

Small Mammals of the Mitchell Plateau Region, Kimberley, Western Australia

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Abstract

This paper presents the background for a series on the biology of small mammals in the Mitchell Plateau region, an area characterised by a wet-dry tropical climate. From June 1981 to December 1982, 19 species of small terrestrial mammals were captured at Mitchell Plateau. Of 17 species captured on eight mark-release grids, 13 clustered into four significant groups which reflected the major habitats of the region: (1) *Sminthopsis virginiae*, *Leggadina* sp. and *Pseudomys nanus* in riparian and plateau escarpment sites; (2) *Phascogale tapoatafa*, *Trichosurus arnhemensis* and *Pseudomys laborifex* in plateau open forest; (3) *Conilurus penicillatus* and *Mesembriomys macrurus* in open woodland and coastal mosaics; (4) the commoner species *Dasyurus hallucatus*, *Isoodon macrourus*, *Melomys* sp. cf. *burtoni*, *Zyzomys argurus* and *S. woodwardi* in an array of habitats. *Rattus tunneyi*, *Pseudantechinus* sp., *Wyulda squamicaudata* and *Planigale maculata* did not cluster significantly with other species. Two species, *Pseudomys delicatulus* and *Mesembriomys gouldii*, were represented by single specimens captured outside the capture-mark-release grids, in sandstone and plateau woodland respectively. Open forests, particularly on the lateritic plateau surfaces, had the richest and most diverse mammal assemblage over the entire study period. The vine thickets and sandstone contained relatively stable populations of fewer species, and several habitats had seasonally variable populations and species.

Introduction

During the last few decades numerous studies have been made integrating genetic, morphologic, physiologic, behaviour and demographic aspects of the biology of small mammals. Such studies, however, have been almost exclusively on northern-hemisphere temperate species. Very few have examined several populations of the same species simultaneously, despite the importance of such an approach as stressed by Lidicker (1978) who stated that 'in short one cannot ignore an organism's physiology and expect to fully understand its population dynamics'.

In Australia the few studies on native small mammals that have followed this integrative approach have been made on temperate marsupials (Lee *et al.* 1977; Barnett *et al.* 1979a, 1979b, 1982; Bradshaw 1983; Main 1983). Fleming (1975) reviewed the extent of studies on small mammals in tropical Australia. Since that review other major studies by Redhead (1979), Begg (1981a, 1981b, 1981c), Begg *et al.* (1983), Friend (1985) and Kerle (1985) have been published. The only tropical study with an ecophysiological aspect is that carried out on the hill kangaroo, *Macropus robustus*, by Ealey and Main (1967).

The Mitchell Plateau region, which is bounded by the Mitchell and Lawley Rivers (c. 14°44'S., 125°44'E.), is noted for its richness of plants and animals and for its physiographic diversity (Anon. 1981). Forty-one species of native mammals are known here (Kitchener *et al.* 1981; unpublished data). In part this is probably due to the variety of

habitats afforded by the topography of the laterite-capped plateau, 340 m high, which has an area of *c.* 220 km² and dominates the region. Of equal importance is the fact that there is an almost complete assemblage of modern mammals. Their survival owes much to the remoteness of the region, for until recently European man has made little impact on the fauna. Only cats *Felis catus*, and a few cattle *Bos taurus* along the creeks, are known to be feral in the region; the large numbers of donkeys, horses, goats or cattle, that have altered the vegetation elsewhere in the region so extensively (Kitchener 1978; McKenzie 1981), are absent. Furthermore, the rugged topography prevents bushfires from exerting the intensive and wide-scale damage noted elsewhere in Western Australia. Most burns in the sandstone and rockier parts of the region are extremely patchy, and ample sanctuaries for plants and animals remain.

Following broad-scale surveys of the Mitchell Plateau region, Kitchener *et al.* (1981) proposed that in many species of small mammals breeding was reduced towards the end of the 'dry' season, and suggested that, unlike the situation in temperate Australia (Tyndale-Biscoe 1973), September–November is a period of environmental stress. Furthermore, some species seemed restricted to particular vegetation types (riparian, deciduous vine thickets, mangal) and others ranged more widely; one species dispersed some distance in the 'wet' season.

This paper examines the environment and the small mammal assemblage of the Mitchell Plateau region, and provides background information essential to a series of papers to follow on the ecophysiology, genetics, taxonomy and parasitology of selected mammal species in this region.

Methods

Major sampling was carried out for 3–4 weeks in September–October 1981, January 1982, April 1982, July 1982 and September–October 1982. A short reconnaissance trip was undertaken in June 1981 to assess prospective grid sites, and in November 1982 three sites (WM, DV, CS) were trapped to collect additional information on key species.

Trapping

Eight trapping grids were selected for the capture–mark–release (CMR) aspects of the mammal study. Each of these CMR grids was paired with a site in similar habitat (removal sites) from which specimens were taken for dissection and preservation. Each CMR grid was a square consisting of 100 traps located at 15-m intervals. In the vine thicket, narrow paths were cut along trap-lines in order to facilitate movement between trapsites. One small Elliott trap (10 by 9 by 32 cm) was placed at each site. Ten cage traps (23 by 23 by 66 cm) were distributed evenly throughout the trapsites on all grids, as were 10 large Elliott traps (15 by 15 by 45 cm). Traps were baited with a mixture of peanut paste, rolled oats, raisins and bacon bits, and placed on the ground, except at the tidal site at Walsh Point where they were placed on branches. They were checked every morning, each grid taking 0.5–7.0 h to complete, depending on the number of animals captured. Trapping was carried out over five nights on each grid; additional trapnights were conducted for specific purposes. At the first capture for each trapping session animals were marked by toe clipping, weighed and measured, and a blood sample was taken by orbital sinus puncture (Riley 1960). Reproductive condition, relative age, moult and sex were also recorded for each animal. At subsequent captures for each trip only the type of trap and its position; and reproductive condition and weight of animals were recorded. A cloacal or rectal swab was taken from each individual and placed into a small vial of transport medium, and later screened for *Salmonella* and *Arizona* (How *et al.* 1983). Animals which accidentally died on CMR grids were processed in the same manner as animals from the removal sites.

Animals from removal sites were returned to the laboratory in calico bags, and then killed with an overdose of Nembutal (Abbott Laboratories, Sydney). They were then weighed and measured, and their sex, age, moult and reproductive condition noted. Reproductive organs were removed and fixed in alcoholic Bouin's solution, and the liver (and sometimes kidney, heart and muscle) was frozen in liquid nitrogen and sent to the Institute of Medical and Veterinary Science, Adelaide, for isozyme screening.

Study Sites

Trapping grids were chosen to represent the variety of habitats in the region. Their locations are shown in Fig. 1. Temperature and relative humidity on selected CMR grids were recorded by hygrothermographs placed on the ground in modified Stephenson screens, or in rock shelters if available,

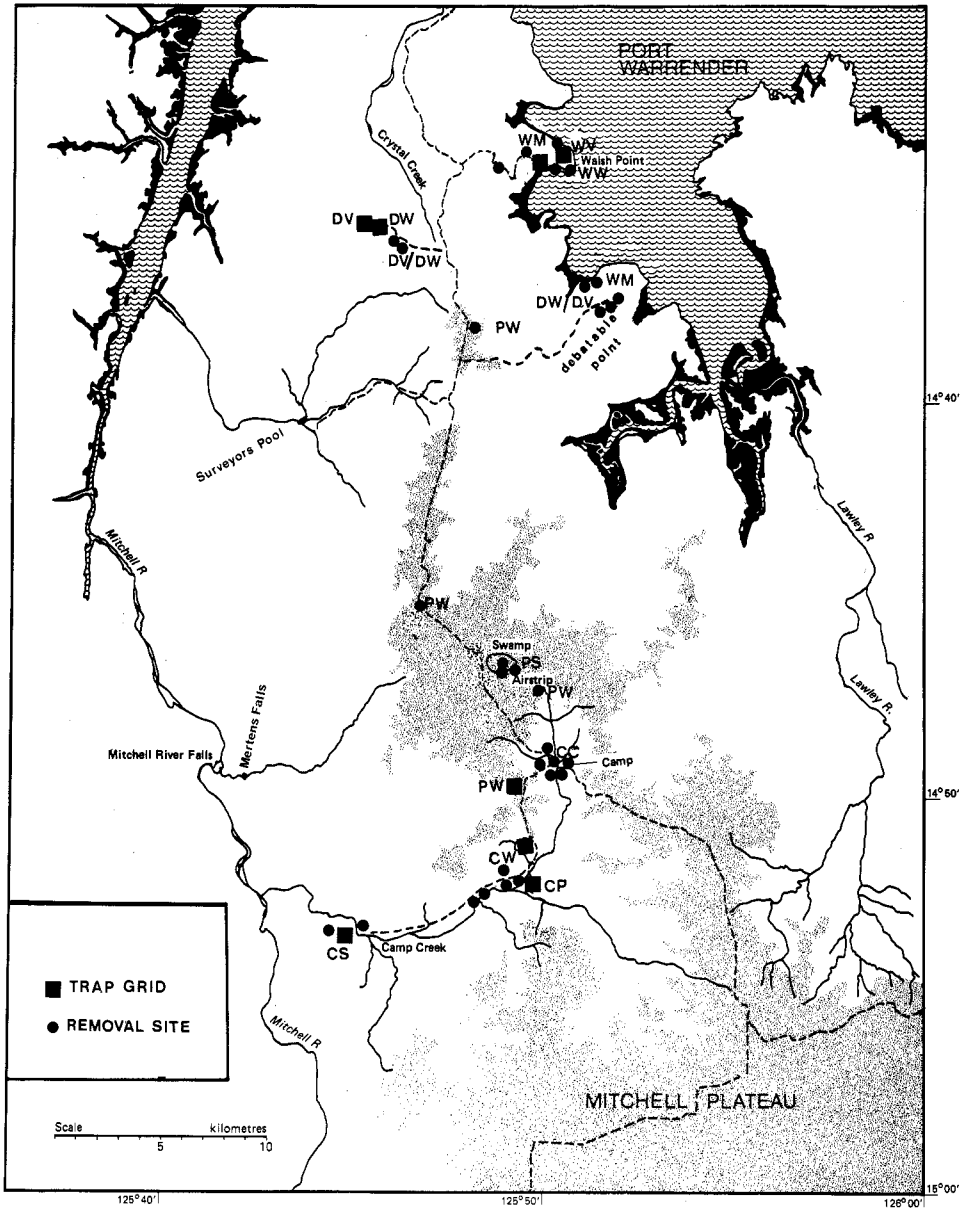


Fig. 1. Map of the Mitchell Plateau region showing the location of the eight CMR grids (■) and the removal sites (●) trapped during 1981–82. Habitat descriptions associated with the grid codes are presented in text (pp. 400–1).

and calibrated in the field against a whirling hygrometer. The extent of litter fall in selected grids was measured by means of 20 buckets (0.049 m^2), each provided with screened drainage holes and placed at ground level.

Removal sites were structurally and floristically similar to, and where possible adjacent to, trapping grids. Individuals removed from these sites provided detailed data on morphometric and reproductive condition and parasite load.

Statistics

Dendrograms of species-groups related to habitat type were produced by WPGMA cluster analysis (Sneath and Sokal 1973) on Jaccard's indices of association for presence/absence data (see Southwood 1978). The statistical significance of the clusters was determined following Strauss (1982), by taking the 95% occurrence of each node level following the accumulation of about 3500 nodes derived from random data sets by the same clustering procedure. In the randomisation process the number of species per site was kept constant but the species present were randomly allocated.

Study Areas

The floristics of the trapping sites have either been described in detail by Hnatiuk and Kenneally (1981) or were similar to habitats described by these authors.

The habitats selected for the study included sites on the plateau (laterite), the scarp (Carson Volcanics), the surrounding lowlands (King Leopold Sandstone) and coastal locations. They are briefly described below.

(i) CMR grids

(CS) *Camp Creek Sandstone*. Adjacent to Camp Creek. Includes both Low Open Woodland and Hummock Grass, on King Leopold Sandstone which occurs as a platform and also deeply fractured into large boulders and intermixed with thickets of dense *Triodia* sp. A small part of the grid was burnt in June 1981.

(CP) *Crusher Plant Volcanics*. A riparian situation on the edge of Camp Creek. *Pandanus* sp. fringing the creek gives way to Low Woodland over Dense Tall Grass. Soils near the creek are deep but become pebbly and shallower with distance from the creek. In June 1981 fires left small areas of tall grass at the creek's edge, and the area was flooded to a depth of 1.5 m in January 1982.

(CW) *Camp Creek Woodland*. Just off the plateau in Low Open Woodland over *Livistona eastonii* palms on a volcanic substrate (which protrudes in places as stones and boulders). Most of the grass layer was burnt in June 1981.

(PW) *Plateau Forest*. On the plateau laterite in the Open Forest representative of much of the Plateau; *Eucalyptus tetradonta* and *E. nesophila* were dominant and intermixed with numerous *Livistona eastonii* over a tall grass layer. Part of the grid is a Low Grassland beneath occasional *E. latifolia*. Burnt by a fire of moderate intensity in mid-October 1981.

(DW) *Lone Dingo Woodland*. An outlying part of the lateritic plateau. This grid is on the top and over the north-east and south-west side of the ridge, includes some rocky boulders along the middle of the ridge, and is adjacent to DV. Vegetation is Open Woodland dominated by *Eucalyptus miniata* with occasional *Livistona eastonii*. Shrub layer is Sparse to Dense Tall Grass. Burnt in late May or early June 1982.

(DV) *Lone Dingo Vine Thicket*. Situated on the south-westward-facing slope of deciduous vine thicket (Dense Low Forest). Vines are more numerous than in Walsh Point Vine Thicket. This area is also much less deciduous than the coastal vine thicket, possibly because of its different aspect.

(WM) *Walsh Point Mosaic*. Three habitat types are included: Mangal, Open Woodland over Dense Tall Grass, and a rocky creek containing large boulders and Vine Thicket elements. The substrate is of Carson Volcanics which drops steeply into mud at mangroves. Woodland adjacent was burnt in June 1981.

(WV) *Walsh Point Vine Thicket*. Deciduous vine thicket (Dense Low Forest over Dense Thicket) between beach and volcanic cliff. The more coastal aspect of the grid was extensively defoliated between June and November. The surrounding vegetation was burnt in June 1981.

(ii) *Removal sites*

(CS) *Camp Creek Sandstone*. Several subsites over 500 m from the CMR grid. Subsites included one in a rocky dry creek bed with some Dense Tall Grass, one on top of a sandstone platform (an area burnt in June 1981), and a major site in deeply fractured sandstones to the west of the main grid. This last site was used as an extension to CS for the larger mobile species, *D. hallucatus* and *W. squamicaudata*, which were marked and released.

(CC) *Camp Creek Mosaics*. Several sites surrounding the exploration camp and encompassing Low Woodlands to Low Open Woodlands with an understorey of scattered shrubs over dense grasses to 2 m high, on fine grey sandy silt which becomes powdery in the dry season. Burnt in October 1981.

(CP) *Crusher Plant Volcanics*. Five subsites in similar riparian habitat 1–4 km from CP. Some subsites were burnt in June 1981, but regeneration of the grasses resulted in good cover to about 0.25 m by September 1981. Unburnt areas are Dense Tall Grass or *Pandanus* sp. fringing dry creek beds.

(CW) *Crusher Forest–Woodland*. On better drained soils with exposures of basalt adjacent to CP sites. Generally with *Livistona eastonii* dominant.

(PW) *North Plateau Forest*. Mixed-eucalypt Open Forest over Tall Grass. Lateritic substrate, soils deep and friable. Differs from PW in that it includes an array of the floristic and edaphic diversity found on the laterite plateau.

(DV/DW) *Lone Dingo Woodland and Vine Thicket*. Similar to DV and DW and sited between 0.3 and 1.5 km from the grid in areas of adjacent Woodland and Vine Thicket on laterite. Two similar sites were trapped at 'debatable point' overlooking the Lawley River mouth in January 1982 and July 1982.

(WM) *Walsh Point Mosaic*. Sites are up to 2 km distant from WM grid, and include mangal, unburnt Tall Grass Woodland, burnt (June 1981) woodland, and rocky volcanic scree along dry creek gullies. In January 1982 some trapping was done near the coastal areas of 'debatable point', in a mosaic of habitats closely resembling these sites.

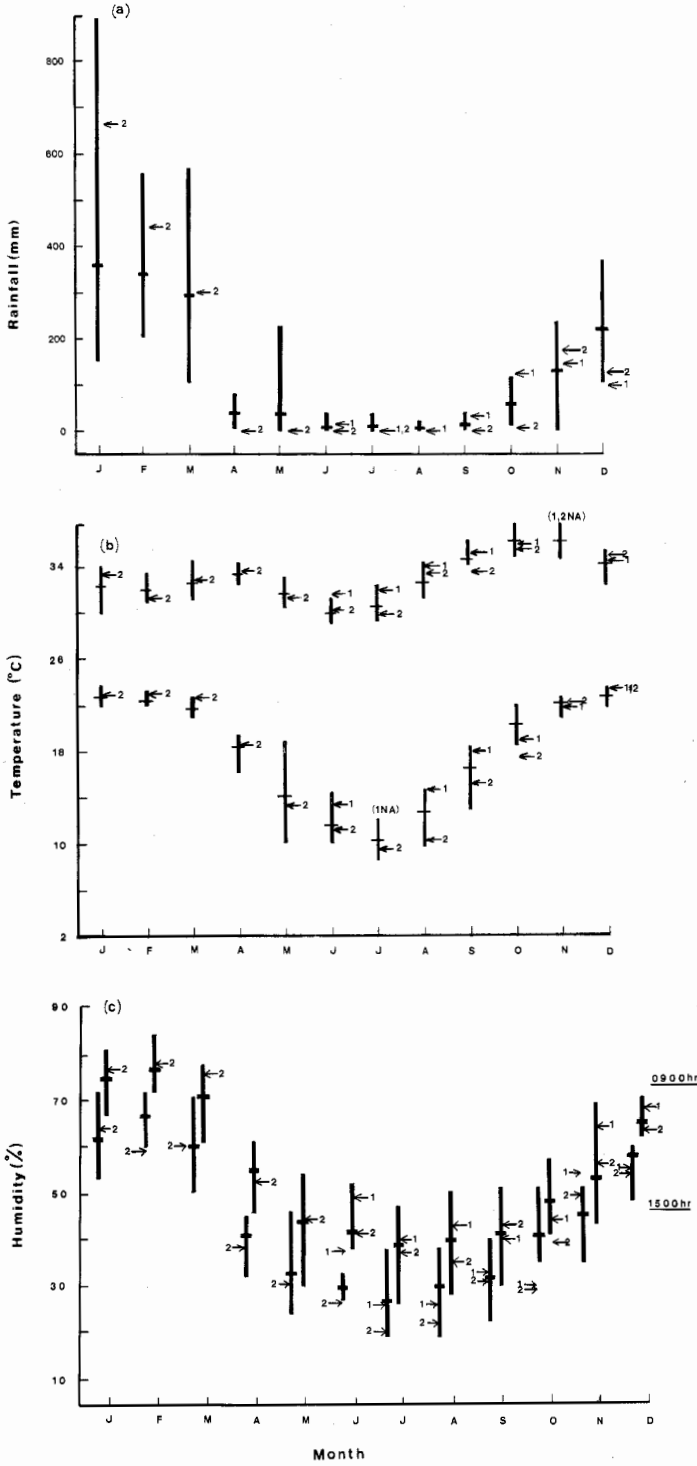
(WV) *Walsh Point Vine Thicket*. One site in the same vine thicket as WV but 300 m from the CMR grid.

(PS) *Plateau Swamp*. Located just north of the airstrip. This site was dry in September–October 1981, and contained Dense Low Forest over Dense Tall Grass with dense *Melaleuca* sp. It was burnt by a cool fire on 15 October 1981 while trapping was in progress. It was flooded during Cyclone Bruno in January 1982, and contained free water for the rest of 1982. This site had no equivalent in the CMR grids.

Climate

The mean monthly rainfall, temperature and relative humidity patterns are illustrated in Fig. 2. Average annual rainfall (1459–1583 mm) place the region in the wettest part of the Kimberley. Beard (1976) estimated that there are usually six 'ombrothermic' wet months each year, from October to March; this provides the region with a longer growing season for plants than is available elsewhere in the Kimberley. Tropical cyclones strike the area about twice in every 3 years (Wilson 1981). Fogs occur occasionally throughout the year; the maximum number of days with fog per month was 13 in August 1972.

Lightning strikes during December–April are unlikely to fire the green, and frequently damp,



ground vegetation; at best they would probably produce very patchy burns. However, the high frequency of potential lightning strikes in October and November, when little rain has fallen and most of the ground vegetation is very dry and readily flammable, suggests that during these months fires occur naturally in the region.

Results

Climate

During the study period rainfall was well above average in October and November 1981, but December 1981 was the driest for the past 12 years. The wet season 'proper' did not begin until 17 January 1982, when Cyclone Bruno passed within 40 km of the campsite, depositing above-average rain for this month. February and March 1982 also were wetter months than average. Both mean maximum and minimum daily temperatures during the study period (Fig. 2*b*) varied irregularly about the 10-year monthly averages. The dry season was marginally warmer than average in 1981, but marginally cooler in 1982.

Table 1. Litter fall at four sites in the Mitchell Plateau region

Values are means \pm standard deviations, dry weight, with coefficients of variation in parentheses. — Litter not removed at that visit. The value for the year is that for the entire study period at that site, which may be more or less than one calendar year. For rank order and site differences, underlining indicates values not significantly different at $\alpha < 0.05$ (ANOVA + LSD)

	Site WV (a)	Site DV (b)	Site WM (c)	Site CS (d)	Site differences
No. of samples	19	20	7	10	
Litterfall ($\text{g m}^{-2} \text{d}^{-1}$)					
Oct.–Jan. (1)	0.53 ± 0.38 (71)	—	0.60 ± 0.41 (68)	—	<u>ac</u>
Jan.–Apr. (2)	0.99 ± 0.42 (42)	0.71 ± 0.25 (35)	0.81 ± 0.88 (109)	0.38 ± 0.30 (79)	<u>dbca</u>
Apr.–July (3)	2.21 ± 0.80 (36)	1.52 ± 0.52 (34)	—	0.39 ± 0.36 (93)	b < a
July–Sept. (4)	1.28 ± 0.74 (58)	1.26 ± 0.37 (29)	0.58 ± 0.46 (79)	0.73 ± 0.73 (100)	<u>cd < ba</u>
Sept.–Nov. (5)	0.54 ± 0.51 (94)	1.57 ± 0.55 (35)	—	—	a < b
All year	403 ± 136 (32)	399 ± 70 (18)	$234^A \pm 147$ (63)	152 ± 134 (88)	<u>dc < ba</u>
F_s	25.8	16.1	0.31	1.4	
Degress of freedom	4,90	3,76	2,19	2,23	
Significance (P)	<0.001	<0.001	NS	NS	
LSD _{0.05}	0.38	0.27			
Ascending rank order (trip)	<u>1 5</u> <u>2 4</u> 3	2 <u>4</u> 3 5	<u>1 2</u> 4	<u>2 3</u> 4	

^A On an annual basis, at site WM the mangroves had greater leaf fall ($432 \text{ g m}^{-2} \text{ y}^{-1}$) than the rest of the grid ($170 \text{ g m}^{-2} \text{ y}^{-1}$) ($F_{s1,20}$, 8.87; $P < 0.01$).

Litter

Litter fall (Table 1) was within the range expected for the wet-dry tropics (Whittaker 1970). Two sites (WV, DV) showed pronounced seasonal variation in leaf fall, which was

Fig. 2 Climatic records for Mitchell Plateau for August 1970–February 1981 for: (a) rainfall, monthly mean and range; (b) temperature, mean daily maximum and minimum; (c) relative humidity, monthly mean at 0900 and 1500 h. Average values and their ranges denoted by horizontal and vertical lines respectively. The monthly values for the period of this project (June 1981–December 1982) are indicated by: 1, 1981; 2, 1982.

Table 2. Numbers of individuals of each species captured on the capture-mark-recapture grids and collected from the removal sites

See pp. 400–1 for coding and description of sites

Family and species	CS	CP	CW	PW	DW	DV	WM	WV	CC	PS
Captured on capture-mark-recapture grids										
Dasyuridae										
<i>Pseudantechinus</i> sp.	5									
<i>Dasyurus hallucatus</i>	40				7	10	6	14		
<i>Phascogale tapoatafa</i>				1						
<i>Planigale maculata</i>			3	6			2			
<i>Sminthopsis virginiae</i>		3	6	2						
Peramelidae										
<i>Isodon macrourus</i>		11			22	31	10	2		
Phalangeridae										
<i>Trichosurus arnhemensis</i>				2						
<i>Wyulda squamicaudata</i>	13							1		
Muridae										
<i>Conilurus penicillatus</i>					1		12			
<i>Leggadina</i> sp. cf. <i>lakedownensis</i>		6	3	1						
<i>Melomys</i> sp. cf. <i>burtoni</i>					1	78	59	33		
<i>Mesembriomys gouldii</i>							1			
<i>Mesembriomys macrurus</i>					5					
<i>Pseudomys delicatulus</i>										
<i>Pseudomys nanus</i>		34	1	2	3					
<i>Pseudomys laborifex</i>				7						
<i>Rattus tunneyi</i>	1	3		3	4					
<i>Zyzomys argurus</i>	106			1	16	2	22	19		
<i>Zyzomys woodwardi</i>	5				1	4	3	27		
Collected from removal sites										
Dasyuridae										
<i>Pseudantechinus</i> sp.	2									
<i>Dasyurus hallucatus</i>	15	1		7	2	3	8	1		
<i>Phascogale tapoatafa</i>										
<i>Planigale maculata</i>				4					1	
<i>Sminthopsis virginiae</i>		7	5						7	2
Peramelidae										
<i>Isodon macrourus</i>		2		16	1	6	5			
Phalangeridae										
<i>Trichosurus arnhemensis</i>				2			2			
<i>Wyulda squamicaudata</i>	3					1				
Muridae										
<i>Conilurus penicillatus</i>				1			7			
<i>Leggadina</i> sp. cf. <i>lakedownensis</i>		2	3	1					5	
<i>Melomys</i> sp. cf. <i>burtoni</i>						15	48	8	8	5
<i>Mesembriomys gouldii</i>				1						
<i>Mesembriomys macrurus</i>					1	1				
<i>Pseudomys delicatulus</i>	3									
<i>Pseudomys nanus</i>		21	1						12	2
<i>Pseudomys laborifex</i>			1	3					3	
<i>Rattus tunneyi</i>		19		10			1		13	72
<i>Zyzomys argurus</i>	63			1	5	15	15	5	10	
<i>Zyzomys woodwardi</i>	5					10	15	10	1	

monophasic at WV (April–July) and biphasic (April–July; September–November) at DV. Litter fall increased by 87% at CS in July–September, but high variance prevents statistical separation. The heterogeneity of vegetation is reflected in the coefficient of variation; it is very low at DV, moderate at WV, and very high at both WM and CS. Both the last sites are vegetation mosaics. Litter fall in both vine thicket grids was similar, but it was much lower at WM and CS. Dividing the WM litter catch into mangrove trees only and the rest of the grid showed that mangroves had the highest litter fall of all sites ($432 \text{ g m}^{-2} \text{ y}^{-1}$) but on the rest of the grid it was close to that of CS. Although samples are small, there is no indication of marked seasonality of mangrove litter fall.

The Small Mammal Community

Nineteen species of mammals were captured during the project, including two (*Phascogale tapoatafa* and *Mesembriomys gouldii*) which were not previously recorded from the region.

From their distribution and abundance, species fell into four groups: (1) those well represented in CMR grids throughout the year in at least two different habitat types (*Dasyurus hallucatus*, *Isodon macrourus*, *Zyzomys argurus* and *Melomys* sp. cf. *burtoni*); (2) those moderately represented in CMR grids throughout the year but numerically abundant in only one habitat type (*Wyulda squamicaudata*, *Conilurus penicillatus* and *Zyzomys woodwardi*); (3) those moderately abundant throughout the year when CMR and removal sites are combined, and present in several habitat types (*Sminthopsis virginiae*, *Pseudomys*

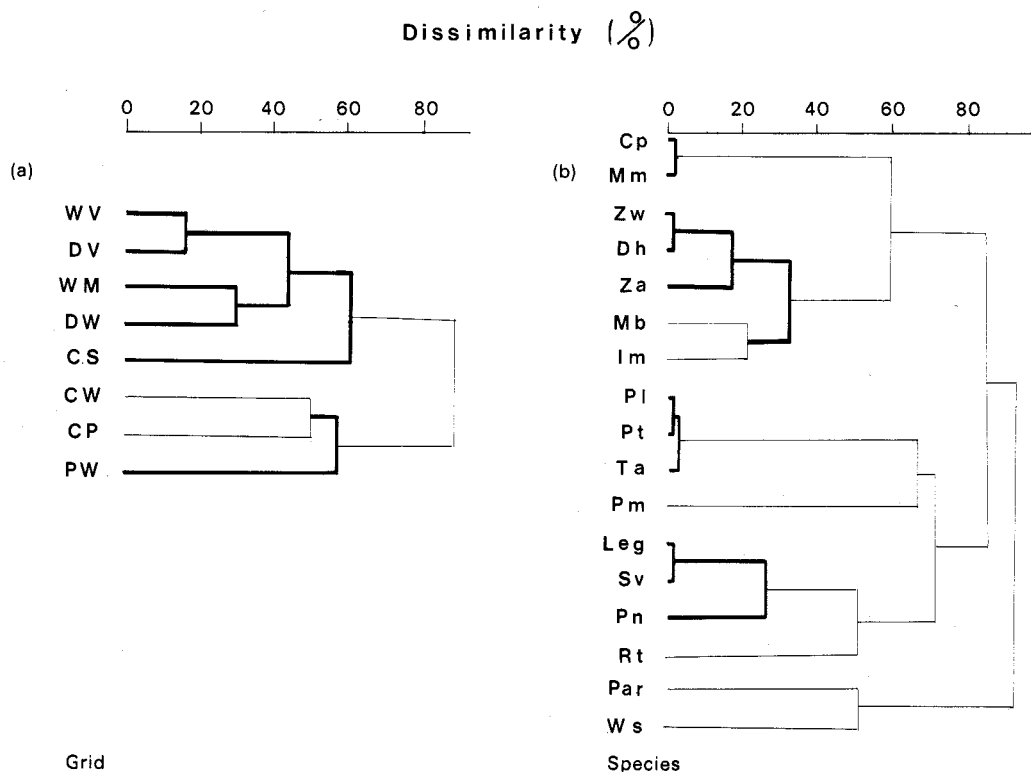


Fig. 3. Dendrogram of similarity of: (a) CMR grids, based on the presence or absence of mammal species during 1981 and 1982; (b) mammal species at Mitchell Plateau, based on their presence on CMR grids during 1981 and 1982. Bold lines indicate significant ($\alpha=0.05$) associations. Codes for species are as for Fig. 4. See text for explanation and description of CMR grids.

nanus, *Rattus tunneyi*); (4) those captured too infrequently to provide much information on basic biology (*Pseudantechinus* sp., *Phascogale tapoatafa*, *Planigale maculata*, *Trichosurus arnhemensis*, *Leggadina* sp. cf. *lakedownensis*, *Mesembriomys gouldii*, *M. macrurus*, *Pseudomys delicatulus*, *Pseudomys laborifex*).

Community Groups

Mammal species varied greatly in the extent to which they utilised the habitats at Mitchell Plateau (Table 2). Cluster analysis of associations of mammal species based on their presence or absence in the different CMR grids revealed four significant groups of species (Fig. 3a). These are as follows: (1) *S. virginiae*, *Leggadina* sp. and *P. nanus*, on the deeper soils of the riparian and escarpment sites and occasionally on the laterites of the plateau itself; (2) *P. tapoatafa*, *T. arnhemensis* and *P. laborifex*, in the plateau Open Forest; (3) *C. penicillatus* and *M. macrurus*, in Open Woodlands and coastal mosaic sites; (4) *D. hallucatus*, *I. macrourus*, *Melomys* sp. cf. *burtoni*, *Z. argurus* and *Z. woodwardi*, which were abundant and widespread species occupying most habitats from coastal to inland sites, although *I. macrourus* and *Melomys* sp. cf. *burtoni* were absent from sandstone. *Rattus tunneyi*, *Pseudantechinus* sp., *W. squamicaudata* and *P. maculata* do not group significantly with other mammal species. *Mesembriomys gouldii* and *P. delicatulus* were recorded from the removal sites only. A single specimen of the former was collected from the northern plateau woodland, which had been burnt 8 weeks previously, and three specimens of the latter were collected from an extension of the CS grid. The above species groupings are similar to data from the removal sites, where trapping was less intensive.

Clustering of CMR grids based on presence or absence of mammal species (Fig. 3b) showed that the coastal and near-coastal grids (WV, DV, WM, DW) clustered tightly together and were similar to the sandstone grid (CS). Interestingly, the woodland site of DW does not cluster with the other (more inland) woodland sites (CW, PW). These more inland woodlands cluster with the inland riparian site of CP, which also has some low woodland vegetation.

Species Abundance

The abundance of each species varied both within and between grids, as indicated by changes in the number of individuals captured on grids for each sampling session (Fig. 4). The percentage of marked individuals during each trapping period shown in Fig. 4 suggests important demographic trends for several species.

The largest population of *D. hallucatus* was at CS, where the proportion of marked individuals increased during much of the study. This population was apparently more stable than the small ones at DW, DV, WV and WM, all of which had a much higher turnover of individuals. As will be detailed elsewhere, this species had home ranges considerably greater than grid area.

Isoodon macrourus at DW, DV and WM had populations with low turnover of individuals. It occurred at CP and WV in September–October 1981, probably as a consequence of fire which burnt part of the former grid and ringed the latter one in June 1981, so that they became important habitat refuges for the rest of the dry season. This may also account for the high proportion of marked individuals captured between June and September 1981 at CP. The complete turnover of individuals at CP by January 1982 was the result of that grid being flooded to a depth of 1.5 m. Unlike Kitchener *et al.* (1981), we did not collect this species on sandstone.

Melomys had large populations at DV and WM, and a smaller one at WV. It was most abundant in the mangroves, where the density was about 40 individuals per hectare. Individuals were seen at night in the centre of the seaward fringe of the mangroves, and along the edges of the channels, together with *Trichosurus arnhemensis*. Although numbers of *Melomys* at these grids fluctuated considerably, only at WV did the proportion of marked

individuals fail to increase consistently throughout the study. This observation, coupled with the lower numbers at WV, suggests that of the three grids, this last has the habitat least favoured by this species.

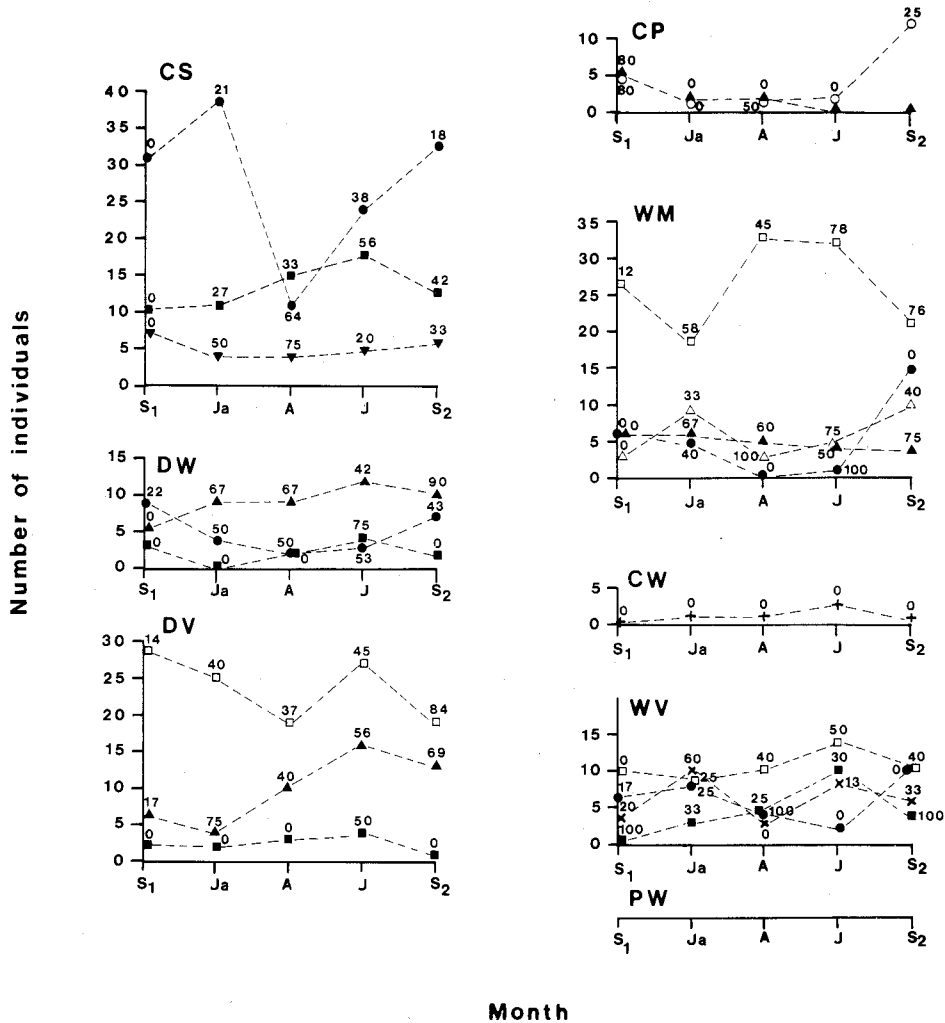


Fig. 4. Numbers of individuals captured on each CMR grid during the 1981 and 1982 survey periods at Mitchell Plateau. Numerals are percentage of recaptures. Plots are only for species captured five or more times. Dh (■), *Dasyurus hallucatus*; Sv (+), *Sminthopsis virginiae*; Im (▲), *Isoodon macrourus*; Ws (▼), *Wyulda squamicaudata*; Mb (□), *Melomys* sp. cf. *burtoni*; Cp (△), *Conilurus penicillatus*; Za (●), *Zyzomys argurus*; Zw (×), *Z. woodwardi*; Pn (○), *Pseudomys nanus*. S₁, September 1981; Ja, January 1982; A, April 1982; J, July 1982; S₂, September 1982.

The pattern of abundance of *P. nanus* at CP was similar to that of *I. macrourus*: 18 individuals were caught at this site in June 1981 as part of the preliminary trapping program, and four of the five captured in September 1981 were recaptures. This species remained at low densities for most of the year, with peak numbers in September–October. At CP it was densest on the deeper alluvial soils adjacent to the creek, where soil moisture remained higher for longer, with a consequent extension of the growing and seeding period for native grasses.

Numbers of *Z. argurus* fell markedly between January and April on all grids. This decline corresponded to a high proportion of recaptures on CS, DW and WV, suggesting an actual decline in population numbers. The local extinction of *Z. argurus* at WM in April is explained by the flooding of this grid at the end of the wet season. The relatively high numbers in September–October 1982 at CS, DW, WV and WM, coupled with low recaptures of individuals, probably reflects recruitment of juveniles into the population, and possibly of some adults from adjacent areas.

Z. woodwardi was most abundant at WV, although its numbers were low there and, like those of *Z. argurus*, declined between January and April. The trend in numbers of recaptures corresponded to numbers of individuals caught.

With the exception of *W. squamicaudata* (discussed by Humphreys *et al.* 1984), the other species were present in low numbers on the CMR grids and nothing is known of their population fluctuations.

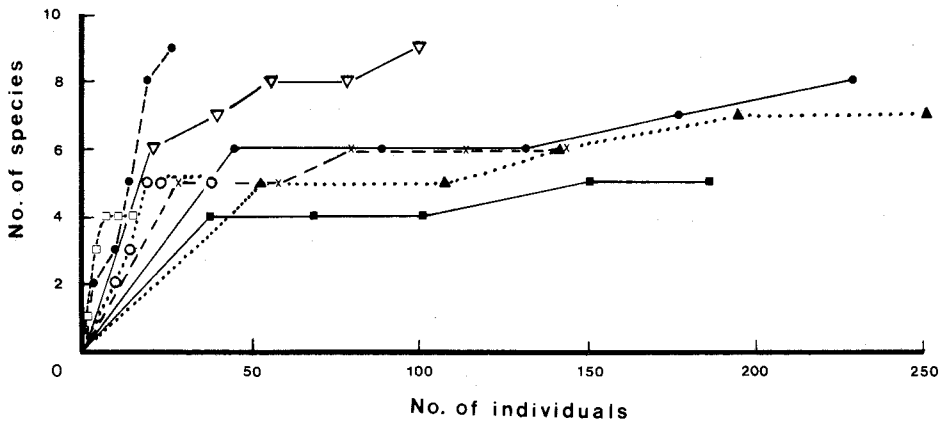


Fig. 5. Relationship between the number of species of mammals and number of individuals trapped on each CMR grid at Mitchell Plateau in 1981 and 1982. □---□ CW; ●—● PW; ○····○ CP; ▽—▽ DW; ×---× WV; ●—● WM; ▲····▲ CS; ■—■ DV.

The low proportion of marked individuals of all species at CP and CW indicates that populations were unstable in these habitats throughout the year. If individuals dispersed from the creek and watercourses (CP) during the wet season, it would be expected that numbers would increase at nearby escarpment (CW) or plateau (PW) sites at the same time. However, numbers were low on these grids throughout the year.

The combined data from all CMR grids showed contrasting seasonal patterns in abundance of species of mammals in the region. Numbers of the larger marsupials (*D. hallucatus*, *I. macrourus* and *W. squamicaudata*) varied less over the study period than did those of the smaller species. *D. hallucatus* and *I. macrourus* had a similar pattern, numbers being at a peak in July and lowest near the end of the dry season (September–October) in those grids where they were most abundant. *W. squamicaudata* and *C. penicillatus* showed no marked seasonal pattern of abundance.

The most pronounced changes in abundance were those in *P. nanus*, *Z. argurus* and *Z. woodwardi*, which declined at the beginning of the wet season (April). *R. tunneyi*, although infrequently captured on CMR grids, increased its numbers slightly in January, coincident with its use of more habitat types in the wet. It was not trapped by us in coastal habitats at Walsh Point or in Vine Thickets at Lone Dingo, although it was recorded in these habitats by Kitchener *et al.* (1981) and Butler and Butler (1978, 1979).

Species Richness and Equitability

There are major differences in species richness and equitability of mammals between habitats, as shown by the relationship between the rate of accumulation of species and the cumulative total of individuals for each CMR grid (Fig. 5).

The plot for the grids CS, WM, DV and WV tends to the asymptote, indicating that few additional species are likely to be captured on these grids. On the other grids, particularly the forests and woodland (PW and DW), the plot continues to rise and suggests that continued trapping will yield more species. The composition of the fauna may depend on the durational stability (rate of change) of the habitat (Southwood 1977); consequently these data may indicate that woodlands are less stable temporally than the other habitats.

Three measures of diversity were calculated from the combined annual species data for each CMR grid: (1) α of the log-series [$S_t = \alpha \ln(1 + \alpha)$]; (2) H of the Shannon-Weaver function [$H = -\sum_{i=1}^{S_t} P_i \ln P_i$]; (3) D of the Simpson-Yule Index [$D = 1/\sum_{i=1}^{S_t} P_i^2$]. Because the values for these diversity indices showed very similar trends, only those of the Simpson-Yule Index are presented in Table 3. On an annual basis, grids that are predominantly open forest had the highest diversity of mammals. The highest diversity was in PW and decreased through DW, WV, WM, CW, CS and CP, to be lowest in DV.

Table 3. Simpson-Yule diversity index and Jaccard's coefficient of similarity for the mammal communities on the eight CMR grids

Grid	Annual		Mean diversity index	Seasonal		
	Diversity index	Total spp.		CV	Mean Jaccard's index	CV
CS	2.48	6	2.57	20	73.4	16.7
CP	2.44	5	2.21	23	32.8	61.9
CW	3.07	4	1.65	57	36.7	100.1
PW	5.73	9	2.39	40	15.7	106.4
DW	4.28	9	3.10	12	52.6	17.1
DV	2.25	5	2.02	21	75.0	20.9
WM	3.11	8	2.68	35	72.4	13.8
MV	3.87	6	3.44	5	84.7	13.4

Mean seasonal diversity indices varied somewhat from the annual data, WV having the highest values. However, the two woodland sites PW and DW again had high values. The woodland CW had a low value, but it was the most variable site seasonally (based on the coefficient of variation), followed by the woodland PW. The least variation occurred in the coastal vine thicket WV and near coastal woodland DW (Table 3). The mean seasonal similarity within grids [based on Jaccard's Coefficient of Similarity: $C_j = j/(a + b - j)$] indicates that the species composition remained more constant, i.e. turnover was least, in the coastal sites WV and WM, the plateau vine thicket DV, and sandstone CS. The species turnover was greater in the woodland sites, reaching a peak in PW (Table 3).

Discussion

Most habitats occupied by mammals during the study confirmed earlier observations on their distribution in the region (Kitchener *et al.* 1981). *M. gouldii* and *P. tapoatafa* were new records for the region; a single specimen of each was trapped in plateau woodland. The only species recorded previously but not during this study was *Petaurus breviceps*.

The group of species in the sandstones and the coastal and near-coastal grids were more closely allied than were those of the other grids. Their major species were present and

abundant throughout the year (*D. hallucatus*, *I. macrourus*, *Melomys* sp. cf. *burtoni*, *C. penicillatus*, *Z. argurus* and *Z. woodwardi*, with *M. macrurus* and *C. penicillatus* mostly in woodland; *P. delicatulus* and *Pseudantechinus* sp. appeared to be restricted to sandstone). The species found in the riparian and plateau escarpment areas were abundant only seasonally (*P. nanus* and *R. tunneyi*), or present in low numbers (*S. virginiae* and *Leggadina* sp. of *lakedownensis*). The other group encompasses species that are essentially Open Forest specialists and occur principally on the plateau (*P. maculata*, *P. tapoatafa*, *T. arnhemensis*, *M. gouldii* and *P. laborifex*).

The coastal and plateau vine thickets are quite dissimilar in their physiognomy and season of leaf fall. Despite this they are occupied by a very similar group of mammal species. Vine thickets appear to offer mammals sanctuary from fires which frequently encircle them, but rarely burn them. The sandstone with its flat exposures, weathered platforms and massive boulders with a relatively cool and dry microenvironment, combined with a diverse flora, supports dense populations of *Pseudantechinus* sp., *D. hallucatus*, *W. squamicaudata* and *Z. argurus*. The mosaic grid at WM showed the importance of closed forest to *Melomys* sp. cf. *burtoni*; the population of this species was densest exclusively in the almost monospecific mangal portion of this grid. The structural and floristic diversity of this grid as a whole accounts for the high species richness of mammals, and will provide valuable data in determining microhabitat preferences of particular species. The alluvial (CP) and volcanic soils (CW) support low numbers of few species, whose populations do not persist over the entire year.

The swamps and creeks on the plateau probably serve as important refuges for populations of some species during the dry season, when conditions on the shallow and better drained soils of the escarpment and plateau dry out, become less productive, and afford individuals less shelter.

Braithwaite *et al.* (1985) reviewed tropical Australian mammal assemblages and concluded that they could be distinguished on the basis of whether they occupied one of two habitat types. Assemblages occupying the 'minor habitat' types where water accumulated in the landscape (includes our riparian situations, paperbark swamp, deciduous vine thicket and mangroves) were less rich in species than those in the drier 'major habitat' types (the rest of our habitats).

Our study of Mitchell Plateau (Fig. 3b) does not support the distinction elaborated by Braithwaite *et al.* (1985). Only two species at Mitchell Plateau (*M. gouldii* and *P. tapoatafa*), each represented by a single specimen, were not collected in the 'minor habitats' in this or in the earlier survey (Kitchener *et al.* 1981). Further, our observations do not support the view of Braithwaite *et al.* (1985) that bandicoots, large arboreal folivore-omnivores (including *Melomys* spp.) and small scansorial folivore-granivores (including *P. nanus*) are less common in the 'minor habitats'.

Braithwaite *et al.* (1985) considered it paradoxical that, compared with the 'major habitats', the more productive and structurally complex vegetation of the 'minor habitats' supported fewer species. They concluded that this resulted from the seasonal flooding of the 'minor habitats' as well as their floristic impoverishment. At Mitchell Plateau, seasonal diversity indices were most variable in Open Forests and Open Woodlands (with the exception of DW), and these sites, together with CP, showed the greatest turnover of species between seasons. However, on an annual basis these Open Forests in particular contained the richest and most diverse mammal assemblage. This probably reflects the considerable structural and floristic variability of these forests on laterites. Braithwaite *et al.* (1985) similarly found that mammal species richness was very high in woodlands and open forests, and related this to the high floristic richness of these habitats. At Mitchell Plateau, patches of *Eucalyptus latifolia* occur on the laterite surfaces, while there is a gradual change from the Open Forest, dominated by *E. tetradonta* and *Livistona eastonii*, of the southern plateau to the Open Woodland, dominated by *E. nesophylla* and *E. miniata*, of northern areas. Coupled with this vegetational transition are complex mosaics resulting from previous fire history, changes

in edaphic texture and in depth, as well as the broad environmental gradient between the coast and inland areas.

Kitchener *et al.* (1981) concluded that the extent and relative importance of the laterite plateau was the most obvious difference between the Mitchell Plateau and the north-east Kimberley which might account for the richer mammal fauna in the former. This study verifies this conclusion. Of the 19 species of terrestrial small mammals recorded during the present study, 16 were in forest-woodland sites associated with laterites. The number of species occupying laterite forests-woodlands contrasts with the statement of Butler and Butler (1979, p. 39) '... it is significant that the laterite plateau is still relatively depauperate'. In the Alligator River region, N.T., 'open forest and woodland' are the habitats richest in vertebrate species (Calaby 1973). At Jabiluka, N.T., sandstones contain a higher diversity of mammal species than either of the two main lowland communities, riparian woodlands and dryland open forests and woodlands (Kerle and Burgman 1984).

The incidence of natural fires is probably highest in the late dry season when lightning strikes are common and the vegetation is most flammable. During this period fires on the laterite plateau are generally intense and extensive, leaving few refugia for mammals. Aborigines, however, traditionally burnt the plateau in the early dry season (I. Crawford, personal communication) in a series of patchy and low-intensity fires. These early fires lowered fuel levels and so reduced the likelihood of extensive hot fires late in the dry season. On the surrounding sandstone country, in all seasons fires appear to burn much more patchily and leave extensive refugia.

The absence of Aborigines from the region could, then, have led to a reversion of burning patterns to the natural, more extensive and intensive fires. The last 10 years have seen Europeans burning the plateau throughout the dry season. The vegetation could, therefore, be still accommodating to these changes, in particular through the structure of the plateau woodlands. These, although rich in mammal species compared to the sandstone country, are very low in numbers of individuals.

The vine thickets, sandstone and, interestingly, DW showed the least seasonal variation in diversity. With the exception of the last site, they had relatively low annual diversity and were characterised by abundant and relatively stable populations of resident species, most of which were captured in each season. The near-coastal laterite woodland DW was strongly influenced by the populations of species it shared with the adjacent vine thicket grid; these accounted for its low seasonal variation in diversity.

Seasonal patterns of movement of mammals on Mitchell Plateau were not as pronounced as those recorded at Jabiluka. For example, Kerle and Burgman (1984) observed that *M. burtoni* migrated along the creeks, apparently in response to rainfall and firing patterns. We did not record any such distinct movement pattern for any species, although *R. tunneyi* did appear to utilise more habitats during the wet season than at other times. Flooding of riparian sites on Mitchell Plateau did not appear to cause dispersal of individual *P. nanus* or *Z. argurus*.

Several species on the Mitchell Plateau showed the same marked fluctuations in numbers as noted by Kerle and Burgman (1984). The most pronounced changes were in the mainly granivorous species: *P. nanus*, *Z. argurus* and *Z. woodwardi*. Their numbers declined towards the end of the wet season (April); this may result from the presumed scarcity of seed at this time, when plant growth was maximal and seed set and fall had not yet begun. Taylor and Dunlop (1985), however, consider that in *Eucalyptus* open forests and woodlands in the Alligator Rivers regions of the Northern Territory seed is available all year round. This indicates that more data are needed on the phenology of flowering and seed set on the Mitchell Plateau to confirm that seed is scarce towards the end of the wet season.

The largest numbers of *P. nanus* were recorded in riparian vegetation (CP) in June 1981, before and immediately after a fire. Numbers fell dramatically by the next sampling period and remained low until September 1982, when they increased slightly. Kerle and Burgman (1984) noted that *P. nanus* numbers were highest in riparian vegetation at Jabiluka in the

season following a burn and suggested that it may be able to recolonise rapidly after fire. Our observations do not support this suggestion.

Habitat distribution patterns for *Zyomys* spp., *D. hallucatus* and *I. macrourus* were similar to observations reported in the Northern Territory for these species by Kerle and Burgman (1984) and Begg (1981*b*, 1981*c*).

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