Dennis, Andrew James (1997) ***Musky Rat-kangaroos, hypsiprymnodon moschatus: cursorial frugivores in Australia's wet-tropical rain forests.*** **PhD thesis, James Cook University.**

Chapter 3.

THE DIET OF MUSKY RAT-KANGAROOS

INTRODUCTION

Knowledge of the diet of Musky Rat-kangaroos is limited and is derived from a few incidental observations of wild animals (Breeden and Breeden 1970; Johnson and Strahan 1982; Schurer 1985) and the feeding preferences of a captive colony (Johnson *et al.* 1983a; Johnson and Strahan 1982). The fleshy pericarps from the fruits of five species of rainforest trees, the seeds of one and invertebrates are known food items (Schurer 1985). Even with this limited information it is clear that the diet of the Musky Rat-kangaroo differs from all other macropodoids which are either grazing/browsing species or mycophagous-omnivores (Dawson 1989; Lee and Cockburn 1985; Seebeck *et al.* 1989).

Although partially compartmentalised, the stomach of Musky Rat-kangaroos is relatively simple compared to those of other macropodoids (Hume 1982). Other macropodoids have complex stomachs which include a sacciform fore-stomach, a tubiform fore-stomach and a hind-stomach (Dawson 1989). The complexity of the stomach is related to a species' ability to digest plant fibre through anaerobic fermentation by micro-organisms. The Musky Rat-kangaroo is unlikely to be able to digest structural carbohydrates in the cell walls of plants as well as other macropods do.

Dawson (1989) has reviewed the general patterns and environmental influences in the diets of Macropodoids. He suggests that body size is the most important influence on diet. Larger species (or individuals) are able to process higher fibre diets than smaller animals. Dawson (1989) points out a trend in the diets of macropodoids. Larger species select grass over forbs and browse. Medium and smaller species shift the balance of intake toward forbs and browse of decreasing fibre content and increasing nutritional value as body size decreases. The Potoroids represent the end point of the continuum. Many consume high proportions of fungus, roots, tubers, invertebrates and succulent herbs (Dawson 1989; Seebeck *et al.* 1989). The Musky Rat-kangaroo as the smallest member of the superfamily is expected to consume the lowest fibre diet of all.

In this chapter, I will examine the diet of the Musky Rat-kangaroo using four main methods. These show that Musky Rat-kangaroos feed primarily on fruits and seeds, consume invertebrates at all times of year and also eat the epigeal sporocarps of some Agaric fungi. These foods are all lower in fibre than the major components in the diets of other macropodoids.

Plate 5 Musky Rat-kangaroo eating the fruit of a Silver Quandong. *Elaeocarpus angustifolia*.

METHODS

The diet of the Musky Rat-kangaroo was determined using a combination of four different methods: 1) identifying teeth marks in fruit; 2) direct observation, both incidentally while radio-tracking and from hides or mobile observation platforms; 3) microscopic examination of faecal pellets; and 4) indirect observations through spool and line tracking. Each method provided information on different aspects of the diet.

Teeth Marks in Fruit

As detailed in Chapters 2 & 4, I established seven transects, totalling 4200m^2, for monitoring the availability of fruits on the forest floor and sampled them at regular intervals. I examined marks left by frugivores in the fruits along these transects, and in many cases, I was able to identify the species of animal involved using a reference collection of photographs and observations (Figure 3.1).

A reference collection of bite marks was established by offering fruits to animals when they were trapped. Many individuals ate readily and I collected the partially eaten samples and recorded the marks left on the fruits (Figure 3.1). Species whose bite marks were collected in this way included: White-tailed Rat, *Uromys caudimaculatus*; Bush Rat, *Rattus fuscipes*; Fawn-footed Melomys, *Melomys cervinipes*; and Musky Rat-kangaroo.

The beak marks of birds were distinguished by comparing the gouge marks in fruits to the beak shapes and sizes on skulls from each species of bird known to eat fruit in the area. In addition, I made many direct observations of feeding in the wild and I was able to collect fruit fed on by: King Parrots, *Alisterus scapularis*; Sulphur-crested Cockatoos, *Cacatua galerita*; Spotted Catbirds, *Ailuroedus melanotis*; Tooth-billed Bowerbirds, *Scenopoeetes dentirostris*; Eastern Whipbirds, *Psophodes olivaceous*; Musky Rat-kangaroos; White Tailed Rats; Red Legged Pademelons, *Thylogale stigmatica*; Feral Pigs, *Sus scrofa*; beetles (Coleoptera); and crickets (Orthoptera).

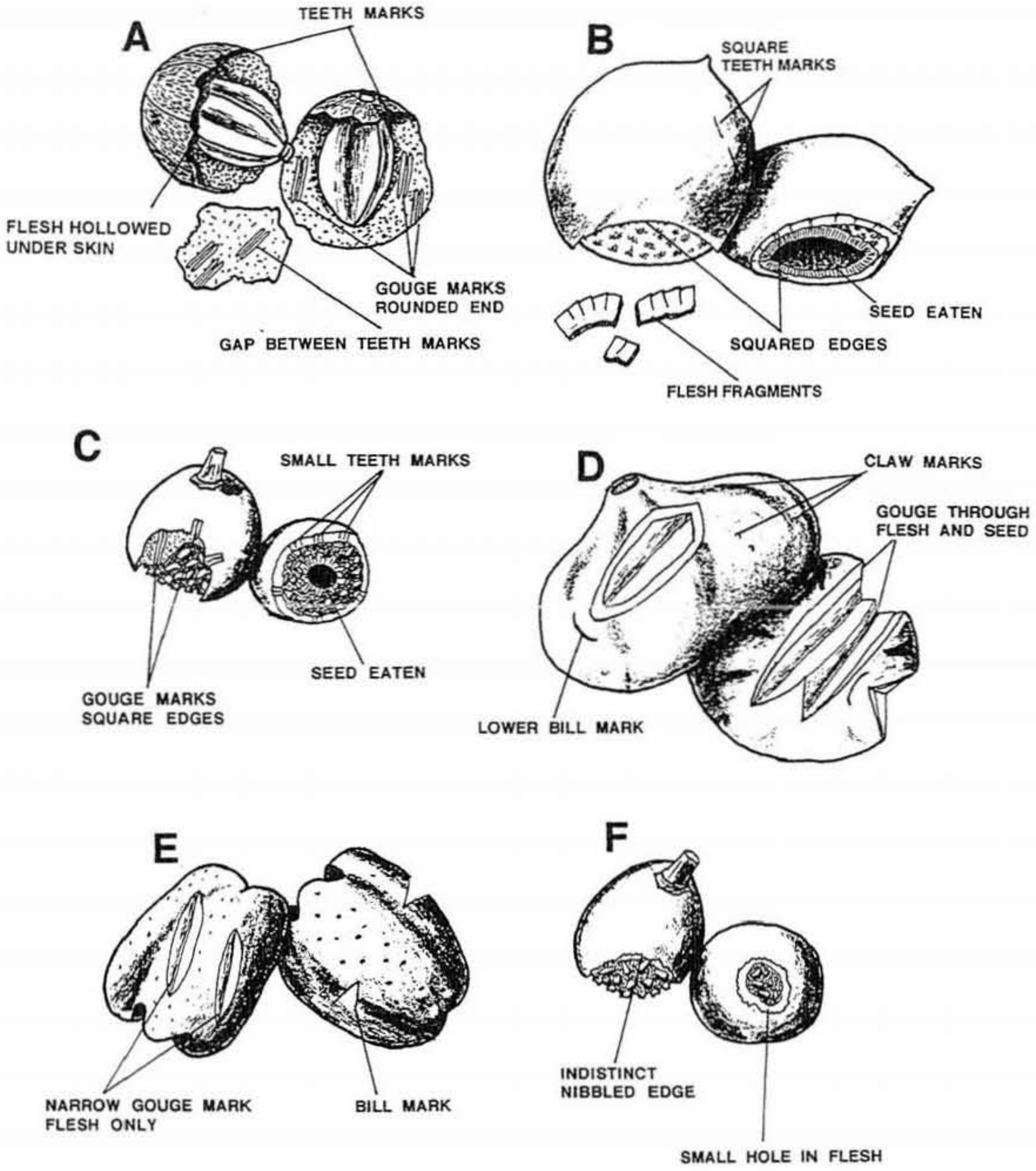


Figure 3.1 Bite marks in fruit commonly encountered along transects - from six different frugivores: A - Musky Rat Kangaroo teeth marks in *Fontainea picrosperma*; B - White Tailed Rat teeth marks in *Athertonia diversifolia*; C - Rattus teeth marks in *Elaeocarpus angustifolia*; D - Parrot marks in *Cryptocarya oblata*; E - Bird marks in *Sysygium papyraceum*; F - Insect marks in *Elaeocarpus angustifolia*. See text for explanation of "Rattus", "Parrot", "Bird" and "Insect".

The marks left on fruit by some frugivores were easily distinguished, while in other cases the differences between species were more subtle. These subtle differences became difficult to differentiate as fruits began to decay. Therefore, I classified frugivores into broad groups in some instances or to species level where the marks were distinct. Bite marks were classified as resulting from: 1) Musky Rat-kangaroos; 2) White-tailed Rats; 3) Other Rats (including: Bush Rat; Cape York Rat, *Rattus leucopus*; Masked White-tailed Rat, *Uromys hadrourus* and; Fawn-footed Melomys); 4) Parrots (including: King Parrot; Sulphur Crested Cockatoo and; possibly Crimson Rosella, *Platycercus elegans*); 5) Other Birds (including: Spotted Catbird; Tooth-billed Bowerbird and; Eastern Whipbird); 6) Pigs; 7) Southern Cassowary, *Casuarius casuarius*; 8) Insects (including beetles and crickets); and 9) unknown marks, where the fruit was decayed so that positive identification was not possible.

In this chapter I will examine the data for the Musky Rat-kangaroo. The data on other species are discussed in Chapter 9.

Size Classes

Each species of fruit encountered on the transects was placed into one of six size classes based on the volume of an entire fruit. The six classes were:

1- <1ml;	**2** - 1 to 5ml;	**3** - 6 to 10ml;
4- 11 to 20ml;	**5** - 21 to 100ml;	**6** - >100ml.

The fruits consumed by Musky Rat-kangaroos were categorized according to their measured volumes, other species were categorised either visually (if obvious) or by calculating their volume based on their measured dimensions or from measurements quoted in Cooper and Cooper (1994).

Volume

I measured the volume of each species of fruit from a sample of 20 - 40 fruits from two or three individual trees using water displacement. The total volume of the entire sample was then divided by the number of fruits in the sample to give the mean volume of one fruit.

Dimensions

The dimensions of individual fruit were measured according to their shape: diameter only for roughly spherical fruit; length and width for those more closely resembling a cylinder; and length, width and height for those with a squashed ovoid shape. The entire sample (20-40) was measured and the mean used as a measure for each species.

Direct Observation

I confirmed that Musky Rat-kangaroos were eating the species of fruits that appeared to have their bite marks by direct observation from a hide or mobile observation platform.

Hides were constructed using triangles of Sarlon Weed Mat sewed into a pyramid supported by four bamboo poles. Four windows were cut, one in each side of the pyramid. The hides were placed at fruiting trees so I could observe directly to determine if Musky Rat-kangaroos were feeding on the fruits of that species of tree. Mobile observation platforms consisted of a hammock, slung at least 2m off the ground, and placed near a fruiting tree. When I sat quietly in a hammock at this height Musky Rat-kangaroos did not detect my presence and would commonly walk beneath me. The mobile observation platform was more effective for observations than the hide because it was off the ground, afforded a wider view of the surrounds and was more comfortable for long periods of waiting. I observed fruits and other foods being consumed, how they were handled and behaviours not related to feeding from the mobile observation platform.

During radio tracking forays and fruit transect walks, I recorded incidental observations of Musky Rat-kangaroo foods which I include here.

Microscopic Examination of Faecal Pellets

Faecal pellets from Musky Rat-kangaroos which defaecated in traps or in holding bags (Chapter 6) were collected and stored in 70% ethanol. Faeces were then prepared for microscopic examination by: lightly grinding two pellets from each sample with a mortar and pestle; soaking in Hertwig's solution (19ml HCl, 150ml H_2O, 60ml glycerol, and 270g chloral hydrate) for seven days to dissolve mucus; straining through a 200 micron sieve to separate the coarse fraction; staining the course fraction with Toluidine Blue to differentiate fruit and fungus; and mounting a subsample of the stained fraction on a slide with glycerine jelly.

After thorough examination of a subsample of slides, I determined that fruit, fungal and invertebrate remains accounted for almost all of the material in the faeces. I therefore examined the mounted faecal material under a light microscope at 40x for the presence of fruit and invertebrate remains and obvious fungal tissue and at 100x and 400x to search more thoroughly for fungal remains (spores and tissue). Each slide was searched until the presence of these items was noted or the entire slide was searched. Any other items seen were also recorded. I then counted each invertebrate fragment (at 40x) on three independent transects across the slide. Invertebrate fragments were few and showed little variation in size. Therefore, I decided that using a method of quantifying fragments in relation to their size was not necessary.

I considered fruit and fungal remains to be unquantifiable beyond presence or absence. The variation in hardness and fibre content of different fruit species was considerable and the Musky Rat-kangaroo avoided eating the skin of some species. The sporocarps of different species of fungi also varied in hardness. This variation in handling (eating the skin or not) and physical characteristics varied at different times of year, making it unlikely that quantification of changes in consumption within each category would be accurate. In addition, the unknown difference in digestability between invertebrates, fruit and fungus precluded comparison across these three categories. As this study was of a more broad ecological nature and many direct observations of feeding were made, I considered fine scale quantification of dietary items unnecessary.

Spool and Line Tracking

Trapped Musky Rat-kangaroos (Chapter 6), were fitted with cotton bobbins and released at the point of capture. A record of their movements (Chapter 7) and evidence of feeding and other behaviour were collected from the trail of cotton left in their wake (see also Berry *et al.* 1987).

Cotton spools consisted of two size 10 bobbins (Penguin Threads) in series. These were super-glued to the fur on the back below the pelvis after trimming the guard hair layer. The bobbins were mounted side by side and the trailing end of the first was tied off to a root or sapling at the release point. The spools totalled about 460m in length. The trails of cotton were mapped and data recorded the day after each Musky Rat-kangaroo was released.

I recorded the following data on the diet and feeding behaviour of each Musky Rat-kangaroo spool trail: 1) the trail often came into contact with a freshly eaten fruit and occasionally a sporocarp, scraping in the litter or digging on a very rotten log, each contact was noted; 2) I recorded the substrate over which the Musky Rat-kangaroo was walking at 5m intervals. The substrate category relevant to this chapter was "Fruitfalls". Where possible, I determined whether any of the fruit with which the line came in contact had been freshly eaten by a Musky Rat-kangaroo. In some instances this was clearly evident but in others many fruits had been freshly eaten by Musky Rat-kangaroos, both on and away from the spool line. In these cases, it was impossible to determine how many fruits were consumed by the spooled individual.

Analyses

Fruit Encounters

I tested whether Musky Rat-kangaroos were encountering fruitfalls at a frequency different from their measured availability. I compared the number of substrate points (5m interval) recorded as fruitfalls from spool and line tracking to data from fruit transects (Chapter 4). To determine the number of fruitfalls available on each transect, I took the central point of each 5x2m quadrat (see Chapter 4) as a substrate point (cf spool and line tracking). If the number of fruits within that quadrat was >5, I considered the central point to be in a fruitfall. Each transect was 300m long while the spool lines varied from 200 to 460m in length. Therefore, I adjusted the number of substrate points identified as fruitfalls along spool lines to a 300m length.

I used a two-way fixed factor Analysis of Variance to examine whether the number of substrate points classified as fruitfalls was different for Musky Rat-kangaroo spool trails and fruit transects (random measures of fruitfalls). I was able to apply this analysis with records from five months in 1991 for which I had sufficient data on both. Due to multiple spool records for some animals and not others, analysis was based on a single record for each animal. Serial sums of squares were used in the unbalanced design. To ensure that the measurements of fruitfalls along transects did not differ from random I performed a Kolmogerov-Smirnov test (K-S $z = 1.1641$, two-tailed $P = 0.133$).

Electivity Indices

To determine the degree of selectivity in the fruit portion of Musky Rat-kangaroos' diet, I compared the fruit availability (total abundance along transects over entire study) to the number of fruits found partially consumed by Musky Rat-kangaroos along transects. I calculated Vanderploeg and Scavia's (1979) relativised index, E^{*}. for each species occurring along transects. When E^{*} is -1 it represents maximum avoidance of a fruit. At 0 it represents random feeding and at +1 maximum selection for a fruit. Because this index is sensitive to small sample sizes I also calculated a simple preference index based on that of Johnson (1980) using the difference between rank of availability and rank of number eaten.

Invertebrate Remains in Faecal Samples

The number of invertebrate remains found in faecal samples were analysed using a 3-way Analysis of Variance. Only a single sample for each Musky Rat-kangaroo was used in the analysis which was performed on data from 1991 (the most complete set). Serial sums of squares were used as the design was unbalanced.

Fungus in Faecal Samples

Fungal remains in faecal samples were recorded as present or absent. These records (one sample per animal) were analysed to determine if the proportion of animals consuming fungus or not consuming fungus varied with season and age class using Hierarchical Loglinear Modelling in a backward elimination process.

RESULTS

General

By far the largest component in the diet of Musky Rat-kangaroos was fruits and seeds. All 165 faecal samples were dominated by their remains. Invertebrate remains appeared in 91.5% of samples in variable quantities and fungus in 44%. All other items, excluding grooming hairs, were found in only 3% of samples (Figure 3.2). Fruits and seeds, invertebrates and fungi were present in samples at all times of year.

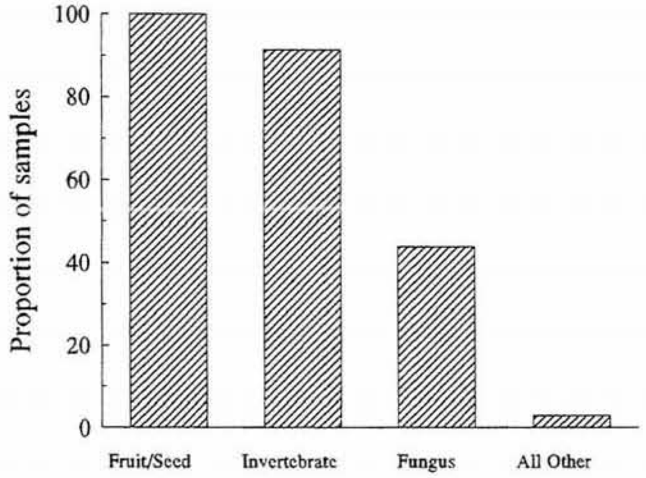


Figure 3.2 Proportion of faecal samples containing the remains of fruits and seeds, invertebrates, fungi or other items.

Other dietary items were few, and included fleshy flowers from the Austrobaileya vine, *Austrobaileya scandens* (direct observation), twigs and leaves (some identified as lilies; faecal samples). Other possible items include foliose lichen and the soft inner bark from several undetermined tree species. Both the latter foods were indicated by circumstantial evidence from spooling records.

Further evidence to suggest that fruits and seeds made up the bulk of the diet of Musky Rat-kangaroos, at least in relation to fungi, was obtained from spool trails. In 57 trails (47 individuals), I noted 80 separate occasions when Musky Rat-kangaroos encountered and ingested fruits (57% of the possible encounters with food; based on the total number of events along spool lines which were assessed as being associated with feeding). A minimum of 201 fruits were partially consumed. I was unable to count how many of some of the smaller fruits were consumed or when only tiny fragments remained. In comparison, only seven records of fungus being ingested were counted (5% of possible food encounters).

Determining if Musky Rat-kangaroos were searching for invertebrates was difficult to quantify using spool records. Musky Rat-kangaroos spent much of their time meandering across the leaf litter, during which they may have encountered and eaten invertebrates. More importantly, there were many occasions when scratchings were made in the litter or in very rotten logs. Taking these events as evidence of searching for invertebrates, they made up 38% of possible encounters with food (litter scratchings 20, logs 34 records). However, it is likely that some of the diggings and scratchings in the leaf litter were associated with re-locating buried seeds and fruits (see Chapter 8).

Fruits and Seeds

Musky Rat-kangaroos consumed flesh from the fruits of 33 species and the seeds of 18 species on my 9ha site (Appendix 1). Only in Watergum fruits, *Syzygium gustavioides* were the seeds alone consumed. Another species (Candlenut, *Aleurites mollucana*), not found on my study site, is known to have only its seed consumed. Both these species have thin woody flesh. Incidental observations by myself and others in other areas indicate that the fruits of at least another nine species are eaten by Musky Rat-kangaroos (Appendix 1). I predict that the list of species consumed by Musky Rat-kangaroos will increase dramatically as their diet is examined in other areas.

The total number of species producing ripe fruit during the study and the biomass available to the Musky Rat-kangaroo are examined in detail in Chapter 4. Musky Rat-kangaroos consumed fruits of 52% (± 3.4% SE; total # spp.=68) of the species falling in each month (range 25 - 82%; Chapter 4). The majority of these had fleshy pericarps or arils which were eaten and varied in colour including: pink; red; orange; purple; blue; black; white; and brown. The seeds they consumed had soft to moderately hard seed coats. Eleven percent of the total number of individual fruits found partially eaten by Musky Rat-kangaroos on fruit transects had evidence of seed predation (n=588). Many of the fruits they did not eat were wind dispersed (e.g. Bull oak, *Cardwellia sublimis*) or housed in hard, indehiscent pods (e.g. Sayer's Silky Oak, *Hollandaea sayeriana*). Some others had seeds covered in very thin arils and housed in furry, dehiscent pods (e.g. Macintyre's Boxwood, *Xanthophyllum octandrum*, Maiden's Blush, *Sloanea australis*). In addition, some fleshy drupes were not consumed (e.g. Northern White Beech, *Gmelina fasciculiflora*, Cribwood, *Corynocarpus cribbianus*). With longer periods of observation or observation in other areas some of these fruits may be found to be in the diet of Musky Rat-kangaroos.

Size Classes

Musky Rat-kangaroos ate fruits from all size classes. Weights of fresh fruits (see Chapter 4) ranged from <0.5g (Rough-barked Satinash, *Syzygium trachyphloium*) to >120g (Hairy Walnut, *Endiandra insignis*). The most abundant fruits were of size class two (1-5 ml; Figure 3.3, 3.4) while the largest number of species fell into size class four (11-20 ml; Figure 3.4, 3.5).

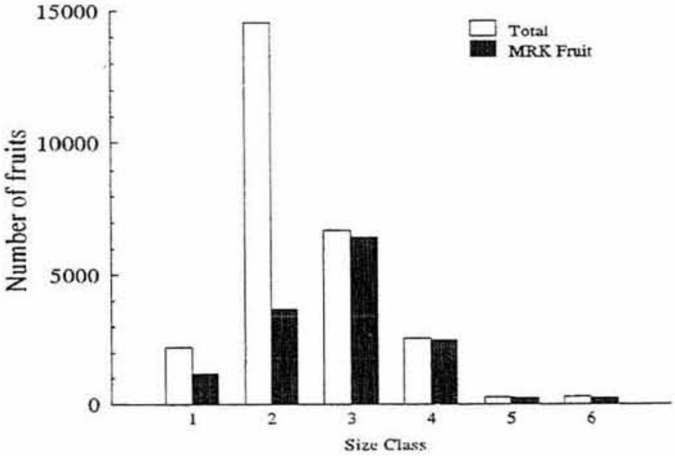


Figure 3.3 Total abundance of fruits along transects during the study including all species (Total) and those consumed by the Musky Rat Kangaroo (MRK Fruit).

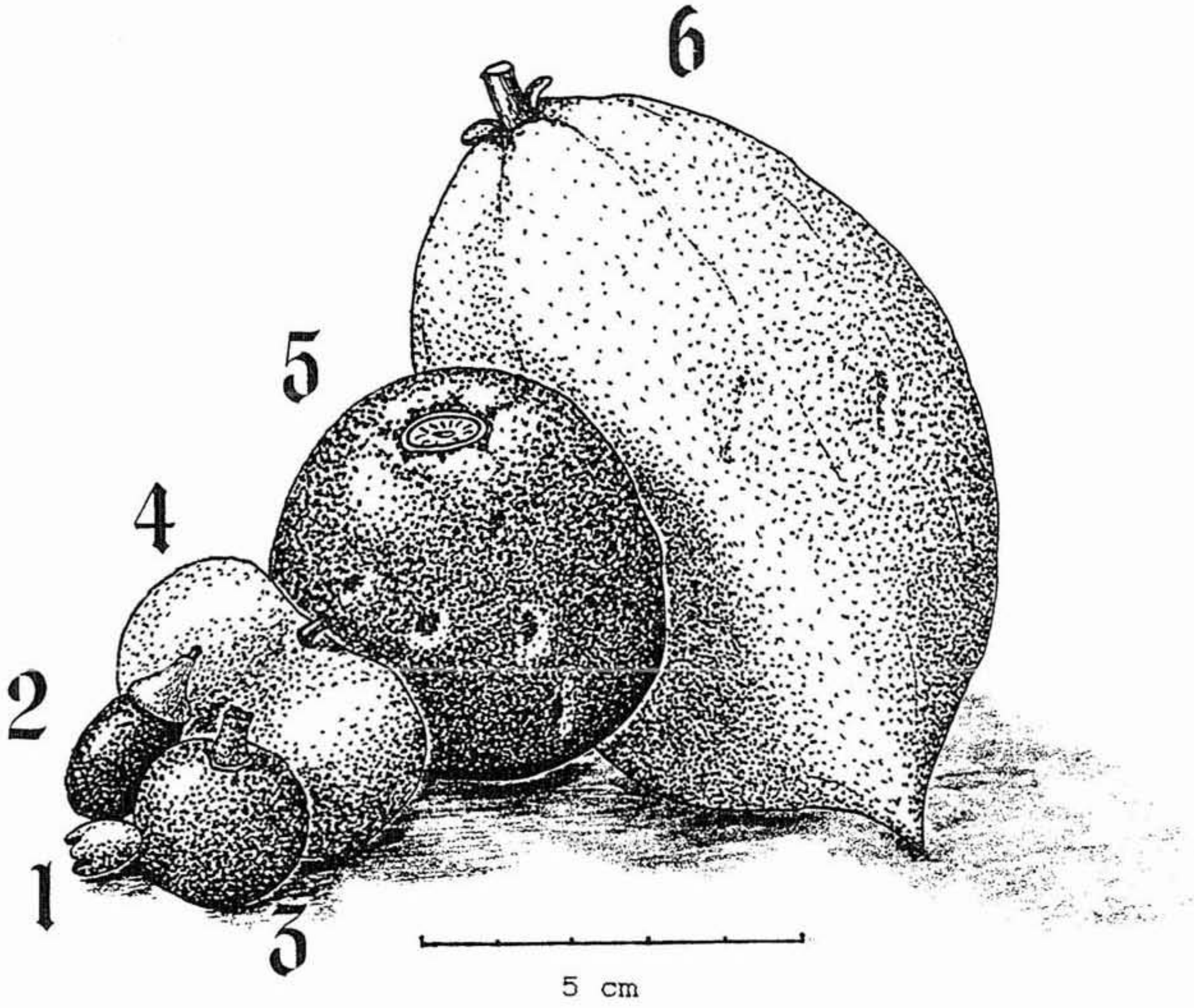


Figure 3.4 Fruit size classes represented by: 1) Rough-barked Satinash, *Syzygium trachyphloium*, <1 ml; 2) Pepperwood, *Cinnamomum laubatii*, 1 - 5 ml; 3) Silver Quandong, *Elaeocarpus angustifolia*, 6 - 10 ml; 4) Baileyoxylon, *Baileyoxylon lanceolatum*, 11 - 20 ml; 5) Boonjie Blush Walnut, *Beilschmiedia volcii*, 20 - 100 ml; 6) Touriga, *Mammea touriga*, >100 ml.

I compared the number of species not eaten to the number of species eaten in each size class using a Chi Square analysis. I combined the counts for the two smaller size classes and the two larger sizes to ensure no cells in the contingency table contained less than five records (Zar 1984). The analysis showed that Musky Rat-kangaroos preferred larger fruits (Chi Square=9.786, DF=3, P=0.0205; Figure 3.5).

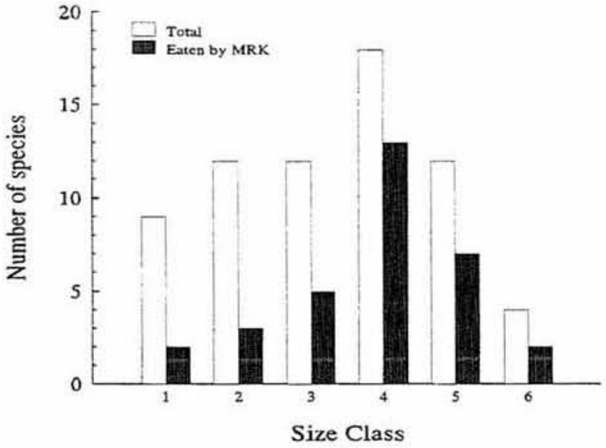


Figure 3.5 Number of species available and eaten by Musky Rat-kangaroos in each size class. Size class: 1<1ml: 2=1-5ml: 3=6-10ml: 4=11-20ml: 5=21-100ml: 6>100ml.

While the abundance of small fruits was large (Figure 3.3) the biomass of fruit parts edible to the Musky Rat-kangaroo was much greater for the larger size classes (Figure 3.6; see Chapter 4 for how biomass of fruits was calculated).

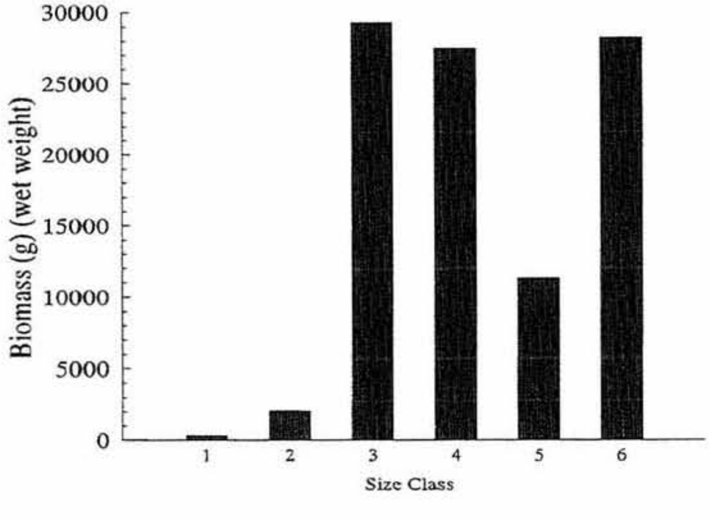


Figure 3.6 Total biomass of fruits and seeds falling on transects during the study and consumed by Musky Rat Kangaroos. Wet weight based on parts consumed.

Preferred Fruits

Species of fruit found on transects which had Musky Rat-kangaroo teeth marks in them are shown in Figures 3.7 and 3.8 (resulting from two alternative systems of relating the abundance of a resource to its use; see methods). Those that were sought at a high rate compared to their availability have a positive value on the electivity index or preference ranking. Those that were eaten at a rate near random feeding are close to zero. While those that were eaten at a low rate compared to their availability have a negative value. Many species not listed in Figures 3.7 and 3.8 (but appearing in Table 4.1 and Appendix 1) showed no evidence of consumption along transects.

The ten most sought after species using either method (Figures 3.7 and 3.8) all belong to size classes four and five which confirms that Musky Rat-kangaroos tend to select large fruits. In addition, 50% of those listed in Figures 3.7 and 3.8 are species from which seeds are sometimes consumed. However, only 11% of all fruits handled by Musky Rat-kangaroos had their seeds consumed (see above).

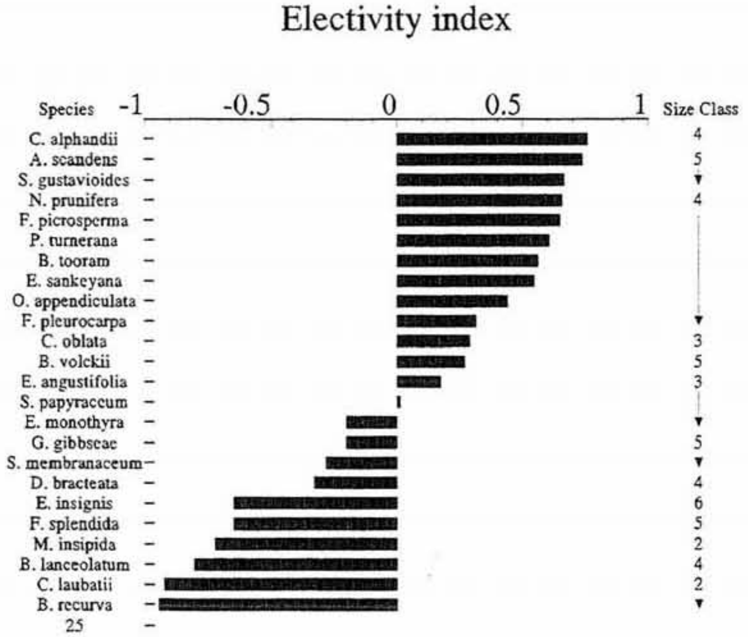


Figure 3.7 Species preferences in the diet of Musky Rat Kangaroos using Vanderploeg and Scavia's (1979) electivity index. Negative values mean a species is eaten at a rate less than its relative availability and positive values at a rate greater than their relative availability. See Appendix 1 for generic names.

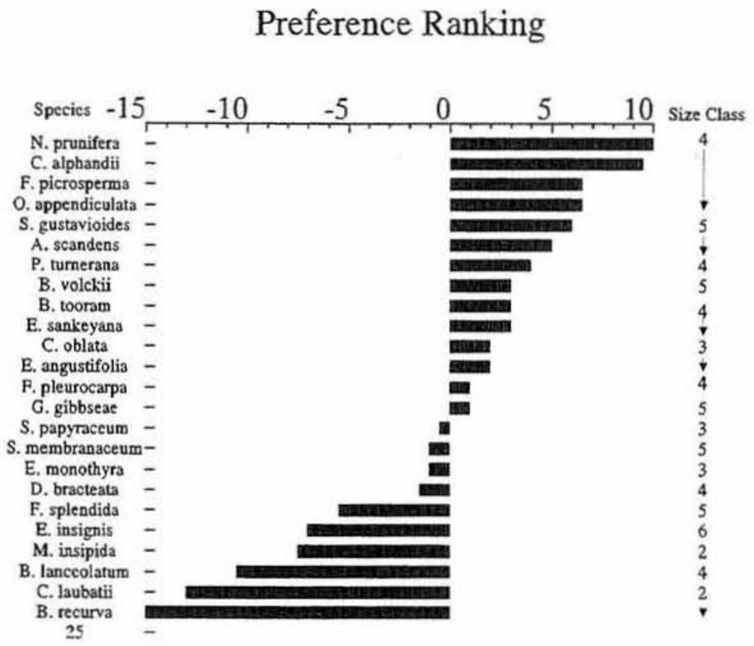


Figure 3.8 Species preferences in the diet of Musky Rat-kangaroos using Johnson's (1980) ranking preference indicator. Negative values indicate that fruits are eaten at a rate less than their availability while positive values indicate species that are eaten at a rate greater than their availability. See appendix 1 for generic names.

Encounters with Fruitfalls

Data on the behaviour of Musky Rat-kangaroos gleaned from spool and line tracking and records of the number of fruitfalls along transects, enabled me to determine if Musky Rat-kangaroos were encountering fruitfalls at a frequency different from their measured availability for five months in 1991. First, I tested whether fruitfalls along transects conformed to a poisson distribution, which they would if they were a random measure of the chance of encountering a fruitfall. The distribution of numbers of encounters with fruitfalls along transects was not significantly different to a poisson distribution (Kolmogorov-Smirnov $Z = 1.641$, $P = 0.133$). Therefore, I considered fruitfalls along transects a random measure. Figure 3.9 shows the rates at which fruitfalls were encountered at random (on transects) and by Musky Rat-kangaroos.

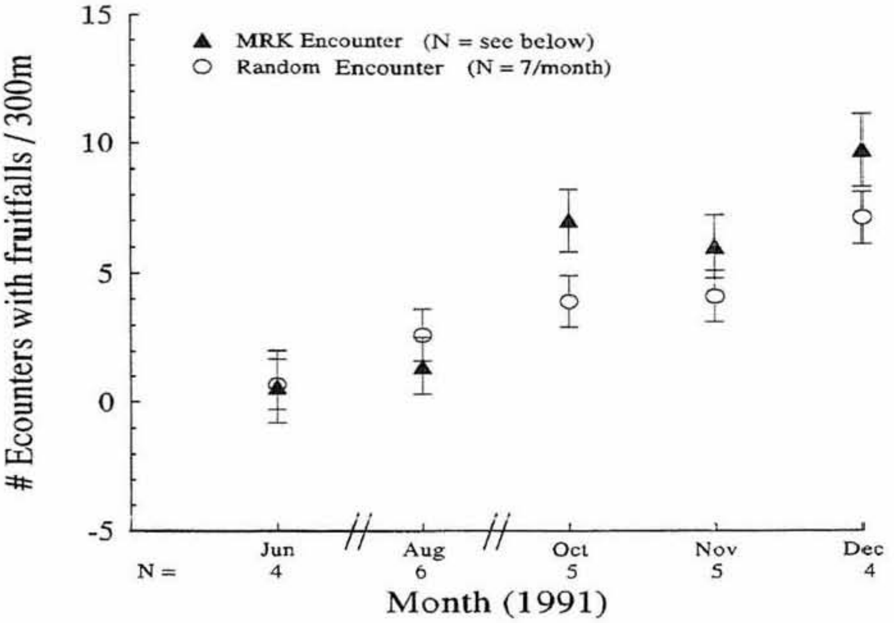


Figure 3.9 Number of encounters with ripe fruitfalls: 1) along transects; and 2) made by Musky Rat Kangaroos with spools.

The data suggest that, during the fruiting peak (October to December), Musky Rat-kangaroos encountered fruitfalls at a rate greater than random. Other studies of frugivores have found changes in foraging strategies when fruits are abundant or rare (e.g. Terborgh 1983). Thus, I analysed the data to differentiate between encounters with fruitfalls during the peak availability of fruit and the period of few fruit. An Analysis of Variance (Table 3.1) showed there was a significant difference between the number of fruitfalls, both on transects and encountered by Musky Rat-kangaroos, in different months. This relates to the seasonal availability of ripe fruit which is explored thoroughly in Chapter 4.

Table 3.1. Results of an Analysis of Variance examining: 1) **Encounters** with fruit falls at random (on transects) and along spool trails left by Musky Rat-kangaroos; in 2) the **Period** of minimum fruit (June, August) and the period of maximum fruit (October, November, December) in 1991.

Source of Variation	DF	Mean Square	F	P
Period[1]	1	300.72	35.63	**0.0001**
Encounter type[1]	1	19.5	2.31	0.134
Period*Encounter type	1	30.04	3.65	0.065
Error	55	8.44		

1. Fixed Factors

Although the difference betweeen the number of fruitfalls available and the number encountered by Musky Rat-kangaroos was not significant, there was a tendency for Musky Rat-kangaroos to encounter fruitfalls more often than they are encountered at random in October, November and December (Figure 3.9). Given that invertebrate fragments were more abundant in faecal samples (see below) in the cold season (May to July) and less so in the storm season (November to January), Musky Rat-kangaroos may have been foraging differentially at different times of year. The limited data presented here hint at the possibility of a change in foraging strategies, with respect to fruitfalls, at different times of year.

Invertebrates

Most invertebrate remains in faeces were masticated to fine particles and identification to species was not attempted. However, a few small semi-intact ants were seen and some ant legs were identifiable in some samples. Musky Rat-kangaroos foraged over leaf litter, in rotting logs and through the crowns of fallen trees. Therefore, they probably ingested a wide range of prey items; a conclusion supported by the diversity in the appearance of invertebrates exoskeleton found in faeces. The smallest invertebrates seen in faecal samples were ants of 2mm length. Worms are eaten with relish in captivity (Johnson, P. M. pers. comm. 1989) but were probably overlooked in faecal analysis due to their near total digestibility. No worm chaetae were identified (see Wroot 1985).

I examined seasonal changes in the number of invertebrate fragments in faecal samples for male and female Musky Rat-kangaroos of different ages (Table 3.2). There was no significant difference between sexes or age groups. However, a significant season and age group interaction showed that subadults consumed significantly more invertebrates during the wet and cold seasons (May - July) than adults, while adults consumed more during the dry season. In addition, the seasonal changes in invertebrate consumption occurred, although this was less pronounced in adults than subadults (Figure 3.10).

Table 3.2 Results of an Analysis of Variance examining the number of invertebrate fragments in faecal samples in male and female, adult and subadult Musky Rat-kangaroos in different seasons in 1991.

Source of Variation	DF	Mean Square	F	P
Season[1]	3	51.19	12.43	**0.0001**
Sex[1]	1	0.027	0.01	0.9352
Age[1]	1	4.66	1.13	0.2920
Season*Sex	3	1.73	0.42	0.7397
Season*Age	3	24.52	5.96	**0.0013**
Sex*Age	1	5.71	1.39	0.2438
Season*Sex*Age	1	2.596	0.63	0.4304
Error	58	4.12		

1. Fixed Factor

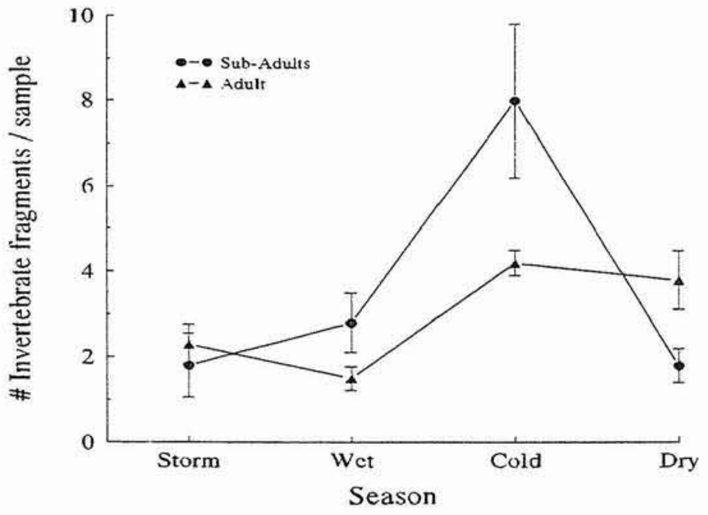


Figure 3.10 Mean (± SE) number of invertebrate fragments occuring in faecal samples of adult and sub-adult Musky Rat Kangaroos in 1991.

I also determined if there was a difference in the rate of consumption of invertebrates between individuals regardless of age or sex class. I used a oneway Analysis of Variance with data for 11 Musky Rat-kangaroos which had multiple samples in 1991 (range 2-9). I found no difference between individual consumption of invertebrates during 1991 (Oneway Analysis of Variance: F=1.64, DF=10,54, P=0.1208). There were insufficient data to examine the difference between individuals in different seasons.

Fungus

Although no effort was made to directly observe Musky Rat-kangaroos eating fungi, I observed them consuming the small white epigeal sporocarps of *Coprinus* sp. on eight occasions. In addition, evidence from spool and line tracking indicated consumption of the sporocarps of three other species of Agaric fungus and the thick white hyphae mass of a fungus penetrating a rotting log (one record). Two species of large (7cm diameter) epigeal sporocarps (unidentified Agarics) had their caps partially eaten (two records, 11 sporocarps), while a small (2cm) red variety had its caps entirely eaten leaving only the stem (one record). The small white *Coprinus* sp., which usually occurred in large clusters, was often heavily "grazed" by Musky Rat-kangaroos. Animals approached a cluster and turned their head and mouth sideways to bite off as many stems and caps as possible at a time. They also picked off single sporocarps with their incisors. *Coprinus* sp. was usally eaten to the substrate. I found no evidence of the Musky Rat-kangaroo consuming hypogeal sporocarps and their digging was limited to scraping at the leaf litter.

The remains of fungi appeared in 44% of faecal samples. However, the proportion of samples containing fungus varied according to season and age class (Table 3.3). All adults consumed fungus during the wet season while only 17% did so in the cold season and 40 to 50% in other seasons (Fungus*season interaction). More Sub-adults (67%) consumed fungus in the wet season than in other seasons (17 - 33%; Figure 3.11) but in general fewer subadults than adults consumed fungus (except in the cold season). This increase in the proportion of animals eating fungus in the wet probably relates to the relative abundance of epigeal sporocarps increasing in the wet.

Table 3.3 Model of best fit resulting from a Hierarchical Log Linear Analysis using backward elimination for data on the number of faecal samples in each Season[1] and age class[2] to have or not to have fungal remains. LR Chi Sq. Change shows if removing the predictor variable/s listed will significantly change the variation explained by the model.

Predictor Variables	DF	LR Chi Square Change	P
Model 1	**0**	**0**	**1**
Age*Fungus*Season	3	4.997	0.172
Model 2	**3**	**4.997**	**0.172**
Age*Fungus	1	1.866	0.172
Age*Season	3	1.075	0.783
Fungus*Season	3	18.41	0.0004
Model 3	**6**	**6.072**	**0.415**
Age*Fungus	1	1.015	0.314
Fungus*Season	3	17.56	0.0005
Model 4	**7**	**7.087**	**0.42**
Fungus*Season	3	17.56	0.0005
Age	1	8.155	0.0043

1. Storm (November to January). Wet (February to April). Cold (May to July). Dry (August to October)

2. Adult. Subadult (including juvenile).

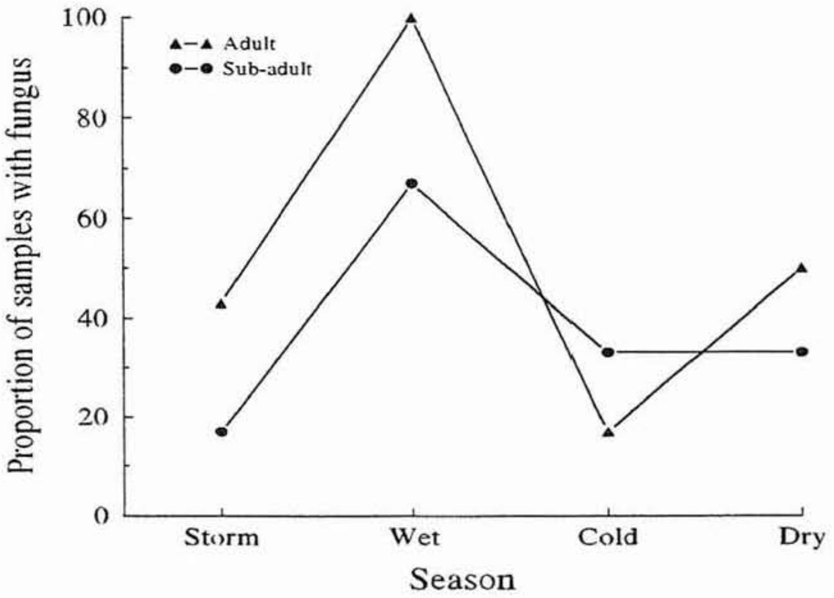


Figure 3.11 Proportion of faecal samples containing fungal remains for adult and sub-adult Musky Rat Kangaroos in different seasons in 1991.

DISCUSSION

Musky Rat-kangaroos eat fruits and seeds at all times of year (Figure 3.2) from a wide variety of fleshy fruited tree species (33 species on my study site; Appendix 1). They focus primarily on large fruits (Figure 3.5 and 3.7) which, although less abundant (Figure 3.3), have a greater biomass of parts edible to Musky Rat-kangaroos than do the smaller fruits (Figure 3.6). In addition, Musky Rat-kangaroos consume invertebrates and the epigeal sporocarps of Agaric fungi.

The peak in consumption of fungus (Figure 3.11) occurred in the wet season (February to April) which was in the period of least fruit availability (see Chapter 4; Figure 4.7) and coincided with the highest availability of epigeal sporocarps (unpublished observations). A peak in consumption of invertebrates followed in the cold season (May to July). Fruits continued to remain low in numbers through this period (Figure 4.5) and the availability of fungus also decreased. Therefore, it is likely that most of the invertebrates that Musky Rat-kangaroos were consuming at this time were from foraging in the litter and fallen logs rather than invertebrates associated with fruit. As the abundance of fruit increased in the dry and storm seasons (August to October; November to January) the other dietary components became less significant. Musky Rat-kangaroos are probably able to obtain a high proportion of their nutritional requirements from fruit when they are abundant.

Subadult Musky Rat-kangaroos ate significantly more invertebrates during the cold season than did adults (Figure 3.10; Table 3.2). This may be due to several factors. Adults may be able to out compete younger animals for the available fruit resources necessitating a higher intake of invertebrates in subadults. In addition, young animals probably have higher protein requirements to maintain growth.

Encounters with Fruit Falls

Musky Rat-kangaroos encountered more fruitfalls than would be expected by foraging at random during the period when more fruit were available but not during the period of few fruit (Figure 3.9). This seems counter-intuitive. In addition, sampling biases should result in the opposite effect. Sampling of fruits on the ground during the times of fewer fruits creates an under-estimate of the availability due to a higher proportion of fruits being consumed (Zhang and Wang 1995). This means that the number of fruitfalls along transects in June is probably an under-estimate of the actual number. Clearly a larger sample size over different seasons is needed to confirm this difference in the foraging behaviour of Musky Rat-kangaroos. However, assuming the pattern to be real, it may be more cost effective for Musky Rat-kangaroos to focus their search effort toward invertebrates and fungi and forage at random with respect to fruits when little fruit is available.

Preferred Fruits

Electivity indices (Figures 3.7 & 3.8) identified species of fruits for which Musky Rat-kangaroos ate high proportions of the available crop during the study. For most species electivity indices agreed with my impressions from direct observation. However, for one species, Baileyoxylon, *Baileyoxylon lanceolatum*, the electivity index under-estimated its importance. This was partly due to its flesh deteriorating extremely quickly and making identification of teeth marks impossible. In 65% of Baileyoxylon fruits with teeth marks in them I was unable to identify the frugivore involved due to the fruits deterioration. In addition, most direct observations of Musky Rat-kangaroos feeding on this species occurred in 1990, before I sampled fruits along transects. Crops in 1990 were small compared to those seen in 1992. This suggests that when a species has a large crop Musky Rat-kangaroos eat relatively less of the crop which would lower the rating on the electivity index. Therefore, the species which appear to be most preferred at any one time probably vary with the size of crops.

Macropodoid Diets

The most significant difference between the diet of the Musky Rat-kangaroo and other macropodoids is the inclusion of a high proportion of fruits. Although other macropodoids are known to consume fruits and seeds, their significance by volume is always low (Bennett and Baxter 1989; Dawson 1989; Horsup and Marsh 1992; Scotts and Seebeck 1989; Seebeck *et al.* 1989).

The diet of Musky Rat-kangaroos is more similar to the diets of other Potoroids than other Macropodoid diets. Bennett and Baxter (1989) found the fruits of two species of plant to be important components in the diet of Long-nosed Potoroos, *Potorous tridactylus* in two months in 1981. Their combined percentage occurrence ranged from 9 - 20%. Seeds were present at all times of year and their occurrence ranged from 0.6 - 30%. Thus, Long-nosed Potoroos consume the most fruit of any potoroid after Musky Rat-kangaroos. However, hypogeal fungi are the most voluminous item in the diets of most potoroids (Bennett and Baxter 1989; Scotts and Seebeck 1989; Seebeck *et al.* 1989), although Burrowing Bettongs, *Bettongia lesueur* and the northern most population of Rufous Bettongs, *Aepyprymnus rufescens* include a larger component of roots and tubers (Dennis 1988; Seebeck *et al.* 1989). In addition, all potoroids are known to consume invertebrates (Seebeck *et al.* 1989).

Dawson's (1989) observed relationship between macropodoid body size and fibre intake holds for the Musky Rat-kangaroo. As expected, Musky Rat-kangaroos appear to have the least fibrous diet, the cellulose and lignin content of cell walls in fruits is much lower than in forbes, browse and grass (Cork and Foley 1991).

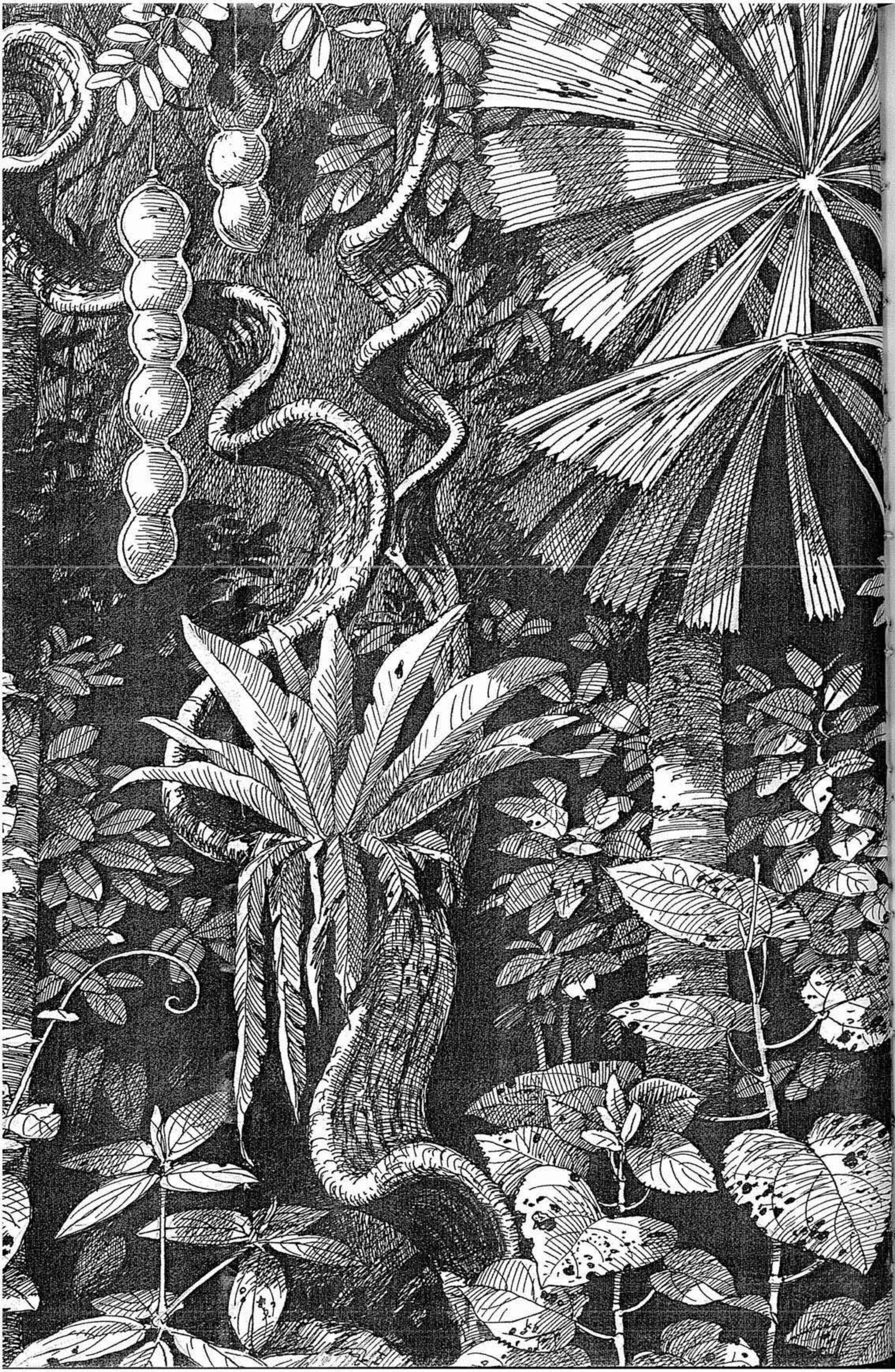
Because Musky Rat-kangaroos have many pleisiomorphic features (Woods 1960) they are often considered to be "a modern example of [the earliest macropodoid] body-form and life-style" (Dawson 1989). Assuming the ancestral macropodoids were also rainforest frugivore/omnivores (which appears likely given the wetter climate and vegetation during the tertiary; Truswell 1990) then all except the Musky Rat-kangaroo have diverged from the ancestral form to become specialised at consuming high fibre diets. As Dawson (1989) points out "complex stomachs are the hallmark of the macropodoids". A parallel can be seen in ungulates. Ungulate feeding strategies are usually classified along a browser grazer continuum. Bodmer (1990a) extended this continuum to include the small ungulate frugivores some of which lack a ruminant digestive system. Bodmer (1989) suggests that ruminant stomachs in Brocket Deer (*Mazama* spp.) evolved in response to digesting hard palm seeds and that this may have also been the case for ancestral artiodactyla. Musky Rat-kangaroos may be the only survivor of a non-ruminant ancestral form of

Macropodoid, where as the Macropodids may be derived from an ancestral form which evolved a ruminant stomach to digest hard seed coats. While Musky Rat-kangaroo retained their ancestral diet the rest of the Potoroids diverged sufficiently to require a ruminant digestive system.

While the diet of the Musky Rat-kangaroo fits into the spectrum of diets found in macropodoids at the low end of the fibre range, it is ecologically very different. Being primarily a frugivore and a terrestrial inhabitant of tropical rain forest, the Musky Rat-kangaroo is ecologically more similar to a range of other mammalian groups around the world. These groups include: Agoutis and Acouchies; small frugivorous Deer; and at the more insectivorous end of the spectrum, an Elephant Shrew (see Chapter 1, Table 1.4).

◆

Plate 6 Musky Rat-kangaroo feeding on the epigeal sporocarps of *Coprinus* sp.



Chapter 4

AVAILABILITY OF FRUITS AND SEEDS

INTRODUCTION

Fleshy fruits, including the seeds of some species, form the bulk of the diet of Musky Rat-kangaroos (Chapter 3). As with most animals that eat fruits or seeds, Musky Rat-kangaroos have a significant impact on their resources both as seed predators and dispersal agents (Chapters 3 & 8; Smythe 1978; Janzen 1983; Herrera 1985; Howe 1989). Conversely, the fruit resources have a significant impact on their frugivores (Terborgh 1986), including Musky Rat-kangaroos. A factor of fruit resources which commonly influences frugivore life histories is the seasonality of production which results in periodic gluts and scarcity (Crome 1975a; Foster 1977; Levey 1988; Marinho-Filho 1991; Moore 1991; Terborgh 1986). This leads to behaviours and life histories which reflect the changing patterns of food resources. For example, many volant frugivores move long distances to access different forest areas which have more fruit available during times of shortage in other areas (Crome 1975a; Innis 1989; Levey 1988; Moore 1991). Some primates in the neo-tropics show distinctive changes in foraging behaviour, feeding on alternative resources during fruit shortages or increasing their foraging ranges (Terborgh 1986). Some frugivores, for example fruit bats and neo-tropical opossums (Lee and Cockburn 1985; O'Brien 1993), are known to have seasonal reproduction which coincides with high fruit availability. Musky Rat-kangaroos are small terrestrial frugivores which do not move large distances in search of new resources (see Chapter 7) and therefore changes in fruit abundance are likely to have significant effects on behaviour and life history attributes.

This chapter examines the species richness, abundance, and seasonality of fruit resources available to Musky Rat-kangaroos on my study site. Significant peaks, troughs and yearly variation in fruit production were evident.

METHODS

Fruit Availability

To assess the availability of fruit to terrestrial frugivores I monitored 2100m of transects from May 1990 to December 1992. This was done monthly for all transects, except where my ill health precluded fieldwork in seven of the 32 months. Transects were arranged systematically as seven 300m long lines spaced at 50 m intervals on the study site (Configuration shown in Figure 2.3). Each transect was two metres wide. After September 1990, I subdivided each transect into 60 contiguous 5 x 2m quadrats to facilitate quantification of fruit numbers. Prior to the transects being divided into quadrats, fruit abundance was recorded according to a scale (sparse - 1-2; few 2-5; common 5-20; abundant - 20+) and position along the transect. Data collected during this period have been used to examine the timing of fruit production only. Data on fruit abundance *per se* is from post-September 1990 quadrat-samples.

Each month, I recorded and removed all fruits within each quadrat. For each individual fruit I recorded: age (juvenile, green, ripe, senescent); species (samples were collected and preserved in 70% ethanol for confirmation of identification); and signs of predation.

My examination of the fruiting phenology of all species is based on ripe fruit, except for species which are consumed as green or senescent fruit by Musky Rat-kangaroos (see Chapter 3; Mountain Mangosteen, *Garcinia gibbseae*, Watergum, *Syzygium gustavioides*).

Identifications of species were confirmed either by Wendy Cooper, author of "Fruits of the Rain Forest" (1994) or Tony Irvine, C.S.I.R.O. Division of Tropical Forest Research.

Biomass Estimates

For those species identified as being consumed by Musky Rat-kangaroos, I recorded average wet weights of the whole fruit and the wet weights and volumes of the seeds and flesh separately. I measured wet weight by combining the entire sample in a bag, weighing it and dividing the net weight by the total number of fruit. The same procedure was repeated separately for flesh and seeds. This was done for a sample of 20-40 fruits from 2-4 different individual trees for each species. Biomass estimates were then calculated for the species eaten by Musky Rat-kangaroos based on the parts chosen (i.e. seed only, flesh only or both from ripe fruit and in two cases green and senescent fruit).

Analysis

Data on both biomass of parts eaten and number of species eaten were analysed using a repeated measures, split plot design, Analysis of Variance. Factors and their error terms are displayed as footnotes to the tables. Biomass data were log transformed (log + 1) in order to stabilise the variance of cells within the Analysis.

RESULTS

I recorded a total of 85 types of fruit from 37 families (Lauraceae being most common) on transects between May 1990 and December 1992. I counted and inspected a total of 30,815 individual fruits after October 1990. The site was species rich, with 68 species of fruit falling within a total area of 0.42 ha (Appendix 1). In addition, 17 individual fruit specimens could not be identified (68 identified + 17 unidentified = 85 types). Un-named specimens consisted mostly of very green fruit (possibly the juveniles of fruit that were identified when ripe) or parts of fruit. They were all represented by only one or two fruits or fruit parts and were excluded from any analyses.

Patterns of Phenology

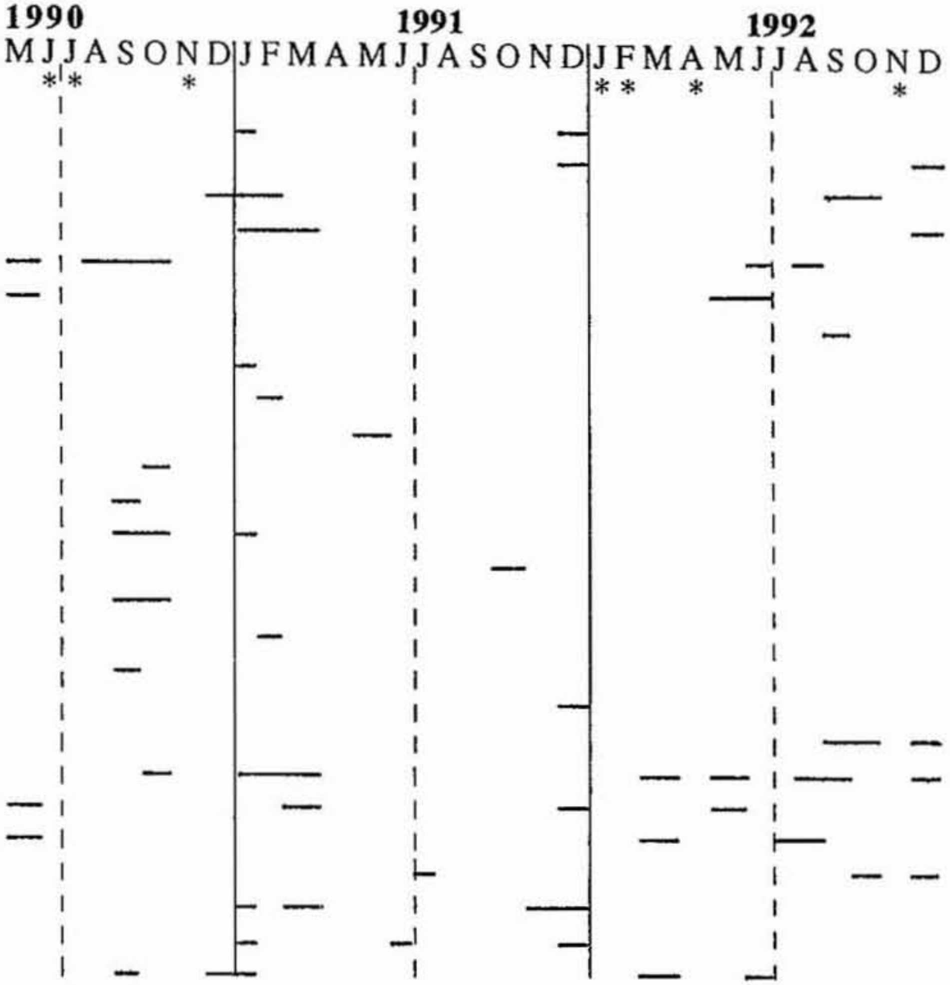
Table 4.1 shows the months in which 54 out of the 68 identified plant species bore ripe fruit. Different species of plants displayed different patterns of fruit production. Several distinctive patterns emerge: (1) some species (e.g.Banana Fig, *Ficus pleurocarpa* and Ivorywood, *Siphonodon membranaceum*) tended to fruit haphazardly at any time of the year, due both to different individuals fruiting at different times as well as the same individual fruiting constantly (pers.obs.); (2) others showed distinctive yearly seasonality (e.g. Sankey's Walnut, *Endiandra sankeyana* and Tooram Walnut, *Beilschmiedia tooram*); (3) some followed this seasonal pattern but skipped years (e.g. Tarzali Silkwood, *Cryptocarya oblata* and Pepperwood, *Cinnamomum laubatii*); (4) others fruited only once during the study, following a longer cycle (e.g. Cribwood, *Corynocarpus cribbianus* and Poison Walnut, *Cryptocarya pleurosperma*); (5) while some fruited for very short periods at different times during the study creating no discernible pattern (e.g. Septic Fig, *Ficus septica* and Umbrella Tree, *Schefflera actinophylla*). Pattern five differs from pattern one primarily in the length of time fruits are ripe, being much shorter for pattern five.

Table 4.1 Occurrence of ripe fruits along transects during 1990, 1991 and 1992. Bars represent when ripe fruit were encountered for each species. * - no data. Numbers correspond to patterns of phenology described in text: 1) haphazard fruiting; 2) yearly seasonality; 3) >yearly seasonality; 4) long cycle and; 5) no discernible pattern. Y and N relate to whether or not the species is consumed by Musky Rat-kangaroos.

Species	Group	MRK
Ficus pleurocarpa	1	Y
Siphonodon membranaceum	1	Y
Piper novaehollandiae	1	N
Prunus turnerana	1	Y
Endiandra insignis	2	Y
Neimeyera prunifera	2	Y
Endiandra sankeyana	2	Y
Beilsciedia tooram	2	Y
Athertonia diversifolia	2	Y
Endiandra monothyra	2	Y
Beilschmiedia recurva	2	Y
Garcinia gibbseae	2	Y
Diploglottis bracteata	2	Y
Beilschmiedia volckii	2	Y
Myristica insipida	2	Y
Fontainia picrosperma	2	Y
Neisosperma poweri	2	Y
Faradaya splendida	2	Y
Hollandia sayeriana	2	N
Leviera acuminata	2	N
Oraniopsis appendiculata	2	Y
Delarbria michieana	2	N
Sysygium gustavioides	3	Y
Cryptocarya oblata	3	Y
Cinnamomum laubatii	3	Y
Castenospora alphandii	3	Y
Pouteria castenosperma	3	N

Table 4.1 Continued......

Species	Group	MRK
Solanum capsicoides	3	N
Syzygium papyraceum	3	N
Elaeocarpus angustifolia	3	Y
Baileyoxylon lanceolatum	3	Y
Halfordia scleroxylla	3	N
Xanthophyllum octandrum	3	N
Acronicia vestita	4	Y
Aglaia australiensis	4	N
Austromyrtus dallachiana	4	Y
Bowenia spectabilis	4	N
Corynocarpus cribbianus	4	N
Cryptocarya pleurosperma	4	?
Dysoxylon papuanum	4	N
Endiandra palmerstonii	4	N
Endiandra xanthocarpa	4	Y
Ficus crassipes	4	Y
Syzygium boonjie	4	N
Syzygium trachyphloium	4	Y
Tetrasynandra lasciflora	4	N
Pothos longipes	5	N
Schistocarpaea johnsonii	5	N
Archidendron ramiflorum	5	N
Austrobaileya scandens	5	Y
Calamus moti	5	?
Ficus septica	5	N
Schefflera actinophylla	5	?



Seasonal Changes in Diversity

The number of species producing falling ripe fruit showed a seasonal pattern with a peak in the later part of each year and in the early part of 1991 (Figure 4.1). An increase in the number of species bearing ripe fruit occurred in the Dry season (August to October), as the ambient temperature increased toward the yearly maximum. The peaks fell just prior to or during the Storm season (November to January), while the period of fewest species fruiting was in the late Wet (March, April) and cold seasons (May to July). I have used the number of rainy days as an inverse measure of the number of hours of sunshine which may effect the ripening of fruits. The number of species producing ripe fruit showed a strong negative correlation with the number of rainy days per month (Pearson Correlation Coefficient = -0.63, P = 0.0007, N = 25) suggesting the number of species producing ripe fruit may relate to the number of hours of sunshine.

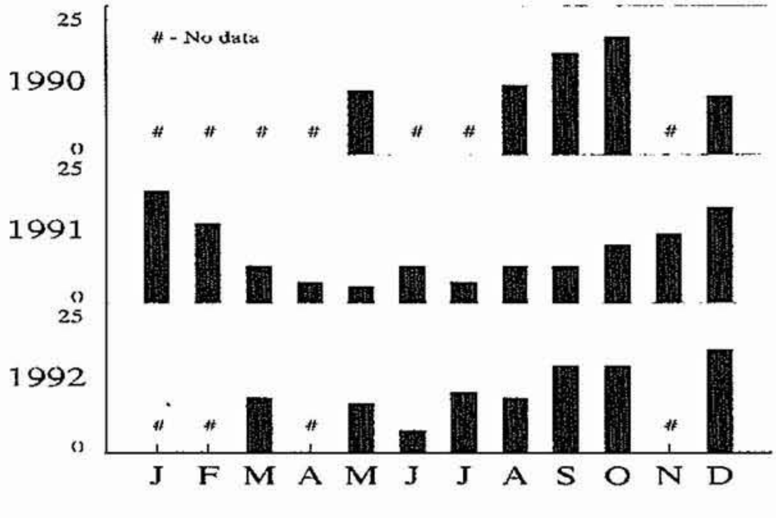


Figure 4.1 Total number of species of plants producing ripe fruit in each month (3 yrs) on my study site.

Although the pattern appears similar between years the number of species which fruited was different. Examination of the number of species fruiting in those months sampled in each year indicates that except for December, 1991 had fewer species fruiting than either 1990 or 1992 (Table 4.2). A larger number of species fruited in 1990 than in 1992 in all five months for which data were available, except December.

Table 4.2 Total number species with ripe fruits falling in 1990, 1991 and 1992 for those months where data were available in each year.

Year	May	Aug	Sep	Oct	Dec
1990	12	13	19	22	11
1991	3	7	7	11	18
1992	10	10	16	16	19

The seasonal pattern of species richness was similar for those that were consumed by Musky Rat-kangaroos (Figure 4.2). About half the species of fruit falling at any particular time were consumed by Musky Rat-kangaroos (mean proportion ± SE = 0.52 ± .034; range = 0.25 - 0.82).

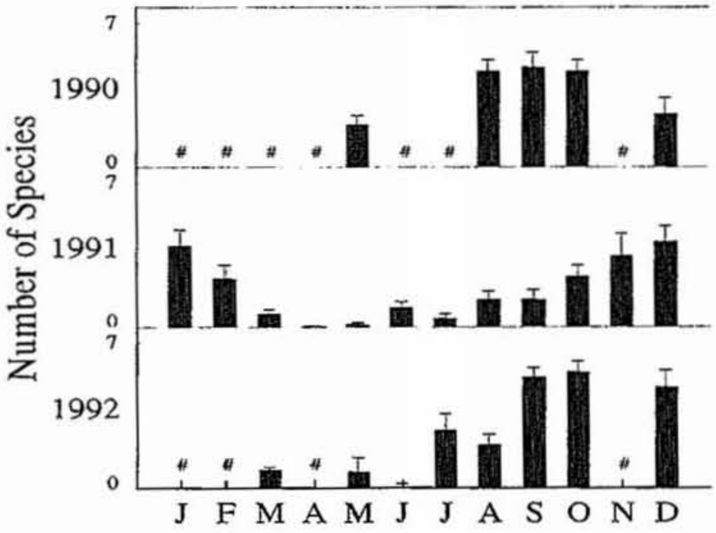


Figure 4.2 Number of species of plants whose fruit were consumed by Musky Rat-kangaroos (means ± SE), as revealed by fruit transects.

For 11 of the 25 months measured (all between March and September), less than five species of plant produced ripe fruits which were being consumed by Musky Rat-kangaroos. In April and May 1991 only one species was producing ripe fruits which were eaten by Musky Rat-kangaroos. In addition, the biomass of fruits being produced was small relative to other months (Figure 4.5). For the other 14 months measured, more than five and up to 13 species were available.

An Analysis of Variance (repeated measures model; Table 4.3) using the species richness data from 1991 and 1992, the most complete sets, showed a significant interaction effect between year and month. This was because the number of species producing fruits eaten by Musky Rat-kangaroos was greater in 1992 than in 1991 during July, September and October (Figure 4.3) but not in the other months studied. The interaction between month and transect was also significant (Table 4.3), due mostly to a larger number of species fruiting on transect four in August and October (Figure 4.4) than on other transects in other months. In addition, all transects had more species fruiting from August to December than in other months, supporting the significance of month *per se* on the number of species producing ripe fruits.

Table 4.3 Results of an Analysis of Variance (repeated measures model) of the number of species of trees producing ripe fruits eaten by Musky Rat-kangaroos in 1991 and 1992.

Source of Variation	DF	Mean Square	F	P
Year[1]	1	26.09	35.36	**0.001**
Month[2]	11	28.14	12.29	**0.0001**
Transect[3]	6	8.37	7.64	**0.0001**
Year*Month[4]	7	8.34	7.61	**0.0001**
Year*Transect	6	0.74	0.67	**0.0001**
Month*Transect	66	2.29	2.09	0.671
Within + Residual	35	1.1		**0.01**

1. Fixed factor. Error term - transect*year.
2. Fixed factor. Error term - transect*month.
3. Random factor. Error term - transect*month*year.
4. Error term for all interactions - transect*month*year.

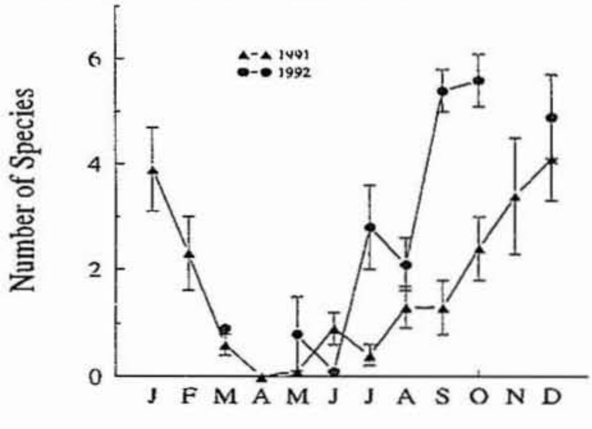


Figure 4.3 Number (± SE) of species of trees producing ripe fruit that were eaten by Musky Rat-kangaroos in 1991 and 1992.

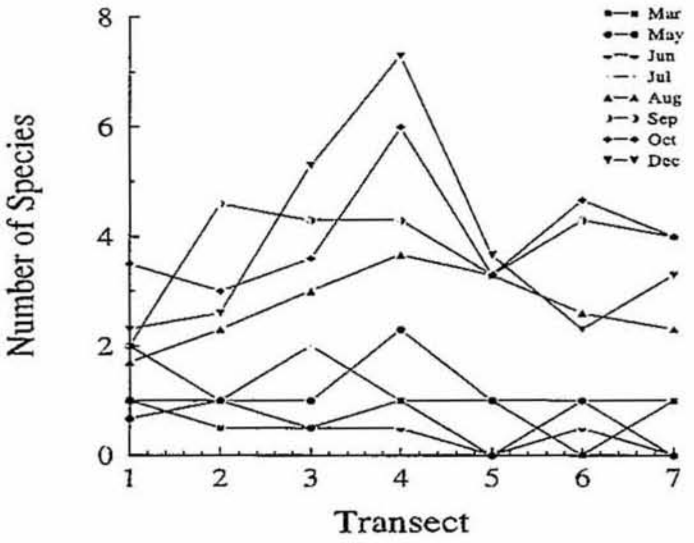


Figure 4.4 Number (± SE) of tree species with fruit eaten by Musky Rat-kangaroos falling on each transect in each month in 1991 and 1992.

Changes in Biomass

An analysis of the trends in biomass of fruits consumed by Musky Rat-kangaroos showed significant interactions between all pairs of factors (Table 4.4; Figure 4.5).

Table 4.4 Results of an Analysis of Variance (repeated measures model) of the biomass of fruits and seeds eaten by Musky Rat-kangaroos in 1991 and 1992.

Source of Variation	DF	Mean Square	F	P
Year[1]	1	1.32	20.88	0.004
Month[2]	11	0.4	15.12	0.0001
Transect[3]	6	1.12	9.18	0.0001
Year*Month[4]	7	0.24	18.68	0.0001
Year*Transect	6	0.06	4.97	0.001
Month*Transect	66	0.03	2.07	0.01
Within + Residual	35	0.01		

1. Fixed factor. Error term - transect*year.
2. Fixed factor. Error term - transect*month.
3. Random factor. Error - transect*month*year.
4. Error term for all interactions - transect*year*month.

The interaction between year and month is due to much greater biomass of fruits and seeds falling in September, October and December in 1992 than in 1991 (Figure 4.5).

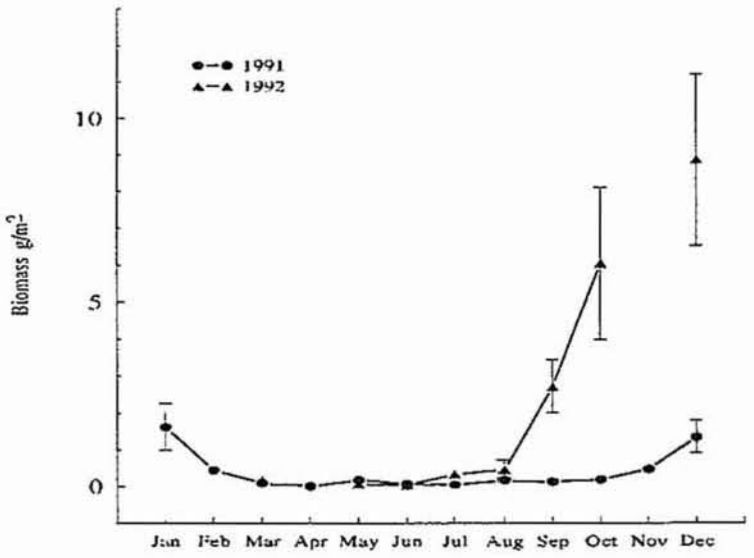


Figure 4.5 Biomass (means ± SE) of fruits and seeds of species eaten by Musky Rat-kangaroos falling on my study site in 1991 and 1992.

The interaction between year and month was due mostly to members of the Lauraceae family (including Boonjie Blush Walnut, *Beilschmiedia volckii*, Tooram Walnut, *B. tooram*, Rose Walnut, *Endiandra monothyra*, Sankey's Walnut, *E. sankeyana*, Hairy Walnut, *E. insignis* and Tarzali Silkwood, *Cryptocarya oblata*) producing large crops of fruit at that time.

A significant interaction between transect and month was also evident (Figure 4.6). This was again due to the large crops of Lauraceae in September, October and December, which were distributed unevenly on the site. Transects three and four contained the largest number of individual trees and species, with crops of Rose Walnut, Sankey's Walnut, Tooram Walnut, and Tarzali Silkwood dominating. In addition, transects one, six and seven had large crops falling in December, which included Boonjie Blush Walnut, Hairy Walnut and October Vine, *Faradaya splendida*.

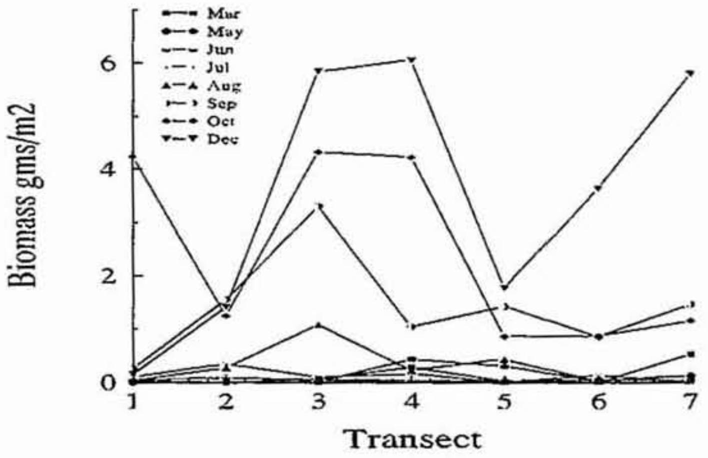


Figure 4.6 Biomass of fruits and seeds eaten by Musky Rat-kangaroos in 1991 and 1992. Displaying the month by transect interaction.

A third interaction, between year and transect, was also evident because of the late 1992 peak in fruits occurring for plants distributed on transects three to seven (Figure 4.7).

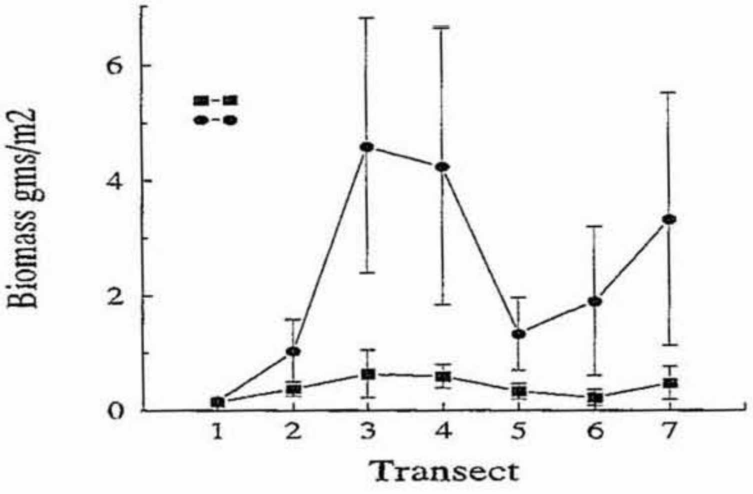


Figure 4.7 Biomass (mean ± SE) of fruits (species consumed by Musky Rat-kangaroos) on each transect in 1991 and 1992.

The amount of fruit available to Musky Rat-kangaroos ranged from 1.97 g/m^2 (± 1.1 SE) in January 1991 to 0.001 g/m^2 (± 0.001 SE) in April 1991. This translates to a seasonality index (Ford *et al.* 1988; ratio of peak to trough measures) of 1970:1. In 1992, a more fruitful year, the seasonality index was 295:1 with biomass ranging from 0.03 g/m^2 (± 0.01 SE) in June to 8.86 g/m^2 (± 2.3 SE) in December. Because 1992 was a masting year for the Lauraceae and had extremely high biomass of fruit during its peak, the seasonal changes in abundance in 1991 are not obvious in Figure 4.5. Therefore, Figure 4.8 displays the biomass changes for 1991 only. I present this figure because analyses in previous (Chapter 3) and subsequent chapters (Chapter 6) relate to the changes in fruit abundance in 1991.

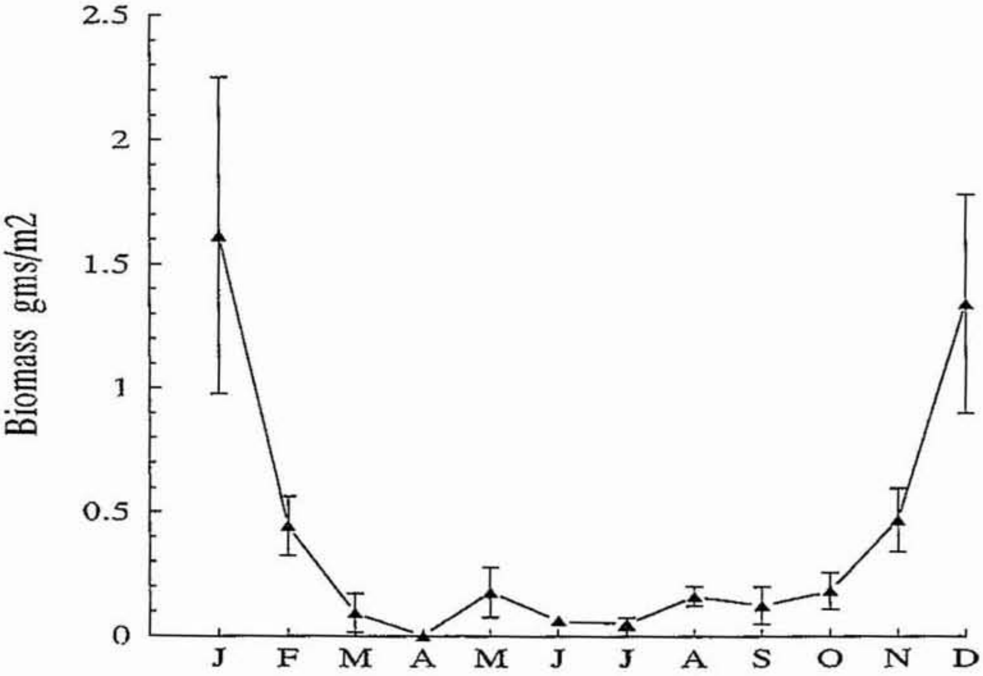


Figure 4.8 Biomass (mean ± SE) of fruits and seeds of species eaten by Musky Rat-kangaroos on my study site in 1991.

DISCUSSION

Species Richness

My study site displayed high species richness with 68 species of plant dropping ripe fruit in an area of 0.42 ha. The only other study conducted in wet-tropical rain forest in Australia that used similar methods was carried out by Moore (1991) at Paluma. Moore (1991) found 45 species in 0.36 ha whereas my study site had 1.3 times the number of species fruiting in a given area. In addition, Moore (1991), in his study on frugivorous birds, used fruit traps which showed that transect walks underestimated the total diversity of fruits by overlooking some of the tiny and rare species. I considered an under-estimate of this sort unimportant for the present study as the species overlooked were probably of little importance to Musky Rat-kangaroos. The lower species richness at Paluma is expected as it is in an area of lower rainfall and near the southern limit of tropical rain forest in Australia. In addition, my study site is part of an area considered to have been a refuge during the Pleistocene contraction of rainforests in Australia (Webb and Tracey 1981) and therefore has higher species richness.

A study conducted in Gabon on the west coast of Africa (White 1994) found strong correlations between both the number of species fruiting and the total number of ripe fruit with the mean number of hours of sunshine per month. Unfortunately I was unable to obtain insolation data for this study. However, the number of rainy days per month showed a strong negative correlation with the number of species fruiting (see "Changes in Diversity" this chapter). If the number of rainy days is considered to be the inverse of the amount of sunshine, then it appears that high insolation values may correlate with the number of species fruiting here as well.

Sampling Methods and Biases

I chose to sample fruits on the forest floor because that was what was available to Musky Rat-kangaroos. Many species of plants may lose a large proportion of their fruits to aerial and scansorial frugivores before the crop falls to the ground (Terborgh 1983). Therefore, sampling the crop sizes in the crowns of trees was not necessarily indicative of what was available to Musky Rat-kangaroos. Fruit traps were also considered and tried in conjunction with transects but all fruits falling into them were consumed by rats each night. Therefore, transects remained the sole and most reliable method of estimating the availability of fruits and seeds to Musky Rat-kangaroos.

Zhang and Wang (1995) examined the three different methods of sampling fruit mentioned above (crops in crowns; fruit traps; terrestrial transects) and explored their relative biases. Sampling by transects on the forest floor over-estimated the amplitude of changes in fruit abundance relative to other methods. This was due to terrestrial frugivores consuming a higher proportion of the supply during times of low availability of fruits. This means that the seasonality indices calculated for 1991 (1970) and 1992 (295) are probably exaggerated. However, they are still a useful measure of the relative availability of fruits to Musky Rat-kangaroos, taking into account the competitive pressures of conspecifics and other terrestrial frugivores.

Australia's Seasonal Wet Tropics

Production of fleshy fruit showed a seasonal pattern with peaks in abundance and in the number of species producing ripe fruit occurring from September to February. This was in the warmest time of year when conditions ranged from dry to wet but generally had a lower number of rainy days per month than at other times. In addition to seasonal changes in abundance and species richness, was the spectacular difference between years. The seasonality and difference between years was similar to the findings of some other studies in tropical rain forests in Australia, including both lowland (Hopkins and Graham 1989), and upland sites (Moore 1991). However, one lowland study, covering 2.5 years at Mission Beach (Crome 1975a), found the peaks in diversity and production falling earlier, July to September, during the cooler dry period.

None of the previous studies in Australia examined the biomass of fruits, at best they used a qualitative scale to give estimates of relative numbers without assessing the sizes of fruits (Hopkins and Graham 1989) or counted the number of fruits on transects and in fruitfall traps, again without any assessment of fruit sizes (Moore 1991). Crome (1975) gave a measure of the seasonal abundance of fruits based on the basal area of fruiting trees as a percentage of the total basal area of trees on his sites. This takes into account only the number of individual trees producing fruits and not the variation in crop sizes within one individual between years. Because of this variation it is difficult to compare data from this study with those of others. However, it is clear that the seasonality index calculated on biomass is far greater than that calculated on abundance scales that ignore the size of fruits. Seasonality indices based on some measure of abundance ranged from 3 at Liverpool creek (Hopkins and Graham 1989) to 52.5 at Paluma (Moore 1991). Whereas the index based on biomass for this study ranged from 295 to 1970.

Spatial and Temporal Heterogeneity

The Analyses of Variance examining both the number of species producing ripe fruits and the biomass of fruits on the study site identified an interaction effect between month and transect. This effect related to the spatial heterogeneity of fruit falls. Some areas (transects) had more species and more fruits than others. The areas with more species or individuals fruiting were dependant upon the month.

One of the most significant aspects of the patterns found was the large difference in biomass of fruit between years (Figure 4.5). While the seasonal pattern remained predictable the absolute quantity of fruit falling varied enormously. This adds an element of unpredictability to the resource base that Musky Rat-kangaroos rely on. The most likely outcome of this level of unpredictability would be a rapid reproductive rate (see Chapter 6).

Availability of Fruits and its Effect on Musky Rat-kangaroos

Both temporal and spatial heterogeneity of fruit availability have significant impacts on Musky Rat-kangaroos which affect aspects of their behaviour and ecology, which will be examined in ensuing chapters. The most significant factors to be gleaned from this chapter are:

1) fruit availability has strong seasonal trends, the peak and trough periods remaining constant between years in this study;

2) the difference between peak to trough fruit availability is large and constitutes a resource bottle-neck;

3) despite similar seasonality a huge difference in the quantity of fruit falling can occur between years, creating unpredictability;

4) fruit falls are patchily distributed in space both at the level of single trees and clusters of trees.

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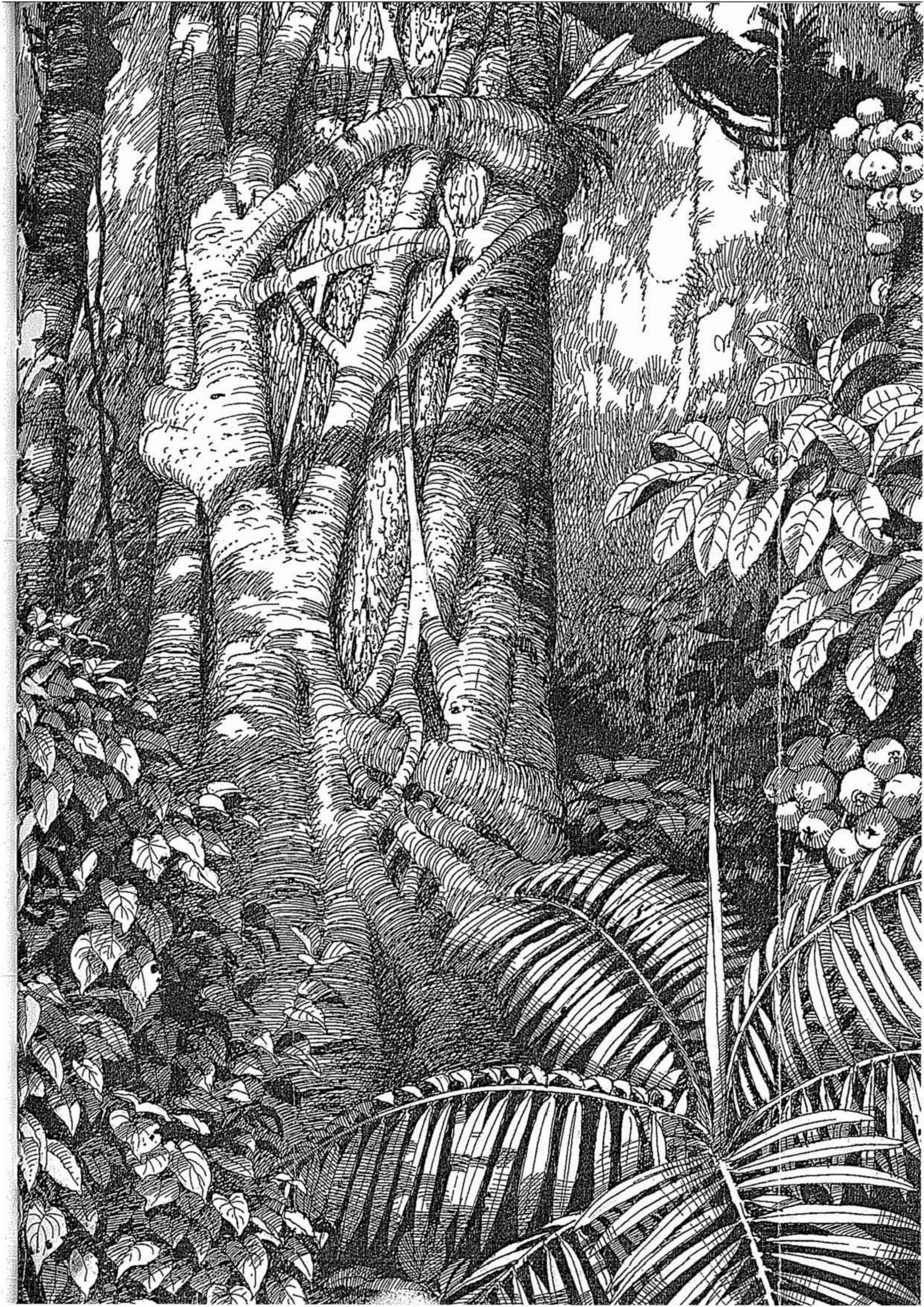

Chapter 5

DISTRIBUTION AND ABUNDANCE OF FAUNA IN LEAF LITTER

INTRODUCTION

Litter fauna forms an important component in the diet of Musky Rat-kangaroos (Chapter 3). As with many animals that rely primarily on fruit, animal protein is an important, high nitrogen supplement (Mack 1990). Terborgh (1983) found that some of the Tamarins, *Saguinus* spp., in his study site at Cocha Cashu (Peru), spent much of their foraging time searching for invertebrates. Like Musky Rat-kangaroos, they fed on invertebrates and fruit but included nectar as well.

Very few studies have examined litter fauna in tropical rain forests of Australia. Those that have (Frith and Frith 1990; Holt 1981; Holt 1985; Jansen 1993), all demonstrate significant seasonal trends in abundance and differences between years. Along with some studies from Panama (Levings and Windsor 1982; Levings and Windsor 1985) and Peru (Pearson and Derr 1986), these studies suggest that moisture (rainfall or relative humidity) is a primary determinant of faunal abundance. In addition, litter quantity was suggested as an important factor (Frith and Frith 1990; Holt 1985). However, only Jansen (1993) measured any of these parameters, finding that both dry litter weight and moisture content were correlated with the abundance of litter fauna. Levings and Windsor (1984) manipulated the moisture levels in previously cleared litter sites and found that arthropod numbers were positively correlated with moisture.

In this chapter, I examine seasonal variation in the abundance of litter fauna in relation to physical parameters of their microhabitat, including: dry litter weight; moisture content; temperature; and topography - ridge, slope or gully. I found that small invertebrates showed seasonal trends in abundance while large invertebrates did not. Abundance correlated with temperature, moisture and dry litter weight.

METHODS

Sample Collection

Samples of litter were collected every second month from January 1991 to November 1992. I collected four samples from each of ridge, slope and gully sites where, on each sampling occasion, the topographical areas were chosen to avoid resampling the same ridge, slope or gully. I chose quadrat locations within each area by spinning on the spot and throwing a section of the quadrat in the air. The location where it landed became the sample. This was repeated four times in each topographical feature being sampled.

I scraped up the litter within the 0.25m^2 quadrat by hand to the depth of the soil layer, placed it into a large plastic bag, weighed and transferred it immediately to the laboratory for extraction. On occasions during collection of the sample large invertebrates (usually spiders or cockroaches) would attempt to escape, these I either re-caught and placed into the sample or made a note of their escape, order and approximate size.

Extraction

Invertebrates were extracted using 30, 25cm berlese funnels (McFadyen 1961)), each with an eight centimetre base covered with one centimetre wire mesh. Each funnel opened into a 700ml container holding approximately one centimetre of 70% ethanol. I fitted the funnels with mosquito netting covers to prevent insects moving in or out of the samples. Each funnel was placed under a 40 watt bulb.

I divided each replicate litter sample between several funnels depending on the volume of litter, with each funnel containing a similar volume. When the litter was extremely wet, the volume per funnel was reduced. On two occasions the litter was so wet that the collection had to be divided into two separate events. I collected and processed six samples on one day and the other six two days later as all would not fit under the lights at one time.

I left the samples for two days, after which I removed the litter for further drying and collected the preserved samples into replicate batches and stored them for sorting. Before this was done, I searched the edge of each funnel for dead invertebrates (mostly oligocheates and amphipods) which I included in the samples. I placed the litter into cloth bags and oven dried it at approximately 40°C to constant weight (usually one week). I then calculated percentage moisture using the wet and dry weights.

Sorting

I sorted the invertebrates under a dissecting microscope into orders and size classes: <1mm; 1 - 2mm; 2 - 5mm; and >5mm. I recorded the actual size of those over 5mm. I chose size classes in preference to biomass estimates because the collection itself represents important reference material for tropical leaf litter fauna and it was therefore undesirable to destroy it for biomass (dry weight) estimates. I examined the possibility of using length-weight ratios to convert the size data into biomass but no information was available for some of the taxa in the samples or for tropical Australian groups in general.

Analysis

Data were analysed by analysis of variance and step down regression. The analyses of variance included year, month, and topography as fixed factors and were performed separately for: 1) invertebrates >2mm and invertebrates >5mm (a subset of those >2mm); 2) moisture content of the leaf litter; and 3) dry litter weight using partial sums of squares due to an unbalanced design (one replicate from March 1991 was lost). The two size classes of invertebrates (>2mm and >5mm) were chosen on the basis of the size of dietary items in faecal pellets. While I observed invertebrates as small as 2mm in faecal samples, the majority of exoskeleton fragments were from organisms larger than 2mm. Therefore, invertebrates >5mm (a subset of those >2mm in analyses) are probably targeted more by Musky Rat-kangaroos. Counts on invertebrate abundance and data for dry litter weight were log transformed (log{n+1}) for both analyses of variance and multiple regressions because of skewed distributions.

RESULTS

A total of 13113 organisms belonging to 37 orders were sorted from 36 m^2 of forest litter. Of these, 4250 were >2mm. The variation in abundance of invertebrates differed for the different size classes (Table 5.1), even though they were not independent (>5mm is a subset of >2mm).

Table 5.1 Analysis of variance tables for invertebrate abundance in 1991 and 1992.

Source of Variation	DF	Mean Square	F	P
Invertebrates >2mm R^2=0.37				
Year[1]	1	0.153	0.39	0.54
Month[1]	5	2.43	6.13	**0.0001**
Topography[1]	2	0.175	0.64	0.64
Year*Month	5	0.646	1.6	0.16
Month*Topography	10	0.584	1.47	0.16
Year*Topography	2	2.52	6.35	**0.0024**
Year*Month*Topography	27	0.603	1.46	0.09
Error	117	0.397		
Invertebrates >5mm R^2=0.25				
Year[1]	1	1.195	2.38	0.13
Month[1]	5	0.604	1.21	0.31
Topography[1]	2	0.521	1.04	0.36
Year*Month	5	0.395	0.79	0.56
Month*Topograph	10	0.961	1.92	**0.0492**
Year*Topography	2	1.402	2.8	0.065
Year*Month*Topography	27	0.801	1.26	0.20
Error	117	0.501		

1.Fixed Factor

The relative abundance of animals >2mm in ridges, slopes and gullies varied in different years (Table 5.1). In 1992, gullies had higher abundances of invertebrates than in 1991 whereas in ridges and slopes invertebrate abundance was similar on both years (Figure 5.1).

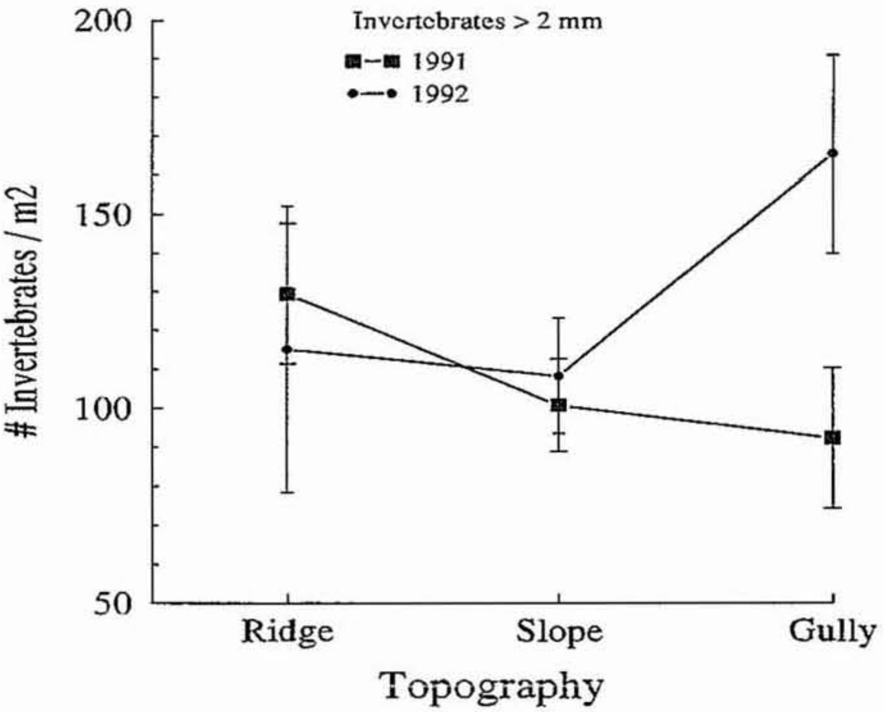

Figure 5.1 Number of invertebrates >2mm (mean ± SE) from ridge, slope and gully samples in 1991 and 1992.

There was also a strong seasonal component to the variation in abundance of invertebrates >2mm, which was in addition to the effects of the interation between topographic location and years. This seasonal effect is illustrated in Figure 5.2. In contrast, the abundance of invertebrates >5mm showed no statistical difference between months (Table 5.1; Figure 5.2). Invertebrates were at their lowest numbers in the cold season (May to July) in both years and at their peak in the storm season (November to January). Numbers of animals >2mm varied from $67m^{-2}$ (± 12.36 SE) during the 1991 July trough to $202m^{-2}$ (± 74 SE) in the 1992 November peak. Invertebrates >5mm varied from $14m^{-2}$ (± 4.4 SE) in the 1992 July trough to $34.3m^{-2}$ (± 12.6 SE) in the 1991 November peak (although this variation was not statistically significant).

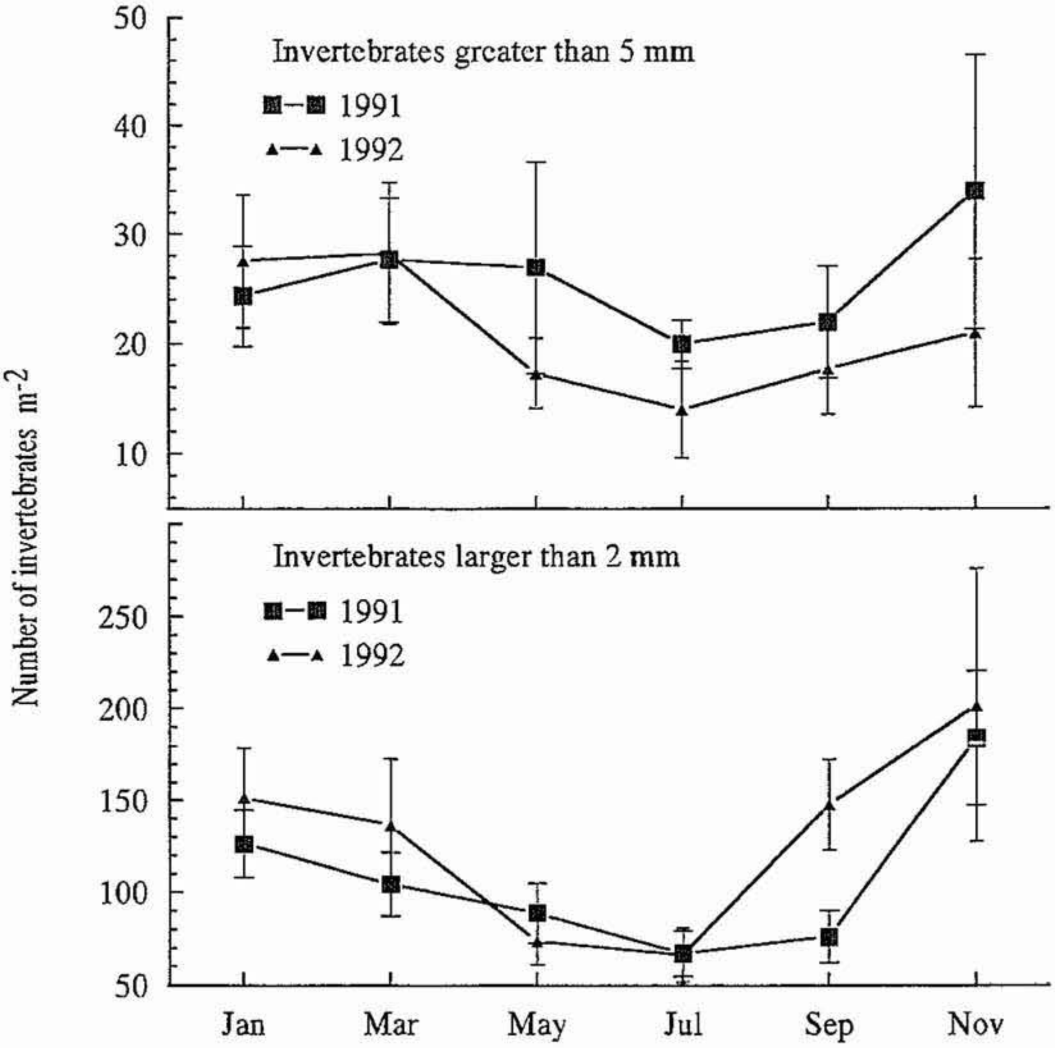

Figure 5.2 Abundance of invertebrates (means ± SE) in each month in 1991 and 1992. All topographical localities combined.

The abundance of invertebrates >5mm differed between ridges, slopes and gullies with the pattern of variation depending on the month (Table 5.1; Figure 5.3). The most outstanding features of this interaction were much higher numbers in gullies in November, a dry period, and much higher numbers on ridges in May, after a wet period (see Figure 2.4 for rainfall patterns).

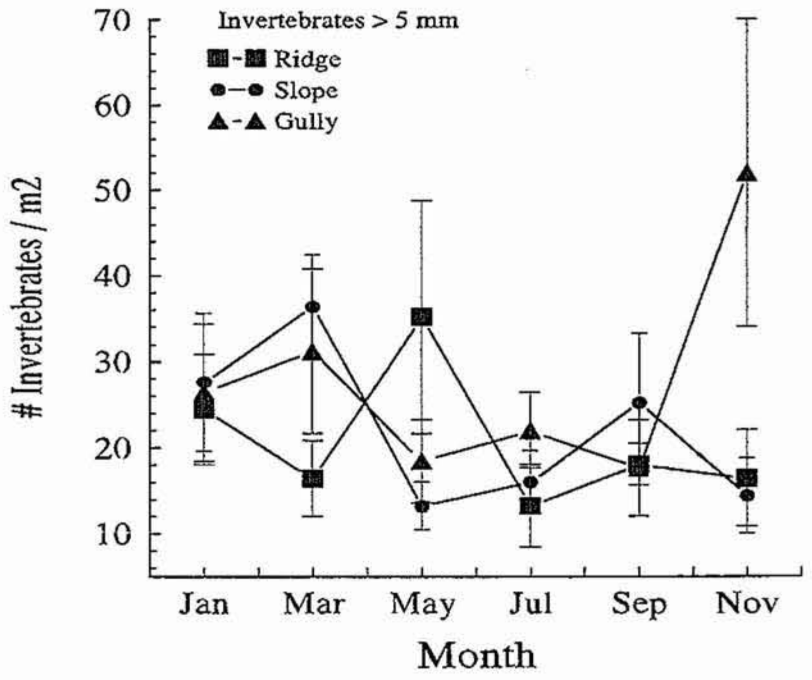

Figure 5.3 Number of invertebrates >5mm (mean ± SE) from ridge, slope and gully sites in each month. Data combined for 1991 and 1992.

Maximum temperature and dry litter weight were the best predictors of the abundance of invertebrates >2mm, while for invertebrates >5mm the best predictors of abundance included maximum temperature, dry litter weight and moisture content of the litter (Table 5.2). However, neither relationship explained more than 21% of the variance in abundance of litter fauna. Litter fauna abundance therefore, is difficult to predict using the parameters measured. Further analysis of seasonal variation in litter moisture and dry litter weight only served to highlight the complex interaction between these parameters and temperature with litter invertebrate abundance.

Table 5.2 Results of step down, multiple regressions for litter fauna >2 mm and litter fauna >5 mm.

Variable	DF	b	SE	T	P
>2mm Regression 1: R^2=0.2					
Intercept	1	-1.31	0.82	-1.6	0.1111
Maximum Temperature	1	0.1	0.02	5.5	**0.0001**
Litter Moisture	1	0.0002	0.003	0.05	0.9601
Dry Litter Weight	1	0.35	0.11	3.27	**0.0013**
>2mm Regression 2:R^2=0.21					
Intercept	1	-1.3	0.78	-1.66	0.0989
Maximum Temperature	1	0.1	0.02	5.6	**0.0001**
Dry Litter Weight	1	0.35	0.11	3.29	**0.0013**
>5mm Regression 1:R^2=0.16					
Intercept	1	-3.06	0.87	-3.526	**0.0006**
Maximum Temperature	1	0.06	0.02	3.256	**0.0014**
Litter Moisture	1	0.007	0.003	2.172	**0.0316**
Dry Litter Weight	1	0.5	0.11	4.37	**0.0001**

DISCUSSION

The abundance of litter fauna >2mm showed strong seasonal variation (Table 5.1; Figure 5.2) which was explained by seasonal temperature fluctuations and changes in the quantity of litter on the forest floor (Table 5.2). Larger invertebrates (>5mm) showed no strong seasonal pattern (Table 5.1; Figure 5.2). However, temperature, dry litter weight and moisture content of the litter were correlated with changes in their abundance (Table 5.2). The most significant feature of these results was the relative stability in abundance of large (>5mm) litter invertebrates (which appeared to be most significant in the diet of Musky Rat-kangaroos; Chapter 3) when compared to the annual variation in fruit availability. Therefore, litter fauna constituted a predictable resource which could be relied upon during times of few fruit.

While the abundance of litter fauna in both size classes varied with topography, the differences depended on year (>2mm) and month (>5mm; Table 5.1). Assuming that invertebrates >5mm were the primary resource sought by Musky Rat-kangaroos then one would expected them to forage more on slopes and gullies in March, Ridges in May and Gullies in November, while during the rest of the year foraging at random with respect to topography would have been profitable (Figure 5.3). However, areas of deep, moist litter would also be profitable whereever they occurred (Table 5.2).

Clearly litter faunal numbers relate to a complex of factors which probably interact synergistically. Some of those factors were measured in this study and may have a causal relationship with invertebrate numbers. Levings and Windsor (1984) showed experimentally that moisture content of the litter significantly effected the recolonisation rates of plots cleared of litter fauna on Barro Colorado Island, Panama. Pearson and Derr (1986), in Peru, found that maximum temperature was correlated with litter faunal biomass in certain sites and Levings (1982; Barro Colorado Island) and Jansen (1993; Wooroonooran National Park, Australia) found correlations with moisture content and quantity of litter. My study was the first to include temporal, topographic and physical parameters - litter moisture, dry weight and temperature (Jansen's [1993] study did not include temperature), and found complicated relationships with all factors and litter faunal abundance. Even so, there was still a significant amount of variation unaccounted for which may relate to other factors like the species of leaves and twigs in the litter and community composition of the fauna.

Studies of the temporal variation in litter fauna abundance have invariably shown seasonal changes (Frith and Frith 1990; Hutson and Veitch 1987; Jansen 1993; Plowman 1979; Wolda 1978) and those from wet tropical Australia have all showed peaks in abundance occurring around November to March (Frith and Frith 1990; Plowman 1990; Jansen 1993). Interestingly Jansen's (1993) study, which was carried out two kilometres away and at the same time as this one using identical methods and equipment, showed peak abundances occuring in January where they occurred in November in this study. Jansen (1993) also recorded twice the density of small invertebrates in her samples. The main difference between the sites was the proximity to the forest edge, Jansen's being closer. These interesting differences suggest that even within a reasonably small area, the litter faunal ecosystem may be cycling and fluctuating at slightly different times within the broad seasonal pattern and may also have very different community composition. These observations of the variability in litter fauna assemblages and abundance over small distances and the stability of abundance for large litter fauna (>5mm) suggest that this resource would have little impact on the seasonality of life history attributes of Musky Rat-kangaroos.

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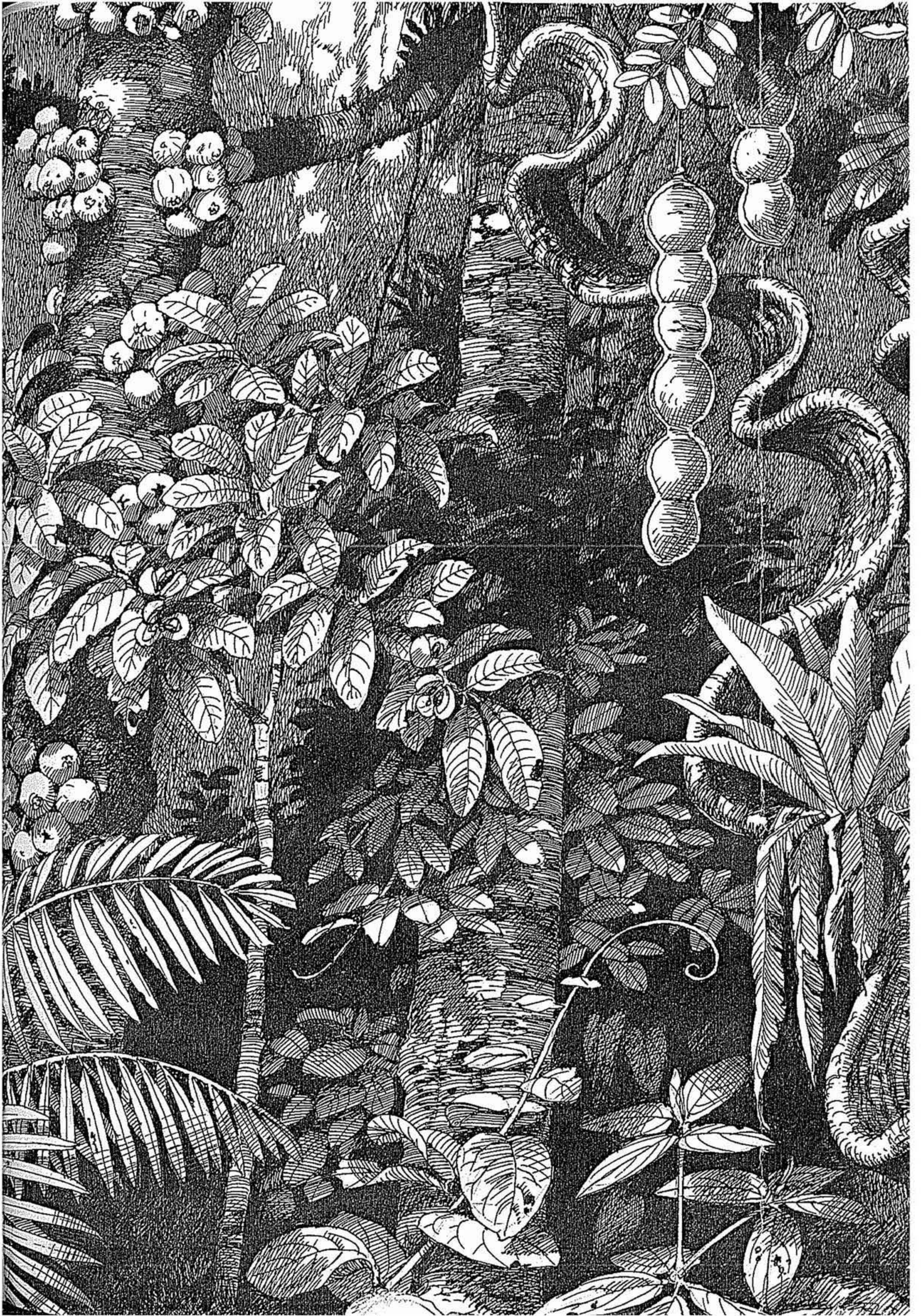

Chapter 6

LIFE HISTORY AND REPRODUCTION

INTRODUCTION

Reproduction in most Macropodoids is unique in that they display embryonic diapause at the unilaminar stage, which is controlled during lactation by the hormonal suppression of corpus luteum development (Hume *et al.* 1989; Tyndale-Biscoe 1989). For most macropodoids reproduction is continuous, although a few at the southern limits of their ranges have developed obligate seasonality, while a few others are facultative seasonal-breeders. The Quokkas, *Setonix brachyurus*, population on Rottnest Island (Western Australia) shows seasonal reproduction, whereas mainland populations are continuous breeders. When animals from Rottnest have continuous access to food, year round breeding resumes (Tyndale-Biscoe 1989). Continuous breeders have a post-partum oestrous and if successfully mated the embryo implants into the uterus and development is arrested until the current pouch young alters its suckling habits. Subsequently, development resumes and by the time birth occurs the current pouch young is permanently evicted but continues to suckle; the mother producing milk of two different qualities from two (out of four) different mammaries (Merchant 1989). This pattern is thought to be ancestral to the current seasonal pattern and probably evolved to take advantage of continuously available food resources and/or in response to unpredictable conditions and drought cycles common in Australia. In addition, during times of severe nutritional stress, usually brought on by drought, some species will enter anoestrus until conditions improve. Others evict young at an early age and resume development of their quiescent embryos, placing less demand on the mother while still being ready to take advantage of a break in the drought (Tyndale-Biscoe 1989).

Rat-kangaroos differ from the normal pattern by having a shorter pouch life which often leads to producing more than one successive young in a year. Otherwise they display a similar reproductive pattern to macropodids and are continuous breeders with delayed gestation during lactation (Rose 1989). All macropodoid males that have been studied appear to be continuously reproductive (but see discussion on Tammar Wallaby; this chapter).

Apart from the rearing of twins (Johnson and Strahan 1982) and Johnson's unpublished observation that males undergo seasonal enlargement of the testes in captivity, nothing is known of reproduction in Musky Rat-kangaroos. This Chapter examines the reproductive patterns seen in wild Musky Rat-kangaroos on the Atherton Tablelands and demonstrates they are seasonal breeders in response to variation in food resources. This is a common pattern in frugivorous animals (Lee and Cockburn 1985; O'Brien 1993; Smythe 1978) and marsupials (Hume *et al.* 1989) but a relative rarity among macropods. Therefore, I will discuss the pattern seen in Musky Rat-kangaroos in relation to both macropods and other frugivores to examine the phylogenetic and ecological influences on their reproduction.

METHODS

To record basic morphometric, weight and reproductive data, animals were trapped from February 1990 to February 1993. Prior to this study no successful method of trapping Musky Rat-kangaroos had been devised despite some attempts (Johnson, P. pers. comm. 1989; Moore, L. pers. comm. 1990). Therefore, the initial capture rates for this project were sporadic until my trapping technique was refined. During this period, I tested numerous methods, including different bait types, trap sizes and trap disguises, before the fence trap described below proved effective. I was unable to trap from January to June 1992 due to ill health.

Trapping

I trapped animals on my 300 m^2 grid with five fence traps, four arranged diagonally across the corners of the grid (as topography allowed) plus one placed centrally (Figure 2.3). Each fence consisted of five 20x1m strips of shade cloth or Sarlon weed mat attached to wooden stakes or trees and pinned into the ground with tent pegs and occasional rocks or logs (Figure 6.1). The five "sub-fences" were then arranged in a zig-zag pattern through the forest, leaving four gaps for traps. Two treadle-release cage traps (Mascott wire works collapsible cat traps 40x40x60 cm), were located between each pair of sub-fences and were left adjacent to the gap when not in use (a total of 20 gaps and 40 traps were used). This allowed resident animals to habituate to moving through the gaps in the presence of traps. No bait was used as animals would continue to use the gap when traps were in use and bait would attract unwanted species such as White-tailed Rats. Early tests showed that Musky Rat-kangaroos did not enter small traps, hence the large size of the traps relative to Musky Rat-kangaroos.

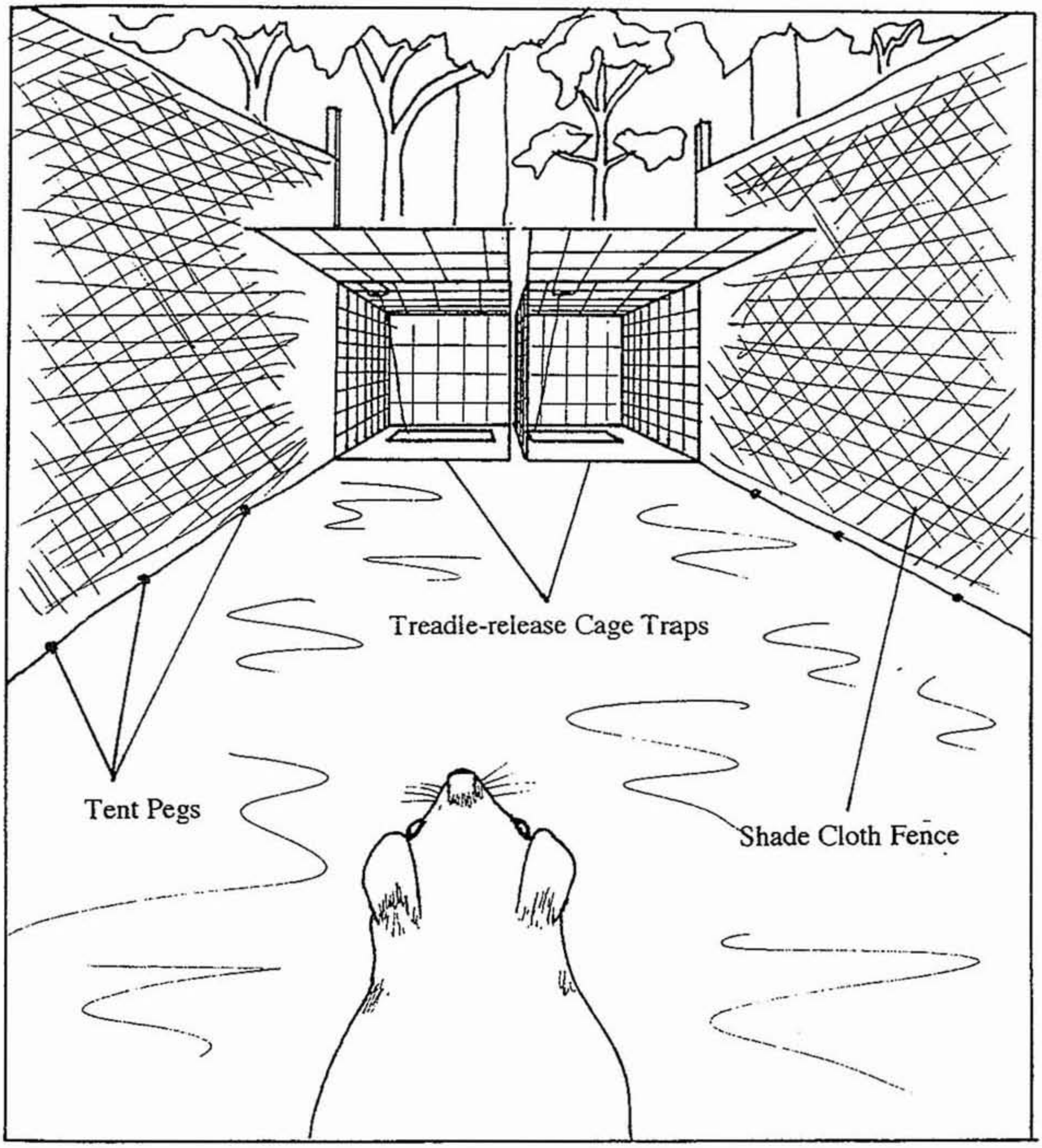

Figure 6.1 Fence trap showing placement of treadle release traps.

This method was successful at catching most terrestrial forest fauna (Table 6.1) and was later modified for a study of pademelons (Vernes 1993). Musky Rat-kangaroos quickly became trap shy. I found trapping at irregular intervals and never more than two days in a row gave the best results.

Table 6.1 List of animals captured in fence traps (other than Musky Rat-kangaroos) with their relative abundance indicated: A - abundant; C - common; O - occasional; R - rare. The method is probably useful for those that are abundant or common.

Common Name	Latin Name	Abundance
Giant White-tailed Rat	*Uromys caudimaculatus*	A
Masked White-tailed Rat	*Uromys hadrourus*	R
Bush Rat	*Rattus fuscipes*	A
Water Rat	*Hydromys chryogaster*	R
Long Nosed Bandicoot	*Perameles nasuta*	A
Red-legged Pademelon	*Thylogale stigmatica*	C
Coppery Brush-tailed Possum	*Trichosurus vulpecula johnsoni*	R
Echidna	*Tachyglossus aculeatus*	R
Spotted-tailed Quoll	*Dasyurus maculatus*	O
Brush Turkey	*Alectura lathami*	O
Orange-footed Jungle Fowl	*Megapodius freycinet*	O
Red-necked Rail	*Rallina tricolour*	R
Chowchilla	*Orthonyx spaldingi*	C
Yellow-throated Scrubwren	*Sericornis citreogularis*	O
Boyd's Forest Dragon	*Hypsilurus boydii*	O

Measurements

I tattooed each animal's ear with a unique number and measured the head, right pes (± claw) and right ear (± 0.1 mm) with Vernier callipers and tail (± 1 mm) with a ruler. In addition, I recorded age and sex class (adult, subadult, juvenile, ♂, ♀); reproductive status; weight (to the nearest 5 g using a 1 kg Pesola scale); and notes on distinctive features, injuries or parasites. Body part measurements followed Sharman *et al.* (1964). The tail was measured on the dorsal surface to the base of the spine. Reproductive data included a description of: pouch; mammary condition (length of nipple in mm, colour - pink or black; and glandular state - no mammary tissue evident, slightly swollen and lumpy, extremely swollen); and number of pouch young. I measured the head and/or tail of pouch young where possible but if a female showed high levels of stress this was not pursued. For males, a measure of testes area was calculated as the product of the length of the right organ and the width of both combined.

Behavioural Observations

Because of the density of the vegetation, systematic observation of behaviour proved unrewarding. Therefore, I abandoned formal sampling in favour of opportunistic observations, recording descriptions of behaviour that were valuable in interpreting and understanding patterns seen in data collected by other methods. Some of the behaviours described enhance understanding of the life history of Musky Rat-kangaroos.

Analysis

Most data were analysed with Analysis of Variance. Due to some animals being caught on several occasions but the majority being caught only once, all repeated measures were removed for each analysis.

Condition Indices

A condition index was calculated for animals based on that used by Bradshaw and De'ath (1991) and modified according to Krebs and Singleton (1993). Initially, body part measurements (head length, pes length and tail length in mm) were analysed, using a single record for each animal to see which measurement was most highly correlated with body weight (Table 6.2). Female body weight was corrected for the presence of pouch young by subtracting the mean weight of young measured in each month multiplied by the number of young being carried by each individual. Weights of early pouch young, still attached to a nipple, were derived from animals freshly killed by domestic dogs or Grey Goshawks, *Accipiter novaehollandeae*.

Table 6.2 Correlation of body part measures with weight for Musky Rat-kangaroos.

Sex/Age Class	Head/P[1]	Pes/P	Tail/P
Males (N=36)	0.58/0.0002	0.45/0.006	0.17/0.32
Females (N=25)	0.83/0.0001	0.38/0.06	0.24/0.25
Subadults (N=34)	0.96/0.0001	0.9/0.0001	0.89/0.0001

[1] Correlation Coefficient/Probability

The variable most highly correlated with body weight was head length. I then calculated the regression relationships between ln(head length) and ln(body weight) (with all repeated measures removed), separately for males, females and subadults (including recently independent juveniles). I then compared the slopes of these equations to assess the possibility of using one equation for all age and sex classes. However, all equations were significantly different (Analysis of Covariance F=310.8, DF=85, P=0.0001; Tukey test) and subsequent calculations of condition indices were done separately for each age and sex class. Table 6.3 shows the resulting regression equations.

Table 6.3 Regression equations to calculate condition indices for Musky Rat-kangaroos. Based on a single measure from each individual. BW - Body Weight, HL - Head Length.

Age/sex Class	Regression Equation	Adjusted R^2	Equation #
Male[1] (N=36)	$\ln(BW)=2.44\times\ln(HL)-4.04$	0.34	6.1
Female[1] (N=25)	$\ln(BW)=2.82\times\ln(HL)-5.63$	0.66	6.2
Subadult (N=34)	$\ln(BW)=3.77\times\ln(HL)-9.75$	0.94	6.3

[1] Adult

The condition index for each animal, each time it was trapped, was then calculated as the ratio of observed body weight to expected body weight. Examination of data for the entire population is based on a single record for each individual.

RESULTS

A total of 198 captures were made of 88 individual Musky Rat-kangaroos, some of which escaped before measurements were completed, leaving 194 records from 86 animals. Males made up 63% of individuals (including pouch young), suggesting a male biased sex ratio (Table 6.4). The sex ratio of pouch young alone was more biased (71% males), suggesting that this represents a truly male biased sex ratio rather than an artefact of trapping or behaviour.

Table 6.4 Number of individuals of each gender and age class encountered on my study site.

Age Class	Gender	Number of Individuals
Adult	male	31
	female	20
Subadult	male	23
	female	14
Pouch Young	male	15
	female	6

Reproduction

Musky Rat-kangaroos showed a highly seasonal reproductive pattern. Males became reproductively active during the period when fruit availability was highest each year.

Male Testes Size

Although the data are patchy, they show a consistent seasonal pattern: testes size increased dramatically between September and October each year (from means of 246 mm^2 ± 22.76 SE in September each year to around 1009 mm^2 ± 98 SE in October 1990, 648.78 mm^2 ± 123.5 SE in October 1991 and 1148.9 mm^2 ± 75.7 SE in October 1992) and contracted between March and May each year (Figure 6.2). Consequently there was a five month period (May to September) when males were presumably incapable of breeding and a seven month period (October to April) when they were in breeding condition.

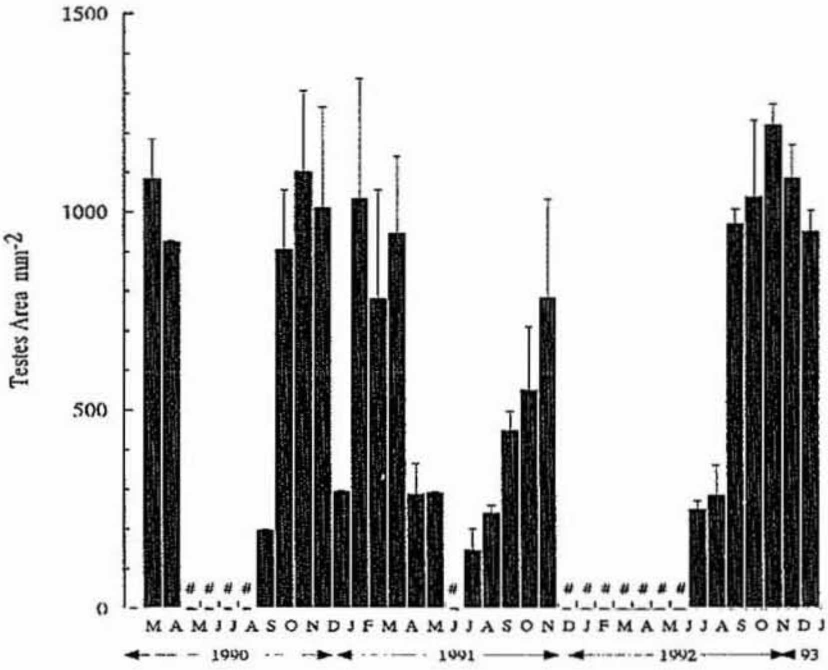

Figure 6.2 Testes area of Musky Rat-kangaroos. means ± SE. # - no data.

The size of testes during the early breeding season (October to December) appeared to be related to the biomass of fruits on the forest floor in each year (see Chapter 4). While the timing of testicular expansion was consistent from year to year, the magnitude of the change was not. I compared mean testes area in the early breeding season, October to December, in 1990 (N=6), 1991 (N=9) and 1992 (N=14) and found that testes were significantly larger in 1992 than 1991, while 1990 was not significantly different to either of the other two years (One-way Analysis of Variance F=7.41, DF=2,26, P=0.0028; Tukey test; Figure 6.3). The difference between 1990 and 1991 is likely to be biologically significant but the sample size was too small for statistical significance. The size of testes during the non-breeding season (May to September) was not statistically different between years (t-test 1991 and 1992: t=-1.04, DF=13, P=0.3191).

A similar pattern was seen with fruit availability (Chapter 4). There was a significant difference between years for the October to December period, with 1992 having much larger crops on the forest floor than either of the previous years and 1990 having more fruit available than 1991. Because of the patchiness of the resource and consequently large variance, the fruit biomass in 1990 did not prove statistically different to the other years (One-way Analysis of Variance F=20.51, DF=2,44, P=0.0001; Tukey Test; Figure 6.3). Figure 6.3 shows the means for testes area and fruit biomass in the October to December period, which display a similar pattern of variation. In addition, condition indices are displayed for comparison and discussed in "Changes in Condition" (this chapter).

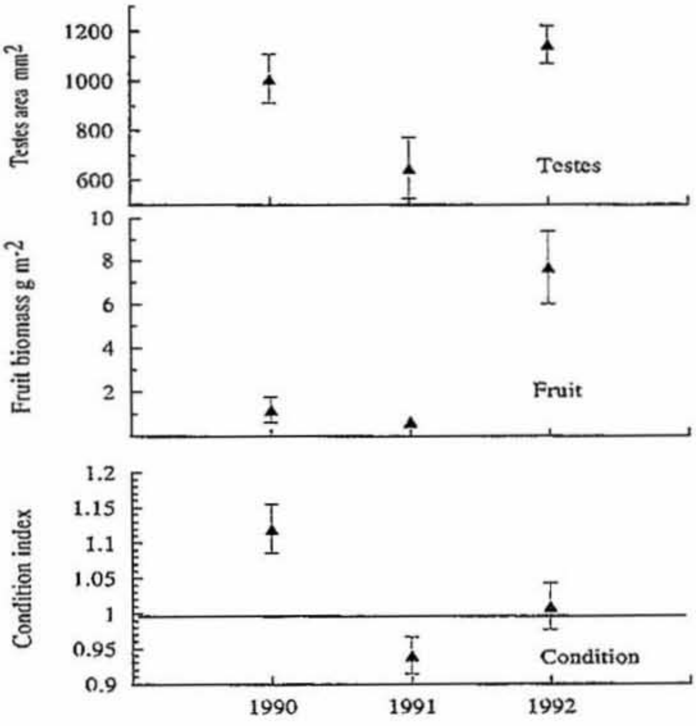

Figure 6.3 Testes size, fruit biomass and condition for Musky Rat-kangaroos in the early breeding season (October to December; means ± SE).

Changes in Male Behaviour

Male Musky Rat-kangaroos in breeding condition (with enlarged testes) were considerably more difficult to handle than non-reproductive males. This was due to an increased frequency of escape attempts and a generally more "nervous" or "aggressive" disposition. In addition, the only time I saw protracted aggressive encounters between males was from September to March each year, when most of the adult population was reproductively active. These encounters involved chases of up to 30 seconds duration and occasionally competition over fruits. Physical contact between combatants was limited to striking out with a forepaw, usually at the rump of a fleeing competitor. Typically, one individual was clearly dominant and easily displaced the other. However, on one occasion each individual alternated between chasing and being chased. In captivity, Musky Rat-kangaroo males are known to be extremely violent toward one another if confined to the same cage in the presence of a female (Johnson, P. pers. comm. 1989).

Female Reproductive Status

The pattern of reproduction in females was consistent with that shown for males. Females carrying pouch young were encountered between the end of February and September each year. Mean head length for those young measured (repeated measures removed) was progressively larger toward September, suggesting that all young were born at a similar time (Figure 6.4; N=13).

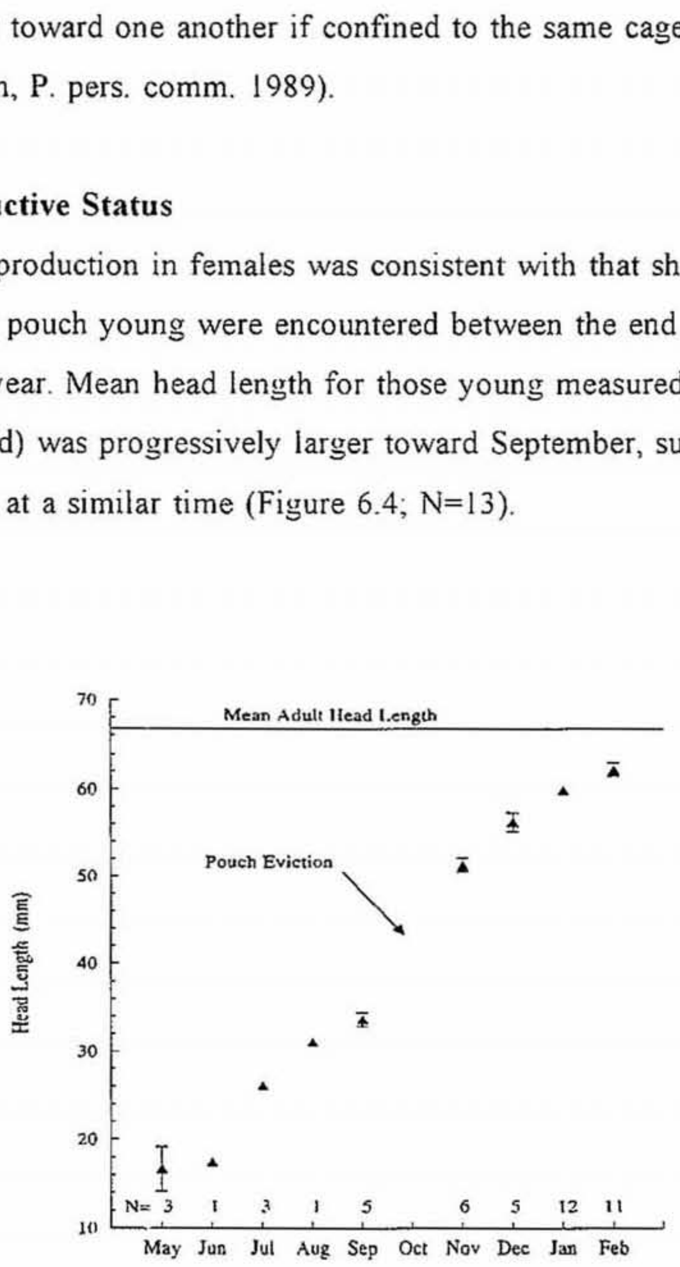

Figure 6.4 Head length (mm) in each month for pouch young and juvenile Musky Rat-kangaroos (repeated measures removed; means ± SE).

Animals that were lactating but not carrying their young, appeared in October in 1990 and 1992 and as early as September in 1991. They were present until December in each year (N=12). During January (N=1, 1993), February and March (N=4, 1991) females that had weaned young were captured (nipples stretched and blackened but no longer producing milk). The earliest month in which a neonate was encountered was the end of February in 1993. No young were encountered until May in 1991 but data for March and April were few (1990 and 1991) or lacking 1992.

As mentioned above, females suckling but not carrying young were first captured in September/October. Juveniles were not caught in the traps until November, when they began to wander independently (N=1 for 1991, N=4 for 1992). In the intervening period they remained at the maternal nest and were periodically visited and fed by the mother (direct observations). As young grew the frequency of independent movements away from the nest increased and therefore larger numbers of juveniles entered traps (N=3 December 1991, N=5 December 1992, N=12 January 1993). At this time juveniles and their mothers re-located each other using vocalisations (a faint hissing squeak) and also spent time foraging together (direct observations).

Several non-reproductive females were caught in 1991. Some of these may have been animals born the previous year which mated for the first time in 1992. However, one was a female (#108) which had produced twins in 1990, did not carry young in 1991 but carried three young in 1992.

Litter Size

Twenty two individual Musky Rat-kangaroos were captured carrying, feeding or having just weaned young during this study. Four individuals carried young in more than one year. Litters consisted of 18 twins, five triplets and three single young. The pattern of variation between years was similar to that seen in male testes size: females in 1991 had the lowest reproductive output (Figure 6.5; Table 6.5; Oneway Analysis of Variance, F=5.48, DF=2,23, P=0.013). The four females that reproduced in two different years were included in the analysis on the basis that litter size was independent in each year regardless of age. However, each of the four females increased their litter size by one in 1992. The ages of the other females were unknown except for two which were subadult in 1991 and produced first litters of twins and triplets in 1992.

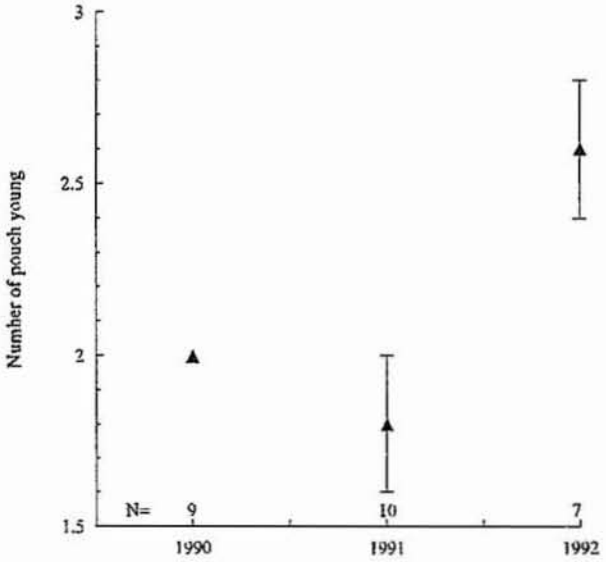

Figure 6.5 Mean (± SE) reproductive output of female Musky Rat-kangaroos. In 1990, all nine females produced twins (Table 6.5).

Table 6.5 Number of female Musky Rat-kangaroos carrying litters of one, two or three in 1990, 1991 and 1992.

	Litter Size		
Year	1	2	3
1990	0	9	0
1991	3	6	1
1992	0	3	4

In 1991, the year of least fruit (see chapter 4), 30% of females had only one young, whereas in the other years none had single young. In addition, female #108, having had twins in 1990, failed to reproduce in 1991. Four females carried triplets in 1992, the year of greatest fruit abundance (see chapter 4), suggesting that the number of young able to be carried through to pouch eviction may relate to the supply of fruit.

Juvenile/subadult Growth

The smallest Musky Rat-kangaroo, a 145 g female, was trapped in November 1992, presumably just after it had begun to wander away from the maternal nest on its own. In September, pouch young had a mean weight of 45.5 g (± 2.1 SE, n=4). They grew rapidly after pouch eviction, particularly in 1992 (Figure 6.6). At the end of 1991, weights were lower and few juveniles were caught (1991 mean ± SE: November 147.5 ± 2.5, N=2; December 170 ± 11.5, N=3; compared to 162.5 ± 14.9 and 279.0 ± 11.6 in November and December 1992).

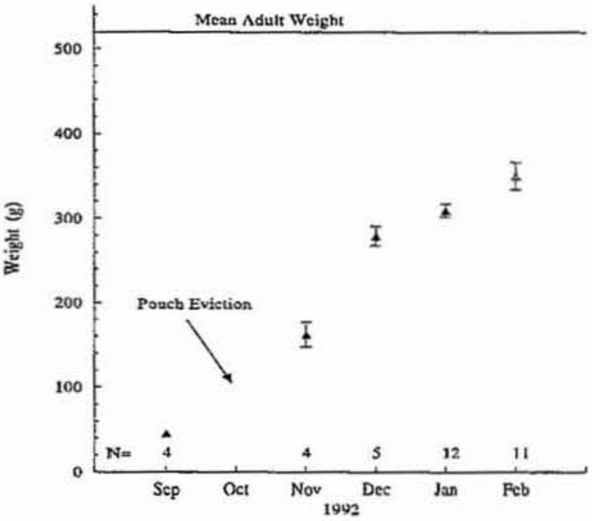

Figure 6.6 Mean weights (± SE) of late pouch young and juvenile Musky Rat-kangaroos in 1992.

In 1991, animals remained distinguishable as subadults by weight (below 400g) until November when fruit availability increased and the next cohort of juveniles appeared. At this time they grew to over 400g and were not identified as subadult (three females reproduced at body weights between 400g and 450g). During 1992, fruit availability increased in July (Figure 4.5), so that by August no subadults were recorded as they had reached a similar weight to adults (range 415g to 650g) earlier than in 1991.

Reproductive Maturity

Six immature animals were followed through to maturity. Female #156 entered the 1991/92 breeding season (October to April) at subadult weight (20+ months old), which places her birth date in early 1990. She was carrying twins in 1992, having mated in the 1991/92 breeding season, over one year after pouch vacation. Four males showed similar patterns to female #156, entering the 1991 breeding season as subadults and maturing during that season. However, male #162, born in 1990, had not reached reproductive maturity in November and December 1991 (testes area 196mm^2) but became mature in October 1992 (testes area >1000 mm^2), two years after pouch vacation.

Longevity

Very little data on longevity were collected as approximately 60% of animals captured were caught once only or for a short period (less than six months). However, some evidence was gathered that is suggestive of lifespan. Female #108 (weight = 575 g, corrected for pouch young) was first caught in 1990 carrying two young. During 1991, she carried no young but had triplets in 1992. By September 1992 (24 months after first being trapped) she was one of the heaviest animals caught (620 g) and her facial hair had become progressively more grey. She was clearly one of the oldest animals I handled. Subadults had uniform pelage colour over the head and shoulders. This began to turn grey after two years.

Four other individuals had young two years in a row and four males were reproductively active for two consecutive years. All of these animals appeared to be among the older members of the population by their second reproductive year. These data suggest that Musky Rat-kangaroos live for at least four years: reproduction usually beginning at 18 to 21 months and continuing for the next two to three years and possibly longer (Table 6.6).

Table 6.6. Significant life history events for Musky Rat-kangaroos. Dates and ages are approximate and are the centre of periods estimated from the status of 88 wild trapped adults and juveniles.

Life History Stage	Date	Age (days)	Age (months)
Birth	31 Mar		
Pouch eviction	1 Oct	180	6
Weaning	1 Jan	270	9
1st Reproduction ♂	31 Oct	576	19
1st Reproduction ♀	1 Jan	635	21
2nd Reproduction			33
3rd Reproduction			45

Changes in Condition

When individual Musky Rat-kangaroos were recaught at different times of year their weight varied considerably. Some adults lost up to 30 - 35% of their peak weight (Mean = 21.1 ± 2.5, N=10) and I found three dead animals on the forest floor between May and August. Changes in condition of individual Musky Rat-kangaroos reflected the changes in fruit availability. For example, males 100 and 106 were in good condition in early 1991 after the fruiting peak but showed a decline in condition after a period of poor fruit availability. Their condition improved again in late 1992, when fruit resources had increased. Similarly, females showed a pattern of condition change that reflected fruit abundance.

Changes in condition in the animals on my study site, considered separately for males and females, showed a similar pattern to that seen in individuals. I have not included the data for subadults because they are patchy and complicated by the growth rates of the juveniles. The condition of male Musky Rat-kangaroos (Figure 6.7) was good during late 1990 and early 1991. As fruit became less abundant (Figure 4.5) condition declined, many animals remaining in poor condition even as fruit availability increased toward the end of 1991. At the end of 1992 condition was more variable with some animals appearing in good condition and others poor. As fruit peaked in December, most animals were in better condition and remained so through January 1993.

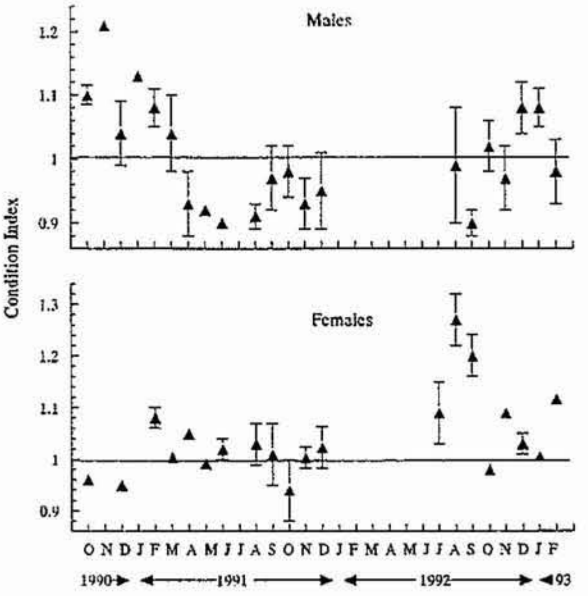

Figure 6.7 Condition indices (means ± SE; Bradshaw and De'ath 1991 modified according to Krebs and Singleton 1993) for male and female Musky Rat-kangaroos. # = missing data.

During the early breeding season (October to December) in 1991, male condition was poor (mean condition ± SE: 0.94 ± 0.026, N=12) while during the 1990 and 1992 seasons condition was better (1.12 ± 0.035, N=6 and 1.01 ± 0.025, N=19 respectively; Figure 6.3). A one Analysis of Variance on condition during October, November and December in each year indicates a significant difference between 1990 and 1991 but 1992 was not significantly different to the other years (based on a single measure for each individual: F=4.75, DF=2,20, P=0.0126; Tukey Test). A similar pattern of variation occurred in testes size and fruit biomass for this period in each year (see section on "Reproduction in Males"; Figure 6.3). Fruits were most abundant in 1992 and testes were largest in 1992 but condition was best in 1990. However, 1991 was the poorest year for all parameters.

To explore the relationships between fruit availability, condition and male reproduction, I performed an Analysis of Variance with testes size as the dependant variable, fruit availability as random factors and condition as a covariate. I used the biomass of fruit from the month before the testes and condition measures on the assumption that the biomass of fruit measured at the same time would not have affected testes size or condition yet. The results of this analysis are presented in Table 6.7 and show a significant interaction between condition and the availability of fruits and seeds during the preceding month. This suggests that some of the factors which may predict reproductive fitness (as measured by testes size) include the condition of animals as they enter the breeding season and how much fruit is available in that year. Condition prior to the breeding season is probably determined by a range of factors including the availability of fruits and seeds in preceding months and years.

Table 6.7 Analysis of variance table examining testes size (dependant variable) in relation to fruit availability in the month preceding the testes measure and condition.

Source of Variation	DF	Mean Square	F	P
Condition[1]	1	0.11	0.49	0.509
Fruit biomass[2]	6	0.0246	1.1	0.455
Condition*fruit biomass	6	0.223	7.7	0.004

1.Covariate

2. Random factor. Error term - Condition*Fruit

For females the situation is less clear due to the presence of pouch young and their eviction during the peak fruiting season. Female condition was consistently poorest through 1991 (Figure 6.7) and showed a trend of improvement while fruits were abundant. I was unable to perform any analysis on data for females as once repeated measures were removed the sample size was too small.

Life Cycle Summary

Young are born from February to April after a seven month period during which males are capable of reproduction (see Figure 6.2). Following this are five months when males are not reproductive. The young are carried in the pouch until October. During the period of pouch life, food resources are at their minimum but the demands placed on the mother by the still small young are also at their minimum. Pouch eviction occurs in October when fruits are abundant. Juveniles are left at a maternal nest after pouch eviction. Through October, November and December young slowly begin to explore and feed themselves until they are weaned in January

(Figure 6.8). The young grow rapidly during the peak fruiting season, increasing from 155g (± 14.5, mean ± SE) in October to 350g (± 15.9, mean ± SE) in February and then maintain their weight or grow more slowly through the ensuing months, weight gain being related to the severity of the fruit shortage. Most subadults become sexually mature during the subsequent breeding season (October to April). However, it appears that some individuals remain immature through this season and mature in their third year. Musky Rat-kangaroos can reproduce in at least two consecutive years, although some individuals may fail to breed in one year but have young again in the following year.

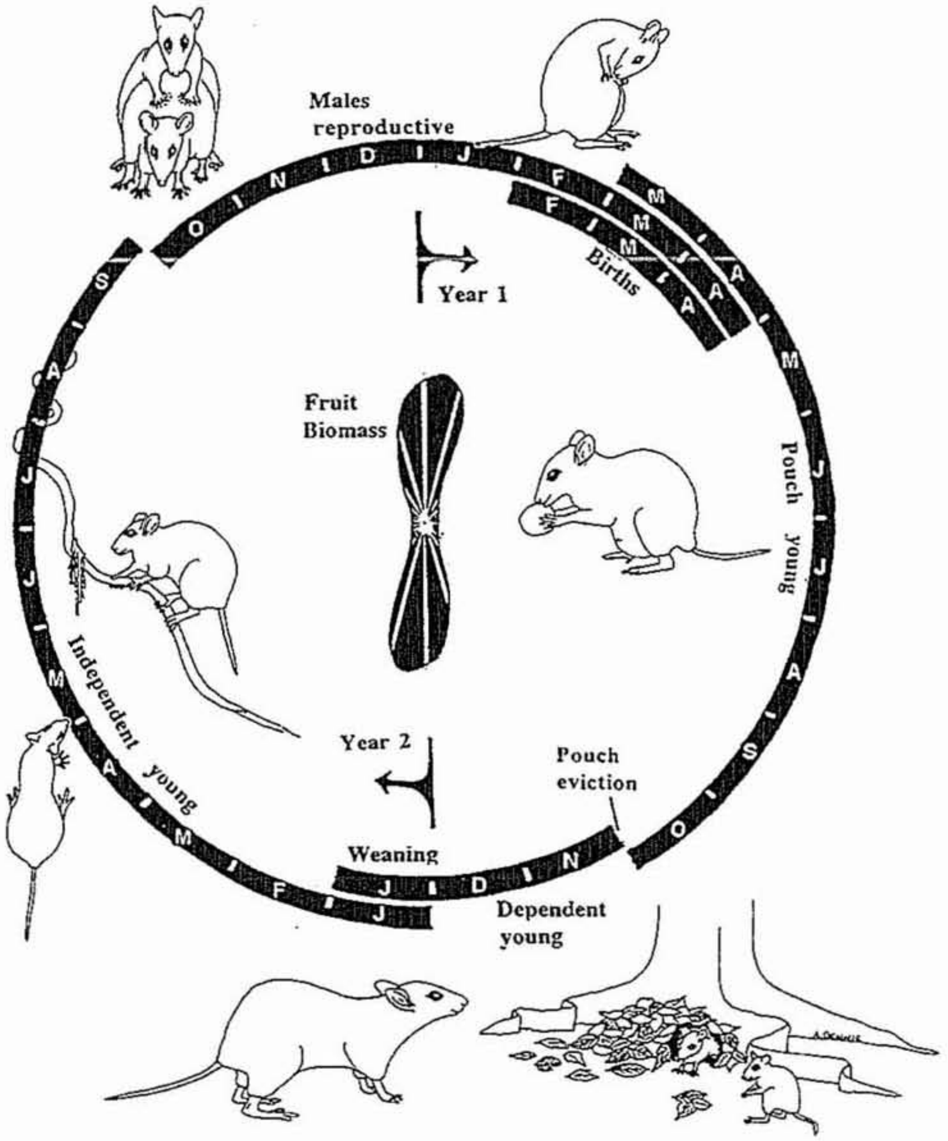

Figure 6.8 Timing of life history events for Musky Rat-kangaroos over a two year period with concurrent changes in fruit availability (centre point = zero fruit). Relative fruit biomass (centre) is derived from data for 1991 (Chapter 4). Although not shown on the figure for ease of reading, adults will reproduce in consecutive years. Illustrations depict different aspects of Musky Rat-kangaroo behaviour. Clockwise from top left: mating pair; cleaning pouch; manipulating fruit; mother returning to young at the nest; dorsal view; climbing a vine.

DISCUSSION

Musky Rat-kangaroos are clearly seasonal breeders, a relative rarity among the Macropodoidea and not known in any other Potoroid (Tyndale-Biscoe 1989). In addition, males display distinctive seasonal enlargement of the testes, and presumably spermatogenesis, which appears to be obligatory. Males in captivity, given food *ad libitum*, continue to undergo seasonal changes in testes size (Johnson, P. pers. comm. 1996). All other macropodoid species that have been studied produce spermatozoa throughout the year. Tammar Wallabies, *Macropus eugenii*, are the only species that shows some seasonality in sperm production (Jones 1989) and is also an obligate seasonal breeder (Tyndale-Biscoe 1989).

The change in testes size in Musky Rat-kangaroos is dramatic and unknown in other macropodoids. This pattern is more reminiscent of other marsupial groups. Some Dasyuridae, such as Northern Dibblers, *Parantechinus bilarni*, which reproduce in more than one year, also display a seasonal enlargement of the testes and an increase in body mass during the breeding season (Lee and Cockburn 1985; Woolley and Begg 1995). Several species of *Antechinus* have a similarly dramatic increase in testes size but this is usually associated with reaching maturity prior to the breeding season (Wilson and Bourne 1984) and the majority of males die after one season.

Female Musky Rat-kangaroos are unique amongst macropodoids in regularly carrying twins or triplets. Despite their reproducing only once per year, this makes them the most fecund macropodoids, rearing up to three young in one year. Most other kangaroos rear one young per year (Bolton *et al.* 1982; Lee and Cockburn 1985). Agile Wallabies, *Macropus agilis*, and Quokkas, *Setonix brachyurus*, are known to approach two young per year, raised in series, at their maximum potential (Lee and Cockburn 1985). Johnson (1997) has recently demonstrated that six other macropodoids (five Potoroids and Bridled Nail-tailed Wallabies, *Onychogalea fraenata*) may be able to produce three young in one year at their maximal rate (based on the length of pouch life being the interval between successive young). However, none of these has been demonstrated to do so and would rarely, if ever, achieve this in the wild, although Woylies, *Bettongia penicillata*, may do so

(Christensen 1980). Therefore, Musky Rat-kangaroos are the first macropodoid to be confirmed to have three young per year in the wild.

Resource Availability

Two of the main food resources of Musky Rat-kangaroos (see Chapter 3), litter fauna (Chapter 5) and fruits (Chapter 4), showed seasonal variation in availability. The greatest variation of food was in the availability of fruits, whereas the variation in the abundance of litter fauna was smaller. A seasonality index (Ford *et al.* 1988), calculated as the ratio of peak to trough measures, was around 3:1 for litter fauna (1991 and 1992) and 300:1 for fruits in 1992. In 1991, the extreme shortage of fruits in April made this ratio even larger (1970:1). The overall abundance in litter fauna was similar between years but differed with topography and/or month depending on the size class of invertebrates examined (Chapter 5; Table 5.1). Despite the variations in physical parameters that correlate with litter faunal abundance and temporal and spatial changes in their distribution pattern, the resource was fairly stable. The availability of fruits and seeds is therefore more likely to have been the selective pressure creating seasonal reproduction in Musky Rat-kangaroos.

Evolution of Reproductive Seasonality

Musky Rat-kangaroos have long been regarded as the most primitive macropodoid in many respects, retaining ancestral features such as the opposable and clawless first digit on the pes (Johnson and Strahan 1982). They commonly produce twins or triplets rather than the single young of other macropodoids. In addition, they are the only Potoroid that is not monovular (Lee and Cockburn 1985) and are presumably monoestrous. These quite profound differences to the usual macropodoid pattern and the pleisiomorphic morphology of Musky Rat-kangaroos raise the question: are these reproductive traits ancestral or are they more recently derived?

The factors of selection for such reproductive traits are clear. The strongly seasonal production of fruits and the unpredictability of peak crop sizes in different years, their correlation with the condition of animals and the changes in reproductive output in relation to condition all suggest strong selective pressure for seasonality and high fecundity.

Testes size, which varied according to fruit availability (Figure 6.3), probably correlates with reproductive potential and certainly reflects, at least in part, the energy invested in reproduction. Similarly, female reproductive output varied between years (Figure 6.5). These changes in reproductive output are evident during the peak fruiting period when condition is generally the best it will get in a given year. The responses are dramatic and given that (even in years of abundant fruit) fruit availability is 300 times greater in the peak than in the trough, the ability of Musky Rat-kangaroos to invest in reproduction outside the fruiting peak must be very small. In addition, young are weaned when fruits are most abundant, allowing them ample resources to grow rapidly. Although unpredictable in the size of crops, the phenology of fruit production in the seasonal tropics seems to follow a reliable pattern (Foster 1977; Hilty 1980; Hopkins and Graham 1989; Marinho-Filho 1991; Moore 1991; White 1994), therefore the evolution of obligate seasonal reproduction is beneficial. Because male Musky Rat-kangaroos undergo seasonal changes in testes size in captivity when food is unlimited (Johnson, P. pers. comm.1990), it is unlikely the pattern seen in this study is an environmental artefact produced by fruit availability during 1990, 1991 and 1992. However, it remains to be seen what the reproductive season for Musky Rat-kangaroos is in the lowlands, where the timing of peak fruit availability is earlier than on the tablelands (Crome 1975a).

Other frugivore/omnivores of the seasonal tropics, for example *Caluromys philander* and *Philander opossum*, two didelphid marsupials from tropical South America, Coatis, *Nasua narica*, and many primates are known to have a breeding pattern very similar to Musky Rat-kangaroos (Lee and Cockburn 1985; Russell 1982; Smythe 1970b; van Schaik and van Noordwijk 1985). All species breed in response to changes in the availability of their primary food resources. Most Megachiropterans are also seasonal breeders, having defined times of testis growth, mating and parturition (O'Brien 1993). Many of these are frugivores or nectarivores and face similar fluctuations in food resources. In addition, Russell (1982) demonstrated that the reproductive output of Coatis varied between years depending on the size of fruit crops in given years.

Although it is not possible to determine whether the reproductive pattern in Musky Rat-kangaroos is pleisiomorphic, it seems likely that it is derived in response to environmental pressures. The same pattern appears in widely varying groups of tropical rain forest animals that feed primarily on fruits. However, if the ancestral habitat showed similar seasonal fluctuations in resources to those seen in tropical rain forests in the present, the pattern of reproduction seen in modern Musky Rat-kangaroos may have evolved early in its history. If that is the case and Musky Rat-kangaroos are representative of the early macropod line then the reproductive patterns seen in other macropods may have been derived from a seasonal pattern.

The number of young carried by females in different years appeared to vary with their condition and the availability of fruits and seeds. This variation raises some interesting questions. Foremost is: by what mechanism is the number manipulated? I witnessed no births and was therefore unable to determine how many young are normally born. However, during 1991 females gave birth while they were still in reasonable condition, similar to that seen in late 1991 just prior to the next birth period (Figure 6.10). Assuming that the number of young born was constant, there are several mechanisms known by which different species manipulate the number of young they carry. Abortion of pouch young is well known in macropods (e.g. Bolton *et al.* 1982). However, unlike other macropodoids, Musky Rat-kangaroos may alter their number of young without complete loss of the litter. Perhaps most likely, is selective abortion by infanticide if the mother's condition deteriorates during early pouch life of the young. Infanticide is well known in *Antechinus* (Dasyuridae) and Cockburn (1994) hypothesised this to be driven by the condition of the mother and her need to select the sex ratio and number of young she was able to rear. Whatever the mechanism of manipulating litter size in Musky Rat-kangaroos, there seems to be a clear response of reproductive success to resource availability.

In summary, Musky Rat-kangaroos have a seasonal reproductive pattern in the wild. The most outstanding feature of this pattern is the dramatic changes of testes size in males, a pattern that does not occur in any species in the same super-family. Another outstanding feature is that females can carry up to three pouch young simultaneously, which is unique to Musky Rat-kangaroos and gives them the highest fecundity of any Macropodoid. These unusual reproductive traits seem to be related to the highly seasonal pattern of fruit production in Australia's tropical rain forests and the enormous variation in peak fruit availability that can occur between years.

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Plate 7 Female Musky Rat-kangaroo with young near nest.