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

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

Key words: community, habitat, microchiroptera, northern Australia, savanna.

INTRODUCTION

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

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

Woinarski *et al.* (1992) did not include systematic sampling of bats, preventing a rigorous examination of the response of the bat fauna to environmental measures. However, data from captures (mist netting, harp trapping, roost searches) indicated that most bat species were present across the environmental range sampled (Woinarski *et al.* 1992). Here we revisit the issue of the response of bats to environmental variables in the tropical savanna of the Northern Territory and north-west Queensland using a more rigorous data set. Our data collection incorporated the use of ultrasonic detectors to sample bats and geographic information system (GIS) derived variables to represent environmental conditions. The study region supports a rich microbat fauna (26 of Australia's 65 species, 15 of Australia's 20 genera), including one endemic species (*Taphozous kapalgensis*), and both of Australia's monotypic genera (*Rhinonicteris*, *Macroderma*).

We assessed environmental factors at two levels, first at the landscape scale, using data available from a GIS, and second at a local scale where information was collected on the physical environment and food resource availability (insects) at individual sampling sites. We predicted that the high vagility of bats would result in species responding broadly to environmental variables. However, specific responses to a number of environmental variables were expected. In particular, we predicted that the distribution, composition and

segregation of bat assemblages would respond to geographical patterns in annual rainfall, presence of rocky escarpments, water bodies and canopy cover. Although a relationship with insect abundance and composition was examined, we predicted that this relationship would not be significant given the generalist feeding ecology of most insect-eating bats (Fenton 1990).

The bat assemblages of tropical Australian savannas are also compared with assemblages elsewhere in Australia. Specifically, we compared our results with community composition and environmental association studies in north Queensland rainforest (Crome & Richards 1988), mangroves in north-western Western Australia (McKenzie & Muir 2000), and open forest/woodland in Victoria (Kutt 1995; Lumsden & Bennett 1995; Herr 1998), south-east New South Wales (NSW) (Law *et al*. 1999) and Tasmania (Taylor & O'Neill 1988).

METHODS

Study area

The study area, called the Top End of Australia, included the tropical savanna of the Northern Terri-tory and north-west Queensland, north of 18°S, but excluding offshore islands (Fig. 1). Across this area, maximum mean weekly temperature ranges between 32°C and 39°C and mean annual rainfall between 360 mm and 1720 mm (Houlder 2000; Fig. 1). Rainfall is highly seasonal with almost all precipitation occurring from November to April. Topographic relief is relatively low. The maximum elevation is 553 m on the Arnhem Land plateau, with the main areas of topographic relief being the Kakadu escarpment and the eastern edge of the Kimberley region in the south-west of the study area. Eucalypt woodlands and forests dominate 78% of the study area (Fox *et al*. 2001). Other notable environments include monsoon rainforests and floodplains dominated by sedgelands and grasslands. On average, over half (52%) of the Top End is burnt every year (A. Edwards, pers. comm. 2004).

Study sites

A total of 39 sampling sites were located across the Top End (Fig. 1). Fieldwork was conducted from 22 September to 1 November 2000 (18 sites), 26 September to 1 November 2001 (19 sites) and 23–25 October 2002 (two sites). Sampling was conducted at similar times of year to reduce possible effects of sea-
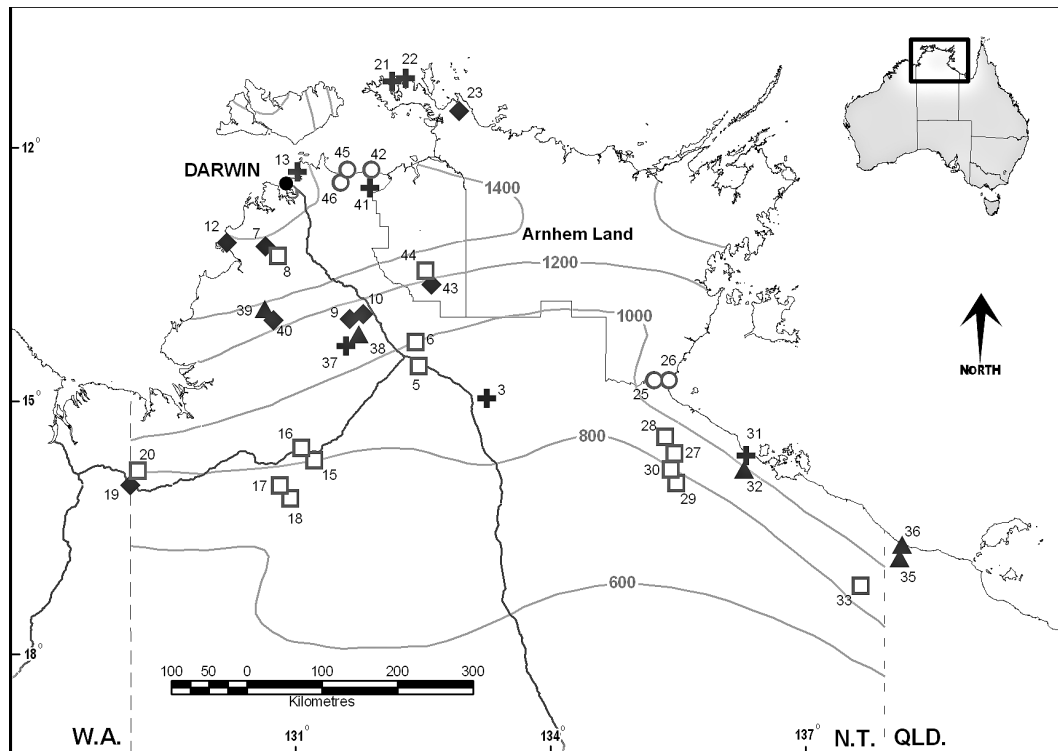

Fig. 1. Map of the study area showing the location of sampling sites and site labels as well as average annual rainfall isohyets (in millimetres). Sites are symbolized according to bat assemblage (diamond = Group 1, square = Group 2, cross = Group 3, triangle = Group 4, circle = Group 5).

sonal variation on species composition. Each site was a circular plot of 100 m radius. Plots were primarily selected to cover a large geographical area and to sample four broad habitat types:

1. Riparian – adjacent to perennial rivers, creeks or permanent waterholes (10 sites).
2. Escarpments – sandstone cliffs (11 sites).
3. Coastal – coastal and near coastal environments (excluding estuaries and mangroves) (eight sites).
4. Woodlands – continuous areas of eucalypt woodlands or open forests not associated with the other habitats types (10 sites).

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

Bat sampling

At each site we used a range of sampling techniques to maximize the likelihood of obtaining a full inventory of bat species (Kuenzi & Morrison 1998; Murray *et al*. 1999; O'Farrell & Gannon 1999). Bats were sampled using two (18 sites) or three (21 sites) harp traps over two consecutive nights as well as one night of shot sampling for a 3-h period after dusk. Harp traps were usually placed across 'flyways' (tracks, streams or other gaps within the vegetation where bats are more likely to be trapped) and were either positioned side by side or spaced between 20 and 30 m apart. We also conducted active searches of caves, road culverts and any other features potentially used as diurnal roosts by bats within 400 m of the centre of the sampling site. In addition, bat calls were recorded at every site with ultrasonic bat-detectors (Anabat II, Titley Electronics, Ballina, Australia) using two methods. The first method involved placing a detector on the ground, elevated to approximately 40°, and operated from dusk for a cumulative total of at least six recording hours over two consecutive nights (maximum 22 h, mean 20 h). This time period has been shown to sample 90% of species calls at a given site (Milne *et al*. 2004). Detectors were connected to either an Anabat II Delay Switch with output recorded to 90-min cassette tape (Sony Chrome UX, Tokyo, Japan) via tape recorder (Optimus CTR-115 D, Fort Worth, USA) (18 sites) or an Anabat V Zcaim and computer (Toshiba Portégé 3440CT or Toshiba Tecra 700CT D, Tokyo, Japan) running Anabat6 software in monitor mode (21 sites). There are no differences in the species detected

between these two recording techniques (Milne *et al*. 2004). For the second method, an Anabat detector was held in the hand and manually activated on detection of a bat-call and actively pointed in the direction of the call. Calls were recorded via tape-recorder and cassette tape, for 3 h after dusk for one night. All recorded calls were identified according to Milne (2002). At several sites (14), shot sampling was not permitted. Instead we trapped bats using mist-nets at these sites. It is likely therefore, that some 'high-flying' bat species that are readily detected using shot sampling, may not have been trapped at these sites. However, we expect this will have a negligible effect on our results as shot sampling at all other sites, used in conjunction with Anabat detectors, enabled us to collect an extensive reference call library for 'high-flying' bat species for the entire study area (Milne 2002). Anabat detectors were systematically used at all sites and will normally detect 'high-flying' species that are not readily trapped (O'Farrell & Gannon 1999).

Environmental data

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

Habitat measurements

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

0   – no trees or rock outcrops
1   – only small trees (<5 cm d.b.h. and <5 m tall)
2   – mostly intermediate sized trees (5–20 cm d.b.h. and 5–15 m tall) OR small trees and rock outcrop showing small (hand size) cracks and holes
3   – mostly large trees (>20 cm d.b.h. and >15 m tall) or small to intermediate trees and rock outcrop with large (body size) cracks and holes

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

We chose to assess whole trees and rock outcrops rather than count individual hollows because small microbats (<10 g) can roost in hollows equivalent to their own body diameter (pers. obs. 2004). Entrances to these hollows are very small and would regularly be overlooked if we attempted to count hollows directly. Large trees have been shown to contain more tree hollows than smaller trees (Whitford 2002) and are preferred roost sites for many bat species (Lunney *et al.* 1988; Herr & Klomp 1999; Law & Anderson 2000; Lumsden *et al.* 2002).

Spatial data

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

Insects

At each site we trapped flying nocturnal insects for one night concurrently with bat sampling. The insect trap was constructed from a white cotton sheet (1.5 m × 2.5 m), suspended off the ground by strings tied to the corners to form a funnel, one end higher than the other. At the bottom of the funnel a hole was cut in the sheet and a plastic jar (65 mm diameter × 130 mm depth) partially filled with 70% ethanol was attached to hang underneath. A 12-V fluorescent light ('Col-Light' brand Col-lite, Maleny, Australia) was hung from the higher end of the sheet to attract insects. The trap was positioned approximately 100 m from the Anabat detector so as not to disturb bats from natural flight habits in the vicinity of the detector, and left unattended for the entire night. Insects that fell into the jar were collected the following morning. In the laboratory, insect samples were filtered through a 2-mm sieve to remove the smallest insects (mostly <3 mm in

length) and then identified to order and assigned to four size (head-body length) classes: <5 mm, 5–10 mm, 10–15 mm and >15 mm. The choice of size classes was based on the range of body sizes found to be prey items of bats in Tasmania (O'Neill & Taylor 1989).

Analysis

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

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

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

Table 1. Environmental variables used in the analysis and other variables that were excluded due to high correlation (i.e. Spearman rank correlation test resulted in a correlation coefficient >0.8)

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

Variables in italics were derived from GIS, field measurements are in plain text

used and a backward stepwise procedure was adopted to generate the minimum adequate model with only those variables having a significant correlation in the vector fitting included in the model development.

RESULTS

Species assemblages

A total of 23 microbat species were identified from the 39 sites, representing over 80% of the species recorded from north-western Australia (Woinarski *et al.* 1992).

Two species known to occur in the Top End, *Macroderma gigas* (Ghost bat) and *Saccolaimus saccolaimus* were not detected in this study. We identified five groups from the classification of all sites by their species composition (Fig. 2). The initial classification divided the sites into four groups. We subdivided the largest of these groups into two and assigned two outlying sites to Group 1 based on the relative position of these sites in the ordination. ANOSIM analysis confirmed that the groups differed significantly in composition ($R = 0.70$, $P < 0.001$) and that there was a significant difference between each pair of groups ($P < 0.01$ or better).
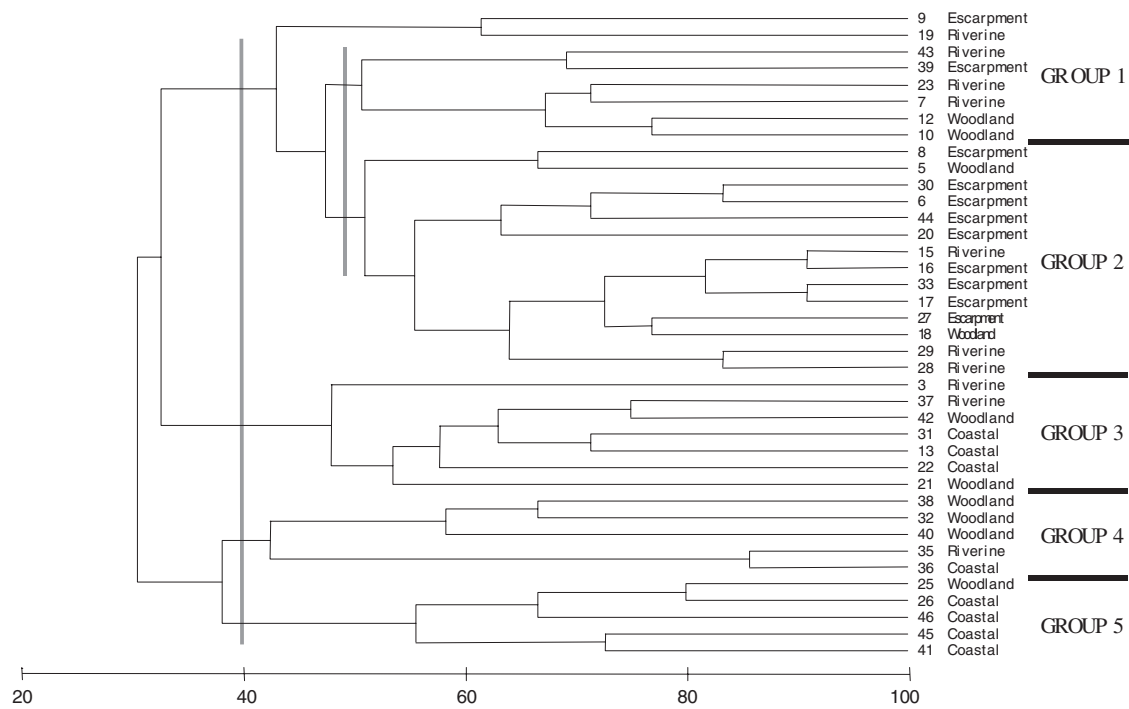
Fig. 2.   Dendrogram showing classification of the 39 sites to form five groups. Grey lines indicate levels at which groups were delineated. Habitat types are shown adjacent to the site numbers.

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

Group 1

Species that were detected most often in this group include *Chalinolobus gouldii* (present in all sites), *C. jobensis,* *S. flaviventris,* *S. greyii*/*S. sanborni* and *P. adamsi. Chalinolobus gouldii* was strongly associated with this group (i.e. tended to occur in Group 1 more than the other four groups). Group 1 had the highest total species richness and mean site species richness of all groups. Sites were characterized by high percent-

age canopy cover, frequent burning and high annual rainfall and were located in the north and west of the Top End.

Group 2

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

Group 3

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

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Table 2.   Comparison of species composition within bat groups and habitats

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

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

Figures represent percentage of sites within each group or habitat in which each species was detected. Differences in proportions were tested using χ^2 statistic and differences in mean species richness were tested using Kruskal–Wallis ANOVA (ns, not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).
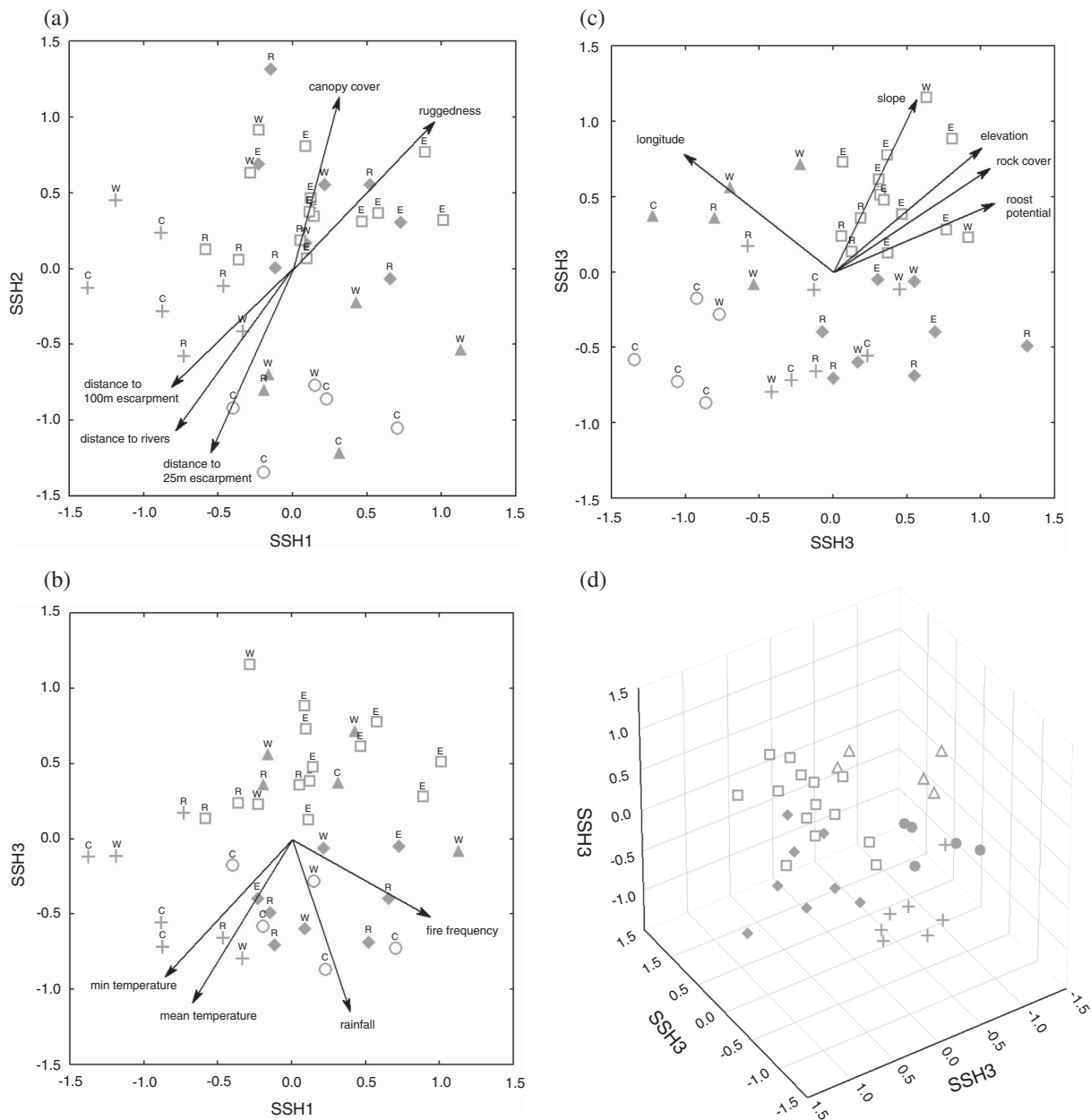
Fig. 3. Ordination of sites by species composition. The ordination is displayed in two dimensions in graphs (a–c) and three dimensions in (d). Significant environmental variables are plotted as vectors on the graphs. The two longest dimensions of the vectors were used to determine on which of the graphs vectors were plotted. Symbols represent groups (refer Fig. 1) and letters represent habitats (R = Riparian, E = Escarpment, C = Coastal, W = Woodland). Three-dimensional stress value = 0.16.

Group 4

This group had equal fewest sites (five) and had the lowest total and mean site species richness. Species detected most often include *C. jobensis* (present at all sites) *S. flaviventris*, *M. loriae* and *C. nigrogriseus*. There were no strong species associations, although *C. nigrogriseus* occurred at proportionately more sites in this group than any other. Sites were characterized

by lower mean annual temperatures, long distances to rivers and no rock cover.

Group 5

Species detected most often include *S. flaviventris*, *P. westralis* (both present at all sites), *P. adamsi*, *M. loriae* and *T. kapalgensis*. *P. westralis* and

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T. kapalgensis were strongly associated with this group. Group 5 also had relatively few sites and low species richness, but was associated with the minima or maxima of several environmental variables including long distances to escarpments, flat terrain at low elevations with no rock, low local roost potential, high annual temperatures and low fire frequency. All five sites were located near the coast (Fig. 1).

Relationships with habitat types

There was a significant difference in species composition between habitat types (ANOSIM, $R = 0.35$,

$P < 0.001$) as well as between all pairwise combinations of habitats except between 'Woodland' and 'Riverine' ($R = 0.037$, $P = 0.27$). *V. caurinus* and *T. georgianus* were detected most often in 'Escarpment' habitat. Both of these species, as well as *Rhinonicteris aurantius* and *C. nigrogriseus*, were absent from 'Coastal' habitat. *P. westralis* was strongly associated with 'Coastal' habitat and absent from both 'Escarpment' and 'Riparian' habitat. *N. arnhemensis* was also absent from 'Escarpment' habitat. All habitats had similar total and site species richness, with slightly lower species richness in the 'Coastal' habitat.

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

Relationships with insects

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

Table 3. Environmental variables with a significant correlation with the ordination of sites by species composition (see also Fig. 3)

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

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

Table 4. Comparison between bat groups for the environmental variables listed in Table 3

Variable	Group 1	2	3	4	5	H
Distance to 25 m escarpments (km)	4.7	1.3	19.3	18.2	28.1	24.16***
Distance to 100 m escarpments (km)	38.9	28.9	119.6	60.6	128.3	24.52***
Elevation (m)	82.8	106.0	30.9	39.2	3.6	16.99**
Canopy cover (%)	53.5	48.5	21.1	28.6	6.7	12.06*
Rock cover (%)	8.7	37.0	0.7	0.0	0.0	14.86**
Minimum temperature (°C)	14.6	12.4	16.5	13.1	15.9	18.91***
Local roost potential	2.1	2.5	2.1	1.6	0.6	17.45**
Slope (%)	6.4	29.7	4.4	5.0	0.2	20.41***
Ruggedness (m)	2.7	10.8	1.2	0.7	0.3	9.03 ns
Fire history (no. times burnt over preceding 7 years)	2.9	1.2	1.0	2.6	0.8	7.71 ns
Longitude (decimal °E)	131.2	132.9	132.6	135.0	133.1	4.92 ns
Annual rainfall (mm)	1210	848	1157	991	1149	12.72*
Distance to rivers (km)	2.7	1.6	6.6	8.5	7.6	8.84 ns
Mean temperature (°C)	26.7	26.5	26.9	26.2	27.0	14.13**

Values are the mean for sites in each group, *H*-values refer to the Kruskal–Wallis statistic (ns; not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

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

Group	Habitat			
	Riparian	Escarpments	Coastal	Woodland
1	4	2	0	2
2	3	9	0	2
3	2	0	3	2
4	1	0	1	3
5	0	0	4	1

Species richness model

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

Table 6. Summary of results from generalized linear modelling (GLM) for site species richness

Variable	Estimate	SE	*P*-value
Species richness (deviance = 18.607; deviance captured = 40.0%; *n* = 39)			
Constant	1.3902	0.2578	
Distance to rivers (km)	−0.0403	0.0130	★★
Annual rainfall (mm)	0.0005	4.6617	★

Minimum adequate models and explanatory power (per cent of deviance captured) are shown. Probability levels *P* < 0.05, **P* < 0.01.

DISCUSSION

As predicted, the insectivorous bat fauna of north-western Australia responded broadly to most environmental variables. The main environmental feature associated with the distribution of microbat assemblages in the study area was topography (variation in elevation, slope, topographic ruggedness and distance to escarpments). Not surprisingly, therefore, species considered to be obligate cave roosters (*Hipposideros ater*, *H. diadema*, *H. stenotis*, *M. macropus*, *M. schreibersii*, *R. aurantius*, *T. georgianus*, *V. caurinus*, *Vespadelus finlaysoni*), mainly occurred in (but were not restricted to) Groups 1 and 2 which were associated with high values for the topographic variables. Although we expected a relationship between microbat assemblages and distance to escarpments, the significant effect of elevation was not predicted. Elevation generally increased away from the coast and was auto-

correlated with 'distance to coastlines', making it unclear which of these features was most important in influencing bat composition.

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

In contrast to the significant relationship identified between bat assemblages and mean climatic variables, there was no significant relationship between ambient temperature (measured at 10 PM each sampling night) at each site and species composition. At the time of year that we sampled, temperature was unlikely to limit the number of bat species that were active. However, during the dry season, low inland temperatures may reduce insect activity, restrict bat activity to the earlier, warmer times of the night and/or induce some species to enter torpor. Therefore, restricting our sampling to one period of the year may have affected our results but sampling at different times of the year would have required a much greater sampling effort. Between years, there was no observable difference in general weather patterns during each sampling period, therefore inter-year variations were unlikely to have affected our results.

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

We assessed several variables involving insect availability at each site. None of the variables showed any significant relationship with microbat assemblages. This suggests that, in the Top End at least, available food resources do not influence the composition of bat communities. This conclusion was consistent with previous research on insect-eating bats that indicated most species capture prey opportunistically (Fenton

1990). Specific research on Tasmanian bats also con-cluded that bat assemblages were generally opportu-nistic foragers (O'Neill & Taylor 1989). Four aspects of our sampling strategy may have influenced our anal-ysis. First, we did not sample non-volant insects and other arthropods that are eaten by some bat species in the Top End (e.g. spiders, C.R. Pavey, unpubl. data 2004). Second, high flying insects that are preyed on by bats such as *Taphozous* spp. were probably not attracted to our light trap. Third, bats may only show a response to insects at certain times of the year. It is likely that at the time of sampling (late dry season), insects were abundant and food resources did not affect the activity of bats. Fourth, insect sampling was limited to one night per site, which may not have been sufficient to provide an adequate representation of overall insect availability. Therefore, we suggest that a combination of insect sampling methods should be used in future assessments of prey availability and bat assemblages, particularly when the diversity of bats is high. These methods should aim to sample volant and non-volant invertebrates.

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

Most sites (34) were sampled in pairs and the min-imum distance between any two sites was 2 km (mean 10 km). Bats can travel long distances during the night. Foraging distances for a selection of species range between 1 km and 10 km (Herr & Klomp 1999; Law & Anderson 2000; Lumsden *et al.* 2002), there-fore some of our results were potentially autocorre-lated due to the same bats being sampled at both sites within a pair. Therefore, we assessed the similarity in site species composition using the Bray-Curtis index. This index was calculated by dividing the number of shared species between pairs of sites by the total num-ber of species of both sites. The resulting value was
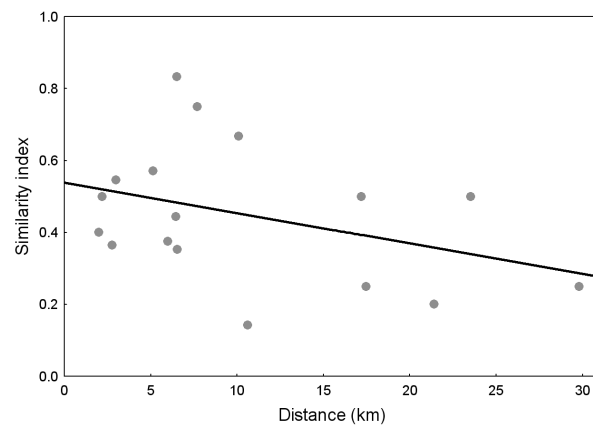

Fig. 4.   Similarity in bat species composition between pairs of sites (using the Bray Curtis similarity index, refer text) plotted against the distance between each pair. Graph also displays the fitted linear regression line.

plotted against the distance between each pair of sites (Fig. 4). The scatter of points was highly variable, however, the slope of the regression line was shallow. This pattern indicated that the relative change in spe-cies composition as a result of geographical separation was small.

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

Comparisons with other studies in Australia

Some of the environmental variables that we found to be significantly correlated with bat assemblages in the Top End differed from those related to bat community variation in other areas of Australia. Waterbodies have been found to support high species diversity and some species are strictly associated with them (Law *et al.* 1998; south-west slopes of NSW.; Young & Ford 2000; central western Queensland). In the Top End, GLM analysis suggested bat species richness increases with decreasing distance to perennial rivers. However, species richness was not exceptionally high at our 'Riparian' sites. Further, Group 2, which was on aver-age closest to rivers, did not have the highest species diversity. Also, we found no significant difference in species assemblages between 'Riverine' and 'Wood-

land' habitats and there was no relationship with distance to available surface water. Given that sampling was carried out during the driest time of the year (late dry season September–November) the likelihood of detecting significant associations with waterbodies was maximized.

A relationship between vegetation structural complexity and microbat diversity has been established in studies in Western Australia (McKenzie & Muir 2000) and NSW (Law *et al*. 1998). By contrast, we found significant correlations of bat species diversity with canopy cover but no associations with structural complexity. Compared with the vegetation in the areas sampled by McKenzie and Muir (2000)and Law *et al*. (1998), the vegetation of the Top End is usually shorter and contains fewer understorey layers (D. Lewis pers. comm. 2004). This limits the degree of vegetation structural complexity in the Top End that likely accounts for the lack of correlation between structural complexity and bat communities.

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

Vegetation corridors beside rivers and surrounding areas (but not the waterbodies themselves) appeared to be important environments as they supported high bat species richness. Bats are regularly characterized by the foraging strategy they employ within their immediate environment (McKenzie & Rolfe 1986; Neuweiler 1989; Schnitzler & Kalko 1998).

Rivers are often associated with environments with tall dense vegetation. These areas do not appear to be of conservation significance because we did not observe high species richness at our 'Riparian' sample sites. However, riverine environments usually have a distinct outer 'edge' and vegetation surrounding these areas is usually shorter and relatively open. We propose that these areas had greater species richness as they provide a diversity of environments for bats that employ different foraging strategies. We recommend that further research be conducted to examine the relationship between rivers and bats in the Top End.

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

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REFERENCES

Andersen A. N., Cook G. D. & Williams R. J., eds. (2003) *Fire in Tropical Savannas: the Kapalga Experiment*. Springer-Verlag, New York.

Belbin L. (1994) *PATN. Pattern Analysis Package*. CSIRO Division of Wildlife & Ecology, Lyneham.

Bowman D. M. J. S., Wilson B. A. & Dunlop C. R. (1988) Preliminary biogeographic analysis of the Northern Territory Vascular Flora. *Aust. J. Bot.* **36,** 503–17.

Churchill S. (1998) *Australian Bats*. Reed New Holland, Sydney.

Clarke K. R. & Green R. H. (1988) Statistical design and analysis for a 'biological effects' study. *Mar. Ecol. Prog. Ser.* **46,** 213–26.

Crawley M. J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.

Crome F. H. J. & Richards G. C. (1988) Bats and gaps: microchiropteran community structure in a Queensland rain forest. *Ecology* **69,** 1960–9.

Dyer R., Jacklyn P., Partridge I., Russell-Smith J. & Williams D., eds. (2001) *Savanna Burning*. Tropical Savannas CRC, Darwin.

Fenton M. B. (1990) The foraging behaviour and ecology of animal-eating bats. *Can. J. Zool.* **68,** 411–22.

Fisher D. O., Owens I. P. F. & Johnson C. N. (2001) The ecological basis of life history variation in marsupials. *Ecology* **82,** 3531–40.

Fox I. D., Neldner V. J., Wilson G. W. *et al.* (2001) *The Vegetation of the Australian Tropical Savannas.* Environmental Protection Agency, Queensland Government, Queensland.

Herr A. (1998) Aspects of the ecology of insectivorous forest-dwelling bats (Microchiroptera) in the western slopes of the Australian alps (PhD Thesis). Charles Sturt University, Albury.

Herr A. & Klomp N. I. (1999) Preliminary investigation of roosting habitat preferences of the large forest bat *Vespadelus darlingtoni* (Chiroptera, Vespertilionidae). *Pac. Conserv. Biol.* **5,** 208–13.

Houlder D. J. (2000) *ANUCLIM* Version 5.1. Centre for Resource and Environmental Studies, Australian National University, Canberra.

Johnson C. N. (1998) Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. *J. Anim. Ecol.* **67,** 689–98.

Johnson C. N. (2002) Determinants of loss of mammal species during the late quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proc. R. Soc. Lond. B.* **269,** 2221–7.

Kantvilas G. & Minchin P. R. (1989) An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest. *Vegetatio* **84,** 99–112.

Kuenzi A. J. & Morrison M. L. (1998) Detection of bats by mist-nets and ultrasonic sensors. *Wildl. Sco. B.* **26,** 307–11.

Kutt A. S. (1995) Activity and stratification of microchiropteran bat communities in thinned, unthinned and old lowland regrowth forest, east Gippsland. *Vic. Natur.* **112,** 86–93.

Law B. S. & Anderson J. (2000) Roost preferences and foraging ranges of the eastern forest bat *Vespadelus pumilus* under two disturbance histories in northern New South Wales, Australia. *Austral Ecol.* **25,** 352–67.

Law B., Anderson J. & Chidel M. (1998) A bat survey in state forests on the south-west slopes region of New South Wales with suggestions of improvements for future surveys. *Aust. Zool.* **30,** 467–79.

Law B. S., Anderson J. & Chidel M. (1999) Bat communities in a fragmented forest landscape on the south-west slopes of New South Whales, Australia. *Biol. Conserv.* **88,** 333–45.

Lumsden L. F. & Bennett A. F. (1995) Bats of a semi-arid environment in south-eastern Australia: biogeography, ecology and conservation. *Wildl. Res.* **22,** 217–40.

Lumsden L. F., Bennett A. F. & Silins J. E. (2002) Location of roots of the Lesser long-eared bat *Nyctophilus geoffroyi* and Gould's wattled bat *Chalinolobus gouldii* in fragmented landscape in south-eastern Australia. *Biol. Conserv.* **106,** 237–49.

Lunney D., Baker J., Priddel D. & O'Connell M. (1988) Roost selection by Gould's long-eared bat, *Nyctophilus gouldi,* Tomes (Chiroptera: Vespertilionidae) in logged forest on the south coast of New South Wales. *Aust. Wildl. Res.* **15,** 375–84.

McDonald R. C., Isbell J. G., Speight J. G., Walker J. & Hopkins M. S. (1998) *Australian Soil and Land Survey Field Handbook*. Department of Primary Industries and Energy and CSIRO Australia, Canberra.

McKenzie N. L. & Muir W. P. (2000) Bats of the southern Carnarvon Basin, Western Australia. *Rec. West. Aust. Mus.* **61 (**Suppl), 465–77.

McKenzie N. L. & Rolfe J. K. (1986) Structure of bat guilds in the Kimberley mangroves, Australia. *J. Anim. Ecol.* **55,** 401–20.

Meakin C., Owen G., Brocklehurst P. & Lewis D. (2001) *NORFOR. Mapping the Forest Cover of the NT. Document 1 Field Methodology and FPC Indexing*. Department of Lands Planning and Environment, Palmerston.

Menkhorst K. A. & Woinarski J. C. Z. (1992) Distribution of mammals in monsoon rainforests of the Northern Territory. *Wildl. Res.* **19,** 295–316.

Milne D. J. (2002) *Key to the Bat Calls of the Top End of the Northern Territory*. Technical report no. 71. Parks and Wildlife Commission of the Northern Territory. Darwin.

Milne D. J., Armstrong M., Fisher A., Flores T. & Pavey C. R. (2004) A comparison of three survey methods for collecting bat echolocation calls and species accumulation rates from nightly Anabat recordings. *Wildl. Res.* **31,** 57–63.

Murray K. L., Britzke E. R., Haley B. M. & Robbins L. W. (1999) Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. *Acta Chiroptol.* **1,** 105–12.

Neuweiler G. (1989) Foraging ecology and audition in echolocating bats. *TREE* **4,** 160–6.

O'Farrell M. J. & Gannon W. L. (1999) A comparison of acoustic *versus* capture techniques for the inventory of bats. *J. Mamm.* **80,** 24–30.

O'Neill M. G. & Taylor R. J. (1989) Feeding ecology of Tasmanian bat assemblages. *Aust. J. Ecol.* **14,** 19–31.

Pardon L. G., Brook B. W., Griffiths A. D. & Braithwaite R. (2003) Determinants of survival for the northern brown bandicoot under a landscape-scale fire experiment. *J. Anim. Ecol.* **72,** 106–15.

Russell-Smith J. (1991) Classification, species richness, and environmental relations of monsoon rain forest in northern Australia. *J. Veg. Sci.* **2,** 259–78.

Schnitzler H.-U. & Kalko E. K. V. (1998) How echolocating bats search and find food. In: *Bat Biology and Conservation* (eds T. H. Kunz & P. A. Racey.), pp. 183–96. Smithsonian Institution Press, Washington and London.

Strahan R., ed. (1995) *The Mammals of Australia*. Reed Books, Sydney.

Taylor R. J. & O'Neill M. G. (1988) Composition of the bat (Chiroptera: Vespertilionidae) communities in Tasmanian forests. *Aust. Mamm.* **9,** 125–30.

Watson M. & Woinarski J. (2003) *Vertebrate Monitoring and Re-Sampling in Kakadu National Park, 2002*. Report to Parks Australia. Department of Infrastructure, Planning and Environment. Darwin.

Whitehead P. J., Bowman D. M. J. S. & Tidemann S. C. (1992) Biogeographic patterns, environmental correlates and conservation of avifauna in the Northern Territory, Australia. *J. Biogeogr.* **19,** 151–61.

Whitford K. R. (2002) Hollows in jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophilla*) trees. I. Hollow sizes, tree attributes and ages. *For. Ecol. Manage.* **160,** 201–14.

Woinarski J. C. Z. & Gambold N. (1992) Gradient analysis of a tropical herpetofauna: distribution patterns of terrestrial reptiles and amphibians in Stage III of Kakadu National Park, Australia. *Wildl. Res.* **19,** 105–28.

Woinarski J. C. Z. & Fisher A. (1995) Wildlife of Lancewood, *Acacia shirleyi* thickets and woodlands in Northern Australia. 1. Variation in vertebrate species composition across the environmental range occupied by Lancewood vegetation in the Northern Territory. *Wildl. Res.* **22,** 379–411.

Woinarski J. C. Z., Braithwaite R. W., Menkhorst K. A., Griffin S., Fisher A. & Preece N. (1992) Gradient analysis of the distribution of mammals in Stage III of Kakadu National Park, with a review of the distribution patterns of mammals across north-western Australia. *Wildl. Res.* **19,** 233–62.

Woinarski J. C. Z., Fisher A. & Milne D. (1999) Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern Territory, Australia. *J. Trop. Ecol.* **15,** 381–98.

Woinarski J. C. Z., Brock C., Armstrong M., Hempel C., Cheal D. & Brennan K. (2000) Bird distribution in riparian vegetation in the extensive natural landscape of Australia's tropical savanna: a broad-scale survey and analysis of a distributional data base. *J. Biogeogr.* **27,** 843–68.

Woinarski J. C. Z., Milne D. J. & Wanganeen G. (2001) Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecol.* **26,** 360–70.

Young R. A. & Ford G. I. (2000) Bat fauna of a semi-arid environment in central western Queensland, Australia. *Wildl. Res.* **27,** 203–15.