ECOLOGY OF *RATTUS LUTREOLUS LACUS* IN TALL OPEN FOREST, NORTH-EAST QUEENSLAND, WITH EMPHASIS ON HABITAT USE AND REFERENCE TO COEXISTANT SMALL MAMMALS

Thesis submitted by

Louise Joan BOSCACCI, BSc *(JCUNQ)*

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in partial fulfilment of the requirements for the Degree of Bachelor of Science with Honours in the Department of Zoology at the James Cook University of North Queensland.

ABSTRACT

A mark-capture program from February to August, 1982 formed the basis of an ecological study of *Rattus lutreolus lacus* in tall open forest on the Paluma Range, North-east Queensland.

Aspects of the ecology of three coexistent small mammals, *Rattus fuscipes, Melomys cervinipes* and *Antechinus flavipes* have also been reported on.

Faecal analyses indicated that *R. lutreolus* has a diet mainstay of grass rhizomes and stems, which is supplemented by fungi and insects.

The species showed substantial diurnal activity.

Microhabitat preferences were assessed in relation to the floristic and structural composition of the vegetation. Avoidance of closed forest-type microhabitat within the open forest reiterates the restriction of *R. lutreolus* to open forest *per se*. An association with dense ground cover below 1 metre was shown. Optimal microhabitat for *R. lutreolus* appears to equate with dense grass situations.

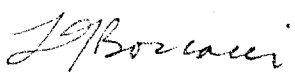
Prolonged breeding activity throughout the year was suggested. Onset of mature breeding condition in young males occurred in May and active breeding condition was noted from the winter months of June and July until the last trapping session in August. *R. lutreolus lacus* has 8 nipples. This is fewer than *Rattus lutreolus lutreolus* which has 10 nipples and may be indicative of smaller litter sizes.

Diet is suggested to be a major determinant of activity pattern, microhabitat preferences and reproductive performance of *R.lutreolus*.

In suitable parts of the forest habitat, *R.lutreolus* was readily trapped and relative to the 3 other species was the most abundant small mammal.

STATEMENT OF SOURCES

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.



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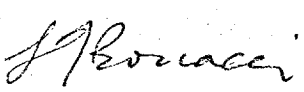

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1. INTRODUCTION

1.1 Australian Native Rodents

The native rodent fauna of Australia (Order Rodentia, Family Muridae) is a diverse group of 53 currently recognised species from 14 genera, comprising some 22 percent of the native land mammals (Watts & Aslin 1981).

The genus *Rattus* (Fischer 1803) is perhaps the best known of all Australian rodents, being widespread with a largely coastal and sub-coastal distribution on the east coast, in south-west Western Australia and in Tasmania (Watts & Aslin 1981). Currently 7 species are described: *R. fuscipes*, *R. lutreolus*, *R. tunneyi*, *R. sordidus*, *R. villosissimus*, *R. colletti*, and *R. leucopus* (Watts & Aslin 1981).

1.2 *Rattus lutreolus*

R. lutreolus (Gray), the eastern swamp rat, is a predominantly south-eastern species, with a coastal and sub-coastal distribution throughout its range on the Australian mainland, from the Adelaide region in South Australia, to at least Lake Barrine on the Atherton Tableland in north-east Queensland (Taylor & Horner 1973a). The species also occurs in Tasmania, in both coastal and highland habitats (Taylor & Horner 1973a; Green 1967).

Three subspecies are described: *R.l. velutinus*, the velvet-furred rat, in Tasmania; *R.l. lutreolus*, on the mainland from Adelaide in South Australia, to near Gympie in south-east Queensland, and *R.l. lacus* in north-east Queensland (Taylor & Horner 1973a).

1.3 *Rattus lutreolus lacus*: Previous Accounts and Known Habitat

Among the *Rattus* taken by a professional collector Gabrielle Neuhauser in northern Queensland in 1937 as part of the American

Museum of Natural History Archbold Expedition, are 5 specimens from Lake Barrine (17°15'S, 145°38'E). From these, Tate (1951) in Taylor & Horner (1967) re-evaluated the status of *R. lacus* and considered that this species and *R. lutreolus* were sufficiently similar to refer *R. lacus* to the species *lutreolus* as *R.l. lacus*.

R.l. lacus (Plate 1) has subsequently been trapped at only 4 other locations in north-east Queensland:

Kirrama State Forest on the Cardwell Range (18°10'S, 145°44'E) (J.W. Winter, personal communication),

Paluma Dam area on Mt Spec (18°56'S, 146°10'E) (Taylor 1975),

Adjacent to the Paluma-Ewan road on the western edge of the Paluma Range (19°2'S, 146°9'E) (J.W. Winter & R.G. Atherton, pers.comm., present study), and

Mt Zero on the Coane Range (19°4'S, 146°8'E) (J.W. Winter & R.G. Atherton, pers.comm.)

This is despite an intensive survey by the Queensland Department of Primary Industries in the Townsville district (Lavery & Johnson 1968), broad surveys of coastal and highland habitats in North Queensland by Queensland National Parks and Wildlife Service (J.W. Winter & R.G. Atherton pers.comm.) and several other trapping programs: throughout Cape York (Tate 1952) and northern Queensland (Taylor & Horner 1970; 1973a); studies in northern cane fields (McDougall 1944, 1946; Redhead 1973); in rainforest on the Paluma Range (Wellesley-Whitehouse 1981); at Kirrama, Cardwell Range (G.E. Heinsohn pers.comm.); on the Atherton Tableland (Preen 1981); and a survey of a series of coastal habitats near Innisfail (Harrison 1962a).

As a consequence, *R.l. lacus* has remained a little known rodent. Its ecology and reproduction are completely unknown. In comparison, Braithwaite (1978) undertook a comprehensive study of several populations of *R.l. lutreolus* in Victoria. This subspecies has also been included in several broader small mammal studies, in Victoria

(Cheal 1978), New South Wales (Posamentier 1976; Press 1976) and in south-east Queensland (Hockings 1981). Similarly, many aspects of the ecology of *R.l. velutinus* have been described (Green 1967).

A pertinent difference already apparent between *R.l. lacus* and its 2 conspecifics, relates to habitat distribution. Habitat descriptions of successful trapping localities of *R.l. lacus*, to date, are given in Table 1. These records indicate 2 similar habitat attributes:

1. All sites are highland localities.
2. All capture sites have been in the tall open forest type which is developed on well drained, friable soils adjacent to rainforest on the western edge of the coastal range systems, not associated with swamp and not closely associated with standing water. Although Lake Barrine was given as the original trapping locality (Taylor & Horner 1973a), and the lake is surrounded by rainforest and beyond that, cleared farm land (Tracey & Webb 1975), open forest patches once occurred within about 5 kilometres of the lake, and hence Lake Barrine may have been given as a general locality (J.W. Winter pers.comm.). *R.l. lacus* has not been trapped in rainforest.

R.l. lutreolus and *R.l. velutinus* have been taken in a variety of habitats (Taylor & Horner 1973a). In Victoria, *R.l. lutreolus* is found in wet and dry coastal heaths, inland heaths, swamps and river banks, sclerophyll forests and semi-commensal situations (Braithwaite 1978). The major habitat of this subspecies is considered to be swamp heath (Taylor & Horner 1973a).

Of note is that throughout the range of *R.l. lutreolus*, open eucalypt forms only a marginal habitat. Similarly, eucalypt forest is considered a marginal habitat of *R.l. velutinus* (Green 1967). *R.l. velutinus* commonly occurs in three major habitat types: Myrtle-predominant rainforest, button grass sedgelands and coastal swamp (Green 1967).

Table 1. Habitat descriptions of trapping localities of *Rattus lutreolus* in north-east Queensland

Locality	Collection Date		
Lake Barrine, Atherton Tableland 17°15'S,145°38'S 760m	1937	'bladey grass' on original labels. Possibly from pockets of open forest within about 5km of Lake Barrine.	Taylor & Horner (1973a) J.W. Winter (pers.comm.)
Kirrama, Cardwell Range 18°10'S,145°44'E 640m	1974	Tall open eucalypt forest. Trapped in dense grass of about 0.5 metres in height. Tall open forest Type 14, *Eucalyptus grandis, E. intermedia, E. resinifera, Syncarpia glomulifera, Allocasuarina torulosa.*	J.W. Winter (pers.comm.) Tracey & Webb (1975)
Paluma Dam Area, Mt Spec 18°56'S,146°10'E 900m	1969	Tall open forest of *E. grandis* (Type 14, Tracey & Webb, 1975). Trapped in dense bracken adjacent to a moist gully, northwest of the dam wall.	P.M. Johnson (pers.comm.) Taylor (1975)
Mt Zero, Coane Range 11.0km S.W.Paluma 19°4'S,146°8'E 940m	1976	Trapped in dense bladey grass up to 1.5 metres in height in an experimental hoop pine plantation. Trees only 1.5 metres. Natural surrounding vegetation: open forest of *E. resinifera, E. intermedia, Syncarpia glomulifera, Allocasuarina torulosa,* grassy understorey or with rainforest elements depending on how recently fired.	J.W. Winter & R.G. Atherton (pers.comm.)
Paluma-Ewan Road, Paluma Range 7.5km W.S.W. Paluma 19°2'S,146°9'E 900m	1976 1982	Trapped in dense grass (bladey grass, *Imperata cylindrica,* the dominant species) and bracken in tall open forest of *E. grandis, E. resinifera, E. intermedia* with co-dominant species *Syncarpia glomulifera.* *Allocasuarina torulosa* understorey. Grassy ground cover with regenerating rainforest elements throughout.	J.W. Winter & R.G. Atherton (pers.comm.) Present Study

1.4 Present Study

In January 1982, *R. lutreolus* was live trapped in tall open forest on the western edge of the Paluma Range (19°2'S, ;46°9'E, altitude 900 metres) in an area where it had previously been located (J.W. Winter pers.comm.).

The aim of the present study, which was conducted from February to August 1982, was to describe the ecology of *R.l. lacus* in this habitat type which appears to be an atypical one for *R. lutreolus*, as a contribution to the total ecological story of this species throughout its range.

A primary objective was to identify the microhabitat preferences of *R. lutreolus* in order to provide a preliminary base to aid further attempts at locating new populations in northern Queensland. In turn, it is hoped that this will aid definition of the geographic distribution and status of *R. lutreolus* in northern Queensland.

Other Species

Three other small mammal species, 2 native rodents *Rattus fuscipes* and *Melomys cervinipes* (Plate 3) (Rodentia Muridae) and a dasyurid *Antechinus flavipes* (Marsupialia, Dasyuridae) (Plate 4) have been trapped in association with *R. lutreolus* on the Paluma Range (J.W. Winter pers.comm.; exploratory trapping this study).

Compared with southern Australia and paralleling the situation which is shown in the extreme by *R. lutreolus* , there is a dearth of basic ecological information on rodents and other small mammals in tropical Queensland. Considerable effort has been devoted to the native rodent pest problem in central and northern canefields with studies on *R. sordidus* (McDougall 1944, 1946) and *Melomys littoralis* (McDougall 1944, 1946; Redhead 1973).

Harrison (1962a) gave a semi-quantitative account of broad habitat

Plate 1. *Rattus lutreolus lacus*

Plate 2. *Melomys cervinipes*

Plate 3. *Antechinus flavipes*

preferences of several small mammal species near Innisfail, and indicated some foods eaten by several species (Harrison 1962b). Wellesley-Whitehouse (1981) compared the ecologies of *R. fuscipes* and *Uromys caudimaculatus* in rainforest at Paluma, and Preen (1981) as part of a broader study, considered the impact of rainforest logging on the small mammal fauna.

Since *R. lutreolus* is a member of the broader small mammal community, aspects of the ecology of the other small mammal species, *R. fuscipes*, *M. cervinipes* and *A. flavipes*, have been considered, on a comparative basis, in this study.

2. STUDY AREA AND GENERAL METHODS

2.1 Study Area

The study site on the western side of the Paluma Range, (19°2's, 146°9'E, altitude 900 metres) is situated approximately 8 kilometres west of the village of Paluma, 85 kilometres north-west of Townsville (Figure 1).

2.1.1 Habitat

2.1.1.1 Vegetation and Soils

The vegetation in the Paluma-Hidden Valley area is related to soils and rainfall, and changes in a transitional series from east to west (Jackes 1980).

The initial vegetation on the eastern range is simple mesophyll vine forest as defined by Webb (1959). This type is developed on deep to moderately deep 'red acid structured earths' with associated yellow earths (Anon. 1970) and, in general, occurs where a minimum of 1500 millimetres of rainfall is received annually (Jackes 1980).

As the soils change on the drier western side of the range to

Figure 1. General locality of the study site on the western side of the Paluma Range, north-east Queensland. Capture sites of *Rattus lutreolus* in this region are also shown.

'yellow mottled acid leached structured earths' (Anon. 1970), an associated vegetation change occurs. A mixed forest (terminology *sensu* Walker & Hopkins 1981) with an open overstorey of the sclerophyllous emergents *Eucalyptus grandis*, *Syncarpia glomulifera* and *Banksia integrifolia* and a closed understorey of rainforest and other mesophyllous elements, leads into a tall open forest community with a predominantly grassy groundflora.

Immediately adjacent to the ecotone is a narrow, 300 to 400 metre wide, belt dominated by *Eucalyptus grandis* and *Syncarpia glomulifera*. This is then developed into a mixed *Eucalyptus* community. Dominants include *Eucalyptus intermedia*, *E. acmeniodes*, *E. polycarpa*, *E. resinifera* and *E. grandis*. *S. glomulifera* is a frequent associate, and an understorey of *Allocasuarina torulosa* (and *B. integrifolia*) occurs. The forest is dissected by moist gullies and creeks of which the larger ones support well developed gallery (closed) forest.

To the east of Hidden Valley, an open woodland community is dominant on sandy soils. *E. shirleyi* dominates in areas with granite outcrops; *E. peltata* and *E. drepanophylla* in moister areas (Jackes 1980).

The present study was centred on the ecotone region between the tall open forest and the transitional-type mixed forest. Trapping was undertaken in both the open forest (within about 1.5 kilometres of the ecotone) and the transitional mixed forest (hereafter referred to as closed forest for ease).

2.1.1.2 Climate

Temperature

A maximum-minimum thermometer was placed in the tall open forest from February to September. Temperatures were averaged over 4 maximum and 4 minimum readings in each month from February to August; only one maximum and minimum reading was taken in September.

Average monthly temperature maxima and minima are shown in Figure 2. An average minimum of 6°C was recorded in July, and an extreme minimum of 2°C was recorded in this month. An extreme maximum of 29.6°C was recorded in February, with an average maximum of 29.5°C.

Rainfall

Rainfall data are not available for the study site. However, rainfall data from the Paluma village (supplied by B. Venn, Ivy Cottage) from 1969 to 1981 (Figure 3) and for 1982, January to September (Figure 4) are presented to indicate general trends; rainfall would be expected to be lower in the study area. Notably, 1982 has been the driest year since records began in 1969.

2.1.1.3 Logging History

The study site was situated in State Forest 268 and the general area has undergone considerable logging disturbance. Logging has been conducted in different sections of the forest from 1960 to 1964 and from 1970 to 1974 (R. Hamwood, Qld. Forestry Dept., pers.comm.). A sleeper log operation involving selective logging of bloodwood species was occurring in an area just west of the study area (R. Hamwood pers.comm.). However, no operations were current in areas being trapped from February to August 1982.

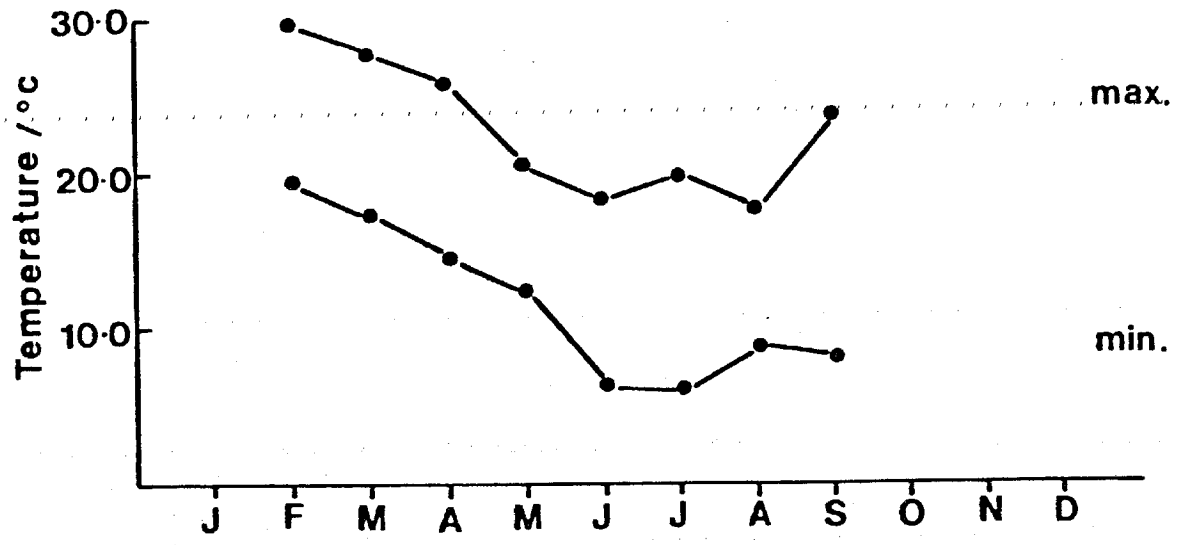
2.1.1.4 Fire

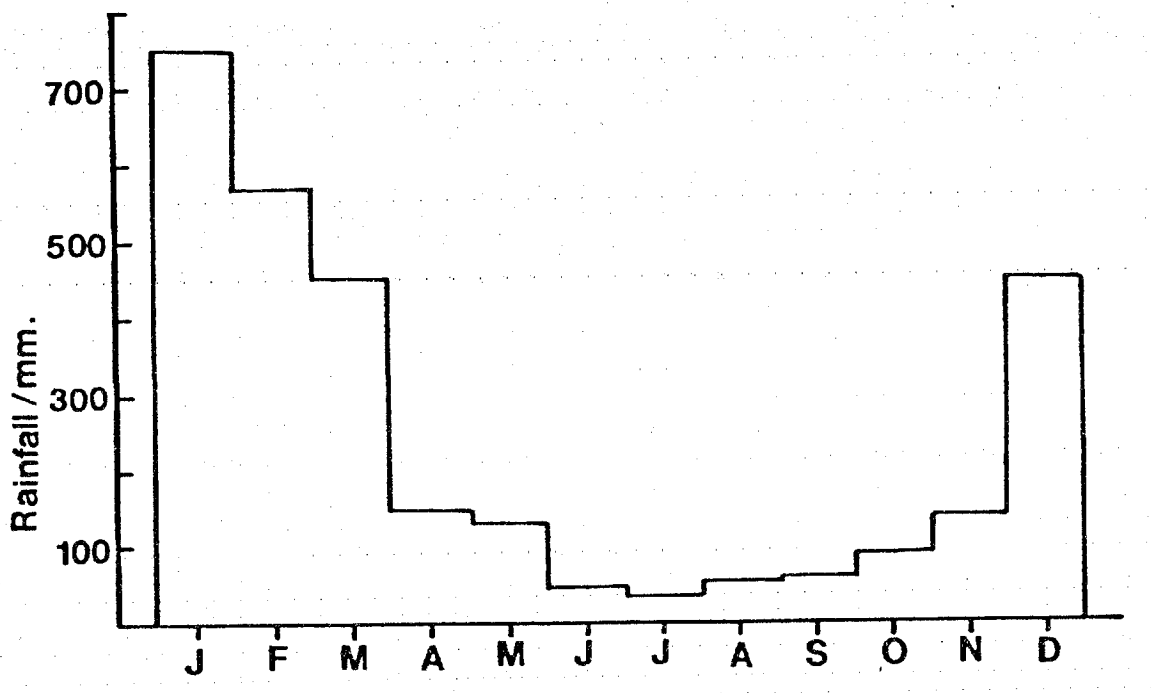
Most tree trunks had scorch burns which extended up to a height of 10 metres in some cases, indicating that fire is a considerable influence in this habitat. Interspersion of closed and open forest is mainly fire-related (R. Hamwood pers.comm.). Fires are fairly regular (every 1 to 2 years) but are generally very patchy (spot burns on ridges) and either largely originate in the southerly coastal region or are due to lightning strikes (R. Hamwood pers.comm.).

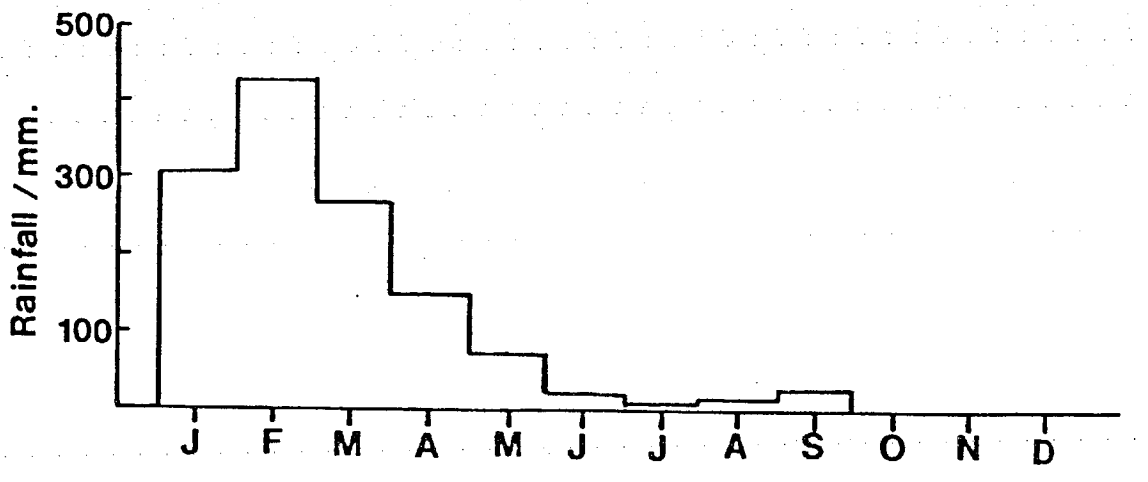
Figure 2. Average monthly maximum and minimum temperatures (^{o}C) at the study site in tall open forest, from February to September 1982. Temperatures were averaged over 4 maximum and 4 minimum readings each month from February to August. A single maximum and minimum reading was taken in September.

Figure 3. Average monthly rainfall (mm) in the Paluma Village from 1969 to 1981 inclusive.

Figure 4. Monthly rainfall (mm) and the number of rainy days in the Paluma Village from January to September 1982.







No. days :	17	18	20	18	7	3	3	6	5

Unnatural causes are probably also involved. The study area was free of fire from January to September 1982.

2.2 General Methods

2.2.1 Trapping Design and Program

Two trapping types (1) a grid and (2) transects were adopted to accommodate the major objective of identifying the microhabitat preferences of *R. lutreolus* and coexistent small mammal species.

The grid was used to enable the analysis of the dispersion of small mammals on a fine scale in relation to the floristic composition and structure of the vegetation. In contrast, transect trapping enabled a broader range of vegetational situations (primarily vegetation densities) to be sampled than would be possible using only a grid arrangement.

Grid

The grid was established across a moist gully with shrubby growth of rainforest elements and other mesophyllous species about 0.8 kilometres west of the ecotone (Figure 5). A small flow of water of a few centimetres in depth was present in parts of the creek from February to April. By May, a small pool of about 50 centimetres in width and a few centimetres in depth and an area of saturated mud remained. The creek bed was dry from June to August.

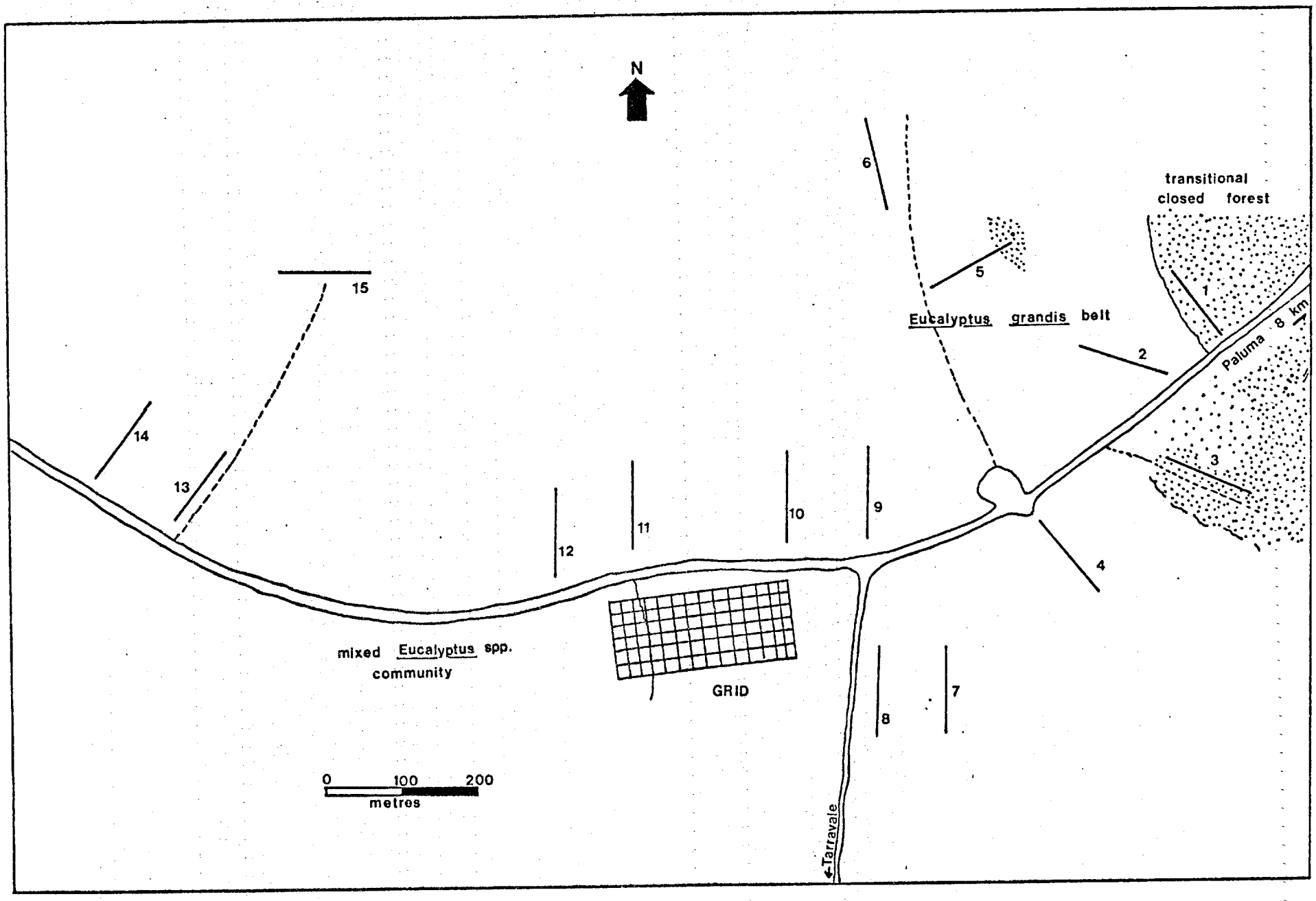
In February, a small grid of 30 sites with an inter-trap distance of 15 metres was established. In March this was doubled to 60 sites and in April extended again to 105 sites. This grid of 105 sites was trapped each month from April to August inclusive. The true trapping area of the grid after the addition of a boundary strip of 7.5 metres or half the inter-trap distance (Brant 1962) was 2.4 hectares.

All sites on the 30 and 60 traps grid were trapped for 3 nights

Figure 5. Trapping Design: positions of the 15 transects and the grid in the study area.

The stippled areas denote closed forest in which trapping was conducted. This included the transitional type mixed forest adjacent to the open forest and a patch of gallery forest which had developed on a moist depression within the open forest.

Dashed lines represent logging snig tracks.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15
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4
3
2
1
8
7
transitional
closed forest
Eucalyptus grandis belt
Paluma 8 km
mixed Eucalyptus spp.
community
GRID
0 100 200
metres
Tarravale

in February and March respectively; from April to August the entire 105 trap grid was trapped for a total of 2 nights each month, with sites on each half of the grid (52 sites and 53 sites respectively) being trapped for 2 nights each. Thus, each site on the grid was trapped for a total of 2 nights in each month from April to August inclusive. This program was largely governed by availability of traps and to enable simultaneous grid and transect trapping.

Transects

Fifteen straight line transects of 10 sites each, with an inter-trap distance of 15 metres (total length 135 metres each) were established in the study area. The positions of the transects in relation to the ecotone and the grid are shown in Figure 5. Two transects were established immediately east of the ecotone in the closed forest; the remaining were positioned in a variety of visually assessed topographical and ground cover situations. With the exception of transect 5 (Figure 5), transects were established in vegetation which was homogeneous within a minimum of 50 metres from the line of traps. This was a visual assessment in order to provide a discreet sample. Transect 5 was deliberately set so that 3 sites sampled a patch of gallery forest which had developed on a moist depression (Figure 5).

One trap was placed at each site. Each site was trapped for a total of 8 nights giving a total of 80 trap nights (1 trap night = 1 trap x 1 night) on each transect. The entire trapping program is summarised in Table 2.

2.2.2 Trap and Bait Type

A single trap type, collapsible aluminium 'Elliott' traps (33cm x 10cm x 10cm) was used from April to August. In February and

March, both 'Sherman' galvanised metal box traps (23cm x 8cm x 8cm) and 'Elliotts' were used. All small mammal species captured using 'Elliotts' were also trapped by the smaller 'Shermans.' Hence, the smaller size of the 'Shermans' is not considered to have influenced the observed capture rate of any species.

A bait of peanut paste, rolled oats and vegetable oil was used throughout the study. This bait has been found to be successful for capturing a range of herbivorous, omnivorous and insectivorous small mammals (e.g. Fletcher 1977; Braithwaite *et al.* 1978).

2.2.3 Daily Trapping Procedure and Animal Handling

Traps were set for the first trapping night in each month from about 1530 hours onwards. They were cleared each morning at first light from 0600 hours to 0645 hours onwards. Clearing took up to a maximum of 5 hours and a minimum of 3 hours from March to August when grid and transect trapping was concurrent.

Due to the large number of traps operated, traps were left open during the day and only cleared once daily, except in July and August when they were cleared twice daily in order to monitor small mammal activity patterns (Table 2). Traps in exposed sites, e.g. in sparse grass, were covered by litter to prevent overheating of potential captures. In the winter months of June and July litter and soil was heaped on traps in exposed sites (closed forest, sparsely grassed areas) and, in some cases, soil and litter was placed inside the traps to provide insulation. The latter proved impractical,however, when attempting to remove captured animals in the least time possible. Despite precautions taken, an unfortunate number of trap deaths was incurred: 9 *R.l. lacus*, 4 *Rattus fuscipes* and 4 *Antechinus flavipes*. Captured animals were shaken from the trap into a soft cloth bag.

Table 2: Summary of trapping program from February to August 1982

Trapping Dates	Trap Nights — Transect 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Transect Total	Grid Total	Transect & Grid Total
Feb. 11-13																	90	90
Mar. 25-27											40					40	180	220
Apr. 24-27	40	40									40			40		160	210	370
May 25-28	40	40												40		120	210	330
June 27-30			40	40	40				40	40						200	210	410
July 28-31						40	40	40		40		40	40		40	280	210	490
Aug. 17-20			40	40	40	40	40	40	40			40	40		40	400		
23-26																	210	610
Total																1200	1320	2520
	Trap Days																	
July 28-30					30		30	30				30	30		30	180	158	338
Aug. 17-19			30	30	30	30	30	30	30			30	30		30	300		
23-25																	158	458
Total																480	316	796

For each capture, body weight was measured to the nearest gram using a 200 gram Pesola spring balance, and sex and reproductive condition were recorded. Criteria used to establish reproductive condition are described in Section 6.

Each animal was individually marked with 7mm monel metal fingerling ear tags (No.FF, Salt Lake Stamp Co.) clipped on the ear. A single tag was placed into each ear pinna of *R. lutreolus*; a single tag on only 1 pinna of the other species. Few tags were lost from *R. lutreolus* probably due to the small thick ears of this species. However, a high loss from *Melomys cervinipes* and *Antechinus flavipes* between trapping sessions occurred. In these 2 species the pattern of ear rips and a combination of other features such as tail notches and sex were used to identify individuals which lost tags. Additionally, tagging in both ears was adopted. However, despite this, the exact number of individuals caught on the grid was not finally determined since in some months all *M. cervinipes* and *A. flavipes* had lost original and subsequent tags and identification became impossible.

Alternative marking techniques have been used in small mammal studies which avoid the problem of tag loss, such as toe clipping and cutting individual patterns of holes in ear pinnae (e.g. Fletcher 1977). However these were considered undesirable. Analyses of the microhabitat preferences of these species on the grid were based on the number of captures rather than the number of individuals. Hence, tag loss was not important in the end.

2.2.4 Standard Measurements

Standard body measurements of *R. lutreolus* were taken in June, July and August when animals were breeding, in order to obtain adult morphometrics. The following measurements considered most appropriate for use on live animals in the field (Fox 1979) were taken: total

body length (tip of nose to tip of tail), tail length (tip to anus), pes length (heel to tip of the longest—the third—toe, excluding claw) and total head length (base of skull to tip of snout). Total body length was measured to the nearest millimetre using a steel ruler, with the animal held horizontally against the ruler. Tail length was similarly measured with the tail horizontal and depressed to the rule. Pes length was measured on the left pes using Vernier Calipers. In this species the pes could be made to relax and flatten out completely by running the thumb along the bottom of it. Total head length was measured with Vernier Calipers with the animal held around the shoulders.

Pes length was also recorded for *Melomys* sp. Two species, *M.cervinipes* and *M.burtoni*, occur in North Queensland (Watts & Aslin 1981). Identification is based on pes length, which is greater than 25mm in *M. cervinipes* (J.W. Winter pers. comm.). All *Melomys* captured in February, March and April were *M. cervinipes*, and subsequent new captures were assumed to be *M. cervinipes*.

2.2.5 Miscellaneous Trapping

Apart from the main trapping program outlined, additional trapping was undertaken in February using wire cage, 'Elliott' and 'Sherman' traps in the open forest and closed forest. This involved 60 trap nights in each habitat. These trapping data have been used only to indicate reproductive status in the rodent species captured, and in a supportive manner when considering microhabitat preferences. The trapping results from the 2 habitats are given in Appendix 1.

3. CHARACTERISTICS OF THE GRID POPULATIONS OF *RATTUS LUTREOLUS* AND OTHER SPECIES; BODY MEASUREMENTS AND WEIGHTS OF *RATTUS LUTREOLUS*

3.1 Methods

Population Size. Population size in each month was determined using the Known-to-be-Alive (KTBA) estimate, which is the number of animals caught at time i plus the number marked and known to be alive prior to time i (Wood 1971). This method avoids the assumptions inherent in the traditional Petersen Estimate (Lincoln Index) and the Jolly-Seber model, that (1) animals do not lose their marks and (2) that marking does not affect probability of survival. Additionally, the Petersen Method assumes that (3) there is no gain or loss of members during sampling and that every animal has the same probability of capture. The Jolly-Seber model also assumes that (4) there is recruitment and immigration but death and emigration affect marked and unmarked animals equally (Smith *et al.* 1975 in Golley *et al.* 1975). The KTBA is also considered to be more realistic than direct enumeration alone, since it allows for individuals known to be present but not captured in a trapping session (Fletcher 1977).

Trappability was calculated as the total number of animals captured per month (from April to August) divided by the number of animals known to be alive, x 100 (Stewart 1979).

Transience. Animals captured in only one trapping session were designated as transients; those caught in 2 or more months as residents (e.g. Wood 1971). Distinction was made between part-residents (captured in 2 or 3 months) and residents (captured in more than 3 months).

Trap Success is the total number of individuals per total number of trap nights in each month (monthly trap success) and the total over the entire study period, February to August (total trap success).

3.2 Results

3.2.1 *Rattus lutreolus*

Population Estimates and Composition. A total of 14 females and 12 males were trapped on the grid from February to August. A total of 162 captures in 1320 trap nights and 316 trap days (Table 3) was recorded. A calendar of individual trap histories is presented in Appendix 2. Monthly KTBA estimates (Figures 6 and 7) indicate that the population size remained relatively stable from April to August (equal monthly trap effort), with a peak of 16 individuals in June and a low of 12 in July.

Five females were classed as residents, and 6 as part-residents (Appendix 2). Two transients to the grid were captured in February and June respectively, and a new animal was caught in August. Four resident and 5 part-resident males were recorded, with 3 males new to the grid being trapped in August (Appendix 2).

The reproductive status of the grid population is discussed in Section 6. In summary, all males caught on the grid in February, March and April were considered to be first-year males, and they commenced breeding in May. Pregnant to post-reproductive females were caught in all months except April. A single juvenile (less than 60 grams—see Section 6) was trapped on the grid in May and June.

Trappability. *R. lutreolus* was readily caught by 'Elliott' live traps; a maximum trappability was recorded in May (93.3%) and a minimum of 83.3% in July (Figure 7).

Density. An estimate of average density of *R. lutreolus* on the grid from April to August, based on monthly KTBA estimates and a true trapping area of 2.4 hectares, was 5.9 individuals per hectare. This is considered to represent average density in equivalent situations to the grid in the open forest.

Figure 6a. Monthly Known-to-be-alive (KTBA) estimates of *Rattus lutreolus* females on the grid from February to August, 1982.


new individuals

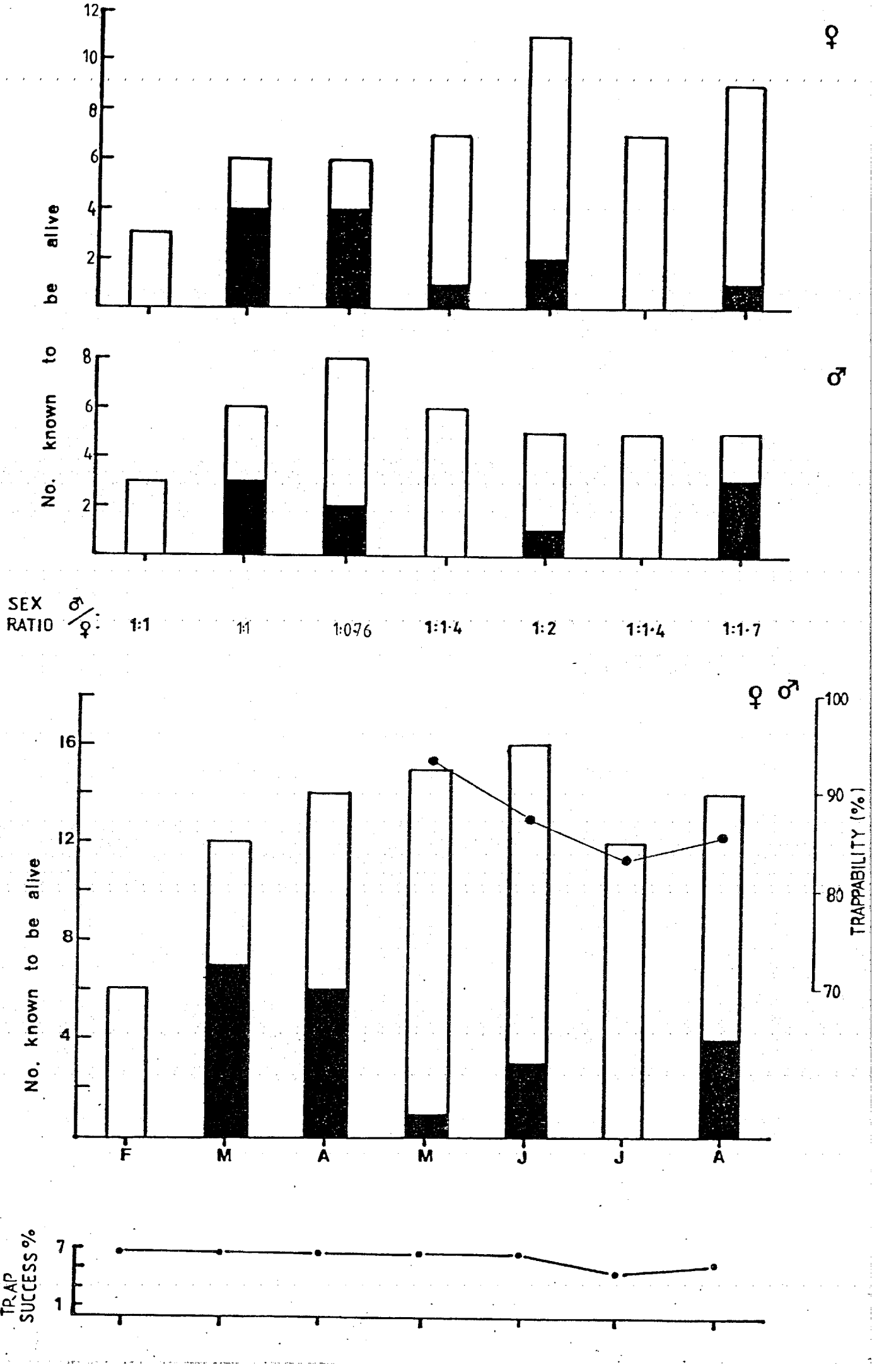
Figure 6. Monthly KTBA estimates of *Rattus lutreolus* males on the grid from February to August, 1982.


new individuals

Figure 7. Monthly total KTBA estimates of *Rattus lutreolus* on the grid from February to August, and trappability of *Rattus lutreolus* on the grid from April to August, 1982.


new individuals

Figure 8. Monthly trap success (%) for *Rattus lutreolus* on the grid from February to August, 1982.


♀
♂
No. known to be alive
12
10
8
6
4
2
8
6
4
2
SEX RATIO ♂/♀:
1:1
1:1
1:0·76
1:1·4
1:2
1:1·4
1:1·7
♀ ♂
No. known to be alive
16
12
8
4
100
90
80
70
TRAPPABILITY (%)
F
M
A
M
J
J
A
TRAP SUCCESS %
7
1

Trap Success. Monthly trap success (trap nights only), based on the number of individuals caught, was low, ranging from a minimum of 4.8% in July to a maximum of 6.7% in February through June (Figure 8). Total trap success based on a total of 26 individuals captured in 1320 trap nights (Table 3) was 2%. Total trap success based on 153 night captures over 1320 trap nights (Table 3) was 11.6%.

Table 3: Monthly captures of *Rattus lutreolus*, *Rattus fuscipes*, *Melomys cervinipes* and *Antechinus flavipes* on the grid from February to August 1982.

Month	Trap Nights	Trap Days	*R. lutreolus* N	*R. lutreolus* D	*R. fuscipes* N	*R. fuscipes* D	*M. cervinipes* N	*M. cervinipes* D	*A. flavipes* N	*A. flavipes* D
Feb.	90		11		5		4		5	
March	180		23		7		11		4	
April	210		32		8		17		9	
May	210		30		9		22		6	
June	210		22		8		16		4	
July	210	158	17	3	6		14		8	4
August	210	158	18	6	6		21		5	
Total	1320	316	162		49		105		45	

Abbreviations: N, night; D, day

3.2.2 Other Species

Rattus fuscipes

A total of 49 captures of 5 individuals of *R. fuscipes* was made on the grid from February to August (total trap success based on captured was 3.7%). A calendar of trap histories is given in Appendix 3. The number of monthly captures are shown in Table 3.

Melomys cervinipes

The actual trap histories of individuals of *M. cervinipes* were not finally determined due to the tag loss problem. However a total of 105 captures from February to August was made (Table 3); total trap success was 7.8%.

Antechinus flavipes

Trap histories are not described due to the tag loss problem. A total of 45 captures (41 night, 4 day) was recorded from February to August. Total trap success based on trap nights and captures only, was 3.1%. Monthly captures are shown in Table 3.

3.3 Body Measurements and Body Weights of *Rattus lutreolus*

3.3.1 Body Measurements

Absolute body measurements and the individual identifications of animals captured from June to August are given in Appendix 4. These data include several immature non-breeding individuals in addition to mature breeding animals (Reproduction criteria are outlined in Section 6).

Table 4 summarises absolute measurements of all animals (male and female) measured in June, July and August.

Table 4: Absolute Measurements of *Rattus lutreolus* (males and females) captured in June, July and August, 1982

Measurement	N	$\bar{X}$±S.D.	Observed Range	C.V.
HBT(mm)	39	249.0±19.5	193-283	7.8
TAIL(mm)	36	103.4± 8.8	77-119	0.5
HB(mm)	38	147.7±11.9	112-170	8.1
HEAD(mm)	39	42.6± 1.8	36.2-46.0	5.3
PES(mm)	43	30.2± 1.5	26.1-33.6	4.9

Abbreviations: HBT, head-body-tail or total length; HB, head-body length; S.D., standard deviation; C.V., coefficient of variation; Pes measurement on the left pes.

Absolute body measurements of mature, breeding males and females captured during June, July and August are summarised below in Table 5.

Table 5: Absolute body measurements of mature (breeding) *Rattus lutreolus*, males and females, captured in June, July and August, 1982. Abbreviations as in Table 4.

Measurement		N	X±S.D.	Observed Range	C.V.
HBT(mm)	♂	19	255.7±16.8	212-283	6.6
	♀	11	245.5±19.6	194-262	7.9
TAIL(mm)	♂	18	104.9± 9.6	77-119	9.1
	♀	9	105.3± 4.7	99-112	4.5
HB(mm)	♂	19	152.2±10.5	135-170	6.9
	♀	11	146.5± 8.6	144-155	5.9
HEAD(mm)	♂	19	43.4± 1.4	40.5-46.0	3.2
	♀	10	42.4± 1.5	40.4-44.7	3.6
PES(mm)	♂	19	31.1± 1.4	28.1-33.6	4.5
	♀	11	29.7± 0.7	28.9-31.3	2.2

Mature males and females were not significantly different in overall body size (HBT, Student t-test comparison: $p>0.05$).

3.3.2 Body Weights

Rattus lutreolus: Male-Female Comparison

Weights of males and females excluding juveniles (less than 60 grams) at first capture in each month from February to August were used in this comparison. The mean body weight of all non-juvenile males captured was 101.6±21.09 (range 67-153 grams, N=54). The mean body weight of all non-juvenile females was 100±17.49 (range 66 to 153 grams, N=58). Mean male and female body weights were not significantly different (Student t-test: $p>0.05$).

Mature breeding males (June to August) had a mean body weight of 11.0±18.5 grams (range 78-153.0 grams, N=38). Mature breeding females on average weighed 113.7±14.5 grams (range 90-151 grams, N=26). Males and females were not statistically compared since this included females designated as pregnant.

The heaviest male at 153 grams was captured in August and was actively breeding. The heaviest female at 151 grams was captured in August and was designated as pregnant.

Comparison of *R. lutreolus lacus* with *R. lutreolus lutreolus* and *R. lutreolus velutinus*

In Victorian heathland populations of *R.l. lutreolus*, Braithwaite and Lee (1979) found that adult males weighed around 130 grams and adult females about 120 grams.

Although Green (1967) did not specify mean adult body weights, the mean weight of animals in October when the population of *R.l. velutinus* under study was breeding, was for males and females respectively: 139.4(129-149) grams and 105.2(87-114) grams.

On the basis of these data, *R.l. lacus* appears to be somewhat smaller than its 2 conspecifics. This trend is most marked in males.

3.4 Discussion

On the grid, *R.l. lacus* was shown to be highly trappable, suggesting that once a population is located animals should be readily caught. Similarly, *R.l. lutreolus* in Victorian heath has been found to be readily trapped in live traps (Braithwaite & Lee 1979). In addition to trap proneness, trap success reflects actual numbers of animals in the trapping area. Trap success has also been found to be markedly affected by trap placement, e.g. Stewart (1979) found that traps placed on runways and near burrows within the general vicinity of a designated grid site produced a much higher return than traps placed at exact grid sites which were not close to such features. This was attributed to most activity of rodents being centred on runways and burrows, and hence traps close to these features would be more frequently detected (Stewart 1979).

Of the 4 species studied, *R. lutreolus* was trapped most frequently. In rainforest at Paluma, Wellesley-Whitehouse (1981) recorded a rodent (*R. fuscipes* and *U. caudimaculatus*) trap success of between 15.3 to 44.4%. Trap success in the open forest at Paluma

in the present study was considerably lower, apparently reflecting lower rodent densities. Notably, a KTBA estimate of only 2-3 *R. fuscipes*, in each month, from April to August, on the 2.4 hectare grid was recorded. In contrast, Wellesley-Whitehouse (1981) gave a KTBA estimate for *R. fuscipes* in 1.53 hectares of rainforest over several months of between 11 and 25. In the rainforest, a much higher trap success was reported for *R. fuscipes* than *M.cervinipes* (Wellesley-Whitehouse 1981). However in the open forest, *M. cervinipes* was caught more frequently than *R. fuscipes* (8.0% versus 3.7%). This appears to reflect a much lower density of *R. fuscipes* in open forest, and possibly a higher trap dominance of *R. fuscipes* in comparison with *M. cervinipes* in the rainforest.

4. DIET, FEEDING HABITS AND ACTIVITY PATTERN OF *RATTUS LUTREOLUS*

4.1 Introduction

One of the major determinants of habitat dispersion in small mammals is likely to be the availability of food resources (Cheal 1978). Additionally, the availability and accessibility of preferred food resources appears to be a major factor in rationalising many aspects of small mammal ecological strategies, in particular, reproductive performance (e.g. Lee *et al.* 1982).

This section reports on the diet, feeding habits and activity pattern of *R. lutreolus*. Activity patterns of *R. fuscipes*, *M. cervinipes* and *A. flavipes* are also reported since these are unrecorded for these species in north Queensland.

4.2 Diet

4.2.1 Methods

Diet was assessed by microscopic analysis of the composition of faecal pellets from animals caught on the grid.

Collection of Faeces

Faeces of first night captures only were collected in order to avoid contamination by other species. From each trap, enough faeces were collected to fill a 20ml glass vial. Samples,collected each month from March to August, were stored in 70 percent alcohol during each trapping session, prior to transfer to the laboratory.

Preparation and Analyses of Faecal Samples

Preparation of samples followed standard preparations described by Watts (1977). Samples were transferred to a petri dish and crushed down into a homogeneous looking mixture using a spatula. They were then sieved and washed for a few minutes using

a fine (0.25mm) nylon mesh sieve to remove soil particles and material in late stages of digestion. Trials were first run using unsieved samples; however large quantities of soil and partly digested homogeneous material made microscopic analysis impossible. The sieved solids were transferred to a petri dish with fresh water immediately prior to analysis.

Both a qualitative and quantitative technique were used to analyse diet.

Qualitative Description: Dietary Range

Each faecal sample was examined under a low power (x10) binocular microscope to obtain a complete list of dietary items. A 3-point scale: +, ++, +++, was used to give a crude index of abundance of each gross item. This approach also gave an indication of item morphology which aided identification of food items at higher magnification.

Quantitative Analysis

Since *R. lutreolus* is a specialist herbivore throughout its range in south-eastern Australia (Watts & Braithwaite 1978; Cheal 1978), it was desirable in this study to attempt to identify specific plant taxa eaten by *R.l. lacus*. For this purpose, a reference collection was prepared of epidermises and cuticles of common groundflora species on the grid. This approach, originally described by Baumgartner and Martin (1939), has subsequently been used with success in numerous analyses of herbivore and omnivore diets (e.g. Cheal 1978; Fitzgerald & Waddington 1979; Marsh *et al.* 1982).

Taxa included in the collection were the grasses *Imperata cylindrica* (bladey grass) and *Sorghum* sp. (Poaceae), and non-grass groundflora *Pteridium esculentens* (bracken fern), native

ginger *Alpinea caerulea* (Zingiberaceae), *Dianella* sp. (Liliaceae) and *Gahnia* sp. (Cyperaceae). Epidermal mounts of rhizome, stem and leaf/blade were prepared as follows:

Thin strips of tissue were excised from the different vegetative parts of each species and soaked overnight in hot hydrogen peroxide to dissolve mesophyll (Cockburn 1981). The remaining epidermises and cuticles were mounted in glycerine on glass slides. Additionally, grass spikelets and seeds were collected, dissected and mounted for use as reference material.

Two glass slides of each faecal sample were prepared by spreading a thin film of faecal mixture over the slide with a pasteur pipette. Ten sites on each slide were examined at x40 magnification , and diet items present in each field listed (Occurrence method, Hynes 1959). The first site was positioned by selecting a pre-determined co-ordinate and subsequent sites were positioned at pre-determined set distances on 2 parallel transects (e.g. Marsh *et al.* 1982). Higher magnification (x100) was used to identify specific plant taxa where necessary.

The diet of *R. fuscipes* is probably the best known of all Australian rodents (e.g. Watts 1977). The contents of one stomach of a collected specimen were examined at low power (x10) and items were indexed using the abundance ranking used in the *R. lutreolus* faecal analysis.

4.2.2 Results

Qualitative Description

Table 6 shows the relative abundances in faeces of gross food items. In all months, grass stem and/or rhizome dominated faecal samples. Grass remnants were present as obvious chunks of grass

Table 6. Dietary range of *Rattus lutreolus* and relative abundances of food items eaten.
Abundance index: +, present; ++, abundant; +++, very abundant. N, number of faecal samples.

Food Item	March	April	May	June	July	August
N=	3	3	3	3	3	2
Grass stem/rhizome	+++	+++	+++	+++	+++	+++
: chunks, strips of stem						
: cross sections of stem						
: rhizome bracts						
Monocot rootstock		+		+	++	+
: matted fibrous tissue						
Grass seed					+	
Fungi—massed fruiting bodies and mycelia	+		+	++		
Fruit and seeds (fleshy)		+				
Flower—*Banksia* sp.?		+				
Fragmented insect cuticle, limbs, wings	+	+	+	+	+	+
Unidentified plant tissue	+	+	+	+	+	+
Ants,* coleopterans* (entire)	+				+	+
Woody stem fragments	+	+		+	+	+

* Considered to be accidental inclusions in samples.

stem and/or rhizome, in some cases as complete cross-sections of culms (above ground stems) in which the dense outer vascular layers and inner aerenchymatous cortex were obvious, and as strips of sheathing leaf bases. Rhizome has also been listed. This was based on the presence of very characteristic rhizome bracts of *Imperata cylindrica*. *Imperata* is a perennial grass which develops an extensive rhizome system which enables rapid colonisation of recently fired sites (Kleinschmidt & Johnson 1977). No other grass species on the grid *Sorghum* sp., *Panicum* sp. and *Themeda australis* (section 5) has a well-developed rhizome system (pers.observ.; Kleinschmidt & Johnson 1977). Fragmented insect cuticle was present, but relatively unimportant, in all months. Whole ants and coleopterans were considered to be accidental inclusions in samples since these were often found active in the traps each morning.

Quantitative Analysis

Table 7 shows the presence and frequency occurrences (%) of diet items in *R. lutreolus* faeces, from March to August 1982. Sixty microscope fields were examined each month from March to July and 40 in August, giving a total of 340. Since monthly sample sizes are not large, the analysis mostly indicates the relative importance of different food items during the entire study period, rather than in each month. Criteria used to identify and classify diet items are outlined below:

Anatomical distinctions between the grasses were not recognised in early analyses and no attempt to distinguish between grasses was made in subsequent analyses. Grasses show several distinctive characteristics which rendered cellular material readily recognisable: parallel venation, epidermal cells with crenulated margins, and silica bodies. Plate 4 shows culm epidermis from *Imperata*. Rhizome

Table 7. Frequency occurrence (%) of diet items in faeces of *Rattus lutreolus*, March to August 1982.
N_F = Number of faecal samples
N_M = Number of microscope fields

Food Item	March	April	May	June	July	August	Total
N_F=	3	3	3	3	3	2	17
N_M=	60	60	60	60	60	40	340
Grass stem/rhizome	100	100	100	100	100	100	100
Grass aerenchymatous cortex	98	100	100	100	100	100	99
Whole root fragments	-	12	2	-	7	-	4
Grass seed (glume/palea)	2	10	2	-	-	-	2
Monocot rootstock?	13	65	18	10	48	20	29
Dianella (Liliaceae)	10	3	-	-	-	10	4
Alpinea (Zingiberaceae)	5	-	-	-	-	-	9
Pteridium stem/rhizome	2	5	3	8	-	3	4
Loose vascular elements	17	32	10	8	23	5	16
Unidentified cellular material	23	82	20	22	8	4	32
Insect cuticle	10	10	10	12	18	20	13
Woody stem fragments	20	32	2	-	2	5	10
Fungal hyphae and/or fruiting bodies	10	7	27	33	7	5	15
Dicot seeds (fleshy)	-	12	-	-	-	-	2
Flower—whole	-	7	-	-	-	-	1
—stamens/ anthers							
Fruit (whole)—berry	-	2	-	-	-	-	0.3

epidermis and cortex tissue is shown in Plate 5. As noted in the qualitative description, much of the grass material occurred as chunks of stem/rhizome and,similarly, this material was readily identifiable on slides. Aerenchymatous cortex was originally associated with grass in the qualitative description. Nodulate fibrous material has been tentatively classed as monocotyledon rootstock. Three non-grass species were recognised on faecal slides on the basis of cellular characteristics: epidermal trichomes rendered *Dianella* epidermis identifiable (Plate 6). Stems and rhizomes of *Pteridium* possess distinctive large vacuolate cells with multicellular hairs (Plate 7). *Alpinea* tissue was not adequately reproducible; however epidermal cell shape and arrangement permitted ready identification. Although they were not included in the frequency occurrence determinations (Table 7), spore masses and pollen grains which were probably incidental inclusions, were noted at x100 magnification. Fragments of charcoal and wood also occurred in most samples.

Stomach contents of a sample *R. fuscipes* contained large amounts of fungi (+++), substantial amounts of insect cuticle (++) and traces of woody stem fragments and unidentifiable plant tissue (+). Unlike all of the *R. lutreolus*, the single *R. fuscipes* had not utilised grass stems/rhizomes.

4.3 Feeding Habits of *Rattus lutreolus*

Shallow diggings, no more than 5 centimetres in depth, into the bases of true grasses (Plate 8) on the grid and on 5 transects (2, 4, 6, 9 and 15) were observed. These were attributed to *R. lutreolus* which was captured on the grid and the above transects (section 5). Diggings were characterised by a shallow hole scooped out around the bases of swards of grasses, predominantly *Imperata cylindrica*,

Plate 4

Outer cell layers of the basal stem of *Imperata cylindrica*. Note the crenulated epidermal cells and parallel venation. Similar fragments were present in faecal material.
(Scale bar is 0.1mm.)

Plate 5

Rhizome epidermis and cortex of *Imperata cylindrica*. Note the crenulated epidermal cells.
(Scale bar is 0.01mm.)

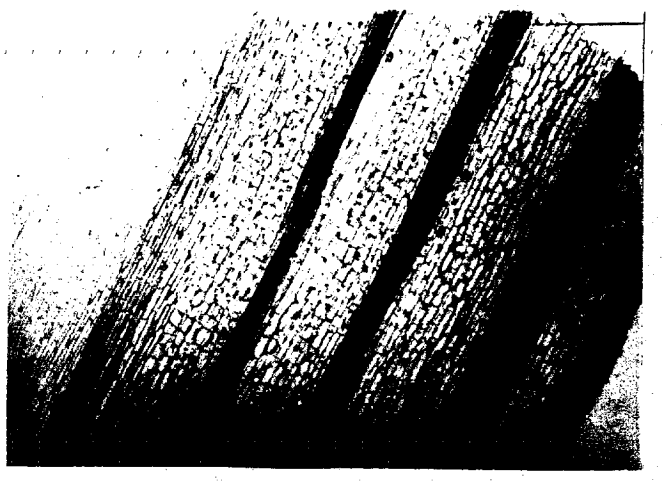
Plate 6

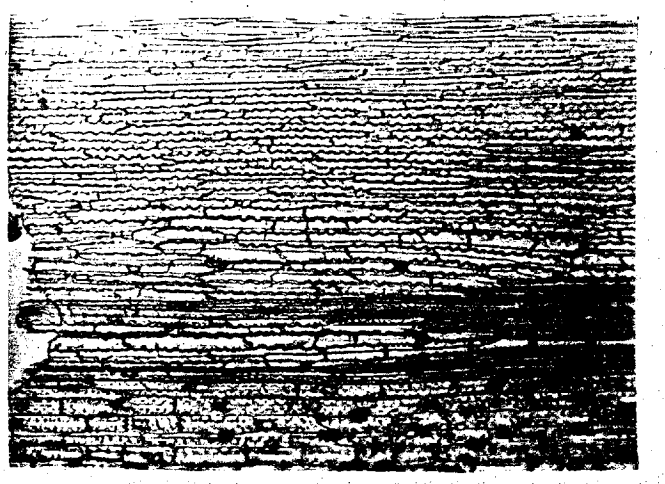
Basal stem epidermis of *Dianella* sp. Note the characteristic epidermal trichomes.
(Scale bar is 0.02mm.)

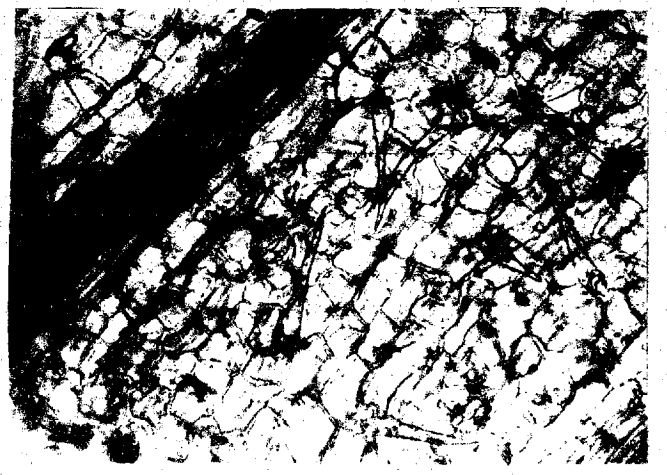
Plate 7

Basal stem epidermis and epidermal hairs of *Pteridium esculentens*. Note the characteristic multicellular hairs and large vacuolate epidermal cells.
(Scale bar is 0.1mm.)

Plate 8. Characteristic ground diggings of *Rattus lutreolus lacus*. The grass species is *Imperata cylindrica*.







with soil from the working face forming a mound of loose workings in front of the hole. Gnawed root, rhizome, lower stem and leaf bases were observed in most cases, with fragments of root and stem often littering the working area.

Although *R. fuscipes* excavates burrows (Watts & Aslin 1981), it has not been reported to produce shallow diggings into the bases of grasses. Grass material was not found in the sample stomach of *R. fuscipes* examined. Throughout its range, *R. fuscipes* is largely an opportunistic generalist omnivore. In Victoria, its diet in forests consists of seeds, berries, drupes, roots, soft-leaf and stem material, macro-fungi and a variety of leaf litter invertebrates (Warneke 1971 in Gullan & Norris 1981). In rainforest on the Atherton Tableland, Watts (1977) found that *R. fuscipes* ate mainly insects with some seeds and herbs. Similarly in rainforest approximately 8 kilometres from the present study site at Paluma, litter invertebrates (mainly arthropods) formed the bulk of the diet, although a variety of vegetable material was also eaten (Wellesley-Whitehouse 1981).

Due to its omnivorous habit, *R. fuscipes* has no digestive or masticatory specialisations for feeding on coarse plant material such as grasses or mature fern fronds (Warneke 1971 in Gullan & Norris 1981). *Melomys cervinipes* is semi-arboreal and vegetarian, eating mainly soft leaf and stem material, and fruit (Harrison 1962b; Wood 1971). *Antechinus* is carnivorous and insectivorous (Ride 1970; Fox 1982). Hindmarsh and Majer (1977) in Fox (1982) have shown that *A. flavipes* is largely insectivorous taking most arthropods in roughly the same proportions in which they occur in their habitat.

Neither *M. cervinipes* and *A. flavipes* are known to produce

ground diggings and on the basis of diet would not be expected to do so. Certainly the faecal composition of *R. lutreolus* would suggest that these diggings are produced by this species.

Watts and Braithwaite (1978) and Cheal (1978) indicated that *R.l. lutreolus* exploits mainly sedge rhizomes and basal stems via diggings. Similarly Green (1967) noted that *R.l. velutinus* almost completely ate away the root system of clumps of button grass. Thus, the feeding behaviour of *R.l. lacus* appears to be very similar to its 2 conspecifics.

4.4 Activity Patterns

4.4.1 Methods

In order to detect diurnal activity, all grid and transect traps were cleared twice daily during the July and August trapping sessions. Traps were cleared from 0600 to 0630 hours onwards in the morning and from 1630 to 1700 hours onwards in the evening (about an hour prior to the onset of darkness). The trapping program and trapping effort was as follows:

July—transects 5, 7, 8, 12, 13 and 15 for 3 trap days each; a total of 180 trap days.

—the grid: 53 traps for 2 trap days each; 52 traps for 1 trap day each; a total of 158 trap days.

August—transects 3, 4, 5, 6, 7, 8, 9, 12, 13, 15 for 3 trap days each; a total of 300 trap days.

—the grid: as in July; a total of 158 trap days.

The total number of traps days was 796 (Table 2).

The number of diurnal captures of each species during these 2 sessions was compared with the number of captures of each species recorded on the first 3 nights of the total 4 night trapping routine

in the same sessions, on each transect, and on the grid (a total of 796 trap nights).

4.4.2 Results

The numbers of day and night captures of each species are shown in Figure 9. Out of a total of 34 captures, equal numbers of *R. lutreolus* were caught during the day and the night. These data do not indicate equal amounts of diurnal and nocturnal activity, since traps were not open and available to animals for equal periods during the day and the night. Morning clearance took up to 5 hours on some days. They do, however, indicate considerable diurnal activity.

Diurnal activity was also shown by *A. flavipes* (Figure 9), although significantly more night captures were recorded (χ^2, $p<0.001$; based on expected 1:1 ratio). *R. fuscipes* and *M. cervinipes* were active only during the night (Figure 9).

4.5 Discussion

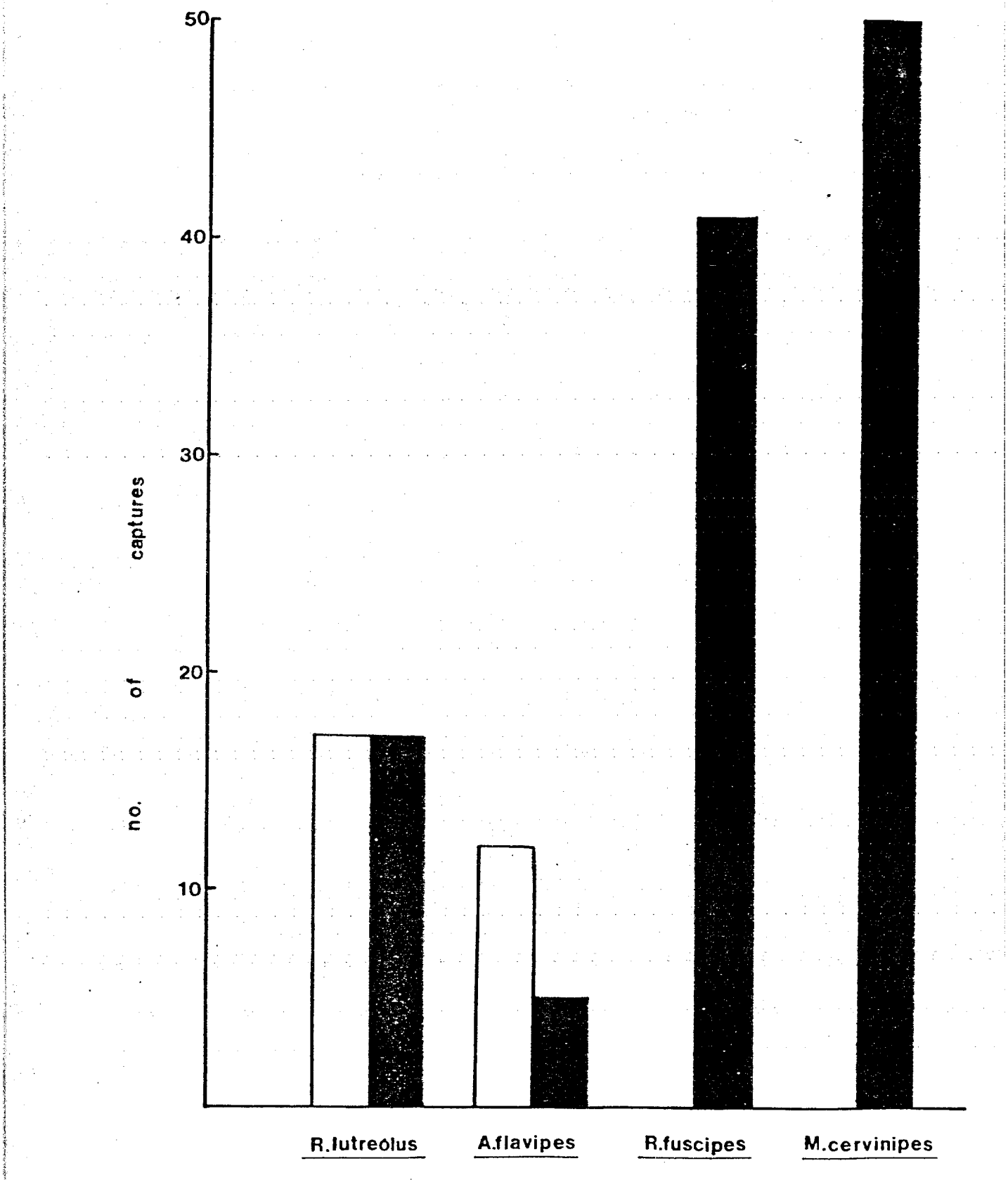
The major limitation of any diet analysis is the limited powers of identification of individual food items. Diet analysis is time consuming and,to be anything but superficial, specific identification of food items, in particular plant species, is considered to be basic. However, the potential scope of a system using reference material can be enormous. Notwithstanding this, the range of food items ingested by *R. lutreolus* was quite narrow and the frequency occurrence of unidentified cellular material averaged over all months was less than 50 percent.

In all samples, grass stem and/or rhizome was recorded and formed the bulk of the diet (qualitative assessment). The grass species *Imperata cylindrica* is considered to have provided the

Figure 9. Number of day and night captures of *Rattus lutreolus*, *Rattus fuscipes*, *Melomys cervinipes* and *Antechinus flavipes* in July and August, 1982.

day

night


50
40
30
20
10
no. of captures
R.lutreolus
A.flavipes
R.fuscipes
M.cervinipes

bulk of this grass material for 2 reasons:

a. On the grid, *Imperata* was the dominant grass species, occurring in more sites and providing the highest mean cover-abundance of all grass species (section 5). Since *R. lutreolus* has been found to have a diet mainstay of grass stem/rhizome, it would be expected to eat proportionately more of the most abundant species.

b. On the grid, diggings into the bases of only *Imperata* were observed; however at least one digging into the roots and lower stem of *Sorghum* was observed on transect 7, a capture site of *R. lutreolus* (section 5).

Grass stem/rhizome was supplemented by insect material and fungi which were taken throughout the year in small quantities. Unidentified cellular material and loose vascular elements (possibly from the grass bulk) also occurred. Three non-grass species *Dianella, Alpinea* and *Pteridium* were eaten infrequently, apparently in small quantities and thus, possibly non-selectively along with grasses, since the 3 species grew in association with grasses on the grid (section 5).

Watts and Braithwaite (1978) found that in Victorian heath, *R. lutreolus* subsisted mainly on sedges (Cyperaceae) which were the dominant groundflora type. However, in non-heath habitats (riparian and semi-commensal), the bulk of the diet consisted of grass stem which reflected the absence of sedges and dominance of true grasses. Insect and underground fungi were reported as being eaten in small quantities. Similarly, Cheal (1978) considered that the diet mainstays of *R. lutreolus* in heath were rhizomes and rootstocks of Cyperaceous species with these being supplemented

by insect and mycorrhizal fungi. Analysis of a single faecal sample from *R. lutreolus* in eucalypt forest indicated the dominance of leaf-bases, rootstocks and leaves of grasses which comprised the dominant groundfora (Cheal 1979).

Thus, the diet of *R. lutreolus* appears to remain largely monocotyledon-based and quite specialised throughout its range. Between-habitat differences in the actual plant species contributing the bulk of the diet appear to be related to different groundflora dominants.

Although sample sizes in this study were insufficient to adequately assess if there were any seasonal changes in diet diversity, the diet of *R. lutreolus* on the grid was generally dominated by grass stem/rhizome, mainly of *Imperata cylindrica*, which was largely exploited by characteristic shallow ground diggings.

Considerable diurnal activity was shown by *R.l. lacus*. *R.l. lutreolus* has been found to display considerable diurnal activity in Victorian heath (Braithwaite 1977), in New South Wales forest-grassland (Press 1976) and south-eastern Queensland heath (Dwyer *et al.* 1979) with diurnal captures varying from 30 to 70 percent in different localities in Victoria (Braithwaite 1977).

The activity patterns of *A. flavipes* at the study site corroborate findings by Dickman (1980) who recorded a few daylight captures of this species near Canberra. Similarly, diurnal activity has been found to be shown by *Antechinus stuartii* (Wood 1970) and *Antechinus swainsonii* (Braithwaite 1977; Hall & Lee 1982). The exclusively nocturnal activity of *R. fuscipes* and *M. cervinipes* (at least in July and August) is similar to findings in subtropical rainforest in south-east Queensland (Wood 1971).

Many factors have been cited to influence activity patterns of small mammals, such as diet, availability of dense cover, rainfall, cloud cover, activity rhythms of competitors, predators and food resources (Ashby 1972; Southern 1964; Doucet & Bider 1974; Park 1940 in Braithwaite 1977). In particular diet has been suggested to be a major determinant. Several herbivorous rodents have been found to show considerable diurnal activity, e.g. the South African swamp rat *Otomys irroratus* (Dieterlen 1968 in Posamentier 1976) and North American *Microtus* spp. (Getz 1961). Ashby (1972) in Braithwaite (1977) postulated that since the diet of herbivorous small mammals is bulky, an animal requires much longer to ingest sufficient nutriment in each 24 hours and thus would be likely to be active and feeding during the day as well as at night. It has also been suggested that diurnal activity in insectivorous small mammals may be related to the time required to locate sufficient food or to the activity rhythm of their insect food species (Braithwaite 1977).

Since *M. cervinipes* is herbivorous and *R. fuscipes* ingests insects, and both have been shown to be exclusively nocturnal, much of the generalised arguments above appear unlikely. However, the observed activity patterns of the 2 exclusively vegetarians, *R. lutreolus* and *M. cervinipes*, may be more specifically related to the nature of the diet. The diet mainstay of *R. lutreolus* is grass stem/rhizome, which is bulky. The argument that slow digestion rates require diurnal feeding may apply. In addition, the nutrient content and caloric value of grasses may be low relative to soft leaf, stem and fruits of dicotyledonous species which are expoited by *M. cervinipes* (Harrison 1962b; Watts & Aslin 1981). In particular *Imperata cylindrica* is sometimes regarded as indicating low soil

fertility (Burbidge 1968). The food types of *M. cervinipes* are less bulky which would be likely to result in greater digestibility and hence, assimilation. Thus differences in bulkiness, nutrient content and calorific value of the plant food resources exploited by *R. lutreolus* and *M. cervinipes* may be sufficient to explain the difference in activity patterns.

Antechinus spp. fossick for insects in leaf litter, under logs and on tree trunks (Wakefield & Warneke 1967). A requirement for successful fossicking may be that prey are active and visible. Observations of *Antechinus* sp. in captivity have indicated that vision played a large part in final prey capture although noise and possibly smell were initial pointers to the presence of prey when animals were not actively searching (pers.observ.). Activity peaks of insects are likely to occur during the day when temperatures are highest, and this may contribute to diurnal activity in this genus.

In contrast, *R. fuscipes* is omnivorous and not entirely dependent on insects. Insects ingested appear to be mainly litter arthropods exploited during general ground fossicking (Warneke 1971 in Gullan & Norris 1981; Wood 1970). Due to its opportunistic dietary habit, the species would be expected to be little restricted by insect activity peaks and less likely to show diurnal activity.

5. MICROHABITAT PREFERENCES OF *RATTUS LUTREOLUS* AND OTHER SMALL MAMMALS

5.1 Introduction

The habitat distribution of *R. lutreolus* in North Queensland appears to be highly restricted. However, although the species has not been trapped in rainforest, its distribution in relation to the open and closed forest ecotone is of interest.

The microhabitat attributes of trapping sites exist only as qualitative accounts from the trapping records (Table 1). In contrast, the microhabitat preferences of several populations of *R. lutreolus* in Victoria have been comprehensively assessed (Braithwaite & Gullan 1978; Braithwaite *et al.* 1978; Cheal 1978). Similarly, quantitative habitat relationships of *R. lutreolus* in coastal heath (Posamentier 1976) and in a grassland area (Press 1976) in New South Wales, have been described. Green (1967) gave a qualitative account of habitat utilisation by *R. l. velutinus* in Tasmania.

Vegetation is the most obvious component of a small mammal's habitat and detailed floristic and physiognomic descriptions of the vegetation are now considered essential to adequately characterise habitat use and apportionment in small mammals (Cheal 1978). The microhabitat preferences of *R. lutreolus* and the 3 co-existent small mammal species, *R. fuscipes*, *M. cervinipes* and *A. flavipes* have been assessed in relation to floristic composition and structure of vegetation.

5.2 Methods

5.2.1 Vegetation Description: Grid and Transects

5.2.1.1 Floristic Description and Analysis

Description

The method used to assess the floristic preferences of *R. lutreolus* and the other species followed that developed by Braithwaite and Gullan (1978) in which the dispersion of small mammals is viewed in relation to the major floristic groups identified on a trapping grid.

At each trap site on the grid, every vascular plant species occurring in a 5-metre quadrat centred on the site was listed Additionally, the cover-abundance of each species was estimated using the Braun-Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg 1974), which is outlined below:

+ - solitary to few individuals with small cover

1 - numerous but less than 5% cover, or scattered with up to 5% cover

2.- any number, with cover 5-25% of the reference area

3 - any number with 5-25% cover

4 - any number with cover 50-75% of the reference area

5 - any number with cover more than 75% of the reference area.

Although the rating is quantitatively crude, it is considered that fairly consistent results are obtained when used by the same person a number of times, and when worked methodically by deciding first if cover/abundance is greater or less than 50% and then working up or down the scale (Mueller-Dombois & Ellenberg, 1974).

Analysis

Floristic data were analysed using a computer based clustering technique, the Clustan I.C. Package (Wishart 1978) to cluster the 105 trap sites into groups on the basis of presence-absence of plant species. The Similarity Index used was the Jaccard Coefficient. Several species which were recorded only once or twice on the entire grid were excluded as background noise in this analysis. These were *Eucalyptus grandis, Helichrysum* sp., *Solanum parvolium* and *Monotoca scorparia.*

Several species of bloodwoods have been recorded in this region: *Eucalyptus intermedia, E. acmeniodes, E. polycarpa* (B. Jackes pers. comm.). These were not consistently distinguished in the field and have been grouped together with *E. resinifera* as *Eucalyptus* spp. in this study. Distinction was made between mature established trees of *Eucalyptus* spp., *Banksia integrifolia, Syncarpia glomulifera* and *Allocasuarina torulosa* (greater than 3 metres in height, characteristic bark features developed) and regenerating individuals (up to 1.5 metres in height), since these represented very different structural types. Thus, some consideration of structure has been incorporated into the floristic analysis to facilitate finer interpretation of the type of habitat presented by the different floristic groups.

5.2.1.2 Structural Description: Grid and Transects

The term vegetation structure describes the vertical layering and horizontal spacing (density) of vegetation (Walker & Hopkins 1981). Structure was assessed independently of floristic data using a point quadrat procedure, following Cockburn (1981):

A 2-metre graduated aluminium pole (1.5 centimetre diameter) was dropped into the vegetation at 10 regular intervals of

50 centimetres along a 5 metre transect which passed through each trap site. On transects, this was run along the axis of the transect. On the grid, this followed the long axis. Intervals were initially measured using string marked off in 50 centimetre intervals; but thereafter a half pace was walked to approximate 50 centimetres on structural transects. The presence or absence of vegetation touching the pole was noted at 6 height intervals: 0-0.25m, 0.26-0.5m, 0.51-0.75m, 0.76-1.0m, 1.01-1.5m and 1.51-2.0m, to give a comparable index of vegetation density from 1 to 10 for each height class at each trap site. Only the vegetative parts of grasses were considered, and both standing, dead and live vegetation (mainly referring to grasses) was included to give an estimate of total cover.

Above 2.0 metres, the presence or absence of vegetation in the height classes: 2.01-3m, 3.01-6m, 6.01-12m, 12.01-20m and 20.01-35m was recorded by sighting along the pole. A Ranging-120 rangefinder was used to measure heights.

The height classes above 2 metres were chosen using a structural classification of rainforest and non-rainforest vegetation developed by Walker and Hopkins (1981) in which the height classes describe the following growth forms:

1.01 - 3m - dwarf trees, tall shrubs

3.01 - 6m - low trees, very tall shrubs

6.01 - 12m - mid high trees, extremely tall shrubs

12.01 - 20m - tall trees

20.01 - 35m - very tall trees.

Emphasis was placed on density of vegetation below 2 metres since this was assumed to be of most significance to ground-dwelling small mammals.

5.2.2 Animal-Vegetation Associations

5.2.2.1 Floristics

Floristic preferences of the 4 small mammal species were analysed by comparing the mean number of captures per site in each floristic grouping identified on the grid. The mean number of captures of each species per site in each floristic group was assumed to indicate the amount of utilisation of different floristic groups; an approach which has been shown to be useful by recent studies on small mammal habitat preferences (e.g. Braithwaite & Gullan 1978; Cockburn 1981). Comparisons for each species are based on total captures from April to August. Since the trapping program on the 105 site grid ran from April to August only, seasonal dispersion patterns are not considered. Both day and night captures of *R. lutreolus* and *A. flavipes* are used in respective analyses.

5.2.2.2 Structure

Transect and grid captures were analysed separately. The total number of contacts in each height class below 2 metres was summed for each trap site to give an index of density at that height class. Spearman Rank Correlation coefficients were calculated for the density index at each height class and captures of each of the 4 mammal species at each trap site from February to August.

This approach was adopted to produce a more descriptive, rather than definitive, account of the relationship between each species and vegetation density at lower height levels. Only transects established in open forest sites, i.e. with grassy groundcovers, were included in the analysis in an attempt to assess the relationship between the 4 species and vegetation density in

the open forest habitat alone. Thus, transects 1 and 3 and sites 8, 9 and 10 of transect 5 were excluded (Section 2, Figure 5).

Structural profile data for heights above 2 metres on the grid were used to summarise the structural features of each of the floristic groupings identified.

5.2.3 Other Habitat Characteristics

The major components of and the cover characteristics of the leaf litter at each trap site on the grid were recorded. Litter was classified as one of 3 cover types: (i) sparse and patchy, (ii) thin continuous layer or (iii) thick continuous layer.

5.2.4 Abundance Index of Food Resources of *Rattus lutreolus* on the Grid

A crude index of the abundance of food resources of *R. lutreolus* in the major floristic types on the grid was calculated as follows: all grass genera on the grid were regarded as potential food species, although it was considered that *Imperata* contributed to the bulk of the diet (Section 4). Each of the Braun-Blanquet cover-abundance scales was converted to an integer, so that + was converted to 1, 1 to 2 and so on to 5 = 6. From the floristic proforma, the mean cover-abundance of each grass genus in each of the major floristic types on the grid was calculated. This was multiplied by the frequency occurrence of each species in each different floristic type (outlined in detail in Section 5.3.2, Table 12). The individual indices for each grass genus were summed to produce a total index of potential food in each floristic type.

5.3 Results

5.3.1 General Trends in the Habitat Distribution of *Rattus lutreolus* and Other Small Mammals

Transects were deliberately positioned on either side of the open-closed forest ecotone in order to establish the distribution of *R. lutreolus* in relation to these 2 habitat types at their junction (Figure 5). The numbers of individuals and captures of each small mammal species on the 15 transects are shown in Table 8. No movement of individuals between transects were detected. In 160 trapnights, no captures of *R. lutreolus* on the closed forest transects 1 and 3 (Figure 5, Plate 9); were made; however the 3 other small mammals co-existent with *R. lutreolus* in the open forest, *R. fuscipes, M. cervinipes* and *A. flavipes* were trapped on these 2 transects (Table 8). Additionally 2 captures of an individual *A. stuartii* were recorded on transect 1. Identification was based on pelage characteristics, in particular (i) uniform grey-brown body colouration and (ii) absence of cream-apricot eye rings/crescents which are characteristic of *A. flavipes* in North Queensland (Van Dyck 1982). In North Queensland, *A. stuartii* is wholly restricted to highland vine forest (Van Dyck 1982). Only *R. fuscipes* was captured during 60 miscellaneous trap nights in the transitional closed forest in February (Appendix 1). Thus, of the 4 species regularly caught in the open forest, only *R. fuscipes, M. cervinipes* and *A. flavipes* used both habitat types. Considering that a maximum of 9 individuals (30 captures) of *R. lutreolus* were recorded in 80 trap nights on transect 2 (Table 8) which was positioned 50 to 100 metres from the closed forest edge (Figure 5), these data are considered sufficient to indicate complete restriction of *R. lutreolus* to the open forest *per se*.

Table 8. Transect trapping results: number of individuals and number of captures (in parentheses) of *Rattus lutreolus*, *Rattus fuscipes*, *Melomys cervinipes* and *Antechinus flavipes* on transects 1-15. Night captures only.

* *Antechinus stuartii*, 1(2) also captured on transect 1.

Transect	Trap Nights	*R. lutreolus*	*R. fuscipes*	*M. cervinipes*	*A. flavipes*
1	80	-	6(21)	-	1(2)
2	80	9(30)	2(4)	1(1)	2(3)
3	80	-	10(23)	5(8)	4(4)
4	80	5(8)	1(2)	1(1)	-
5	80	2(3)	8(16)	3(7)	-
6	80	2(3)	1(2)	3(9)	1(4)
7	80	7(11)	-	-	3(3)
8	80	-	2(7)	2(7)	-
9	80	6(13)	1(3)	-	1(1)
10	80	-	1(2)	2(2)	-
11	80	-	3(4)	3(6)	1(1)
12	80	-	1(2)	-	2(3)
13	80	-	-	5(11)	1(1)
14	80	-	1(7)	1(1)	1(1)
15	80	2(2)	5(11)	2(1)	2(2)
Total	1200	33(70)	42(104)	28(54)	19(25)

A similar rodent distribution pattern was found on transect 5 (Figure 5) which included both open forest sites with a grassy groundcover and sites in a patch of gallery (closed) forest. Table 9 below summarises the number of individuals and captures of each small mammal species on transect 5.

Table 9. Number of individuals and number of captures (in parentheses), of 3 live-trapped rodent species on transect 5 (Figure 5), June and August, 1982

	Open Forest							Closed Forest			Total
Trap Site	1	2	3	4	5	6	7	8	9	10	
Trap Nights	8	8	8	8	8	8	8	8	8	8	80
R. lutreolus		1(2)				1(1)					2(3)
R. fuscipes				1(1)	1(3)		2(2)	1(1)	5(6)	2(3)	8(16)
M. cervinipes			1(1)	2(2)		1(1)		2(3)			3(7)

A. flavipes was not captured on this transect. *R. lutreolus* was confined entirely to open forest sites. *R. fuscipes* was caught on both open and closed forest sites. A total of 8 individuals of *R. fuscipes* were trapped; however only 1 individual was common to both the open and closed forest sites. Two were caught only on open forest sites, 5 only in the closed forest island. Similarly, *M. cervinipes* was caught at both open and closed forest sites. Of the total 3 individuals which were captured, the 2 individuals caught in the closed forest were also trapped on the open forest sites. One was trapped only in closed forest.

Comparison of the number of individuals of *R. fuscipes* captured on the closed forest transects 1, 3 and 3 closed forest sites on transect 5, with the remaining open forest transects (Figure 5) indicated that a significantly higher number were caught at closed

forest sites (Table 10, χ^2, $p<0.05$; based on trap nights completed in each habitat type). This suggests that open forest is a sub-optimal habitat for *R. fuscipes*. *M. cervinipes* and *A. flavipes* were not compared due to low numbers.

Open Forest Transects

Transects in the open forest (excluding transects 1 and 3) were classified into one of 3 broad topographical situations: ridge-top (Plate10), midslope (Plate 11) or lower slope adjacent to a moist gully (Plate 12). Positions were referenced in relation to prominent ridge-top and gully situations.

From the structural profile data, the mean number of contacts in each height class below 2 metres (Section 5.2.1.2) was calculated for each transect. Transect 5 was excluded since it was deliberately heterogeneous. An index of ground cover volume on each transect was obtained by summing the individual height class means. Figure 10 indicates the transects on which *R. lutreolus* and the 3 other species were captured in relation to the index of vegetation volume and topographical position.

R. lutreolus was captured on transects which were positioned in lower to mid-slope situations, correlating with the upper range of vegetation densities. The species was totally absent from all ridge transects. The absence of *R. lutreolus* from a transect over 80 trap nights is considered meaningful since high trappability was established earlier (Section 3.3.1).

R. fuscipes, *M. cervinipes* and *A. flavipes* were trapped across the range of vegetation densities and topographical situations.

Table 10. Numbers of individuals and number of captures (in parentheses) of small mammal species in the 2 habitat types, open and closed forest.

Closed Forest: Transects 1, 3 and sites 8, 9 and 10 of transect 5.

Open Forest: Transects 2, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15 and sites 1 to 7 of transect 5.

χ^2 comparison is based on the number of live trapped individuals of *Rattus fuscipes*.

Figure 10. Occurrence of live-trapped *Rattus lutreolus*, *Rattus fuscipes*, *Melomys cervinipes* and *Antechinus flavipes* in relation to topographical situation and volume of vegetation below 2 metres on open forest transects.

Abbreviations: LS - lower slope adjacent to gully
MS - mid-slope
R - ridge top

Horizontal lines indicate transects on which each species was captured.

Trap Nights	Closed Forest 184	Open Forest 1016	χ^2 Comparison
R. lutreolus	0	33 (70)	
R. fuscipes	22 (54)	21 (50)	$p<0.05$
M. cervinipes	7 (11)	23 (44)	-
A. flavipes	5 (6)	14 (19)	-
A. stuartii	1 (2)	0	-

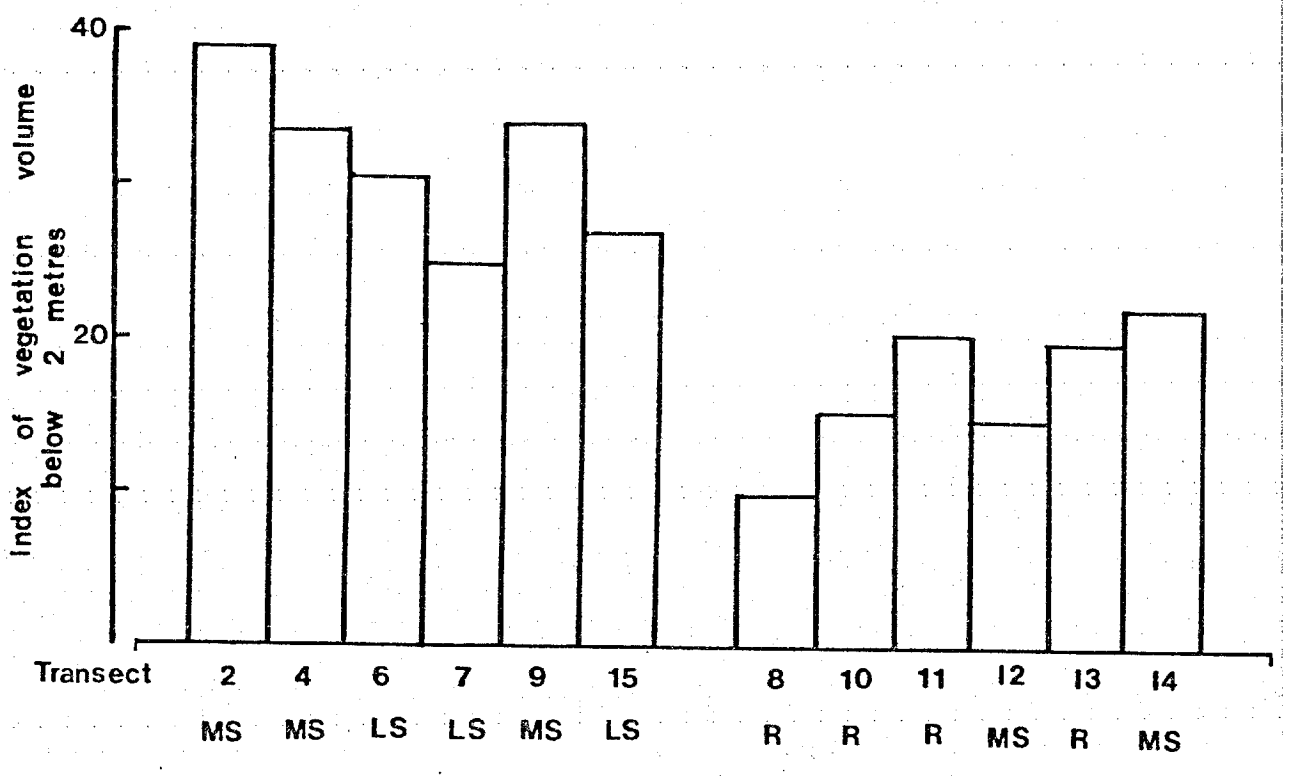


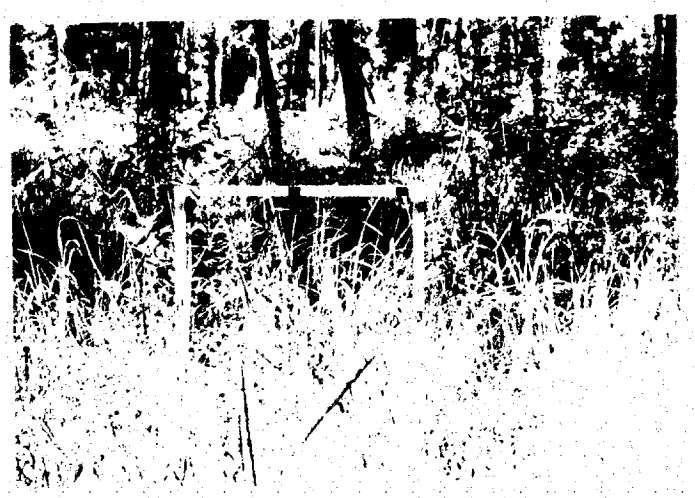
Plate 9. Transitional type mixed forest, transect 3. Note the regenerating understorey of rainforest and mesophyllous shrubs and the open overstorey of sclerophyllous tree species including *Eucalyptus grandis* and *Syncarpia glomulifera*. The stake is 1 metre in height.

Open Forest Transects:

Plate 10. Example of groundcover density in a ridge position within the open forest. Transect 10. The quadrat is 1 metre x 1 metre.

Plate 11. Example of groundcover density in a mid-slope position. Transect 9. The quadrat is 1 metre x 1 metre.

Plate 12. Example of groundcover density in a lower-slope position. Transect 7. The quadrat is 1 metre x 1 metre.



5.3.2 Description of Floristic Groupings on the Grid (105 Sites)

Seven floristic groups were classified at the first major grouping produced by the clustering procedure, at a Jaccard Coefficient of 0.284. Two sites at this level of similarity remained unclassified. A dendrogram, showing site groups and their associated similarity coefficients, which was produced by procedure TREE of the Clustan Package is presented in Figure 11. The seven groups on the grid are plotted in Figure 12. Table 11 lists the plant taxa recorded on the grid and the frequency occurrence (%) of taxa in each floristic group. Designation of taxa as rainforest elements is based on Francis (1981) and descriptions of James Cook University herbarium reference material.

A brief description of the seven groups is given below:

Floristic Group 1

This group included most of the grid (Figure 12) and generally was represented by sites with a grassy groundflora adjacent to the creek on the western grid section and separated from the creek by several smaller groups on the eastern grid section. Sites were characterised by grass taxa *Imperata cylindrica* (dominant species), *Themeda australis*, *Sorghum* sp. and *Panicum* sp., with other groundflora taxa *Pteridium esculentens*, *Dianella* sp. and *Alpinea caerulea* contributing variable cover-abundance (5 to 25% cover-abundance). Sites were also characterised by the regenerating mesophyllous shrubs, *Trema*, *Rhodomyrthus*, *Melastoma*, *Maesa*, and several regenerating rainforest elements, *Mischocarpus*, *Macaranga*, *Wilkiea*, *Guioa*, *Jagera*, *Schizomeria*, *Glochidion* and the disturbance genus *Rubus*. *Eucalyptus* spp. were the dominant overstorey trees (12.01–20 metres) with the codominant *Syncarpia glomulifera* present. An open understorey (6.01–12 metres) of *Allocasuarina torulosa* and *Banksia integrifolia*

Figure 11. Dendrogram showing classification of 105 grid trap sites into 7 floristic groups and 3 floristic types. (See text for description of floristic groups and types.)

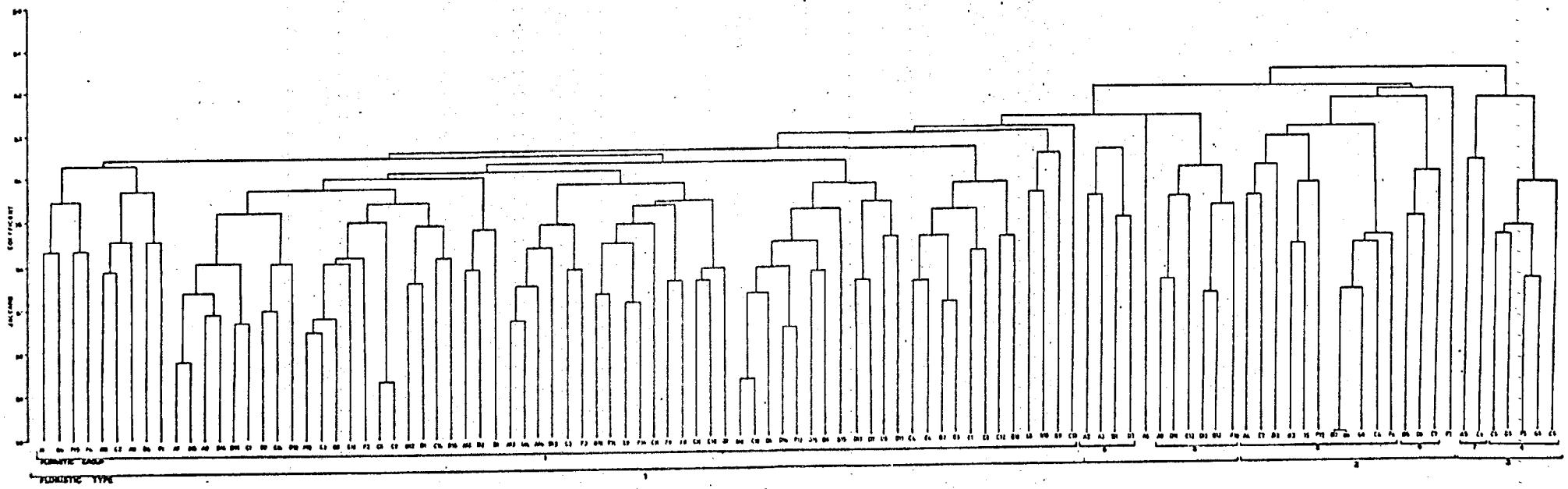

COEFFICIENT
FLORISTIC GROUP
FLORISTIC TYPE

Figure 12. A plot of the 7 floristic groups on the grid.

Figure 13. A plot of the 3 floristic types on the grid.

FLORISTIC TYPE

1 2 3

FLORISTIC GROUPS

1 2 3 4 5 6 7 unclassified

N

creek

creek

Table 11. Frequency occurrence (%) of plant taxa in 7 floristic groups on the 105-site grid in tall open forest on the Paluma Range. +indicates cover-abundance values for plant taxa in the 2 unclassified sites.

Plant Taxa	Frequency Occurrence (%) Floristic Group							Unclassified	
	1	3	5	2	6	7	4	A6	F7
No. of Sites	72	6	4	11	3	2	5	1	1
Imperata cylindrica	100	100	100	45	33				
Themeda australis	24	17							
Sorghum sp.	92	50	75	9					
Panicum sp.	56	33	50	9					
Pteridium esculentens	78	50	100	100	100	100	80	+	+
Other Pteridiophytes						50	100		
Gahnia spp.	14		50	18			100		
Dianella sp.	85					50	20		
Cordyline sp.	7					50	100		
Alpinea caerulea	43			100				+	
Pimelia sp.	21							+	
Trema aspera	13	100	25						
Melastoma polyanthum	29	67	25		33	50	60	+	
Rhodomyrthus trineura	64	67	50		33		20	+	
Rubus spp.	46	17		9		100	40		
Maesa dependans	36			36	100		100		
Macaranga subtendata	22		75	45	100		100		
Mischocarpus lachnocarpus	10		75		9			+	
Wilkiea huegeliana	1			18	33	50	20		
Guioa acutifolia	56		25	27	33	20			
Eucalyptus spp.(M)	15								
Eucalyptus spp.(R)	18	50							
Banksia integrifolia (M)	7								
Banksia integrifolia (R)	6		25						
Syncarpia glomulifera (M)	8	17		9					
Syncarpia glomulifera (R)	8	17	75						
Allocasuarina torulosa (M)	43	50	25	9					
Allocasuarina torulosa (R)	4		75						
Jagera pseudorhus	13			9			60		
Smilax australis	18			27		100	40		
Schizomeria ovata	6			9			20		
Glochidion ferdinandi	15					50	20		
Eupomatica laurina				9					
Cryptocarya sp.							60		
Sloanea sp.							20		
Syzygium sp.							40		
No. of Taxa	31	13	15	18	7	9	19	7	1

occurred. Floristic group 1 showed highest floristic diversity with 31 taxa (Table 11).

Floristic Group 2

This group was comprised of sites adjacent to the creek and one site at the eastern edge of the grid (Figure 12). In contrast to floristic group 1, *Pteridium* was the characteristic and dominant (in terms of cover-abundance) groundflora species. *Alpinea* was also characteristic. *Imperata* and the other grass genera were unimportant to absent. Various regenerating rainforest and mesophyllous shrubs were present, although *Eucalyptus* spp. were absent. The group was floristically less diverse (18 taxa) than group 1 (Table 11).

Floristic Group 3

This group (Figure 12) was very similar to group 1 (Table 11). The characteristic groundflora species was *Imperata*. Notably the associated groundflora of *Dianella*, *Gahnia* and *Alpinea* were absent, resulting in a floristically less diverse ground layer. All sites were characterised by the mesophyllous shrub *Trema*. No rainforest elements occurred. The group was represented by 6 sites only.

Floristic Group 4

This group was represented by 5 sites in the actual creek bed (Figure 12) and represents a major floristic discontinuity from groups 1 and 2. Notably, grasses were absent and other groundflora genera, *Pteridium*, *Gahnia* and *Dianella*, were insignificant in the provision of ground cover (cover abundance, + to less than 5%). Thus, vegetation was absent to negligible at ground level. Cover was provided by well developed rainforest shrubs and trees and other mesophyllous species *Melastoma*, *Rhodomyrthus* and *Maesa* which also occurred as regenerating shrubs in other groups. The group was characterised by the rainforest understorey tree genera *Cryptocarya* sp., *Sloanea* sp. and *Syzygium* sp.

which occurred at no other sites on the grid. Other characteristic features were the presence of ferns (other Pteridiophytes) and mosses (not included in the analysis).

Floristic Group 5

Group 5 was very similar to groups 1 and 3 in that ground cover was characterised and dominated by grasses, in particular *Imperata* (Table 11). Although *Pteridium* was present in the 4 sites (Figure 12), cover-abundance was low and did not exceed 5-25%. Floristic diversity (15 taxa) was comparable to group 3 (13 taxa) although lower than group 1 (31 taxa).

Floristic Groups 6 and 7

These groups were represented by 3 and 2 sites respectively (Figure 12). Ground cover was characterised and dominated by *Pteridium*. Group 6 differed from group 7 by the presence of *Imperata*, although this was insignificant in terms of cover-abundance (<5%). Along with the absence of *Imperata*, the presence of the rainforest shrub *Glochidion* and the vine *Smilax* in group 7 appears to have separated it from group 6.

Unclassified Sites

The 2 unclassified sites were floristically similar to group 2. The characteristic and dominant groundflora species was *Pteridium*. Shrub species, *Melastoma*, *Rhodomyrthus* and *Mischocarpus*, added structural heterogeneity to site A6.

From the floristic description above, there appeared to be 3 major floristic discontinuities on the grid, which are described by the last major classification produced by the clustering technique. Thus floristic type 1 comprises groups 1, 3, 5 and the unclassified site A6 (a total of 83 sites), floristic type 2 comprises groups 2, 6 and the unclassified site F7 (a total of 15 sites) and floristic

type 3 is comprised of groups 4 and 7 (a total of 7 sites). Since the purpose of this analysis was to analyse small mammal dispersion in relation to major floristic types, the 3 major floristic discontinuities will be considered only.

The 3 floristic types are plotted in Figure 13. Table 12 summarises the floristic features of the 3 types. A brief description of each of the 3 types is given below:

Floristic type 1 (Plate 13) was characterised by a grass dominated groundflora, the species *Imperata* being present in all sites. Regenerating sclerophyllous, rainforest and mesophyllous species provided a scattered shrub layer. An open overstorey and understorey was provided by sclerophylls. This type was representative of most of the open forest habitat.

Floristic type 2 (Plate 14) was represented by sites with a dense homogeneous ground cover of *Pteridium*. The shrub layer extended into this type.

Floristic type 3 (Plate 15) describes creek bed and creek bank vegetation dominated by well developed rainforest and mesophyllous shrubs and understorey trees. Groundflora was sparse and grasses were absent.

5.3.2.1 Structural Characteristics of Major Floristic Types

The main structural characteristics and the litter features of the 3 types are summarised in Figure 14.

Type 1 was characterised by dense ground cover below 1 metre, negligible vegetation at 1.5 to 2 metres and from 2 to 3 metres. Understorey (3-12 metres) and overstorey (>12 metres) trees were present.

Type 2 was characterised by medium dense vegetation below 0.25 metres and apparently denser vegetation from 0.76 metres to 1 metre.

Plant Taxa	Frequency Occurrence (%) Floristic Type 1	2	3
No. of Sites	83	15	7
Imperata cylindrica	100	39	
Themeda australis	22		
Sorghum sp.	88	6	
Panicum sp.	54	6	
Pteridium esculentens	73	100	80
Other Pteridiophytes		6	100
Gahnia spp.	15		100
Dianella sp.	74	17	20
Cordyline sp.	6	6	100
Alpinea caerulea	38	61	
Pimelia sp.	20		
Trema aspera	20		
Melastoma polyanthum	32	17	60
Rhodomyrthus trineura	62	11	20
Rubus sp.	41	17	40
Maesa dependans	32	39	100
Macaranga subtendata	23	28	100
Mischocarpus lachnocarpus	12	11	
Wilkiea huegeliana	1	22	20
Guioa acutifolia	50	22	20
Eucalyptus spp. (M)	13		
Eucalyptus spp. (R)	20		
Banksia integrifolia (M)	6		
Banksia integrifolia (R)	6		
Syncarpia glomulifera (M)	9	6	
Syncarpia glomulifera (R)	12		
Allocasuarina torulosa (M)	43	6	
Allocasuarina torulosa (R)	7		
Jagera pseudorhus	11	6	60
Smilax australis	16	28	40
Schizomeria ovata	5	6	20
Glochidion ferdinandi	13	6	20
Eupomatica laurina		6	
Cryptocarya sp.			60
Sloanea sp.			20
Syzygium sp.			40
No. of Taxa	31	23	19

Table 12. Frequency Occurrence (%) of plant species in 3 floristic types on a 105-site grid in tall open forest, Paluma Range.

Plate 13. Floristic Type 1

Note grass dominated groundflora, open understorey of *Allocasuarina torulosa, Banksia integrifolia,* and open overstorey of *Eucalyptus* species and *Syncarpia glomulifera.*

Plate 14. Floristic Type 2

Note dense homogeneous groundcover of *Pteridium esculentens* (bracken-fern). Open understorey of *Allocasuarina torulosa* and open overstorey of *Eucapyptus* species and *Syncarpia glomulifera.*

Plate 15. Floristic Type 3

Creek associated gallery forest. Note dense stand of mesophyllous and rainforest understorey trees and shrubs, sparse groundcover and the absence of grasses.
Stake is 1 metre in height.

The latter reflects the morphotype of *Pteridium*, the groundflora dominant, in which overlapping fronds provided complete cover at this height. There was negligible vegetation above 1.5 metres. Overstorey trees were absent.

In contrast to types 1 and 2, there was negligible vegetation below 1 metre in floristic type 3. Densest vegetation occurred at 1.5 to 2 metres. Most sites had foliage at 2 to 3 metres. Understorey and overstorey trees were present.

In summary, the 3 types showed basic differences in the nature and amount of vegetation providing cover at lower height levels.

5.3.3 Abundance of Food Resources for *Rattus lutreolus* in the 3 Major Floristic Types on the Grid

Individual abundance indices of each grass genus and the total index of food resources in the major floristic types 1 and 2, in which grasses were present, are shown in Table 13 (below).

Table 13. Abundance Indices of *Rattus lutreolus* Food Resources in Floristic Types 1 and 2

Grass Genus	Floristic Type 1			Floristic Type 2		
	*Mean cover abundance	Frequency Occurrence (x100)	Food Index	Mean cover abundance	Frequency Occurrence (x100)	Food Index
Imperata	4	100	400	1	39	39
Themeda	1	22	22	0	0	0
Sorghum	2	88	176	1	6	6
Panicum	1	54	54	1	6	6
Total			652			51

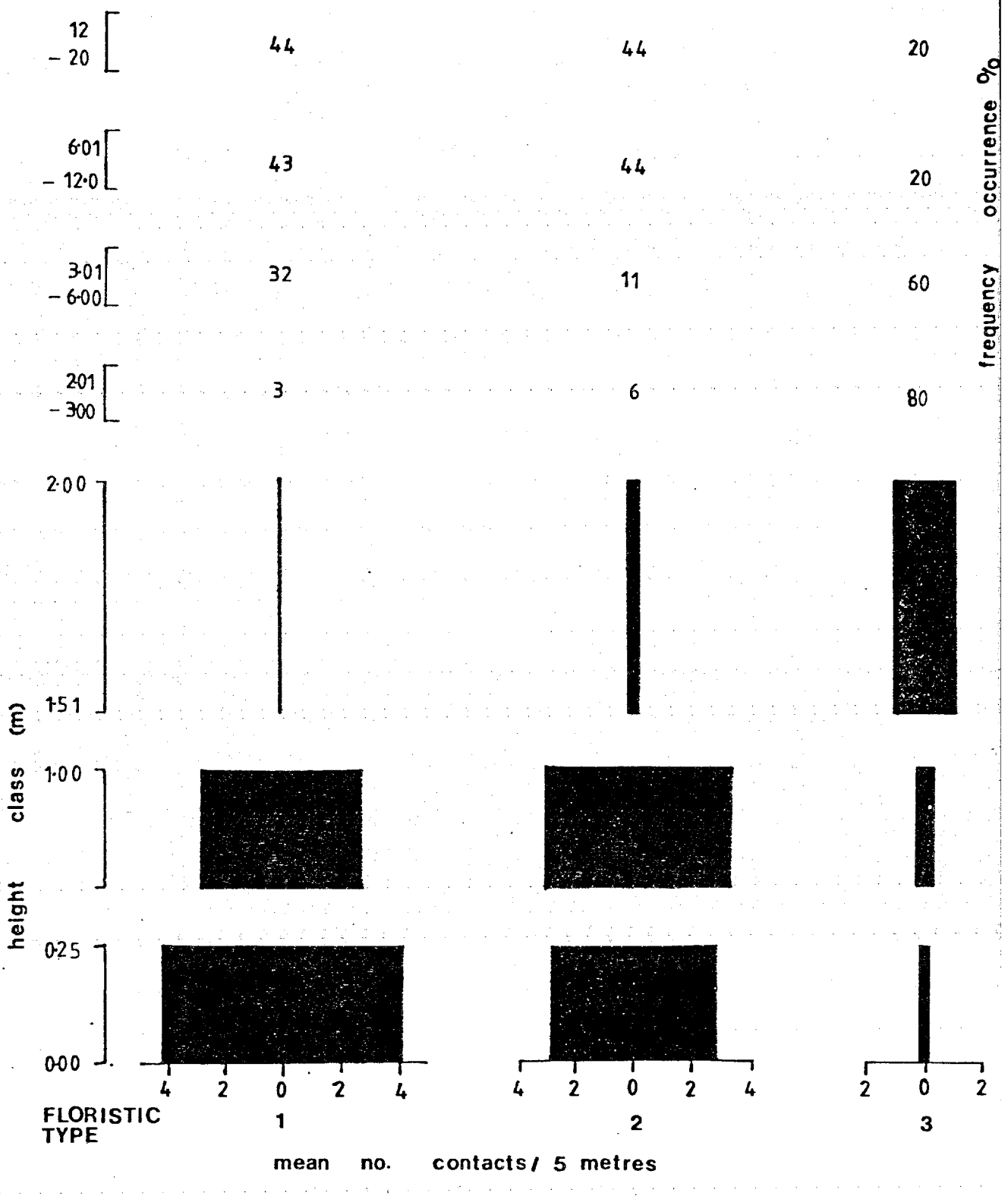
*Reconverted to original Braun-Blanquet rank values.

Figure 14. Summary of structural and litter characteristics of the 3 floristic types on the 105-site grid.

Height classes below 2 metres:
mean number of contacts per 5 metres = total number of vegetation contacts at each site in the floristic type, summed and averaged over the total number of sites in the floristic type.

Height classes above 2 metres:
frequency occurrence (%) - number of sites of the total number in each floristic type (x100), in which vegetation was present at a particular height class.

Litter Characteristics		
Sclerophyllous leaves and dead grass; patchy, discontinuous	*Pteridium* fronds and *Allocasuarina* needles; thick, continuous	Mesophyllous leaves; thin, continuous



5.3.4 Mammal - Vegetation Relationships

The 4 small mammal species are considered separately in the following discussion of relationships with vegetation floristics and structure.

5.3.4.1 *Rattus lutreolus*

a. Floristic Preferences

The dispersion of 129 captures of *R. lutreolus* on the grid from April to August (Table 3) is plotted in Figure 15a. Captures were made over a large part of the grid,although it is notable that no captures were recorded at creek sites. Considering dispersion in relation to the 3 major floristic types, the species showed complete avoidance of type 3 and utilisation of the 2 non-creek types 1 and 2 (Figure 15a). The total numbers of captures and the mean number of captures per site in types 1 and 2 are given in Table 14. The mean number of captures per site per floristic type is plotted in Figure 16. Comparison of the means using a Student t-test indicated that there was no significant difference ($p>0.05$) in the amount of utilisation of the 2 floristic types. However the nature of the captures in the 2 types should be analysed. Table 15,which is based on the individual trap histories of grid animals (Appendix 2), indicates the number of captures of individual males and females in floristic types 1 and 2.

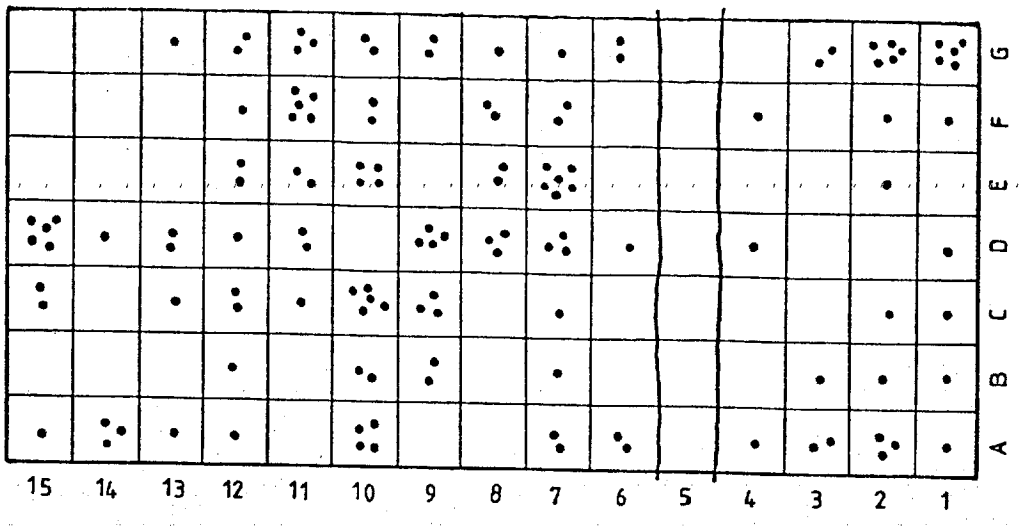
Floristic type 1 captures were of grid residents (caught in more than 3 months on the grid), part-residents (caught in 2 or 3 months), a transient animal (caught in 1 month only) and new animals caught in August. Floristic type 2 captures were of grid residents, one part-resident female and a new male captured in August. However, all resident animals caught in types 1 and 2 were caught more often in type 1.

Figure 15a. Dispersion pattern of captures of *Rattus lutreolus* on the grid from April to August 1982.

Figure 15b. Dispersion of *Rattus fuscipes* on the grid from April to August 1982.

Figure 15c. Dispersion of *Melomys cervinipes* on the grid from April to August 1982.

Figure 15d. Dispersion of *Antechinus flavipes* on the grid from April to August 1982.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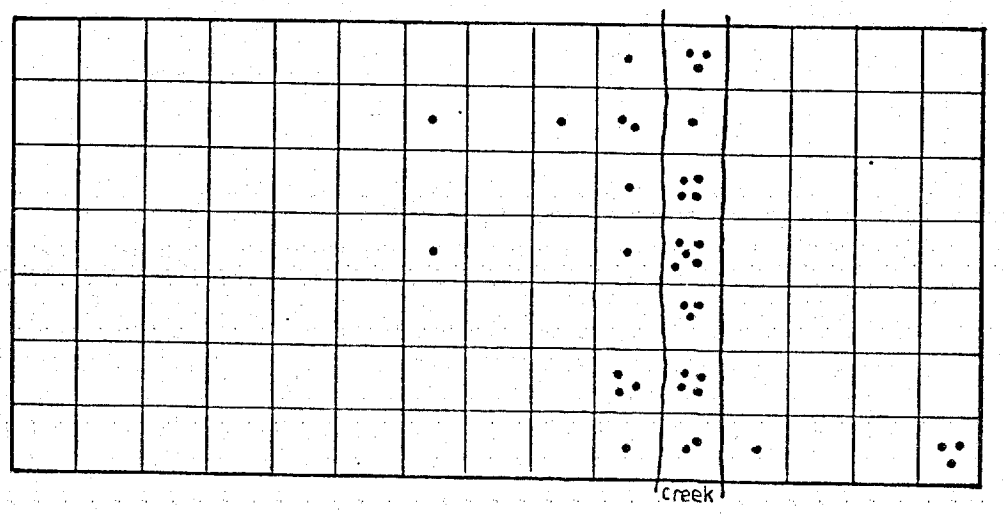
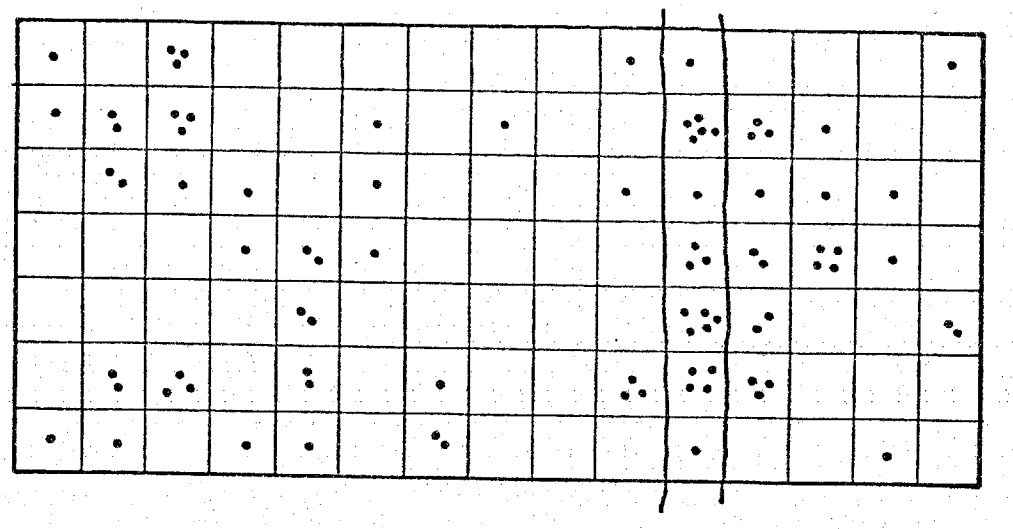

creek



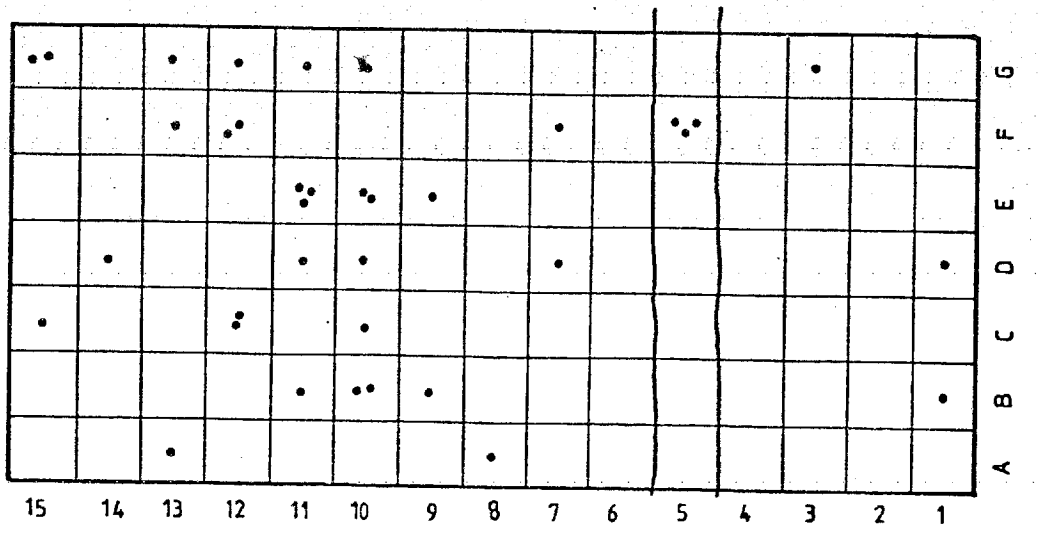

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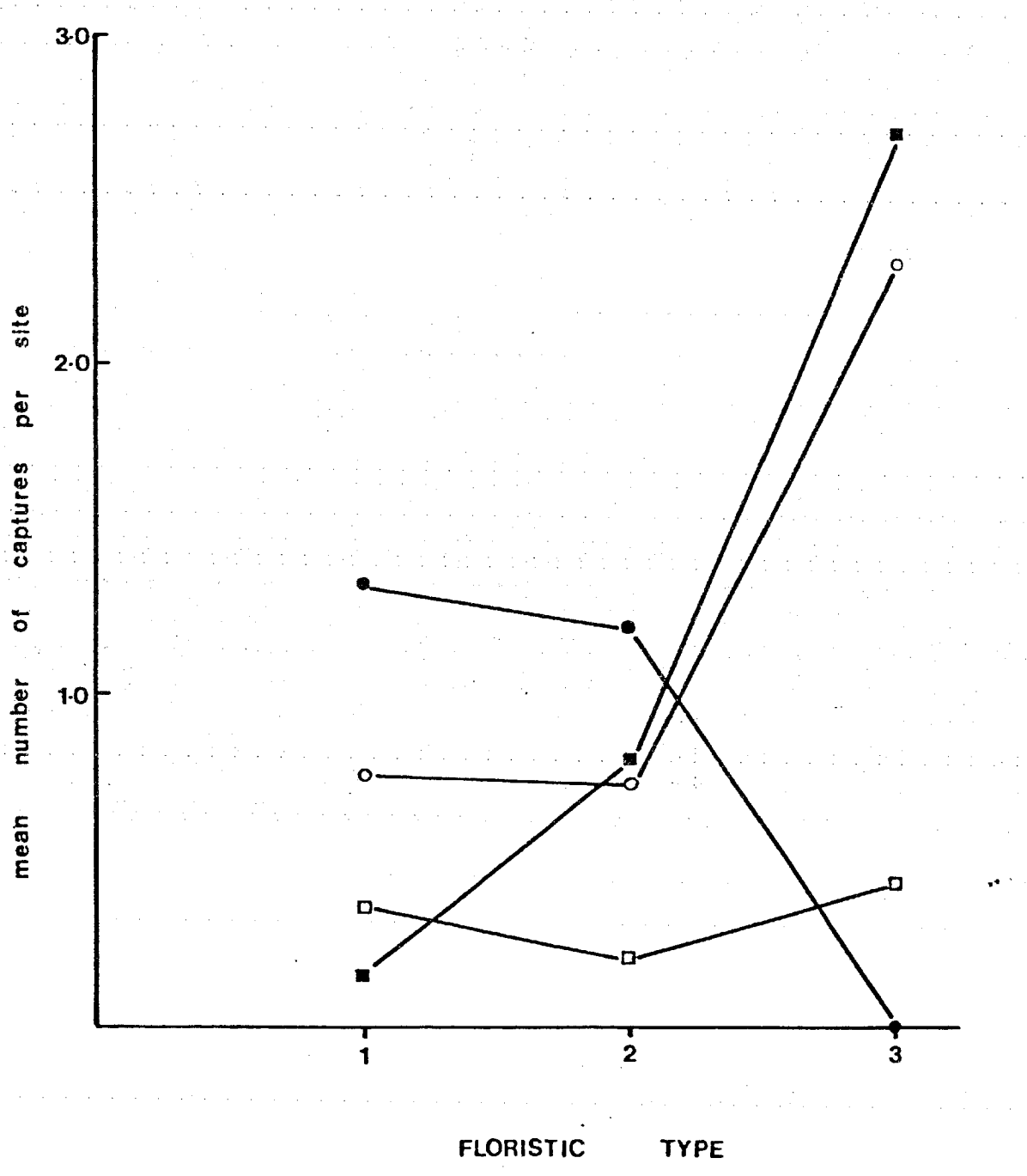
Table 14. Abundances of live-trapped *Rattus lutreolus*, *Rattus fuscipes*, *Melomys cervinipes* and *Antechinus flavipes* in 3 floristic types on the 105-site grid, April to August, 1982: total number of captures and mean number of captures per site (in parentheses).

Figure 16. Mean number of captures per site of each small mammal species, *Rattus lutreolus*, *Rattus fuscipes*, *Melomys cervinipes* and *Antechinus flavipes* in the 3 floristic groups, April to August, 1982.

- ● *Rattus lutreolus*
- ■ *Rattus fuscipes*
- ○ *Melomys cervinipes*
- □ *Antechinus flavipes*

	Floristic Type			Total
	1	2	3	
No. of Sites	83	15	7	105
Rattus lutreolus	112(1.35)	17(1.13)	0(0)	129
Rattus fuscipes	6(0.07)	13(0.87)	19(2.71)	38
Melomys cervinipes	63(0.76)	11(0.73)	16(2.29)	90
Antechinus flavipes	30(0.36)	3(0.20)	3(0.43)	36



This breakdown suggests that *R. lutreolus* captures in type 2 comprised new animals (possibly transients) and exploratory sallies of type 1 residents. No grid residents were caught only in type 2, although 2 grid males were caught only in type 1.

Table 15. Number of captures of *Rattus lutreolus* individuals in floristic types 1 and 2, April to August 1982.

♂ Individual Tag Numbers	Floristic Type 1	2	♀ Individual Tag Numbers	Floristic Type 1	2
Residents			Residents		
1804/1805	8	3	1815/1816	9	2
1821/1822	13	–	1886/1887	8	1
1911/1913	9	–	1900/1901	8	4
1986/1988	3	1	1919/1920	8	2
			1928/1929	5	1
Part-residents			Part-residents		
1806/1807	4	–	1906/1907	3	–
2095	4	–	2011/2012	3	–
1921/1922	1	–	2001/2002	–	2
1964/1965	2	–	2006/2007	4	–
1904/1905	4	–	2009/2010	6	–
			2040/2055	6	–
Transients			Transients		
			2099/2100	1	–
New Animals			New Animals		
2122/2124	1	–	2128/2129	1	–
2114/2116	1	–			
2118/2119	–	1			

Structural Association

Spearman Rank Correlation coefficients and their associated probability levels for transect and grid data are shown in Table 16. On both the grid and the transects, captures of *R. lutreolus* showed significant positive correlations with density of vegetation in the 4 height classes below 1 metre. Thus, a strong association with dense groundcover on both the grid and the transects was indicated.

		Height Class/m	GRID r_s	GRID p	TRANSECTS r_s	TRANSECTS p
a.	*R. lutreolus*	0.0 -0.25	0.2829	<0.005*	0.5019	<0.001*
		0.26-0.5	0.2882	<0.005*	0.5152	<0.001*
		0.51-0.25	0.2781	<0.005*	0.5597	<0.001*
		0.76-1.0	0.2654	<0.01*	0.4517	<0.001*
		1.01-1.5	0.1422	>0.1	0.1517	>0.05
		1.51-2.0	-0.1377	>0.1	0.0203	>0.5
b.	*R. fuscipes*	0.0 -0.25	-0.3870	<0.0001*	-0.2160	<0.05*
		0.26-0.5	-0.3667	<0.001*	-0.1754	<0.05*
		0.51-0.75	-0.0658	>0.1	-0.0724	>0.05
		0.76-1.0	0.0215	>0.5	0.0220	>0.05
		1.01-1.5	0.1189	>0.1	0.2046	<0.05*
		1.51-2.0	0.4528	<0.005*	0.0849	>0.05
c.	*M. cervinipes*	0.0 -0.25	-0.2146	<0.05*	-0.1547	>0.05
		0.26-0.5	-0.2596	<0.005*	-0.0474	>0.5
		0.51-0.75	-0.2578	<0.005*	-0.1323	>0.1
		0.76-1.0	-0.2446	<0.01*	-0.1474	>0.05
		1.01-1.5	-0.1652	>0.05	-0.1993	<0.05*
		1.51-2.0	0.0964	>0.1	0.0280	>0.5
d.	*A. flavipes*	0.0 -0.25	0.2561	<0.005*	0.1737	p=0.05*
		0.26-0.5	0.2877	<0.005*	0.1094	>0.1
		0.51-0.75	0.1974	<0.05*	0.2537	<0.005*
		0.76-1.0	0.2011	<0.05*	0.1022	>0.05
		1.01-1.5	0.0837	>0.01	0.0356	>0.5
		1.51-2.0	-0.0516	>0.5	-0.0833	>0.1

Table 16. Spearman Rank Correlation Analyses for Grid and Transects. Correlations between captures of each small mammal species and vegetation density below 2.0 metres.

a. *Rattus lutreolus*
b. *Rattus fuscipes*
c. *Melomys cervinipes*
d. *Antechinus flavipes*

r_s = correlation coefficients
p = associated probability level.

(An asterisk indicates significant correlations.)

5.3.4.2 *Rattus fuscipes*

A total of 38 captures of *R. fuscipes* was recorded from April to August (Figure 15b). The breakdown of the total and mean number of captures in the 3 floristic types is shown in Table 14. The mean number of captures per site per type is plotted in Figure 16. A preference for floristic type 3 over 1 and 2 was suggested. The mean number of captures per site in type 3 was significantly greater than the mean in floristic type 2 (Student t-test, $p<0.001$), indicating a highly significant preference for type 3. The mean for type 1 was not tested since only 5 captures were recorded. However, the preference for type 3 is further highlighted when the capture success of types 1 and 2 combined (0.19 captures per site) is compared with the mean capture success of type 3 (2.7 captures per site). Means were significantly different (Student t-test comparison, $p<0.001$).

Table 17 is a breakdown of captures in the 3 floristic types, based on individual trap histories of grid animals. Captures in type 1, at D9 and F9 (Figure 15b), were of resident male (1802/1803) in May and June. In the other months, the individual was caught in types 2 and 3. Captures at A1 and A6 were of a resident female (1817/1818) in May, June and July. The same individual was caught in type 2 and 3 in the other months. No individuals were caught only in type 1. A single transient was captured only in type 2; however this was a single capture only. The part-resident individual was captured more often in type 3 than 2, and a new animal in August was captured only in type 3 (Table 17).

The breakdown in Table 17 indicates that captures in floristic type 1 represented transient forays of type 2 and 3 resident individuals.

Table 17. Number of captures of *Rattus fuscipes* individuals in floristic types 1, 2 and 3 from April to August, 1982.

♀				♂			
Individual Tag Numbers	Floristic Type 1	2	3	Individual Tag Numbers	Floristic Type 1	2	3
Resident	4	3	7	Resident	2	8	5
1817/1818 Part-Resident				1802/1803 Part-Resident	-	1	4
Transient				1908/1009 Transient	-	1	-
New animal				2036/2037 New animal	-	-	2
				2120			

Structural Association

Table 16 lists Spearman Rank Correlation coefficients and their associated probability levels for transect and grid data. On both the transects and the grid, significant negative correlations between captures of *R. fuscipes* and vegetation density below 0.5 metres were indicated, suggesting avoidance of dense vegetation at low levels. It is notable that this is opposite to the association with dense ground layer vegetation which was shown by *R. lutreolus*. Additionally, transect captures showed a significant positive correlation (r_s=0.2046, $p<0.05$) with vegetation density at 1.0 to 1.5 metres. On the grid there was a significant positive correlation (r_s=0.4528, $p<0.005$) between captures and vegetation density at 1.51 to 2.0 metres. The relationship of increasing numbers of captures of *R. fuscipes* with decreasing ground cover (below 0.5 metres) density on the transects reflects the floristic preference on the grid. Strong preference for floristic type 3 which was characterised by negligible ground-cover below 1.01 metre and increased vegetation density at 1.51 to 2.0 metres (Figure 14), which was provided by shrubs and understorey trees, indicates a preference for sparse groundcover.

5.3.4.3 *Melomys cervinipes*

Floristic Preferences

The dispersion of 90 captures of *M. cervinipes* on the grid is shown in Figure 15c. The species was caught in all 3 floristic types (Table 14). The mean number of captures in each floristic type is shown in Figure 16. Student t-tests, used to assess the significance of the differences in the mean number of captures per site in the 3 types, indicated that the mean capture success for type 3 was significantly greater than that of type 2 ($p<0.05$) and type 1 ($p<0.001$). However means for types 1 and 2 were not significantly different ($p>0.05$).

In summary, a preference for type 3 over type 1 and 2, with no difference in the amount of use of type 1 and 2, was indicated.

Structural Association

On the grid, captures of *M. cervinipes* were significantly negatively correlated with vegetation density for each of the 4 height classes below 1 metre (Table 16). Association with sparse groundcover can be related to the floristic preference; the preferred floristic type 3 was characterised by sparse vegetation below 1 metre with relatively more vegetation from 1.5 to 2 metres (Figure 14). This relationship with vegetation density was corroborated by the transect data, although the correlation coefficients were not statistically significant for height classes below 1 metre (Table 16). However a significant negative correlation with vegetation density at 1.01-1.5 metres ($r_s=-0.1193$, $p<0.05$) occurred.

5.3.4.4 *Antechinus flavipes*

Floristic Preference

A total of 36 captures of *A. flavipes* from April to August was recorded. The dispersion of these captures is compared with the

patterns shown by the 3 other species in Figure 15d. Captures were made in both creek sites and sites not associated with the creek, largely on the eastern grid section. Captures were made in the 3 major floristic types (Table 14). The mean number of captures per site in each type (Figure 16) suggests a preference for type 1 over type 2 and 3. Since only 3 and 3 captures were recorded in types 2 and 3 respectively, statistical comparisons between the 3 types were not made. On this basis, floristic preferences are considered to be undefined.

Structural Association

On the grid, significant positive correlations between captures of *A. flavipes* and vegetation density in each of the 4 lower height classes (Table 16) indicated an association with dense ground cover. On the transects, significant positive correlations with vegetation density at 0-0.25m (r_s=0.1737, p=0.05) and 0.51-0.75 metres (r_s=0.2537, p<0.05) suggest a similar reaction to density of groundcover.

5.4 Discussion

The 3 floristic types, which showed quantitative and qualitative differences in vegetation floristics and structure, represent 3 different microhabitats for small mammals. Workers who have successfully used floristic classifications to define perferred or required microhabitats have contended that the usefulness of this approach stems from the close relationship between the floristic composition of vegetation and the type and availability of food resources, edaphic conditions and vegetation seral stages (Braithwaite & Gullan 1978; Braithwaite *et al.* 1978; Gullan & Norris 1981; Gullan & Robinson 1980; Stoddart & Braithwaite 1979).

In relatively homogeneous open forest in Victoria, this approach was found to be less useful for describing preferred

microhabitats of *Antechinus stuartii* and *A. swainsonii*. Lack of any floristic associations was attributed to interspecific competition between the 2 *Antechinus* species and *Rattus fuscipes*, with habitat use being influenced by moment to moment interspecific avoidance (Hall & Lee 1982).

In the present study, floristic microhabitat preferences of the 3 species, *R. lutreolus*, *R. fuscipes* and *M. cervinipes*, have been described; the association between *A.flavipes* and floristics remained inconclusive. The floristic associations of *R. lutreolus* and the 2 other species appear to be directly interpretable in relation to known niche occupation, being mediated in particular by diet.

Rattus lutreolus

R. lutreolus demonstrated equal preference for floristic types 1 and 2 with complete absence from type 3. The major differences between the 3 groups was related to the nature of and amount of vegetation providing cover at lower levels. The absence of *R. lutreolus* from type 3 reiterates the restriction of this species to the open forest *per se*.

The creek-associated floristic type 3 essentially represented a small strip of rainforest habitat which was surrounded by open forest. Thus, within the open forest, complete avoidance of rainforest type microhabitat is confirmed.

It is suggested that the dispersion of food resources on the grid, in addition to the structural preferences of *R. lutreolus* would be sufficient to explain the floristic association of this species. The bulk of the diet of *R. lutreolus* was found to be grass lower stems, leaf blade bases and rhizomes, with a variable amount of insect material and fungi ingested from March to August (Section 4, Table 7). Since grasses (the dominant species was

Imperata) were the dominant groundflora in floristic type 1, the utilisation of this type by *R. lutreolus* would relate to the dispersion of food. However, equal preference for type 2 does not appear to relate to the dispersion and abundance of food resources. The food abundance indices (Table 13) indicated that floristic type 1 was superior in the provision of the main food resource of *R. lutreolus*. The major plant food items available in type 2 would include tubers, roots, rhizomes and frond material of *Pteridium* and *Alpinea* (Table 12). Additionally, the deep moist litter layer would be expected to support a large invertebrate fauna. In the dietary analysis, *Alpinea* was absent and *Pteridium* cellular material occurred infrequently, which suggested that rhizome material may have been included while digging for grass rhizomes and basal stems. The apparent transient nature of captures in floristic type 2 suggests a primary dependance on type 1 in terms of food resources. The analysis of the relationship between *R. lutreolus* and density of vegetation below 2 metres indicated an association with dense groundcover on both the transects and the grid. A similar structural requirement has been cited for *R. lutreolus* in an area of grassland (Press 1976) and in coastal heathland (Posamentier 1976) in New South Wales. Association with, or a requirement for, dense ground level vegetation by herbivorous rodents has invariably been related to a requirement for protection from diurnal predators (e.g. Getz 1961; Posamentier 1976). Such a requirement would be conferred by diurnal activity, which has, in turn, been related to herbivory (Section 4.5).

The high level of diurnal activity shown by *R. lutreolus* in July and August may rationalise the observed structural association. However, as Braithwaite and Gullan (1978) reasoned, dense ground

cover may be correlated with the densest concentration of food resources.

The average structural characteristics of each floristic type were summarised in Figure 14. Both types 1 and 2 supported medium dense to dense groundcover which was provided by the dominant groundflora of true grasses and *Pteridium*, respectively. The dispersion of *R. lutreolus* in type 1, then, may be interpreted as a response to both the availability and abundance of the grass resource and the cover resource by which to expedite the exploitation of food. Although floristic type 2 groundflora was not directly utilised, dense ground cover would have allowed transient sallies.

The summarised structural characteristics of floristic type 3 (Figure 14) indicated an open ground situation. However, although it was not fully described by the structural profiling method, almost complete cover was provided at height from about 1.5 to 3 metres, by the closed canopy of rainforest and mesophyllous shrubs. Thus, absence of the grass resource may be sufficient to dictate complete avoidance of floristic type 3.

The role of interspecific relationships in moulding the microhabitat dispersion pattern of *R. lutreolus* should be considered. In contrived laboratory encounters, *R. l. lutreolus* was shown to be interspecifically subordinate to *R. fuscipes*, although *R. lutreolus* was far more aggressive (Braithwaite 1978). Highly significant preference for floristic type 3 by *R. fuscipes* has been established and this was an almost complementary trend to that of *R. lutreolus*.

Avoidance of *R. fuscipes* by *R. lutreolus* in type 3 may have been involved, although only a small population of *R. fuscipes* was present

on the grid (Appendix 4). Additionally, overlap in the dispersion of the 2 species occurred in floristic type 2 and to a lesser extent in type 3, which suggests spatial separation was not rigid. Instead, avoidance of closed forest type microhabitat and habitat appears to be better related to the absence of the grass food resource.

Rattus fuscipes

The diet of *R. fuscipes* in forest habitats is well known. Throughout its range the species is largely an opportunistic generalist omnivore (Section 4). If the potential food resources offered by the 3 floristic types are assessed, floristic type 3 would be expected to be superior in the provision of the primary food resources of this species, such as litter arthropods, fungi and other soft plant resources. Invertebrate populations vary with soil types, plant species and leaf litter characteristics (Matthews 1976 in Gullan & Robinson 1980). The moist continuous cover of mesophylls in type 3 and the deep continuous cover of *Pteridium* fronds and *Allocasuarina* needles of type 2, would be likely to support a greater biomass of litter and soil invertebrates than the patchy drier litter of sclerophylls and dead grass in type 1. Additionally, floristic type 3 was the wetter of the 3 microhabitats and supported macro-fungi, mosses and lichen throughout the year. Macro-fungi were noted in floristic type 2 only in the wetter months of February and March.

The summarised structural characteristics of floristic type 3 (Figure 14) indicated a sparse groundcover to open ground situation. The association with sparse groundcover on the grid appears to reflect the strong association with floristic type 2. However, the association with sparse groundcover was repeated on the transects

which traversed only open forest, grass-dominated groundflora.

A similar relationship with vegetation was detected by Press (1976) for *R. fuscipes* in forest-grassland in New South Wales, and may suggest an adaptation to unimpeded ground movement (Press 1976). The latter, in turn, would be related to an omnivorous foraging habit, since the various food resources exploited by this species are spatially dispersed in contrast to *R. lutreolus*, and unimpeded ground movement would be likely to optimise foraging activity.

R. fuscipes shows poor tolerance of water deprivation relative to *R. lutreolus* (Baverstock 1976). This may have been an additional contributing factor to the microhabitat preference of *R. fuscipes*.

Captures of *R. fuscipes* in floristic type 1 were recorded only in May and June. Use of floristic type 1 by this species was possibly facilitated by access walking tracks through the dense grass, which were well established by that time as a result of regular grid traverses.

Melomys cervinipes

M. cervinipes is a generalist herbivore (Section 4). Preference for floristic type 3 over types 1 and 2 may have been a reaction to the dense stand of mesophyllous and rainforest elements which would have provided abundant soft leaf and stem material. Mosses, ferns and a common soft leaved species in this type, *Cordyline* sp., would have supplemented the vegetarian diet of this species. Additionally, semi-arboreality has been noted for *M. cervinipes* (Wood 1971; Watts & Aslin 1981). Floristic type 3 was the only area on the grid which supported a dense stand of well developed shrubs and spreading understorey trees (Plate 12) which would have offered abundant foraging surfaces.

The association with sparse ground cover on the grid mainly reflects the floristic preference, although not entirely, since *M. cervinipes* showed a more general dispersion pattern than *R. fuscipes*. Although correlations were not significant, possibly due to the fewer data, an association with sparse groundcover on the transects was also suggested.

The microhabitat preferences of *M. cervinipes* have not previously been quantified. Wood's (1971) demonstration of arboreal foraging and nesting in this species exists as the only assessment of habitat utilisation for this species.

Antechinus flavipes

Antechinus is insectivorous and carnivorous (Section 4). Microhabitat preferences have either been difficult to define in relation to floristics and structure (Hall & Lee 1982), have been found to be complex and temporally variable (Fletcher 1977), or have been best defined by structural rather than floristic characterisation (Fox & Fox 1981).

The floristic preferences of *A. flavipes* were not defined in the present study and will not be commented on further.

An association with dense vegetation below 1 metre and at lower height levels on the transects suggests a cover requirement which may be conferred by the diurnal activity which is shown by this species. Similarly, Dickman (1980) contended that *A. stuartii* in relatively unstructured woodland near Canberra used whatever cover was available and showed strong association with features such as logs and tree-log complexes, which provided maximum cover.

5.5 Summary

The microhabitat preference of *R. lutreolus* was described in relation to vegetation floristics and structure. Of 3 broad microhabitat types in the open forest, which were defined in terms of floristics and characterised by different structural attributes, a preference for sites with grass dominated groundflora was demonstrated. Over and above this, a strong association with dense groundcover was established. Distinct avoidance of creek-associated closed forest-type microhabitat within the open forest biotope reiterated the restriction of this species to the open forest *per se*.

In contrast, *R. fuscipes* and *M. cervinipes* showed strongest preference for the creek associated strip of closed forest-type microhabitat; in the case of *R. fuscipes*, the sub-optimal nature of the open forest in comparison with the closed forest, corroborated this.

The association of *R. lutreolus* with dense groundcover and monocotyledon-dominated microhabitat was related to primary dependance on true grasses as the major component of the diet.

6. REPRODUCTIVE PATTERNS OF *RATTUS LUTREOLUS*

6.1 Introduction

The reproductive biology and behaviour of *R. lutreolus lacus* is unknown. In a major assessment of the reproductive characteristics of wild native Australian *Rattus*, Taylor and Horner (1973b) considered 13 of the 14 subspecies recognised at that time, excluding *R. lutreolus lacus* due to lack of material. The number of abdominal nipples of this subspecies has remained unknown since they were found to be indistinguishable on the Lake Barrine holotypes. The reproductive biology of *R. lutreolus lutreolus* has been thoroughly assessed (Braithwaite 1979). Green (1967) reported observations on breeding in wild and captive *R. lutreolus velutinus*.

This section presents observations on the reproductive biology of *R. lutreolus lacus* which were made during the mark-recapture program, concerning (1) pattern of breeding throughout the February to August period, and (2) mammary formula. The reproductive performances of the 2 coexistant rodent species, *R. fuscipes* and *M. cervinipes* are also considered, in an attempt to identify the ecological factors which might be influencing the pattern of breeding in *R. lutreolus lacus* in the study area.

6.2 Methods

6.2.1 Timing of Onset and Duration of Breeding

Information on the reproductive condition of the 3 rodent species in each month from February to August was collated from exploratory trapping in February (Appendix 1) and from grid and transect trapping.

Reproductive Classes

Animals were assigned to several reproductive classes which

were recognised in the field. The criteria used in constructing these classes largely follows Dwyer (1978).

Rattus lutreolus

Males

Three classes were recognised in the field:

1. Juveniles: animals weighing less than 60 grams, testes abdominal. This upper weight limit follows Braithwaite (1979), but additionally below about 60 grams, animals clearly formed a separate cohort of lighter and hence younger animals compared with the majority of animals captured during the study period.
2. Immature, non-breeding: abdominal testes and a small (2x2mm) smooth pigmented patch just anterior to the anus which expands to form the cauda-epididymal protrusion. First year males.
3. Mature, breeding:
   a. First year males at the onset of testicular descent and breeding: testes at the base of the penis or in upper scrotum. Cauda-epididymal sacs showing obvious enlargement to about 5x5mm.
   b. Actively breeding: testes scrotal, cauda-epididymal sacs expanded, scrotum balding.

Females

1. Juveniles: animals weighing less than 60 grams, with imperforate vaginae, nipples minute (less than 1mm) and covered by dense ventral pelage. No animals in the weight range 60 to 70 grams were captured.

2. Immature, non-breeding: greater than about 70 grams, imperforate or perforate vaginae, nipples less than 1mm. and covered with dense ventral pelage.

Note that perforation of the vaginae in the genus *Rattus* usually occurs spontaneously and is unrelated to whether or not mating has occurred, e.g. in *R.l. lutreolus*, perforation occurs between 26 to 45 days following birth (Fox 1979).

3. Mature, breeding: all animals with perforate vaginae. Two subcategories were recognised:

   a. Animals in early pregnancy or post-reproductive condition. Braithwaite (1979) found that females of *R.l. lutreolus* with medium sized nipples (1-2mm) were either in early pregnancy or were post-reproductive. Post-reproductive refers to animals which have bred previously in at least one breeding season. In the absence of autopsy data in this study, females with this nipple size were classified likewise.

   b. Late pregnancy to lactating: nipples large (2-4mm), ventral pelage around nipples thinned.

The nature of the pubic symphysis has been used to indicate pregnancy in rodents; an open symphysis denoting pregnancy (Wellesley-Whitehouse 1981). This index was found to be highly subjective on unetherised animals and was not used. Abdominal palpation for embryos was unsuccessful and no importance has been placed on this method for deciding whether an animal was pregnant or not.

Rattus fuscipes

Males

Animals were assigned to one of 3 classes:

1. Juvenile-immature: testes abdominal, cauda-epididymal sacs still

a small patch anterior to the anus.

2. Mature, breeding: testes scrotal, scrotum full, cauda-epididymal protrusion prominent.

2. Mature:

   a. Animals at breeding onset: testes at penis level or in upper scrotum; cauda-epididymal sacs showing obvious enlargement.

   b. Post-reproductive: testes at penis level or in extreme upper scrotum; cauda-epididymal sacs large, flaccid and wrinkled.

Females

1. Juvenile-immature: imperforate vaginae, nipples minute and covered by dense ventral pelage.

2. Mature, non-breeding: perforate vaginae, nipples small (1-2mm).

3. Mature, breeding (pregnant to lactating): perforate vaginae, nipples large (2-4mm).

Melomys cervinipes

Males

Cauda-epididymal protrusions are not obvious in *Melomys*. Two categories were recognised on the basis of the position of the testes:

1. Non-breeding: testes abdominal.

2. Breeding: testes scrotal, scrotum full.

Females

1. Immature, non-breeding: imperforate vaginae, nipples minute.

2. Mature, non-breeding: perforate vaginae, nipples small (1mm).

3. Mature, breeding (pregnant to lactating): vaginae perforate or imperforate. (In *M. cervinipes*, the vagina may become imperforate again during pregnancy (Wood 1971). Captures of

females with imperforate vaginae and very large teats, in this study, also suggested this.) Teats medium to large (2-4mm).

6.2.2 Mammary Formula of *Rattus lutreolus lacus*

Females were carefully examined in July and August when nipples were enlarged and when thinning of the ventral pelage allowed accurate counts of nipples. The mammary formulas of females with enlarged nipples only, were considered.

6.3 Results

6.3.1 Breeding Pattern

Rattus lutreolus: Males

The number of individuals in each reproductive class each month from February to August and the total monthly sample sizes are shown in Figure 17. One actively breeding male was captured in February during exploratory trapping. On the grid, only first year immature animals were captured in February. In March, *R. lutreolus* was caught only on the grid, and all males were of immature status. In April, the onset of testicular descent in grid animals was detected. By May, all males had scrotal testes and most were considered to be in mature breeding condition. Active breeding condition was obvious from June to the last trapping session in August.

Thus, the onset of mature breeding condition in first year males occurred in late April to early May. On the grid, the descent of testes was synchronous in the small population of males. No post-reproductive males (a class described for *R. fuscipes*) were captured on the grid or on the transects. The mean body weights, with standard deviations, of grid-caught males, in each month from February to August are shown in Figure 18. An increase in weight from the immature non-breeding condition to the actively breeding

Figure 17. Numbers of *Rattus lutreolus* males in each reproductive class from February to August, 1982.

Reproductive classes:

Juveniles are shown separately each month.

juveniles (testes abdominal, less than 60 grams).

immature, non-breeding males (testes abdominal, cauda-epididymal patch only).

males at onset of mature breeding condition (testes in upper scrotum, cauda-epididymal sacs enlarged).

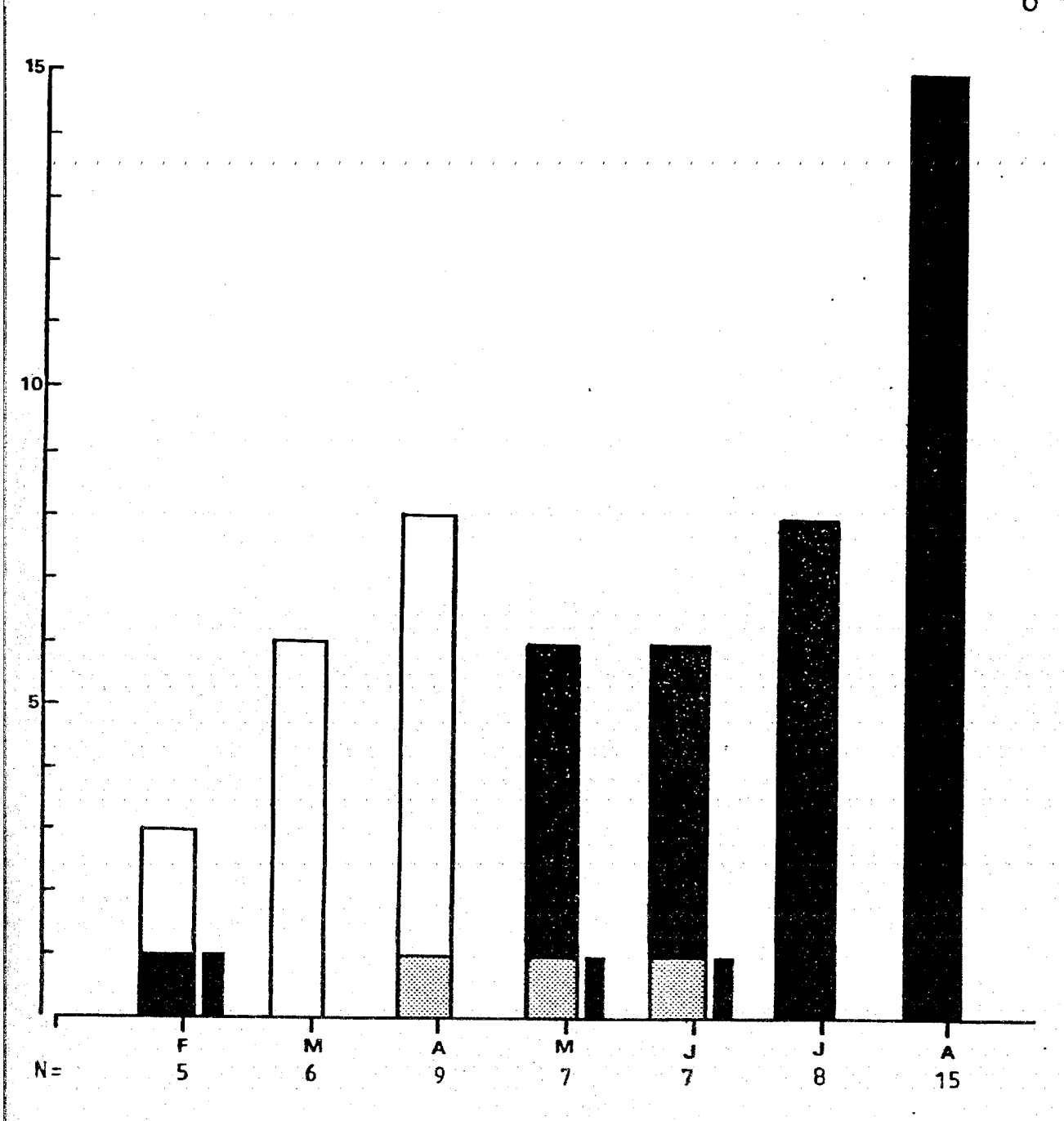
males in active breeding condition (testes fully descended, cauda-epididymal protrusion prominent).

N = total number of individuals caught each month.

Figure 18. Monthly mean body weights (grams) of *Rattus lutreolus* males caught from February to August on the live-trapping grid.

Horizontal line is the mean.

Vertical line is ± 1 standard deviation.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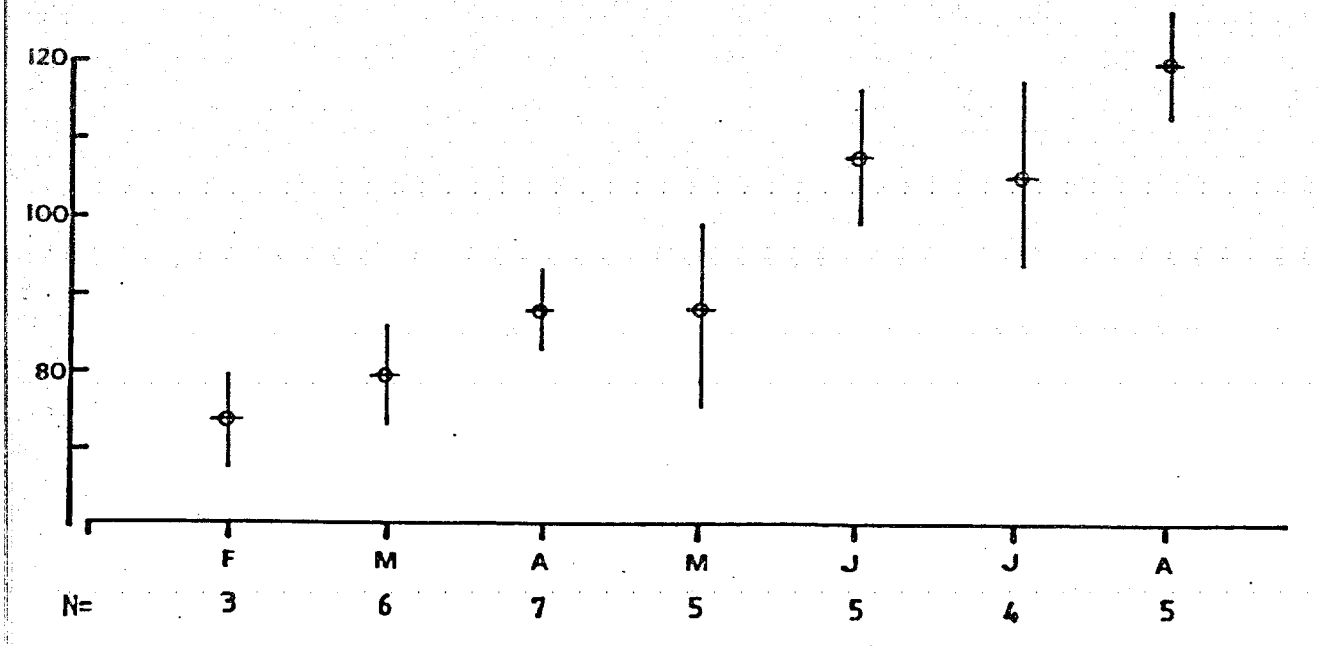
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condition was well marked. Mean body weight continued to increase to August. Five males captured at Mt Zero (Figure 1) in late September 1976 had scrotal testes (J.W. Winter pers.comm.).

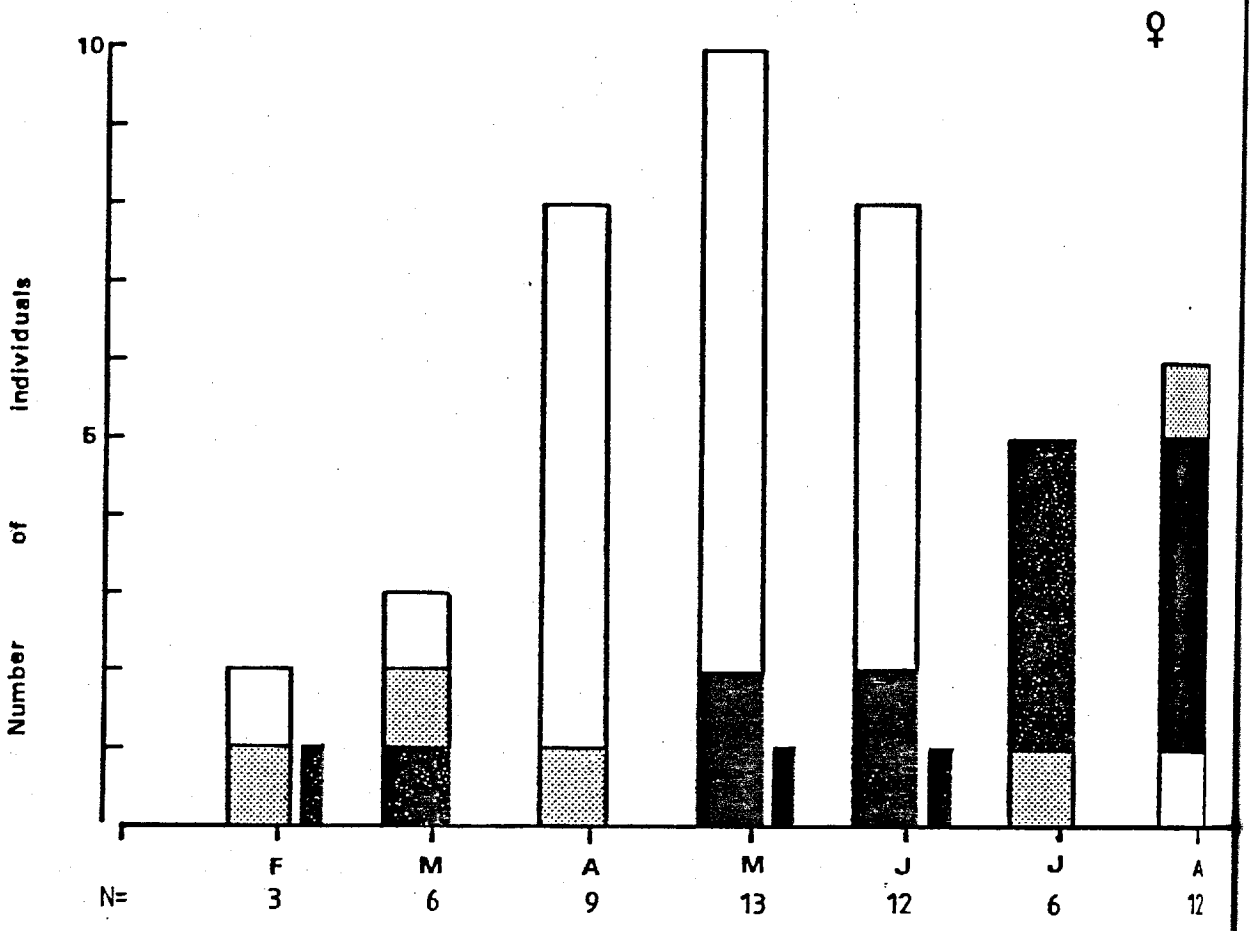
Females

The number of captured females in each reproductive class and the total sample sizes from February to August are shown in Figure 19. Pregnant or lactating females were present in all months except May and June. Females with enlarged nipples (1-2mm) were captured in all months; however difficulty in distinguishing between post-reproductive animals and those in early pregnancy prevented further distinction. Most females captured from February to June were immature, non-breeding animals and probably consisted of first year animals. In July and August, all females which were earlier classed as immature were obviously pregnant.

In summary, some individuals appeared to be pregnant or lactating from February to April. From June to August all females appeared to be breeding. The monthly mean body weights with standard deviations of grid-caught females are shown in Figure 20. An increase in mean body weight from May to August correlates with the onset of breeding and pregnancy in grid individuals.

Juveniles

The presence of juveniles in a population is a good indicator of the timing of reproductive activity (Taylor & Horner 1973b). Three different juveniles weighing 30, 45 and 47 grams respectively, were trapped in February, May and June. Braithwaite (1979) reported a mean gestation period for a laboratory colony of *R.l. lutreolus* of 23 days, which was extended to a span of 28 to 33 days when coincident with lactation and postpartum oestrus. Taylor & Horner (1973b) contended that the gestation periods of all Australian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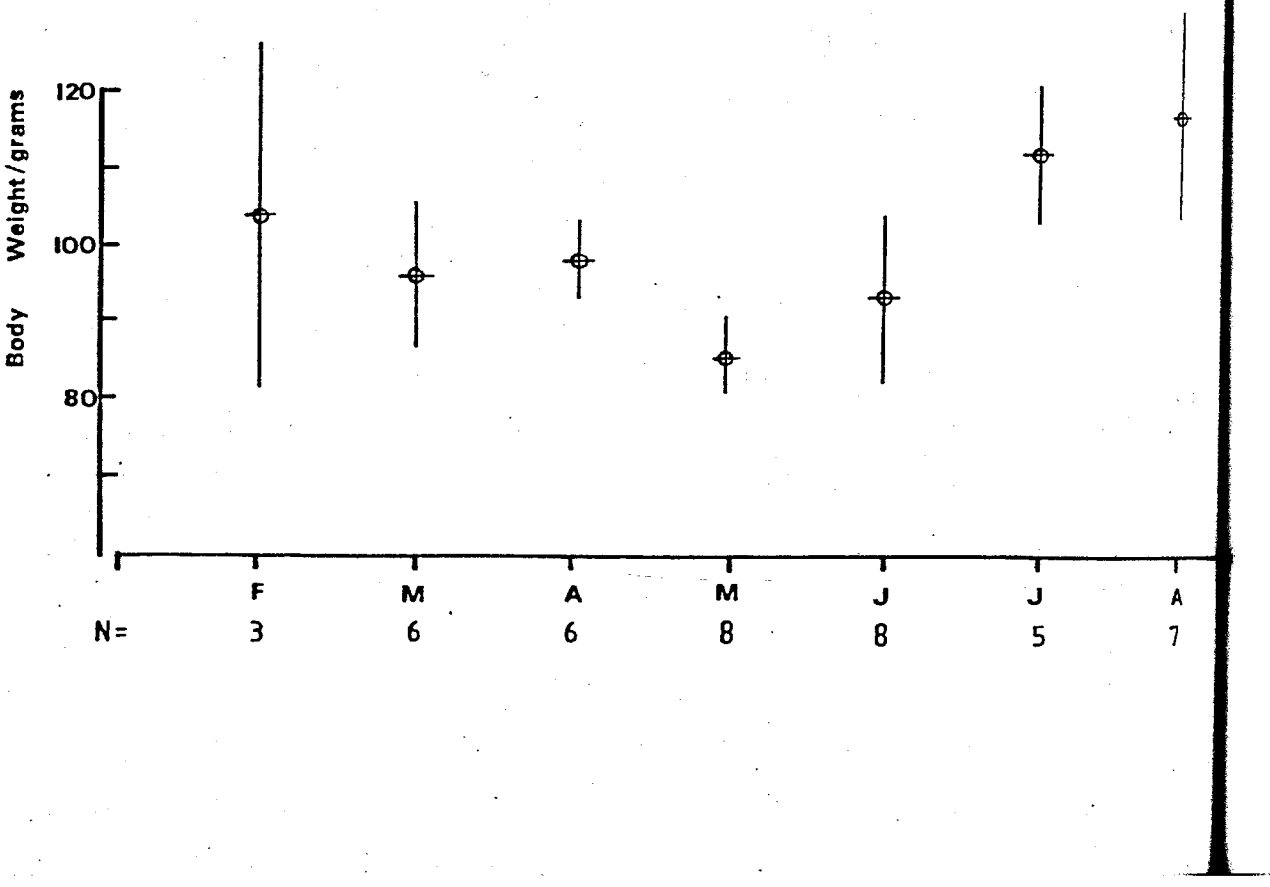
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Figure 19. Numbers of *Rattus lutreolus* females in each reproductive class in each month from February to August, 1982.

Reproductive classes:

Juveniles are shown separately each month.

juveniles (imperforate vaginae, nipples minute, less than 60 grams).

immature, non-breeding females (imperforate or perforate vaginae, nipples small, greater than 70 grams).

early pregnant or post-reproductive females (vaginae perforate, nipples medium, 1-2mm).

late pregnant or lactating females (vaginae perforate, nipples large, 2-4mm).

N = total number of individuals caught each month.

Figure 20. Monthly mean body weights (grams) of *Rattus lutreolus* females caught from February to August on the live-trapping grid.

Horizontal line is the mean.

Vertical line is ± 1 standard deviation.

Rattus were comparable, with a span of 21 to 24 days. Assuming a maximum gestation length of 33 days and allowing 4 weeks for young to be recruited into the trappable population (Braithwaite 1979), the presence of juveniles in February, May and June suggests mating in December, March and April.

Summary of Breeding Pattern of *Rattus lutreolus*

The following observations:

1. Inferred mating in December, March and April,
2. Presence of a scrotal male in February, and
3. Development of mature breeding condition in males on the grid in May, and the continuation of breeding until at least late April,

suggest prolonged breeding activity. Most Australian *Rattus* species show seasonal breeding in spring and summer when levels of vegetative productivity are highest (Taylor & Horner 1973b). Assuming that *R.l. lacus* continues breeding over the normally wet summer, almost continuous year-round breeding may occur.

Rattus fuscipes: Males

Figure 21 shows the number of animals caught monthly in each reproductive class. All males in February and March were in mature breeding condition. Testes were fully descended. Regression of testes occurred from April, and most males caught in May, June and August were post-reproductive. Partial descent of testes in newly mature males occurred from June onwards. However, no fully scrotal males were present by late August. Immature males were present from May to August.

Females

Pregnant and/or lactating females were present in all months from February to August (Figure 22). Most females caught in May

Figure 21. Number of *Rattus fuscipes* males in each reproductive class in each month, from February to August, 1982.

Reproductive classes:

Juveniles are shown separately each month.

juvenile-immature males (testes abdominal).

mature, breeding males (testes scrotal, cauda-epididymal protrusion prominent).

males at onset of breeding (testes in upper scrotum, cauda-epididymal protrusion small).

post-reproductuve males (testes regressed, cauda-epididymal sacs flaccid and wrinkled).

N = total number of individuals caught each month.

Figure 22. Number of *Rattus fuscipes* females in each reproductive class in each month from February to August, 1982.

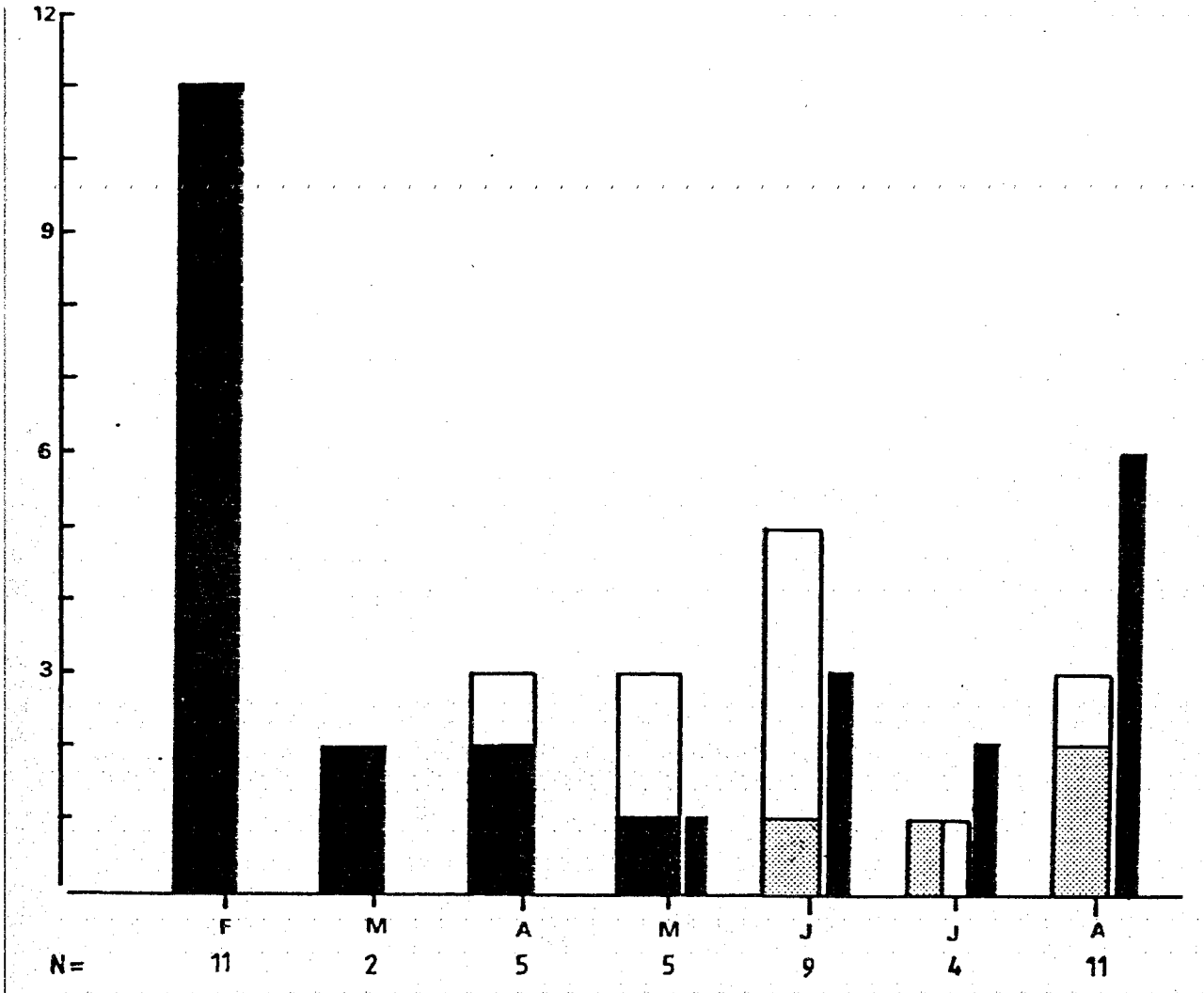
Reproductive classes:

juvenile-immature females.

mature, non-breeding females (perforate vaginae, nipples small).

mature, breeding females: pregnant to lactating (perforate vaginae, teats large).

N = total number of individuals caught each month.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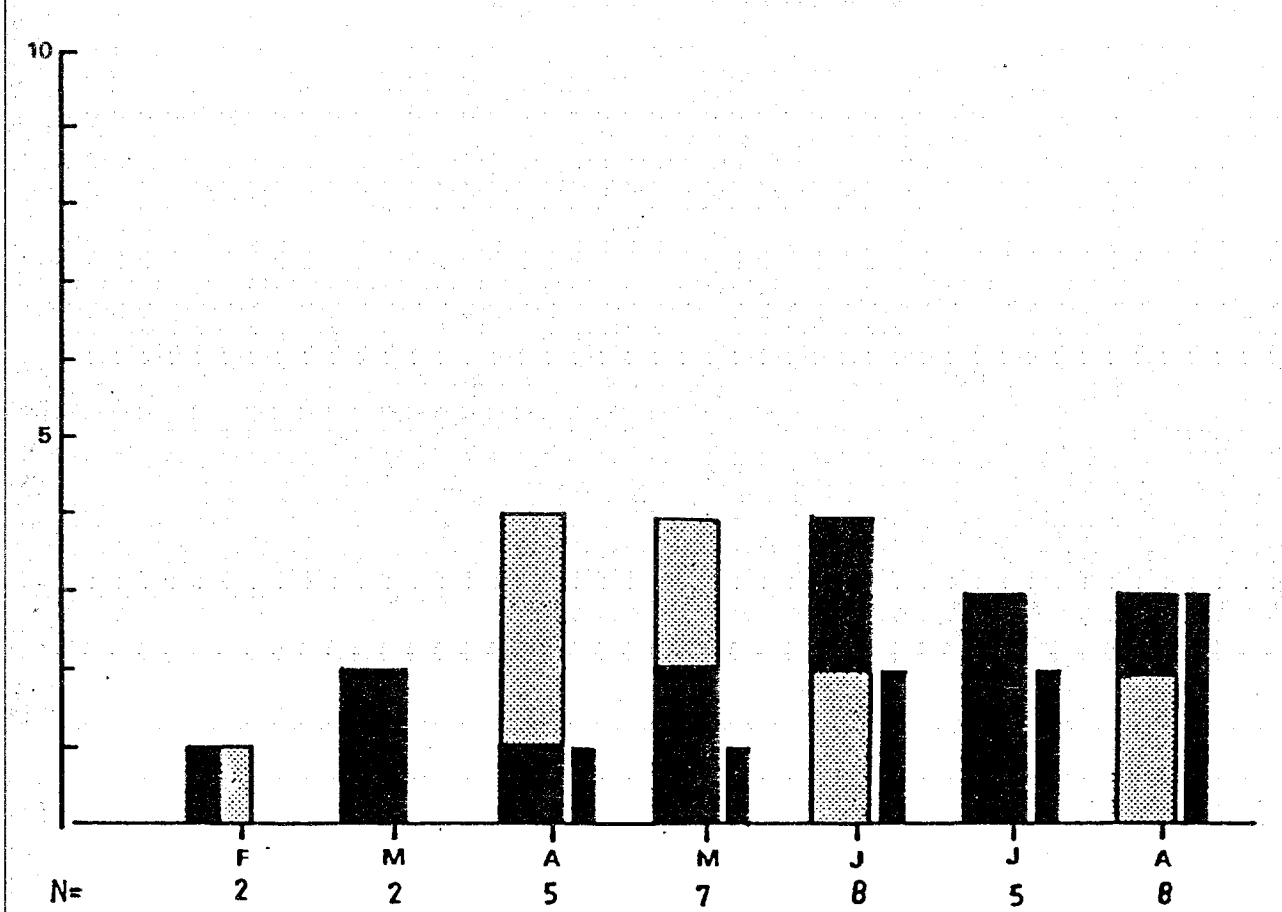
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and June were mature, non-breeding individuals which were possibly post-reproductive. Immature animals were recruited from April to August.

Summary

Regression of testes in males from May until at least late August and the absence of fully scrotal mature individuals in late August suggest an over-winter lull in breeding.

Melomys cervinipes: Males

Several trends are indicated by Figure 23. Fully mature scrotal males and immature non-breeding males were trapped in all months except May, when only immature non-breeding animals were caught. However only 4 males were trapped in May. Most males caught in June, July and August were mature animals with descended testes. Fewer immature, non-breeding animals were also caught in these 3 months.

Females

Immature individuals were caught from March to August; no females being trapped in February (Figure 24). Most females caught from March to May were immature. Apparently mature but non-breeding females were caught in March, May and August. Pregnant and/or lactating females were caught in March, April, June, July and August.

Summary

The observations above suggest prolonged breeding activity. Assuming that breeding continues through the summer months, and this has been reported for *M. cervinipes* near Brisbane (Wood 1971) and noted for a few other Queensland localities (Taylor & Horner 1970), almost continuous year-round breeding may occur. A brief non-breeding period, in May, in which no mature breeding males or pregnant-lactating females were caught, was suggested. However, it should

Figure 23. Numbers of *Melomys cervinipes* males in each reproductive class in each month from February to August, 1982.

Reproductive classes:

immature, non-breeding males (testes abdominal).

mature, breeding males (testes scrotal).

N = number of individuals caught each month.

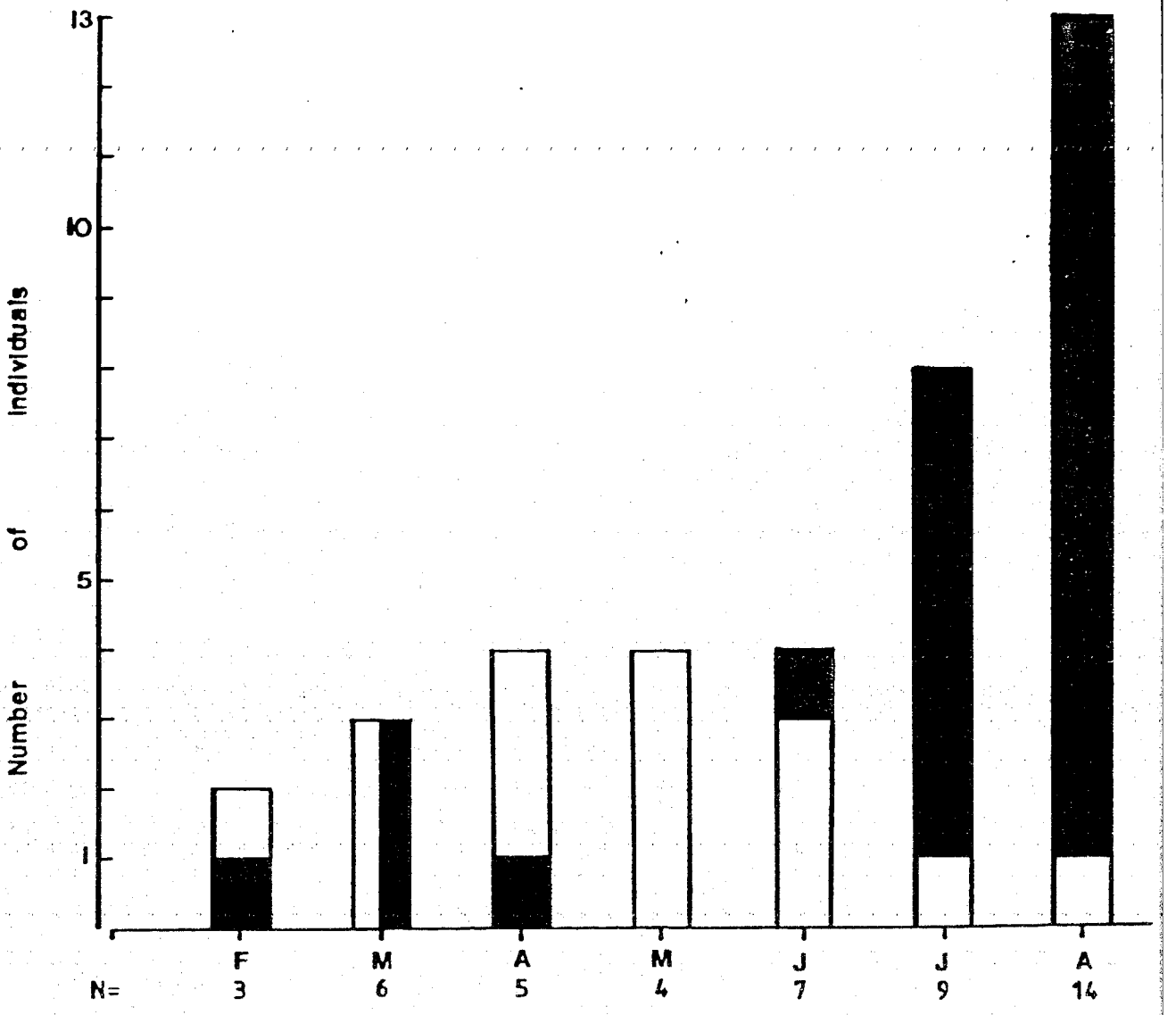
Figure 24. Numbers of *Melomys cervinipes* females in each reproductive class each month from March to August, 1982.

Reproductive classes:

immature, non-breeding females (imperforate vaginae, nipples minute).

mature, non-breeding females (perforate vaginae, nipples small).

mature, breeding females: pregnant to lactating (perforate or imperforate vaginae, nipples large, 2-4mm).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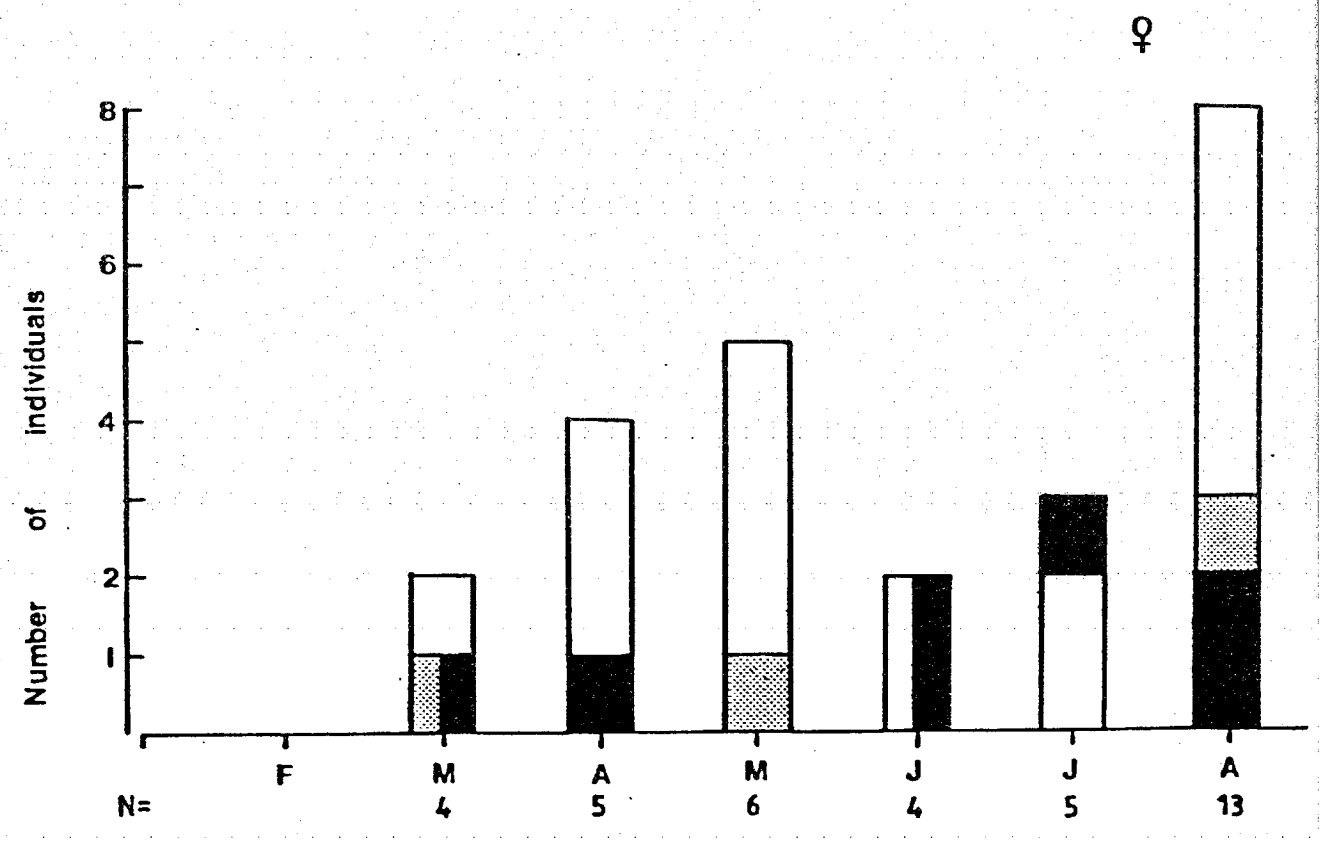
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be noted that the numbers of animals caught in all months except August were low, and while the presence of mature animals is indicative of breeding activity, their absence may merely reflect small sample sizes.

6.3.2 Mammary Formula of *Rattus lutreolus lacus*

The total number of nipples possessed by *R.l. lacus* was found to be 8, 2 pairs of pectoral and 2 pairs of abdominal nipples (mammary formula is 2,2=8). This was based on counts from 10 individuals. Eight nipples represents a reduction in comparison with *R.l. lutreolus* which possesses 10 nipples (2,3=10) (Taylor & Horner 1973b), but is the same as the number possessed by *R.l. velutinus* (2,2=8) (Green 1967; Taylor & Horner 1973b).

6.4 Discussion

McDougall (1946) stressed the importance of rainfall on the breeding pattern of *R. sordidus*, a vegetarian species, due to the effect on food availability. When green plant material was available throughout the year, *R. sordidus* bred almost continuously. Taylor and Horner (1973b) reviewed the importance of climate on the pattern of breeding in native Australian *Rattus*, contending that most species bred in distinct breeding seasons when vegetative productivity was at its highest, usually in spring and summer. It was suggested that in tropical areas, populations bred over a less punctuated season since variability in vegetative productivity was less markedly seasonal than in temperate areas of Australia. Braithwaite (1979) considered that rainfall was the main factor controlling reproduction in *R.l. lutreolus* in Victorian heathland. In summer when Victorian soils undergo a severe water deficit due to low rainfall, many plants die, growth of sedge rhizomes and stems is severely curtailed and accessibility by digging is

restricted. As a consequence, breeding is curtailed (Braithwaite 1979).

In the present study, the onset of breeding in first year males correlates with decreasing monthly rainfall in 1982 (Figure 3). Breeding commenced in May and continued over the dry winter months of June and July. This suggests that in the tall open forest habitat on the Paluma Range, *R. lutreolus* was not limited by availability and accessibility of grass resource over the driest part of the year. Hence, dry season breeding may be the norm for this species in North Queensland, since 1982 has been an extremely dry year (Section 2).

Differences in the pattern of breeding were shown by *R. lutreolus* and *R. fuscipes* in the study area and appear to be attributable to dietary differences. Breeding in *R. fuscipes* was shown to be reduced or to cease in June and July. Similarly, Wellesley-Whitehouse (1981) reported an over-winter cessation of breeding in *R. fuscipes* in rainforest at Paluma. This correlates with lowest monthly maximum and minimum temperatures, and rainfall. Abundance of the main dietary components of *R. fuscipes* (Section 4) would be expected to be reduced by low temperature and rainfall, resulting in a food stress situation in winter which would conceivably limit breeding activity. In contrast, the grass resource appears to be a more stable dietary mainstay which did not become limiting during the drier, cooler winter months.

Dwyer (1975) commented on a similar phenomenon in New Guinean *Rattus* species. Reduction or cessation of breeding in the drier winter months was least evident for grassland species. Periods of sustained high breeding were at least one or 2 months shorter

for rainforest species, and this phenomenon was attributed to different levels of food availability in rainforest and grassland habitats.

Prolonged breeding activity was shown by *M. cervinipes* at Paluma. *M. cervinipes* is a generalist herbivore (Section 4) and relative to *R. fuscipes* would be less likely to suffer a food stress situation in the colder, drier winter months.

Following the trend shown by *R.l. velutinus* in Tasmania (Green 1967), *R. lutreolus* in North Queensland shows a reduced nipple number relative to *R.l. lutreolus* from south-east Queensland to Victoria. Taylor and Horner (1973b) showed that mammary formula was a reliable subspecific characteristic for all Australian *Rattus* species, except for *R. fuscipes*. Mean litter size and nipple number appear to be positively related in *R. lutreolus*. *R.l. velutinus* in Tasmania (with 8 nipples), has a mean litter size of 4. In Victoria, although litter size was found to vary widely in different habitats, mean litter size of *R.l. lutreolus* (with 10 nipples) averaged over a range of habitats was 5 (Braithwaite 1979). Based on these trends, a reduced mean litter size would be predicted for *R.l. lacus*. The only available data on litter sizes of *R.l. lacus* is the observation that a litter of 4 was produced by a trap-held female captured at Mt Zero (Figure 1) (J.W. Winter pers.comm.).

It is interesting that the reduced number of nipples of *R. lutreolus* in North Queensland is paralleled by a reduced number in *R. fuscipes*, from 10 (2,3=10) in *R.f. assimilis* from south-east Queensland to south-eastern Victoria, to 8 (1,3=8) in *R.f. coracius* in North Queensland (Taylor & Horner 1973b).

Wellesley-Whitehouse (1981) gave a mean litter size of 4, from 8 laboratory-reared litters of *R. fuscipes coracius*. In

comparison, mean litter sizes of 4.5 and 4.4 were recorded for *R. fuscipes* in south-east Queensland (Wood 1971) and 4.5 for a population in New South Wales (Taylor & Horner 1961 in Wellesley-Whitehouse 1981).

It should be noted that a number of factors have been cited as correlating with litter size. Mean litter sizes were positively correlated with latitude in *R. rattus* in North America, varying from 3.2 in the tropics to 7 at higher latitudes (Jackson 1965 in Braithwaite 1979). Lloyd (1966) in Braithwaite (1979) found no correlation between latitude and litter size. Other factors such as number of previous litters, maternal body size and the time of year in which a litter is produced (Braithwaite 1979) may also be implicated.

Cody (1971) in Braithwaite (1979) considered reduced litter sizes and adult mortality to be characteristic of a stable environment.

Relative to temperate habitats, comparative stability of food resources appears to have allowed prolonged breeding by *R. lutreolus* in the tall open forest habitat. As a result, it might be predicted that prolongation of the period suitable or possible for production of young might lead to selection of a reproductive trait such as smaller litter sizes. A reproductive pattern in which few young are produced at any one time, but over an extended period, rather than a larger number in a major seasonal effort, may be selectively advantageous when there is little seasonal variability in food resource abundance.

7. DISCUSSION

The primary objective of this study, as part of a broader ecological study of *Rattus lutreolus lacus* , was to identify microhabitat preferences of the subspecies within the open eucalypt forest. Since open eucalypt forest forms only a marginal habitat of *R. lutreolus* in south-eastern Australia, the study afforded the opportunity to determine how the species uses such a habitat. The adjunct, then, is to identify the major determinants of the microhabitat preferences and other aspects of ecology.

A diet mainstay of grass stem/rhizome (it is likely that the bulk is provided by *Imperata cylindrica*) is suggested to be a major determinant of the observed microhabitat preferences, activity pattern and reproductive performance of *R. lutreolus*. *R. lutreolus* was found to be restricted to the open forest, being absent from the adjacent transitional type closed forest (described in Section 2). Microhabitat preferences appeared to be mainly related to the spatial dispersion and abundance of the grass resource. However, a cover requirement may also be important. On the live-trapping grid, which was situated in a lower to mid-slope position, spanning a moist creek bed, avoidance of the creek-associated rainforest type microhabitat was pronounced. The 2 preferred floristic types differed in groundflora dominants, which separately were grasses and *Pteridium esculentens* (bracken-fern). Use of the grass dominated floristic type 1 appeared to reflect primary dependance on grasses as the main dietary component (Section 4). However, abundance of grasses and a high food resource index in this type, corresponded with dense groundcover. As previously outlined, a small mammal's requirement for, or association with dense groundcover

has largely been related to a need for protection from diurnal predators (e.g. Getz 1961; Posamentier 1976). *R. lutreolus* has been found to show a requirement or preference for dense vegetation at low height levels in heath communities (Braithwaite *et al.* 1978; Cheal 1978; Posamentier 1976) and in forest-grassland (Press 1976).

Unlike heath vegetation where cover is provided mainly by low shrubs (see Cheal 1978), dense low cover on the grid in the 2 preferred floristic types was provided by grasses and *Pteridium*. Although transects through the open forest were not described floristically, all traversed grassed terrain (e.g. Plates 10, 11 and 12) and densities below 2 metres are considered to have largely described grass densities.

Dense homogeneous belts of *Pteridium* are commonly developed adjacent to gullies and creeks in this forest type and probably reflect a combination of moist soil conditions and the absence of fire from the localised area for some time. Use of this floristic type by *R. lutreolus* was shown to be of a transient or temporary nature. Diet analyses indicated that *Pteridium* and *Alpinea* (a common associate in this floristic type) were eaten infrequently, despite this concentration of root, rhizome and stem material. However, digestibility of *Pteridium* and *Alpinea* tissue, relative to grasses, remains an unknown factor.

It seems, then, that the dispersion of *R. lutreolus* relates to both abundant food and cover. Both may be essential components of suitable microhabitat which is capable of supporting resident animals. Both food and cover requirements are satisfied by dense grass situations.

Whereas *R. fuscipes* ceased breeding during the coolest and driest months of June, July and August, young males of *R. lutreolus* showed mature breeding condition in May, and active breeding condition was observed from June until the last field observations in late August. This ability of *R. lutreolus* to breed during the winter months was related to the grass resource being a temporally more stable food base than litter invertebrates and fungi which have been reported to be important dietary items for *R. fuscipes* in forest (e.g. Warneke 1971 in Gullan & Norris 1981; Watts 1977; Wellesley-Whitehouse 1981).

Insect productivity appears to be variously governed by temperature and rainfall, and the individual and combined effects of the 2 factors may vary considerably with latitude (e.g. Van Dyck 1982). Perhaps arthropod abundance is affected more by temperature, so that the lower winter temperatures reduce arthropod productivity. Equally well, the combined effects of low temperature and rainfall may limit arthropod abundances. On the grid, macro-fungi was abundant in the wetter months of February and March, yet was notably absent in the drier months of June, July and August. The diet of *R. fuscipes* has been shown to change seasonally, depending on food resource availability (e.g. Cheal 1978). In winter, the high protein summer diet of mainly arthropods and fungi may become proportionately more vegetarian as arthropod abundances become limiting (Cheal 1978). Relative to an arthropod dominated diet, a vegetarian diet is likely to be richer in carbohydrates than proteins (e.g. Braithwaite 1978; Cheal 1978). Such a change in nutritional quality, combined with a straight food stress situation in which insufficient quantities of preferred food items such as arthropods and fungi are available, would be likely to limit

breeding by *R. fuscipes* during winter.

In contrast, growth of vascular plants such as grasses is likely to be largely controlled by rainfall. The apparent temporal stability of the grass resource in the Paluma Range study area is most likely related to the high annual rainfall regime of the area. The proximity of the rainforest which develops where a minimum of 1500 millimetres of rain is received annually (Section 2) indicates a moist forest habitat. Evidence for this suggestion of stability of plant food resources in the study area was provided by the patern of breeding which was shown by *M. cervinipes*. This species showed mature breeding condition in all months except May. (However the May observation was based on only a small sample size of 4.) In the winter months of June and July, *R. fuscipes* showed regressed testes. In contrast, in these months, testicular descent was noted for *M. cervinipes*.

R. lutreolus is a member of a broader small mammal community and as such, it might be expected that aspects of its ecology could be influenced by coexistant species. Interspecific effects are not limited to congeners, although they seem to be particularly common where species of the same genus are sympatric (Cheal 1978). Cheal (1978) contended that where the 2 species were coexistant in an area of closed heath in Victoria, there was little evidence of any competitive exclusion of *R. fuscipes* by *R. lutreolus* and vice versa. It was found that the most suitable areas for *R. lutreolus* also supported *R. fuscipes*, and elsewhere in the vegetation type where *R. lutreolus* abundance was lower, *R. fuscipes* was absent (Cheal 1978). In contrast, Braithwaite (1978) contended that *R. fuscipes* had an important effect on the distribution and abundance of *R. lutreolus*. In other Victorian heathland where the 2 species were coexistant,

R. fuscipes was common throughout most vegetation groups, whereas *R. lutreolus* was restricted to wet community groups (Braithwaite 1978).

At the Paluma Range study area, the 2 species showed almost opposite responses to vegetation floristics and structure. On the live-trapping grid, *R. fuscipes* was largely restricted to the creek associated strip of rainforest-type microhabitat and made only transient movements into the *Pteridium* and grass dominated floristic types. Indeed, open forest appears to be a suboptimal habitat for *R. fuscipes* since a significantly higher number of individuals were captured at closed forest sites than at grassy open forest sites. Within the open forest, the species may ultimately be dependent on the moist gully and creek vegetation.

Rather than suggesting competitive exclusion, it was suggested that the microhabitat preferences of *R. fuscipes* and *R. lutreolus* appear to be better related to the different dietary requirements of the 2 species. Generalised foraging by *R. fuscipes* might be optimal when unimpeded ground movement is allowed (e.g. Press 1976). The almost clear ground situation in closed forest microhabitat would enhance the species' ability to exploit spatially dispersed ground-based food resources. It was suggested that a diet including large amounts of litter invertebrates and fungi would be better satisfied in closed forest microhabitat.

R. fuscipes has been shown to have lower tolerance of water deprivation relative to *R. lutreolus* (Baverstock 1976), and this may contribute to the species preference for creek associated closed forest microhabitat.

The strong within-habitat separation of the 2 species suggests there is little potential for field interactions. Competitive

interactions result in apportionment of habitat and food resources (e.g. Krebs 1978). Hence, the almost complementary microhabitat preferences of *R. lutreolus* and *R. fuscipes* may be indicative of strong ecological displacement as a result of former competitive interactions.

In many aspects of ecology, *R.l. lacus* appears to be in close ecological harmony with its 2 conspecifics. The diet remains largely monocotyledon based. In Victoria and New South Wales, *R. lutreolus* appears to be best adapted to swamp-heath (Braithwaite 1978; Taylor & Horner 1973a) where sedges rather than grasses are common. The diet of *R. lutreolus* in this habitat reflects this dominance of sedges (e.g. Cheal 1978; Watts & Braithwaite 1978). However it has also been shown that when grass forms the major groundflora type, *R. lutreolus* is equally capable of utilising it as a diet mainstay (e.g. Watts & Braithwaite 1978; Cheal 1978). In Tasmania, where *R. fuscipes* is absent, *R. lutreolus* occupies a wider range of habitats including temperate rain forest where it may be more insectivorous than elsewhere (Braithwaite 1978).

Substantial diurnal activity appears to be characteristic of this species throughout its range and, as suggested earlier, is probably diet related.

The major ecological difference between *R.l. lacus* and its 2 conspecifics, *R.l. lutreolus* and *R.l. velutinus*, relates to reproduction. A reduction in the number of nipples possessed by *R.l. lacus* relative to *R.l. lutreolus* was equated with a potential for producing smaller litters. This trend is shown in Tasmania, by *R.l. velutinus* which also possesses 8 nipples (e.g. Braithwaite 1979; Green 1967). In Tasmania, this may be a result of lower vegetative productivity in the highland habitats which prevents

R. lutreolus rearing larger litters (Braithwaite 1979).

The reproductive strategy of *R.l. lacus* needs to be clarified by longer term study. However, from the theoretical literature (comprehensively reviewed by Braithwaite 1979), smaller litter sizes would be expected to be adaptive where temporal stability of food resources facilitates extended breeding periods. Larger litter sizes might be predicted for populations with shorter breeding seasons (e.g. Spencer & Steinhoff 1968 in Braithwaite 1979). Cody (1971) in Braithwaite (1979) recognised that characteristics normally associated with island populations, such as a mature age structure, long pre-reproductive periods, reduced clutch or litter sizes, and reduced adult mortality would be associated with a stable environment. A relationship between reproductive effort and adult survivorship has been recognised, so that the higher the reproductive effort, the higher the mortality of adults (e.g. Braithwaite 1979). Due to the short term nature of the present study, a detailed analysis of the dynamics of the small grid population of *R. lutreolus* was not attempted. Hence, other population characteristics such as levels of recruitment and mortality which would normally be important correlates to consider when attempting to identify the reproductive strategy of a small mammal population are unknown.

It was unfortunate that some data on litter sizes of *R.l. lacus* was not able to be obtained during the study. It would be an interesting adjunct to obtain field data on litter sizes in order to establish the pattern of reproduction of *R. lutreolus* in North Queensland. This would provide insight into the influence of latitude on the reproductive characteristics of *R. lutreolus* which is the only native Australian rodent species with a

distribution from Tasmania to north-east Queensland (Watts & Aslin 1981).

Recognising the north-south cline of increasing commonness and habitat generality of *R. lutreolus* (Section 1), Braithwaite (1978) speculated about the status of the species in North Queensland. Due to the apparent habitat restriction of *R.l. lacus* it was suggested that a narrower range of food resources would be available to this subspecies relative to *R.l. lutreolus* and *R.l. velutinus* which both occupy a broader range of habitats. As a result, *R.l. lutreolus* and *R.l. velutinus* are able to exploit a broader range of food resources, e.g. in temperate rainforest in Tasmania insects may form an important dietary component, and in Victoria, the diet mainstay largely reflects the dominant monocotyledonous food resource. Following on from this, Braithwaite (1978) suggested that *R.l. lacus* was probably highly specialised in diet so that it was at the point of rarity, close to extinction.

If *R. lutreolus* is restricted to the open forest habitat in north-east Queensland, which is the picture that has emerged to date, a diet mainstay of the dominant monocotyledonous groundflora in this habitat - true grasses - represents a narrower food base than that exploited by populations of *R. lutreolus* in south-eastern mainland Australia and Tasmania. However, the habitat distribution of *R. lutreolus* in north-east Queensland needs to be clarified by further extensive and intensive trapping efforts before conclusions on the status of the species can be made. All intensive trapping programs in highland situations have been in rainforest (Section 1). It is possible that this lack of intensive trapping in adjacent sclerophyll forest has contributed to the apparent

rarity of *R.l. lacus*.

Within the open forest study area on the Paluma Range, *R. lutreolus* was found to be readily trappable, and relative to *R. fuscipes*, *M. cervinipes* and *A. flavipes*, the species was common. On the open forest transects, more individuals of *R. lutreolus* were live-trapped than any of the 3 other species. On the grid, a density of around 5.9 individuals per hectare was recorded. However, dispersion of *R. lutreolus* within the forest was not uniform. Avoidance of ridge situations which were characterised by sparser groundcover, was notable. Hence, it is suggested that within the coarsely grained open forest, the availability of suitable microhabitat-dense grass situations - is probably the major parameter controlling the dispersion and abundance of *R. lutreolus*.

8. GENERAL CONCLUSIONS

In tall open forest on the Paluma Range, *Rattus lutreolus*, a specialist herbivore, is coexistant with 3 other small mammal species, *R. fuscipes*, *M. cervinipes* and *A. flavipes*. The importance of diet as a major determinant of the ecology of *R. lutreolus* has been stressed. The spatial dispersion of food resources was considered to be a major influence on the dispersion of the species within the habitat. Use of the habitat on a temporal basis was related to the nature of the vegetarian diet. Reproductive characteristics and performance were suggested to be related to the temporal stability of food resources throughout the year.

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APPENDIX 1

Individual tag numbers and sex of small mammal species captured during 60 trap nights in both open and closed forest (transitional type mixed forest with an open overstorey of sclerophylls and closed understorey of rainforest and mesophyllous species) in February 1982. M = male; F = female.

Closed Forest (60 trap nights)		Open Forest (60 trap nights)			
Rattus fuscipes		*Rattus lutreolus*		*Antechinus flavipes*	
1838/1839	M	1852/1853	M	1835	M
1844/1845	F	1866	M		
1836/1837	M				
1842/1843	M				
1840/1841	M				
1856/1857	M				
1860/1861	M				
1858/1859	M				
1854/1855	M				
1834/1868	M				
Total:	10		2		1

APPENDIX 2

Individual trap histories of *Rattus lutreolus* males and females caught on the grid from February to August, 1982

Tag Numbers		February	March	April	May	June	July	August
1804/1805	M	A6,C7,E7	D8,D8,D8	D8,D8-E7	B9,B9-D6	C10,A12-E7	C9,C10	T.D.
1806/1807	M	E8,E8,E8	F9,F9,F9	D9,D9,E8, E8				
1821/1822	M	--F10	G10,G10, G10	--G11,G11	--F10,F10	---G8	-D11,G11-(D)G2	C11,B12,E10, E10,(D)E10
1904/1905	M		-C4,G4	--E2,F4	--D1,F2			
1911/1913	M		-G2-	--G2-	--G3,G2	--G1,G2	-E10,G2,G3, (D)G2	T.D.
1921/1922	M		--B10	C9	T.D.			
1964/1965	M			-C2--	-C1--			
1986/1988	M			---G13		--F12-	C10---	C12---
2095	M					--G12	A13---	C10--E11
2122/2124	M							--G12-
2118/2119	M							----(D)F7
2114/2116	M							---G2
1906/1907	F	-D10-	-D9,C10	-C10,F11,F11				
1815/1816	F	-G8,F7	G6,G6,F7	--F8,F7	--G9,G9	--G6,G7--	--F11-(D)E11	--G11,F11, (D)F11
1823/1827	F	--D6						
1886/1887	F		C4--	B3,A3,B1,D4	A2,A2--	-A3--	A1,A2--	
1900/1901	F		-C8,B9	A10,A10,E7, E7	B10,B10,E7, E7	A10,A10--	D9,D9--	
1919/1920	F		--B6	A6,B7--	A7,A7--	C9,C7-D7	--D7-	--D7-(D)D8
1928/1929	F		--G2	--G1,G1	-G1,G1-	---F1		(D)G6
2011/2012	F				D13,D13--	-C12--		
2001/2002	F				-A4--			(D)B2
2006/2007	F				A14,A14--			A15,A14--
2009/2010	F				D15,D15, E12,E12	D11,D12	T.D.	
2099/2100	F					-A6--		
2040/2055	F					-D14--	-C15,D15-	-D15,D15,D15
2128/2129	F							--C13-
Trap Nights		90	180	210	210	210	210	210
Trap Days							158	158

Abbreviations: T.D., trap death; (D) day capture.
M, male; F, female.

APPENDIX 3

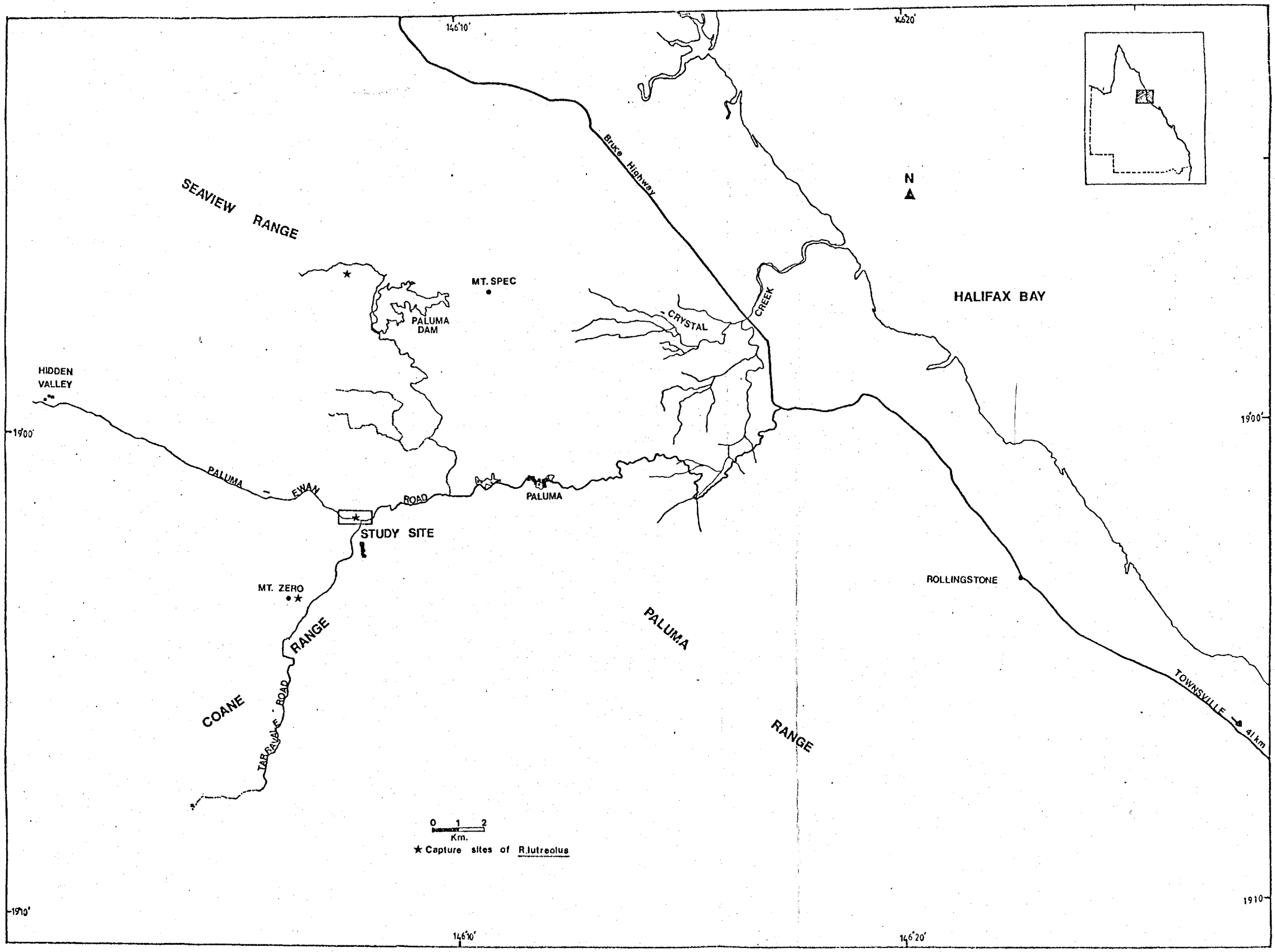
Individual trap histories of *Rattus fuscipes* caught on the grid from February to August, 1982

Tag Numbers		February	March	April	May	June	July	August
1802/1803	M	D5--	-G5,G6	-B5,D5,E5	D9,C5,E5,E6	B5,B6,F7,F9	B5,B6,G6,E5	
1828/1829	M	G5- G5						
1908/1909	M		-F5,F5	-C5,F5,F6	--G5,G5			
2036/2037	M				--D6-			
2120	M							--E5,G5
1817/1818	F	C5- E5	G5,E6,D5	C5,B6--	A1,A1--	A1,B5,D5,D5	A5,A6--	A4,A5,D5,D5
Trap Nights		90	180	210	210	210	210	210

APPENDIX 4

Absolute Body Measurements of *Rattus lutreolus* captured in June, July and August 1982, at Paluma. Abbreviations: HBT, head-body-tail or total length (mm); HB, head-body length (mm). Weight = weight at time of measurement. U.T./T.D. - Untagged trap death.

Tag Numbers	Sex	HBT(mm)	TAIL(mm)	HB(mm)	HEAD(mm)	PES(mm)	Weight (grams)
2099/2100	F	242	109	133	41.2	29.6	79
2011/2012	F	240	100	140	41.7	28.7	80
1913/2031	M	243	96	147	40.5	30.5	107
1876/1880	F	194	damaged	141	41.3	29.4	104
1910/1977	M	230	damaged	160	42.4	30.8	108
1928/1929	F	262	110	152	43.5	29.3	90
1900/1917	F	244	damaged	155	40.4	30.0	108
1805/1877	M	257	102	155	42.5	30.3	101
1927/2041	F	249	100	149	42.0	29.4	103
2040/2055	F	245	103	142	44.7	29.4	105
2009/2010	F	193	81	112	36.2	26.1	46
1935/2003	F	251	95	156	41.0	29.5	90
1986/1988	M	251	91	160	44.1	30.0	122
2095	M	250	110	140	42.6	30.1	99
2128/2129	F	245	100	145	-	30.0	132
2122/2124	M	244	108	136	42.8	29.2	111
2188/2119	M	280	110	170	45.1	32.5	125
2114/2116	M	-	-	0	45.0	30.2	112
2194/2195	M	270	110	160	43.2	31.9	135
2175/2176	F	258	112	146	41.4	29.1	98
2163/2164	M	265	100	164	46.0	31.8	148
2092/2152	M	257	110	140	44.0	33.6	131
2150/2151	M	-	-	-	-	28.5	105
2153/2154	F	260	110	150	42.7	30.0	113
2132/-	M	245	107	138	42.0	31.8	97
2065/2066	F	218	93	125	40.8	28.1	79
2140/2141	M	264	110	154	44.3	32.0	140
2161/2162	M	212	77	135	41.0	28.1	88
2159/2160	M	283	119	164	45.1	32.9	153
2138/2139	F	230	105	125	40.5	29.5	109
2136/2137	M	250	100	150	43.0	30.3	101
2189	F	249	102	147	43.8	29.5	132
U.T./T.D.	M	269	108	161	44.5	31.0	103
2148/2149	M	-	-	-	-	29.0	124
2042/2087	M	265	107	158	43.3	30.6	107
2050/2051	F	255	105	150	41.5	28.4	98
2045/2047	F	265	112	153	41.9	30.6	99
2044/2076	M	263	114	149	43.3	31.6	112
2157/2158	M	260	109	151	44.4	33.0	140
2145/2146	F	260	107	153	43.8	31.3	151
2071/2197	F	254	99	155	41.5	28.9	111
1981/1982	F	240	93	147	41.4	30.0	93


146°10'
146°20'
Bruce Highway
SEAVIEW RANGE
N
MT. SPEC
PALUMA DAM
CRYSTAL CREEK
HALIFAX BAY
HIDDEN VALLEY
19°00'
PALUMA - EWAN ROAD
PALUMA
STUDY SITE
MT. ZERO
ROLLINGSTONE
COANE RANGE
TABAVAC ROAD
PALUMA RANGE
TOWNSVILLE 41 km
0 1 2
Km.
★ Capture sites of R.lutreolus
19°10'
146°10'
146°20'