi* as distinct (*N. g. geoffroyi* and *N. g. pallescens*). These subspecies are distinguished on external and cranial measures presented in Thomas (1913).

Reference call dictionary

During field work between 1992 and 2007, echolocation call sequences by free-flying bats of known identity were recorded from: (1) bats captured in mist nets or bat traps set over pools, in riparian woodlands, in mangroves or across the entrances of caves and mines, then released with bioluminescent tags (Buchler 1976) and recorded on subsequent passes; (2) bats that we shot while their echolocation calls were being recorded (CALM Animal Ethics Permit No. 14/93); (3) bats from surrounding regions if we were unable to record sequences by at least 10 individuals from the study area. We excluded sequences when echolocation calls by more than one individual were present in the sequence.

Call sequences were recorded using the frequency-division function of Anabat II ultrasound detectors (Titley Electronics, Australia), set to divide by 16. The frequency-division function using Zero-crossing analysis within these detectors is known to operate on the strongest harmonic present (Parsons *et al.* 2000), normally the fundamental harmonic. Output was stored directly onto Metal IV cassette tapes using a Sony Walkman Professional (WMD6C) tape recorder and, after 2003, a Sony Minidisc recorder (MZ-N510) in SP-mono mode.

COOL EDIT 2000, now ADOBE AUDITION 2 (Adobe Systems, USA), was used to convert the recordings to '.mp3' files, display call sequences in spectral view, then analyse consistently shaped, regularly spaced, sequential sets of 'search' mode calls with clean, well-defined shape (see McKenzie and Bullen 2003 for details). Unlike the 'approach' or 'interception' phases of sequences, search mode calls are emitted at a rate of one call per wing-beat or fewer (Schnitzler *et al.* 1987; Kalko and Schnitzler 1993, 1998; McKenzie and Bullen 2003). Since microbat species all flap their wings at similar frequencies (7 to 12 Hz: Schnitzler *et al.* 1987; Bullen and McKenzie 2002b), call repetition rates can be used to distinguish periods of 'search mode' in sequences recorded from free-flying bats.

We used COOL EDIT 2000 to carry out a 2048-point Blackmann-Harris fast-Fourier transformation of each search-mode call. This analysis provided the frequency spectrum (profile) of the call's strongest harmonic (Figure 2, modified

Table 1 The Pilbara microbat fauna.

Family	Species	Code
Megadermatidae	*Macroderma gigas* (Dobson, 1880)	Mg
Hipposideridae	*Rhinonicteris aurantia* Gray, 1845	Ra
Emballonuridae	*Taphozous georgianus* Thomas, 1915	Tg
	Taphozous hilli Kitchener, 1980	Th
	Saccolaimus flaviventris (Peters, 1867)	Sf
Molossidae	*Tadarida australis* (Gray, 1838)	Ta
	Chaerephon jobensis (Miller, 1902)	Cj
	Mormopterus beccarii Peters, 1881	Mb
	Mormopterus loriae Thomas, 1897	Ml
Vespertilionidae	*Nyctophilus arnhemensis* Johnson, 1959	Na
	Nyctophilus bifax daedalus Thomas, 1915	Nbd
	Nyctophilus geoffroyi geoffroyi Leach, 1821	Ngg
	Nyctophilus g. pallescens (Thomas, 1913)	Ngp
	Chalinolobus gouldii (Gray, 1841)	Cg
	Chalinolobus morio (Gray, 1841)	Cm
	Scotorepens greyii (Gray, 1843)	Sg
	Vespadelus finlaysoni (Kitchener, Jones and Caputi, 1987)	Vf

from McKenzie and Bullen 2003). The frequency that was maintained for the greatest number of cycles (F_{peakC}) could be determined from the frequency profile. We also measured the quality factor of the strongest harmonic ($Q = F_{peakC}/$ bandwidth), an index of sharpness of tuning (Laverghetta 1981). Because of the noise levels associated with field recordings, we measured *Q6dB* (subsequently referred to in this paper as *'Q'*) at 50% of the cycle-count at F_{peakC} (equivalent to 6 dB below peak from the fast-Fourier transformation), rather than at the -10 dB (i.e. *Q10dB*) normally used under laboratory conditions when assessing the frequency tuning properties of auditory neurones (e.g. Casseday and Covey 1992).

Echolocation survey

Between 2004 and 2007, Anabat II ultrasound detectors connected to minidisc recorders in 'mono, short-play' mode were placed at ground level in 69 sites scattered throughout the Pilbara (Figure 1). The detector's microphone was orientated within 30° of vertical. Sites were not randomly arrayed; there were two to four sites in each of the 24 survey areas into which the region was divided (McKenzie *et al.*). Most sites were on watercourses with pools of varying size and permanence, but scree slopes, sandplains, mulga flats and low open woodlands were also sampled (10 sites), along with mangroves

(5 sites). Some sites were near caves and abandoned mines. At each site, echolocation calls emitted by passing bats were recorded for an average of 150 min from late dusk on one or more nights in spring, autumn, winter and/or summer (we averaged 1.9 recording nights totalling 4.5 h per site). Repeated sampling depended on logistical opportunities offered by a trapping program that focused on ground mammals and reptiles, a constraint that precluded a more systematic sampling regime for bats and any multivariate statistical analysis requiring a balanced sampling design. For this reason, analysis of habitat-use was confined to species presence/absence data at sites, rather than the relative abundance of detections and issues of seasonality (Gannon *et al.* 2003). Overall sampling efficiency for microbat species was assessed using both the Chao2 (Chao 1987) and the incidence-based (ICE, Lee and Chao 1994) estimators in the EstimateS software (Colwell 2006).

F_{peakC} and Q values were determined for the search-mode calls in the recordings, and identified to species using the reference call data in conjunction with the spectral diagnostics previously published by:

• Bullen and McKenzie (2002a) for Western Australian *Nyctophilus* spp. (which covered populations of the four Pilbara *Nyctophilus* species), and
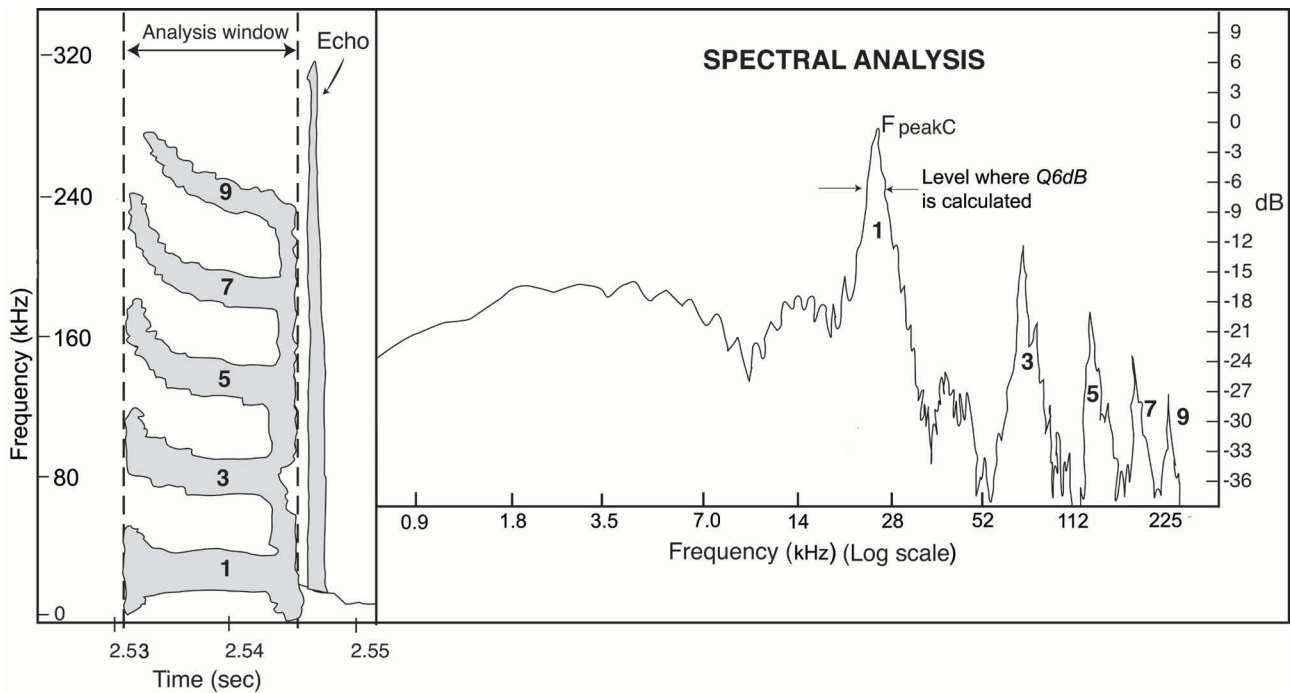
Figure 2 *Mormopterus beccarii* search mode call recorded using an ANABAT II detector, and displayed in frequency-time domain using COOL EDIT (modified from McKenzie and Bullen 2003). Results of the spectral analysis (frequency profile) of the entire call ('Analysis window') are included on the right-hand side of the figure as a plot of 'dB' (a direct measure of the number of cycles) versus 'frequency'. The fundamental harmonic (1), as well as higher harmonics (3 to 9), are visible in both displays. ANABAT II produces a square-wave output, so these higher harmonics are artifacts produced by COOL EDIT's Fast Fourier Transform routine.

- McKenzie and Bullen (2003) for discriminating *Saccolaimus flaviventris* from *Chaerephon jobensis*, and *Taphozous* spp. from *M. beccarii*.

Habitat

This analysis assumes that spatial distribution reflects an underlying correlation with environmental factors (Austin 1991; Clarke 1993), '… *a habitat paradigm*' Armstrong 2005), and treats metacommunity relationships (e.g. microhabitat and resource availability hypotheses, *sensu* Hernandez *et al.* 2005) as second order effects at regional scales. Because we do not yet have an explicit model to provide an explanatory framework for our results, our interpretation of this inherently exploratory design was based on deductive logic (Oksanen 2001; Dickman and Crowther 2008) and, as no experimental or mensurative design has been implemented to construct a null hypothesis (Austin and McKenzie 1988), alternative hypotheses are not excluded. Inferential statistics are used to test patterns observed in the empirical data.

Numerical clustering analyses from the computer package PATN (Belbin 1995) were used to expose patterns of species composition and species co-occurrence in the site data matrix (species presence/absence). The Czekanowski measure was used to compare the 69 sites according to their species similarities and Two-step (Belbin 1980) was used to determine the quantitative relationships between species in terms of their co-occurrences. These procedures yielded dissimilarity matrices for sites and species, respectively. Flexible UPGMA (unweighted pair-group mean averaging, Sneath and Sokal 1973; Belbin 1995), with the clustering parameter (Beta) set to -0.1, was used to derive classification partition structures (dendrograms) from both matrices so that the sites could be clustered according to compositional similarities, and species clustered according to co-occurrences. ANOSIM (Clarke and Green 1988) was then used to test if there was a significant difference in the *F*-ratio of the association values between or within classification groups, compared with 100 iterations in which sites were randomly re-allocated between groups.

The species-dendrogram partitions were interpreted in terms of the previously known habitat associations and roost preferences of their component species across their wider distributions in Australia (e.g. van Dyck and Strahan 2008). The site-dendrogram partitions were compared statistically in terms of several environmental attributes of the sites. These attributes were chosen because of their biological relevance as gradients likely to influence microbat distributions, either

Table 2   Category definitions for 'gestalt' environmental attributes listed in Appendix 1.

Riparian Development (combinations of freshwater availability and vegetation complexity)

1 = not in riparian zone (grass, shrubs and/or low trees mostly less than 7 m high).

2 = on dry creek (shrubs and/or low trees to 7 m).

3 = on creek with semi-permanent or permanent pools nearby and fringed by tall shrubs and low trees about 4 m high, and usually with a narrow and intermittent fringe of trees 7 to 15 m high).

4 = on creek with permanent freshwater pools, with rush-beds and a wide zone of tall trees > 15 m high and > 30% canopy cover.

M = mangroves

Atmospheric Conditions (assessed on the most favourable night for bat activity if data for more than one night have been pooled)

1 = cold, windy and >half moon

2 = cold + [windy and/or < half moon] or [still and/or > half moon]

3 = warm, windy and moonless

4 = hot, still and moonless

Caves (distance to nearest ranges, massive scree or mine)

1 = > 20 km

2 = 10–20 km

3 = 3–10 km

4 = 0.1–3 km

5 = < 0.1 km

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directly or indirectly, and also on the basis that they were not highly intercorrelated (Spearman Rho < 0.5), thereby avoiding multi-collinearity. On these criteria, we retained only two of the climatic attributes, 'minimum temperature in the coolest period annually' and 'annual average precipitation'. These were generated for the sites using ANUCLIM (McMahon *et al*. 1995). Temperature and rainfall attributes have direct effects on the ecophysiology of many mammal species (e.g. Prosser and Brown 1961; McNab 1980; Spicer and Gaston 1999; Meynard and Quinn 2007). Attributes such as riparian development (combining vegetation complexity and freshwater pool permanence in creeks), distance to coast, distance to ranges (rock crevices, caves and/or underground mines), and atmospheric conditions on the sampling night/s (windiness, cloud cover, moon phase and temperature) were recorded on-site, or derived from Google Earth and from the nearest Bureau of Meteorology weather station (Table 2). Their biological relevance for Australian microbats has been well documented (e.g. McKenzie and Rolfe 1986; Lumsden and Bennett 1995; Law *et al*. 1998; McKenzie and Muir 2000; Young and Ford 2000; Williams and Dickman 2004; Milne *et al*. 2005a,b). To determine whether spatial autocorrelation caused by proximity between landward sites should to be treated as a factor influencing composition (e.g. Diniz-Filho *et al*. 2003), we plotted compositional

dissimilarity (Czekanowski) against Euclidean distance apart (km) for all pairs of sites, then tested for significance in the relationship using 999 randomisations. The matching of environmental to biotic patterns was carried out using group statistics module of PATN (Belbin 1995), and assessed using Kruskall-Wallis one way analysis of variance by ranks.

Foraging niche data for metacommunity analysis

To quantify aspects of resource partitioning in Pilbara microbat guilds, three aspects of niche were documented: microhabitat, flight speed and turn capability. In addition, data on species' foraging strategies were extracted from relevant literature and supplemented with observations made during the field work. These data were collected to provide a basis for assessing the influence of metacommunity interactions on assemblage composition.

1. Usual foraging microhabitat

Microbat records from our fieldwork were assigned to one of four foraging microhabitats, depending on differences in the degree of air-space clutter (obstruction to straight flight) at the point where the free-flying bat was first seen. Observations were made with a spotlight, in the glow of a floodlight or at dusk or when bats

returned to forage nearby after being released carrying bioluminescent tags ('Cyalume'). They were recorded if the bat was seen to be foraging or if its 'search-approach-interception' echolocation sequences were detected. Nearly half of the microhabitat data came from observations we made while recording ultrasound sequences emitted by bats of, at the time, unknown identity. Microhabitat definitions follow McKenzie *et al.* (2002), and were modified from McKenzie and Rolfe (1986):

1. Open airspaces more than 5 m above or beside canopies, cliffs, hill-slopes or hilltops (OC).

2. Semi-open airspaces a few metres above (> 2 but < 5 m) the top of the canopy or bare hills (AC).

3. Semi-cluttered airspaces within a few metres (> 2) of the sides and underside of the canopy or rock faces (BS/O).

4. Cluttered airspace inside stands of vegetation (IS) or within two metres of foliage, bark, ground or surface of pools (BS/A). IS and BS/A could not be discriminated in the open vegetation of the Pilbara region.

2. Flight speeds

These were measured from passing bats, either at dusk as they foraged around vegetation or departed their roosts in caves or abandoned mines, or at night if they were partially illuminated using a 12-V neon floodlight ('Versa-Light' by Burn-Brite Lights, Australia). In such situations they were subsequently identified from their ultrasound sequences. The speeds were measured using a hand-held K-band radar unit (Doppler-shift meter model TS3, supplied by Municipal Electronics, UK), calibrated for a speed range of 1–28 m sec^{-1} (4–100 kph). Additional flight speed data were measured from bats released in the field within a few hours of capture carrying bioluminescent tags or released the next morning in daylight. In this case, sub-adults, pregnant females and animals with scarred wings were excluded, as was the period while bats accelerated from rest. All readings for a species were pooled. Mode rather than average speed values were used for our analysis because the readings did not have normal distributions, even when pooled by species. Speed data from individuals captured on the periphery of the adjacent Ashburton and Little Sandy Desert Regions were incorporated to increase sample sizes for four widespread species (*M. beccarii*, *N. geoffroyi*, *S. flaviventris*, *T. australis*).

3. Turn capability

Turn capability, in conjunction with flight speed, provides a basis for rating bat airframes in terms of agility (see Table 10 in Bullen and McKenzie 2001), i.e. the ability to generate roll acceleration and/

or side force when entering and exiting a turn. A manoeuvrable bat has a small radius of turn while an agile bat can enter these tight turns at moderate to high speeds, and can abruptly tighten the radius of its turn. Therefore, by definition, agile bats are inherently manoeuvrable, but manoeuvrable bats are not necessarily agile. Agility is most readily recognised when bats enter and exit level turns at speed so that we can estimate the aerodynamic loading (normal acceleration in the sagittal plane = $\cos(\Phi)^{-1}$, where 'Φ' is the bank angle). During these turns, agile bats can roll quickly to bank angles that exceed 70° (> 2.9 gravities; Bullen and McKenzie 2001) so that turns appear abrupt rather than radiused. Tight wing-overs, stall-turns, half hammer heads and flick rolls induce airframe loadings quickly, equal to or greater than those generated during 70° or 80° 'level banking turns', implying agility (airframe loading of 2.9 and 5.8 gravities respectively; Bullen and McKenzie 2001).

Turning manoeuvres were identified using slow motion video recordings of individual bats released to fly around in a large, well-lit room. Rooms chosen as flight chambers had floor areas of between 50 and 60 m^2 (7–9 m long, 8–6 m wide, 2.7–3 m high), large enough to provide all but the largest of the microbats with a considerable margin for manoeuvring (Bullen and McKenzie 2001). Bat flight manoeuvres were filmed using a video camera (Sony Video8 Professional CCD-V100E) set to 25 frames s^{-1}, so that the types of manoeuvre undertaken by each species could be identified. Observations on the turns used by the large microbats (*C. jobensis*, *M. beccarii*, *T. australis*, *S. flaviventris* and *Taphozous* spp.) were recorded from free-flying bats in the field while microhabitat and flight-speed data were being collected, and were also available from our previous studies in adjacent regions (e.g. McKenzie *et al.* 2002). Turn capabilities of the largest microbat (*Macroderma gigas*) were observed by partially obstructing a bend at the entrance of a day-roost in the abandoned Klondyke Queen Mine from dusk onwards so that emerging *M. gigas* had to turn back, pitch-upwards to exit through a gap in the tunnel's ceiling, or use a rolling manoeuvre to avoid the obstacle and exit in level flight.

RESULTS

Call spectral characteristics

Tables 3 and 4 summarise search-mode echolocation call characteristics of the 17 species (6 families) known from the region, and include statistics on the number of individual bats, call sequences and calls used for characterisation. Three of the species are restricted to the mangrove stands scattered along the Pilbara coast (*M. loriae*,

N. g. pallescens and *N. arnhemensis*; McKenzie and Start 1989). Western Australian Museum and literature records show that all three are replaced by allopatric con-generic counterpart species in the region's landward environments (*M. beccarii*, *N. g. geoffroyi* and *N. bifax daedalus*, respectively). In this paper we use the term 'landward' to encompass the Pilbara's terrestrial, aquatic and riparian environments, but not marine inter-tidal ecosystems such as mangroves. For clarity, the spectral characteristics of species comprising these two compositionally distinct communities have been considered separately, even though they share

a number of species.

Figure 3a plots F_{peakC} against Q for reference search-mode calls by the 14 microbat species found in the Pilbara's landward environments (excluding mangroves). It shows that search-mode sequences by 13 of the 14 microbat species could be identified using a combination of F_{peakC} and Q, provided that departure call sub-sequences (*sensu* 'rising' and 'falling' sub-sequences in Bullen and McKenzie 2002a) were ignored in separating *Nyctophilus bifax daedalus* from *N. g. geoffroyi* sequences (Figure 4). The exception is *Taphozous hilli* which was too similar to be resolved from *T. georgianus* (except
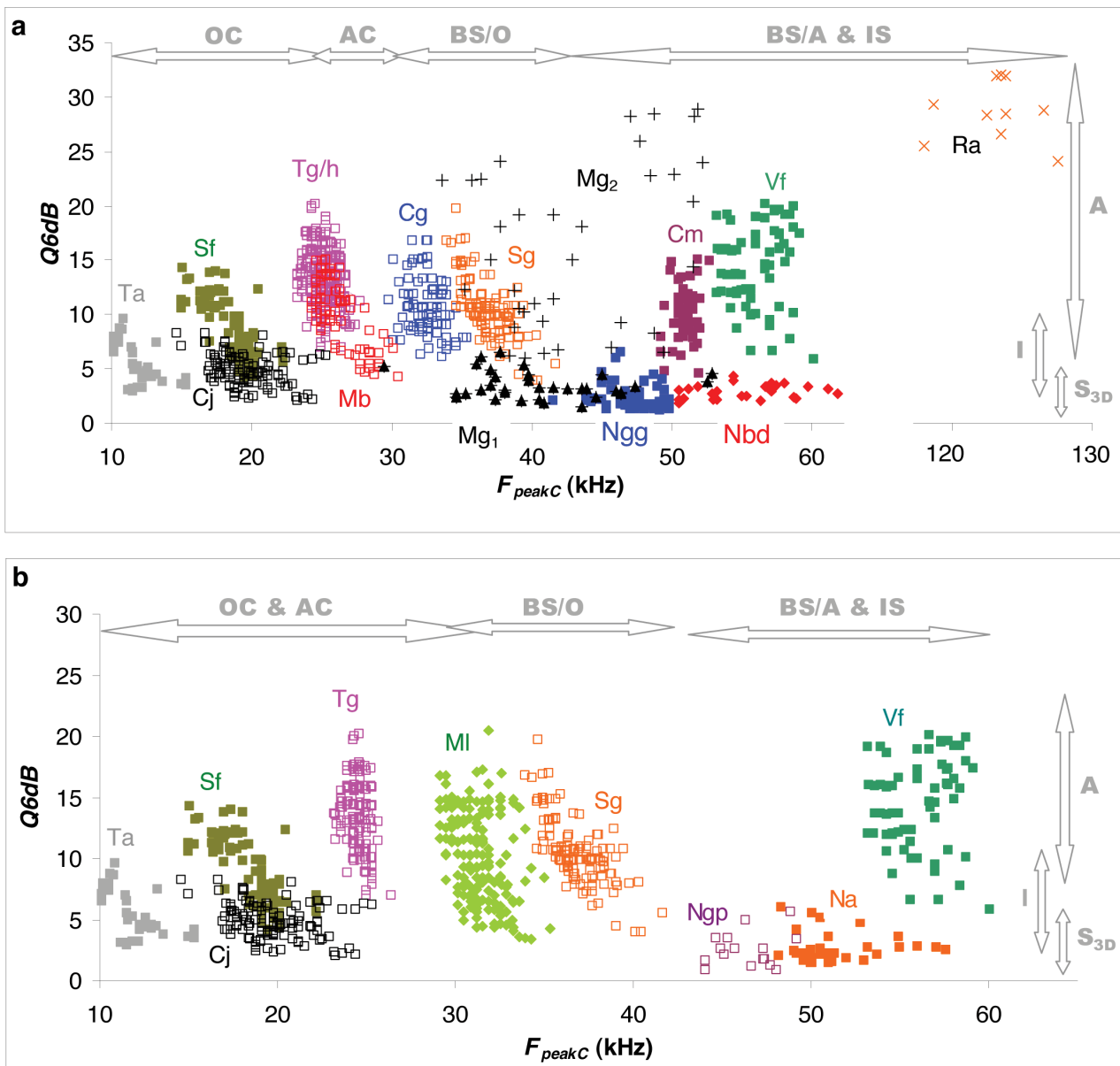
Figure 3   Scatterplot of F_{peakC} versus Q of the strongest harmonic in reference search-mode echolocation calls by (a) the 14 species found in the Pilbara's landward environments, and (b) the 9 species found in the Pilbara's mangrove environments. Species codes comprise the first letter of the genus and species names (see Table 1). Sample sizes are provided in Tables 3 and 4. Microhabitat and foraging strategy categories from Tables 5 and 8 are superimposed.

Table 3 Search-mode echolocation call statistics of Pilbara microbats derived from free-flying call sequences by known bats, including data on number of individuals and sequences used to characterise species. 'Shape' refers to the call's appearance in spectral view (see Figure 6), either constant frequency (CF) or frequency modulated (FM). FM calls can be steep (st), shallow (sh) or nearly constant (cf).

	Species											
	Cg	Cj	Cm	Mb	Ml	Ra[a]	Sf	Sg	Ta	Tg[b]	Th[c]	Vf
av F_{peakC} (kHz)	32.5	19.7	50.9	26.3	31.4	120.2	18.3	36.9	11.4	24.5	25.6	55.8
sd F_{peakC}	1.2	2.1	0.7	1.6	1.6	3.6	1.6	1.5	0.9	0.5	0.6	1.8
av Q	10.7	4.8	10.0	10.5	10.6	33.2	9.3	10.6	6.7	14.5	13.3	14.5
sd Q	2.7	1.4	2.3	3.2	3.5	7.8	2.8	2.8	1.6	2.1	1.5	3.5
call duration (ms)	7–11	8–15	7–8	8–13	7–14	5–8	12–21	7–13	12–23	9–18	4–8	4–8
call shapes	FM, stFM	shFM, FM	FM, stFM	shFM, FM	cfFM–stFM	CF	cfFM,FM	FM, stFM	cfFM, FM	cfFM, shFM	cfFM, shFM	FM, stFM
calls/WB[d]	1/1, 1/2	1/1–1/5	1/1, 1/2	1/1–1/3	1/1–1/3	N/A	1/1–1/8	1/1, 1/2	1/2–1/7	1/1–1/7		1/1
# individuals	12	20	1	6	37	56	14	10	3	25	16	18
# sequences	12	20	13	6	37	56	14	10	3	25	16	18
# calls	86	124	63	85	212	87	103	124	19	149	109	77
av calls/seq[e]	7.2	6.2	5.9	14.2	5.7	1.6	7.4	12.4	6.3	6.0	6.8	4.3
sd calls/seq	8.2	5.5	6.6	9.1	5.4	2.3	5.4	17.3	0.6	5.1	6.3	6.1
range[f]	1–30	1–24	1–26	1–25	1–21	1–16	1–10	1–59	6–7	1–17	1–27	1–26

[a] weak signals had F_{peakC} values as low as 88 kHz or even as low as 55 kHz
[b] from McKenzie and Muir (2000)
[c] from McKenzie and Bullen (2003)
[d] e.g. 1/2 = 1 call per 2 wingbeats
[e] number of calls per sequence analysed
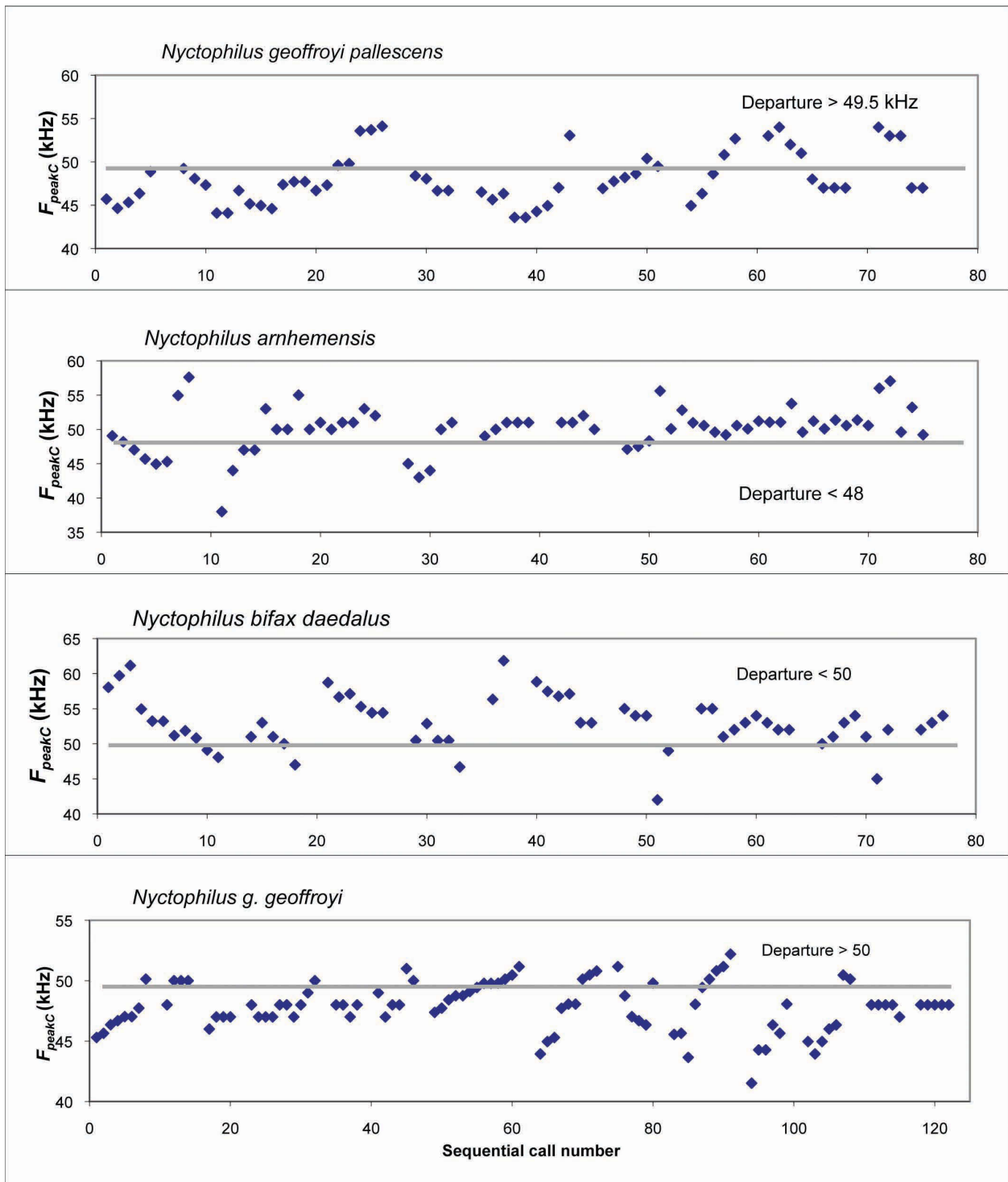[f] range in number of calls per sequence analysed

Figure 4   Search-mode sequence data for four *Nyctophilus* species. Individual bat sequences are separated by spaces. The grey horizontal lines represent the arbitrary boundary used to distinguish between the normal and the departure subsequences for species recognition. Individual dots represent the F_{peakC} value of each call within a sequence.

statistically; see McKenzie and Bullen 2003).

Macroderma gigas has a surface foraging strategy with two modes. It perches in vegetation to ambush passing prey (either on the ground or in the air), and it also gleans surfaces such as the ground while in-flight (e.g. Churchill 1998). Its echolocation calls showed wide variation in both F_{peakC} and Q values, but occupied the spectral spaces between, above and below *Scotorepens greyi* and *Chalinolobus morio*, with some overlap (Figure 3a). Unlike other microbats using the same frequency band, *M. gigas* calls were often prolonged (av. *ca.* 15 ms, ranging up to 50 – see Figure 5), usually complex in terms of frequency when displayed in time domain (W-, M-, N-, or U-shaped FM, or stepped CF – see Figures 6a and 6b), and usually irregularly spaced call-to-call in sequences (examples are illustrated in Figure 6a, sequences 2 to 4). Where sequences were regular, the call repetition-rate corresponded to their relatively low wing-beat frequency (6.96 +/- 0.71 Hz; Bullen and McKenzie 2002b), eliminating the possibility of confusion with approach-mode and intercept-mode calls of smaller microbats, with their much higher wing-beat frequencies, using the same spectral space. The call complexity distinguished them from the search-mode calls of all other species. Our reference calls were recorded in two separate contexts, and the sub-clustering recorded for *M. gigas* in Figure 5 suggests context-specific use of these spectral spaces:

1. Recordings of flying *M. gigas* observed just after leaving a mine adit (Klondyke Queen, 21°20'S,

119°53'E) after dark: brief (<8 ms), low Q (<6) calls with peak frequencies between 34 and 55 kHz (labelled 'Mg₁' in Figure 3a, and plotted as solid triangles in Figure 5). Call complexity in combination with low Q distinguishes *M. gigas* calls in this category from calls by all other microbats in the same frequency band and were used to identify unknown sequences (see Figure 6a sequences 1 to 6, and the first 5 calls displayed in Figure 6b).

2. Recordings of *M. gigas* flying back and forth after attempting to to re-enter the mine entrance at Whim Creek (20°50'S, 117°49'E) past the observers: prolonged (10–50 ms), high Q (6–36), CF and complex FM calls with peak frequencies between 33 and 53 kHz (hollow squares in Figure 5). Call duration is sufficient for diagnosis. Call complexity in combination with 'call duration' distinguishes these calls from other species using the same band, and calls from these recordings were used as reference calls to identify unknown sequences.

The second category is labelled 'Mg₂' in Figure 3a. In addition, *M. gigas* sequences often included characteristic sub-sequences of audible chitter-calls (see Figure 6a), described by Churchill (1998) as 'audible twitter' (see below). Examples of the call complexity compared to other species that use the same frequency band are displayed in Figure 6 (Figure 6b *versus* 6d). In the Pilbara, *M. gigas* also emits the loud audible 'chirping sounds' described by Kultzer *et al.* (1984).

$$y = 0.8x + 6.7$$
$$R^2 = 0.31$$
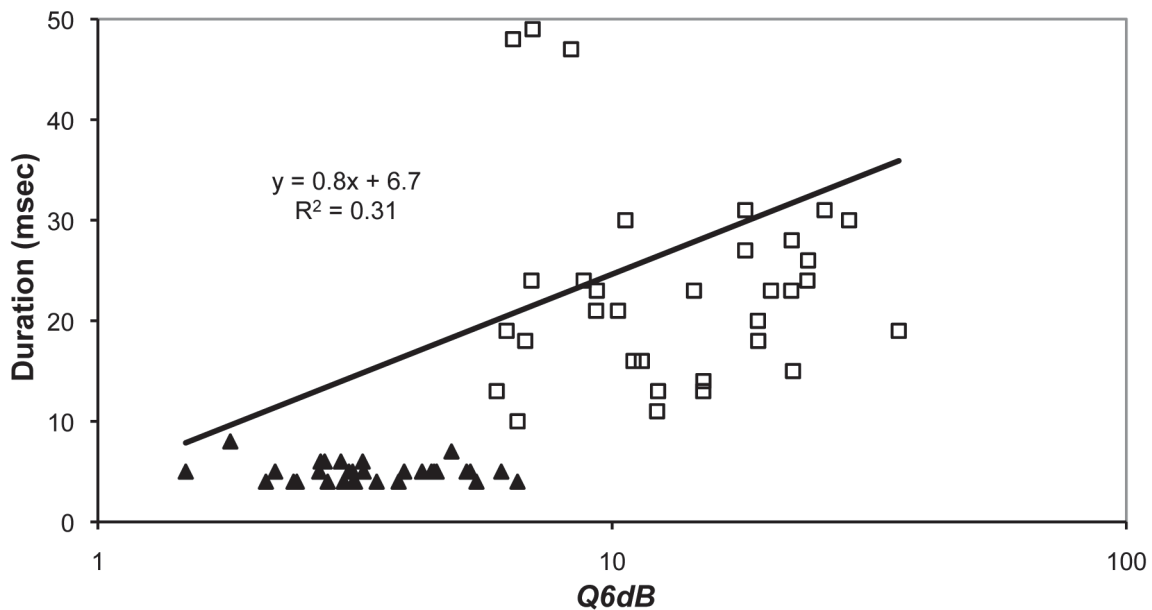
Figure 5 Scatterplot of Q versus '*Duration*' for the strongest harmonic of *M. gigas* calls recorded in two different contexts: in-flight soon after emerging from a roost (solid triangles), and attempting to re-enter a roost-adit past the observers (hollow squares).
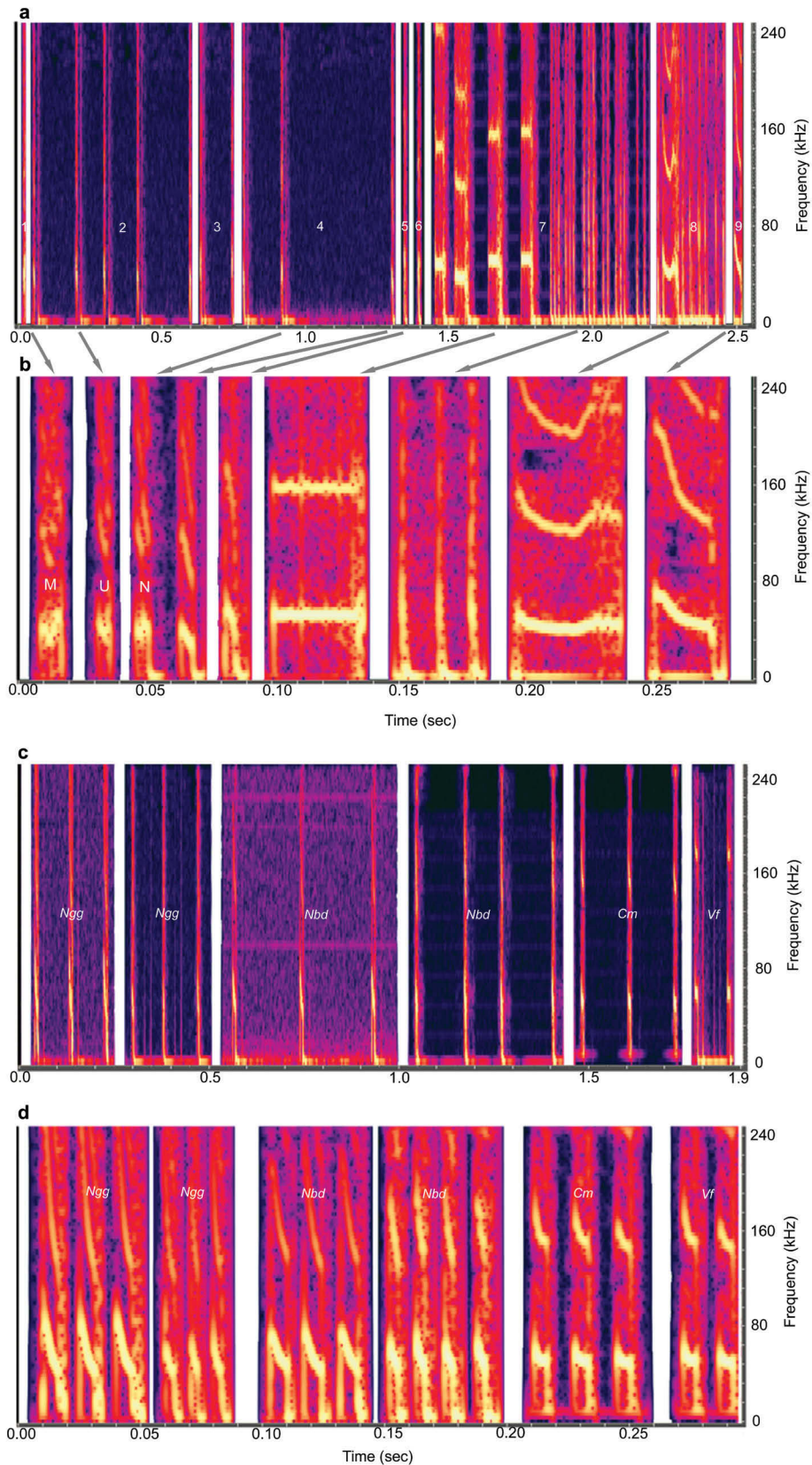
Figure 6   Search-mode call sequences in time domain by *M. gigas* and other Pilbara species that use the same frequency band. (a) Sections from nine in-flight sequences by *M. gigas* showing different call types and durations, and including sequences (labelled 2, 3 and 4) showing the characteristically irregular call-repetition rates. Chitter calls are also illustrated (the second half of sequences 7 and 8). (b) Close-up views of the variation seen in *M. gigas* calls, with spacing between calls removed. (c) Sections from typical sequences by Pilbara *N. g. geoffroyi*, *N. bifax daedalus*, *C. morio* and *V. finlaysoni* showing typically steady call repetition rates. (d) Close-up views of calls shown in (c) with the spacing between calls removed.

Additional call attributes were also required to separate some of the nine species comprising the mangrove microbat community (Figure 3b):

- Departure sub-sequences (*sensu* Bullen and McKenzie 2002a) had to be ignored to separate *N. arnhemensis* from *N. g. pallescens* sequences (Figure 4).

- Two call characteristics were useful in resolving the spectral overlap between the mangrove specialist *M. loriae* and the common landward species *Chalinolobus gouldii* (Figures 3a and b), which ventured into the landward edge of mangroves occasionally (McKenzie and Start [1989] recorded 1 *C. gouldii* for every 20 *M. loriae*). *M. loriae* sequences often include calls with Q values well below 5.1 (the lower limit for *C. gouldii*), and its calls had a narrower bandwidth (F_{min} to F_{max} range and less curvilinear shape in time domain) for any given F_{peakC} value (Milne 2002).

Organisation of echolocation calls in spectral space

From an ecological perspective, the 'spectral' space between species in the Pilbara's landward community is almost entirely occupied below 60 kHz (Figure 3a). Except for *T. georgianus* and *T. hilli* in the eastern Pilbara, and for the occasional *C. gouldii* venturing into mangroves, species' normal, in-flight, search-mode calls show no more than partial overlap in both communities, and species are regularly arrayed to occupy the available spectral space. The reasons for the partial overlaps between *S. flaviventris* and *C. jobensis*, and between *M. beccarii* and *T. georgianus/hilli* calls, were explored in McKenzie and Bullen (2003).

The Pilbara's landward community also includes one hipposiderid, *Rhinonicteris aurantia*. Its distinctive echolocation calls are of constant frequency (rather than frequency modulated), and have a very high Q and frequency (F_{peakC} between 112 and 128, averaging 120 kHz, Table 3). However, individual weak calls in these sequences sometimes returned low readings, between 55 and 110 kHz, that we treated as artefacts of the recording equipment representing inharmonic partials that

Table 4 Search-mode echolocation call statistics of Pilbara *Nyctophilus* spp. and *M. gigas* derived from free-flying call sequences by known bats (individuals observed outside roost sites, cyalume releases etc., see 'Methods'). Data on number of individuals and sequences used to characterise species are included. The three columns for *M. gigas* provide statistics for their constant frequency (CF), prolonged frequency modulated (FM) and brief FM calls, respectively. The first two columns may not be search-mode calls.

	Species						
	Mg	**Mg**	**Mg**	**Na**[a]	**Nbd**[a]	**Ngg**[a]	**Ngp**[a]
av F_{peakC} (kHz)	46.3	42.4	40.5	51.3	53.8	47.3	47.5
sd F_{peakC}	7.7	5.0	5.5	2.1	2.9	2.0	2.6
min	35.7	33.6	29.0	48.2	50.5	41.5	43.6
max	52.6	52.2	55.6	57.6	61.8	49.8	49.2
av Q	26.3	13.0	3.5	2.5	2.9	2.3	2.4
sd Q	6.8	6.0	1.2	1.0	0.6	1.3	1.6
av call duration (ms)	26.8	22.9	4.9	5.6	5.0	5.4	5.1
sd call duration	4.9	10.0	0.9	1.0	0.8	1.4	1.9
duration range (ms)	18 - 31	11 - 50	4 - 8	3 - 7	4 - 7	3 - 7	3 - 9
call shapes	complex CF	complexFM	complex FM	ststFM	ststFM	ststFM	ststFM
calls/WB	--	--	4/1–1/1	1/1	1/1, 1/2	1/1	1/1
av calls/seq[b]	1.5	1.2	4.4	10.8	6.1	7.5	9.5
sd calls/seq	1.0	0.5	3.1	9.3	2.5	3.2	8.7
range in calls/seq	1–3	1–3	1–10	4–28	2–11	4–14	5–30
# individuals (N)	4	24	10	6	10	14	8
# sequences	4	27	10	6	10	15	8
# calls (n)	6	31	44	65	59	91	63
Departure F_{peakC}	--	--	--	48.0–38.0	42.0–50.0	50.0–52.2	49.5–54.1

[a] includes data from Bullen and McKenzie (2002a)
[b] number analysed

Table 5   Foraging microhabitats of Pilbara microbats (n = number of observations, N = numbers of individuals). Microhabitat codes are explained in 'Methods'.

Species	Foraging microhabitats				n	N
	OC	AC	BS/O	BS/A-IS		
Tg[a]	59	2			61	61
Ta[a]	34		1		35	34
Sf	33	3			36	26
Cj[a]	113	35	14		162	153
Mb	8	15	10		33	19
Ml[a]	21	66	59	46	192	159
Cg	6	34	105	11	156	131
Mg	1	4	21	6	32	32
Sg		13	133	28	174	121
Vf[a]			12	52	64	60
Ra			9	79	88	34
Cm			1	6	7	4
Nbd			7	78	85	69
Na[a]				45	45	39
Ngg[b]				3	3	3
Ngp[a]				46	46	38

[a] includes data from McKenzie and Start (1989)
[b] consistent with Carnarvon Basin and Little Sandy Desert populations (McKenzie and Muir 2000; McKenzie et al. 2002)

were not integer multiples of the fundamental frequency (first harmonic).

Species foraging niche

Clear patterns in microhabitat-use emerged from the observational data (Table 5), which allowed species to be compared in terms of the airspace clutter they encountered in their usual foraging microhabitat. At the two extremes *T. australis, S. flaviventris* and *T. georgianus/hilli* hunted in open airspace well clear of obstructions, while the four *Nyctophilus* spp., *C. morio, R. aurantia* and *Vespadelus finlaysoni* hunted in cluttered airspace, close to surfaces. The remaining species hunted in various intermediate levels of clutter.

Six agility classes could be distinguished when we compared species in terms of their manoeuvres (Table 6, final column); four of these (classes 3 to 6) considered to be agile on the basis of their asymmetric turn capabilities. Of the species in agility class 3, however, we noted that *N. b. daedalus* and *N. arnhemensis* performed their most energetic turns at relatively low flight speeds compared to *T. georgianus* and *M. loriae,* and that *M. gigas* sacrificed altitude during these turns. These observations suggest that *N. b. daedalus, N. arnhemensis* and *M. gigas* are less agile than *T. georgianus* and *M. loriae.* Further evidence for this difference was provided

by our flight chamber observations that the *Nyctophilus* were the only species to hover (Table 6). *Nyctophilus g. pallescens* hovers lasted nearly three seconds, and some *N. arnhemensis* hovers lasted five to seven seconds. The uncertainty about *S. flaviventris* agility reflected the lack of flight chamber test data, but free-flight observations of social dog-fighting reported by Churchill (1998) and of it foraging between tree canopies in the Little Sandy Desert (McKenzie et al. 2002), indicate that it is capable of tight turns.

Two of the flight speeds reported in Table 7 are based on small sample sizes. The *N. g. geoffroyi* value of 4.7 m sec^{-1} is based on only 8 readings from 6 individuals, while the value of 5.6 m sec^{-1} for *C. morio* is based on 4 readings from 1 individual. These speed values are consistent with published data from southern Western Australia (Bullen and McKenzie 2001), that were based on 213 readings from 19 individual *N. g. geoffroyi* (4.4 m sec^{-1}), and 526 readings from 57 individual *C. morio* (5.3 m sec^{-1}).

Taken together, the data on agility and flight speed are consistent with published foraging strategies from elsewhere and our field observations of foraging behaviours (Table 8). This includes observations on 19 *N. b. daedalus* that were captured in mist nets set from late dusk onwards at canopy,

Table 6 Number of manoeuvres observed for bats flying either outside (free flight) or in an observation chamber. Slow-motion video analysis was used to score manoeuvres in observation chambers (standard deviation of individual scores are shown in parenthesis). N = number of individual bats; n = number of minutes of video recording in flight chamber. For both the coordinated turns and the asymmetrical turns, the more energetic manoeuvres are shown in the columns on the right hand side.

Species	Location	N	n	Coordinated turns				Skidding turn	Open wingover	Tight wingover	Stall turn	Half hammer head	Flick roll	Hovers	Agility
				>20°	>40°	>60°	>80°								
Ta	chamber	2	9.0	11	1				1						1[a]
Cj	outside	2, 43		2, 28	0, 15										1
Mb	outside	14		9 (0.8)	3 (0.5)										1
Sf	outside	4		1	2	1									2
Ngg	outside	2		23	14			7	9						2[b]
Ngp	chamber	3	15.5	91 (10.0)	48 (4.4)	5 (0.6)		41 (6.4)	21 (3.0)					43	2
Mg	chamber	3, 2	12.0, 22.0	2, 20	0, 10	0, 1		0, 1	0, 5	0, 1					3[c]
Mg	outside	4, 26		6, 5	5, 12	0, 4			0, 5						
	in adit	97			37	11, 9			39	1					
Na	chamber	3	4.5	14 (5.7)	108 (29.7)	7 (2.5)			61 (13.2)	3 (1.0)				4 (1.2)	3
Na	outside	1		7	6				2						
Nbd	chamber	1	12.3	18	33	10		3	45	17				18	3
Tg	chamber	5	18.0, 4.0	31 (3.1)	13 (1.9)	4			6 (1.3)	3 (0.9)					3[d]
Tg	outside	4								1					
Ml	chamber	5	19.0, 3.5	76 (3.8)	71 (5.5)	4 (0.8)		6 (1.4)	31 (3.1)	11 (1.9)					3[e]
Ml	outside	13		7	4				2						
Sg	chamber	2, 2	16.0, 9.5	25, 27	30, 32	2, 12		0, 6	12, 27	1, 17	1, 10				4
Sg	outside	1, 3				0, 24			0, 12	0, 10	0, 4				
Cg	chamber	2	10.1	11	13	6			14	4	9	1			5
Cg	outside	5, 9				2, 3	0, 1		0, 2	2, 0	1, 3	1			
Ra	chamber	1	12.5	27	31	23	11		62	29	6	3			5
Cm	chamber	2	10.9	2	18	102	71		46	53	54	1	3		6[f]
Vf	chamber	4, 1	12.5, 6.0	26, 23	48, 41	55, 46	20, 23		26, 20	13, 27	23, 16	0, 1	2, 10		6
Vf	outside	7				1	1		1	1	3		7		

[a] *Ta*: data from Bullen and McKenzie (2005) are used, but belong to the same population

[b] *Ngg*: includes data from the adjacent Little Sandy Desert (McKenzie *et al.* 2002)

[c] *Mg*: 180° turn, 1m diameter @ 15 kph = 3.5 G (gravity).

[d] *Th*: did a 3.5 G pull-up at bottom of shaft in Tallering Peak mine, equivalent to the co-ordinated turns of > 60° by free-flying Pilbara *Tg* (see McKenzie *et al.* 2002).

[e] *Ml*: two individuals released at Cape Keraudren used an upward corkscrew manoeuvre to evade birds in open air: 1. pitch down, 2. pull-up in wing-over condition, 3. climbing corkscrew.

[f] *Cm*: level turn measured at 15 kph with 0.7 m radius = 4.0 G.

lower branch and shrub height at Weeli Wolli Spring (site RHNC48) in February 2006, and released with bioluminescent tags. After release, six were observed foraging among the upper branches and canopies of River Gum woodland, up to 20 m above the ground. They would perch for several minutes at a time, and/or spiral slowly around and through the canopy before commuting to the next canopy at higher flight speeds, behaviours consistent with ambushing and gleaning. Even moderately agile turns (Agility class 3 in Table 8) performed at high flight speeds (>7.5 m sec^{-1}) imply an air superiority strategy and are consistent with field observations of the relevant species out-turning their prey. Species observed to intercept their prey during a straight, high speed pass had the lowest agility ratings and high flight speeds. Bat species with a 'surface' foraging strategy (S_a, S_H or S_{3D} in Table 8) all showed moderate to low agility in conjunction with low flight speeds. Exceptions were the large predator (*M. gigas*), which has the highest wing loading of all the surface strategists (13.5 versus 4.7–5.5 N m^{-2}) and consequently needs proportionally higher flight speed to generate sufficient lift even for level flight, and *M. loriae*, which has a dual-mode airframe (Bullen and McKenzie 2002b, 2004, 2007). This mode-change was observed during fieldwork at Cape Keraudren in November 2007, when four *M. loriae* individuals foraging close above the mangrove canopy at a mode flight speed of 7.8 m sec^{-1} were seen to gain altitude, then depart at measured velocities exceeding 11 m sec^{-1}. Equivalent instances of very fast flight by this species were noted during a previous visit in February 2006.

Echolocation survey

Figure 7 overlays reference calls (as solid squares) with unknown calls (as hollow squares) recorded at landward sites in the Pilbara. Unknown calls that plotted on the periphery of a reference call cluster were identified only if they were in continuous sequence with calls that fell within the cluster. Sequences of *Saccolaimus flaviventris* and *Taphozous* spp. sometimes included one or two second harmonic calls that were in the same frequency band as *C. gouldii* and *N. geoffroyii* calls, respectively, but with distinctively flat CF shapes in time domain and high *Q* values. Examples for *S. flaviventris* are plotted in Figure 7. On the basis that we have never recorded a reference call of *S. flaviventris* in the 8 or the 24 kHz range, or heard an 8 kHz echolocation sequence in Western Australia, we conclude that the frequency of its fundamental harmonic is about 16 kHz (range 15 to 19).

Almost all sequences and most of the individual search-mode calls that we recorded were identifiable unless the recording was visibly distorted by atmospheric attenuation, echoes or over-saturation. Only *Taphozous* sequences remain unresolved, so they are listed as *T. georgianus-hilli* (*Tgh*) in the site compositional analysis below. With the same restrictions, the equivalent result was obtained for bats belonging to the mangrove community; unknown sequences could be identified unambiguously although, in this case, the site species lists were based on captures rather than call identification, and were published in McKenzie and Start (1989). On the basis that all clear sequences by 16 of the region's 17 microbat species were identified, we concluded that spectral parameters provided a viable survey tool.

ICE and Chao2 procedures in EstimateS both produced an estimate of 13 species from the 64
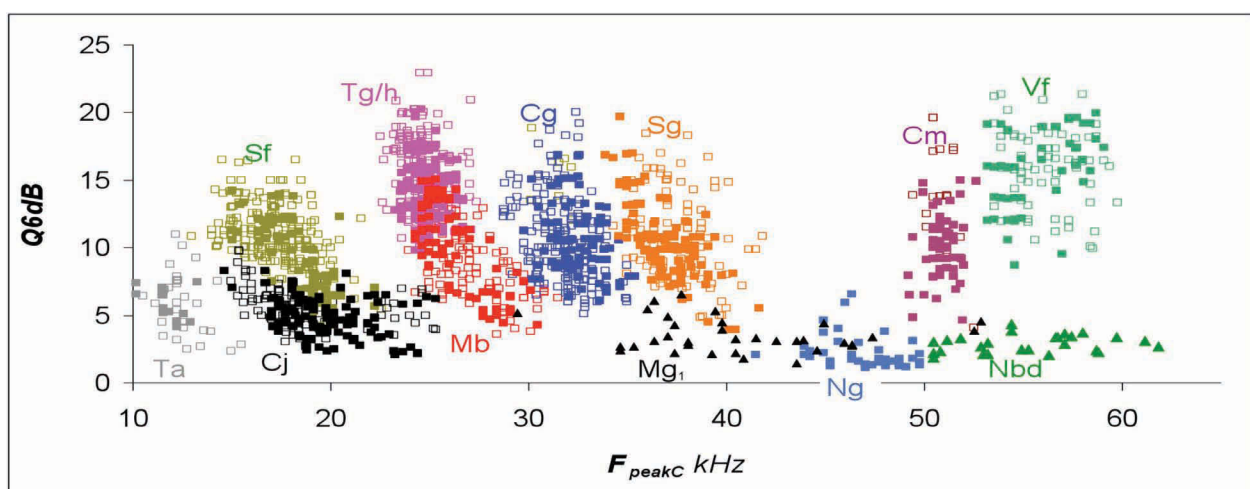

Figure 7   Scatterplot of strongest harmonic F_{peakC} versus Q of 'unknown' search-mode echolocation calls (hollow squares) overlaid onto reference calls (solid squares), for identification purposes.

Table 7 Mode flight speed of Pilbara bats measured in the field (*N* = number of individual bats; *n* = total number of speed measures). Species codes as in Table 1.

Species	Flight speed (m s^{-1})	N	n	av *n/N*	sd *n/N*
Cj	8.6	101	307	3.1	3.0
Cg	6.9	122	243	2.0	2.6
Cm	5.6 [a]	1	4		
Mb	7.8	14	69	4.9	6.6
Mg	6.9	106	283	2.5	1.5
Ml	7.8	16	140	5.4	4.5
Na	5.3	6	40	5.0	3.7
Nbd	5.6	28	182	6.3	3.4
Ngg [b]	4.7	6	8	1.3	0.5
Ngp	5.0	14	75	5.0	3.4
Ra	6.1	79	119	1.5	0.7
Sf	8.1	13	29	2.2	1.4
Sg	6.1	120	398	3.3	3.9
Ta	8.6 [c]	>30	461	<10	
Tg & Th [d]	8.1	76	191	2.4	1.6
Vf	5.6	53	85	1.6	1.0

[a] mode flight speed for Coolgardie population = 5.3 m sec^{-1} (*N* = 57, *n* = 256) (Bullen and McKenzie 2001)
[b] data from adjacent Little Sandy Desert population (McKenzie and Bullen 2003)
[c] adjusted from Bullen and McKenzie (2001) because hand-launch measurements of molossids under-rate V_{mode} by 10%
[d] unable to distinguish *Tg* from *Th* echolocation calls

Table 8 Foraging Strategy (from Bullen and McKenzie 2004): interceptor (I), air-superiority (A), ambusher surface and level air-to-surface (S$_a$ & S$_H$), and 3D air-to-surface (S$_{3D}$).

Species	Agility (from Table 6)	Flight speed (from Table 7)	Published data and field observations
Mb	1	7.8	I [a]
Cj	1	8.6	I [a]
Ta	1	8.6	I [a b c]
Ngg	2	4.7	S$_{3D}$ [a b c]
Ngp	2	5.0	S$_{3D}$ [d e]
Na	3	5.3	S$_{3D}$ [f]
Nbd	3	5.6	S$_{3D}$ [e]
Mg	3	6.9	S$_H$, S$_a$ [c g]
Ml	3	7.8	I & A [e]
Sf	2	8.1	A [a c]
Tg	3	8.1	A [a]
Th	3	8.1	A [a]
Sg	4	6.1	A [a]
Ra	5	6.1	A [b e]
Cg	5	6.9	A [a b e]
Cm	6	5.6	A [b]
Vf	6	5.6	A [a c]

[a]McKenzie *et al*. (2002); [b]Bullen and McKenzie (2001); [c]Churchill (1998); [d]McKenzie and Start (1989); [e]Authors' empirical observations of field behaviour, including information on *N. b. daedalus* in Results; [f]McKenzie and Churchill (2008); [g]Richards *et al*. (2008).

Table 9   Sub-region and survey area faunas (excluding mangrove sites), incorporating literature and WA Museum records.

Survey area (Figure 1)	Cg	Cj	Cm	Mb	Mg	Nbd	Ng	Ra	Sf	Sg	Ta	Tg	Th	Vf	Distance to coast (km)
BDRS	1	1		1	1		1	1	1	1	1	1		1	390
BDRN	1	1		1	1		1	1	1	1		1		1	330
RHNC	1	1	1	1	1	1	1	1	1	1	1	1	1	1	310
RHNE	1	1		1		1	1	1	1	1	1			1	250
TCMBC	1	1		1	1		1	1	1	1		1	1	1	230
RHNW	1	1		1	1		1		1	1		1		1	210
TCMBE	1	1		1	1	1	1	1	1	1	1	1	1	1	210
TCMBW	1	1		1	1		1		1	1	1	1	1	1	200
NE	1	1		1	1		1		1	1	1	1	1	1	180
NW	1	1		1	1		1	1	1	1	1	1		1	180
WYE	1	1		1	1		1	1	1	1				1	150
MBE	1	1		1	1			1	1	1	1	1		1	130
PE	1	1		1	1		1		1	1	1	1	1	1	130
PHYC	1	1		1	1		1	1	1	1	1	1	1	1	100
PHYE	1	1		1	1		1	1	1	1	1	1	1	1	100
MBW	1	1		1	1		1	1	1	1	1	1		1	90
OYE	1	1		1			1	1	1	1	1	1		1	80
PW	1	1		1	1	1	1		1	1	1	1		1	80
WYW	1	1		1	1		1		1	1		1		1	80
OYW	1	1		1	1	1	1	1	1	1	1	1		1	40
DRC	1	1		1	1	1	1	1	1	1	1	1		1	20
DRE	1	1		1	1		1		1	1	1	1		1	20
PHYW	1	1		1			1	1	1	1	1	1		1	20
DRW	1	1		1	1	1	1	1	1	1				1	10
# survey areas	24	24	1	24	21	7	23	17	24	24	19	21	8	24	
# sub-regions	4	4	1[a]	4	4	3[b]	4	3[c]	4	4	4	4	2[d]	4	

[a] only in Hamersley RHNC
[b] not from Chichester
[c] not from Fortescue
[d] not from Roebourne or Fortescue

sites sampled in landward environments. These indicated that no further species would be added after the 14th (ICE) and 19th (Chao2) sites were sampled. The field survey result was 100% of the estimation (of 13 species), bearing in mind that the region's two *Taphozous* species were not discriminated by the sampling method used. Nine species were estimated (Chao2 as well as ICE) for the 5 mangrove sites sampled, with no further species predicted to be added after the 3rd site was sampled. Again, the field sampling result was 100% of the estimated richness. Both the terrestrial and the mangrove community accumulation curves were asymptotic.

Species distributions and conservation status in the Pilbara

Table 9 combines the landward site lists according to survey areas, which allows available Museum and literature records to be added to the echolocation survey results, and *T. georgianus* to be separated from *T. hilli*. It shows that five species belonging to the landward community are more widespread than previously supposed, or are localised or have consistent gaps in their regional distributions, and that a sixth is ubiquitous but seasonal (Table 10). In combination, these two tables reveal that:

1. *Taphozous hilli* is not known from the

Roebourne and Fortescue sub-regions, and has been found only in inland areas of the Hamersley and Chichester sub-regions that are in the 'desert bioclimatic zone', more than 100 km from the coast (Figure 1).

2. Under Western Australia's *Wildlife Conservation Act (1950)*, the Pilbara population of *Rhinonicteris aurantia* is listed as rare and likely to become extinct and, under Australia's *Environmental Protection and Biodiversity Conservation Act (1999)*, it is listed as vulnerable. Our results indicate that it is more common than previously recognised (Hall *et al.* 1997; Armstrong 2001), occurring in 17 of the 24 Pilbara survey areas. In 12 of these, the records are based on recordings made in the dry season, and in some cases in survey areas with no known roosts, suggesting that additional roost colonies remain to be discovered. We detected its calls at new sites in 10 of the 24 survey areas, despite *R. aurantia*'s low detectability (bat detector range is < 3 m for this species) and the sparsity of our sampling (total of < 10 hours recording across 3 sites per survey area). There are no records from the Fortescue, the only sub-region in which suitable cave roosts are scarce or absent.

3. The Pilbara population of *Macroderma gigas* is listed as vulnerable in the IUCN Red List (2002), and as priority 4 (in need of monitoring) by the Department of Environment and Conservation, Western Australia. Our results suggest that it is more common than previously supposed, occurring in 21 of the 24 survey areas, and in all 4 sub-regions. Its calls were detected at new sites in 10 of the 24 survey areas despite the sparsity of the sampling and the low intensity of *M. gigas* calls (bat detector range is < 3 m for *M. gigas*).

4. *Nyctophilus b. daedalus* is known from 3 of the region's 4 sub-regions (not from the Chichester), but only 7 of the 24 survey areas. Its apparent rarity may be an artefact of detectability assumptions '6' and '9' in Gannon *et al.* (2003, p. 48), and it is probably more widespread in these situations than the available data indicate. Pilbara bat species are not randomly distributed in 3-dimensional space and their calls do not have equal probability of detection (Gannon *et al.*'s assumptions '6' and '9', respectively) because they have different frequencies and intensities, so they were not equally detectable from ground-level. We observed *N. b. daedalus* foraging among the branches of the River Gum and paperbark trees, 15–25 m high, that form these riparian forests (Table 8). The problem was that its low intensity calls are detectable only to distances of 3–4 m, but our detectors

were placed on the ground because recordings made nearer to the tree canopy were almost always swamped by insect calls, mainly bush-crickets.

5. In the Pilbara, *C. morio* is known only from the Weeli Wolli-Marillana Creek system in the RHNC survey area of the Hamersley sub-region. Despite our focus on sampling riparian environments, we did not detect this species at any other site in the Pilbara. In contrast to *N. b. daedalus*, search-mode calls by *C. morio* that were released carrying bioluminescent tags were detectable to distances of at least 15 m, so our echolocation records should have detected *C. morio* at the other Pilbara sites sampled, if it was present. Elsewhere in Australia, this species is characterised by having isolated extra-limital populations to the north of its otherwise temperate distribution (Young *et al.* 2008). Also, over the last four years, one of the authors (RB) has identified bat calls from ultrasound recordings from more than 200 sites scattered across the Gascoyne and Murchison bioregions, immediately south of the Pilbara. Taken together, these observations suggest that this extra-limital Pilbara population is indeed geographically localised.

6. Although nearly all previous records of *T. australis* from the Pilbara came from its coastal areas, additional records collected during this survey provide evidence for its presence throughout the region in winter (Tables 10 and 11). Even in winter, it was not recorded everywhere, partly because of the limited mid-winter sampling (see Appendix 1), but recordings from landward environments were uncommon compared even to species with less powerful calls. Elsewhere, this species can be detected within 2 h of dusk on most nights (Bullen and McKenzie 2005). There was only one summer record from the Pilbara – a call sequence recorded at Weeli Wolli Spring in February 2006.

Assemblage composition

The environmental attributes of the 69 recording sites (Figure 1) are listed in Appendix 1. When species were classified according to their co-occurrences at the 69 sites, the dendrogram's partition structure could be interpreted to the 4-group level (Figure 8) in terms of known habitat associations and roost preferences of their component species across their wider distribution in Australia. At this level, an ANOSIM test showed that association distances between species in different partitions were significantly greater than the distances between species in the same partition (real-F = 4.2, best-F = 2.0, % randomised > real = 0):
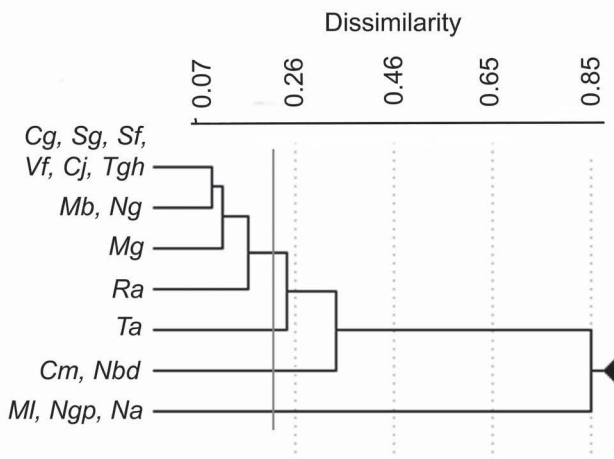
Figure 8   Species classified into four groups (grey line) according to their co-occurrences at the same sites. Dendrogram partition structure to the seven-group level is shown.

1. Ten species that are widespread in the region, some of which also occur in mangroves. This group includes species that prefer to roost in or on trees (*N. g. geoffroyi*, *C. gouldii*, *S. greyi*, *S. flaviventris*, *M. beccarii* and *C. jobensis*), as well as species that roost in caves and/or crevices (*T. georgianus/hilli*, *V. finlaysoni*, *M. gigas* and *R. aurantia*) and consequently have higher occupancy of sites in ranges (rugged outcrop country with rock crevices, slots, caves and often underground mine workings).

2. One tree-roosting molossid of the Australian temperate zone (*T. australis*), that expands its geographic range in winter to include northern arid areas of the continent, including the Pilbara region (Bullen and McKenzie 2005).

3. Two specialists of productive riparian environments. *N. b. daedalus* normally forages in the canopy and upper branches of riparian forest. In contrast, despite having a detectability range > 15 m, *C. morio* was detected only from the Weeli Wolli-Marillana Creek complex of the RHNC survey area, which is consistent with available Museum records.

4. The three mangrove specialists (*M. loriae*, *N. arnhemensis* and *N. geoffroyi pallescens*) all have mesic tropical distributions elsewhere in Australia where they occur in rainforest, monsoon forest, riparian zones and mangrove communities (McKenzie and Rolfe 1986; van Dyck 2008).

The presence and absence matrix (69 site × 16 species) from the echolocation survey was re-ordered according to the site and species classification analyses (Figure 9). Two communities

were revealed, with up to 12 species in landward assemblages and up to 9 in the mangrove assemblages. Differences between the four site-dendrogram groups (Figure 10) could be explained using three environmental attributes: riparian development, distance to ranges and distance to coast (see Figure 11):

1. This group comprised landward sites more than 3 km from ranges (see Figure 11a). Obligate cave dwellers were rare or absent (*T. georgianus/hilli*, *V. finlaysoni*, *M. gigas* and *R. aurantia*). In this cluster, well-developed riparian sites with permanent or semi-permanent pools were richer (> 4 species/site) than dry sites with open low vegetation. *M. beccarii*, *C. jobensis*, *S. flaviventris* and *N. g. geoffroyi* favoured the sites with well-developed riparian zones.

2. Landward sites in or close to ranges that were also in well-developed riparian zones characterised by permanent pools and, at sites with the highest species richness (> 8 species), by tall paperbark forests with areas of bulrush swamp. These were the most specious sites; highest site occupancy for the obligate cave dwellers (*T. georgianus/hilli*, *V. finlaysoni*, *M. gigas* and *R. aurantia*) as well as large tree-roosting microbats such as *S. flaviventris*, *C. jobensis*, *M. beccarii* and *N. g. georgianus*, and the two riparian specialists (*C. morio* and *N. b. daedalus*), were recorded in this group.

3. Landward sites that were as close to ranges as the sites in Group 2, but were on smaller, less permanent watercourses and/or had more open riparian vegetation (see Figure 11b). The relatively poor riparian zone at most of these sites was reflected in the scarcity of *M. beccarii*, *C. jobensis*, *S. flaviventris* and *N. g. geoffroyi*.

4. The five mangrove sites formed a group because of three species, the mangrove specialists *N. geoffroyi pallescens*, *N. arnhemensis* and *M. loriae*. These species were unique to, and ubiquitous in, the mangrove sites sampled (see Figure 11c), and each of these species has its allopatric con-generic counterpart in the region's landward environments. For consistency, occasional mangrove records of the common landward species *C. gouldii* have been retained for this analysis, even though they were encountered on only three occasions, all on the landward edge of the mangroves.

Nestedness in species composition (Atmar and Patterson 1993, 1995) is overt in the landward site-groups [$T = 18.4$, $P < 0.001$ for group-1; $T = 20.4$, $P < 0.001$ for Groups 2+3 combined), with nearly all community members present at the best-developed riparian sites, closest to ranges (Figure

12). This plot of species richness *versus* 'caves' (an alternative measure of distance to ranges) and 'riparian development' summarises the importance of rugged landscapes and riparian zone quality as influences on assemblage richness in the landward microbat community.

No significant relationship was detected when we plotted the similarity in site species composition (Czekanowski) against Euclidean distance apart (km) for all pairs of landward sites (Kendall Tau = 0.02, $P > 0.05$). Consequently, spatial autocorrelation was not treated as a factor liable to influence species composition.

DISCUSSION

Spectral characters as a survey tool

We could identify 16 of the 17 microbat species known in the Pilbara from their search-mode echolocation call sequences, a useful survey technique. The only constraint was the broad overlap in spectral characters observed between *T. georgianus* and its arid zone counterpart, *T. hilli*, in the landward community (Figure 3). *Taphozous georgianus* occurs throughout the region throughout the year (including its mangrove communities), while all 48 records (museum specimens) of *T. hilli* from the Pilbara are restricted to the region's 'desert bioclimate zone', more than 100 km inland (Figure 1, Table 9). Both species have large allopatric ranges elsewhere in northern Australia, and the reason for sympatry between two such morphologically and spectrally similar congenerics in the eastern Pilbara is unknown. It might reflect the seasonal heterogeneity in atmospheric conditions.

The two mangrove-dwelling *Nyctophilus* (*N. arnhemensis* and *N. g. pallescens*) have calls with spectral characteristics similar to their allopatric landward counterparts (*N. bifax daedalus* and *N. g. geoffroyi*, respectively), so the survey data on the mangrove pair were based only on capture records, and we recommend that future ultrasound recordings made in mangroves be identified using Figure 3b. Also, particular care has to be taken with the spectral identification of the mangrove specialist *M. loriae* because the common landward species *C. gouldii* occasionally ventures into the landward edge of the mangroves and has very similar search mode calls. We do not consider *C. gouldii* to be a member of the mangrove community, and have excluded it from the spectral plot (Figure 3b).

Despite small sample sizes (N < 10), the call frequencies listed in Tables 3 and 4 for *T. australis*, *M. beccarii*, *N. arnhemensis* and *C. morio* were consistent with previously published data from other regions (e.g. McKenzie and Bullen 2003).
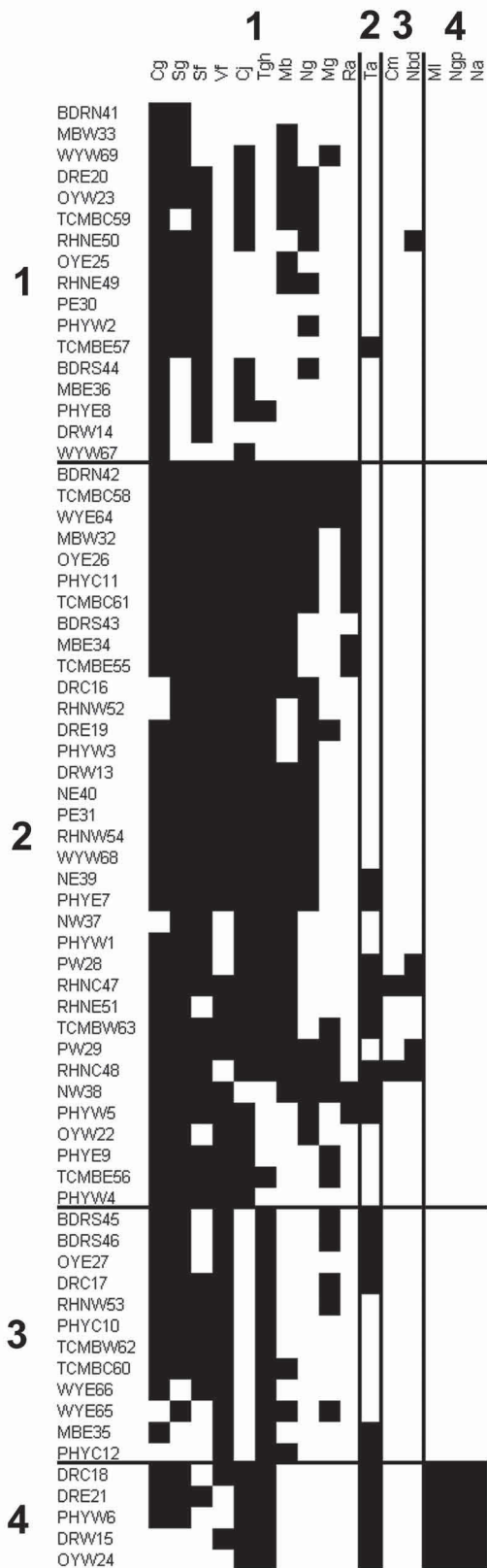

Figure 9 Microbat data matrix, with sites re-ordered according to similarities in their species composition, and the species re-ordered according to their co-occurrences at the same sites. Lines indicate classification partition boundaries at the four-group level (Figures 8 and 10). Site locations by survey area are shown in Figure 1.

In particular, the values for *C. morio* were based on multiple passes by a single cyalume-tagged individual to minimise our interference with the Pilbara's isolated and apparently very localised population. Nevertheless, small sample sizes can cause problems in species recognition. In the Pilbara, *N. g. geoffroyi* typically emits sequences of search-mode calls with frequencies ranging from 42–50 kHz (average 47.3, with departures to 52), rather than the 47–48 kHz range that we reported earlier using a total of 38 calls (a single sequence from each of 8 individuals, Bullen and McKenzie 2002a). Similarly, in the Pilbara, *N. g. pallescens* calls range from 44–49 kHz (average = 47.5, with departures to 54.1, Figure 4) rather than 47–53 (50.7, with no departures) that we reported earlier based on 14 calls (single sequences by 3 individuals).

We noted earlier that recordings of *S. flaviventris* and *Taphozous* spp. sometimes included calls in the second harmonic, as has been noted for emballonurids from elsewhere (e.g. Obrist *et al.* 1993). Most of these were calls interspersed among first harmonic calls in sequences, but occasional calls were found that switched between the first and second harmonic in the middle of a call. In neither case were other species of echolocating bats present.

Call spectral characteristics and foraging niche

Differences in call structure are thought to contribute to resource partitioning by sympatric species through niche differentiation (Heller and Helversen 1989; Neuweiler 1990). Foraging niche categories have been superimposed on Figure 3. Clearly, these 'spectral' plots can be treated as representations of resource allocation because the species' call parameters showed clear, functionally appropriate relationships with foraging niche: call frequency with foraging microhabitat, and the

Figure 10 Sites classified into four groups according to similarities in their species composition. Dendrogram partition structure to the four group level is displayed.

combination of Q and F_{peakC} with foraging strategy. For instance, fast-flying species that foraged in open airspace are characterised by having low-frequency echolocation calls that are less attenuated by the atmosphere, while species that hunt in clutter have airframes adapted for slower but more manoeuvrable flight, and use higher-frequency echolocation that sacrifices detection-range for detail-in-imagery (see also Simmons 1989; Kingston *et al.* 1999; McKenzie *et al.* 2002; McKenzie and Bullen 2003; Wund 2006; Surlykke and Kalko 2008).

Environmental influences on composition

A number of other studies have concluded that distance to coastline, to ranges with caves/crevices, and to a riparian zone are important factors explaining patterns in the composition of microbat assemblages (Crome and Richards 1988; Williams and Dickman 2004; Milne *et al.* 2005b).

The coastal factor differentiated the distinctive bat community found in Pilbara mangroves. Caves or crevices provide obligate day-roosts for a range of species, including five that occur in the Pilbara (e.g. Armstrong 2001; van Dyck and Strahan 2008). Well-developed riparian zones provide the most complex, productive vegetation structures found in semi-arid and arid regions such as the landward environments of the Pilbara. Since bats partition airspace according to clutter-levels (e.g. McKenzie and Rolfe 1986; Schnitzler and Kalko 1998; Bullen and McKenzie 2001), it is not surprising that high microbat species diversity has been associated with freshwater bodies such as perennial rivers elsewhere, and that some species are confined to these situations (e.g. Cross 1988; Law *et al.* 1998; Young and Ford 2000; Seidman and Zabel 2001). *Nyctophilus b. daedalus* and *C. morio* are the two species in the Pilbara's landward community that show this particular habitat specificity. Despite their different foraging strategies, both have specialised aerodynamic cleanliness characteristics (Bullen and McKenzie 2007) and/or flight muscle-mass ratios (Bullen and McKenzie 2004) that require productive foraging niches: *C. morio* because it needs surplus power to perform highly agile turns close to clutter, and *N. b. daedalus* which incurs high energy costs in manoeuvring and hovering at low speeds (Table 8) while gleaning in clutter because of its airframe's high wing loading (5.6 *versus* 4.7 N m^{-2} for its counterpart, *N. g. geoffroyi*). Riparian areas provide greater abundances of insects than wooded habitats, and that has been correlated with higher feeding rates (Thomas 1988). Furthermore, bat activity along intermittent streams in California was related to size, being least along small ephemeral examples, especially when the channels were dry (Seidman and Zabel 2001). Well-developed riparian areas also
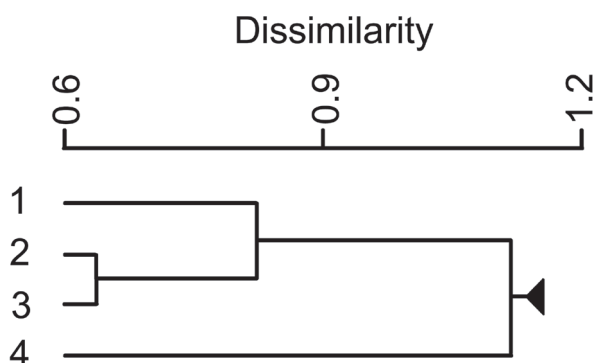
Table 10 Total numbers of microbat records from the Pilbara, including the results of this survey, WAM collections and existing literature (e.g. McKenzie and Start 1989). Y = Western Australian Museum specimen record, E = echolocation record, – = ultrasound recordings made but species not detected, empty cell = no ultrasound recordings made.

	Records[a]	PBS[b]	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	newest	Sub-region gaps[c]
Cj	40	24	Y	Y	E	Y	Y	Y	E	Y	Y	Y	Y	Y	2007	F
Cg	99	24	Y	Y	Y	Y	Y	Y	–	Y	Y	Y	Y	Y	2003	eR
Cm	6	1	–	Y				–	E	E	–		Y		2007	all but RHNC
Mg	386	21	Y	Y	–	Y	Y	Y	Y	Y	Y	Y	Y	Y	2007	e&wR
Mb	71	24	Y	Y	Y	Y	Y	E	E	Y	Y	Y	Y	Y	2007	C,R,F
Ml	182	5	Y	Y	Y	Y	Y	Y	–	Y	–	Y	Y		2007	all but mangle
Na	33	5	Y	Y	–	Y	Y	Y	–	Y	–	Y	Y		2007	all but mangle
Nbd	61	7	Y	Y	Y	Y	Y	Y	Y	Y	Y	–	Y	Y	2007	C, eF,e&wR
Ngg	9	23	–	Y	E	Y	E	–	E	E	E	Y	–	Y	2006	C, eFwR
Ngp	37	5	Y	Y	–	Y	Y	Y	Y	Y	–	Y	Y		2007	all but mangle
Ra	81	17	Y	–	Y		Y	Y	Y	Y	–	E	Y		2007	F, w&eR
Sf	15	24	Y	E	E		Y	E	E	Y	Y	E	Y		2007	eF, R, sC
Sg	61	24	Y	Y	Y	Y	Y	Y	E	Y	Y	Y	Y	Y	2007	wH, e&wR
Ta	21	18	–	E	Y[d]	Y	Y	Y	E	E	Y	–	–		2007	none
Tg	363	17	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	2007	eF
Th	47	8	–	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	2005	eF, wH, R, wC
Vf	587	24	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	2007	none
Number of ultrasound recording nights			4	5	4	0	44	8	8	7	10	26	1	0		

[a] Number of individuals as vouchers (Western Australian Museum collections), captured/released or seen

[b] Number of Pilbara 'survey areas' in which species has been captured or detected

[c] C = Chichester (east, west, south and/or north), R = Roebourne (e, central, w), H = Hamersley (e, w) and F = Fortescue (e, w) (Figure 1)
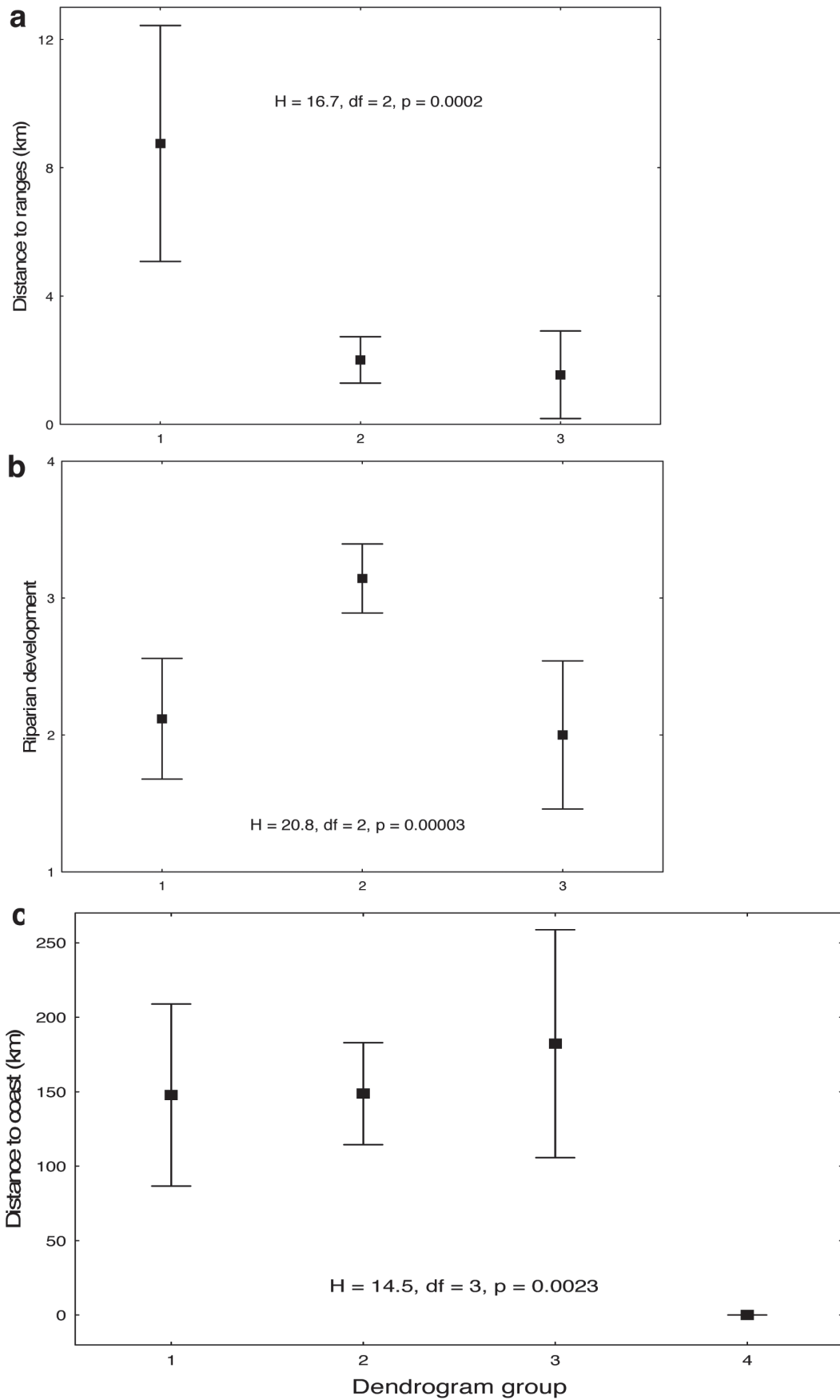
[d] 27 March

Figure 11   Site attributes that best separated the four dendrogram groups derived from the site classification (Figure 10). In statistical terms, the combination of 'Distance to ranges' and 'Riparian development' separated each of the three landward site-groups, while 'Distanct to coast' separated group-4 (the mangrove sites) from the rest. Mean and 95% confidence intervals are displayed (H = Kruskall-Wallis coefficient).

provide roost sites and areas for drinking (Cross 1986, 1988; Tidemann and Flavel 1987). Interaction between the 'distance to ranges' and the 'riparian development' factors explained the nestedness in species composition overt in the Pilbara's landward site-groups of Figure 9.

The assemblage analysis herein is based on 2.5 h recording sessions that commenced at dusk, the period of peak activity for most microbat species (Law *et al.* 1998; Kuenzi and Morrison 2003; Milne *et al.* 2005a). Even so, richer species lists might have been achieved from sites that were remote from riparian pools and ranges if the recording sessions had been more prolonged, covering the later parts of the night, and if all sites had been sampled in at least two seasons. Richards (2001) recommended 3 h of recording from dusk to detect 90% of species present at a site, and Duffy *et al.* (2000) recommended 5 h. We averaged 1.9 recording nights, totalling 4.5 h per site.

In terms of their structural complexity, the regional bat faunas of Western Australia's tropical arid zone conform to a diversity productivity hypothesis (Nijs and Roy 2000), with the most arid regions having species-poor faunas dominated by fast-flying species of open airspace, rather than surface and air superiority strategists that hunt in more cluttered microhabitats (Table 11, also see McKenzie *et al.* 2002). The Pilbara study confirms that the additional species found in the least arid of these regions are confined to productive landscape mosaics (e.g. *C. morio*, *N. arnhemensis*, *N. bifax daedalus* and *M. loriae*), or depend on physiologically benign day-roosts in caves and rock-crevices (e.g. *M. gigas* and *R. aurantia*; Armstrong 2001). Positive, exponential relationships between productivity and community diversity (richness, evenness and degree of difference between species) are well recognised (e.g. Rosenzweig and Abramski 1993; Srivastrava and Lawton 1998; Nijs and Roy 2000),

Table 11 Structural diversity of microbat faunas in tropical arid regions of Western Australia, listing number of species in each foraging strategy, a measure of overall productivity (annual average rainfall), occurrence of productive landscape mosaics, and availability of physiological refuges (updated from McKenzie *et al.* 2002). Species codes from Table 1. [a]*Sb = Scotorepens balstoni* (Thomas 1906).

Foraging Strategy	Pilbara	Gascoyne	Carnarvon	Great Sandy Desert	Little Sandy Desert	Gibson Desert
Interceptor	*Ta* *Cj* *Mb* *Ml*	*Ta* *Cj* *Mb*	*Ta* *Cj* *Mb* *Ml*	*Ta* *Cj* *Mb*	*Ta* *Mb*	*Ta* *Mb*
Air Superiority – open	*Sf* *Th* *Tg* *Ml*	*Sf* *Th*	*Sf* *Th* *Ml*	*Sf* *Th*	*Sf* *Th*	*Th*
Air Superiority – highly agile	*Cg* *Sg* *Vf* *Ra* *Cm*	*Cg* *Sb*[a] *Vf* *Ra*	*Cg* *Sg* *Vf*	*Cg* *Sg* *Vf*	*Cg* *Sg* *Vf*	*Cg* *Sb*[a] *Vf*
Surface – 3-D	*Ngg* *Nbd* *Na* *Ngp*	*Ngg* *Nbd*	*Ngg* *Na* *Ngp*	*Ngg*	*Ngg*	*Ngg*
Surface – ambusher	*Mg*	*Mg*				
TOTAL	17	12	12	9	8	7
Productivity						
Rainfall (mm)	350	240	250	240	230	220
Mangroves	present	none	present	none	none	none
Cavernous ranges	widespread	widespread	sparse	rare	rare	rare
Complex riparian woodlands with permanent pools	widespread	widespread	sparse	rare	rare	none

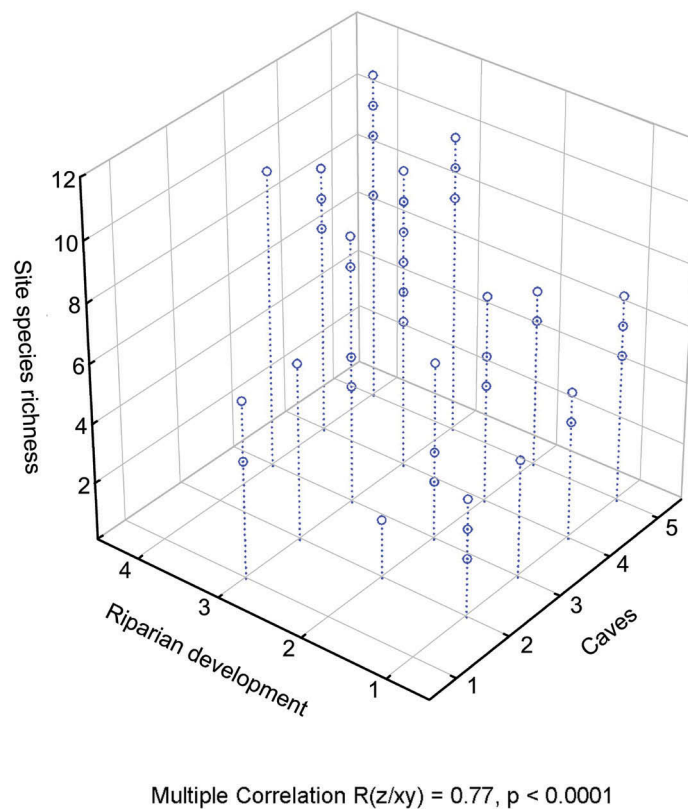Multiple Correlation R(z/xy) = 0.77, p < 0.0001

Figure 12   Species richness plotted against 'Riparian Development' and 'Caves' (distance to ranges and other cavernous habitat, see Table 2) for the 64 landward sites.

particularly in the context of strong interspecific competition.

Determinants of community structure

It appears that spectral variables can be used to characterise free-flying bats according to their foraging niche without distorting the outcome by disrupting their normal activities. Spectral variables may allow the organisation of microbat communities to be reliably and quickly related to environmental factors, including disturbance heterogeneity (*sensu* Urban 2004), even in communities of unknown species composition.

Given the ecological relevance of the spectral variables, the near-regular spacing of species across the spectral plots implies that Pilbara microbat communities are organised deterministically, according to specialisations related to resource partitioning. Niche-assembly models of meta-community organisation have been reported previously for guilds and faunas of Australian microbats (McKenzie and Rolfe 1986; McKenzie and Start 1989; McKenzie *et al.* 2002), although these studies used measures of flight capability, rather than echolocation, as surrogates of realised foraging niche. However, this niche-assembly

model of metacommunity is insufficient to explain the structure of microbat assemblages at regional scales in the Pilbara because nestedness in assemblage species composition that related to environmental factors was exposed by the habitat analysis, implying the influence of environmental controls (see Mouquet and Loreau 2002; Urban 2004; Armstrong 2005). Several species were absent from those landward sites that were remote from well-developed riparian habitats (e.g. *C. morio*, *N. b. daedalus*) while others were absent from the sites that were remote from ranges (e.g. *T. georgianus /hilli* and *V. finlaysoni*).

Nestedness in species composition was not restricted to the Pilbara's landward community; it was also overt among faunas of the adjacent regions when they were arrayed using rainfall as an approximate measure of regional productivity (Table 11). Where the nestedness was disrupted, the species turnover involved a congeneric replacement (*S. greyi* by *S. balstoni* in the Gascoyne and Gibson Desert Regions). Equivalent congeneric replacements discriminated the two Pilbara communities: as we noted earlier, three landward species — *N. g. geoffroyi*, *N. bifax daedalus* and *M. beccarii* — are replaced in the mangroves by their ecological counterparts *N. g. pallescens*, *N.*

arnhemensis and *M. loriae*, respectively (Table 1). Given the tight relationship between foraging ecology and phylogeny in Western Australian microbats (e.g. McKenzie *et al*. 2002), we suggest that metacommunity as well as habitat interactions are important determinants of organisation in Western Australian microbats at local and regional scales.

Conservation

Armstrong (2005) argued that metapopulation and habitat paradigms have to be integrated to understand broad-scale declines in species, and to provide sound management advice. Our study has revealed that metacommunity and habitat paradigms are both required to explain assemblage composition in Pilbara microbats, and we identify several factors relevant to planning for their conservation. Loss of complexity in riparian vegetation, reduced permanence of pools, loss of mangrove stands and loss of suitable cave roosts, are all likely to reduce microbat populations. Any resource development liable to affect these sites should be accompanied by non-intrusive monitoring of microbats; the call library provided in this paper will allow monitoring to be implemented inexpensively. For microbats belonging to the landward community, we need to ensure that well-developed riparian sites in 'range country' are included in conservation reserves (e.g. Weeli Wolli, Cattle Gorge and Turee Creek). For the mangrove bat community, at least five mangrove stands must be included in the conservation reserve system (i.e. Gales Bay, Dampier, Cossack, Balla Balla Harbour and Cape Keraudren); loss of any of these stands will substantially reduce the area of this habitat in the region.

The valley of Weeli Wolli Spring appears to be regionally unique from a microbat viewpoint. It supports the richest microbat assemblage recorded during our survey, and is also the only area in northern Western Australia known to support a population of *C. morio* (Young *et al.* 2008). Additionally, data presented herein make it the only location known in northern Western Australia where *T. australis* can persist through the hot and humid summer months (see Bullen and McKenzie 2005). We speculate that occasional cool air that floods through the Weeli Wolli valley during summer nights may reduce atmospheric enthalpy to levels at which this otherwise temperate-adapted species can forage for long enough to meet its metabolic requirement. Atmospheric enthalpy represents the variation in the combination of temperature, specific humidity and pressure of air.

Pilbara microbats have not yet suffered the extinctions experienced by the region's other (non-volant) indigenous mammals (McKenzie *et al.* 2006; Baynes, *Records of the Western Australian Museum* Supplement 78). We found no evidence that microbat species have been extirpated from parts of the Pilbara; even the 'whispering' bats (so-called because of their seemingly weak call) were recorded in all sub-regions where appropriate habitats were present (*R. aurantia*, *M. gigas* and *Nyctophilus* spp.). Nevertheless, a smart reserve system is required to preserve these intact, interesting microbat communities.

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APPENDIX 1

Microbat sampling site locations and environmental attributes (defined in Methods).

Site # (Figure 1)	Latitude (°S)	Longitude (°E)	Caves	Distance to ranges (km)	Riparian development	Atmospheric conditions	Distance to coast (km)	Minutes recorded	Nights sampled
1	-20.2672	119.2022	4	3	3	3	28	152	11 Oct 05
2	-20.1619	119.3667	1	20	3	4	19	304	28, 29 May 06
3	-20.2839	119.1558	4	0.3	2	4	27	310	7, 10 Mar 07
4	-20.3167	119.1889	5	0.001	1	3	32	162	13 May 07
5	-20.3117	119.2536	3	6.1	3	4	34	314	13 May 07, 6 Nov 07
6	-19.9717	119.7744	4	0.2	M	4	0	434	1980s, 22 Feb 06, 3, 4 Nov 07
7	-20.8806	120.6942	3	4.8	3	4	120	465	18, 23 May 06, 17 Jun 05
8	-20.6994	120.8894	2	11.4	1	3	108	152	6 Oct 05
9	-20.7944	120.3281	3	4	2	3	100	150	16 Jun 05
10	-20.8472	119.7667	3	6	3	3	89	152	18 Jul 05
11	-20.9111	119.6500	5	0.03	3	4	93	460	12, 13, 16 May 06
12	-20.4297	119.9689	4	3	1	4	53	152	28 Sep 05
13	-20.8553	116.6117	4	1.5	4	4	12	696	5 Aug 04, 4 Oct 04, 20, 21 May 05, 24 Feb 06
14	-21.0519	116.1606	3	4	2	3	7	152	30 Sep 04
15	-20.7317	116.6242	5	0.01	M	4	0	292	1980s
16	-20.8511	116.9436	4	2	3	4	14	305	4 Oct 04, 25 May 05
17	-21.0742	116.9319	5	0.01	1	4	39	154	12 May 07
18	-20.6300	117.0000	5	0.1	M	4	0	422	1980s, 27, 28 May 05, 2 Nov 05
19	-20.9289	1179753	4	2.5	4	4	41	364	4, 5 Oct 04, 2 May 05
20	-20.7003	118.2975	1	21	3	4	36	156	14 May 07
21	-20.6744	117.7828	3	6	M	4	0	520	1980s, 31 Oct 07

Site # (Figure 1)	Latitude (°S)	Longitude (°E)	Caves	Distance to ranges (km)	Riparian development	Atmospheric conditions	Distance to coast (km)	Minutes recorded	Nights sampled
22	-21.7333	115.8089	3	5	3	3	42	155	28 Sep 05
23	-21.7792	115.4083	1	14.9	3	3	22	306	12 May 06, 27 Sep 05
24	-22.4739	114.2297	3	6.6	M	4	0	292	1980s
25	-21.7119	116.7639	2	10.2	1	3	106	152	6 Oct 05
26	-21.7189	116.2150	4	2.2	4	4	68	461	20, 23 May 06, 2 Oct 05
27	-21.9925	116.5072	5	0.05	2	1	113	155	9 Jun 05
28	-21.5908	117.0700	4	2	4	3	98	385	4, 5 Aug 04, 14 May 05
29	-21.3336	117.2525	5	0.03	3	4	67	456	9 Oct 04, 10, 14 May 05
30	-21.7917	117.8617	3	3.9	2	3	125	309	12 Oct 04, 18 May 05
31	-21.7733	117.9203	4	2	3	3	127	152	16 May 05
32	-21.0475	118.7950	4	0.17	3	4	84	757	14 Jun 05, 25, 26, 27 Sep 05, 14 May 06
33	-21.1025	118.8875	3	4.6	2	2	92	150	15 Jun 05
34	-21.3203	119.3783	4	0.2	3	3	131	464	12 Oct 05, 3, 6 May 06
35	-21.0661	119.4422	4	1.4	2	3	112	153	11 Jun 05
36	-21.3528	119.4522	3	3.6	2	2	137	150	13 Jun 05
37	-21.8125	120.0875	4	1.5	2	2	201	150	12 Aug 04
38	-21.8317	120.1583	4	0.2	3	3	206	465	18, 20 May 05, 21 Oct 04
39	-21.2036	121.0214	4	0.8	3	4	165	450	15 Oct 04, 7 May 05, 13 Oct 06
40	-21.2261	120.4942	4	2	3	2	153	152	16 Jul 03
41	-22.6419	120.6167	2	15	1	4	303	154	3 Sep 05
42	-22.6275	120.7633	3	6	4	4	318	150	9 Oct 05
43	-23.3075	119.8628	4	0.9	4	4	361	302	13, 14 Feb 06
44	-23.5353	120.3250	3	3.6	3	4	398	155	22 May 06

45	-23.5083	120.2672	4	0.5	3	4	388	155	23 May 06
46	-23.4706	120.1958	5	0.02	1	4	389	155	1 Sep 05
47	-22.8928	119.2233	5	0.03	4	4	294	361	2 Jul 02, 3, 4 Aug 04, 17 Oct 04, 17 Feb 06
48	-22.9156	119.2056	5	0.03	4	4	294	152	17 Feb 06
49	-22.1825	119.9386	4	2.6	3	3	237	306	20, 22 Oct 04
50	-22.6631	119.9242	2	15	3	4	270	153	6 May 05
51	-22.0764	119.6733	4	1.2	3	4	219	152	10 May 05
52	-22.3347	118.9889	3	3.5	2	4	231	307	18 Oct 04, 6 May 05
53	-22.1067	119.0006	5	0.02	2	4	206	152	4 May 05
54	-22.2219	119.0228	4	2.1	3	3	218	290	15 May 07
55	-22.4258	118.4531	5	0.02	3	4	214	174	11, 12 Jan 96
56	-22.4778	118.5506	5	0.03	4	4	217	269	28 Sep 05, 18 Feb 06
57	-22.5831	118.4572	4	1.25	1	1	233	158	15 Jul 05
58	-23.3703	117.8222	5	0.04	4	4	298	458	12, 13 Oct 05, 6 May 07
59	-23.3439	118.0217	4	0.31	3	4	296	153	31 May 06
60	-23.2817	118.1017	4	1	3	2	294	153	2 Jun 06
61	-23.2081	117.5353	5	0.1	4	4	274	272	5 May 07, 13 Nov 07
62	-22.6403	117.7094	4	1	3	3	223	309	4, 5 Oct 05
63	-22.5080	117.6941	3	7	3	4	201	277	25 May 06, 8 May 07
64	-22.6850	116.3069	4	3	3	4	160	303	7 Oct 04
65	-22.4869	116.5658	5	0.04	2	3	161	152	19 May 05
66	-22.4467	116.0017	3	5.5	1	3	121	153	22 May 05
67	-22.0283	115.4300	2	17	2	4	51	152	3 May 05
68	-22.0933	115.6197	3	6	3	4	65	152	3 Oct 04
69	-22.1858	115.5556	4	0.5	1	4	72	152	2 Oct 04