

Recent developments in studies of the community structure, foraging ecology and conservation of Western Australian bats

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ABSTRACT

Surveys of microbat communities in several regions of Western Australia have revealed a diversity–productivity model of community structure in which co-occurring species occupy different foraging niches, but environmental factors influence turnover in species composition across landscapes.

Detailed studies of species airframe morphologies, echolocation call designs, wingbeat frequencies and amplitudes, and flight muscle masses have revealed that bat sensory systems and aerodynamic packages (including fur and flight muscles) are fully integrated and functionally appropriate to empirical data on flight speeds, foraging strategies and microhabitats.

We also report on progress towards the development of a general model for estimating species energy budgets and quantifying the deterministic relationships between their energetics, aerodynamics, geographical ranges and foraging niches.

Key words: bats, Western Australia, echolocation, foraging ecology, aerodynamics, metacommunity, habitat associations

Introduction

The 37 bat species known from WA can be grouped into two distinct faunas, one temperate and the other tropical. Regional and community species richness decreases with rainfall in both faunas, although there is also some species-level turnover.

This programme began in 1972. Originally a series of bat surveys, it soon became an investigation of the ecological basis of resource partitioning in Western Australian bat communities. Most of the early papers reported on survey work in the eastern Goldfields, Nullarbor, Kimberley and inland desert regions (e.g. Kitchener *et al.* 1981; McKenzie and Youngson 1983; McKenzie 1983; Boscacci *et al.* 1987; McKenzie *et al.* 1992; McKenzie *et al.* 1994; McKenzie and Rolfe 1995; McKenzie *et al.* 1995a; Burbidge *et al.* 1995).

Other early papers reported detailed ecological studies that focussed on the structure of bat guilds in tropical mangrove communities (McKenzie and Rolfe 1986; McKenzie and Start 1989), on the ecomorphological structure of an entire bat fauna (McKenzie *et al.* 1995b) and on a zone of faunal interchange between temperate and tropical environments (McKenzie and Muir 2000). They revealed functionally appropriate relationships between species flight morphology (wing aspect ratio, wing-loading and tip index), echolocation call characteristics, foraging microhabitats and community organisation. Relationships between phylogeny and foraging ecology were apparent at the family level, implying that morphological specialisations related to foraging strategy commenced early in the evolution of bats (McKenzie *et al.* 1995b).

These papers also introduced a classification of foraging microhabitats for Western Australian microbats that,

modified from Fenton (1982), was based on the use of open, semi-cluttered or fully cluttered airspace. Microhabitats were defined as open air (OC), above clutter (AC), beside clutter (BS/O), against clutter (BS/A) and inside clutter (IS). Geographical turnover in species composition of Western Australia's microbat faunas was shown to conform to the zone of transition from temperate to tropical climates (McKenzie and Muir 2000, p. 471), similar to that reported in European, North American and Australian faunas (e.g. Pagel *et al.* 1991, Nowak 1994, Burbidge *et al.* 2009), and to include species that are seasonally absent (McKenzie and Muir 2000) – *Tadarida australis* and *Saccolaimus flaviventris*. At more local scales, guilds in stable environments were found to have a deterministic structure that related to differences in species potential foraging niche (McKenzie and Start 1989) and, as elsewhere, assemblage composition correlated with structural complexity in vegetation (McKenzie and Muir 2000, Milne *et al.* 2005).

Collaboration between the authors began in 1996, when we combined our knowledge of airframe design (RDB) and bat ecology (NMCK) to interpret data on bat airframe structures in relation to differences observed in species flight performance and foraging behaviours. The project on Western Australian bats now has five discrete components that aim to:

1. Document the geographic distribution of species, assess their conservation status and identify factors limiting their distributions.
2. Document the composition of bat communities (from local assemblages to regional faunas).
3. Characterise species in terms of their foraging habitats and strategies.

4. Build a library of species echolocation calls as a field survey tool and an additional perspective on foraging niche.
5. Assess differences between species airframes that relate to flight performance and control, foraging behaviours and energetics.

In combination, these datasets are expanding our understanding of the mechanisms that structure bat communities and determine the geographical ranges and conservation vulnerabilities of their component species.

We chose to begin the collaboration in an accessible region with a relatively simple bat fauna.

Coolgardie Woodland Study (Bullen and McKenzie 2001)

The arid to semi-arid Coolgardie Bioregion of WA has a bat fauna of eight obligate insectivores. Their foraging behaviours were described between 1976 and 1983 during field survey work across the diverse mosaic of woodlands and shrublands that cover this region's gently undulating landscapes (cited earlier). From these notes, we recognised two discrete facets to the microbats' foraging behaviour, and assessed them separately: (1) where they hunted, defined in terms of differences in airspace clutter and, (2) how they find and catch their prey. These were termed 'usual foraging microhabitat' (defined earlier) and 'foraging strategy', respectively.

The strategy categories ('interceptor', 'air superiority' and 'surface') were refined from the traditional 'hawking' and 'gleaning' descriptors (e.g. Fenton 1982). The region's molossids were intercepting their airborne prey during a direct, high-speed pass. The small-eared vespertilionids were observed to out-turn their airborne prey (hence the term 'air superiority'), while the long-eared *Nyctophilus* species were surface foragers that hunted either air-to-surface (previously gleaning) or surface-to-air (previously ambushing).

The Coolgardie study developed understanding of bat flight morphology to a new level. It showed that ear, tail, wing leading edge flap and wing camber geometry were functionally appropriate to species foraging microhabitats and foraging strategies, and that the differences were not merely a phylogenetic artefact. After testing the Coolgardie woodland community's eight microbats in terms of flight performance, stability and control, we presented the first systematic classification of bat flight manoeuvres. These tests included measuring species' flight speeds using hand held radar, obstacle course experiments to assess species ability to turn, and slow motion analysis of video recorded in a flight chamber to describe the various manoeuvres performed by each species and assess the induced aerodynamic forces. These data were used to produce an agility rating for each species: interceptors and surface foragers had low scores, while air superiority foragers were highly agile. Agility in this context is a measure of the ability of an airframe to generate and sustain lateral acceleration.

Our study revealed that the tail, ears and main wing all contribute to a bat's flight capabilities. In combination, six airframe ratios provided robust predictions of species'

foraging microhabitats and foraging strategies (aspect ratio, wing loading, tail area ratio, tail length ratio, ear area ratio and ear length ratio). The first two could be used to predict their foraging microhabitat (Fig. 1), while their foraging strategy was linked to functionally appropriate ear and tail ratios. Interceptors had small tails with long tail arms, surface foraging bats had medium-size tails with shorter tail arms, while the air-superiority species all had medium to large tails with longer tail arms (Fig. 2).

The size of the bat's ears and their distance forward on the airframe were linked to agility, but the ratio of 'tail area ratio' to 'ear area ratio' (TEAR) gave cleaner separation of the agility classes (Fig. 3). Highly agile bats had small ears and large tails giving highest TEAR values (*Chalinolobus gouldii*, *C. morio* and *Vespadelus regulus*), while the least-agile bats had the lowest TEAR values (*Nyctophilus geoffroyi* and *Tadarida australis*). From the functionally appropriate linkage between ear design, agility and foraging strategy we concluded that the ears were operating as canard wing aerodynamic surfaces and were not simply auditory appendages.

Next, we tested the repeatability of the Coolgardie study by selecting another region of comparable faunal complexity, but different composition.

Little Sandy Desert Study (McKenzie et al. 2002)

Part of Australia's red centre, the Little Sandy Desert has a tropical arid climate based on summer rainfall. Sand dune fields with interdune plains that support spinifex and mulga, respectively, dominate the region. River gums such as *Eucalyptus camaldulensis* fringe drainage lines that traverse the dune fields and the watercourses that drain its abrupt sandstone ranges (Beard 1990).

The desert's bat fauna comprises nine species, which are all obligate insectivores. During the study, the nine species were classified into the foraging strategy and microhabitat-use categories defined during our earlier studies, and the relevant airframe parameters were measured. The assignment of each species to a category of foraging strategy and preferred microhabitat was based on hunting behaviours observed in the field, combined with published observations from elsewhere. Detailed descriptions of these behaviours are included in the paper, and allowed the air superiority strategy to be divided into two sub-categories: the first comprised the two emballonurid species, which were fast and semi-agile fliers; the second comprised the three small-eared vespertilionid species, which were highly agile. Emballonurids do not occur in the Coolgardie fauna. As in the Coolgardie study, the molossids were observed to be interceptors and the long-eared bat (*Nyctophilus geoffroyi*) had a surface foraging strategy.

Airframe design parameters relating to flight performance, stability and control again showed tight, functionally appropriate relationships with the foraging niches of all nine species as well as with their search mode echolocation call parameters (F_{peakC} and bandwidth ratio). As in the Coolgardie study, the airframe parameters were found to segregate into two nearly independent groups. The first, comprising the overall

wing-based parameters of aspect ratio and wing loading, related to microhabitat-use (Fig. 4), and the second, comprising the ear and tail morphology, related to foraging strategy. Again, bats characterised by higher wing loading and aspect ratio values foraged in the open air, and these values reduced as the level of clutter increased. In addition, ear and tail design was shown to be related to the bat's agility (and manoeuvrability) giving its overall foraging strategy (Fig. 5).

The absence of specialist components in the bat faunas of desert bioregions, compared to adjacent but more

productive bioregions in Western Australia's tropical arid-zone, implied a diversity-productivity model of faunal organisation that is consistent with the 'specialisation hypothesis' (Srivastrava and Lawton 1998) in which co-occurring species occupy different foraging niches. Clear functionally appropriate family-level relationships between phylogeny and foraging ecology were apparent, supporting the implication of our earlier studies: that morphological specialisations related to foraging strategy commenced early in the evolution of bats (McKenzie *et al.* 1995b; Bullen and McKenzie 2001).

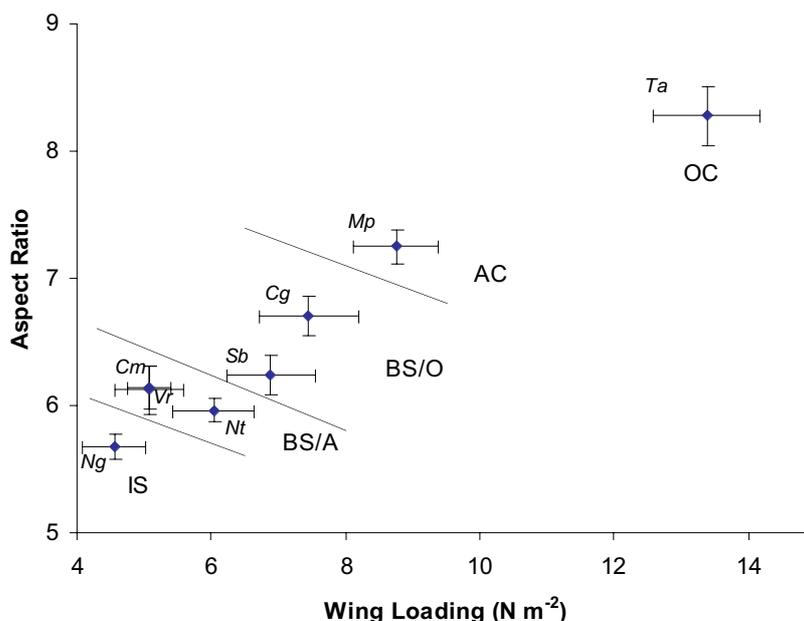


Figure 1. Cross-plot of aspect ratio versus wing loading, with usual microhabitat superimposed (IS = Inside clutter; BS/A= Beside clutter / against; BS/O = beside clutter / open; AC = above clutter; OC = open air). Bars indicate standard deviation. Reproduced from Australian Journal of Zoology.

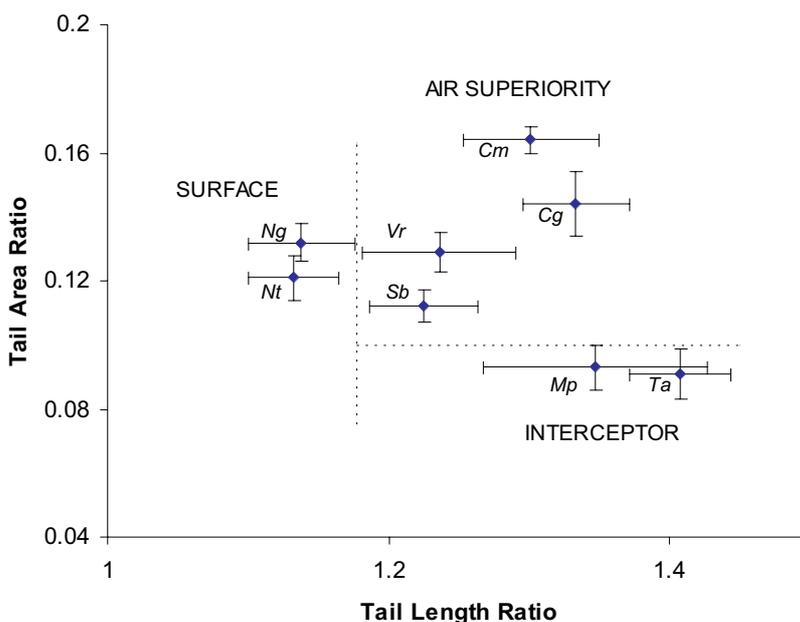


Figure 2. Cross-plot of tail area ratio versus tail length ratio with three foraging strategies superimposed. Bars indicate standard deviation. Reproduced from Australian Journal of Zoology.

The seasonal absence of the Desert's large molossid previously documented in the Carnarvon region (McKenzie and Muir 2000), combined with the opportunity provided by our expanding data set, prompted a specific investigation.

Tadarida australis distribution study (Bullen and McKenzie 2005)

Tadarida australis (white-striped free-tailed bat) is a relatively large (35 g), obligate insectivore that is not

known to hibernate and is seasonally sparse or absent in tropical northern areas of WA during the spring and summer (Churchill 1998; McKenzie and Muir 2000; McKenzie *et al.* 2002). To confirm and characterise this range contraction, we compiled presence and absence data from various sources including previous publications, Western Australian Museum records and data from our own field surveys. These data revealed a northward range expansion of up to 1200 kilometres for the winter and a corresponding southward contraction for the summer. At full expansion, this species range covers approximately

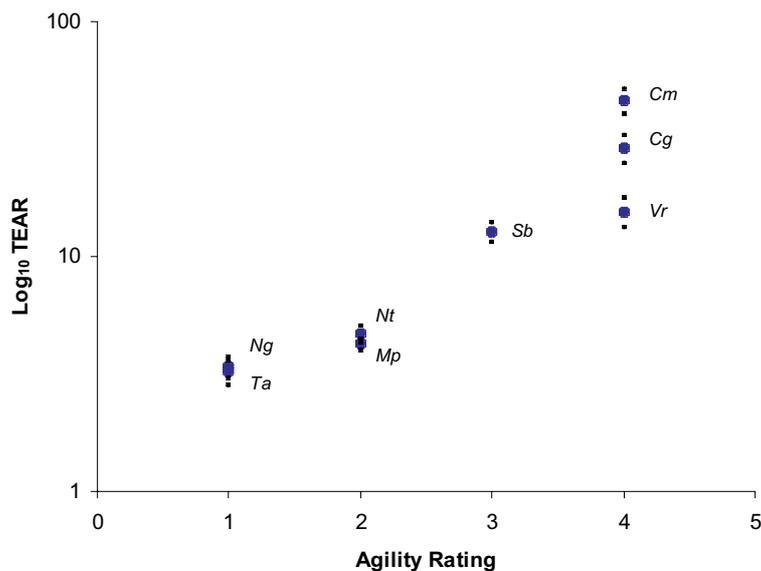


Figure 3. TEAR (large dots) in relation to observed manoeuvrability and agility rating. Small dots indicate standard deviations. Reproduced from Australian Journal of Zoology.

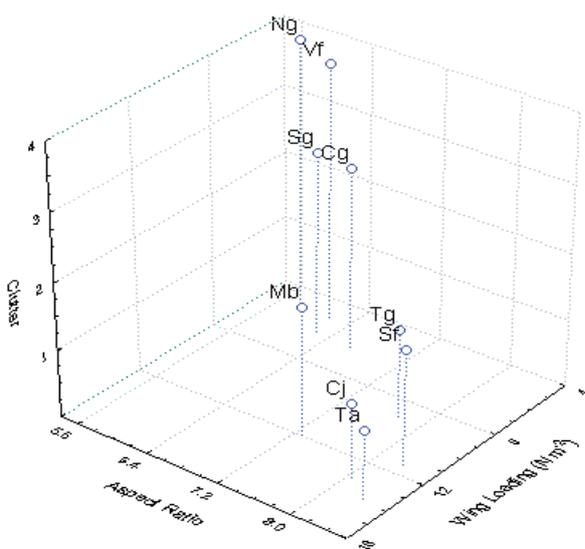


Figure 4. Three dimensional scatter plot of foraging microhabitat (clutter) against average aspect ratio and average wing loading ($N\ m^{-2}$). Species codes are Cg *Chalinolobus gouldii*, Cj *Chaerephon jobensis*, Mb *Mormopterus beccanii*, Ng *Nyctophilus geoffroyi*, Sf *Saccolaimus flaviventris*, Sg *Scotorepens greyii*, Ta *Tadarida australis*, Tg *Taphozous georgianus*, Vf *Vespadelus finlaysoni*. Reproduced from Australian Journal of Zoology.

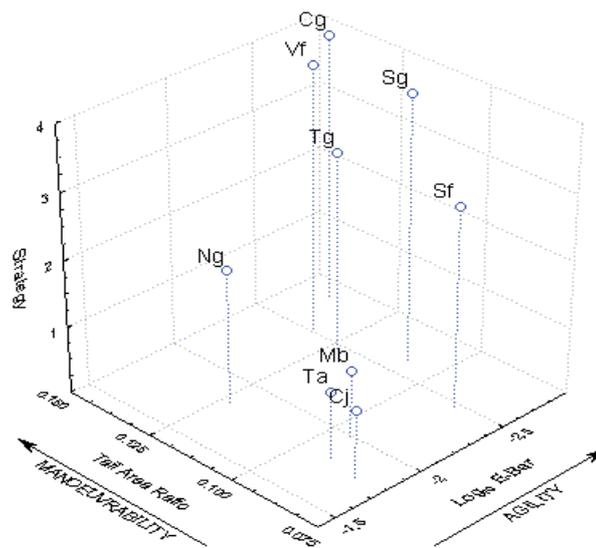


Figure 5. Three-dimensional scatterplot of foraging strategy against Tail Area Ratio and E-bar. Species codes are given in figure 4. Reproduced from Australian Journal of Zoology

80% of the state. Its northern range limits, for both summer and winter, do not correlate with any geographical barrier.

The available literature relates temperate bat migration to resource availability as a consequence of changing season so, in search of an explanation, we plotted monthly changes in the boundaries of the species range in terms of available meteorological and geographical data. The summer range limit of *T. australis* correlates with an interaction of temperature and humidity, which is best summarised by atmospheric enthalpy. Three climatic thresholds enclose this enthalpy envelope – average overnight minimum temperature <20°C, average annual rainfall >10 mm per month, and < 50 mm per month. Its winter distribution is expanded northward within the enthalpy threshold as far north as the middle of the Great Sandy Desert. The range boundaries for winter and summer are presented in figure 6 and are compared with the published 20°C overnight minimum temperature isotherm (refer to Fig. 7). Our study highlighted, for the first time, a tight correlation with atmospheric enthalpy that pointed to flight muscle heat dissipation as a limiting factor. Data on the distribution of *T. australis* from elsewhere in Australia reveal that the ‘enthalpy range limit’ relationship applies throughout Australia (Fig. 7).

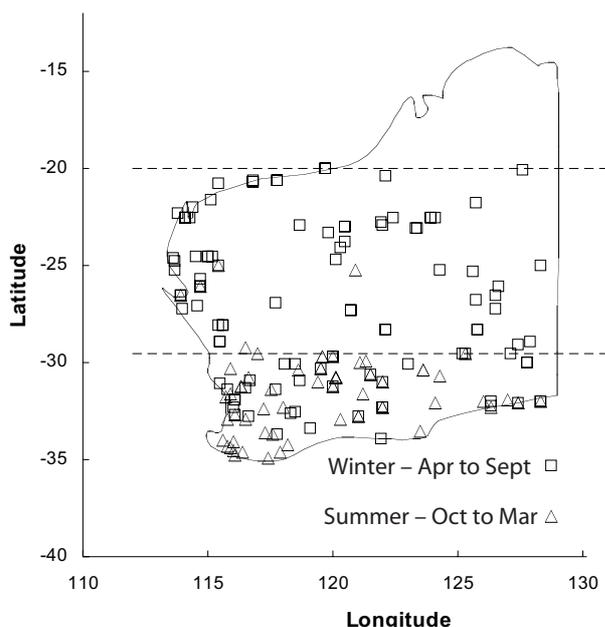


Figure 6. Presence of *Tadarida australis* with winter and summer months noted. Absence of the species from the range north of -29.5deg is apparent. The four presence points in this region represent March and October records. Reproduced from Australian Journal of Zoology.

If the ability to dissipate heat limits the geographical range of *T. australis*, it was suggested that the effects of global warming over the next century would reduce this range substantially, possibly confining the species to the south-eastern corner of the continent, south of the Murray River, by 2100 (Bullen 2005).

Echolocation

Our echolocation studies have been undertaken in parallel with the regional fauna and flight morphology studies.

They aimed to provide an additional perspective on species foraging ecology as well as a call library as a non-intrusive microbat survey tool. The call sequences were recorded and stored on cassette tapes and, later, onto MiniDisks (Sony, Japan) using an Anabat detector. Initially, the recordings were processed through ZCAIM analysis to characterise the bat calls present. Unfortunately, echolocation surveys of areas the size of the WA bioregions have proved to be very time consuming due, in part at least, to a trade-off between detecting weak bat calls and recording huge amounts of insect noise. Examples of these early bat surveys in WA include McKenzie *et al.* (1995a) with echolocation call variables for 10 tropical species from Koolan Island, and McKenzie and Muir (2000) with echolocation variables for 11 tropical and temperate species from the Carnarvon Bioregion. This early work revealed species pairs or sets with overlapping geographical ranges that could not be uniquely identified from one another in WA using the time domain variables provided by ZCAIM analysis. These included most Western Australian *Nyctophilus*, two tropical broad-nosed bats (*Scotorepens greyii* and *S. sanborni*), three of WA’s other tropical vespertilionids (*Chalinolobus nigrogriseus*, *Pipistrellus westralis* and *Myotis macropus*), *Chaerephon jobensis* and *Saccolaimus flaviventris*, and even *Tapochozous georgianus*, *T. hilli* and *Mormopterus beccarii*.

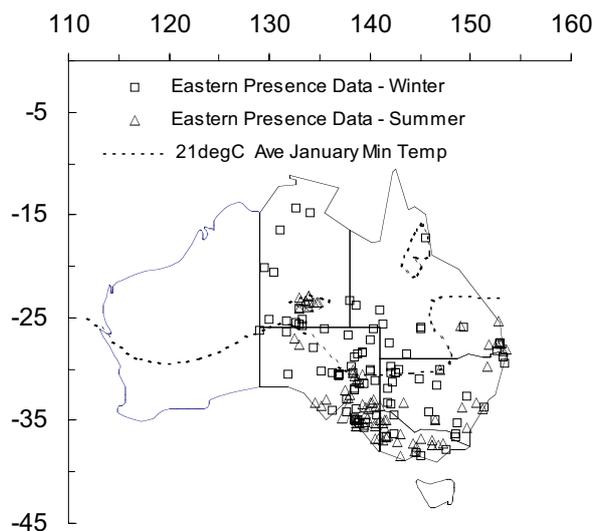


Figure 7. *T. australis* presence data from Australia other than W.A. reveal that the ‘enthalpy range-limit’ relationship applies Australia-wide.

We continue to build this library of Anabat generated recordings in digital format, which now covers all but six of Western Australia’s 26 bioregions (Environment Australia 2004). However, instead of ZCAIM analysis, we have adopted sound processing software that allows the recordings to be reviewed for the bat calls present using frequency domain as well as time domain variables. Since the bats were operating in a frequency dominated sound environment, we reasoned that the key to separating species calls would be found by analysing calls in that domain. Computer packages such as Cool Edit 2000 (now available as AUDITION; Adobe Systems USA) can scan and display call sequences in both of these sound domains in real time. From the frequency domain

spectrogram of one or more calls, it measures the frequency with the peak number of cycles (F_{peakC}) and displays the corresponding frequency profile while, at the same time, displaying the calls in time domain so that their clarity, steep, shallow or flat frequency variation through time and their repetition rate are visible. The last parameter is relevant because it reflects the wing beat frequency of the species, which allows search mode call sequences (useful for species identification purposes) to be distinguished from approach and interception mode sequences (e.g. Lancaster *et al.* 1995; McKenzie and Bullen 2003). This processing strategy was adopted for our bat surveys after 2000.

Nyctophilus Call Study (Bullen and McKenzie 2002a)

This study showed that spectral analysis could be used to differentiate ultrasound sequences by the seven *Nyctophilus* species that occur in WA. The call-to-call trends in peak frequency (F_{peakC}) values are species-specific if care is taken to select clear calls from genuine search mode sequences. Such sequences have repetition rates of one call per wingbeat, or less. These spectral differences were too subtle to be separated in time domain using the processing tools then available.

In addition, the three temperate species separated their usual F_{peakC} values, with *N. timoriensis* using a range of 43 – 47 kHz, *N. geoffroyi* using a range of 47 – 48 kHz and *N. gouldi* using a range of 50 – 53 kHz. In the tropical regions it was found that the five species also staggered their preferred F_{peakC} range with *N. geoffroyi* using the lower range of 47 – 48 kHz (since shown to extend from 43 – 48 kHz), *N. arnhemensis* using the range 50 – 52 kHz, *N. bifax dadaelus* using the range 50 – 54 kHz and *N. walkeri* using the highest range of 54 – 58 kHz.

Little Sandy Desert Call Study (McKenzie and Bullen 2003)

This study used spectral variables to differentiate the search mode echolocation sequences (but not all individual calls) of the species comprising the Little Sandy Desert's (LSD's) microbat fauna. Five species have distinctive sequences, with calls that are easily assigned using the frequency domain variable F_{peakC} (Fig. 8). However, calls by the other species form two clusters from which species cannot be reliably identified using either time domain variables or the frequency domain variable, F_{peakC} . To resolve this issue, we adapted a second frequency domain variable (Q factor) that provides further discrimination between the relevant species. A measure of the bandwidth ratio of the call's peak frequency at 50% of the peak's cycle-number (6 dB below the peak), it allowed unique identification of four of the five relevant species. Across a range of F_{peakC} values, *S. flaviventris* calls could be reliably differentiated from those by *C. jobensis*, and *M. beccarii* calls from those by *Taphozous*, figure 9. However, while calls by the two *Taphozous* species showed spectral characteristics that were statistically different en-mass, the sample differences were too small to be useful in discriminating species. The paper also showed that the different Q factors of emballonurid and molossids calls were functionally consistent with differences in their

airframe agility and that their F_{peakC} values were consistent with their different pinna tuning characteristics, reflecting the evolutionary divergence of these two families towards different foraging strategies.

We were beginning to understand the highly integrated relationship between bat sensory systems and their aerodynamic and ecophysiological packages.

Some additional funding, and the presence of genera representing three more families of bat (*Macroderma*, *Pteropus* and *Rhinioncteris*), caused our focus to shift to the Pilbara fauna.

Pilbara Studies

The Pilbara region of WA is extremely rich in minerals, primarily gold and iron ore, and its mining industry is currently a powerhouse of Australia's economy. Its fauna comprises 17 species of bat, including two megabats, and it has been the subject of several studies. Three of the region's microbats are confined to mangroves (McKenzie and Start 1989), while three others occur as geographical isolates from their main populations elsewhere in Australia (*Chalinolobus morio*, *Macroderma gigas* and *Rhinioncteris aurantia*) and have a limited number of known roosting locations that are often associated with mines (e.g. Hall *et al.* 1998; Armstrong and Anstee 2000; Armstrong 2001; Bullen 2006). *M. gigas* and the Pilbara population of *R. aurantia* are listed as Vulnerable (IUCN 2008 and EPBC Act 1999, respectively).

Building on work done by Dunlop (Hall *et al.* 1998) and Churchill (Churchill *et al.* 1988) during the 1970s and 80s, and by Armstrong during the 1990s (Armstrong and Anstee 2000; Armstrong 2001), one of the mining companies active in the region employed consultants to assess the sensitivity of *R. aurantia* colonies to nearby mining operations. This project began in 2004 and included one of the authors (RB) for a period. A large population of *R. aurantia* was discovered in the Goldsworthy district. This population centred on two gorges (Cattle and Callawa Gorges), also used by *M. gigas*. The gorges included several caves that were considered to be possible *R. aurantia* roosts. The company limited the distance that their iron ore mining operations could approach these caves to several hundred meters, and began to monitor the *R. aurantia* populations. The initial studies (Ecologia Environment 2005) and other work that followed (Ecologia Environment unpublished data) indicated that:

1. Colonies remain at their roost cave location in the face of closely adjacent mining operations as long as the temperature and humidity conditions within the caves remain unaffected.
2. Like their northern Australian counterparts, Pilbara *R. aurantia* scatter in the wet season when foraging and roosting opportunities increase, then return to the preferred primary roosts during the dry season.
3. *R. aurantia* do not abandon primary roosting caves when the area is reduced by fire as long as the local water resource is not affected, and presumably the local insect populations remain in place at the water resource. In contrast, *M. gigas* populations leave the area and then return as the undergrowth regenerates.

A recent visit (2007) by one of us (NMcK) confirmed that numerous *R. aurantia* were still present in Cattle Gorge.

A second project on Pilbara bats commenced in 2004 (McKenzie and Bullen 2009) as part of a regional biodiversity survey supervised by one of the authors (NMcK) for the WA Department of Environment and Conservation. We systematically surveyed microbats at 69 sites dispersed across the region, and collected data on species foraging ecology. Echolocation call sequences were identified using a library of known calls

accumulated during fieldwork. In combination, the frequency maintained for the greatest number of cycles (F_{peakC}) and the bandwidth ratio of this peak (Q) readily separated search-mode echolocation calls by 13 of the 17 species comprising the region's microbat fauna, but not the four species-pairs with allopatric ranges. Even so, the spectral characters provided an ecologically informative, viable and non-intrusive survey tool.

Classification of the sites in terms of their species composition revealed two compositionally distinct

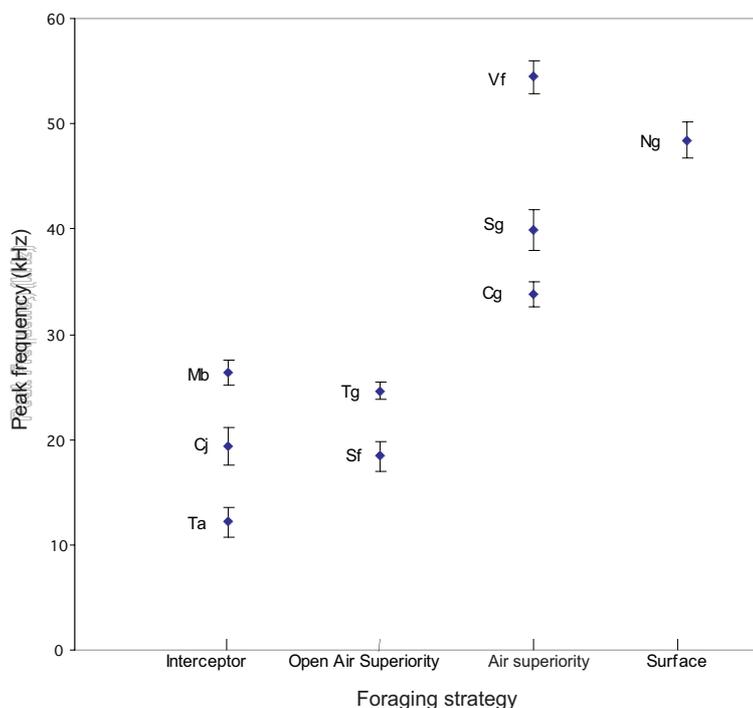


Figure 8. Peak frequency of search mode calls by Little Sandy Desert microbats plotted against usual foraging strategy (from McKenzie et al. 2002). Species codes are given in figure 4. Reproduced with permission from Australian Mammalogy.

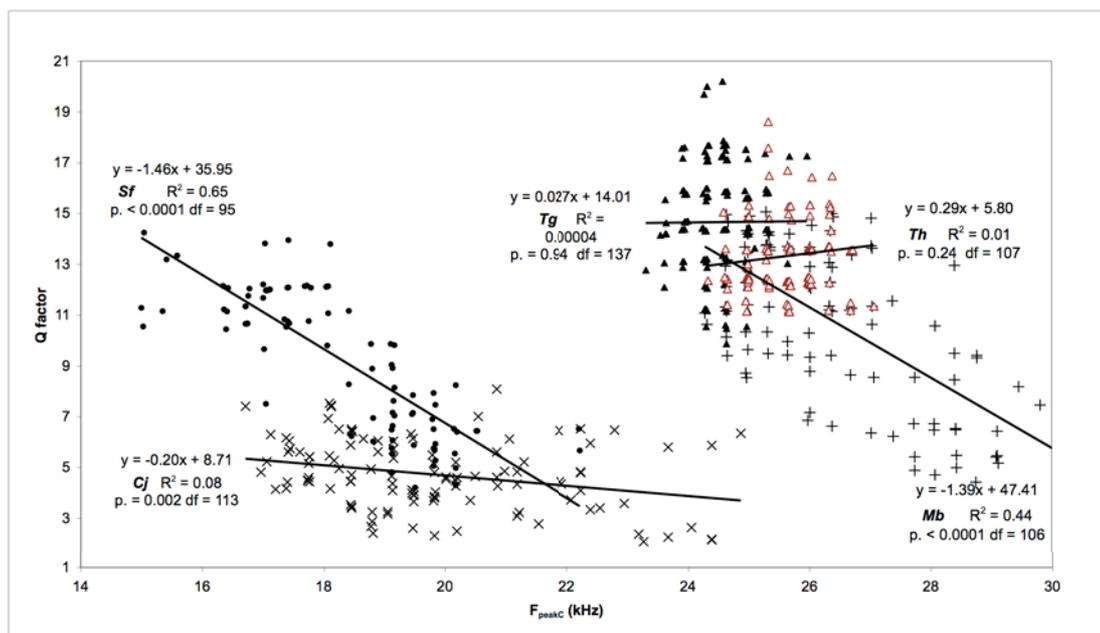


Figure 9. Scatterplot of F_{peakC} versus Q-factor of the strongest harmonic in “search mode” echolocation calls by Little Dandy Desert bats. Species codes are given in Figure 4. Reproduced with permission from Australian Mammalogy.

communities. One comprised 14 species and occupied landward environments, while the other comprised 9 species and occupied mangroves. 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 implied 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, which were set in cavernous landscapes. Two species were found to be widespread and more common than previously supposed despite detectability constraints caused by their cryptic calls (*Macroderma gigas* and *Rhinonictis aurantia*). Three riparian sites and four mangrove stands were identified for reservation.

Energetics

The feasibility of developing a general model for understanding bat community structures had been considered early in our collaboration. Simply measuring the flight morphology of the various species comprising Western Australian bat communities and linking this to their echolocation parameters and foraging behaviours might not be enough to explain the compositional organisation of these communities and the conservation vulnerabilities of their component species. The essence of this was to collect relevant ecological, behavioural and morphological data on species by using available

technology and equipment, and to assess and interpret species flight morphologies in terms of aircraft design principles. We recognised that no model would be complete without a robust method of calculating each species' ability to acquire and transform the energy needed for growth, survival and reproduction. This model had to include an understanding of the physiological mechanisms for saving energy such as torpor, and of the differences between the species that allow some to persist in regions where others do not. Without this model, the likely effects of latitude, rainfall and global warming on composition could not be predicted. Ultimately, we hoped to produce a general energy model covering the entire Western Australian bat fauna. If this was to be achieved, it needed to be in discrete steps.

Wingbeat frequency study (Bullen and McKenzie 2002b)

Wingbeat frequency (f_w) and amplitude (θ_w) were measured for 23 species of Australian bats, representing two sub-orders and six families. This was done by video recording the flight of the species and correlating the wing beat time histories collected with flight speed measurements taken with our hand held radar. Maximum values were between 4 and 13 Hz for f_w , and between 90 and 150° for θ_w , depending on the species.

We needed a wingbeat equation that was scaled to a readily available parameter, such as species mass, and that readily explained the variation between species over the full climatic range of Western Australia, tropical to temperate, mesic to arid. Recognising that the wingbeat frequency is controlled by the duration of the muscle's contraction and that the performance of the muscle is affected by the resistance it works against, we were looking for gross variations in the speed of operation of the muscles of bats with different phylogenies, foraging strategies or habitats to determine the level of complexity that needed to be modelled.

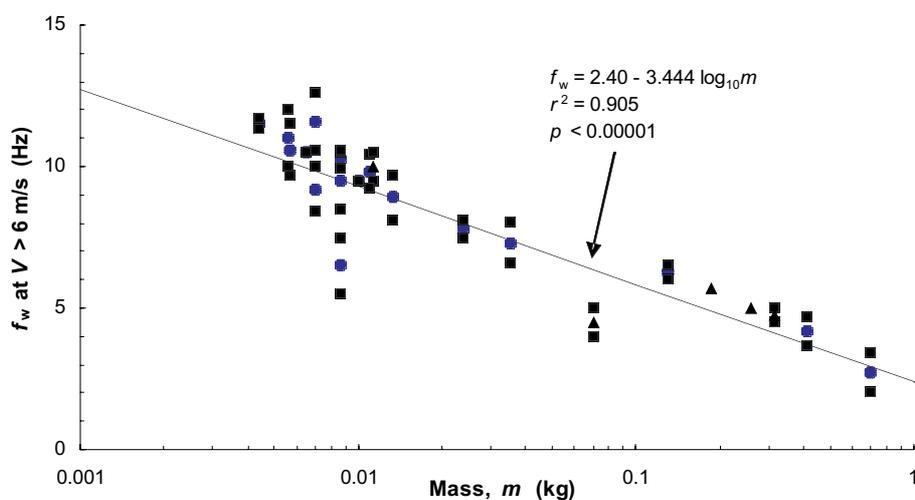


Figure 10. Summary of high flight speed wingbeat frequency data. For each species the mean values \pm S.D. of the data for $V > 6$ m s⁻¹. Reproduced with permission from Journal of Experimental Biology.

Wingbeat frequency for each species was found to vary only slightly with flight speed over the lower half of the speed range. At high speeds, frequency was found to be almost independent of velocity. Wingbeat frequency (Hz) depends on bat mass (m , kg) and flight speed (V , m/s) according to the equation: $f_w = 5.54 - 3.068 \log_{10} m - 2.857 \log_{10} V$ (Fig. 10). This simple relationship applies to both sub-orders and to all six families of bats studied. For 21 of the 23 species, the empirical values were accurate to within 1 Hz of the model values. One species, *Mormopterus planiceps*, was found to have a second mode of flight in which f_w was up to 3 Hz lower for all flight speeds.

A simple relationship predicting wingbeat amplitude to within $\pm 15^\circ$ from flight speed and wing area (S_{REF} , m^2) was also developed. This equation is based on data up to and including speeds that require maximum wingbeat amplitude to be sustained. For most species, the maximum wingbeat amplitude was found to be 140° reflecting the inability of the bats to raise their wings to a vertical position at the top of their stroke.

Muscle mass paper (Bullen and McKenzie 2004)

“How big is the bat’s engine”? The primary method of bat locomotion is medium to high-speed flight. Apart from thermoregulation and reproduction, a large proportion of the energy it expends in its daily cycle is expended on flapping the wings during flight (Speakman and Thomas 2003), generally 50 to 70% in insectivores and frugivores. We therefore focussed on the muscles that generate and control the upstroke and downstroke of

the wings as the primary “engine” of the bat, weighing the primary flight muscles of the chest, shoulder, back and upper arms for 29 species of Australian bat, representing two sub-orders and six families.

Flight muscles were found to total between 9 and 23 % of the mass of the bat (m_{bat}). When plotted against m_{bat} , they aligned into three statistically distinct classes. These classes represent ‘high energy’, ‘general’ and ‘low energy’ foraging strategies (Fig. 11). Differences in the foraging ecologies and geographical distributions of the bats were reflected in these classes as well as in the bats’ airframe designs. The majority of carnivores, frugivores and insectivores that forage using the interceptor strategy were found to fall into the low-energy class. The rest of the temperate insectivores fell into the general muscle class, except for the high energy *Chalinolobus morio*. In contrast, the rest of the tropical insectivores were split equally between the general and high-energy classes, perhaps reflecting the higher productivity of the tropical wet season.

The equation derived from the study allows a simple calculation of the flight muscle mass based on bat mass and the parameter TEAR that, as discussed earlier, corresponds to overall agility. The flight muscle mass ratio of male bats average 0.75% greater than do females of the same species.

Aerodynamic cleanliness (Bullen and McKenzie 2007, 2008a, 2008b)

Next, we evaluated species aerodynamic cleanliness (of the wing, body and pelage) to quantify species-specific lift and drag coefficients for the general energetic model and

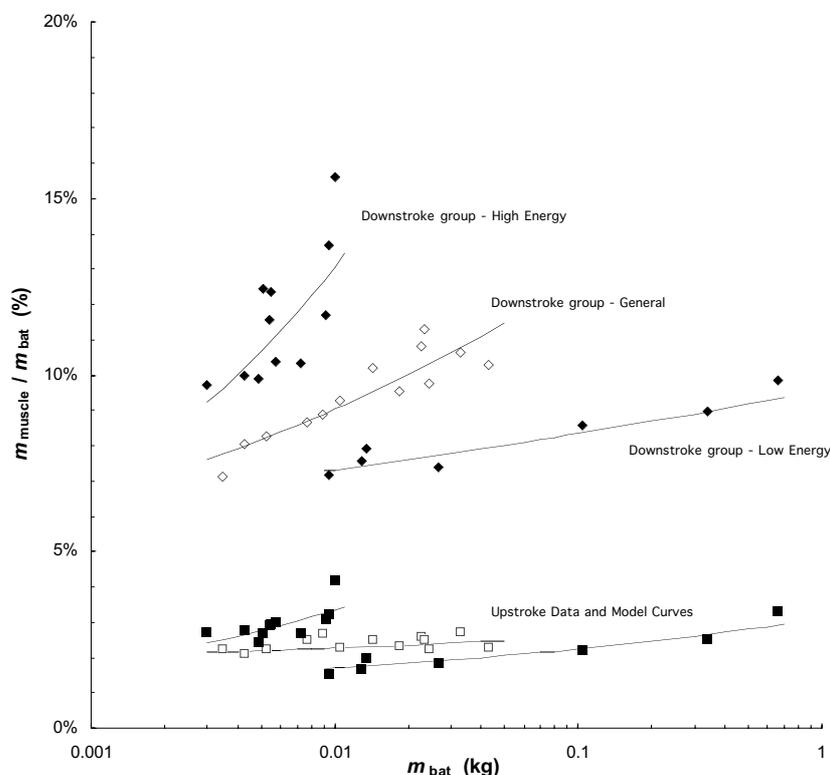


Figure 11. Downstroke (diamonds) and Upstroke squares) group flight muscle mass fractions plotted against bat mass. Reproduced from Australian Journal of Zoology.

show their functionally appropriate correlations with foraging niche. This contributes to a baseline for real appraisal of the empirical observations collected during the regional fauna studies.

Aerodynamic cleanliness can be assessed as the ratio of the unavoidable drag figure divided by the total drag figure at a given flight condition (Bullen and McKenzie 2008b). Given that skin friction and lift induced drag are unavoidable, clean optimisations that minimise avoidable drag is shown to be functionally appropriate. Head/body and wing relative cleanliness was consistent with aspects of species foraging niche such as foraging strategy. Cleanliness of face and fineness ratio of head and body were found to be related to minimum foraging drag. Blending of the wing and body, the presence of a wing/body fillet and the texture of the pelage, and the presence of a riblet like surface, were found to be important. The aerodynamic optimisation of ears and tail membrane were found to correlate with foraging strategy. The interceptors had optimisations for minimum drag generation consistent with their higher foraging flight speed. Rather than being optimised for minimum drag, the air-superiority bats' wings, tails and ears were and were consistent with their highly agile but slower foraging flight speeds. Surface bats were characterised by the absence of optimisations for low drag. The frugivore plus the nectarivore and the carnivore studied appear to

be discrete optimisations. Figure 12 presents the species studied classified according to similarities in their cleanliness attributes.

Relevance to conservation (McKenzie *et al.* 2006, Burbidge *et al.* 2009)

Unlike other mammals, bat surveys in Western Australia have revealed little evidence for regional extirpations during the period since European settlement (Burbidge and McKenzie 1989, McKenzie *et al.* 2006). *Macroderma gigas* shows evidence of an historical contraction from the State's arid regions, and there is an unexplained gap in the range of *Nyctophilus timoriensis* that corresponds to the virtually cleared woodlands of the Avon Wheatbelt region. Elsewhere in Australia and its territories however, a number of bats are endangered.

The understanding of species flight capabilities and foraging strategies has provided a basis for understanding the effect of vegetation simplification associated with over-grazing, inappropriate fires regimes, land clearing and destruction of productive riparian sites in arid regions, on the composition of Western Australia's microbat communities. In this context, industries in the Pilbara are now more aware of the environmental needs of

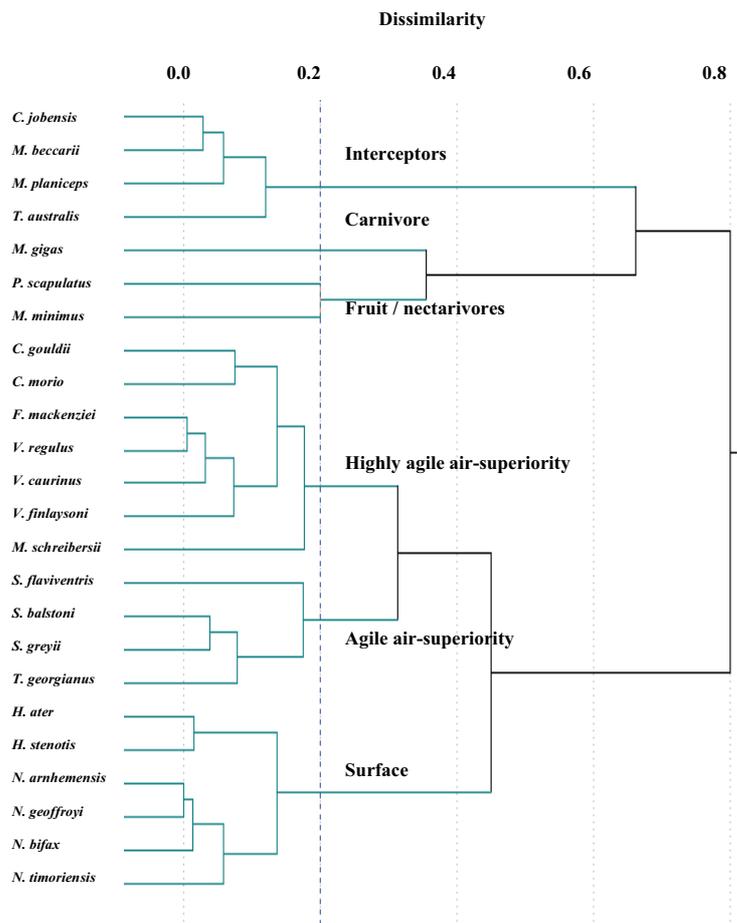
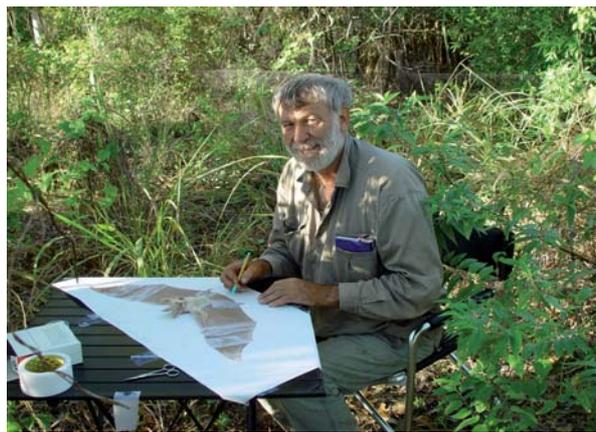


Figure 12. Species classified according to similarities in their aerodynamic cleanliness attributes. Modified from figure 8 of Bullen and McKenzie 2008b. This shows the functionally appropriate correlation of cleanliness with foraging niche.



Bob Bullen at work in the laboratory in April 2009.



Norm McKenzie at work on a Kimberley Island field study in June 2004.

potentially vulnerable species such as the cave-dependent *Rhinonictes aurantia* and *Macroderma gigas*, and the region's riparian-dependent population of *Chalinolobus morio* (McKenzie and Bullen in press). Also, as discussed earlier, our studies of *Tadarida australis* have revealed its physiological vulnerability to climate change.

Our compilation provision of robust call libraries for regional faunas across WA is providing an efficient and rapid survey and monitoring tool for assessing development applications and for documenting patterns in microbat species composition across landscapes as a basis for improving the State's network of conservation reserves.

Finally, given the predictable metabolic costs of flight and reproduction, and changes that might occur with global warming changing geographical patterns in productivity, the general bat energetic model should provide a prediction of species geographical range limits.

The Future

Regional studies on bat status, distribution, ecology and community organisation are also continuing. We are

currently carrying out a microbat study as part of a biodiversity survey of the near pristine islands along the North Kimberley coast. This tropical mesic region is facing increasing pressure for development, and has the most complex bat fauna found in Western Australia, comprising 21 microbat and 3 megabat species. Besides opportunistic mist netting and cave searches, bat echolocation sequences are being recorded at three locations on each of 19 islands, two in the dry season and one in the wet. The islands being sampled range in size from 800 to 30 000 ha and, together, provide a microcosm of landscapes found on the adjacent mainland. As part of this project, we are compiling a library of reference call sequences recorded from free-flying individuals of known identity. They were recorded by the authors at various locations across the Kimberley region during the last 20 years, along with data on their airframes and observations on their foraging ecology.

Our next step in generating a general energy model is to investigate the mechanical efficiency of microbat airframes, yet another coefficient necessary to model species flight power curves.

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