

Echolocation Ecology and Flight Morphology of Insectivorous Bats (Chiroptera) in South-western Australia

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Abstract

A small community of obligate insectivorous microchiropterans in the Perup forest reserve of south-western Australia was sampled to determine species flight morphologies, diets and echolocation call designs. The aspect ratio: wing loading relationships of the seven species analysed indicate a loose clustering of species into closed, edge and open microhabitats with substantial interspecific overlap. Non-parametric correlations of the bats' aspect ratios and wing loadings with their echolocation call characteristics support these foraging zone classifications. Diet analyses indicate that this community of bats forages on a wide variety of insects, although certain preferences for Lepidoptera, Hymenoptera and Coleoptera were noted. We use these results and observations of the same species from other sites to propose a microhabitat separation for the bats of the Perup forest.

Introduction

Recent evidence suggests that microchiropteran, insectivorous bats partition their environment into microhabitats by means of their flight morphologies (Fenton 1972; Findley 1976; McKenzie and Rolfe 1986; Norberg 1987; Crome and Richards 1988), diets (McNab 1971; Black 1972; Freeman 1979; O'Neill and Taylor 1989), and echolocation designs (Neuweiler 1984; Barclay 1988). There appears to be substantial correlation amongst these variables (Neuweiler 1984; Aldridge and Rautenbach 1987; Norberg and Rayner 1987; Barclay 1988), although there is debate regarding how well such statistical relationships accurately define the foraging niches of bats (Fenton 1990). If reliable correlations do exist for these variables in different bats from around the world, it may be possible to use such correlations to predict microhabitat usage in unstudied communities of bats.

We studied a small community of insectivorous bats in the Perup forest reserve of south-western Australia to seek correlations amongst flight morphologies and echolocation variables. We compare these correlations with those described from studies of more complex bat communities in other parts of the world, and use our results to predict the microhabitat use of the bats of the Perup forest.

Materials and Methods

Our study was carried out from January to March 1988 at the Conservation and Land Management (C.A.L.M.) research station in the Perup forest of southern Western Australia (34°15'S., 116°40'E.), a nature reserve with restricted access. The Perup site is an open forest consisting primarily of jarrah (*Eucalyptus marginata* Donn ex Smith, 1802) and marri (*E. calophylla* Lindley, 1841) with seasonal swamps and streams. Precipitation is low throughout the year (< 800 mm p.a.); during our study (dry

season) there was no rain and virtually the only water sources were fire-control holes. These small waterholes are a focus of bat activity at dusk and serve as convenient collecting sites.

Bats were captured (C.A.L.M. license SF000027) at the waterholes from dusk to 2000 hours with mist nets and non-collapsible harp traps (Tuttle 1974), and were immediately placed into cloth bags. After the traps and nets were collapsed the bats were taken to the laboratory at the research centre, where they were weighed and banded (approximate time between capture and weighing, 1 h). No record was made of the ages of the bats caught in our study.

We calculated aspect ratio: wing loading (AR:WL) relationships by two methods. In the first (Norberg and Rayner 1987), live individuals were placed on tracing paper, ventrum down, and one wing and the tail membrane were extended to maximum span. The outline was traced and the positions of the shoulders, foot and tail tip included for references. Traces were measured with a Hipad Digitizer (Houston Instruments) coupled to a planar area software package (Sigma-Scan). Half wingspan, in metres, is the linear distance from wingtip to body midline, passing through the shoulder; doubling this gives the total wingspan. Half wing area is the area enclosed by the outline of the wing and tail membranes and the midline of the body; doubling this value gives the wing area. Dividing the square of the wingspan by wing area results in aspect ratio. Mass, in grams, of the bat times gravitational acceleration, divided by wing area, results in wing loading ($N\ m^{-2}$). In the second method (McKenzie and Rolfe 1986), preserved specimens from the Western Australian Museum were measured in a similar fashion except that the head and ears were included in the wing outline.

Faeces were collected from the bags in which the bats were individually stored (approximate holding time, 2 h). Pellets were sun-dried and taken to laboratories at the University of Toronto, where they were analysed by the methods of Belwood and Fenton (1976). Insect remains were identified from exoskeletal remains and, when available, head capsules. Pellets were recorded as containing Lepidoptera, Coleoptera and/or Hymenoptera. No attempt was made to quantify the percentage of pellets containing the relative insect fragments, but pellets containing single insect orders were tallied for each bat examined.

For echolocation recordings bats were flown in the laboratory room at the Perup Research Centre (width 5 m; length 10 m; height 2.5 m), which was dimly illuminated and partly sound-attenuated with carpets and drapes. All bats described in this study, with the exception of *Tadarida australis*, flew freely around the room while their echolocation signals were recorded with either a Brüel and Kjaer $\frac{1}{2}$ -in. condenser microphone (type 4135 without protecting grid) or a QMC S100 Bat detector, onto a Racal Store 4D Instrumentation Tape Recorder running at 30 i.p.s. (system frequency response range with B&K microphone: ± 0.5 dB, 50 Hz–130 kHz; with QMC microphone: ± 2 dB, 5 kHz–100 kHz). We assume that the bats were emitting search-phase calls while in this flight mode. Free-flying *T. australis* were recorded as they foraged over roadways within the research centre. We caution that our recording techniques for this bat did not permit us to know its exact position relative to the microphone and we may have underestimated the high-frequency content of its calls. In all recording sessions echolocation call amplitudes were monitored with a Non-linear Systems oscilloscope (MS-15). The recordings were analysed at the University of Toronto with a fast Fourier transform spectrum analyser (Nicolet 100A Mini-analyser). The following acoustic parameters were measured from 10 calls of two individuals of each species recorded: (1) duration (ms) (DURATN of Woodside and Taylor 1985); (2) lowest frequency (kHz), the lowest frequency measurable above baseline spectrum noise (at least 20 dB below maximum); (3) highest frequency (kHz), the highest frequency (including harmonics) measurable above baseline spectrum noise; (4) peak frequency (kHz), the frequency of maximum spectral power (usually the fundamental) (EMAX of Woodside and Taylor 1985); (5) frequency span (kHz), the highest minus lowest frequencies. Correlations of the morphological and acoustic variables use the non-parametric Kendall rank procedure because the data revealed considerable skewness.

During the echolocation recordings we made qualitative assessments of the bats' flying abilities (e.g. low or high from the floor, straight or manoeuvrable flight, etc.). These observations were continued when the bats were released at the waterholes where they were captured. After their confinement (2–3 h) all the bats were fed sugar water and released. None of the bats died during these studies.

Results

At Perup we captured 79 bats of the following species (numbers of each in parentheses): *Eptesicus regulus* (Thomas, 1906) (36); *Chalinolobus morio* (Gray, 1841) (14); *C. gouldii* (Gray, 1841) (4); *Nyctophilus gouldi* Tomes, 1858 (18); *N. geoffroyi* Leach, 1821 (5); *Mormopterus planiceps* (Peters, 1866) (2). Individuals of *Tadarida australis* (Gray, 1838)

Table 1. Morphometrics of Perup bats, the two methods of wing measurement

All values are averages ± 1 standard deviation; values in parentheses are sample sizes. NORB, value obtained from live specimens by method of Norberg and Rayner (1987); M&R, values obtained from preserved specimens by method of McKenzie and Rolfe (1986). All weights taken on field-caught specimens

Species	Weight (g)	Aspect ratio		Wing loading	
		NORB	M&R	NORB	M&R
<i>C. morio</i>	7.5 \pm 0.5 (14)	4.8 \pm 0.4 (10)	6.3 \pm 0.2 (9)	6.7 \pm 0.7 (10)	6.5 \pm 0.8 (9)
<i>C. gouldii</i>	13.1 \pm 1.1 (4)	5.5 \pm 0.9 (2)	6.6 \pm 0.1 (15)	9.1 \pm 1.9 (2)	6.9 \pm 0.6 (15)
<i>N. geoffroyi</i>	6.3 \pm 0.5 (6)	5.1 \pm 0.3 (2)	5.8 \pm 0.2 (11)	5.7 \pm 0.3 (2)	5.4 \pm 0.3 (11)
<i>N. gouldi</i>	10.0 \pm 1.7 (17)	5.5 \pm 0.5 (3)	6.0 (1)	7.0 \pm 0.4 (3)	5.6 (1)
<i>E. regulus</i>	5.5 \pm 0.6 (36)	5.3 \pm 0.4 (21)	6.2 \pm 0.2 (6)	6.8 \pm 0.9 (21)	5.2 \pm 0.3 (6)
<i>M. planiceps</i>	9.9 \pm 0.5 (2)	6.1 \pm 0.1 (2)	7.2 \pm 0.1 (5)	12.3 \pm 0.2 (2)	12.5 \pm 0.2 (5)
<i>T. australis</i>	36.0 ^A	11.1 ^A	8.3 \pm 0.3 (17)	19.6 ^A	16.0 \pm 1.3 (17)

^A Values from Norbert and Rayner (1987).

Table 2. Echolocation call characteristics of Perup bats

Values are averages ± 1 standard deviation from 10 pulses sampled from each of two bats

Species	Duration (ms)	Lowest (kHz)	Highest (kHz)	Peak (kHz)	Span (kHz)
<i>C. morio</i>	3.4 \pm 0.6	50.4 \pm 0.4	125.8 \pm 0.1	63.0 \pm 0.9	75.4 \pm 0.3
<i>C. gouldii</i>	2.7 \pm 0.1	29.6 \pm 0.5	106.1 \pm 16.2	41.3 \pm 0.5	76.5 \pm 15.7
<i>N. geoffroyi</i>	2.0 \pm 0.3	52.7 \pm 0.2	106.8 \pm 10.5	67.8 \pm 4.9	54.1 \pm 10.2
<i>N. gouldi</i>	4.1 \pm 0.1	54.2 \pm 5.5	112.7 \pm 9.1	71.6 \pm 8.8	58.5 \pm 3.6
<i>E. regulus</i>	4.5 \pm 0.4	38.7 \pm 0.3	110.2 \pm 2.7	52.6 \pm 2.0	71.5 \pm 3.0
<i>M. planiceps</i>	6.4 \pm 0.5	31.3 \pm 3.0	84.1 \pm 0.3	39.2 \pm 3.0	52.8 \pm 3.0
<i>T. australis</i>	19.2 \pm 1.5	11.4 \pm 0.1	19.8 \pm 5.1	12.6 \pm 0.4	8.4 \pm 5.0

were readily detected by their human-audible echolocation calls every night, although none were caught. Two of the species recorded from this area (Christensen *et al.* 1985) were not encountered: *Nyctophilus major* Gray, 1844, and *Pipistrellus tasmaniensis* (= *Falsistrellus mackenziei* Kitchener, Caputi and Jones, 1986). Most of the bats were captured within 45 min after sunset; after 2000 hours few bats were observed near the waterholes. Tables 1 and 2 summarise the bats' morphometric (by both measurement methods) and echolocation characteristics, respectively. Although we recognise that small samples may have influenced the variance reported for some of the species in these tables (e.g. *M. planiceps*), we are confident the means are representative of the species in the Perup region. Comparison of our survey with Woodside and Taylor (1985) must be limited to the echolocation parameters of signal duration and maximum (spectral intensity) frequency, because the -dB criteria which Woodside and Taylor (1985) used in determining their highest and lowest echolocation frequencies (FMAX and FMIN respectively) are not given.

Fig. 1A compares the AR:WL relationships of the Perup bats determined by the two methods described in our study, and the values (using preserved specimens) given by Norberg

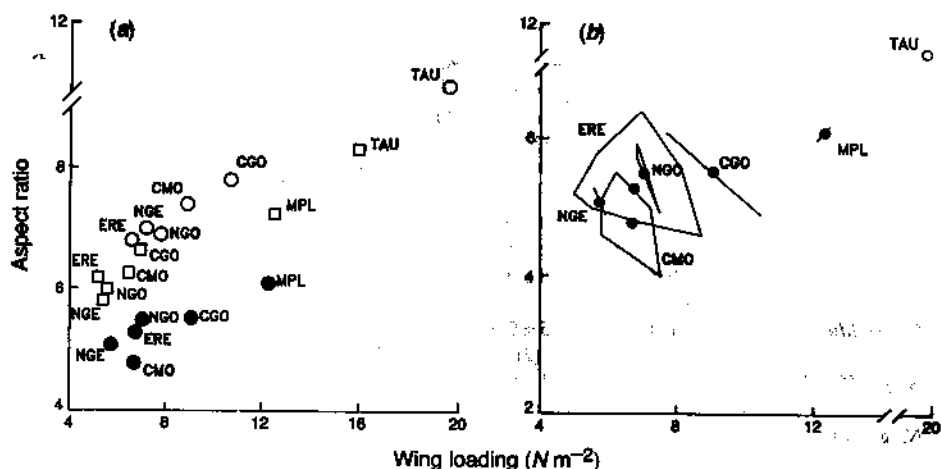


Fig. 1. (A) Plot of aspect ratio versus wing loading values measured for the Perup forest bats. Values from Norberg and Rayner (1987) (\circ), by McKenzie and Rolfe (1986) method on preserved specimens (\square), and by Norberg and Rayner method on live specimens (\bullet). Species names: NGE, *Nyctophilus geoffroyi*; NGO, *N. gouldi*; ERE, *Eptesicus regulus*; CMO, *Chalinolobus morio*; CGO, *C. gouldii*; MPL, *Mormopterus planiceps*; TAU, *Tadarida australis*. (B) Ranges of the values measured using the Norberg and Rayner (1987) method with live specimens, value for TAU from Norberg and Rayner (1987).

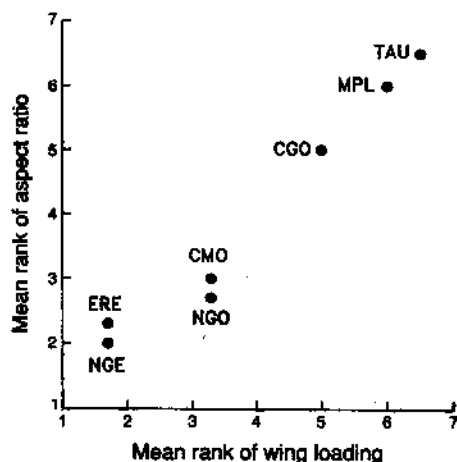


Fig. 2. Aspect ratio:wing loading relationships following the averaging of the ranks of each species determined by the three methods of Fig. 1. Species names as in Fig. 1.

and Rayner (1987). There are differences in the actual values amongst the three measurements, those methods using preserved specimens giving consistently higher aspect ratio values. Fig. 1B shows the ranges of the values measured by the Norberg and Rayner (1987) method on live bats. The values measured by the three methods were ranked, 1 to 7 from lowest to highest, and then averaged to produce the AR:WL relationship in Fig. 2. In this Figure species with low AR:WL values cluster loosely (*N. geoffroyi* and *E. regulus* in the lowest group, *N. gouldi* and *C. morio* somewhat higher). *C. gouldii* occupies a central zone and *M. planiceps* and *T. australis* are progressively more isolated from the other species. Actual AR:WL values place *T. australis* considerably outside the rest of the Perup species, regardless of the morphometrical method used (Fig. 1).

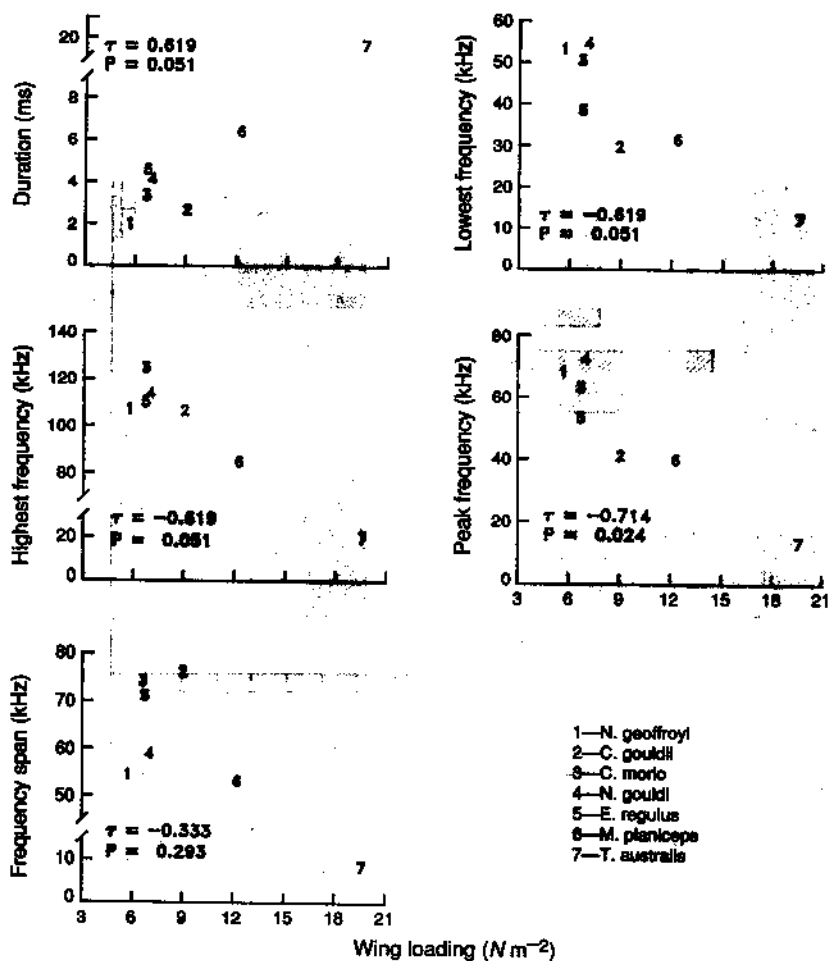


Fig. 3. Correlations of echolocation characteristics to wing loading values for the Perup bats. For each plot the Kendall tau statistic and accompanying probability are reported; *Tadarida australis* wing loading values from Norberg and Rayner (1987).

The morphological separation of Perup bats is reflected in the correlations of wing-loading values and echolocation characteristics. Fig. 3 shows the correlations between the Perup bats' wing-loading values [by the method of Norberg and Rayner (1987) on live specimens] and their echolocation variables (from Table 2). We use the wing-loading values reported for *T. australis* by Norberg and Rayner (1987) in our correlations because all of the morphometric analyses indicate that this species has the highest wing loading of all of the species used. In our non-parametric correlation analysis this places *T. australis* in the top rank regardless of its actual wing-loading values. For Perup bats at this time of the year there is a strongly significant ($P < 0.05$) correlation between wing loadings and echolocation-call peak frequencies; weakly significant ($P = 0.051$) correlations exist with call duration, lowest frequencies and highest frequencies, and insignificant ($P > 0.05$) correlations with echolocation spans. When peak frequency is used as the most highly correlated acoustic variable to body morphology, three species-clusters appear, with *N. geoffroyi*, *N. gouldi*, *C. morio* and *E. regulus* in one group, *C. gouldii* and *M. planiceps* in another, and *T. australis* alone.

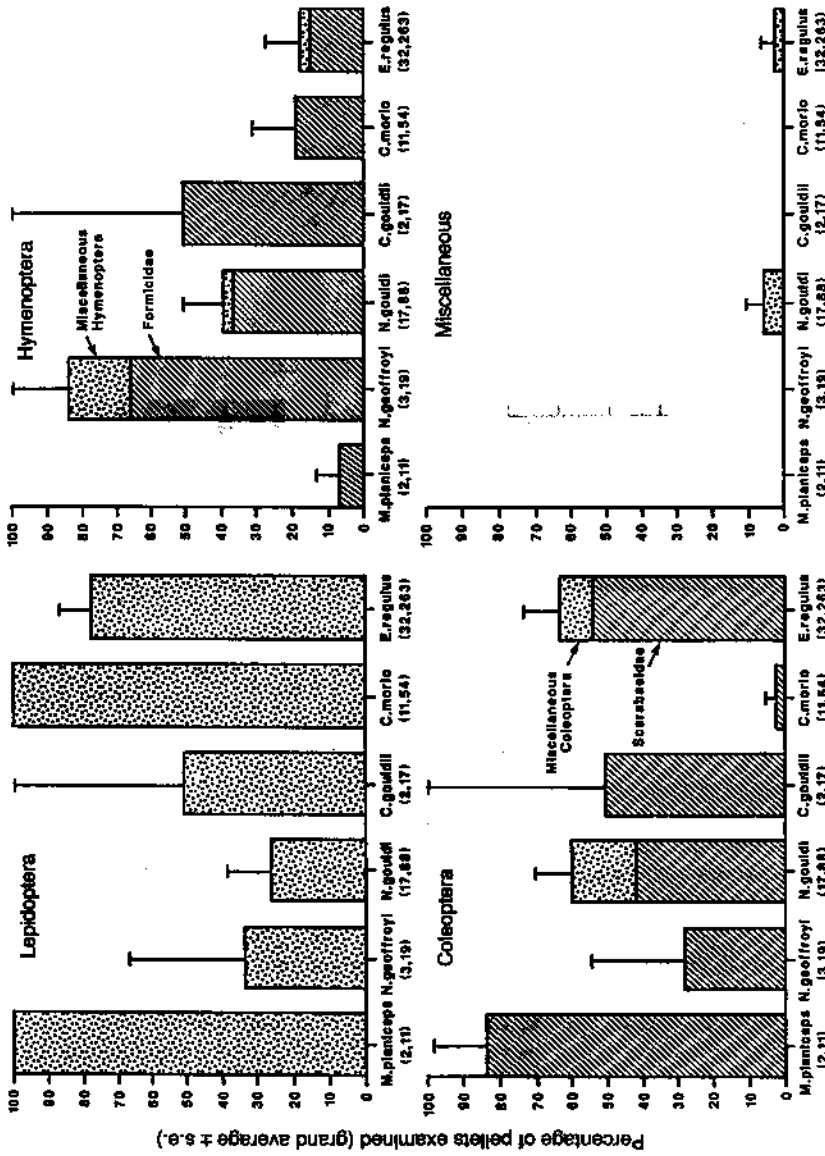


Fig. 4. Faecal analyses of the Perup forest bats. Bar heights represent the averaged percentage of pellets from the bats of each species that contained the specified insect order. Numbers beneath species names indicate total numbers of bats and pellets inspected, respectively.

Table 3. Comparison of the correlations of Perup bat aspect ratio and wing loadings with echolocation variables with the two methods of wing measurement

NORB, value from live specimens by method of Norberg and Rayner (1987); M&R, from preserved specimens by methods of McKenzie and Rolfe (1986). Values are Kendall tau statistics, with probabilities in parentheses

Parameter	Method	Correlation coefficient of:				
		Peak	Lowest	Highest	Span	Duration
Aspect ratio	NORB	-0.586 (0.068)	-0.488 (0.129)	-0.683 (0.033)	-0.488 (0.129)	0.586 (0.068)
	M&R	-0.809 (0.011)	-0.714 (0.024)	-0.524 (0.098)	-0.048 (0.881)	0.524 (0.098)
Wing loading	NORB	-0.714 (0.024)	-0.619 (0.051)	-0.619 (0.051)	-0.333 (0.293)	0.619 (0.051)
	M&R	-0.619 (0.051)	-0.524 (0.098)	-0.524 (0.098)	-0.238 (0.453)	0.333 (0.293)

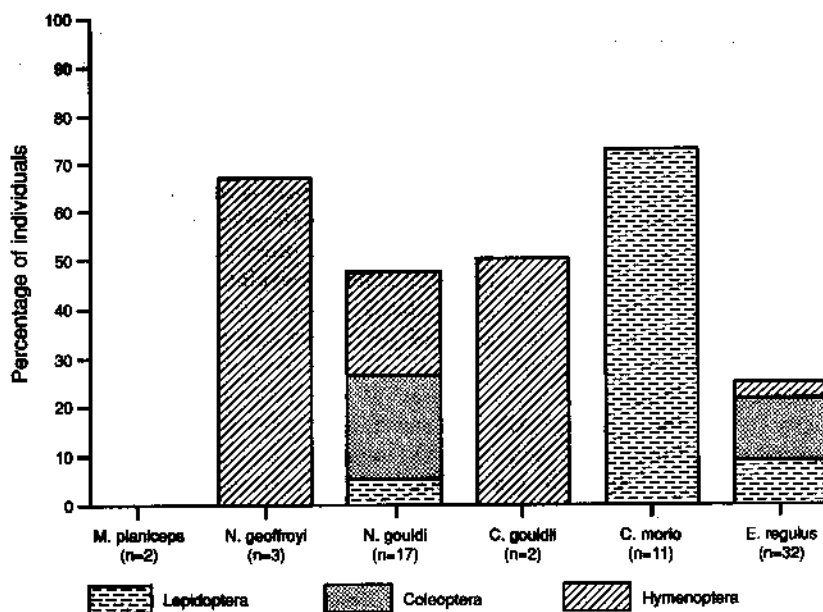


Fig. 5. Analyses of those faecal pellets containing single insect orders. Bar heights represent the percentage of individual bats captured that produced pellets consisting entirely of the specified insect order; numbers beneath species names are total numbers of bats from which pellets were collected.

Table 3 describes the different correlations of echolocation with aspect ratios and wing loadings, by means of the commonly reported method of Norberg and Rayner (1987) on live specimens and the alternative method of McKenzie and Rolfe (1986) on preserved specimens. This table shows that strongly significant ($P < 0.05$) correlations exist most often between flight morphology and echolocation peak frequency. Lowest and highest frequencies reveal both strongly and weakly ($P = 0.051$) significant correlations in half of the cases, but frequency span does not. Echolocation duration weakly correlates only to the wing loading of live specimens.

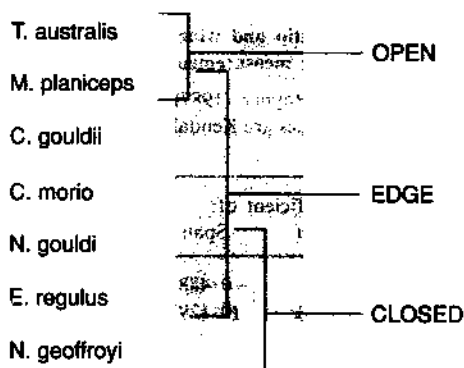


Fig. 6. Proposed microhabitat distribution of Perup forest bats from the echolocation and flight morphology and behaviour data of the present study, and from observations of same species in other studies. Microhabitat classification is adapted from Fenton (1990).

Faecal analyses revealed no particular concentrations of any insect order in the bats' diets for the short time they were sampled (Fig. 4). All species fed upon all of the insect orders identified, although Lepidoptera (presumably moths) were found in particularly high incidence in the faeces of *C. morio* (70% of the individuals captured produced pellets that were completely lepidopteran in origin: Fig. 5). Winged reproductive ants (Hymenoptera) were taken in large numbers by *N. geoffroyi* and *C. gouldii*, beetles (Coleoptera) were heavily taken by all but *C. morio*, and *E. regulus* and *N. gouldi* appeared to have the widest prey preferences.

Discussion

Fenton (1990) suggests that behavioural variability in bats is sufficiently high to warrant caution in formalising their foraging niches. He proposes three categories of microhabitats, which are (along with equivalent categories proposed by other authors): (1) closed ['inside stand' and 'beside stand' of McKenzie and Rolfe (1986), 'gleaning' and 'between canopy and close to obstacles' of Neuweiler (1983) and 'zones 2, 6 and 7' of Aldridge and Rautenbach (1987)]; (2) edge ['beside stand in the open' and 'just above canopy' of McKenzie and Rolfe (1986), 'between or below canopy' of Neuweiler (1983) and 'zones 3, 4 and 5' of Aldridge and Rautenbach (1987)]; (3) open ['over canopy' of McKenzie and Rolfe (1986), 'open air' of Neuweiler (1983) and 'zone 1' of Aldridge and Rautenbach (1987)]. Gleaning bats appear to be a special case of closed-microhabitat bats, many (perhaps all) species not using echolocation for detecting prey but listening for the sounds generated by their prey (Faure *et al.* 1990).

Neuweiler (1984), Aldridge and Rautenbach (1987) and Barclay (1988) suggest that flight morphology constrains bats' foraging niches, and this, in turn, influences the echolocation designs used by the bats within their particular microhabitats. The background vegetation of closed zones present both physical and acoustic objects, so that echolocation used in these microhabitats is hindered by background acoustic contamination (clutter). Bats flying in these zones typically use calls that are short (<2 ms), faint (<70 dB SPL), high in peak frequency (>50 kHz) and generally broad-banded (Neuweiler 1983; Fenton 1990). Bats flying in very open habitats (e.g. above the canopy) require long-distance resolution for their calls and emit longer (>10 ms), lower frequency (10–30 kHz) and more intense (>100 dB SPL) signals. Whereas bats at the extreme ends of microhabitat spectra follow these arbitrary classifications [e.g. Old World molossids (Neuweiler 1984; Aldridge and Rautenbach 1987); neotropical phyllostomids (Belwood 1988)], there is considerable overlap for most bats. The most constrained species appear to be those which forage in open areas, because of their physical inability to negotiate the cluttered spaces within forests. 'Closed' bats may exploit the other zones, as suggested by Fenton (1990), but could face severe flight limitations (e.g. especially in windy conditions) because of their low wing loadings and aspect ratios. For these bats, feeding would be energetically very costly in open zones. 'Edge' bats,

with their moderate aspect ratio and wing loadings and multipurpose echolocation design, should exhibit both the greatest flexibility in foraging microhabitat and the highest species richness as a group.

There is, at present, no agreement upon which of the two morphometric variables commonly reported, aspect ratio or wing loading, is the most relevant to a bat's echolocation patterns. Indeed, the behavioural flexibility exhibited by bats and the very different aspect of flight performance that these indices measure (Norberg and Rayner 1987) might make single-variable correlations unwise when we attempt to predict microhabitat use in bats. Although wing loading may be a better measure of flight speed, agility and manoeuvrability (critical for slow-flying 'edge' and 'closed' bats), aspect ratio relates to energy cost per unit distance (important for open-air bats that fly long distances during their nightly foraging bouts) and may be the stronger correlate against echolocation design for niche prediction. The statistics in Table 3 imply that peak frequency is the most commonly correlated echolocation variable and may serve as the bat's most critical sonar parameter. Even so, correlations arising from such analyses must, at present, be viewed only as predictions and not conclusions. Unless variables such as resource availability were constants, one would not expect a species' flight indices or echolocation characteristics to provide more than a rough picture of its optimum foraging zone within a given vegetation type. Six of the seven species used in this study are known to forage in vegetation that ranges from dense forests to savannah grasslands, and the Perup area is itself a mosaic of shrubland, woodland and forest patches in which seasonality and disturbances such as the successional changes following bushfires cause fluctuations in the availability of food and other resources. In these conditions, the nature of a species' optimum foraging zone might vary seasonally and from vegetation type to vegetation type (e.g. we have only theoretical ideas of what is 'cluttered' vegetation to a bat). Such factors may explain some of the differences in the nature, number and precision of bat flight zones described in different studies.

Using the categories of Fenton (1990) and the aforementioned qualifications, we propose the microhabitat separation of the Perup bats illustrated in Fig. 6. We predict the bat species of the Perup forest community during the dry season will forage as follows:

Tadarida australis. This species possesses the most distinctly separate AR : WL relationship of all those examined. Its long, narrow wings and heavy body mass will limit it almost exclusively to an open zone. Foraging-zone observations for this species in mangrove communities are quantified by McKenzie and Start (1989) as 'over canopy'. At Perup this bat was routinely heard flying above the forest canopy but we never caught it at the waterholes, presumably because of the confined nature of these sites. Even on windy nights at Perup, when smaller bats were presumably unable to fly in the open, *T. australis* were still commonly heard. Its echolocation resembles that of other above-canopy molossids, e.g. *T. aegyptiaca* (Fenton and Bell 1981), and we predict that at Perup it is an obligate open-zone bat.

Mormopterus planiceps. This bat has a AR : WL relationship that predicts a mixed open and edge microhabitat usage. Although we caught it at the waterhole, our observations of its flight in the laboratory qualitatively suggest that it is not well suited for close-quarter manoeuvring. Its echolocation call is higher in frequency than that of *T. australis*, but lower than those of the other species in the community. The congeneric *M. loriae* is similar in that its echolocation frequency is one of the lowest in a New South Wales community (Woodside and Taylor 1985). *M. planiceps*' faecal samples indicate preference for no particular insect order, further suggesting a range of foraging zones. We predict that this bat forages primarily in open, above-canopy zones but commonly enters edge habitats, as does *M. loriae* in mangrove communities (McKenzie and Start 1989).

Chalinolobus gouldii. This species has a AR : WL plot similar to that of *M. planiceps*, an affinity shared by its echolocation : wing loading correlations. Its calls are middle-range

in frequency and duration, like those of *M. planiceps*. The body morphology and echolocation frequency design of this bat are similar to those of individuals studied in Tasmania (O'Neill and Taylor 1986) and New South Wales (Woodside and Taylor 1985) but its echolocation duration differs from those of New South Wales individuals in an interesting way. Our results differ from those of Woodside and Taylor (1985) in this species' echolocation pulse duration (2.7 v. 1.3 ms). Its calls suggests it is adapted for open habitats, as reported in other Australian sites (McKenzie and Rolfe 1986; McKenzie and Start 1989), and it may alter its pulse durations to suit the particular forest environment it forages in. At Perup we expect to find it primarily in edge habitats, occasionally venturing into open zones.

Chalinolobus morio, *Nyctophilus gouldi* and *Eptesicus regulus*. These group together in both their AR:WL plots and echolocation correlations. They have been described as 'closed' species that forage along the outlines of the canopy with considerable agility (O'Neill and Taylor 1986). All three bats exhibit considerable variety in their diets, further suggesting a wide range of habitat choices. Echolocation: wing loading correlations further suggest that *E. regulus* spends more time in a closed microhabitat than do the other two species, a prediction supported by O'Neill and Taylor's (1986) description of its manoeuvrable flight and gleaning ability. In flight trials, *N. gouldi* could be induced to pick fluttering insects from the hand, an observation in keeping with others about this bat (Guppy and Coles 1988). We predict that at Perup these three species routinely use edge habitats, occasionally moving into closed zones (particularly *E. regulus* and *N. gouldi*). The echolocation frequencies for our samples of *C. morio* and *E. regulus* are very similar to those from Woodside and Taylor (1985) but, as with *C. gouldii*, our bats emitted consistently longer pulses. The maximum frequency of our *N. gouldi* was considerably higher than those reported by Woodside and Taylor (1985) (71.6 v. 54.1 kHz) and, though we recognise the need for caution in direct comparisons of potentially variable acoustic parameters, these differences may reflect something of the genetic changes this species is undergoing in widely disparate locations.

Nyctophilus geoffroyi. This bat may not deserve special mention except for an increased time spent gleaning in the closed zone. Various authors have described its slow, fluttering flight, and have mentioned gleaning as part of its foraging behaviour (Dwyer 1965; O'Neill and Taylor 1989). Specimens of this bat and its sympatric congener *N. major* have been recovered from pitfall traps (e.g. Western Australia Museum mammal specimen records M17676, M23364 and M20637), presumably drawn there by the sounds of previously captured insects. Our flight observations qualitatively indicate that this bat readily alights to glean fluttering insects. The very low aspect ratio of this bat and its characteristic gleaning-type echolocation signal also agree with those reported in Woodside and Taylor (1985). Its mean call durations (2.0 ms: Table 2) are longer than those measured from gleaners in the Panama rainforest (Fullard, unpublished data) but are comparable to those from a North American temperate gleaner, *Myotis evotis* (Faure *et al.* 1990). The more open character of the Perup forest may allow longer signals from its gleaning bat species, which would improve their echolocation signal: noise ratios. We predict that in Perup *N. geoffroyi* strongly favours the closed zone and spends a considerable amount of its foraging time gleaning insects.

In conclusion, we feel that a flexible microhabitat usage best describes the assemblage of bats in the present study. Since considerable variability has been reported in the diets of bats exposed to seasonal changes that are no more severe than those experienced in the Perup forest (Fenton and Thomas 1980), it is parsimonious to assume that Perup bats are as opportunistic as necessary to exploit the greatest array of insects. Since our study was conducted during Perup's dry season, we would have been less likely to witness pronounced specialisation on prey. During the wet season certain bats (e.g. gleaners) may specialise more on insects associated with growing vegetation (e.g. caterpillars).

We feel that the morphological and echolocation correlations reported for the bats in this site are strong enough to warrant studies testing the zone preferences described in Fig. 6. It would be particularly interesting to document whether these relationships change for Perup bats during the wet season and whether certain of the bats' behaviours (e.g. gleaning) change to accommodate new foraging-zone preferences.

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References

- Aldridge, H. D. J. N., and Rautenbach, I. L. (1987). Morphology, echolocation and resource partitioning in insectivorous bats. *Journal of Animal Ecology* 56, 763-78.
- Barclay, R. M. R. (1988). Echolocation strategies of aerial insectivorous bats and their influence on prey selection. In 'Animal Sonar'. (Eds P. E. Nachtigall and P. W. B. Moore.) pp. 595-9. (Plenum Press: New York)
- Belwood, J. J. (1988). Foraging behavior, prey selection, and echolocation in phyllostomine bats (Phyllostomidae). In 'Animal Sonar'. (Eds P. E. Nachtigall and P. W. B. Moore.) pp. 601-5. (Plenum Press: New York.)
- Belwood, J. J., and Fenton, M. B. (1976). Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 54, 1674-8.
- Black, H. L. (1972). Differential exploitation of moths by the bats *Eptesicus fuscus* and *Lasiurus cinereus*. *Journal of Mammalogy* 53, 598-601.
- Christensen, P., Annels, A., Liddelow, G., and Skinner, P. (1985). Vertebrate fauna in the southern forests of Western Australia. Forestry Department of Western Australia, Bulletin No. 94.
- Crome, F. H. J., and Richards, G. C. (1988). Bats and gaps: microchiropteran community structure in a Queensland rain forest. *Ecology* 69, 1960-9.
- Dwyer, P. D. (1965). Flight patterns of some eastern Australian bats. *Victorian Naturalist* 82, 36-41.
- Faure, P. A., Fullard, J. H., and Barclay, R. M. R. (1990). The response of tympanate moths to the echolocation calls of a substrate gleaning bat, *Myotis evotis*. *Journal of Comparative Physiology Series A* 166, 843-9.
- Fenton, M. B. (1972). The structure of aerial-feeding bat faunas as indicated by ears and wing elements. *Canadian Journal of Zoology* 50, 287-96.
- Fenton, M. B. (1990). The foraging behaviour and ecology of animal-eating bats. *Canadian Journal of Zoology* 68, 411-22.
- Fenton, M. B., and Thomas, D. W. (1980). Dry-season overlap in activity patterns, habitat use, and prey selection by sympatric African insectivorous bats. *Biotropica* 12, 81-90.
- Fenton, M. B., and Bell, G. P. (1981). Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy* 62, 233-43.
- Findley, J. S. (1976). The structure of bat communities. *American Naturalist* 110, 129-39.
- Freeman, P. W. (1979). Specialized insectivory: beetle-eating and moth-eating molossid bats. *Journal of Mammalogy* 60, 467-79.
- Guppy, A., and Coles, R. B. (1988). Acoustical and neural aspects of hearing in the Australian gleaning bats, *Macroderma gigas* and *Nyctophilus gouldi*. *Journal of Comparative Physiology Series A* 162, 653-68.
- McKenzie, N. L., and Rolfe, J. K. (1986). Structure of bat guilds in the Kimberley mangroves, Australia. *Journal of Animal Ecology* 55, 401-20.
- McKenzie, N. L., and Start, A. N. (1989). Structure of bat guilds in mangroves: environmental disturbances and determinism. In 'Patterns in the Structure of Mammalian Communities'. (Eds D. W. Morris, Z. Abramsky, B. J. Fox and M. R. Willig.) pp. 167-78. (Texas Technical University, Special Publications of the Museum No. 28.)

- McNab, B. K. (1971). The structure of tropical bat faunas. *Ecology* **52**, 352-8.
- Neuweiler, G. (1983). Echolocation and adaptivity to ecological constraints. In 'Neuroethology and Behavioural Physiology'. (Eds F. Huber and H. Markl.) pp. 280-302. (Springer-Verlag: Berlin.)
- Neuweiler, G. (1984). Foraging, echolocation and audition in bats. *Naturwissenschaften* **71**, 446-55.
- Norberg, U. M. (1987). Wing form and flight mode in bats. In 'Recent Advances in the Study of Bats'. (Eds M. B. Fenton, P. Racey and J. M. V. Rayner.) pp. 43-56. (Cambridge Press: Cambridge.)
- Norberg, U. M., and Rayner, J. M. V. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera); wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London (Series B)* **316**, 335-427.
- O'Neill, M. G., and Taylor, R. J. (1986). Observations on the flight patterns and foraging behaviour of Tasmanian bats. *Australian Wildlife Research* **13**, 427-32.
- O'Neill, M. G., and Taylor, R. J. (1989). Feeding ecology of Tasmanian bat assemblages. *Australian Journal of Ecology* **14**, 19-31.
- Tuttle, M. D. (1974). An improved trap for bats. *Journal of Mammalogy* **55**, 475-7.
- Woodside, D. P., and Taylor, K. J. (1985). Echolocation calls of fourteen bats from eastern New South Wales. *Australian Mammalogy* **8**, 279-97.

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