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

Chapter 11

MUSKY RAT-KANGAROOS: CURSORIAL FRUGIVORES

How do Musky Rat-kangaroos Relate to their Environment ?

Musky Rat-kangaroos can be classified as frugivores because fruits and seeds accounted for the bulk of their diet throughout the year (Chapter 3). In addition, they scatterhoarded many fruits and seeds, to the benefit of at least some species of plants (Chapters 8 & 9). They consumed most of the available fruits which had a fleshy pericarp or aril but also included the seeds of some species that did not. They ate fruits from over half the species producing fruits on my study site, many of those they did not eat were wind dispersed, housed in hard, indehiscent pods or had furry, dehiscent pods. In addition, some fleshy drupes were not consumed. Like many other frugivores, Musky Rat-kangaroos supplemented their diet from other sources, particularly when the seasonal availability of fruits is at its minimum (see Terborgh 1983). During the late wet, cold and early dry seasons, when fruit abundance was minimal, their search effort was random with respect to fruit falls (Figure 3.8; Table 3.2). Larger quantities of fungus (late wet season; Figure 3.10), and then invertebrates (cold season; Figure 3.9) appeared in their diet at this time. During the peak in fruit abundance, their search effort focused on fruit. Although invertebrates and fungus still occurred in their diet they appeared less sought after than during the period of minimum fruit abundance, a pattern similar to many other frugivores (e.g. Smythe 1978; Terborgh 1983; Terborgh 1986).

The availability of fruits displayed seasonal changes of extremely high amplitude (Chapter 4), while invertebrate abundance did not (Chapter 5). Seasonal reproduction in Musky Rat-kangaroos reflected the changes in fruit abundance (Chapter 6): a common pattern for frugivores of tropical rain forests which is rare amongst macropodoids (Smythe 1970b; Russell 1982; Lee and Cockburn 1985; van Schaik and van Noordwijk 1985; O'Brien 1993; Tyndale-Biscoe 1989). Several features of Musky Rat-kangaroo reproduction are exceptional amongst macropodoids and are probably a result of their unique niche as the only frugivorous macropodoid. The most significant features were: seasonal changes in testes size for males (Figure 6.2); and multiple young per litter for females (Table 6.4). The close links between reproductive timing and the abundance of fruits were also reflected in reproductive output varying between years when the biomass of fruits differed from one to the next. The condition of Musky Rat-kangaroos was lowest when fruit biomass was lowest and also tracked the inter-year difference in peak fruit biomass. This was reflected by male testes size and litter size being smaller when condition, and the biomass of fruits during the peak, were lowest (Figures 6.3 & 6.5).

Musky Rat-kangaroos were common on my study site, occurring at an average density of 2.4/ha (Chapter 7). Changes in their population density reflected their reproductive pattern with an approximately twofold increase in density when juveniles were becoming independent of their mothers. In addition, population density was slightly higher in 1992 (when the availability of fruits was greater) than in the other years of my study (Figure 7.5). This jump in population density was followed by a rapid decline, probably due to their numerous predators taking advantage of inexperienced Musky Rat-kangaroos entering the population (Chapter 10). Like some other cursorial frugivores (e.g. Agoutis and Acouchies, Dubost 1988), Musky Rat-kangaroos had a small home range (mean male range 2.1ha; mean female range - 1.4ha; Chapter 7). However, unlike the former species which defended family territories (Smythe 1978; Dubost 1988), Musky Rat-kangaroos were solitary and promiscuous with extensively overlapping home ranges. Like Acouchies, they covered most of their range in each day's foraging (Dubost 1988).

Are Musky Rat-kangaroos Effective Dispersers ?

Schupp (1993) reviewed literature on the effectiveness of dispersers and outlines a hierarchical set of components for assessing disperser effectiveness (see Chapter 1: "Effectiveness"). While I did not obtain specific data on several of the components he listed, I use Schupp's (1993) outline here to assess the effectiveness of Musky

Rat-kangaroos as dispersers. As I discussed in Chapter 1 ("Animals that disperse" section), the effectiveness of a disperser probably varies for different species of plant in space and time. Therefore, I will examine Musky Rat-kangaroo effectiveness for Fontain's Blushwood, whose fruits they fed on and cached and for which I have direct and indirect data on caching rates and seed survival (Chapters 8 & 9).

Summary of Feeding on Fontain's Blushwood

Musky Rat-kangaroos were a significant member of the frugivore coterie visiting Fontain's Blushwood. They accounted for 18% of the teeth marks found in their fruits on my fruit transects (N total = 222). While rats (excluding White-tailed Rats) accounted for more (41%), they consumed 81% of their seeds immediately, whereas Musky Rat-kangaroos consumed only 46% of seeds (Figure 10.5). White-tailed Rats (14%), Parrots (1%) and untouched fruits (26%) accounted for the remainder of the Fontain's Blushwood fruits. White-tailed Rats consumed all the seeds they handled and parrots one third (Figure 10.5). Of the seeds remaining viable after predation, Musky Rat-kangaroos were responsible for 21%, rats 17%, parrots 2% and untouched fruits 59% at the time of sampling. The majority of fruits remaining at the parent plants were probably consumed by rats or died of fungal attack (see Chapter 9). Assuming a similar caching rate to simulated fruits (see Chapter 8), an additional 9% (20 fruits) had probably been dispersed or cached by Musky Rat-kangaroos and were not found on the transects (see Equation 8.2). I estimate (using Equation 9.3a) that 15 seeds survived for at least three months or until germination due to handling by Musky Rat-kangaroos.

Case Study: Effectiveness of Musky Rat-kangaroo dispersal of Fontain's Blushwood

According to Schupp's (1993) hierarchical outline of disperser effectiveness, Musky Rat-kangaroos are effective dispersers of Fontain's Blushwood (Table 11.1) and due to their catholic tastes in fruit, are probably effective dispersers for many other species.

Table 11.1 Aspects of disperser effectiveness (based on Schupp 1993) and the corresponding data for Musky Rat-kangaroos in relation to Fontain's Blushwood. Data are from my seed survival experiment (Chapter 9), dispersal of imitation fruits (Chapter 8), population estimates (Chapter 7) and diet (Chapter 3) (see text for details).

Aspects of Disperser Effectiveness			Musky Rat-kangaroos
Quantity	# of visits	Abundance of disperser:	2.4/ha.
		Diet:	Primarily frugivorous.
		Reliability of visitation:	Reliable throughout fruiting period.
	# of seeds/visit	# of seeds handled/visit:	? (few).
		Probability of dispersing a handled seed:	34%.
Quality	Treatment	# seeds left intact:	54%.
		Germination rate:	improved ?
	Deposition	Habitat:	Rainforest only.
		Microsite:	Random, 21% in canopy gaps.
		Rate of deposition:	Rapid, seeds not swallowed.
		Direction of deposition:	Random, 30% >5m from parent plant.
		Seed mixing:	None, placed singly.

Musky Rat-kangaroos were certainly abundant on my study site and in some areas a fruiting tree could be visited by at least five individuals simultaeneously (see Chapter 7). They were primarily frugivorous (Chapter 3) and displayed reliable visitation to Fontain's Blushwood. My raw data from fruit transects showed that Musky Rat-kangaroos visited Fontain's Blushwood trees throughout their fruiting season in January and February, 1991. Dispersal experiments with simulated fruits (Chapter 8) showed that Musky Rat-kangaroos handled 56% of available fruits and the probablity of dispersing or caching a handled fruit was 34% (calculated from number cached and number moved >5m in Figure 8.1). I was unable to determine the number of fruits handled per visit although hide observations and spool and line tracking showed that they commonly fed from 1 - 7 fruits or pieces of bait before moving on and carrying an item with them.

Fifty-four percent of the Fontain's Blushwood seeds handled by Musky Rat-kangaroos were left intact, and caching by Musky Rat-kangaroos may have increased the germination rate of seeds (only seeds buried in rain forest soil had germinated after three months; Figure 9.4; Chapter 9 "Control seeds"). It is also possible that consumption of flesh from seeds may remove germination inhibitors or decrease the chances of mould infection (Howe and Smallwood 1982), although this was not tested here. Musky Rat-kangaroos cached or otherwise dispersed 34% of the imitation fruits they handled (see above), 30% of those handled being carried >5m from the parent plant. These seeds were placed singly and at random with respect to vegetation density and surrounding objects, resulting in 21% of those handled immediately ending up in canopy gaps (Chapter 8). No seed mixing occured with fruits dispersed by Musky Rat-kangaroos as they were dispersed singly.

Musky Rat-kangaroos are clearly effective dispersers in this case and are probably the most effective disperser of Fontain's Blushwood. To my knowledge this is the first case where a frugivore's effectiveness has been examined for all the criteria listed by Schupp (1993). Therefore, direct comparisons with other frugivore/plant interactions are not possible. However, many other studies demonstrate that one or a few species among a large frugivore coterie are more effective dispersal agents of a tree species than other frugivores in the coterie, based on a few of these criteria (e.g. Howe 1975; Becker and Wong 1985; Howe 1985; Murray 1988).

Musky Rat-kangaroos were more effective dispersers for the seeds of Fontain's Blushwood than Acouchies and Agoutis are for the seeds of *Vouacapoua americana* (Caesalpinaceae) in the Neotropics. Acouchies and Agoutis in combination are primarily predators, destroying 78% of the seeds they handle (cf Musky Rat-kangaroo's 46%). In addition, they only handle between 2.5 and 10.5% of seeds falling from parent plants during the fruiting period (Forget 1990; cf Musky Rat-kangaroo's 18%). The proportion of fruits moved >5m by Agoutis and Acouchies is 14% while for Musky Rat-kangaroos it was 30%. Acouchies and Agoutis have long been recognised as important (and effective) dispersal agents (Smythe 1989). The data I presented for Musky Rat-kangaroos suggest that they were more effective dispersers than Agoutis and Acouchies.

Advantages of Dispersal by Musky Rat-kangaroos

Escape in Time

The most significant advantage of dispersal by Musky Rat-kangaroos for the two species examined in Chapter 9 (Baileyoxylon and Fontain's Blushwood), was seed burial. Caching removed seeds from the 100% predation by mammals (mostly rats) experienced by seeds left on the surface of the litter. Burial allowed many seeds to escape predation for long enough to be able to germinate and use up endosperm reserves so they were no longer attractive to seed predators. This suggests that agents dispersing seeds, but not burying them, would be of little value to these tree species. This raises an interesting question about the presumed effectiveness of volant frugivores which disperse the seeds of various rainforest plants. In Chapter 1, I outlined a series of advantages which may be gained by plants whose seeds are dispersed. The least significant, in terms of its exploration in the literature examined, appears to be the most significant advantage in this case: burial to escape density and distance independent mortality (see "Escape in Time" Chapter 1).

Further studies on the advantages of seed burial by scatterhoarding animals for a range of plant species in different countries will help to identify how common this advantage is to rainforest plants. Many of the frugivore coterie/plant relationships examined in the literature fail to take into account the attractiveness of seeds to mammalian and insect seed predators which may effect their survival after dispersal (e.g. Howe 1975; Howe 1985; Murray 1988). While Becker and Wong (1985), in their study of *Aglaia* sp. in Malaysia, found that rodent seed predators attacked seeds below the parent crown at a greater rate than those further away, my study demonstrated that the seeds of some species may be attacked at the same rate at any distance from their parent. Thus, if the seeds of the plant *Casearia corymbosa* in Howe's (1975) study in Costa Rica were palatable to terrestrial seed predators, the two species of Toucan identified as their most effective dispersers may be far less effective than previously thought. Forget (1990) also found that seed burial conferred advantages to *Vouacapoua americana* seeds by removing them from insect and mammal attack, suggesting that seed burial confers advantages that warrent further study.

Escape in Space

For Fontain's Blushwood, removal from density- or distance-dependent mortality (100%), brought about primarily by Fawn-footed Melomys and fungus, was also an important advantage to being dispersed by Musky Rat-kangaroos. Tables 1.2 and 1.3 (Chapter 1) show studies from many tropical countries in which escape from density-dependent mortality was important or of no consequence respectively. Similarly, in my study, the two tree species examined showed different responses. The buried seeds of Baileyoxylon did not have 100% mortality under the parent (cf the buried seeds of Fontain's Blushwood), so would probably not gain great advantage from escaping density-dependent mortality under the parent tree. However, seeds dispersed by Musky Rat-kangaroos are removed from the possibilities of allelopathy and root and nutrient competition from conspecific seedlings and the parent as they are dispersed singly through the forest and not in clumps.

These results reiterate the conclusion I drew from reviewing the literature (see Chapter 1): for some species of plant seeds under parents experience such high levels of predation or other mortality that dispersal away from the parent is essential if any are to survive; for other species mortality under the parent is low enough that some seeds survive and are able to germinate without leaving the parental seed shadow. Larger numbers of seeds usually accumulate below a parent tree than away from it. Therefore, unless mortality is near or reaches 100% under the parent (as in the case of Fontain's Blushwood) equal or greater numbers of seeds may survive below the parent as survive away even when the proportions killed are higher below the parent. For Baileyoxylon, seed survival was higher away from the parent but a significant number also survived under it (see Figure 9.3). In natural circumstances this would probably lead to a larger number of seeds surviving under the parent than away from it, depending on what proportion of the crop is dispersed.

Finding Suitable Sites

Light Environments

Another advantage is that 21% of fruits handled by Musky Rat-kangaroos ended up in canopy gaps (Chapter 8). Seedling growth and survival in canopy gaps is generally better than in the understorey (Augspurger 1983b; Augspurger 1984; Dirzo and Dominguez 1986; Howe and Schupp 1985; Osunkoya *et al.* 1993; Osunkoya 1994; Sork 1987). However, Fontain's Blushwood is an understorey tree and therefore probably gains relatively fewer advantages from being dispersed into a canopy gap than Baileyoxylon. In addition, many large seeded rain forest trees are able to establish in the understorey and wait for a canopy gap to form overhead (Connell, J. pers. com. 1995), suggesting that direct dispersal into a gap may be only a small additional benefit for these species. In addition, Osunkoya (1993) found that seedlings in gaps were subject to higher rates of herbivory than those in the understorey, a pattern which offsets the advantages of more vigorous growth. However, net seedling growth was still better in gaps than in the understorey.

The advantages of dispersal to gaps for some plants is clearly greater than for Fontain's Blushwood or Baileyoxlon. Some species are unable to germinate unless they are in canopy gaps (Brokaw 1982b; Denslow 1980; Foster and Jansen 1985; Murray 1988). Murray (1988) demonstrated that three species of gap-dependent plants at Monte Verde, Costa Rica, benefitted by a 16 - 36 fold increase in reproductive output from dispersal by three volant frugivores, although he did not calculate directly the proportion of seeds that end up in gaps. Some of the plants whose seeds Musky Rat-kangaroos disperse may be more gap-depedent than the two examined in my study. The results of Murray's (1988) study suggest that the 21% of seeds dispersed to gaps by Musky Rat-kangaroos could be a significant advantage to some species.

Colonisation

Musky Rat-kangaroos are unlikely to be important dispersal agents for the colonisation of new areas or unused pastures because they do not disperse seeds over long distances (up to 68m; Chapter 8) nor do they traverse open areas. However, rain forest that is re-establishing and abutting mature forest may benefit over the long term from the short-distance dispersal of large seeded species not well dispersed by other frugovore groups (see "Ecological implications in todays landscape" below).

Genetic Advantages

Short distance dispersal by Musky Rat-kangaroos is probably insignificant to maintenance of gene-flow between populations of a tree species. However, it may aid in maintaining gene flow at the intrapopulation level. Hamrick and Loveless (1986) showed that animal dispersal of seeds in general was less effective than predicted for the maintenance of gene flow between populations of a tree species. Pollen dispersal may be the more significant factor maintaining interpopulation gene flow (Hamrick and Loveless 1986; Hamrick *et al.* 1993). Wind dispersed trees appeared to have greater genetic structure in their populations than trees dispersed by other methods (Hamrick and Loveless 1986). Many trees in rain forest with wind dispersed seeds are tall emergents which, when in flower, are clearly visible accross the canopy. This may lead to better pollen mixing by strong flying pollinators flying from one individual to the next than is experienced by canopy and subcanopy trees whose seeds are dispersed by animals. Thus, pollination patterns may have been responsible for the genetic pattern found by Hamrick and Loveless (1986) and Hamrick *et al.* (1993) rather than seed dispersal methods.

Overall, Musky Rat-kangaroos are effective dispersers that clearly convey several different levels of benefit to rain forest trees. These include: 1) escape from predation by burial; 2) escape from density- or distance-dependent mortality at the parent tree by dispersal and/or burial; and 3) an increased probability of finding a suitable germination site. Several other advantages to dispersal discussed in Chapter 1 were clearly not relevent to dispersal by Musky Rat-kangaroos.

Ecological Implications in Today's Landscape

The landscape in the Wet Tropics of Australia, as with many regions of the world, consists of fragmented patches of natural vegetation and remaining stretches of continuous forest. Many fragments and some of the remaining continuous forest have been disturbed to varying degrees by humans (Winter *et al.* 1987a). The species composition of animals in fragmented landscapes is drastically different from that in continuous forest, both in species present and in species abundances (Laurance 1994; Laurance and Laurance 1995). Musky Rat-kangaroos only use large fragments or fragments that are nearly contiguous with continuous forest (see Chapter 7) and continuos forest. In contrast, many rats (including White-tailed Rats) are more abundant in fragments of most sizes and distances from continuous forest (Laurance 1994; Laurance and Laurance 1995). One of the reasons for this is that rats are better suited to using the matrix of vegetation types between fragments than are Musky Rat-kangaroos. This means that in fragments, plants whose seeds are palatable to rats are probably subject to much higher rates of predation than in continuous forest.

Without Musky Rat-kangaroos caching some of these seeds, and therefore removing them from rat predation (see Chapter 9), fewer seeds would be able to survive to germination in fragmented forests. Harrington *et al.* (1997) found 100% predation by White-tailed Rats for certain taxa in fragmented forests. While they also found 100% predation by rats in continuous forest, they used seeds that had been stripped of their flesh as experimental units. Had they used complete fruits they would probably have found that a portion of their samples in continuous forest were cached by Musky Rat-kangaroos and therefore removed from predation by rats. In addition, Cassowaries tend to use only large fragments or those close to continuous forest (Crome and Moore 1990). However, many volant frugivorous birds use the mosaic of fragmented forest patches and probably bias the dispersal of plants toward small seeded species. Together, these data suggest that forest fragments are operating under radically different seed-dispersal and seed-predation patterns compared to continuous forest. The expected outcome would be a decline in large seeded, rat-palatable species which are dispersed by Musky Rat-kangaroos and Cassowaries, and an increase in relative abundance of small fruited, bird-dispersed plants. Harrington *et al.* (1997) examined one aspect of this question and found no discernable difference in the population structure and abundance of large seeded plants between fragments and continuous forest. Either the effects of dispersal and escape from predation for these species are not a major factor contributing to population structure and abundance or the time frame under examination (~40 years) is too short to find significant changes in community structure.

The loss of terrestrial frugivores from fragmented forests may be a significant problem in most tropical countries. Estrada *et al.* (1993) found that non-flying mammals were the most affected by forest fragmentation at Los Tuxtlas, Mexico. Many plants with large seeds seem to rely on the terrestrial component of frugivore assemblages to disperse their seeds (Stocker and Irvine 1983; Smythe 1989; Forget 1990; Harrington *et al.* 1997; this study), particularly when frugivorous primates are absent from the system. As described above, the absence of cursorial frugivores which scatterhoard seeds may also have implications for species who need to avoid heavy, post-dispersal seed predation.

Perhaps most importantly, it is terrestrial frugivores and seed predators which create the ultimate size and shape of a plant's seed shadow after dispersal by volant and arboreal frugivores. Changes in the community composition of terrestrial frugivores and seed predators may drastically change the survival rates and dispersal distances of seeds for different species. Whether or not this will drastically affect the community composition of the plants in fragments will depend on how stable, over the long term, the effects of terrestrial frugivores and predators have been on the ultimate size and shape of their seed shadows. If plants have been subjected to similar pressures from terrestrial frugivores for long enough, seedlings of plants with heavy seed predation may have become well protected from herbivore attack to compensate for high seed losses, and thus be able to recruit from only small numbers of seeds surviving to seedling stage. Those whose seeds are not heavily predated may be less well protected from herbivore attack but still able to recruit from a larger pool of seedlings than the former species.

Lack of cursorial frugivores and other terrestrial frugivores which disperse large seeds may result in the inability of large seeded plants to recolonise fragments when adults die. Given the spatial heterogeneity of tree species in most forests (see Connell 1978), the frequency of tree deaths due to windthrows and storms (see Brokaw 1982) and the many chance events which lead to the survival of a seedling to maturity (see Chapter 1), plants whose dispersal agents are unable to carry seeds in from other areas will be less likely to be able to replace themselves in a fragment than plants whose seeds and seedlings are constantly replenished from outside sources. Thus, species relying primarily on terrestrial frugivores would decrease in relative recruitment rates and when an adult dies, recolonisation from neighbouring areas may not be possible. Therefore, to maintain tree species diversity in fragments in the long term, establishing connectivity for terrestrial (and arboreal) frugivores will be necessary in most tropical regions (see "Management Implications Arising from this Study" below).

The Australian Frugivore Community in Tropical Rain Forest

The Australian frugivore community appears depauperate when compared to communities in other tropical rain forest countries (see "Communities and Coteries" Chapter 1). This is probably due to the general low diversity of mammals in Australian rain forests (Jones and Crome 1990). The low diversity may be due to the severe contraction of rain forest as Australia's climate dried during the continental plate's northward drift (White 1986) and to more recent contractions into a series of small refugia, from which rain forest has expanded only in the last 10,000 years (Webb and Tracey 1981). Despite this low diversity, only one of the major functional subdivisions outlined in Chapter 1 (Figure 1.2; Table 1.4) remains unrepresented in Australian rain forest (Diurnal, arboreal frugivores; Figure 11.2 pg. 221; Table 11.2 pgs 222 - 223).

Jones and Crome (1990) list the number of species and families of plants whose fruits are consumed by "major rain forest frugivores" in Australia's Wet Tropics. Musky Rat-kangaroos do not appear on their list because, at the time of writing, it was not generally known that Musky Rat-kangaroos were significant frugivores. I reproduce their table here (Table 11.2; Figure 11.1) and include my Musky Rat-kangaroo data and data for Cassowaries from an extensive study at Mission Beach (Bentrupperbaumer, J. pers. comm. May 1997) for comparison with the other "major frugivores".

Table 11.2 Number of species and families of plants whose fruits are consumed by some of the major rain forest frugivores. Based on Jones and Crome 1990 with additions from Bentrupperbaumer, J. per. comm. May 1997; and this study.

Common Name	Latin Name	# Species	# Families
Brown Cuckoo-dove	*Macropygia amboinensis*	32	23
Rose-crowned Fruit Dove	*Ptilinopus regina*	16	11
Superb Fruit Dove	*Ptilinopus superbus*	54	27
Topknot Pigeon	*Lopholaimus antarcticus*	20	10
Torresian Imperial Pigeon	*Ducula spilorrhoa*	37	20
White-headed Pigeon	*Columba leucomela*	14	9
Wompoo Fruit Dove	*Ptilinopus magnificus*	61	30
Southern Cassowary	*Casuarius casuarius*	115	46
		107[1]	37+
Musky Rat-kangaroo	*Hypsiprymnodon moschatus*	49[2]	24

1. Mission Beach only (from an area of ~320ha). Bentrupperbaumer pers. com.

2. This Study

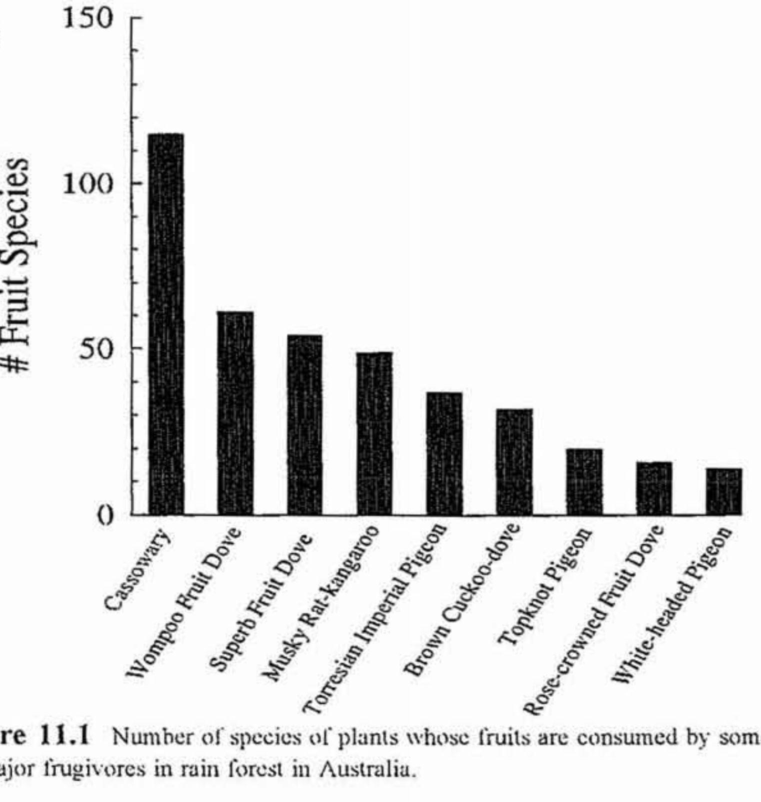

Figure 11.1 Number of species of plants whose fruits are consumed by some of the major frugivores in rain forest in Australia.

At the current level of knowledge, Musky Rat-kangaroos consume fruits from the fourth largest number of species. However, none of the numbers in this list can be considered exhaustive as studies or observations have been limited spatially and/or temporally. My Musky Rat-kangaroo data is particularly spatially limited as the data are derived from a 9ha study site with only a few additional observations from elsewhere (see Appendix 1). Examination of the diet of Musky Rat-kangaroos in other areas and over larger areas is likely to find that they consume considerably more species. They may even consume as many species as Cassowaries do, which would highlight even further the previously unrecognised importance of Musky Rat-kangaroos as members of Australia's frugivore community.

In Chapter 1, I outlined a functional classification for frugivores in tropical rain forests. Here, I give details of Australia's frugivore community and list the species falling into each category described in Chapter 1 (Table 1.4). The number of species listed as corresponding to each category differ between Table 1.4 and Figure 11.2 and Table 11.2. This is because Table 1.4 combines Australia and New Guinea into the Australasian region, where insufficient work has been done to list the community in as much detail as in tropical rain forest in Australia only. Two other studies of frugivores have been conducted in the general area of my study. One focussed on 13 species of tree with large seeds (>2cm; Harrington *et al.* 1997), the other on White-tailed Rats (Goldberg 1994). Only a few other studies have been conducted around the Wet Tropics of Australia. These have focussed on a particular tree species (Lott 1995), ecological processes (Hopkins *et al.* 1990; Hopkins and Graham 1987; Hopkins and Graham 1989; Osunkoya *et al.* 1993; Osunkoya 1994; Willson 1988), particular frugivores (Crome 1975a; Crome and Moore 1990; Richards 1990; Moore 1991; Bentrupperbaumer, J. in progress] and also include a review (Jones and Crome 1990). Therefore, the following outline of Australia's frugivore community in tropical rain forest will be for the wet tropical region and two small blocks of rain forest to the north: the Macilwraith and Iron Ranges. The total combined area of these three rain forests covers 9,800 km^2 (Winter *et al.* 1987a).

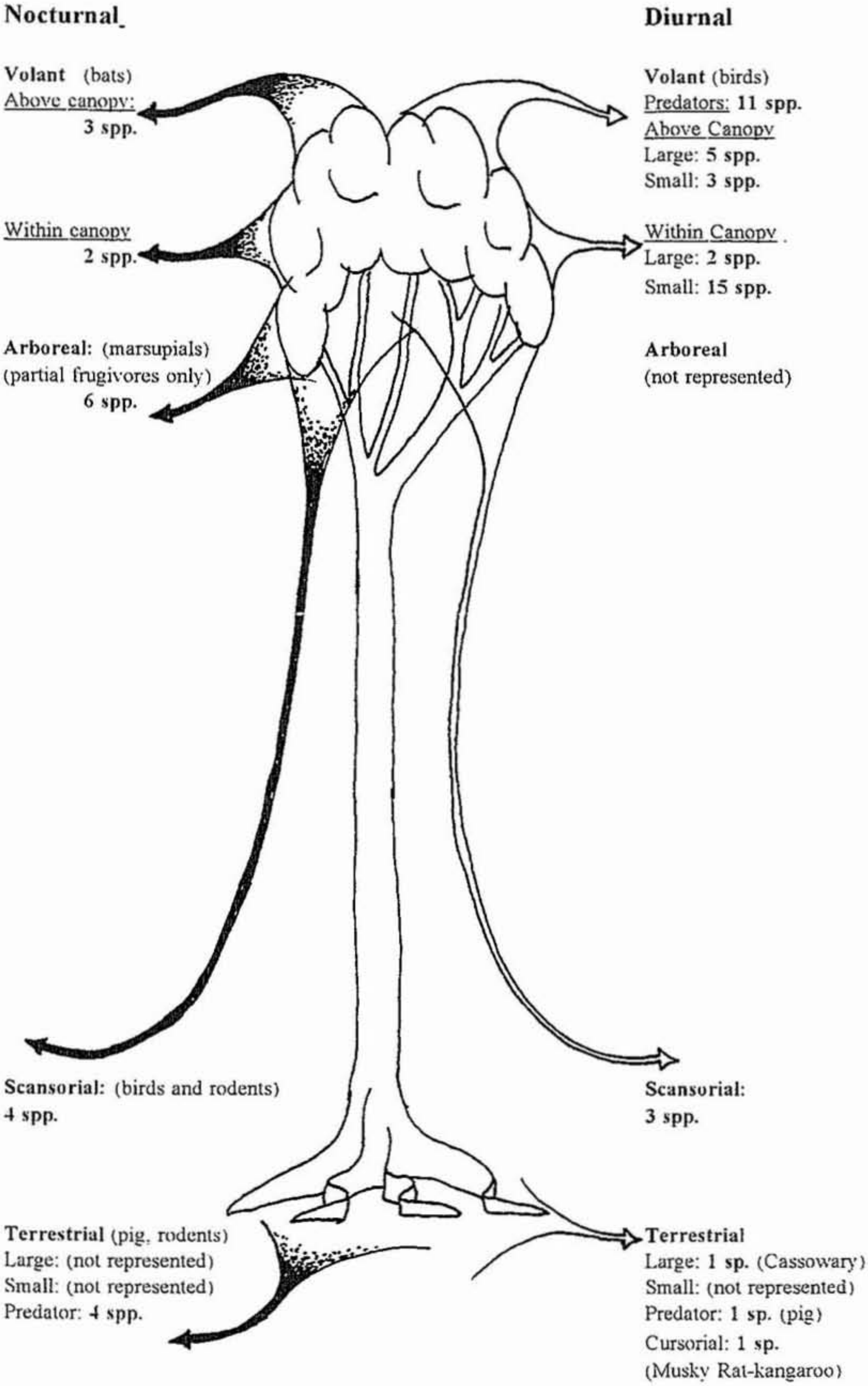

Figure 11.2 Number of species occupying different functional roles in tropical rain forest in Australia.

Table 11.3 Species occupying different functional roles in tropical rain forest in Australia. Categories outlined in Table 1.4: "Predators" may still be important dispersal agents for some species.

Category	Common Name	Latin Name
Volant		
Diurnal		
Predators:	Brown Cuckoo-dove	*Macropygia amboinensis*
	Emerald Dove	*Chalcophaps indica*
	Sulphur-crested Cockatoo	*Cacatua galerita*
	Palm Cockatoo	*Probosciger atterrimus*
	Rainbow Lorikeet	*Trichoglossus haematodus*
	Little Lorikeet	*Glossopsitta pusilla*
	Double-eyed Fig-parrot	*Psittaculirostris diophthama*
	King Parrot	*Alisterus scapularis*
	Red-cheeked Parrot	*Geoffroyus geoffroyi*
	Eclectus Parrot	*Eclectus roratus*
	Blue-cheeked Rosella	*Platycercus elegans*
Above canopy		
Large:	Pied Currawong	*Strepera graculina*
	Torresian Imperial Pigeon	*Ducula spilorrhoa*
	Topknot Pigeon	*Lopholaimus antarcticus*
	White-headed Pigeon	*Columba leucomela*
	Channel-billed Cuckoo	*Scythrops novaehollandiae*
Small:	Yellow-eyed Cuckoo-shrike	*Coracina lineata*
	Figbird	*Sphecotheres viridis*
	Metallic Starling	*Apionus metallica*
Within canopy		
Large:	Wompoo Fruit-dove	*Ptilinopus magnificus*
	Common Koel	*Eudynamis scolopacea*
Small:	Superb Fruit-dove	*Ptilinopus superbus*
	Rose-crowned Fruit-dove	*Ptilinopus regina*
	Varied Triller	*Lalage leucomela*
	Yellow Oriole	*Oriolus flavocinctus*
	Olive-backed Oriole	*Oriolus sagittatus*
	Golden Bower-bird	*Prionodura newtoniana*
	Victoria's Riflebird	*Ptiloris victoriae*
	Mistletoebird	*Dicaeum hirundinaceum*
	Silvereye	*Zosterops lateralis*
	Bridled Honeyeater	*Lichenostomus frenatus*
	Graceful Honeyeater	*Meliphaga gracilis*
	Yellow-spotted Honeyeater	*Meliphaga notata*
	Lewin's Honeyeater	*Melipaga lewenii*
	Macleay's Honeyeater	*Xanthotis macleayana*
	Helmeted Friarbird	*Philemon buceroides*

Table 11.3 (cont.)

Category	Common Name	Latin Name
Volant		
Nocturnal		
Above canopy:	Black Flying-fox	*Pteropus alecto*
	Spectacled Flying-fox	*Pteropus conspicillatus*
	Little Red Flying-fox	*Pteropus scapulatus*
Within canopy:	Common Blossom-bat	*Syconycteris australis*
	Eastern Tube-nosed Bat	*Nyctimene robinsoni*
Arboreal		
Diurnal:	Not represented	
Nocturnal:[1]	Herbert River Ringtail Possum	*Psuedochirulus herbertensis*
	Daintree River Ringtail Possum	*Psuedochirulus cinereus*
	Green Ringtail Possum	*Pseudochirops archeri*
	Lemuroid Ringtail Possum	*Hemibelideaus lemuroides*
	Lumholz's Tree-kangaroo	*Dendrolagus lumholtzi*
	Bennett's Tree-kangaroo	*Dendrolagus bennettianus*
Scansorial		
Diurnal:	Satin Bowerbird	*Ptilinorhynchus violaceus*
	Tooth-billed Bowerbird	*Scenopoeetes dentirostris*
	Spotted Catbird	*Ailuroedus melanotis*
Nocturnal:	Coppery Brush-tailed Possum	*Trichosurus johnstonii*
	Fawn-footed Melomys	*Melomys cervinipes*
	White-tailed Rat	*Uromys caudimaculatus*
	Prehensile-tailed Rat?	*Pogonomys loriae*
Terrestrial		
Large:	Cassowary	*Casuarius casuarius*
Small:	Not represented	
Predators:	Feral Pig	*Sus scrofa*
	Bush Rat	*Rattus fuscipes*
	Cape York Rat	*Rattus leucopus*
	Masked White-tailed Rat?	*Uromys hadrourus*
Cursorial:	Musky Rat-kangaroo	*Hypsiprymnodon moschatus*

[1] All are primarily folivorous but take varying quantities of fruit.

Coevolution between Musky Rat-kangaroos and the Trees whose Fruit they Disperse ?

While I did not attempt to address this question directly in this study, it seems clear from the data presented here that Musky Rat-kangaroos have not coevolved with the plants they currently disperse. Musky Rat-kangaroos certainly convey advantages to some of the species they disperse but this cannot be interpretted as coevolution. The reasons I conclude this are as follows: 1) Musky Rat-kangaroos consume fruits from a broad range of syndromes, colours and sizes, therefore not applying any direct selective pressures on these attributes; 2) they place seeds singly and at random through the forest and therefore are not able to develop specific relationships with plants that require dispersal to be directed to specific microsites; and 3) they occur in Australia's seasonal tropics, a region which is subject to irregular but common disturbance by cyclones and storms, a pattern of disturbance with variable intensity that probably has impacts that override the more subtle effects of dispersal by animals (see Connell 1979). No studies have adequately demonstrated that coevolution occurs between frugivores and the plants they disperse and Herrera (1986) concludes that what coevolution does occur must be diffuse at best.

Although it seems apparent that coevolution between Musky Rat-kangaroos and the trees whose fruit they disperse has not occurred, they may be partly responsible for the continued existence of some species over geological time. Along with Cassowaries and perhaps some Flying-foxes (which also handle all or most size classes of fruit; Bentrupperbaumer, J. pers. comm.1997; pers. obs.), Musky Rat-kangaroos are able to handle and disperse the largest fruits which occur in Australian rain forests. None of the other frugivores occurring here are known to handle large sized fruits, except White-tailed Rats which kill almost 100% of the seeds they handle (Goldberg 1994; Harrington *et al.* 1997; this study). Assuming dispersal, other than by gravity or water, is important for the long term persistance of a species of plant, then many large-seeded species would have perished from the system but for the efforts of this small subset of Australia's frugivores.

Musky Rat-kangaroos, Cassowaries and Flying-foxes are likely to have been the primary agents transporting large seeds into areas newly colonised by rain forest plants. Although none of these species carries large seeds over long distances, all carry them sufficient distances to facilitate an incremental spread of large-seeded taxa. Around 18,000 years ago, wet tropical rain forests in Australia are thought to have contracted into a series of small refugia due to a drier, cooler climate at the time (Nix and Switzer 1991). These refuges appeared to occupy two main areas; one in the centre of the current distribution of rainforest in the Wet Tropics and one in the north of it (Nix and Switzer 1991). Palynological evidence from volcanic craters and crater lakes, suggest that much of the Atherton Tableland (the area of my study site) was covered in dry, fire-prone Eucalypt forest as recently as 10,000 years ago (Walker 1990). Prior to European invasion of the Atherton Tablelands (mid 1800's; Smith 1991), it was again covered in rain forest (Walker 1990). Most of the area is now pasture but enough fragments remain to confirm that many of the plant species in fragments have large seeds. Colonisation of Eucalypt forest by large- seeded plants in distant refuges would have required greater dispersal capabilities than those supplied by gravity or water. An established rain forest community with fruit bearing plants would be required to attract Cassowaries, Musky Rat-kangaroos and Flying-foxes, and by doing so, would encourage the dispersal of the large seeded species into the area. This stepwise regeneration of rain forest has been recorded in the neotropics for rainforest recolonising alluvial deposits on riverbends (Foster 1986). Thus, it is likely that the species composition of plants in rain forests outside refugia is a direct result of the species composition of the frugivore community.

Management Implications Arising from this Study

Several key issues are raised by this study which are significant to the management of Australia's tropical rain forests, much of which is on the World Heritage List and currently undergoing active management planning (Wet Tropics Management Authority 1995). The first and most positive is that Musky Rat-kangaroos appear to be abundant and secure in continuous forest which has been disturbed by selective logging. Their population densities, previously unknown, were high on my study site, which was last selectively logged in the mid-1970's (Chapter 7). In addition, my findings concerning their diet and dispersal capabilities and the ecological implications of these factors have already led to many trees with large fruits eaten by Musky Rat-kangaroos being included in rain forest replanting projects (Tucker, N., Department of Environment, Community Nature Conservation. pers. comm. 1996). Perhaps the most significant of these is a corridor being planted on private property between Lake Barrine (a large isolated fragment) and the nearest continuous forest in the hope of allowing ready movement of terrestrial animals between the two. The purpose of planting trees with large fruits is to re-establish a fully functional ecosystem more rapidly and to attract Musky Rat-kangaroos and Cassowaries into the corridor.

Another implication, which arises from the discovery that many predators (including domestic dogs and cats) feed on Musky Rat-kangaroos, is managing the boundaries of World Heritage rain forest where it abutts human habitation. It may be necessary to implement some control over access to rain forest by domestic dogs and cats in neighboring suburban and farming communities so that Musky Rat-kangaroo populations will not suffer added predatory pressure.

Questions Arising from this Study

As with most initial studies, many questions have been raised by this study, some of which I have already outlined in preceding chapters. Here I list some of those I see as most interesting to pursue.

Functional ecology

With respect to determining the ecological significance of Musky Rat-kangaroos in the entire Wet Tropics region of Australia, it is important to determine:

- What fruits occur in the diet of Musky Rat-kangaroos in other forest areas?
- What is the total number of species they consume?
- Do Musky Rat-kangaroos cache the seeds of all the species they consume?
- What is the retrieval rate of cached seeds?
- Are there any plant species which are totally reliant on dispersal by Musky Rat-kangaroos?
- What quantity of fruit do they disperse in relation to other frugivores in the

community?

The first two questions will give a more thorough indication of how broad their diet is than the present study has and will help to determine their significance in relation to other frugivores (last question). However, I judge the most important questions to answer are those which centre around their caching behaviour. This is particularly important for plants whose seeds: 1) are eaten by rats; 2) are large or; 3) are not well dispersed by other frugivores. Currently, proposed management directions for Australia's Wet Tropics World Heritage Area centre around the management of biodiversity, vegetation types and special, rare and threatened species (Wet Tropics Management Authority 1995). This does not directly include ecological processes such as the dispersal of seeds by frugivores. To ensure long term protection of all the aspects of tropical rain forests (particularly in fragments), ecological processes need to be considered and the possible effect of frugivores, through seed dispersal, on the biodiversity of plants is foremost among them.

Reproduction

From an autecological perspective and a desire to understand the effects of the environment and its resources on the life history of Musky Rat-kangaroos the following questions are of interest:

- Does the different timing of seasonal peaks in fruit availability in different areas change the timing of their reproduction?
- What is the physiological control over reproductive seasonality and male testes size?

My study has demonstrated a strong correlation between fruit availability and reproductive timing and output in Musky Rat-kangaroos. If the seasonal changes in male testes size are driven purely by nutritional requirements, then I expect that individuals living on the coastal plain will have an earlier and perhaps longer reproductive period than those on the Atherton Tablelands, reflecting the earlier and longer peak in fruit abundance (see Crome 1975). However, many seasonally breeding animals have developed obligate seasonality (Tyndale-Biscoe 1989) and respond to changes in day length. Therefore a study of the physiological control over testes growth and reduction would indicate whether seasonality is facultative or has become obligate.

Other aspects of reproduction also warrent further study. Foremost among them is:

- How do females manipulate their number of pouch young?

This is particularly interesting given the evidence of changes in litter size tracking changes in peak fruit availability presented in my study. In addition, Musky Rat-kangaroos are the only macropodoid which has multiple young simultaeneously. Therefore, further study of litter size manipulation will help to understand the relative merits of the single young and multiple young strategies in marsupials.

Populations

Also of interest are questions relating to the maintenance of populations, gene flow between populations, and the likelihood of chance events causing local extinctions.

- Why do Musky Rat-kangaroos have a male biased sex ratio?
- Do young males disperse from, and females remain in, the natal range?
- How do population sizes vary over longer time frames and in different areas than examined in this study?

These questions will help to understand why Musky Rat-kangaroos do not occur in isolated forest fragments and may aid in determining the necessity of re-establishing links between regional discontinuities which have been created by humans in the last 200 years.

Nutrition

From a nutritional and physiological ecology perspectives several additional questions are of interest:

- What nutrients do Musky Rat-kangaroos derive from: fruits; invertebrates; fungus?
- How do they deal with the toxic compounds in certain fruits and seeds?
- Do their foraging strategies change from season to season? (more data needed)

Terborgh (1983) demonstrated that monkeys in Peru dramatically alter their foraging strategies on a seasonal basis. My data indicated that Musky Rat-kangaroos probably did also. These changes in foraging strategies were intimately linked to changes in fruit availability, suggesting that fruit are the most significant nutritional requirement for these animals. However, other foods are also eaten year round, suggesting that a purely fruit diet is limiting in some way. This may be due to a lack of certain nutrients in fruit, greater ease of obtaining certain nutrients from non-fruit sources or perhaps secondary compounds in fruit limiting their ability to maintain a totally frugivorous diet during the peak (Mack 1990).

Biogeography

Finally, from a biogeographic and management perspectives it is essential to determine:

- What is the entire distribution and abundance of Musky Rat-kangaroos?

Present observations suggest that they are distributed throughout most of the Wet Tropics region but they do not occur in the rain forest south of the Wallaman Falls area (145°45'E, 18°40'S). In addition, they appear to be found at different densities in different parts of their range with several areas of high density (Winter, J. pers. comm.1989; pers. obs.). The high density areas may correspond to those identified by Crome and Moore (1990) as high density areas for Cassowaries (pers. obs.). Musky Rat-kangaroos also appear to be in lower densities at altitudes greater than 800m above sea level than below this altitude. It would be valuable to define high density areas and examine plant species composition and fruiting phenology in them to determine if high density areas have sigificantly more species with large fruits than other less densely populated areas. These data will help to understand if Musky Rat-kangaroo (and possibly Cassowary) populations are limited by the plant species composition of forests.

To estimate population size over such a large area using trapping methods would be impractical. However, simple relative abundance could be examined using a method first suggested by Dr John Winter, further refined in this study and tested by Gray (1994). This involves using a mobile observation platform (see Chapter 3) and sitting for periods in the mornings and evenings and counting the number of sightings per unit time. These data would give a better understanding of the species' conservation status and help identify priority areas for management strategies such as dog and cat control.

Closing Remarks

Musky Rat-kangaroos are one of the few frugivorous mammals in Australia's rain forests. They are the only non-volant mammal that is primarily a seed disperser rather than a seed predator. Given the depauperate nature of mammal communities and the total lack of primates in rain forest in Australia, this places them in a position of great significance in relation to frugivory and seed dispersal. In most tropical countries with rain forests of similar plant species diversity to Australian rain forests, seed dispersal is carried out by a diverse community of both birds and mammals. Primates are significant contributors to the total biomass of frugivores in those countries. Musky Rat-kangaroos are significant contributors to the biomass of frugivores in Australia, despite their small individual size. They also have a relatively greater biomass than functionally similar (cursorial) frugivores do in the neotropics. The reason for this is most likely the difference in mammalian frugivore diversity between the countries. Musky Rat-kangaroos therefore, are filling an ecological role which is shared by a much larger number of species in other countries. In addition, they appear to be the only marsupial in the world that is terrestrial and frugivorous and are clearly of great ecological significance in tropical rain forests in Australia.

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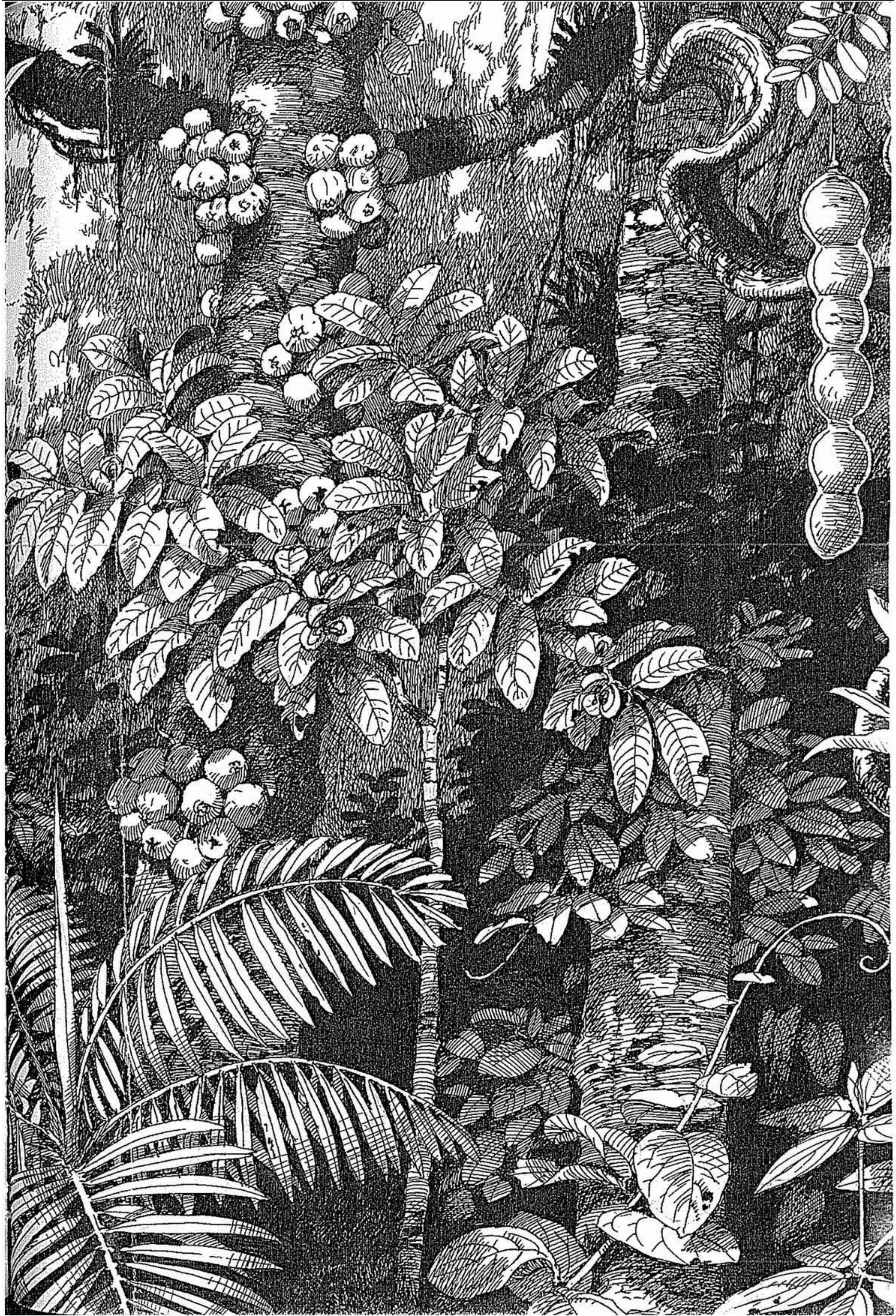

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APPENDIX 1

Species of plants producing ripe fruit on the Gourka Rd study site (145° 44' 43"E, 17° 22' 38"S, 740m Elevation) showing the size class of the fruits they produce (S: 1 - 1ml; 2 - 1 to 5ml; 3 - 6 to 10ml; 4 - 11 to 20ml; 5 - 21 to 100ml; 6 - >100ml), E - if Musky Rat Kangaroos consume them (Y- yes; N - no; ? - probably but no confirmation), the parts eaten (F - flesh; S - seed; B - both flesh and seed), and the method of determining if they were eaten (SALT - spool and line tracking; MOP - direct observation from a mobile observation platform or hide; BOFAT - bite marks on fruit found along transects. Also included are other fruit species known to be eaten by Musky Rat-kangaroos in other areas along with the source of the observation.

GENUS	SPECIES	FAMILY	S	E	P	CONFIRMATION
Acronicia	vestita	Rutaceae	3	Y	F	SALT
Aglaia	australiensis	Meliaceae	4	N		
Apodytes	brachystylis	Icacinaceae	2	N		
Archidendron	whitei	Mimocaceae	4	N		
Athertonia	diversifolia	Proteaceae	4	Y	F	BOFAT, MOP
Austrobaleya	scandens	Austrobaileyaceae	5	Y	B	SALT, MOP, BOFAT
Austromyrtus	dallachiana	Myrtaceae	1	Y	B	SALT
Baileyoxylon	lanceolatum	Flacourtiaceae	4	Y	B	BOFAT, MOP
Beilschmeidia	tooram	Lauraceae	4	Y	F	SALT, MOP, BOFAT
Beilschmeidia	recurva	Lauraceae	2	Y	F	SALT, BOFAT
Beilschmeidia	volcii	Lauraceae	5	Y	F	SALT, MOP, BOFAT
Bowenia	spectabilis	Zamiaceae	6	N		
Calamus	moti	Arecaceae	1	?		
Cardwellia	sublimis	Proteaceae	5	N		
Castenospora	alphandii	Sapindaceae	4	Y	F	MOP, BOFAT
Cinnamomum	laubatii	Lauraceae	2	Y	B	BOFAT
Corynocarpus	cribbianus	Corynocarpaceae	4	N		
Cryptocarya	oblata	Lauraceae	3	Y	F	MOP, BOFAT
Cryptocarya	pleurosperma	Lauraceae	5	?		
Delarbria	michieana	Araliaceae	2	N		
Diploglottis	bracteata	Sapindaceae	4	Y	F	MOP, BOFAT
Dysoxylon	papuanum	Meliaceae	2	N		
Eleocarpus	angustifolia	Eleocarpaceae	3	Y	F	SALT, MOP, BOFAT
Endiandra	insignis	Lauraceae	6	Y	B	SALT, BOFAT
Endiandra	monothyra	Lauraceae	3	Y	B	SALT, MOP, BOFAT
Endiandra	palmerstonii	Lauraceae	5	N		
Endiandra	sankeyana	Lauraceae	4	Y	F	MOP, BOFAT
Endiandra	xanthocarpa	Lauraceae	5	Y	F	MOP, BOFAT
Faradaya	splendida	Verbenaceae	5	Y	B	SALT, BOFAT
Ficus	crassipes	Moraceae	4	Y	B	BOFAT
Ficus	pleurocarpa	Moraceae	4	Y	B	SALT, MOP, BOFAT
Ficus	septica	Moraceae	3	N		
Flindersia	bourjotiana	Rutaceae	5	N		
Fontainea	picrosperma	Euphorbiaceae	4	Y	B	SALT, MOP, BOFAT
Freycinettia	scandens	Pandanaceae	4	N		
Garcinia	gibbsiae	Clusiaceae	5	Y	B	SALT, BOFAT
Gmelina	fasciculiflora	Verbenaceae	3	N		
Halfordia	scleroxylla	Rutaceae	1	N		
Hollandia	sayeriana	Proteaceae	6	N		
Irvingbaileya	australis	Icacinaceae	3	?		
Legnephora	moorei	Menispermaceae	2	N		
Lethodon	setosa	Thymelaeaceae	3	Y	S	SALT
Levieria	acuminata	Monimiaceae	2	N		
Mammea	touriga	Clusiaceae	6	Y	F	MOP, BOFAT
Myristica	insipida	Myristicaceae	2	Y	B	SALT, MOP, BOFAT
Neisosperma	poweri	Apocinaceae	3	Y	F	MOP, BOFAT
Niemeyera	prunifera	Sapotaceae	4	Y	B	MOP, BOFAT
Oraniopsis	appendiculata	Arecaceae	4	Y	F	MOP, BOFAT
Piper	novaehollandiae	Piperaceae	1	N		
Pittosporum	rubiginosum	Pittosperaceae	2	N		
Podocarpus	dispermus	Podocarpaceae	3	Y	F	MOP
Polyosma	hirsuta	Escalloniaceae	1	N		
Polyscias	murrayi	Araliaceae	1	?		
Pothos	longipes	Araceae	1	N		
Pouteria	castanosperma	Sapotaceae	4	N		
Prunus	turneriana	Rosaceae	4	Y	B	SALT, MOP, BOFAT
Randia	hirta	Rubiaceae	2	N		
Schefflera	actinophylla	Araliaceae	2	?		
Schistocarpaea	johnsonii	Rhamnaceae	1	N		
Siphonodon	membranaceum	Celastaceae	5	Y	F	SALT, MOP, BOFAT
Solanum	capsicoides	Solanaceae	3	N		
Sysygium	gustavioides	Myrtaceae	5	Y	S	MOP, BOFAT
Sysygium	papyraceum	Myrtaceae	3	Y	F	MOP, BOFAT

Appendix 1 (cont.)

GENUS	SPECIES	FAMILY	S	E	P	CONFIRMATION
Syzygium	boonjee	Myrtaceae	5	N		
Syzygium	trachyphloium	Myrtaceae	1	Y	B	SALT
Tetrasynandra	lasciflora	Monimiaceae	2	N		
Triunia	erythrocarpa	Proteaceae	4	Y	B	MOP. BOFAT
Xanthophyllum	octandrum	Xanthophyllaceae	3	N		

ADDITIONAL SPECIES KNOWN TO BE EATEN						SOURCE
Aleurites	moluccana	Euphorbiaceae	5	Y	S	Breeden & Breeden 1970
Archontophoenix	alexandrae	Arecaceae	2	Y	F	Troughton 1967
Beilschmiedia	oligandra	Lauraceae	5	Y	F	Cooper & Cooper 1994
Endiandra	montana	Laurceae	5	Y	F	A. Dennis
Melodinus	australis	Apocynaceae	6	Y	F	A. Dennis
Omphalia	queenslandiae	Euphorbiaceae	6	Y	B	A. Irvine
Perapentadinia	mearsii	Elaeocarpaceae	3	Y	F	A. Dennis
Syzygium	kuranda	Myrtaceae	5	Y	F	Johnson and Strahan 1982
Trichosanthes	sp.	Cucurbitaceae	6	Y	F	A. Dennis

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APPENDIX 2.

Derivation of formula (Equation 5) used to calculate 95% confidence intervals for estimates of the number of fruits/seeds cached by Musky Rat Kangaroos (Chapter 8). Formula derived by John Hunter, Mathematics Department, James Cook University of North Queensland, Townsville. Equation 5 was used to calculate the probability of Musky Rat Kangaroos caching a number of fruit from zero upwards. The probabilities were summed and at the point where the cumulative probability was 0.05 or 0.95 the estimated number cached was used as the lower and upper 95% confidence intervals respectively.

Previous Data

x - number cached during spool and line tracking of fruit experiments (35)

y - number eaten and left *in situ* during spool and line tracking experiments (92)

s - number left *in situ* on fruit transects with Musky Rat Kangaroo teeth marks in each month

r - number cached in each month (unknown)

Let probability of being cached = Θ (unknown)

Given x, y, s, we need to estimate r

$$\Pr(r/x,\ s,y) = \int \Pr(r/s,\Theta)\ \Pr(\Theta/x,y)d\Theta \qquad \textbf{Equation 1}$$

This is a standard probability expression with s or y omitted on the right-hand side if there is no dependence.

Using Bayes' theorem

$$f(\Theta/x,y) = \frac{f(x/\Theta,y)f(\Theta/y)}{f(x/y)} = \frac{f(x/\Theta,y)f(\Theta)}{f(x/y)\text{[1]}}$$

Put this in Equation 1
[Notation change pr - f on right hand side]

$$\Pr(r/x,\ s,y) = \int f(r/s,\Theta)\frac{f(x/y,\Theta)f(\Theta)}{f(x/y)}\ d\Theta$$

---

[1] omitting "y" where there is independence.

But $f(x/y) = \int f(x/y,\Theta)f(\Theta)d\Theta$ [standard probability expression]

$$\Pr(r/x,\ s,y) = \frac{\int f(r/s,\Theta)f(x/y,\Theta)f(\Theta)d\Theta}{\int f(x/y,\Theta)f(\Theta)d\Theta}$$ **Equation 2**

Let $N = r+s$

i.e. r out of N are cached
s out of N are not cached

$$f(N/s) = \frac{f(s/N)f(N)}{f(s)}\text{[2]} \quad \alpha \quad f(s/N)f(N)\text{[3]} \quad \alpha \quad f(s/N)\text{[4]}$$ **Equation 3**

$f(s/N)$ is the binomial distribution

i.e. $f(s/N) = {}^{N}C_{s}(1-\Theta)^{s}\Theta^{N-s}$

Therefore from Equation 3

$$f(N/s) \ \alpha \ f(s/N) = {}^{N}C_{s}(1-\Theta)^{s}\Theta^{N-s}$$

i.e. $$f(N/s) = K.{}^{N}C_{s}(1-\Theta)^{s}\Theta^{N-s}$$

The sum of the probabilities must add to 1

$$1 = \Sigma^{\infty}_{N=s}f(N/s) = K\Sigma^{\infty}_{N=s}{}^{N}C_{s}(1-\Theta)^{s}\Theta^{N-s} = K.\frac{1}{1-\Theta}$$

i.e. $K = (1-\Theta)$

$$f(N/s) = {}^{N}C_{s}(1-\Theta)^{s+1}\Theta^{N-s}$$

Substitute $N = r+s$

$$f(r/s) = {}^{r+s}C_{s}(1-\Theta)^{s-1}\Theta^{r}$$

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[2] - Bayes theorum

[3] s is given - denominator the same for different N

[4] Taking $f(N)$ = constant. Little effect on result if most of information is in the data

Substitute this expression (and similar one for $f(x/y)$) in Equation 2

$$\Pr(r/x,s,y) = \int_0^1 {}^{r+s}C_s(1-\Theta)^{s+1}\Theta^r . {}^{x+y}C_y(1-\Theta)^{y+1}\Theta^x . 1 d\Theta$$

$$\int_0^1 {}^{x+y}C_y(1-\Theta)^{y-1}\Theta^x . 1 d\Theta$$

Where $f(\Theta)$ is assumed to be equal to 1, thus assuming little prior information about Θ. This has little effect on the result.

$$\text{i.e. } \Pr(r/x,s,y) = \frac{{}^{r+s}C_s . {}^{x+y}C_y}{{}^{x+y}C_y} \quad \frac{\int_0^1 \Theta^{r+x}(1-\Theta)^{s+y+2} d\Theta}{\int_0^1 \Theta^x(1-\Theta)^{y+1} d\Theta} \qquad \textbf{Equation 4}$$

The integrals can be integrated by parts.

For a,b integer $\int_0^1 \Theta^a(1-\Theta)^b d\Theta = \dfrac{1}{a+b+1} \bullet \dfrac{1}{{}^{a+b}C_a}$

Use this in Equation 4

$$\Pr(r/x,s,y) = \frac{{}^{r+s}C_s . \quad {}^{x+y+1}C_{y+1}}{{}^{r+x+s+y+2}C_{s+y+2}} \quad \bullet \quad \frac{x+y+2}{r+x+s+y+3} \qquad \textbf{Equation 5}$$

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Appendix 3

Analysis of Variance tables for seed survival experiment (see Chapter 9).

1) Baileyoxylon Analysis on total number viable and germinated
Run A. R-squared = 0.956
Adjusted R-squared = 0.547

Source of Variation	DF	Mean Square	F	P
Within + Residual	3	0.32		
Tree	3	0.19	0.58	0.666
Position	1	0.22	0.69	0.468
Depth	1	5.81	18.18	**0.024**
Cage	1	10.3	32.24	**0.011**
Tree*Position	3	0.32	0.99	0.503
Tree*Depth	3	0.24	0.76	0.587
Tree*Cage	3	0.08	0.24	0.865
Position*Depth	1	0.07	0.21	0.677
Position*Cage	1	0.08	0.25	0.653
Depth*Cage	1	0.15	0.46	0.546
Tree*Position*Depth	3	0.07	0.23	0.870
Tree*Position*Cage	3	0.01	0.02	0.994
Tree*Depth*Cage	3	0.45	1.41	0.393
Position*Depth*Cage	1	0.24	0.75	0.450
Model	28	0.75	2.34	0.265
Total	31	0.71		

Run B. R-squared = 0.859
Adjusted R-squared = 0.727

Source of Variation	DF	Mean Square	F	P
Within + Residual	16	0.19		
Tree	3	0.19	0.97	0.433
Position	1	0.22	1.14	0.302
Depth	1	5.81	30.12	**0.000**
Cage	1	10.3	53.43	**0.000**
Tree*Position	3	0.32	1.64	0.220
Tree*Depth	3	0.24	1.26	0.322
Tree*Cage	3	0.08	0.45	0.758
Model	15	1.25	6.50	**0.000**
Total	31	0.71		

Baileyoxylon total viable
Run C. R-squared = 0.772
Adjusted R-squared = 0.717

Source of Variation	DF	Mean Square	F	P
Within + Residual	25	0.19		
Tree	3	0.19	0.97	0.433
Position	1	0.22	1.14	0.302
Depth	1	5.81	30.12	**0.000**
Cage	1	10.3	53.43	**0.000**
Model	6	1.25	6.50	**0.000**
Total	31	0.71		

2) *Fontainea* Analysis on total number viable and germinated
Run A. R-squared = 0.977
Adjusted R-squared = 0.757

Source of Variation	DF	Mean Square	F	P
Within + Residual	3	0.14		
Tree	3	0.04	0.69	0.828
Position	1	1.34	9.45	0.054
Depth	1	1.00	7.05	0.077
Cage	1	11.51	81.02	**0.003**
Tree*Position	3	0.19	1.33	0.410
Tree*Depth	3	0.14	1.00	0.500
Tree*Cage	3	0.19	1.33	0.410
Position*Depth	1	0.35	2.45	0.216
Position*Cage	1	0.19	1.31	0.335
Depth*Cage	1	0.35	2.45	0.216
Tree*Position*Depth	3	0.03	0.21	0.887
Tree*Position*Cage	3	0.04	0.30	0.828
Tree*Depth*Cage	3	0.03	0.21	0.887
Position*Depth*Cage	1	1.00	7.05	0.077
Model	28	0.63	4.46	0.121
Total	31	0.59		

Fontainea total viable
Run B. R-squared = 0.960
Adjusted R-squared = 0.896

Source of Variation	DF	Mean Square	F	P
Within + Residual	12	0.14		
Tree	3	0.04	0.69	0.828
Position	1	1.34	9.45	0.054
Depth	1	1.00	7.05	0.077
Cage	1	11.51	81.02	**0.003**
Tree*Position	3	0.19	1.33	0.410
Tree*Depth	3	0.14	1.00	0.500
Tree*Cage	3	0.19	1.33	0.410
Position*Depth	1	0.35	2.45	0.216
Position*Cage	1	0.19	1.31	0.335
Depth*Cage	1	0.35	2.45	0.216
Position*Depth*Cage	1	1.00	0.21	0.887
Model	19	0.63	4.46	0.121
Total	31	0.59		

3) Baileyoxylon Analysis on total number germinated
Run A. R-squared = 0.989
Adjusted R-squared = 0.884

Source of Variation	DF	Mean Square	F	P
Within + Residual	3	0.06		
Tree	3	0.26	4.14	0.137
Position	1	0.14	2.14	0.240
Depth	1	3.58	56.42	**0.005**
Cage	1	7.13	112.22	**0.002**
Tree*Position	3	0.18	2.89	0.203
Tree*Depth	3	0.06	0.94	0.521
Tree*Cage	3	0.22	3.40	0.171
Position*Depth	1	0.01	0.11	0.767
Position*Cage	1	0.37	5.89	0.094
Depth*Cage	1	0.83	13.12	**0.036**
Tree*Position*Depth	3	0.18	2.78	0.211
Tree*Position*Cage	3	0.14	2.15	0.273
Tree*Depth*Cage	3	0.27	4.20	0.135
Position*Depth*Cage	1	0.81	12.71	**0.038**
Model	28	0.60	9.43	**0.044**
Total	31	0.55		

Baileyoxylon germination

Run B. R-squared = 0.886
Adjusted R-squared = 0.706

Source of Variation	DF	Mean Square	F	P
Within + Residual	12	0.16		
Tree	3	0.26	1.63	0.234
Position	1	0.14	0.84	0.377
Depth	1	3.58	22.28	**0.000**
Cage	1	7.13	44.31	**0.000**
Tree*Position	3	0.18	1.14	0.372
Tree*Depth	3	0.06	0.37	0.776
Tree*Cage	3	0.22	1.34	0.307
Position*Depth	1	0.01	0.04	0.842
Position*Cage	1	0.37	2.33	0.153
Depth*Cage	1	0.83	5.18	**0.042**
Position*Depth*Cage	1	0.81	5.02	**0.045**
Model	19	0.79	4.92	**0.004**
Total	31	0.55		

Run C. R-squared = 0.805
Adjusted R-squared = 0.712

Source of Variation	DF	Mean Square	F	P
Within + Residual	21	0.16		
Tree	3	0.26	1.63	0.204
Position	1	0.14	0.86	0.364
Depth	1	3.58	22.75	**0.000**
Cage	1	7.13	45.26	**0.000**
Position*Depth	1	0.01	0.04	0.839
Position*Cage	1	0.37	2.38	0.138
Depth*Cage	1	0.83	5.29	**0.032**
Position*Depth*Cage	1	0.81	5.13	**0.034**
Model	10	1.37	8.67	**0.000**
Total	31	0.55		

4) Fontainea Analysis on total number germinated
Run A. R-squared = 0.991
Adjusted R-squared = 0.907

Source of Variation	DF	Mean Square	F	P
Within + Residual	3	0.05		
Tree	3	0.05	0.97	0.509
Position	1	0.51	10.82	**0.046**
Depth	1	8.01	170.89	**0.001**
Cage	1	2.20	47.02	**0.006**
Tree*Position	3	0.07	1.52	0.369
Tree*Depth	3	0.05	0.97	0.509
Tree*Cage	3	0.08	1.73	0.332
Position*Depth	1	0.51	10.82	**0.046**
Position*Cage	1	0.40	8.56	0.061
Depth*Cage	1	2.20	47.02	0.006
Tree*Position*Depth	3	0.07	1.52	0.369
Tree*Position*Cage	3	0.05	1.00	0.500
Tree*Depth*Cage	3	0.08	1.73	0.332
Position*Depth*Cage	1	0.40	8.56	0.061
Model	28	0.56	11.86	**0.032**
Total	31	0.51		

Run B. R-squared = 0.953
Adjusted R-squared = 0.879

Source of Variation	DF	Mean Square	F	P
Within + Residual	12	0.06		
Tree	3	0.05	0.74	0.548
Position	1	0.51	8.25	**0.014**
Depth	1	8.01	130.24	**0.000**
Cage	1	2.20	35.84	**0.000**
Tree*Position	3	0.07	1.16	0.365
Tree*Depth	3	0.05	0.74	0.548
Tree*Cage	3	0.08	1.32	0.315
Position*Depth	1	0.51	8.25	**0.014**
Position*Cage	1	0.40	6.52	**0.025**
Depth*Cage	1	2.20	35.84	**0.000**
Position*Depth*Cage	1	0.40	6.52	**0.025**
Model	19	0.79	12.81	**0.000**
Total	31	0.51		

Fontainea germination
Run C. R-squared = 0.915
Adjusted R-squared = 0.875

Source of Variation	DF	Mean Square	F	P
Within + Residual	21	0.06		
Tree	3	0.05	0.72	0.552
Position	1	0.51	8.00	**0.010**
Depth	1	8.01	126.33	**0.000**
Cage	1	2.20	34.76	**0.000**
Position*Depth	1	0.51	8.00	**0.010**
Position*Cage	1	0.40	6.33	**0.020**
Depth*Cage	1	2.20	34.76	**0.000**
Position*Depth*Cage	1	0.40	6.33	**0.020**
Model	10	1.44	22.67	**0.000**
Total	31	0.51		

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Appendix 4

Publications resulting from this study:

1) Dennis, A. J. and Johnson, P. M. 1995. Musky Rat-kangaroo, *Hypsiprymnodon moschatus*. in Strahan, R. (ed) *The Mammals of Australia* Australian Museum/Reed Books, Chatswood. pp 282 - 284.;

2) Dennis, A. J. and Marsh, H. D. 1997. (in press) Seasonal reproduction in Musky Rat-kangaroos, *Hypsiprymnodon moschatus*: a response to changes in resource availability. *Wildlife Research*.

1.

2.

Seasonal Reproduction in Musky Rat-kangaroos *Hypsiprymnodon moschatus* : a Response to Changes in Resource Availability

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Running head: Musky Rat-kangaroo reproduction

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Abstract

Musky rat-kangaroos had a seasonal reproductive pattern. Males underwent a dramatic testicular expansion in October and remained enlarged until April when they reduced in size again. Females carried one to three pouch young from around March until October which continued to be suckled until late December. Two primary food resources, fruits and litter fauna, underwent regular seasonal changes in abundance. The availability of fruits fluctuated to a greater degree than litter fauna, both within and between years and probably constituted the main selective pressure for a seasonal pattern of reproduction and high fecundity relative to most other macropodoids. Variation in the availability of fruits between years correlated with changes in the reproductive output of both male and female musky rat-kangaroos during breeding seasons.

Introduction

Musky rat-kangaroos, Australia's smallest kangaroo (Macropodoidea), are diurnal, terrestrial and restricted to Australia's tropical rain forests (Johnson and Strahan 1982). They have long been considered 'primitive' members of the group, retaining many gross morphological features similar to those found in the early Macropodoid line (Woods 1960). However, some characters of their dentition are specialised and are not considered to be the surviving macropodoid ancestral form (Woods 1960). Among the extant kangaroos features which are unique to musky rat-kangaroos include: the presence of an opposable first digit on the pes; an unspecialised digestive tract; a running gait; and the preponderance of twin births.

Little is known of musky rat-kangaroo ecology. Breeden and Breeden (1970) described their diurnal behaviour, observed them feeding on the seeds of the Candle-nut tree (*Aleurites mollucana*) and noted that they fed on insects. Johnson and Strahan (1982) confirmed that females normally rear two young simultaneously, a behaviour unknown in any other macropodoid, and confirmed their diet of fruit and litter fauna. Dennis' observations (to be published separately), based on direct observation and microscopic examination of faecal pellets, confirmed that fruits and seeds form the bulk of their diet. Litter fauna are eaten all year and epigeal sporocarps of a few Agaric fungi are also consumed when available.

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 was known of their reproductive biology. The research reported here, which is part of a broader study of the species ecology, examines the reproductive patterns seen in wild musky rat-kangaroos on the Atherton Tablelands and demonstrates they are seasonal breeders and that their reproductive pattern correlates with variations in food resources.

Study Site and Climate

The study was conducted from March 1990 to February 1992. The study site was in complex mesophyll vine forest (Type 1b; Tracey 1982) on basalt derived soil at an average elevation of 740 m (range 720 - 760; 145°44'43"E, 17°22'38"S). The site is on the eastern side of the Atherton Tableland and within the 94000 ha Wooroonooran National Park. Prior to its listing as National Park in 1992, the area was part of a State forest system (SF 310, Gadgarra) and was last selectively logged during the mid-1970's.

Forest and topography

The forest is tall (canopy 30 - 40 m; emergents 50 - 60 m) with high species diversity (up to 200 tree species and hundreds of other plants on the 9 ha site; Tony Irvine pers. comm.). The understorey varies with the degree of closure of the canopy and ranges from extremely dense thickets of regrowth (sometimes including the exotic *Lantana camara*) where recent cyclone disturbance has broken the canopy, to a very open understorey of scattered saplings or understorey plants where the forest has remained undisturbed with no recent treefall gaps. Approximately one third of the site consists of level ground, the remainder slopes away into a perennial stream with three main tributaries, some with smaller branches.

Climate

Records from a farm 1 km from the site (I. and F. Bean, Ghurkha Rd) show that over the 11 years from 1984 to 1994 the mean yearly rainfall was 3187 mm (± 173 se; range 2128 - 4072). A highly seasonal pattern is evident (Figure 1). Usually there are three very wet months in a year (February, March and April), five wet months (January, May, June, July and December) and four dry months (August to November).

During 1990 the three wettest months of the wet season were later than normal (March to May instead of February to April) while in 1991 the wet season was early (December to February). Subsequent to the 1991 wet season, rainfall was almost continuously below average throughout 1991 and 1992.

Mean monthly maximum temperatures, taken at Malanda 13 km from the study site in 1991 and 1992, ranged from 29°C between November and January each year to 19°C in July, while minimums ranged from around 20°C in the warmer season to around 10°C in the cold seasons. Temperatures recorded under the rainforest canopy 3 km from the study site fluctuated in a similar pattern (Pearson's correlation $r = 0.98$, $Pr < 0.0001$) but did not reach the extremes of temperatures recorded in Malanda.

Methods

We established a 300 x 300 m grid with the assistance of a qualified surveyor. It was marked with colour coded and numbered pegs at 25 m intervals.

Fruit Availability

To assess the availability of fruit to terrestrial frugivores, we monitored 2100m of two metre wide transects monthly from October 1990 to December 1992. Transects were arranged systematically as 7 x 300 m lines along the 300 x 300 m grid (configuration shown in Figure 2). Each transect was further subdivided into 60, 5 x 2 m quadrats for ease of quantification of the number of fruits.

Each month we recorded and removed all fruits within each quadrat. Those species consumed by musky rat-kangaroos were identified by the presence of their distinctive bite marks and later confirmed and added to with direct observations from a hide. Biomass estimates of fresh fruit were 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). To calculate biomass estimates we took a sample of 20 to 40 fruits of each species from two to four trees and weighed them to the nearest gram using a Pesola spring balance. We then calculated the average weight of edible parts of a single fruit for each species.

Litter Fauna

We sampled litter fauna bimonthly from January 1991 to November 1992. We collected 12, 1/4 m^2 samples of litter on each occasion, four from each of ridge, slope and gully sites. Ridge sites were chosen at random from the extensive level area and systematically from the true ridges. We chose slope and gully sites systematically from the six gullies available on the grid. The four sample sites taken within each topographical feature were chosen at random.

Invertebrates were extracted from the samples using 30, 25 cm wide Berlese funnels (McFayden 1961) with 40 watt bulbs over two days. We preserved the animals in alcohol and sorted them under a dissecting microscope. We sorted invertebrates into orders and size classes and recorded the numbers within each. The size classes were: <1 mm; 1 - 2 mm; 2 - 5 mm; >5 mm.

Trapping

Animals using the 300 m^2 grid were trapped in five fence traps, four arranged diagonally across the corners of the grid (as topography allowed) and one centrally (Figure 2). Each fence consisted of five 20 x 1 m strips of shade cloth or Sarlon weed matting attached to wooden stakes or trees and pinned into the ground with "tent pegs" or occasional rocks or logs. The 20 x 1 m strips (sub-fences) were then arranged in a zig-zag pattern through the forest (Figure 2). Two treadle-release cage traps (Mascot 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 gap in the presence of traps. No bait was used as animals continued to use the gap when traps were in place and bait attracted unwanted species such as white-tailed rats *Uromys caudimaculatus*. Early tests showed that musky rat-kangaroos did not enter small traps, hence the large size of the traps relative to musky rat-kangaroos.

We trapped at irregular intervals from September 1990 to February 1993 and never for more than two days in a row, because musky rat-kangaroos quickly became trap shy in the short term. Included are some data from May 1990 when trapping techniques were being developed.

Measurements

We tattooed each animal's ear with a unique number and measured the head, right pes and right ear (± 0.1 mm) with Vernier calipers and the tail (± 1 mm) with a ruler. In addition we recorded age and sex class (adult, subadult, juvenile, ♂, ♀), reproductive status, weight, and notes on distinctive features, injuries or parasites. Reproductive data included pouch and mammary condition and the number of pouch young. We measured the head and/or tail of pouch young where possible but did not persist if a female showed high levels of stress. For males, a measure of testes area was calculated from the length of the right organ and their combined width.

Analyses

Fruit Availability

We have analysed data from 1991 and 1992 with general linear models using SAS to examine seasonal patterns in biomass of fruits and seeds. Because fruit availability was measured in only three months in 1990, these data were used only in analyses relating to testes size during that period.

Litter Fauna

Data on invertebrate abundance were normalised by log transformation ($\ln\{n+1\}$) because of a skewed distribution of counts.

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. Female body weight has been corrected for the presence of pouch young by subtracting the mean weight of young measured each month multiplied by the number of young being carried by each individual. Weights of early pouch young, still attached to the nipple, were derived from animals freshly killed by domestic dogs or grey goshawks *Accipiter novaehollandiae*.

The linear measurement most highly correlated with body weight was head length (for males $r = 0.58$ $P=0.0002$; for females $r = 0.83$ $P=0.0001$; for subadults $r = 0.96$ $P=0.0001$). We then calculated regression equations of ln(head length) on ln(body weight) data (with all repeated measures removed) separately for males, females and subadults (including recently independent juveniles). The slopes of these equations were then compared to assess the possibility of using one equation for all animal classes. All equations were significantly different (ANCOVA $F=310.8$, $DF=85$, $P=0.001$; Tukey test) and subsequent calculations of condition indices were done separately for each age and sex class. The condition index for each animal was then calculated as the ratio of observed body weight to expected body weight.

Results

Fruit Availability

The biomass of fresh fruits and seeds available to musky rat-kangaroos varied seasonally and between years (Figure 3; Table 1). Least fruits were available in April 1991 (mean 0.001 g m^{-2} ± 0.001 se), whereas in the peaks of that year (January and December) 1.61 g m^{-2} (± 0.64 se) and 1.34 g m^{-2} (± 0.44 se) were available. In 1992 fruits and seeds were more abundant than in 1991, the lowest biomass measure being 0.03 g m^{-2} (± 0.014 se) in June. From September on, a large crop of fruit was available in 1992, peaking in December with 8.86 g m^{-2} (± 2.34 se). Seventy five percent was due to large crops of Lauraceae. Fruit biomass also varied between transects in different years and in different months. This was due to the large crops of Lauraceae in 1992 which were spatially heterogenous.

Litter Fauna

A total of 13113 organisms belonging to 37 orders were sorted from 36 m^2 of forest floor litter. During microscopic examination of faecal pellets fragments, invertebrates below 2 mm body legnth were not found. Therefore, we have examined data from the 4250 animals in size classes above 2 mm body length. We also analysed the abundance of animals above 5 mm separately, on the basis that many fragments in faecal pellets corresponded to fauna of this size and patterns of abundance differed with size class.

The abundance of invertebrates >2 mm varied seasonally by a factor of three (Figure 4; Table 2: ANOVA), ranging from 67.3 m^{-2} (± 12.4, means ± se's) during the trough in July 1991 to 184 m^{-2} (± 36.4) in the peak in November 1991. A similar pattern occurred in 1992 and while slightly larger in magnitude (67 ± 12.4 in July to 202 ± 74.1 in November) was not statistically different to 1991. The seasonal pattern was not significant for larger fauna (greater than 5 mm; Figure 4; Table 2).

Trapping Data

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.

Reproduction in Males

Musky rat-kangaroos showed a highly seasonal reproductive pattern. Although the data are patchy, they show a consistent seasonal pattern: testes size increased between September and October each year (from means of 246.87 mm^2 ± 22.76 se to 1009 mm^2 ± 98 se 1990, 648.78 mm^2 se 1991 and 1148.93 mm^2 se in 1992) and contracted between April and May (Figure 5). 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 capable. While the timing of testicular expansion was consistent from year to year the magnitude of the change was not. We compared testes area in the early breeding season, October to December, in 1990 (N=6), 1991 (N=9) and 1992 (N=14) and found that they were significantly larger in 1992 than 1991, while 1990 was not significantly different to either of the other two years. (One-way ANOVA, repeated measures removed, F=7.41, DF=2,26, P=0.0028; Tukey test). The size of testes during the non-breeding season was not significantly different between years (1991 & 1992 t-test: t=-1.04; DF=13; P=0.3191 based on single measure for each individual).

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 Dennis saw protracted aggressive encounters between males was from September to March each year, when most of the adult male population was reproductively active. These encounters involved chases of up to 30 seconds duration and occasionally involved 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 extremely violent if confined to the same cage in the presence of a female (P.M. Johnson pers. comm.).

Female Reproductive Status

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; N=13). Animals that were lactating but not carrying their young appeared in October in 1990 and 1992 and as early as September in 1991 and were present until December in each year (N=12). In 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, 1991) or lacking (1992).

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

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

Litter Size

Twenty two individual musky rat-kangaroos were captured carrying, feeding or having just completed feeding 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 in reproductive output between years was similar to the variation in male testes size: females in 1991 had the lowest reproductive output (Figure 7; Table 3; Oneway ANOVA 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, it must be noted that each of the four females increased their litter size by one in 1992. The ages of other females were unknown except for two females who were subadult in 1991 and produced first litters of twins and triplets in 1992

Juvenile/subadult Growth

The smallest musky rat-kangaroo, a 145g female, was trapped in November 1992, presumably just after it had begun to wander away from the maternal nest on its own. In September, juveniles still in the pouch had a mean weight (±se) of 45.5g (± 2.1, N=4)). They grew rapidly after pouch eviction (Figure 8). At the end of 1991 weights were lower and few juveniles were caught (mean ± se: November 147.5 ± 2.5, N=2; December 170 ± 11.5, N=3).

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 sub-adult (three females reproduced at body weights between 400 and 450g). During 1992, fruit availability increased in July (Figure 3), so that by August no subadults were recorded as they had reached a similar weight to adults (range 415 to 650) 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, 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 1991/92 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 196 mm) but became mature in October 1992 (testes area >1000 mm), two years after pouch vacation.

Longevity

Very little data on longevity were collected as approximately 60% of animals caught were caught once only or several times over a short period (less than six months). However, some evidence was gathered that is suggestive of lifespan. Female 108 (Weight 575g) was first caught in 1990 carrying two pouch young. During 1991 she carried no young but had triplets in 1992. By the end of 1992 she was one of the heaviest animals caught (620g) and her facial hair had become progressively more grey. She was clearly one of the oldest animals handled. Subadults had uniform pelage colour over the head and shoulders which began to turn grey after 2 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 amongst the older members of the population. These data suggest that musky rat-kangaroos may live for at least four years with reproduction usually beginning at 18 - 21 months and continuing for the next two to three years and possibly longer (Table 4).

Changes in Condition

When individuals were re-caught at different times of year, their weight varied considerably. Some adults lost up to 30 - 35% of their peak weight (mean deviation from peak weight ± se = 21.1% ± 2.5, N=10) and Dennis found 3 dead animals on the forest floor from May to August. These changes in weight have been expressed as condition indices and are examined separately for males and females. 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 9) was good during late 1990 and early 1991. As fruit became less abundant (Figure 3) condition declined, many animals remaining in poor condition even as fruit availability increased toward the end of the year. 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.

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). A oneway ANOVA on condition during October, November and December in each year indicated 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 ocurred in fruit biomass and testes size (Figure 10). 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. I performed an ANOVA with testes size as the dependant variable, fruit availability as a random factor 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 so rapidly. The results of this analysis are presented in Table 5 and show a significant interaction between condition and fruit availability. This suggests that some of the factors involved in determining 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 fruit availability in the preceding years.

For females the situation is less clear due to the presence of pouch young and their eviction during the peak fruiting season. Compared with 1992/93 female condition was consistantly poorest through 1991 (Figure 9) and showed a trend of improvement while fruits were abundant. I was unable to perform any analysis on the 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 11). Following this is five months where 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 and the demands placed on the mother by the still small young are at their minimum. Pouch eviction occurs in October when fruits are abundant. Juveniles are left at the maternal nest after pouch eviction. Through October, November and December the young slowly begin to explore and feed themselves until they are weaned in January. 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 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.

Discussion

Musky rat-kangaroos clearly produce young seasonally, a relative rarity among the Macropodoidea, especially in the tropics, and not known in any other Potoroidae (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 (P.M. Johnson pers. comm. 1996). All other macropodoid species that have been studied produce spermatozoa throughout the year. The tammar wallaby *Macropus eugenii* is 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 macropods. This pattern is more reminiscent of other marsupial groups. Some Dasyuridae, such as *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; Wooley 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 reproducing only once a year, this makes them the most fecund of the Macropodoids. 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). P. M. Johnson (pers. comm.) has recently demonstrated that six other macropodoids (five Potoroids and the Bridled Nail-tailed wallaby *Onychogalia 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 has been demonstrated to do so and it is expected that they would rarely, if ever, achieve this in the wild.

Resource Availability

Two of the main food resources of musky rat-kangaroos, litter fauna and fruits, showed seasonal variation in availability (Figures 3 & 4). The variation in abundance of litter fauna was smaller than the variation in the availability of fruits. 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 large (1615:1). Litter fauna are a stable and reliable resource, having low seasonal variation in abundance and high predictability in the years examined. The availability of fruits and seeds is therefore more likely to have been the selective pressure to which the reproductive cycle of musky rat-kangaroos is responding.

Evolution of Reproductive Seasonality

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

The mechanisms of selection for such reproductive traits are clear. The strongly seasonal production of fruits and the unpredictability of peak crop sizes in diferent 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, probably correlates with reproductive potential and certainly reflects, at least in part, the energy invested in sperm production. Similarly, female reproductive output varied between years. 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 at any other time 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; Levey 1991; Mahrino-filo 1991; Moore 1991; White 1994), therefore the evolution of obligate seasonal reproduction is beneficial.

Other frugivore/omnivores of the seasonal tropics, for example two opossums *Caluromys philander* and *Philander opossum* from tropical South America, are known to have a breeding pattern very similar to the breeding pattern of musky rat-kangaroos (Lee and Cockburn 1985). 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.

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. This is suggested by the appearance of the same pattern 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, the pattern of reproduction seen in modern musky rat-kangaroos may have evolved early in their history.

The high fecundity of musky rat-kangaroos is also of clear benefit. The extreme loss of weight (and condition) during poor seasons and the increase in mortality at these times suggests that populations may undergo periodic crashes. High fecundity allows a rapid recovery when conditions improve. Further evidence that populations undergo periodic crashes is apparent from the fact that musky rat-kangaroos do not occur in isolated forest fragments unless they are large (minimum 438 ha) or in very close proximity to continuous forest (Gray unpubl.). Given that individual musky rat-kangaroos have small home ranges (unpubl. data), it appears likely that populations in fragments die out completely in difficult years and are unable to recover because of the species inability to cross intervening pastures.

The number of young carried by females in different years varied 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? We 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 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 macropodoids (e.g. Bolton *et al* 1982). However, this differs from the musky rat-kangaroo case where the number of young may change without complete loss of the litter. Perhaps more 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*, 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 litter size manipulation 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. In addition, females can carry up to three pouch young simultaneously, which is unique to musky rat-kangaroo 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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Table 1. Analysis of variance table for fruit biomass (repeated measure design).

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	0.12	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.

Table 2. Analysis of Variance Table for litter fauna.

Source of Variation	DF	Mean Square	F	P
Litter fauna >2 mm				
Year[1]	1	0.1239	0.28	0.5965
Month[1]	5	2.4846	5.65	0.0001
Year * Month	5	0.6378	1.45	0.2108
Litter fauna >5 mm				
Year	1	0.5687	0.84	0.3617
Month	5	0.6849	1.01	0.4152
Year*Month	5	0.0243	0.04	0.9993

1. Fixed factor.

Table 3. Number of musky rat-kangaroos carrying litters of one, two or three in 1990, 1991 and 1992.

Includes four females which reproduced in two years, one in 1990 and 1992 and three in 1992 and 1992.

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

Table 4. Significant life history events for musky rat-kangaroos.

Dates and ages were estimated from the status of 88 wild trapped adults and juveniles and an arbitrary starting point in the birth season (31st March).

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

Table 5. Analysis of variance table for testes size.

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

Figure 1 Rainfall data during the study period (Bars) with the mean monthly totals (± se) averaged over 11 years from 1984 to 1994 (mean yearly total ± se = 3187 ± 173).

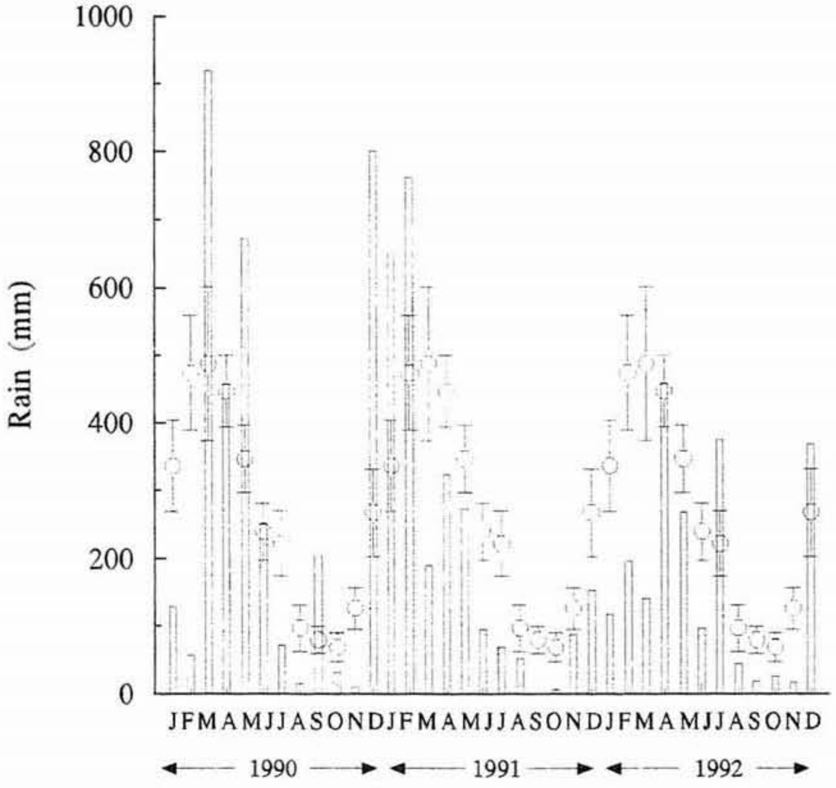

Figure 2 Study site grid showing configuration of transects to examine the availability of fruits and the position of fence traps.

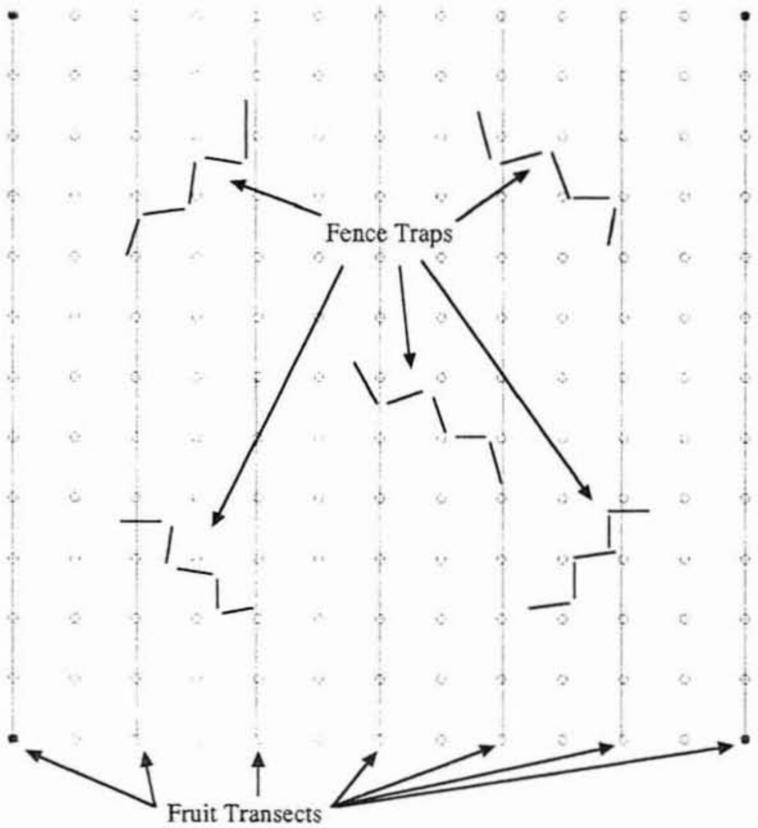

Figure 3 Biomass of fruit species (mean ± se) consumed by musky rat-kangaroos in 1991 and 1992. Biomass is estimated from the parts consumed (i.e. flesh, seeds, or both) from ripe fruits or where these are eaten, green and senescent fruits. Missing data are due to periods of ill health of the chief investigator.

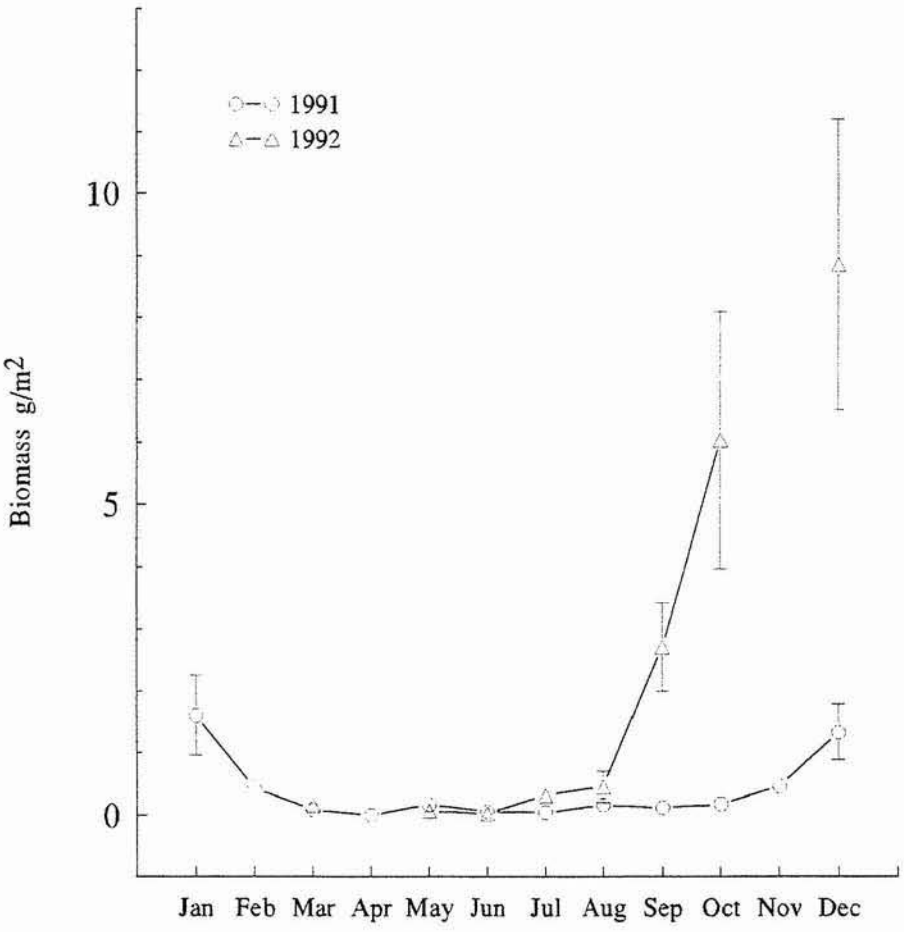

Figure 4 Abundance of litter fauna (mean ± se) on the study site in 1991 and 1992 for animals >5 mm and animals >2 mm.

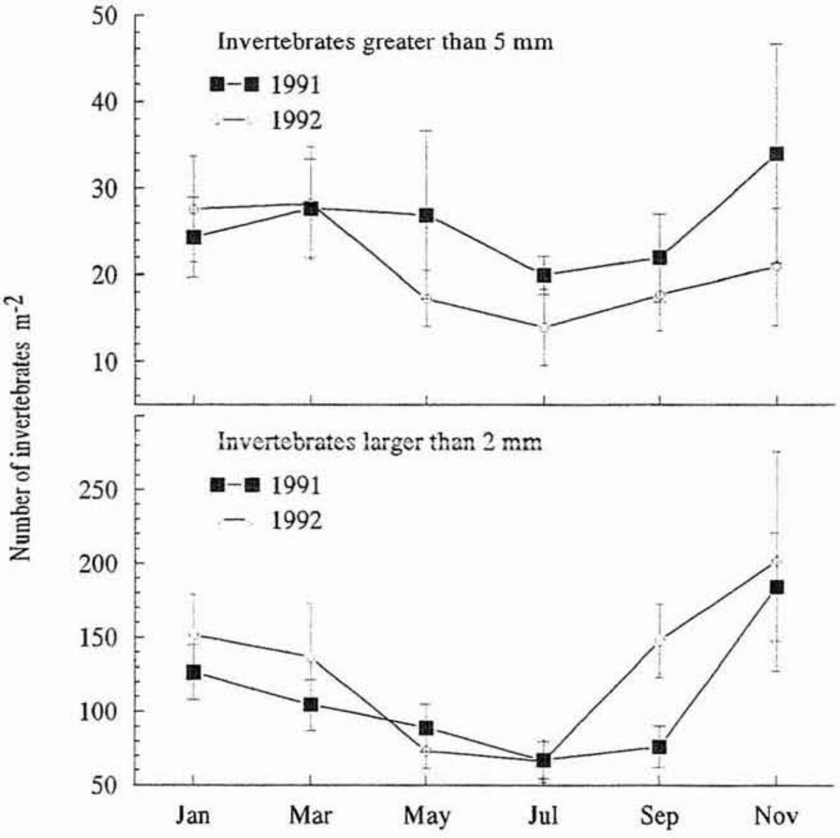

Figure 5 Size of testes (mean area ± se) of musky rat-kangaroos trapped during the study. # - no data due to ill health of chief investigator.

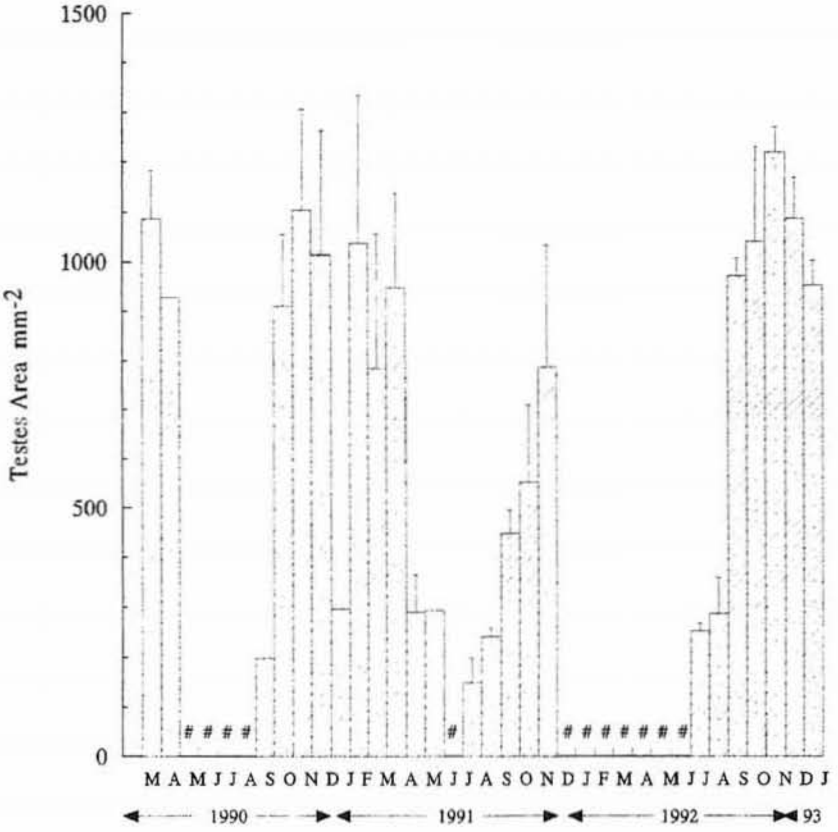

Figure 6 Head length (mean ± se) of pouch young and juvenile musky rat-kangaroos during 1991 and 1992. Data for pouch young are primarily from 1991 and for juveniles are primarily from 1992. The means and se's are calculated from a single measure of each individual.

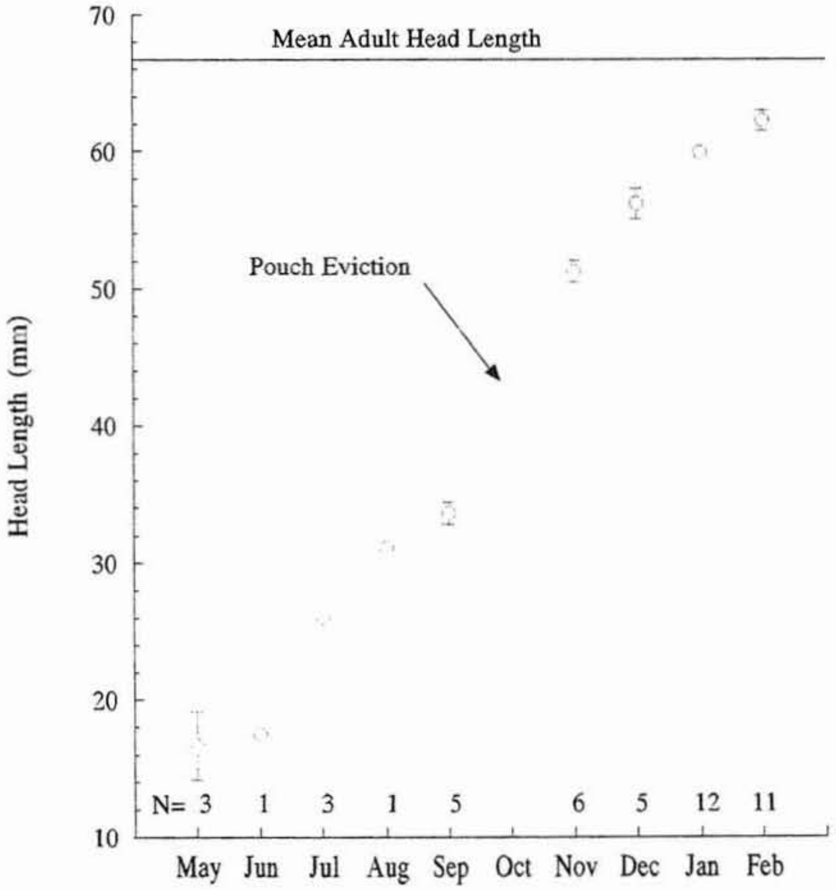

Figure 7 Number of pouch young (mean ± se) carried by musky rat-kangaroos in 1990, 1991 and 1992.

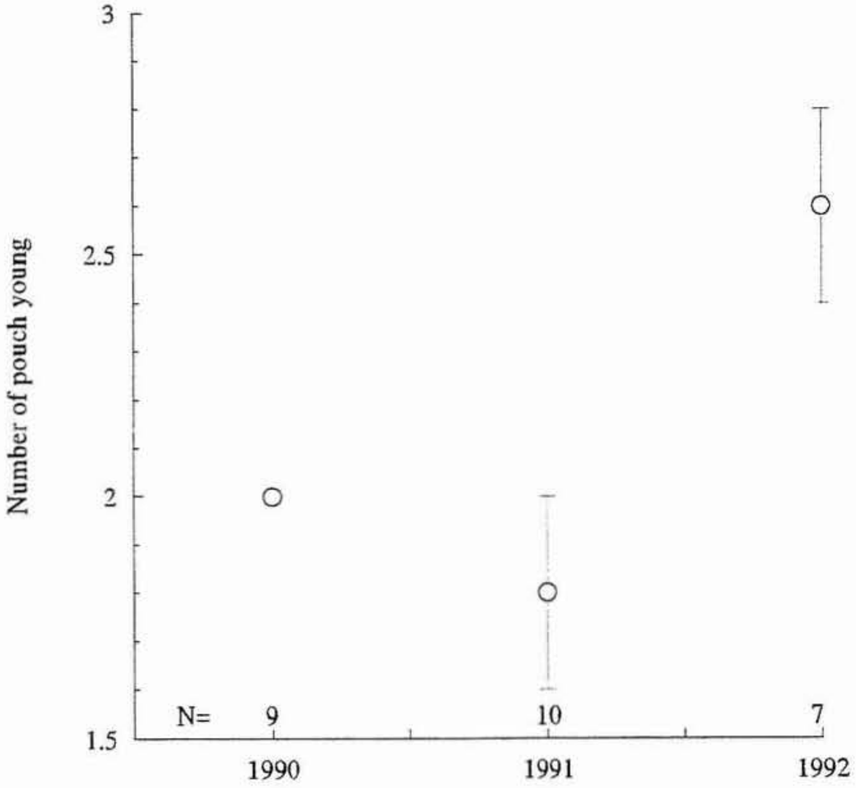

Figure 8 Weights of musky rat-kangaroo pouch young before eviction and juveniles after pouch eviction. No data were available in October because young were left at the nest and did not move about sufficiently to enter traps.

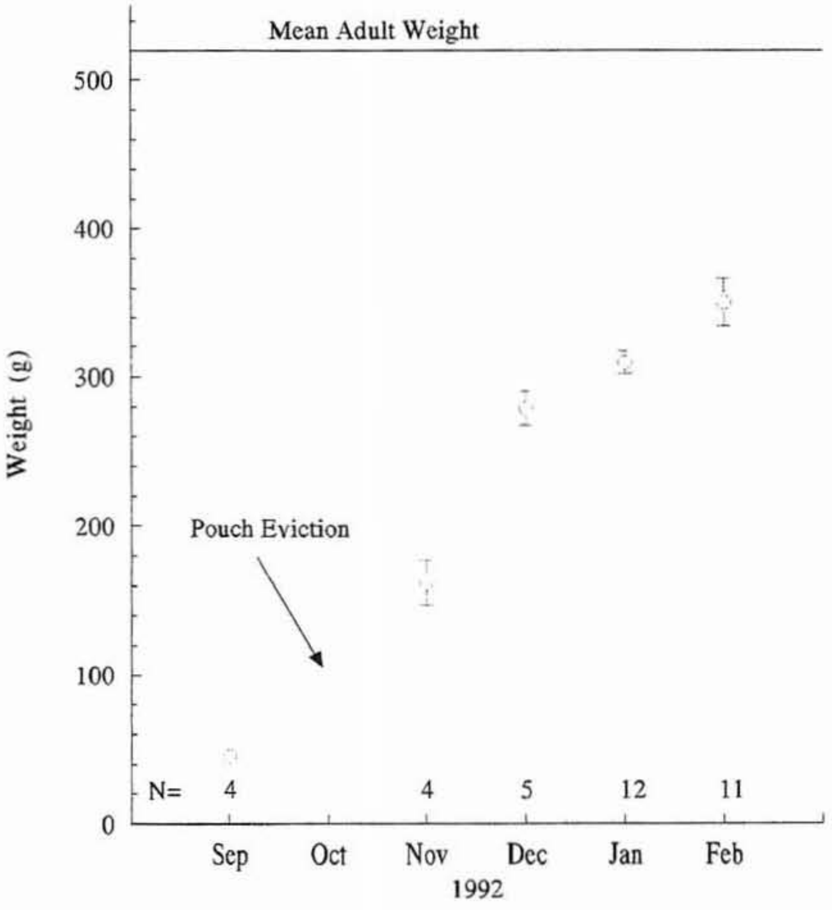

Figure 9 Condition indices (mean ± se; see methods) for male and female musky rat-kangaroos over the study period.

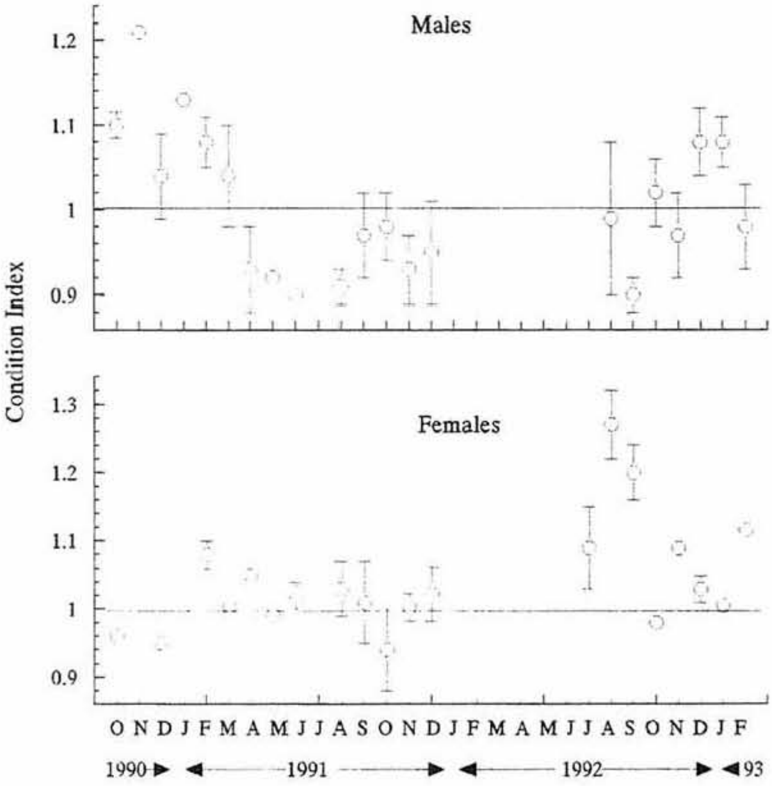

Figure 10 Differences between years (means ± se's) for: testes area; the availability of fruits and seeds; and condition indices during the early breeding season (October to December) in 1990, 1991 and 1992.

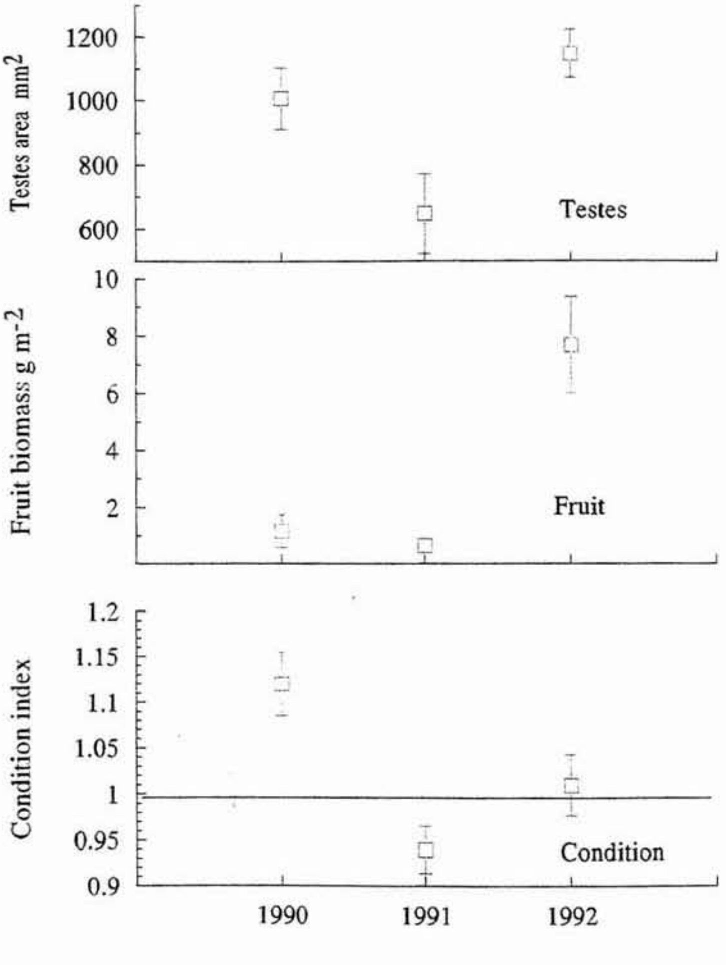

Figure 11 Timing of life history events for musky Rat-kangaroos over a two year period with concurrent changes in fruit availability. Relative fruit biomass (centre) is derived from data for 1991. Although not shown on the figure for ease of reading, adults will reproduce in consecutive years.