

## Bats of the southern Carnarvon Basin, Western Australia

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**Abstract** – We present the results of the first systematic survey of bats in the southern Carnarvon Basin. Two megabat and eleven microbat species were recorded. A twelfth microbat species, *Macroderma gigas*, is known from sub-fossil material. We demonstrate tight, functionally appropriate relationships between species' foraging microhabitats, flight performance indices, and echolocation call parameters. Patterns in the species composition of microbat assemblages across the study area conform with a 'temperate to tropical' climatic gradient, but are modified by variation in the structural complexity of the vegetation. Within the study area, these relationships allow the species composition of microbat assemblages to be predicted from vegetation structure and local availability of roost sites, and provide an explicit basis for assessing the reserve system from the perspective of microbats.

### INTRODUCTION

This paper reports the results of the first systematic field survey of the bats extant in the southern Carnarvon Basin (Figure 1). The lack of systematic regional bat surveys in Western Australia has precluded explicit assessments of:

- species' conservation status,
- geographic patterns in the species-composition of bat guilds, and
- resource allocation among co-occurring species.

All three are important considerations for reserve system development. The only other systematic bat surveys covering areas of Western Australia as extensive as our study area were carried out between 1977 and 1985 in the Eastern Goldfields (e.g. McKenzie and Rolfe, 1995b) and in tropical mangrove communities (McKenzie and Start, 1989).

At the outset of this study, the Western Australian Museum held 77 bat specimens from the study area. All were collected opportunistically, with virtually no ecological data. The earliest record was of *Pteropus scapulatus* (WAM2644) from Tamala Homestead (26°42'S, 113°43'E) in 1944. The single, most species-rich collection comprised three species from Kalbarri National Park in 1969–70 (*Chalinolobus gouldii*, *Vespadelus finlaysoni* and *Tadarida australis*).

The aim of our study was to provide a regional context for conserving the study area's bat fauna. Specifically to:

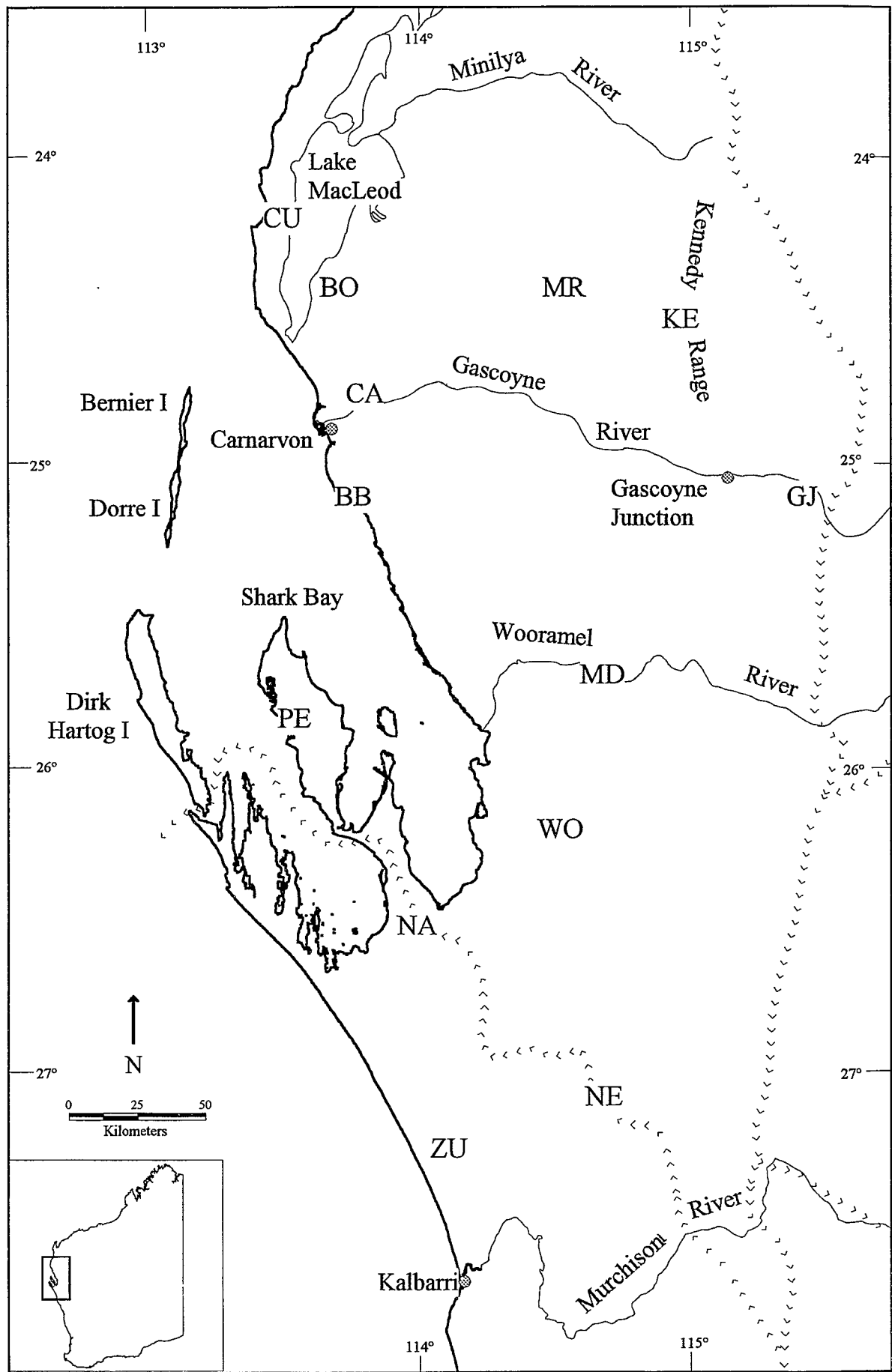
- carry out the first systematic field survey of the bats that are extant in the study area, and lodge voucher specimens in the Western Australian Museum for detailed taxonomic appraisal in the future,

- develop a dictionary of species' ultrasound calls to enhance the efficiency of our field inventory of Irwin-Carnarvon bats, and to provide a basis for more detailed population and ecological studies in the future,
- integrate our field survey data with existing historical records and with late-Holocene sub-fossil records (Baynes, 1990; Appendix 2 in McKenzie, Hall and Muir, 2000) to provide an overview of the status of bat species across the study area,
- identify attributes of the physical environment that provide predictors of gradients in species richness and composition across the study area, and of assemblage composition locally, and
- relate differences in species' foraging microhabitats (realised foraging niches) to a set of eco-morphological measures related to flight performance (potential foraging niche), and echolocation call characteristics, to provide an understanding of guild structures and resource allocation.

### METHODS

#### Study Area

The southern Carnarvon Basin covers 75 000 km<sup>2</sup> on Australia's west coast (28°00'S to 23°30'S, and 112°30'E to 115°30'E). It is centred on Shark Bay, and extends northwards from the Murchison River to the Manilya River, and eastwards to beyond Gascoyne Junction (Figure 1). Its physical environments are detailed by Wyrwoll, Courtney and Sandercock (2000) and Wyrwoll, Stoneman,



**Figure 1** The Carnarvon Basin study area. Survey Area locations are indicated: ZU, NE, NA, WO, PE, MD, BB, GL, CA, CU, MR and KE. Broken lines indicate phylogeographic boundaries.

Elliott and Sandercock (2000). The area south from Shark Bay has a semi-arid temperate climate with mainly winter rainfall. From Shark Bay northwards, the climate is influenced by both tropical and temperate systems; semi-arid at the coast, but arid with locally unreliable summer and winter rainfall further inland.

Descriptions of the vegetations in the study area are provided in Beard (1976a, 1976b) and Keighery *et al.* (2000). In the brief overview provided herein, we follow the structural terminology of Muir (1977). Low open-woodlands to tall open shrublands of *Acacia* cover the extensive alluvial plains that dominate the study area. The plains are traversed by two large ephemeral rivers lined with groves of River Gum (*Eucalyptus camaludulensis* and *E. victrix*). Low-lying saline areas of the plains support dwarf scrub communities of samphire and saltbush. Scattered across the plains are low sand hills that support open shrublands over hummock or tussock grasslands. In the north, these plains grade into dunefields with patches of Mulga low open-woodland on the interdune plains. South of Shark Bay, the plains support woodlands of eucalypts and *Callitris* over an *Acacia* sub-canopy, with areas of dense mallee, *Banksia* and *Actinostrobus* scrub. Vegetations near the coast are mainly grasslands, low shrublands or shrublands that seldom exceed two metres in height.

### Historical Review

A listing of previous bat records from the study area was compiled from a literature review and from the specimen register of the Western Australian Museum. The museum specimens, as well as the voucher specimens collected during our field survey program, were compared with published taxonomic descriptions so that the species determinations were contemporary.

Recent sub-fossil records are listed in Appendix 2 of McKenzie *et al.* (2000). We compared the sub-fossil and historical data-sets with the lists of species encountered during our field survey program to see if any post-European changes are detectable.

### Field Sampling Strategy

The southern Carnarvon Basin vertebrate survey focussed on a series of quadrats that were clustered around each of 12 campsites (Figure 1). These 12 survey areas were positioned to sample the geographic extent and main vegetations of the study area (see McKenzie *et al.*, 2000). Unfortunately, there were insufficient resources to inventory the bats on every quadrat, so we surveyed the bats present in each of the survey areas (except EL), noting the location, date, behavioural activity and microhabitat (in relation to the vegetation structure) of each record. Bat data

were also collected from the plantation and riparian areas at Carnarvon (CA).

Data were recorded during the three programmed mammal sampling sessions (October 1994, May 1995 and March 1996), and during various brief visits to survey areas for other purposes (January 1995, November 1995, March 1996, September 1996). Taxonomic voucher specimens were taken from each survey area, and have since been lodged in the Western Australian Museum collection. Nomenclature follows Strahan (1995).

Bat echolocation call sequences were recorded at each survey area as part of the vertebrate sampling program. The calls were transformed using D940 (Pettersson Elektronik, Sweden) or Anabat II (Titley Electronics, Australia) ultrasound detectors, and the transformed call frequencies (divided by 10 or 16, respectively) stored on TDK XG60 Metal IV cassette tapes using Sony Walkman Professional (WMD6C) tape recorders. Species calls were characterised in terms of five attributes using zero crossing analysis (ZCA): 'shape' (of the time-frequency sweep), ' $F_{min}$ ' (the frequency of the shallowest section of the frequency-sweep near the end of the frequency modulated call), ' $F_{max}$ ' (the highest detected frequency), 'duration', and 'TBC' (time between each call in a sequence). Only consistently shaped, regularly spaced, sequential sets of calls with a clean, well-defined, low-frequency component were included in the analysis. In general we noted that these were calls of bats in 'search' or 'approach' modes, rather than 'interception' or 'departure' modes (see Figure 3, and also Kalko and Schnitzler, 1998). A sub-set of species calls were characterised in terms of a sixth attribute using spectral analysis. The frequency of peak power in the first harmonic ( $F_{peak}$ ), was determined by digitising and analysing the search mode calls using COOL EDIT 95 (Syntrillium Software, USA); calls recorded using the Anabat II detector were normalised prior to the spectral analysis.

Search-mode echolocation calls are emitted during the wings' down-stroke in most species (Lancaster *et al.*, 1995). A search-mode call is emitted during every down-stroke, or every second or third etc, so the time between successive calls is an integer multiple ( $\times 1, \times 2 \dots \times 6$ , etc.) of wing beat frequency. However, average TBC can be meaningless because sets of two or three calls can be separated by several wing beat cycles during which no calls are emitted. Given this variation, and since Carnarvon microbat species all flap their wings at similar frequencies (9 to 13 Hz, author's unpublished data), mean TBC values are not useful for species recognition, so we have not used this attribute in subsequent analysis.

A reference library of bat call sequences was compiled during the course of the field program. It comprised calls by free-flying bats of known

identity, and was compiled from bats captured in mist nets set over pools and mill tanks, then released with bioluminescent tags (Cyalume), and bats that we collected, using a spotlight and shotgun, while their echolocation calls were being tape-recorded. The library included the call sequences of species known from the surrounding regions.

Canonical Discriminant Analysis (STATGRAPHICS, 1991) was used to test whether all of the microbat species could be separated in terms of the five ultrasound attributes measured using the zero crossing analysis. In this analysis, the average ultrasound attributes of each call sequence in the reference library were used as the data points, and their species identity was the classification variable. The results were compared with separations based on the peak frequency attribute derived from spectral analysis of the calls.

The bat echolocation sequences recorded during our nighttime traverses of survey areas were identified using the discriminant scatterplot derived from the analysis of the reference library.

#### Analysis of Biogeographic Patterns

The analysis package PATN (Belbin, 1995) was used to seek patterns in bat species composition across the study area. The assemblages of microbats recorded from the 13 survey areas were used as the input data. We analysed the presence and absence of species at the survey areas, rather than their relative abundance, because limitations in sampling techniques, aggravated by staff and time limitations, precluded reliable abundance estimates (Austin, 1984; McKenzie *et al.*, 1991a). The clustering techniques selected were described in McKenzie *et al.* (1991b). Briefly, the survey areas were classified according to similarities in their species composition using the Czekanowski (1932) similarity algorithm, and the species were classified according to their co-occurrence at the same survey areas using the association measure 'Two-step' (Austin and Belbin, 1982). For both measures of association, a modified version of UPGMA (Sneath and Sokal, 1973; Belbin, 1995) hierarchical clustering strategy was used to re-order the data matrix.

The biological patterns revealed by these analyses were interpreted in terms of the location and environments of the survey areas, and the known habitat preferences of the species throughout their ranges elsewhere in Australia. For this purpose, a set of climatic attributes were derived for each survey area using ANUCLIM (McMahon *et al.*, 1995). Also, a vegetation complexity measure was derived for each survey area. It was based on the number of vegetations or vegetation strata represented: shrublands or grasslands to 1 metre high; shrublands to 2 metres; tall shrublands or low woodlands to 4 metres; woodlands or mallees to 7

metres; woodlands 7 to 15+ metres high. Thus, a value of 2 indicates the presence of the first two strata, either as vegetation patches or as different strata in the same vegetation; a value of 4 indicates either the presence of the first four of the vegetations listed above, or of some combination of the first four as vegetation patches and/or strata.

#### Analysis of Ecological Patterns

The relationship between flight morphology and resource partitioning, and its role in structuring microbat assemblages has been established previously (McKenzie and Rolfe, 1986; Aldridge and Rautenbach, 1987; McKenzie and Start, 1989; Fenton, 1990; Findley, 1993). Data on flight morphology and foraging ecology were needed to quantify this relationship for the study area's microbats, and to assess its effect on the species composition and richness of their assemblages (given that structurally complex vegetations offer a wider array of foraging niches for bats than do open vegetations with few strata).

Wing span, wing area and body weight measurements were taken from a sample of live, non-pregnant adults belonging to each microbat species that we captured during the field program. These measures allowed us to calculate three flight performance parameters: aspect ratio, wing loading and tip shape. The measurement protocols and references for relevant formulae are provided in McKenzie *et al.* (1995a).

Microbat records were assigned to one of three foraging strategies depending on differences in the degree of air-space clutter at the point the free-flying bat was observed, and on whether they were observed to pursue flying prey or glean surfaces (McKenzie *et al.*, 1995a). Their position in terms of the vegetation strata (cf McKenzie and Rolfe, 1986) allowed the second behavioural category to be subdivided on the basis of observed differences in microhabitat-use: AC and BS/O (defined below). Relatively few bats were actually captured, so microhabitat observations were stored on the same tape as the ultrasound recordings that were used to determine the species' identities. The three strategies, and four foraging microhabitats, were defined as follows:

- clutter foragers that glean prey from surfaces such as the ground, bark and foliage, or take airborne prey in the cluttered airspace inside stands of vegetation (IS) or by 'contouring' within a metre of foliage, bark, ground or surface of pools (NS/A). In the open vegetations of the Southern Carnarvon Basin, the differences between IS and NS/A foraging microhabitats of McKenzie and Rolfe (1986) could not be discriminated,
- mainly aerial foragers for flying insects in the partially cluttered to semi-open air spaces within

- a few metres (>1, but <4 m) of the sides and underside (BS/O), or top (AC) of the canopy, and
- species that intercept or hawk insects in the unobstructed air-spaces found well above the canopy, and well above the ground in large clearings (OC).

The proportion of observations in each microhabitat was used as a measure of each species preferred foraging habitat.

Rank Correlation Analysis (Kendall's tau) (STATGRAPHICS, 1991) was used to test for significant relationships between:

- average flight indices, echolocation call attributes and foraging microhabitats; thus, the study area's microbat species were distinguished in terms of their foraging niche, and
- the vegetational complexity (number of vegetational strata present) in a survey area, and the species richness of its microbat assemblage.

RESULTS

Historical Review

The Western Australian Museum's specimen register lists eight microbat species from the study area (Table 1), although the *Scotorepens balstoni* specimen (WAM15192) that was listed in Kitchener and Caputi (1985) is actually *S. greyii*.

One *Taphozous* voucher specimen is listed (*Taphozous georgianus*, WAM34469, skeletal, Kennedy Range), but could not be found (N. Cooper, personal communication). The Kennedy Range is 60 km south-east of the southern-most record of *T. georgianus*, and about 100 km west of the known range of its allopatric congeneric, *T. hilli*. We made several specific searches for this genus during the course of the field sampling program, both by exploring crevices and caves in the daytime, and by traversing different sections of the Kennedy Range at night using spotlights in conjunction with ultrasound detection equipment. These searches were carried out during October 1994, January 1995, May 1995, November 1995, March 1996 and September 1996, and covered sites at various points on top, and along the western and eastern faces, of the range. Recognisable *Taphozous georgianus* ultrasound call sequences were recorded in the KE survey area (see below), but they were rare compared to other species, and we were unable to capture a specimen or locate caves with the height and depth typical of *Taphozous* roosts elsewhere.

The Western Australian Museum holds specimens of *Pteropus alecto* from Carnarvon, and of *P. scapulatus* from Tamala Homestead and Kalbarri (Table 1). The earliest of these flying-fox specimens was registered in 1944. Most *Pteropus* sightings are from homestead gardens (e.g. at Mardathuna and

Table 1 Bat species known from the Southern Carnarvon Basin prior to our field survey program. We have included the registration numbers and localities of selected voucher specimens.

Species	WA Museum specimen	Locality
<i>Tadarida australis</i>	WAM23448	Carnarvon 24°53'S 113°40'E
	WAM15164	Peron 25°48'S 113°33'E
<i>Taphozous georgianus</i>	WAM34469	Kennedy Range 24°40'S 115°10'E
<i>Chalinolobus gouldii</i>	WAM15482	Woodleigh 26°15'S 114°37'E
<i>Scotorepens greyii</i>	WAM15192	Carnarvon 24°53'S 113°40'E
<i>Vespadelus finlaysoni</i>	WAM11915	Dirk Hartog 25°43'S 113°03'E
	WAM11916	Bernier 24°52'S 113°08'E
	WAM 16320	25°44'S 112°59'E
	WAM7886	Mary Spring 27°42'S 114°27'E
<i>Nyctophilus geoffroyi</i>	WAM10015	Peron 25°48'S 113°33'E
	WAM36795	Monkey Mia 25°48'S 113°43'E
	WAM28183	Binthalya 24°41'S 114°50'E
	WAM18468	Woodleigh 26°11'S 114°33'E
<i>Pteropus alecto</i>	WAM15397, 15866-8	Carnarvon 24°53'S 113°40'E
<i>Pteropus scapulatus</i>	WAM23845	Kalbarri 27°42'S 114°12'E
	WAM2644	Tamala 26°50'S 113°23'E
Adjacent Areas		
<i>Chaerephon jobensis</i>	WAM21023	25°42'S 115°59'E
	WAM7482	22°50'S 114°57'E
<i>Mormopterus beccarii</i>	WAM21018	25°42'S 115°59'E
<i>Taphozous georgianus</i>	WAM4338	23°24'S 116°10'E
	WAM21040	22°16'S 113°46'E
<i>Taphozous hilli</i>	WAM13728	28°06'S 115°38'E
<i>Scotorepens greyi</i>	WAM21081	25°42'S 115°59'E
	WAM19701	22°47'S 114°58'E
<i>Macroderma gigas</i>	WAM36687	23°01'S 115°48'E

Tamala), from locations on the coast (e.g. Kalbarri) or along the Gascoyne River (particularly near Gascoyne Junction and Carnarvon), or from valleys along the western face of the Kennedy Range. These latter sites all have extensive stands of River Gum, that would provide a rich if intermittent source of pollen and nectar. Flying foxes were reported in Carnarvon as recently as October 1996, but not in numbers sufficient to cause damage to fruit crops (M. Mahoney, pers. comm.).

*Macroderma gigas* is the only sub-fossil species identified from the study area that is not known from modern collections. The *M. gigas* records are based on bone material from single individuals found in an exposed coastal deposit at 27°50'10"S 114°06'28"E, 10 km south of Kalbarri, and at three locations at Useless Loop in Shark Bay (26°10'S 113°25'E). Bone from the first deposit was less than 1000 years old, while the other deposits were Late Holocene (Martin, unpubl. Ph.D. Thesis, University of Western Australia; Appendix 2 in McKenzie *et al.*, 2000).

### Echolocation Attributes

Table 2 provides summary statistics for the call sequences comprising the reference library. Discriminant analysis of these sequences showed that most of the bat species are distinct in terms of the echolocation attributes determined by zero crossing analysis. The first discriminant function [ $F_n(1) = 1.07F_{\min} + 0.14F_{\max} + 0.35Dur$ ] had a canonical correlation coefficient of 0.99 and accounted for 97.9% of the observed variance in the echolocation data ( $P < 0.00001$ ). The second function [ $F_n(2) = -0.40F_{\min} + 0.75F_{\max} - 0.61Dur$ ] had a canonical correlation coefficient of 0.72 and accounted for 1.63% of the remaining variation, and was also significant ( $P < 0.00001$ ). The coefficients in these functions have been standardised; they reveal the relative contributions of the echolocation

attributes in separating the 11 species. Minimum call frequency ( $F_{\min}$ ) accounted for most of the between-species variation. It was tightly inter-correlated with  $F_{\text{peak}}$  ( $R^2 = 99.7\%$ ,  $p < 0.0001$ ), so  $F_{\text{peak}}$  was not used in the discriminant analysis.

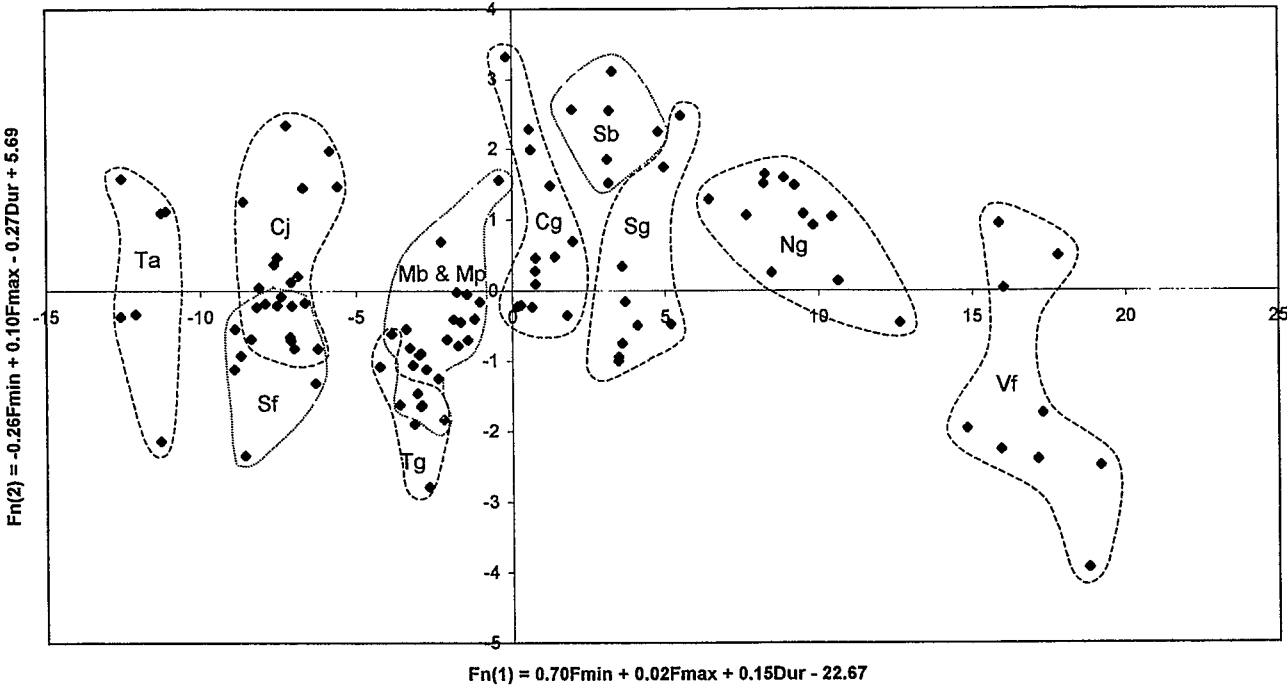
So that the unknown sequences could be identified from their echolocation attributes, unstandardised coefficients were used to generate the discriminant scatterplot (Figure 2). Although *Mormopterus beccarii* was not separable from *M. planiceps*, these congeners are allopatric. The other three overlaps (*Taphozous georgianus* with *Mormopterus* spp., *Scotorepens balstoni* with *S. greyi*, and *Saccolaimus flaviventris* with *Chaerephon jobensis*) were a result of similarities between the search-mode call sequences of one species and the approach-mode call sequences of another. In general, we noted that search-mode calls had a narrow frequency range and a prolonged low frequency component, whereas approach-mode calls began at higher frequencies and had an increased repetition rate (Figure 3). Attenuated recordings of bats in approach-mode (i.e. those by bats flying away or distant from the microphone) also resembled search-mode calls, thereby increasing the observed variance in the data. Because of such problems we could not accurately identify 55% of the 701 apparently well defined ultrasound recordings made during the survey.

### Extant Fauna

Table 3 lists the extant fauna of the southern Carnarvon Basin, as determined from our field sampling program. In combination with the historical records, our results indicate that the study area's post-European bat fauna comprises 13 species (2 megabats and 11 microbats), and that they are all still extant. Most of the microbat species are widespread in the study area, although *Scotorepens* and *Mormopterus* are each represented

**Table 2** Free-flight echolocation call attributes of species comprising the Southern Carnarvon Basin's microbat fauna (mean, standard error, maximum, minimum). Attributes are defined in 'Methods'. 'Seq' = number of call sequences. Because only two sequences from each species were analysed for  $F_{\text{peak}}$ , we list the range of values (rather than the average) and the number of calls analysed (n).

Species	Seq	$F_{\min}$	SE (Min-Max)	$F_{\max}$	SE (Min-Max)	Dur	SE (Min-Max)	$F_{\text{peak}}$ range	(n)
<i>Tadarida australis</i>	6	11.4	0.4 (10.5–13.0)	18.1	2.8 (11.0–30.0)	16.1	1.9 (11.0–24.1)	11.5–14.0	(15)
<i>Saccolaimus flaviventris</i>	11	17.6	0.5 (15.0–19.0)	20.8	0.9 (16.0–24.5)	14.7	0.8 (11.4–21.1)	16.9–20.1	(35)
<i>Chaerephon jobensis</i>	15	18.6	0.4 (16.5–22.0)	28.0	1.4 (20.0–40.0)	11.8	0.8 (6.6–15.1)	18.4–23.1	(20)
<i>Taphozous georgianus</i>	6	23.8	0.2 (23.0–24.5)	24.9	0.4 (24.0–26.5)	13.3	1.1 (9.5–17.3)	23.0–27.5	(11)
<i>Mormopterus beccarii</i>	15	25.9	0.4 (24.5–29.0)	32.2	1.7 (26.0–50.0)	10.1	0.4 (6.1–13.2)	24.5–26.7	(21)
<i>Mormopterus planiceps</i>	6	26.2	0.4 (25.0–27.5)	33.0	2.3 (27.0–40.0)	11.1	0.6 (9.8–13.3)	27.1–28.4	(15)
<i>Chalinolobus gouldii</i>	13	30.5	0.3 (29.0–32.0)	50.1	2.7 (39.0–66.0)	7.6	0.4 (5.6–10.5)	30.7–34.1	(27)
<i>Scotorepens balstoni</i>	6	34.3	0.5 (32.5–36.5)	65.8	2.4 (57.0–74.0)	4.2	0.2 (3.5–4.9)	34.1–38.7	(7)
<i>Scotorepens greyi</i>	9	35.6	0.5 (34.0–37.5)	51.6	3.4 (43.0–73.0)	5.8	0.7 (3.0–9.2)	35.1–38.9	(22)
<i>Nyctophilus geoffroyi</i>	12	42.5	0.7 (38.5–47.5)	73.9	1.1 (66.5–78.0)	4.3	0.3 (2.8–5.8)	40.1–49.4	(22)
<i>Vespadelus finlaysoni</i>	9	53.4	0.7 (51.0–56.5)	78.3	4.6 (64.0–99.0)	4.5	0.3 (3.2–6.0)	51.5–58.2	(14)



**Figure 2** Microbat call sequences from the Carnarvon Basin study area, arrayed according to the linear discriminant functions. The dotted lines are superimposed to indicate species boundaries.

by two allopatric species. In Table 4, the extant records have been compiled as lists for each survey area. *Tadarida australis* appears to be rare in the study area during spring and summer (Table 5).

**Analysis of Biogeographical Patterns**

The results of the numerical classifications are presented as a re-ordered data matrix in Table 6. These analyses revealed a gradient in the composition of the microbat assemblages across the study area that could be explained in terms of climatic patterns. The survey areas in Group-1 have higher rainfall in the coldest quarter (winter, June to August) than the survey areas in Group-2, and similar differences were found when other climatic attributes that distinguish temperate from tropical weather patterns were analysed (Table 7). The

species groups conform to the same climatic gradient. The species comprising Assemblage-A range across tropical Australia, Assemblage-C species have temperate distributions, while the species comprising Assemblage-B are ubiquitous in arid tropical and temperate regions of Australia (Strahan, 1995).

**Analysis of Ecological Patterns**

Tables 2, 8 and 9 provide data on the echolocation characteristics, flight performance and observed microhabitat-use of Irwin-Carnarvon bat species. Table 10 reveals the strong, significant correlations between these three aspects of the ecology of Irwin-Carnarvon microbats. Microbats that foraged in more cluttered air-spaces had higher frequency echolocation calls and tip index, but lower call

**Table 3** Bats recorded from survey areas in the southern Carnarvon Basin during the field sampling program (except *Pteropus scapulatus*). Records from outside of the quadrats are listed in brackets.

<i>Saccolaimus flaviventris</i>	BO4; (CA); GJ1; KE3,5; MD3; MR2; WO3.
<i>Taphozous georgianus</i>	(KE)
<i>Tadarida australis</i>	BB2,5; BO5; (CA); GJ1,3,4; KE1-3,5; MD3; (MR); NA3; NE3-5; (PE); WO3-5; ZU3.
<i>Chaerephon jobensis</i>	(BO); (CA); GJ1; KE1,3,5; MD3; MR1,2,5.
<i>Mormopterus beccarii</i>	(CA); GJ1,3; KE5; MD3; MR5; (WO).
<i>Mormopterus planiceps</i>	NA2,4; NE4; ZU2,5.
<i>Chalinolobus gouldii</i>	(BB); BO4; (CA); CU3,4; GJ1-3; KE1-3,5; MD3; MR2; NA2,4; NE1,3-5; (WO); ZU3,5.
<i>Scotorepens balstoni</i>	NE1,3.
<i>Scotorepens greyii</i>	(BB); (CA); GJ1-4; KE1,2,3; MD3; MR1,2,5.
<i>Vespadelus finlaysoni</i>	CU2,3,4; GJ1; KE3; NE1,3-5; ZU3.
<i>Nyctophilus geoffroyi</i>	BB2; BO4; (CA); CU3; GJ1,2; KE3,5; MD3; MR2; (NA); NE3; PE4; (WO); ZU5.
<i>Pteropus scapulatus</i>	(Kalbarri)
<i>Pteropus alecto</i>	(CA); (KE); (GJ).

**Table 4** Microbat records from the southern Carnarvon Basin, listed by survey area and method (x = echolocation sequence, v = voucher specimen).

Species	ZU	NE	NA	PE	WO	MD	BB	CA <sup>1</sup>	BO	CU	GJ	MR	KE
<i>Saccolaimus flaviventris</i>					x	v		x	x		x	x	v
<i>Taphozous georgianus</i>													v
<i>Tadarida australis</i>	x	x	v	v	v	x	x	v	x		x	x	v
<i>Chaerephon jobensis</i>						v		x	v		v	v	v
<i>Mormopterus beccarii</i>					x	x		x			v	x	v
<i>Mormopterus planiceps</i>	x	x	x										
<i>Chalinolobus gouldii</i>	x	v	v		v	v	x	x	x	x	v	v	v
<i>Scotorepens balstoni</i>		v											
<i>Scotorepens greyii</i>						x	x	v			v	v	v
<i>Vespadelus finlaysoni</i>	x	v								v	v		v
<i>Nyctophilus geoffroyi</i>	x	v	x	v	v	x	x	x	v	x	x	v	x
Richness	5	6	4	2	5	7	4	7	5	3	8	7	9
Veg <sup>2</sup>	4	5	4	2	3	5	3	5	3	2	5	4	5

<sup>1</sup> CA = banks and bed of Gascoyne River at Carnarvon  
<sup>2</sup> Veg = vegetational complexity in survey area (see Methods).

durations, aspect ratios and wing loadings, than did the bats of more open microhabitats. These relationships are the result of ecological processes, rather than mere artifacts of phylogeny, because they are functionally appropriate (McKenzie *et al.*, 1995a). For instance, high frequency echolocation provides detailed imagery at the expense of range, so it needs to be frequently refreshed. It is appropriate to cluttered airspaces, in which manoeuvrability (high tip index and low wing loading) is required, rather than speed and low drag coefficients (high wing loading and aspect ratio) (Norberg and Rayner, 1987).

The strong, functionally appropriate relationships between species' microhabitat use, flight capability and echolocation attributes is consistent with previous studies (see Discussion). It may be a sufficiently pervasive theme in microbat ecology to provide a basis for understanding the structure of their assemblages, and for predicting their compositional components in terms of:

1. the pool of potential colonisers available in a region (the faunal composition),
2. the structural complexity of the vegetation at a study site,
3. the presence of roosts suitable for obligate cave

**Table 5** Microbat records from each survey area by season. Note that sampling methods and effort were very different, both between survey areas and between visits. In each matrix cell, a comma is used to separate the autumn and winter records from the spring and summer records.

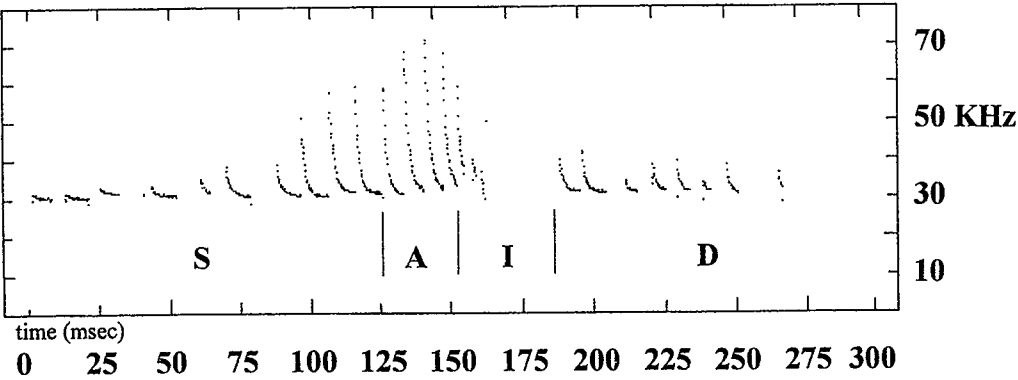
Autumn:	March 1996 (a) and April 1994 (b).
Winter:	May 1995 (c), June 1993 (d).
Spring:	October 1994 (e), November 1995 (f), September 1996 (g), October 1996(h).
Summer:	January 1995 (i).
Not sampled:	(-).

Species	ZU	NE	NA	PE	WO	MD	BB	CA <sup>1</sup>	BO	CU	GJ	MR	KE
<i>Saccolaimus flaviventris</i>					f	c,e	-	d,-	a,-		ef	?e	ac,efgi
<i>Taphozous georgianus</i>							-	-	-				a,
<i>Tadarida australis</i>	c,	c,	ba <sup>2</sup> c,	*	c,h	c,	c,-	c,-	c,-		c,e	c,	c,
<i>Chaerephon jobensis</i>						c,	-	ad,-	a,-		ef	b,e	ac,efgi
<i>Mormopterus beccarii</i>					f	c,ef	-	d,-	-		c,f	b,	a,f
<i>Mormopterus planiceps</i>	c,	c,ef	f				-	-	-				
<i>Chalinolobus gouldii</i>	ac,ei	ac,ef	ba,f		c,ef	c,ef	c,-	ad,-	a,-	a,	c,efi	e	ac,ef
<i>Scotorepens balstoni</i>		ac,ef					-	-	-				
<i>Scotorepens greyii</i>						c,ef	c,-	ad,-	-		c,efi	c,e	ac,e
<i>Vespadelus finlaysoni</i>	c,ei	ac,ef					-	-	-	ba,e	c,ef		ac,e
<i>Nyctophilus geoffroyi</i>	c,	a,f	a,	a,efi	ac,efi	c,	c,-	ad,-	a,-	b,	c,e	e	ef

<sup>1</sup> CA = Carnarvon (Figure 1).  
<sup>2</sup> Emaciated sub-adult found on the ground in the Nanga Caravan Park in March 1996.  
\* Found dead in a building at Monkey Mia in February 1995.



True time (calls expanded x 10)



Gaps between calls deleted, calls magnified

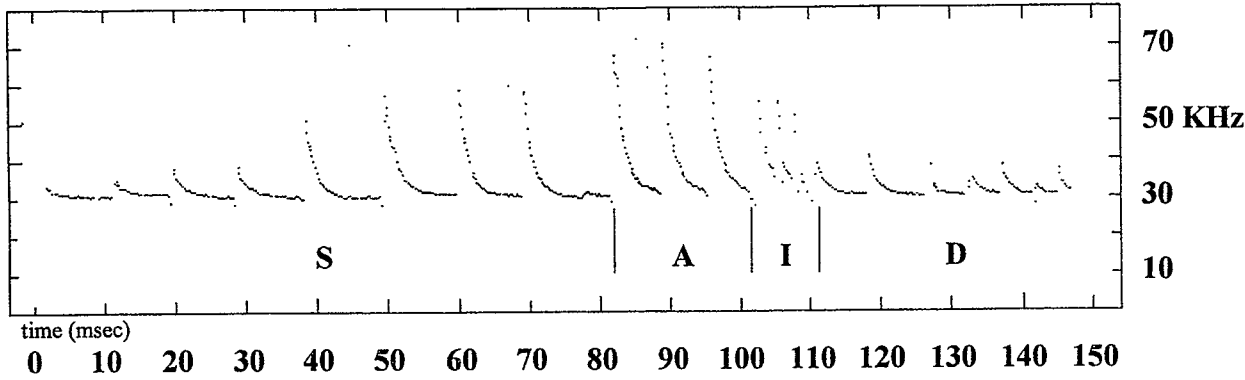


Figure 3 Complete echolocation call sequence for *Chalinolobus gouldii*, illustrating search (S), approach (A), interception (I) and departure (D) modes (quadrat GJ1, 13 November 1995, specimen number FM48036).

Table 6 Microbat data-matrix re-ordered according to UPGMA. The survey areas were classified according to similarities in their species composition; and species were re-ordered according to their co-occurrences. Note that survey area codes are typed vertically.

	Group									
	1					2				
Assemblage	Z	N	N	C	P	B	W	B	M	C
	U	E	A	U	E	B	O	O	D	A
A	S	a	c	c	o	l	a	i	m	u
	l	a	i	m	u	s	f	l	a	v
	h	a	e	r	e	p	h	o	n	j
	m	o	r	m	o	p	t	e	r	u
	s	b	e	c	c	a	r	i	i	
	s	c	o	t	o	r	e	p	e	n
	s	g	r	e	y	i				
	t	a	p	h	o	z	o	u	s	
	g	e	o	r	g	i	a	n	u	s
B	T	a	d	a	r	i	d	a	a	u
	c	h	a	l	i	n	o	l	o	b
	n	y	c	t	o	p	h	i	l	u
	s	c	o	t	o	r	e	p	e	n
	s	g	e	o	f	f	r	o	y	i
	v	e	s	p	a	d	a	l	u	s
	f	i	n	l	a	y	s	o	n	i
C	M	o	r	m	o	p	t	e	r	u
	s	p	e	c	i	p	e	s		
	s	c	o	t	o	r	e	p	e	n
	b	a	l	s	t	o	n	i		

dwellers such as *Taphozous georgianus* and tropical populations of *Vespadalus finlaysoni*.

To test this proposition for the southern Carnarvon Basin, we investigated the microbat species richness ( $R_s$ ) of the survey areas in terms of their vegetation complexity ('Veg' from Table 4) and then considered the actual species composition of these assemblages in terms of species' microhabitat-use (from Table 9). We found that complex southern Carnarvon Basin vegetations (with a variety of foraging spaces to partition) supported the richest microbat assemblages:

$R_s = 0.19Veg^{1.1}$ ,  $R^2 = 79\%$ ,  $p = 0.0001$   
Kendall's Tau = 0.76,  $p = 0.001$   
 $n = 13$

When assemblage composition was considered in terms of species' microhabitat-use, we noted that survey areas with open, low vegetations comprising few strata were relatively poor in the sorts of bat species that favour AC, BS/O and NS/A-IS microhabitats — *Mormopterus* spp. and *Scotorepens* spp. were absent, although *Chalinolobus gouldii* and *Nyctophilus geoffroyi* remained. Thus, the species composition of survey areas was predictable.

**Table 7** Climatic differences between the two groups of survey areas that were distinguished in terms of their microbat species composition (from Table 6). Mean (s.d.) Minimum–Maximum value.

Attribute	Group-1 (n=6)	Group-2 (n=7)	Kruskall-Wallis H	Probability
Temperature (warmest quarter) °C	28(0.4)27–29	29(0.9)28–31	7.4	0.007
Precipitation (coldest quarter) mm	136(27)109–191	87(12)70–104	9.0	0.003

### DISCUSSION

Available data indicate that the study area's extant fauna comprises 13 species, 2 megabats and 11 microbats. Most species are widespread throughout the study area, although congeners are allopatric (*Scotorepens greyii* with *S. balstoni*; *Mormopterus beccarii* with *M. planiceps*), and *Taphozous georgianus* records are restricted to the Kennedy Range (KE), the only part of the study area with substantial escarpments and gorges. *Tadarida australis*, *Saccolaimus flaviventris* and the two flying foxes are rare or absent in some seasons. Our survey substantially increased the known geographical ranges of *Saccolaimus flaviventris*, *Chaerephon jobensis*, *Mormopterus beccarii*, *M. planiceps* and *Scotorepens balstoni*, although the *M. planiceps* records are based solely on ultrasound recordings.

The extent of the inter-species overlaps in Figure 2 would have been reduced if we had been able to distinguishing between each species 'search', 'approach' and 'departure' mode echolocation calls with more certainty. This problem thwarted the identification of nearly half of the sequences recorded during the field survey program. If data on the bats' orientation and range had been noted for more of the call sequences, we would have been able to decide whether the absence of high frequency components was an artifact of attenuation or indicated search mode calls. We might also have been able to identify sequences affected by Doppler shift.

The study area straddles the boundary between

the Eremaean and South-west Botanical Provinces (Beard, 1980). Since these provinces have somewhat different bat faunas, the study area was expected to include biogeographical gradients in bat assemblage composition. Analysis of the compositional pattern in Table 6 revealed a tropical-to-temperate biogeographic boundary for bats that approximately corresponds to the phytogeographic boundary (Beard, 1980). From WO northwards the microbat assemblages include a component of tropical species such as *Saccolaimus flaviventris*, *Chaerephon jobensis*, *Mormopterus beccarii* and *Scotorepens greyi*, whereas those to the south include temperate species (*Scotorepens balstoni* and *Mormopterus planiceps*). Species such as *Tadarida australis*, *Chalinolobus gouldii* and *Nyctophilus geoffroyi* are ubiquitous.

Finer-scale patterns in assemblage composition and richness are apparent in Table 6. These can be explained in terms of ecological processes related to resource partitioning. For volant animals like bats, woodland patches offer a greater array of different foraging niches than grasslands because nuances of wing shape have a substantial effect on flight performance and, in combination with echolocation characteristics, on foraging strategy (Fenton, 1990; McKenzie and Rolfe, 1986; Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; McKenzie *et al.*, 1995a). Thus we expected that the structure of the assemblage present in each survey area would depend on the availability of suitable foraging microhabitats and on the differences in

**Table 8** Average aspect ratio (AR), wing loading (WL g cm<sup>-1</sup>) and tip shape (TI) estimates for the microbat species recorded in the southern Carnarvon Basin (se = standard error, N = number of specimens measured).

Species	N	AR	seAR	WL	seWL	TI	seTI
<i>Tadarida australis</i>	4	8.33	0.03	0.141	0.006	0.95	0.02
<i>Saccolaimus flaviventris</i>	3	8.28	0.05	0.129	0.003	0.96	0.04
<i>Chaerephon jobensis</i>	7	8.24	0.09	0.132	0.003	0.99	0.01
<i>Taphozous georgianus</i> *	15*	7.64	0.05	0.101	0.002	0.83	0.01
<i>Mormopterus beccarii</i>	1	7.49		0.125		0.94	
<i>Mormopterus planiceps</i> *	3*	7.47	0.20	0.085	0.001	1.03	0.01
<i>Chalinolobus gouldii</i>	6	6.73	0.07	0.075	0.004	0.96	0.04
<i>Scotorepens balstoni</i>	1	6.28		0.066		1.05	
<i>Scotorepens greyii</i>	3	6.24	0.07	0.065	0.001	1.14	0.06
<i>Nyctophilus geoffroyi</i>	9	5.74	0.05	0.054	0.002	1.15	0.03
<i>Vespadalus finlaysoni</i>	3	6.11	0.10	0.053	0.002	1.23	0.06

\* *Taphozous georgianus* from Karijini (22°20'S 118°30'E), *Mormopterus planiceps* from Goongarrie (30°01'S 121°04'E).

**Table 9** Numbers of bats recorded in each foraging microhabitat. Microhabitats were defined in terms of their obstruction to straight-ahead flight (see Methods for definitions).

	OC	AC	BS/O	NS/A-IS	Clutter <sup>1</sup>
<i>Saccolaimus flaviventris</i>	29	1	1	0	1.1
<i>Taphozous georgianus</i>	3	0	0	0	1.0
<i>Tadarida australis</i>	38	1	0	0	1.0
<i>Chaerephon jobensis</i>	37	3	0	0	1.1
<i>Mormopterus beccarii</i>	11	10	6	0	1.8
<i>Mormopterus planiceps</i>	1	3	0	0	1.8
<i>Chalinolobus gouldii</i>	4	18	30	2	2.6
<i>Scotorepens balstoni</i>	0	0	3	0	3.0
<i>Scotorepens greyii</i>	1	2	27	0	2.9
<i>Vespudalus finlaysoni</i>	1	1	12	11	3.3
<i>Nyctophilus geoffroyi</i>	0	1	3	28	3.8

<sup>1</sup> Each microhabitat was assigned an arbitrary clutter value from 1 (OC) to 4 (NS/IS). Thus the average clutter value of *Saccolaimus flaviventris* = (29x1 + 1x2 + 1x3 + 0x4)/(29 + 1 + 1 + 0) = 1.1

species' flight capabilities and echolocation characteristics. This view was consistent with the strong positive correlation we observed between the vegetational complexity and microbat assemblage richness of survey areas, and the tight, functionally appropriate, relationship between species' flight/echolocation capabilities and their observed microhabitat-use (Table 10). The actual species membership of each assemblage depended on the pool of potential colonising species that was available in the surrounding fauna to supply the appropriate array of ecomorphological types, and

**Table 10** Correlations between the echolocation call parameters, flight performance indices and foraging microhabitats of Carnarvon Basin microbats. Kendall's tau and probability values are listed. Echolocation call minimum frequency ( $F_{min}$ ), maximum frequency ( $F_{max}$ ) and duration (DUR) are defined in Methods. AR = aspect ratio, WL = wing loading, TI = wingtip shape and Clut = clutter (from Table 9).

$F_{max}$	.93					
	.0001					
Dur	-.78	-.85				
	.0008	.0003				
AR	-.96	-.89	.82			
	.0000	.0001	.001			
WL	-.93	-.85	.71	.89		
	.0001	.0003	.002	.0001		
TI	.70	.70	-.55	-.62	-.59	
	.003	.003	.019	.008	.013	
Clut	.75	.82	-.82	-.78	-.75	.62
	.001	.001	.001	.001	.001	.008
	$F_{min}$	$F_{max}$	Dur	AR	WL	TI

on the availability of suitable roosts for certain obligate cave-dwellers.

Since these ecomorphological and vegetational relationships allow us to predict the composition of microbat assemblages across both biogeographical regions of the study area, they provide an explicit basis for designing a system of reserves that encompasses a representative selection of the study area's microbat assemblages. For instance, reserves centred on KE, NE and CA survey areas would satisfy reserve system comprehensiveness and representativeness criteria for bats at the species level.

A comparison of sub-fossil, historical and contemporary bat records revealed no evidence of the range contractions and extinctions that are overt among indigenous non-volant mammals (see McKenzie *et al.*, 2000). *Macroderma gigas* (as sub-fossil records) is the only species known from the study area that we did not record extant during our field survey. The scattered sub-fossil records of single individuals in Late Holocene deposits suggests that vagrant *Macroderma gigas* venture into the study area from time to time, but there is no reason to suppose that the species is resident; suitable roosting/breeding caves are unknown, and the closest post-European records are from Barlee Range (23°30'S 116°00'E, 1995), 50 km north-east of the study area's northern boundary, where it is still extant.

Perhaps bats have persisted because they are less exposed (than non-volant mammals) to the following extinction mechanisms (*sensu* Smith and Quin, 1996):

1. they are rarely caught by introduced predators and, as frugivores and insectivores, they encounter little or no direct competition from the introduced herbivores and granivores (rabbits, cattle, sheep, goats, camels and *Mus musculus*) that are now ubiquitous in the region, and
2. the energetic efficiency of foraging by flight rather than on foot (Calder, 1984) should have mitigated the impact of the reduced environmental productivity (Burbidge and McKenzie, 1989), as well as any effect of direct competition from the facultative insectivores that have been introduced (mice, cats and foxes).

Nevertheless, bat population densities are likely to have declined throughout the region in response to the widespread disturbance of soil A-horizons, and the decline in the architectural complexity and biomass of most vegetations, that has occurred since European settlement (Beard, 1976b; Payne *et al.*, 1987; Wyrwoll, Stoneman, Elliott and Sandercock, 2000).

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