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

Chapter 7

POPULATION SIZE AND SPACE USE IN MUSKY RAT-KANGAROOS

INTRODUCTION

To understand the interactions between animals and their environment and resources more fully, it is useful to have measures of population density and movement patterns. As Musky Rat-kangaroos are the only frugivorous macropodoid (Chapter 3) comparisons across phylogenetic groups are appropriate. Clutton-Brock and Harvey (1977) demonstrated a strong correlation between home range area and the diversity of food plants eaten by primates, showing that those with larger ranges consumed a larger number of plant species. Home range size also relates to the way in which a species' deals with seasonal shortages in fruit resources and population density may be regulated by the forest's carrying capacity during resource bottlenecks (Terborgh 1986). Terborgh (1983) found several patterns amongst a community of five primates at Cocha Cashu in Peru. Squirrel Monkeys, *Saimiri sciureus*, are able to feed more extensively on figs during the seasonal shortage of fruits than are two Capuchins (*Cebus apella* and *C. albifrons*) which switch to feeding on alternative resources. This is due primarily to the home range of Squirrel Monkeys being larger than that of the two Capuchins. Two smaller Tamarins (*Saguinus imperator* and *S. fuscicollis*) change their feeding strategies during the period of few fruit to use available resources within a much smaller area than any of the other species. In the peak fruiting period, the diets of all five species are similar (Terborgh 1983).

Given that Musky Rat-kangaroos are small (comparable to Tamarins) and show a tendency to feed more on fungus and invertebrates during periods of low fruit availability (Chapter 3), then I expected they would have small home ranges in which they intensively used the available resources and their population density would probably vary with the intensity of the fruit shortage. In this chapter, I show that at least some Musky Rat-kangaroos maintained small home ranges and their population size tended to vary with the availability of fruits in different years.

METHODS

Population Estimates

The methods used to trap Musky Rat Kangaroos are described in Chapter 6. I trapped from October 1990 until February 1992. However, I use only data subsequent to February 1991 for the purposes of population estimates as the traps were still being refined and established prior to this.

I used capture records in each month as a single trapping period and calculated population size, number recruited and survival rates for an open population model using the Jolly-Seber estimate ("Jolly"; Hines unpubl.). Although the Jolly-Seber estimate has some shortcomings, such as internally derived standard errors, it has the advantage of calculating survival rates, is robust (Begon 1983) and was suitable for my data. Jolly-Seber estimates are based on three assumptions.

1) **All animals have an equal probablility of capture**. By using fence trapping without bait I believe all animals that lived in the vicinity of traps had an equal probability of capture. However, after mapping all spool trails from trapped animals it became clear that the traps did not service all the area of my 9 ha gridded site (Figure 2.2). Therefore, I measured the area encompassed by all spool trails (see below) to convert the population estimate to a measurement per hectare. Coincidentally, the area encompassed by all spool trails was also approximately 9 ha but of a different shape to my study site.

2) **Emmigration is permanent**. I was unable to determine if this was the case for this study. However, a large proportion of animals (51%) were caught only once and not seen again. Either these animals became permanent emmigrants or learned to avoid traps and were never re-captured. If trap-wise animals were present then the population size is under-estimated.

3) The third assumption of the Jolly-Seber estimate, that the **probability of survival is constant for all individuals**, was probably not met as subadults

seem to have higher mortality than adults and may be more likely to emmigrate. The majority of Musky Rat-kangaroo remains found under the roosts of Lesser Sooty Owls, *Tyto multipunctata*, were from subadult animals (Burnett, S. pers. comm.1996) and the time of year that Dingo scats had Musky Rat-kangaroo remains was when subadults had recently become independent (Chapter 10). Violation of this assumption would again under-estimate the population size.

Despite these violations, I believe it is still worthwhile to make an estimate of population size because of the lack of information for this species. In addition, the Jolly program's (Hines unpublished) internal testing procedure (using Chi Square) confirmed that the data were suitable.

Spool and Line Tracking

Spool and line tracking methods are described in Chapter 3. I estimated that each spool represented 3-4 hours of movements and spools were deployed at all times of year. I mapped spool trails (± 2m) using my 300m² grid (Chapter 2). When spool trails went beyond the grid system I used compass bearings and distance from known points of reference to map the trail. As spool trails never went more than 50 m beyond the limits of my grid and a test of accuracy on the original establishment of my grid by a qualified surveyor showed a total error of 2 m in 300 m, I believe spool trail maps beyond the grid are comparable to those within it.

I estimated home range areas from accumulated spool trails for animals that had been spooled more than twice. I calculated the area covered by tracing a line around the extremities of the accumulated trails and, using a digitising tablet (Summa-graphics Summersketch tablet using Sigma Scan) and cross-hair stylus, measured the area. I considered this method comparable to using the 100% minimum convex polygon (Mohr 1947) method of Calhome (Kie *et al.* 1994) because both methods measure the area within the limits of the outer points of reference. Cumulative area curves for increase in home range size with number of spools indicated that in most cases increase in area began to level off quickly (Figures 7.1 and 7.2). However, in only two cases (female 54, female 56) was there a clear asymptote suggesting that the area may continue to increase slightly with added spool trails for the other animals.

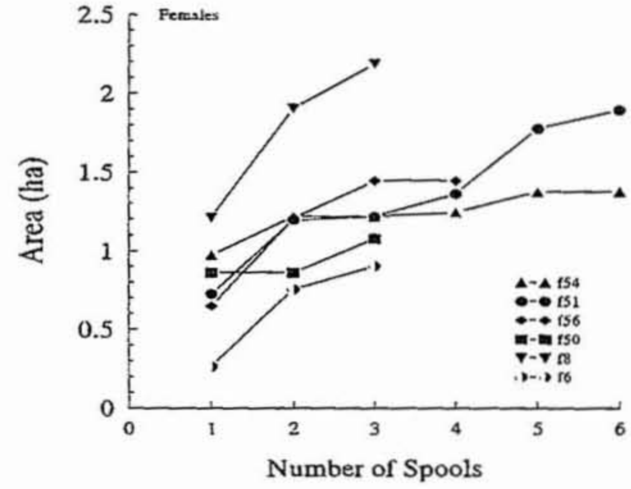

Figure 7.1 Cumulative area with additional spool trails for the home ranges of female Musky Rat-kangaroos.

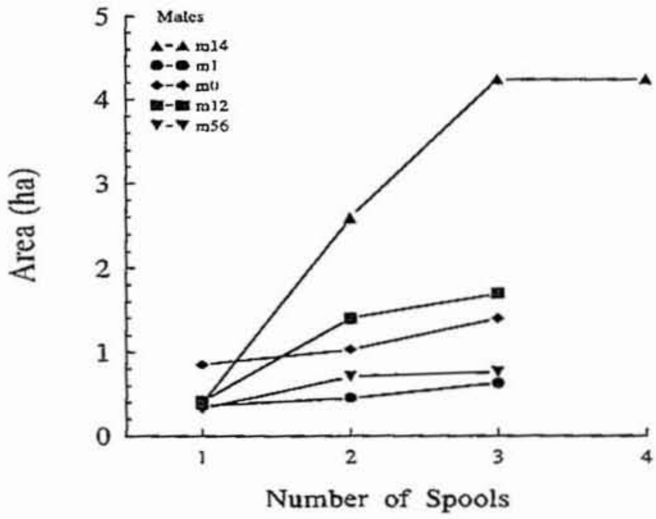

Figure 7.2 Cumulative area curve with additional spool trails for the home ranges of male Musky Rat-kangaroos.

Radio-telemetry

I fitted collar-mounted radio-transmitters (Sirtrack, Havelock North, NZ; 150 - 152 MHz; 1 pulse/second) to 12 Musky Rat Kangaroos and recorded locations based on their position on or near my grid using homing. The transmitters were single stage (11g, approximately 2% body weight) or two stage (17g, approximately 2.75% body weight for larger animals) with lithium batteries housed in an epoxy coating and fitted to a ball-chain collar (Figure 7.3; final design after trying many mounting methods). The whip antenna was attached to the collar for half its length and stood upright at the back of the animal's neck for the remainder.

Figure 7.3 Ball chain collar with radio-transmitter used on Musky Rat-kangaroos.

I attempted to obtain location points at greater than two hourly intervals between 0700 and 1800 hr at least two days each week while animals retained a collar. However, Musky Rat-kangaroos frequently removed their collars so only short term observations were achieved for most individuals. The longest period an animal retained its collar was seven months but due to an intermittant fault in the transmitter only 20 fixes were obtained for this animal.

After trialling radio-telemetry methods with Musky Rat-kangaroos for 15 months I concluded that the animals were unsuited to tracking using telemetry, given the technology available to me at the time. The main problems included: 1) transmitter faults due to extremely wet conditions; 2) interference of direction finding capabilities of the recieving antenna due to large tree trunks and signal bounce (which was exacerbated in wet weather); and 3) inability of Musky Rat-kangaroos to tolerate collars or harnesses. Musky Rat-kangaroos groomed frequently and worried their collars until they were stretched or broken. I ceased using telemetry equipment when an animal was found seriously injured with its forelegs caught in its collar. I collected enough data (Figures 7.4 and 7.5) to estimate home range area for two animals, one male and one female.

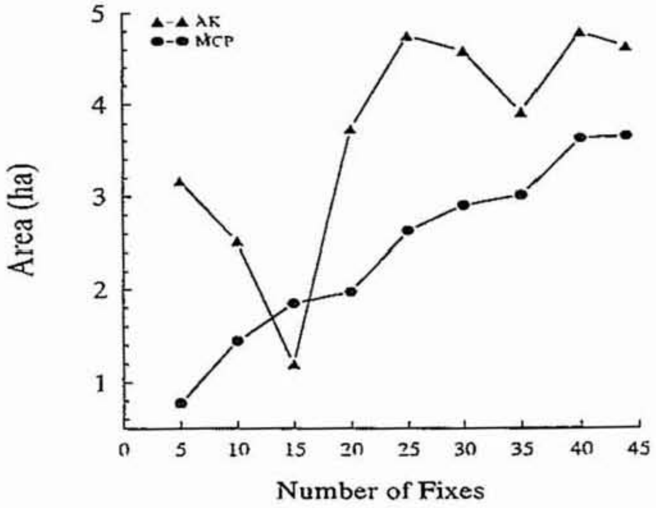

Figure 7.4 Cumulative home range area with increasing number of fixes for male 16. **AK** - Adaptive Kernel; **MCP** - Minimum convex polygon.

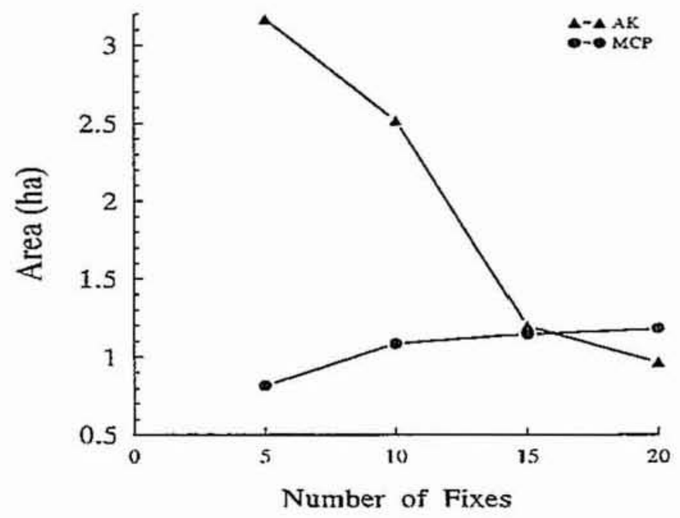

Figure 7.5 Cumulative home range area with increasing number of fixes for female 35. **AK** -Adaptive Kernel; **MCP**- Minimum Convex Polygon.

The graph of cumulative increase in home range area with increasing number of fixes for male 16 would suggest that the maximum extent of his range was not yet determined (Figure 7.4). The home range estimate using Adaptive Kernel analysis (Worton 1989) stabilised at 4.6 ha (95% isopleth). This suggests that the minimum convex polygon estimate was not complete. For female 35, the minimum convex polygon estimates stabilised while the adaptive kernel estimate was below the minimum convex polygon estimate suggesting estimates for female 35 were more accurate than those for male 16.

RESULTS

Population Size

Musky Rat-kangaroo population density ranged from 1.4 to 4.5/ha on my study site during 1991, 1992 and January 1993 (Figure 7.6; mean 2.4 ± 0.31 SE).

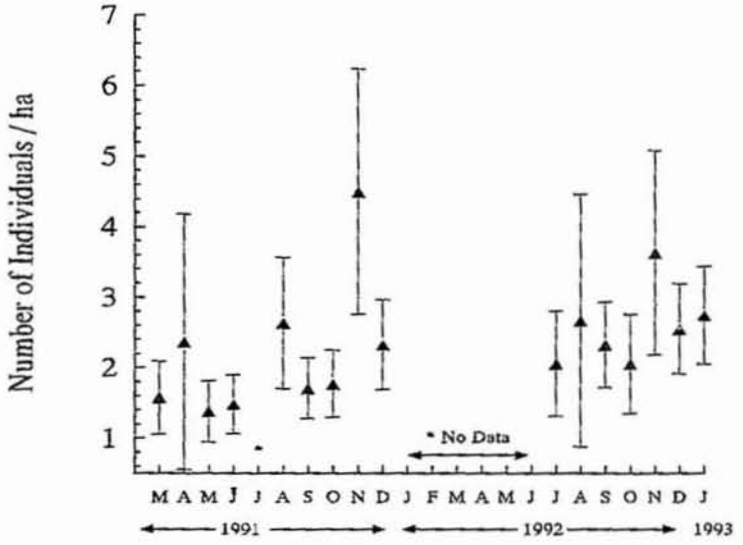

Figure 7.6 Musky Rat-kangaroo population estimates (± SE) for my study site during 1991, 1992 and early 1993 (Jolly-Seber esimates).

The validity of these estimates of population parameters are limited by the small sample size and failure to meet at least one of the assumptions inherent the Jolly-Seber method. However, the density estimates agree with measures of the number known to be alive (Figure 7.7).

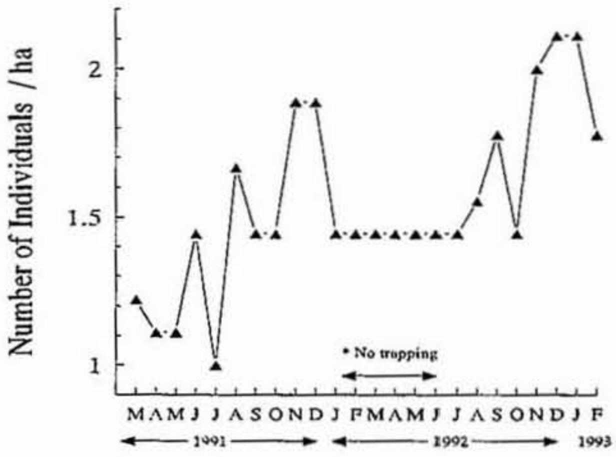

Figure 7.7 Density of Musky Rat-kangaroos known to be alive on my 9 ha study site in 1991, 1992 and 1993.

The maximum number known to be alive in any one month was 2.1/ha for December 1992 and January 1993 and fence traps did not appear to catch all animals on the site. The pattern of change in the number of animals known to be alive is similar to the pattern of Jolly-Seber estimates and suggests a slightly larger population in 1992 than 1991.

The high population estimate in April 1991 may have been due to Musky Rat-kangaroos being more mobile and in search of food due to the extreme shortage of fruit (Chapter 4) and therefore more prone to being trapped. In August 1991, the high estimate may be due to no animals being caught in July. In July 1992, all nine animals caught were recaptures, whereas in August 1992 changes in the population that had occurred in the six months without trapping became evident with two new animals being caught, resulting in an elevated population estimate. The recruitment estimates (Figure 7.8) show a similar pattern in April and August 1991 and August 1992 as that in the population estimates (Figure 7.6) and are probably due to the same data anomolies. In both 1991 and 1992 the highest population estimates occurred in November, the time of year that juvenile Musky Rat-kangaroos began to wander away from the maternal nest and enter traps (Chapter 6). Thus, the November increases in population size related to recruitment of juveniles into the trappable population, which is demonstrated by recruitment estimates (Figure 7.8).

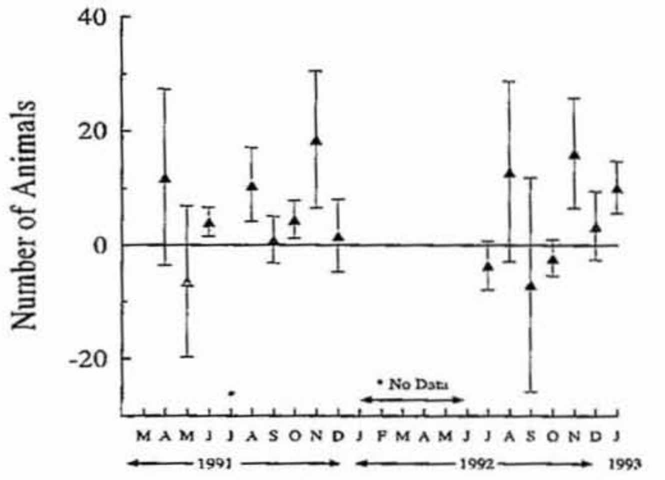

Figure 7.8 Mean (± SE) recruitment estimates of Musky Rat-kangaroos in 1991 and 1992.

The mean population size in 1991 (2.2\ha ± 0.32) was slightly below that for 1992 (2.6\ha ± 0.2) although not statistically different (t-test t = -0.9287, DF = 14, P = 0.3688). Fruit availability was greater in 1992 than in 1991 (Figure 4.7) and while fruit biomass during the seasonal trough was similar in both years, a significant increase in available fruit began earlier in 1992 (July) than in 1991 (November). This shortening of the resource bottleneck was coincident with better condition in Musky Rat-kangaroos (Figure 6.7), more rapid attainment of adult weight by subadults (see Chapter 6) and a greater survival rate (Figure 7.9; three of the urvival rate estimates were calculated as greater than one and were adjusted to one).

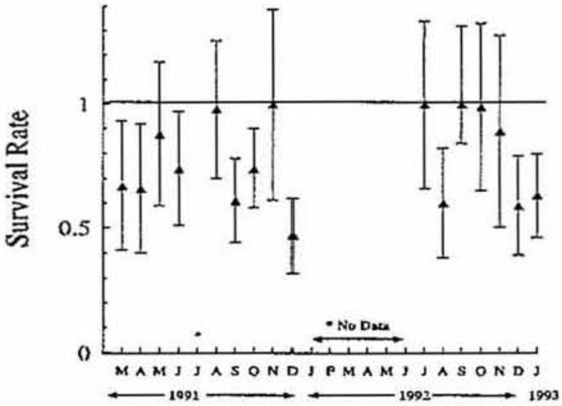

Figure 7.9 Survival rates (± SE) for Musky Rat-kangaroos during 1991 and 1992.

While the mean survival rate in 1991 (0.75 ± 0.06 SE) was lower than in 1992 (0.81 ± 0.07), the two were not statistically different (t-test t = -0.672, DF = 14, P = 0.509). However, during 1991 I encountered three dead animals during the period of few fruit whereas in 1992 I encountered none, suggesting that mortality may have been greater in 1991.

Musky Rat-kangaroo Movements

Home Range Area

Musky Rat-kangaroos resident on my study site occupied small home ranges (0.76 to 4.2 ha) and remained within those ranges for long periods (up to 17 months recorded; Table 7.1). All animals that were re-trapped, with the exception of a juvenile male, were re-trapped in the same vicinity as their original capture, regardless of the interval of time between captures (from one to 17 months). In addition, radio-tagged individuals were frequently located at points near opposing extremes of their ranges in one day so that both short term (one day) and long term (four to seven months) locations covered similar ranges of movement. I tested for differences in the distance between four fixes (all six combinations of fixes) in one day in January 1991 and one day in April 1991 and the distances between fixes taken in January to those taken in April for the Musky Rat-kangaroo male 16. A oneway Analysis of Variance showed that the mean distance between fixes taken in one day (January 165 m ± 31 SE; April 119 m ± 22 SE) was not different from the mean distance between fixes taken three months apart (January to April 112 m ± 26 SE; April to January 186 m ± 33 SE; F = 1.59, DF = 3,20, P = 0.2231). This and the fact that, in the short term, thread from the 460 m spools fitted to Musky Rat-kangaroos remained in a confined area within which the spool trail doubled or tripled back on itself (e.g. Figure 7.10) suggest that Musky Rat-kangaroos tend to cover most of their range in a day and three or more spool trails for an individual is sufficient to give an indication of their pattern of movements. The one exception to this was male 14 who, although trapped four times in either of two traps, on one occasion walked in one general direction for a straight line distance distance of 220m before his spool trail ended. The event was during the breeding season and may have been related to searching for mates.

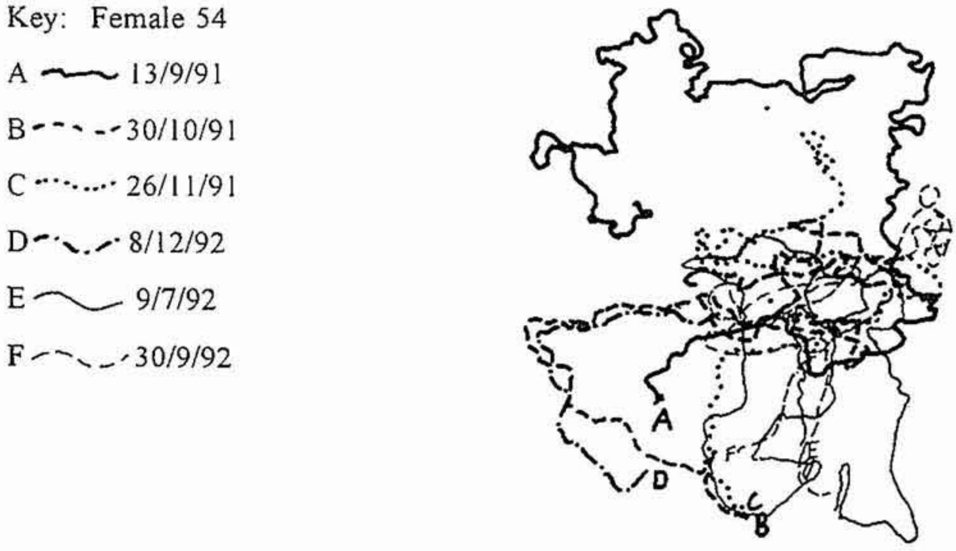

Figure 7.10 An example of cumulative spool trails for the Musky Rat-kangaroo female 54.

Table 7.1 Estimated home range areas (ha) for Musky Rat-kangaroos during the study showing the number of months between the first and last records. Estimates are based on both spool and line tracking records (* = number of spool trails) and radio telemetry data (Bold: # = number of fixes).

Individual	# Records	# Months	Area (ha)
Male 16	**#45**	**4**	**3.7**[1]
Male 6	*3	1	0.8
Male 1	*3	10	0.6
Male 12	*3	11	1.7
Male 14	*4	13	4.2
Male 0	*3	17	1.4
Mean (± SE) males	*3.2 ±0.2	9.3 ±2.4	2.1 ±0.62
Female 35	**#20**	**7**	**1.2**[1]
Female 6 (subadult)	*3	2	0.9
Female 8	*3	13	2.2
Female 56	*4	13	1.4
Female 59	*3	13	0.8
Female 54	*6	15	1.4
Female 51	*6	15	1.9
Female 50	*3	17	1.1
Mean (±SE) females	*4.2 ±0.6	13.3 ±1.2	1.4 ±0.18

1. Minimum convex polygon estimate.

Home Range Overlap

There was no evidence of territoriality in Musky Rat-kangaroos. Home ranges overlapped extensively within and between each gender (Figure 7.11). In addition to the 13 ranges shown in Figure 7.11, the ranges of an unknown number of other individuals, including at least one male and one female whose ranges are not shown (radio-tagged individuals), also occurred on the study site. A minimum of 19 (2.1/ha Figure 7.7) animals were known to be alive on the site in November and December 1992 and the Jolly-Seber population estimates suggest the number of animals on the study site may have been up to 40 at its peak (4.4/ha Figure 7.6). The home range overlap between individuals is therefore far more extensive than Figure 7.11 demonstrates.

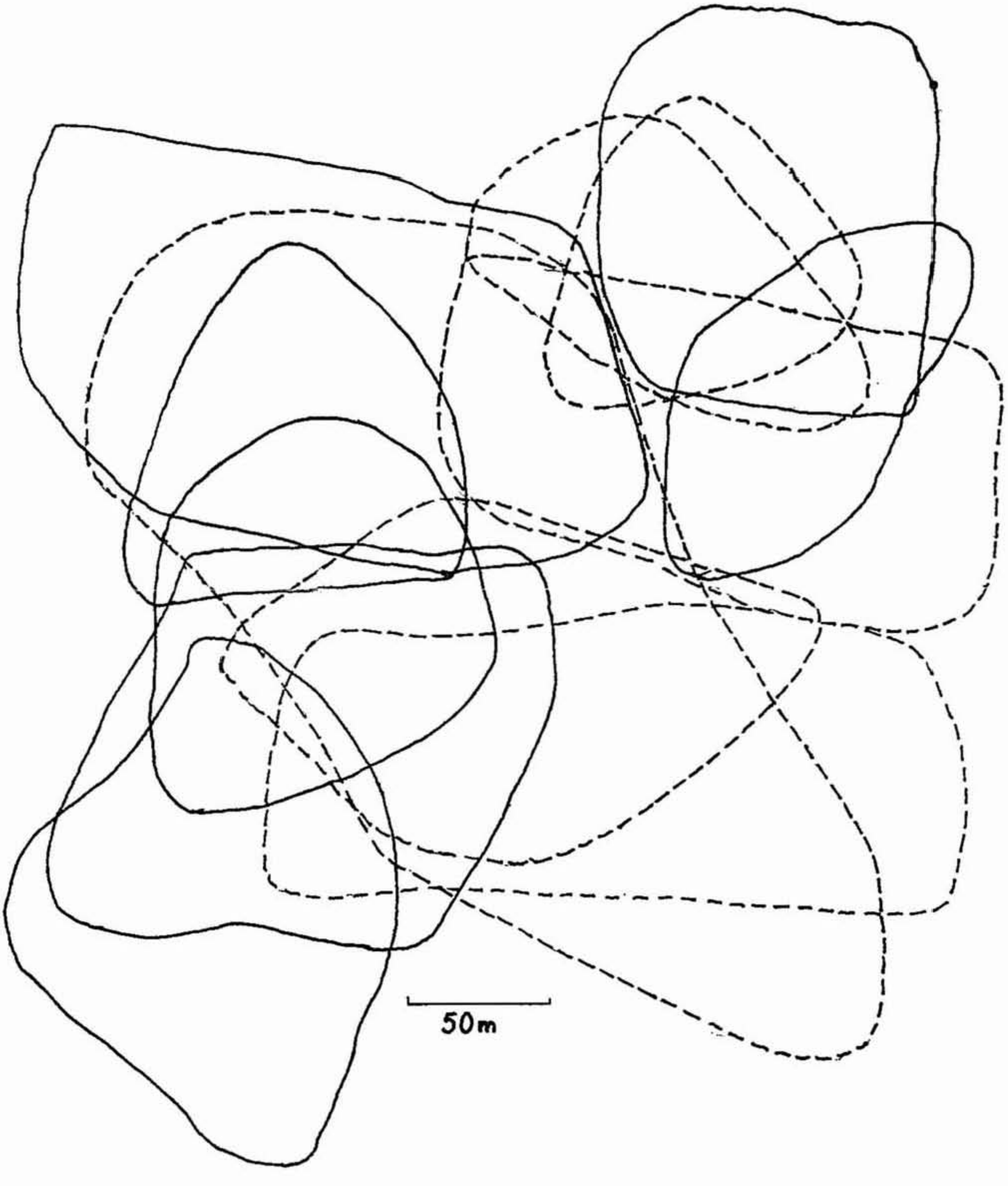

Figure 7.11 Overlap in home ranges for 13 Musky Rat-kangaroos (measured by spool and line tracking). The dashed line represents males and the solid line is females. The four black dots represent the corners of my gridded site.

DISCUSSION

Population Size

Although the data did not show statistical differences in population size between years, there was some indication both in the Jolly-Seber estimates and the minimum number known to be alive that the density of Musky Rat-kangaroos on my study site was lower in 1991 than in 1992. In addition, the mean survival rate was lower in 1991 than 1992. The period of fruit scarcity varied from eight months in 1991 to five months in 1992 (Chapter 4; measured as fruit biomass being below 0.4 g/m^2). These data coupled with the Musky Rat-kangaroos high fecundity (relative to other macropodoids) and extreme loss of condition during periods of fruit scarcity (Chapter 6) suggest that the population density of Musky Rat-kangaroos may be regulated by a yearly resource bottleneck in fruit availability.

Several years with long periods of fruit scarcity may cause populations to undergo serious declines. The high fecundity of Musky Rat-kangaroos (see Chapter 6) is also of clear benefit in this situation. 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 the fragments are large (minimum 438 ha) or in very close proximity to continuous forest (Gray unpubl.; pers. obs.). Given that individual Musky Rat-kangaroos have small home ranges (see Chapter 7), 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.

Movement Patterns

Musky Rat-kangaroos had small home ranges within which they switched to feeding on fungi and invertebrates during periods of few fruit (Chapter 3). However, I retrapped a larger number of females (on more than two occasions) than males and therefore was able to obtain more home range estimates for females (Table 7.1). Given that the sex ratio of Musky Rat-kangaroos was biased toward males in all age groups (62% males; Chapter 6) this is a surprising result. One possible explanation is that Musky Rat-kangaroos display two patterns of movements, one being more nomadic or wide ranging while the other is more sedentary. An alternative explanation is that males become trap shy. Other macropodoids are known to have a dispersal phase in which young animals have much larger ranges than adults until they settle into one place (Johnson 1989). Considering the male biased sex ratio in Musky Rat-kangaroos and the smaller number of males recaptured more than twice, it is likely that a proportion of males are more wide ranging than the sedentary population. However, there was no evidence to suggest that young females showed a higher degree of philopatry than males. Seventy one percent of juvenile and subadult females were caught only once whereas 45% of young males were caught only once. However, there was no statistical difference between the numbers of each gender caught only once (Chi Square 2.33, $DF = 1$, $P = 0.1266$). This is similar to findings for the Long-nosed Potoroo, *Potorous tridactylus*, where both genders disperse (Johnson 1989). However, many other macropods including another Potoroid are philopatric or show male-biased dispersal from the natal area which appears to be accompanied by slightly male biased sex ratios (Johnson 1989).

Comparisons with other Terrestrial Frugivores

I estimated the biomass of Musky Rat-kangaroos to be 125 kg km^{-2} based on their mean population density (2.4/ha) and average adult weight (520 g). Terborgh (1983) estimated that Acouchies (500 g body weight and ecologically similar to Musky Rat-kangaroos) at Cocha Cashu (Peru) had a biomass of only 2 kg/km^2. However, the diversity of diurnal, terrestrial frugivores at Cocha Cashu was greater and in addition to Acouchies included: Agoutis (2 kg body weight); Coatis, *Nasua nasua* (2.5 kg body weight); and squirrels (600 g body weight). Despite the higher diversity of diurnal terrestrial frugivores their combined biomass is still below that of the Musky Rat-kangaroo (43 kg/km^2 compared to 125 kg/km^2). Cassowaries are the only other diurnal, terrestrial frugivores in Australian rain forests and in high density areas, such as Mission Beach, total 150 kg/km^2 (data from Bentrupperbaumer, J. pers. comm.1997) which brings the total biomass of this class of frugivore to 275 kg/km^2 in Australian forests. The large difference in diurnal terrestrial frugivores between sites can be explained by the diversity and biomass of all frugivores. The most significant frugivore group at Cocha Cashu, the primates (650 kg/km^2; Terborgh 1983), is entirely lacking from Australian forests and the total number of primarily frugivorous mammals in Australia's wet tropics is five species (Jones and Crome 1990) compared to 28 species at Cocha Cashu (excluding Bats).

Both Acouchies and Agoutis differed from Musky Rat-kangaroos in having partially defended home ranges occupied by family units or bonded pairs (Dubost 1988; Smythe 1978) whereas Musky Rat-kangaroos occupied solitary ranges which overlapped considerably with conspecifics of both genders. In addition, Acouchy and Agouti ranges were small in comparison to Musky Rat-kangaroo ranges. Acouchi home range areas covered 0.65 to 1.2 ha while Agoutis, a much larger species, occupied ranges from 2 to 5 ha (Dubost 1988; Smythe 1978). There appear to be no phylogenetic constraints on Musky Rat-kangaroos developing social systems similar to Agoutis and Acouchies as Macropodoids are known to form monogamous pairs (Horsup 1996; Seebeck *et al.* 1989) and various other social groups (Croft 1989). Therefore, the difference in social and spatial patterns between otherwise ecologically similar species may again relate to a higher diversity of terrestrial frugivores in South America than Australia, necessitating different spatial and social strategies to deal with interspecific competition for resources.

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Plate 8 Musky Rat-kangaroo using cable root as a pathway.

Chapter 8

SEED DISPERSAL BY MUSKY RAT-KANGAROOS

INTRODUCTION

Plant propagules are dispersed in a variety of ways including by animals, on wind, in water, and by a variety of self dispersal mechanisms such as explosive pods (see Chapter 1, "Modes of Dispersal"). In tropical rain forests most fruits are fleshy and adapted for dispersal by animals (Howe and Smallwood 1982). In Australian rain forests between 70 and 95% of species produce fleshy fruit, depending on the site (Jones and Crome 1990; Webb and Tracey 1981).

With the exception of studies on a few frugivorous birds (Crome 1975a; Crome 1975b; Crome 1976, Stocker and Irvine 1983; Bentrupperbaumer, J. unpubl.] and some studies of a few tree species (Harrington *et al.* 1997; Osunkoya 1994; Irvine, A. unpubl.; Harrington, G. pers. comm. 1996), little is known of frugivory and dispersal in Australia's tropical rain forests. Frugivorous mammals are the most poorly known group, and despite the large proportion of fleshy fruited plant species, non-flying mammals are few in number relative to other tropical countries. The low diversity of non-flying mammals known to eat primarily fruits is a product of a relatively low diversity of mammals (Jones and Crome 1990) and the lack of investigation.

In Chapter 3, I demonstrated that Musky Rat-kangaroos are predominantly frugivorous, eating the fruits of at least 44 species of plants from 23 families. This is not an exhaustive list as the majority of the observations are from one very small area. Given their diet and terrestrial nature one might expect them to behave similarly to other terrestrial frugivores living in tropical rain

Agoutis (*Dasyprocta* spp.) and Acouchies (*Myoprocta* spp.) of Central and South America are well known as scatterhoarders of fruits and seeds (Smythe 1978; Dubost 1988). While Agoutis are much larger animals (4 - 5.9kg; Dubost 1988) than Musky Rat-kangaroos (0.4 - 0.62kg), Acouchies are only slightly larger (1 - 1.45kg; Dubost 1988). All species are diurnal, terrestrial frugivores (see Chapter 1, Table 1.4) and are subjected to intra-specific competition for resources and a seasonal fluctuation in food availability. It is therefore likely that Musky Rat-kangaroos also scatterhoard fruits and seeds.

In this chapter, I demonstrate that Musky Rat-kangaroos disperse fruits and seeds and examine the distance they are dispersed and how many fruits and seeds are dispersed.

Plate 9 Musky Rat-kangaroo dispersing the fruit of a Tarzali Silkwood, *Cryptocarya oblata*.

METHODS

Observations of Behaviour

I used four methods to observe the behaviour of Musky Rat-kangaroos: **1)** from a mobile observation platform; **2)** from a hide; **3)** at a feeding station; and **4)** using radio-tracking. The mobile observation platform and hide are described in Chapter 3. Radio-telemetry equipment and its use are described in Chapter 7.

The feeding station was directly behind my home in rain forest that was contiguous with my study site, 4km away. I used 10x25 binoculars to observed the station from the back door of my house (10m away). I placed baits (banana and sweet potato) within an area of 4m^2 at 0700hr or 1600hr daily during June 1991 and recorded Musky Rat-kangaroo behaviour. After June 1991, I continued with haphazard baiting and observed behaviours without recording them. Table 8.1 lists the four methods I used, the time engaged in each, the number of encounters with Musky Rat-kangaroos and the average time spent before I made one observation of a Musky Rat-kangaroo.

Table 8.1 Summary table for each method of observation used to examine Musky Rat-kangaroo behaviour. Showing: 1) hours spent in method; 2) The total number of sightings; and 3) the average number of hours spent for each sighting.

Method	Hours	# Sightings	Hours/Obs.
Mobile Observation Platform	17.4	9	2
Hide	22.8	5	5
Feeding Station	31.4	15	2
Radio-telemetry	103.7	71	0.7
Total	**175.1**	**100**	**1.67**

Spool and Line Tracking of Fruits

To determine how far, where and how many fruits were cached by Musky Rat-kangaroos I developed a technique of spool and line tracking fruits. Initially, I tried attaching cotton bobbins (size 10, Penguin Threads) to native fruits. Success was limited due to difficulties in attaching cotton bobbins to fruit. Therefore, I used "simulated fruits". Each simulated fruit consisted of a cotton bobbin housed in clear plastic wrap and Gaffa tape, which was placed inside a chinese date. The resulting "fruit" resembled an aging Sankey's Walnut *Endiandra sankeyana* and was palatable to most frugivorous animals.

Apart from Cassowaries, Musky Rat-kangaroos are the only known diurnal, terrestrial frugivores in Australia's tropical rain forests. Therefore, fruits were placed on the forest floor during daylight hours. This ensured that nocturnal frugivores (rodents) did not handle the fruits. All handling of simulated fruits was attributable to Musky Rat-kangaroos. This was confirmed, when possible, by examining teeth marks left in dates. The few avian frugivores that forage on the ground leave obvious marks in fruit (Catbird, Tooth Billed Bowerbird) or ingest it whole (Cassowary). I found no evidence to suggest that any frugivores other than Musky Rat-kangaroos interfered with the simulated fruits.

Simulated fruits were set in clusters of three (September 1994) or 10 (November 1995) on the forest floor. The trailing end of each cotton bobbin was tied to a conveniant root or sapling. Clusters were placed at 24 sites over a broad area which encompassed two ridges, two slopes and a gully. Each cluster was placed on the forest floor between 0630 and 0730hr. They were then checked between 1700 and 1900hr daily for three days and then removed. Each evening those fruits that remained untouched were removed and replaced the following morning. Those fruits that had been cached by a Musky Rat-kangaroo during the day were left overnight and checked early the next morning. None was interfered with by nocturnal animals. I chose a length of three days to leave simulated fruits out based on the results of my experiments in 1994 where eighteen simulated fruits were left out for two weeks. All handling of fruits by Musky Rat-kangaroos occurred within the first three days. The remainder of the time they remained undisturbed.

Each time the simulated fruits were checked their status was recorded in the following way: 1) untouched; 2) eaten *in situ*; 3) moved and eaten; or 4) cached. For each fruit that was moved, I measured the straight line distance from its origin to its final resting point. If the distance moved was <5m the fruit was re-classified as eaten *in situ*. I estimated a fruit needed to be moved >5m to be outside a fruitfall, and therefore dispersed, for most species consumed by Musky Rat-kangaroos. For those that were cached, I described the cache site including: 1) depth buried (± 0.25cm); 2) immediate cover (leaves, twig, root, log etc.); 3) density of the surrounding vegetation (number of stems within 50cm); 4) distance to nearest object (± 0.5cm); and 5) evidence of teeth marks in the cotton bobbin which was taken as evidence of attempted predation of the seed.

Estimating the Number of Fruits Moved

I estimated the number of fruits moved by Musky Rat-kangaroos based on data obtained from fruit transects (see Chapters 3 & 4) and fruit spooling experiments (see below). I used the following equation:

$$D/ha = \#H/0.42 * 47/92 \qquad \textbf{Equation 8.1}$$

Where: **D/ha** is the number of fruits cached or dispersed (>5m) per hectare; **#H** is the number of fruits along transects which had Musky Rat-kangaroo teeth marks in each month (Chapter 3); **0.42** is the area (ha) covered by the transects; and **47** was the number of simulated fruits which were cached or moved >5m and **92** was the number of simulated fruits with teeth marks that were left *in situ*. I then added the number of fruits cached or dispersed (D/ha from equation 8.1) to the number handled along transects in each month (#H/0.42) to estimate the total number handled (Ntot):

$$Ntot/ha = D/ha + \#H/ha \qquad \textbf{Equation 8.2}$$

To calculate the number cached, I used equation 8.1 replacing 47 with 35, which was the number of simulated fruits that were cached. I calculated 95% confidence intervals for the estimates of the number of fruits cached (scatterhoarding was the behaviour most significant to plants: Chapter 9) using standard probability expression and Bayes' theorum (Hunter, J. pers. comm. 1996; Appendix 2).

Estimations of the number of fruits dispersed or cached were based on the number along fruit transects found with Musky Rat-kangaroo teeth marks (see above). However, fruits with teeth marks counted along transects clearly do not represent the total number of fruits that have fallen and been handled during each month. The decomposition of fruits is very fast, particularly after they have been partially consumed by an animal. Based on observations of regularly-visited ripe fruit on the forest floor, I estimated that identification of an animal whose teeth marks were in fruit would become impossible after three to five days. Consequently, I was unable to identify the predator for 33% of partially eaten fruits along transects. Thus I considered each month's count of the number of fruits handled by Musky Rat-kangaroos to be for the previous five days. Therefore, to get a more realistic estimate of how many fruits were handled and cached I have corrected the estimate from Equations 8.1 and 8.2 for the number of days in each month assuming that each monthly measure represented only five days of activity.

RESULTS

Behaviours Resulting in Dispersal of Seeds

Musky Rat-kangaroos have three main patterns of behaviour at a fruit fall (or a feeding station). Either they: 1) feed *in situ*, taking small amounts of flesh from several fruits (up to 9; 10/29 observations); 2) choose a fruit and immediately leave the area to consume it or cache it (12/29 observations); or 3) begin to feed and are displaced by a conspecific (7/29 observations). Behaviours two and three both result in dispersal of seeds outside the fruitfall area.

Displacement at Feeding Sites

I recorded individual Musky Rat-kangaroos being displaced by conspecifics at fruitfalls on seven occasions but observed this behaviour regularly (without recording it) while I was involved in other activities. On only one occasion did I record two animals feeding at a fruitfall in close proximity, although I witnessed up to five animals feeding under a single, very large fruitfall. At the feeding station, displacement of conspecifrcs followed a regular pattern which is described below.

Individual Musky Rat-kangaroos entered a fruitfall area cautiously. An individual usually meandered around the area sniffing the litter surface. On finding a suitable fruit (usually some were passed over) the Musky Rat-kangaroo would pick it up in its mouth and sit back on its hind feet, transferring the fruit to its hands to manipulate it and feed on the flesh. When a conspecific approached, the Musky Rat-kangaroo transferred the fruit back to its mouth and ran away from the fruit fall area. The distance Musky Rat-kangaroos carried fruits ranged from 5 - 50m (unpublished observation; Irvine, A. pers. comm.1992). The Musky Rat-kangaroo would then stop and consume the flesh of the fruit and either drop the seed, consume it or cache it. Once the flesh and/or seed were consumed the Musky Rat-kangaroo would often return to the fruitfall and displace the animal that had displaced it. The newly displaced animal would also carry off a fruit. I saw this reciprocated displacement continue for up to four displacement events. There did not appear to be an age or gender based hierarchy with respect to this form of displacement as I witnessed a subadult displace an adult and both sexes displacing members of the same and opposite sexes.

Scatterhoarding

I first witnessed scatter hoarding behaviour while in a mobile observation platform at a fruitfall of Baileyoxylon, *Baileyoxylon lanceolatum*. An individual Musky Rat-kangaroo approached the fruitfall, chose a fruit and ran approximately 5m away. It consumed the flesh while manipulating the fruit in its hands, then transferred the seed to its mouth, scratched a shallow hole in the litter, dropped the seed into the hole and pushed it into the soil with its nose. The Musky Rat-kangaroo then covered the area with leaf litter, which it manipulated using its nose and mouth, and left the area. I subsequently witnessed scatter hoarding on two other occasions and indirectly observed caching behaviour during spool and line tracking of Musky Rat-kangaroos (Chapter 7). These observations led to the development of a method of spool and line tracking fruit to determine how far, where and how many fruits were cached and/or dispersed in the ways described above.

Sizes of Fruit Moved and Cached

I observed Musky Rat-kangaroos carrying the fruits of 11 species of plants. Their size classes ranged from three to six (Table 8.2; see Chapter 4 for description of size classes) which includes the largest size classes of fruit available.

Table 8.2 Size classes and species of fruit carried by Musky Rat-kangaroos and therefore potentially scatter hoarded or dispersed.

Common Name	Latin Name	Size Class
Blue Quandong	*Elaeocarpus angustifolia*	3
Brown Pine	*Podocarpus dispermus*	3
Baileyoxylon	*Baileyoxylon lanceolatum*	4
Brown Tamarind	*Castanospora alphandii*	4
Fontain's Blushwood	*Fontainea picrosperma*	4
Plum Boxwood	*Neimeyera prunifera*	4
Almond Bark	*Prunus turnerana*	4
Austrobaileya	*Austrobaileya scandens*	5
Boonjee Blush Walnut	*Beilschmiedia volckii*	5
Watergum	*Syzygium gustavioides*	5
Omphalea	*Omphalia queenslandiae*	6

Spool and Line Tracking of Fruits

Musky Rat-kangaroos appeared not to differentiate between simulated fruits and real fruits. The flesh was partially or wholly devoured from simulated fruits, the cotton bobbins were cached instead of a seed and in some instances animals attempted to eat the cotton bobbins. Simulated fruits were cached either entire, partially eaten or as the seed (bobbin) only.

A total of 248 simulated fruits were placed on the forest floor. Forty four percent remained undisturbed after three days. The majority (56%) were either eaten *in situ* (moved <5m), moved and eaten (>5m) or cached (Figure 8.1). Those fruits moved >5m were moved a mean distance of 16.51m (± 2.08 SE). Those from which the flesh was consumed and the cotton bobbin was left on the litter surface were carried a mean distance of 15.2m (± 2.9 SE). While those that were cached were carried a mean distance of 17m (± 2.7 SE). The maximum distance a simulated fruit was moved was 68m in a caching event.

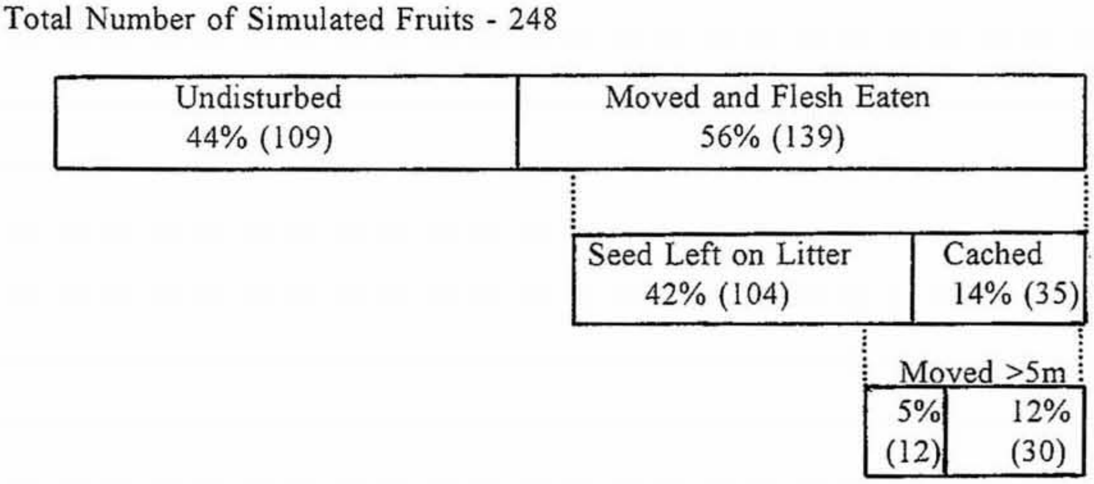


Figure 8.1 Final fate (at the end of three days) of simulated fruits during spool and line tracking experiments. All percentages based on total number (248).

Figure 8.1 represents a broad summary of the ultimate fate of simulated fruits. Some fruits were handled in a complex series of events over the three day period. Table 8.3 lists all ways in which simulated fruits were handled and the frequencies with which each handling method was encountered. When simulated fruits were cached more than once (Table 8.3), the first caching event was of either a whole fruit or a partially eaten fruit. The end product that was eventually re-cached was invariably the cotton bobbin.

Table 8.3 Methods by which simulated fruits were handled and the number of times each handling method was encountered.

Handling Method	Frequency
1. Undisturbed	109
2. Eaten "*in situ*" (moved <5m)	92
3. Moved (>5m) and eaten	12
4. Cached and not retrieved	20
5. Cached retrieved re-cached	1
6. Cached retrieved flesh eaten dropped	13
7. Cached retrieved flesh eaten re-cached	12
8. Cached retrieved re-cached retrieved eaten dropped	1
9. Cached retrieved re-cached retrieved eaten re-cached	2

Cache Sites

On no occasion was more than one simulated fruit found at a cache site. Therefore, Musky Rat-kangaroos are scatter-hoarders. Simulated fruits were cached from 1.1m to 68m away from their point of origin (mean 14.9m ± 2.5 SE). They were always covered with leaves, twigs or tucked under a root or log. Only 2/35 were cached without soil covering. The rest were cached from 1cm to 5cm under the soil surface (mean - 1.5cm ± 1.6 SE).

Cached fruits were placed at random with respect to objects such as logs, saplings, roots or buttresses. I compared the distances from the nearest objects for 34 caches, 34 simulated fruits that were moved, eaten and left on the litter surface and 34 randomly chosen points on the forest floor (random points were chosen by deriving random coordinates from a random number table and locating them on a grid). The mean distances were not significantly different for cached and random sites. However, simulated fruits that were dropped onto the litter by a Musky Rat-kangaroo were significantly further from objects than random points in the forest (Figure 8.2; Oneway Analysis of Variance F=10.95, DF=2,99, P=0.0001).

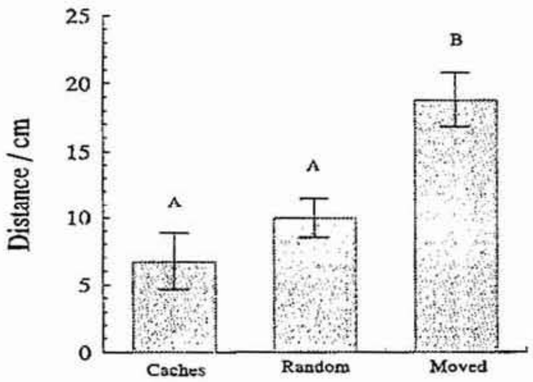


Figure 8.2 Mean (± SE) distances to objects for imitation fruits cached or moved and random points. A & B - Tukey test groupings.

In addition, cache sites were not significantly different from random with respect to the density of surrounding vegetation (T-Test: cache sites compared to randomly chosen sites; T=1.42, DF=30, P=0.1656). Thus Musky Rat-kangaroos cache seeds at random with respect to obviously discernable cues. Twenty nine seeds (out of 139 moved; 21%) were placed in canopy gaps.

Number of Fruits Dispersed

Musky Rat-kangaroos dispersed and/or cached significant numbers of fruits and seeds during this study (Figure 8.3). I calculated that Musky Rat-kangaroos were handling between 22 and 2738 fruits/ha/month on my study site (mean 696.9/ha ± 194 SE) with between 7 and 926/ha/month being dispersed (mean 271.9/ha ± 71.9 SE). The number of fruits I estimated to be scatterhoarded ranged from 5 to 689/ha/month (mean 175.3/ha ± 48.8 SE; Figure 8.4; see Equations 8.1 & 8.2). Musky Rat-kangaroo fed on the fruits of 35 species of plants on my study site. During eight months in 1991, I calculated they dispersed 1002 seeds/ha from those 35 species and in eight months in 1992 they dispersed 2576 seeds/ha (see Equations 8.1 & 8.2).

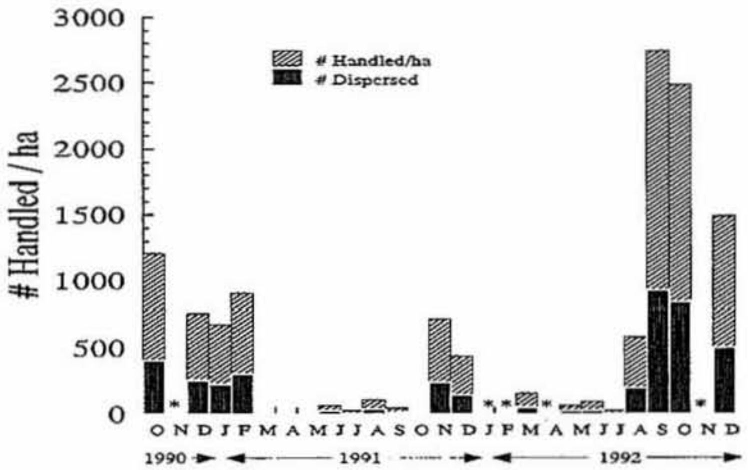


Figure 8.3 Estimated number of fruits handled and dispersed by Musky Rat-kangaroo in each month in 1990, 1991 and 1992.* = No Data.

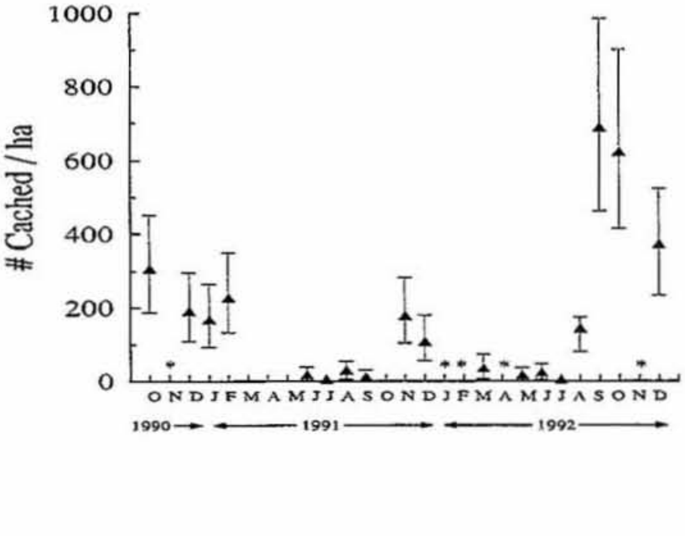


Figure 8.4 Estimated number (± 95% CI) of fruits and/or seeds scatterhoarded in each month in 1990, 1991 and 1992. * = No Data.

DISCUSSION

Musky Rat-kangaroos disperse significant numbers of seeds in several ways: 1) by carrying fruit away from a fruitfall to consume it; 2) by being displaced by a conspecific while feeding; and 3) through scatter hoarding fruits and seeds. By doing so Musky Rat-kangaroos fulfill the role for which plants provide fleshy fruit, the dispersal of their propagules (Howe and Smallwood 1982).

Terrestrial frugivores that occupy tropical rain forest in other countries also disperse seeds (Dubost 1988; Forget 1990; Forget 1991; Kiltie 1981; Smythe 1978). The way in which seeds are dispersed varies between species. Agoutis, Acouchies (Central and South America), some rats (South America and Australia) and an African ground Squirrel (*Epixerus ebii*) are known to scatter hoard (Emmons 1980; Dubost 1988; Forget 1990; Forget 1991; Goldberg 1994; Kiltie 1981; Smythe 1978). In certain large seeded species of plants burial (mimicking that done by Acouchies and/or Agoutis) results in a germination rate 3.6 times higher than in seeds that are not buried (calculated from Forget 1990).

Other terrestrial groups (e.g. Cassowaries, Elephants, Pigs and Deer) from tropical rain forests which consume fruits, do so by ingesting them whole and defaecating the seeds in clumps (Bodmer 1989; Howe 1989; Janzen 1983; Stocker and Irvine 1983). In many of these animals the majority of seeds are digested or destroyed through mastication (Bodmer 1989). Presumably however, a few are defaecated while still viable and in some cases (e.g. the cassowary; Stocker and Irvine 1983) the majority of seeds remain viable after passage through the gut.

Cassowaries have long been considered the most important terrestrial dispersal agent in Australia's rain forests (Jones and Crome 1990), due both to the large number of species and size classes of fruit it eats and its ability to walk long distances. However, this study has shown that Musky Rat-kangaroos consume and carry fruits of all the larger size classes (Chapter 3; this Chapter) which are not well dispersed by other frugivores except the cassowary. In addition, the cassowary defaecates seeds in high density clumps, which will generate little advantage to plants whose seedlings do not tolerate such high densities well (Howe 1989). Whereas Musky Rat-kangaroos disperse seeds singly throughout the forest which may confer advantages to species that are adapted to scatter disperal as well as those adapted to clump dispersal.

White-tailed Rats are also known to scatterhoard (Goldberg 1994; Harrington *et al.* 1997). They are known to scatterhoard the seeds of Atherton Oaks *Athertonia diversifolia* and probably scatterhoard other species as well. However, in some studies of its hoarding behaviour (Harrington *et al.* 1997) all seeds were re-found and eaten. Presumably however, this is not always the case. An animal may be killed by a predator and a good number of its caches remain undetected by conspecifics. Goldberg (1994) found two percent of caches remained unrecovered after four days. Therefore, Musky Rat-kangaroos, Cassowaries and White-tailed Rats (particularly the first two species) are probably the primary dispersal agents for the majority of plants with large fruits and/or seeds in Australian tropical rain forests.

Cache Sites

Musky Rat-kangaroos cached seeds at random with respect to objects on the forest floor and the density of surrounding vegetation. White-tailed Rats, on the other hand, cache seeds in areas with high densities of surrounding vegetation and close to saplings (Goldberg 1994). White Tailed rats are clearly one of the most important seed predators in Australian rain forests and are able to recover seeds from mock caches at a similar rate to their own caches (Goldberg 1994). It is therefore likely that they compete with Musky Rat-kangaroos for the recovery of seeds from caches. Smythe (1986) suggests that competition between terrestrial frugivores may be important in determining carrying capacity, partcularly during times of fruit scarcity. Further, he suggests that the abundance of peccaries (Tayasuidae), which are able to locate caches made by Agoutis (Kiltie 1981), may affect the abundance of agoutis in a given forest area. However, I found none of the Musky Rat-kangaroo caches disturbed by nocturnal animals, suggesting that the difference in cache location cues is sufficient to avoid theft from Musky Rat-kangaroo caches by White-tailed Rats. In addition, White-tailed Rats tend to consume seeds with much thicker testas than do

Musky Rat-kangaroos (Unpublished observation). Therefore, while White-tailed rats and Musky Rat-kangaroos may compete for some resources (see Chapter 10) they are unlikely to have a major impact on each others populations due to differences in activity periods and cache site selection.

Number of Fruit Dispersed

Estimates of the number of fruits dispersed are based on three main assumptions which need to be explained. Firstly, the proportions of fruits cached are based on the data collected using simulated fruits (chinese dates). It is likely that the caching rates vary depending on the nutritive value or palatability of each species of fruit/seed to Musky Rat-kangaroos. Squirrels in temperate pine forests are known to cache and retrieve seeds of different nutritive value at different rates (Smith and Reichman 1984). I was unable to calculate caching rates for the fruit of each species of tree due to logistical difficulties Therefore, I have assumed that the rate of caching for chinese dates is similar to that for at least a large proportion of fruits.

Secondly, I have assumed, that Musky Rat-kangaroos cache seeds of all species whose flesh they consume, regardless of the palatability of the seed. I witnessed Musky Rat-kangaroos caching the seeds for species in which they consumed the seed. I also witnessed Musky Rat-kangaroo leave a fruitfall carrying fruits whose seed they do not eat. Given that the cotton bobbins in simulated fruits were cached, it is likely that the seeds of most species would also be cached, regardless of whether the seed is palatable to Musky Rat-kangaroos. Therefore, I considered it worthwhile to use the available data to estimate the number of seeds cached.

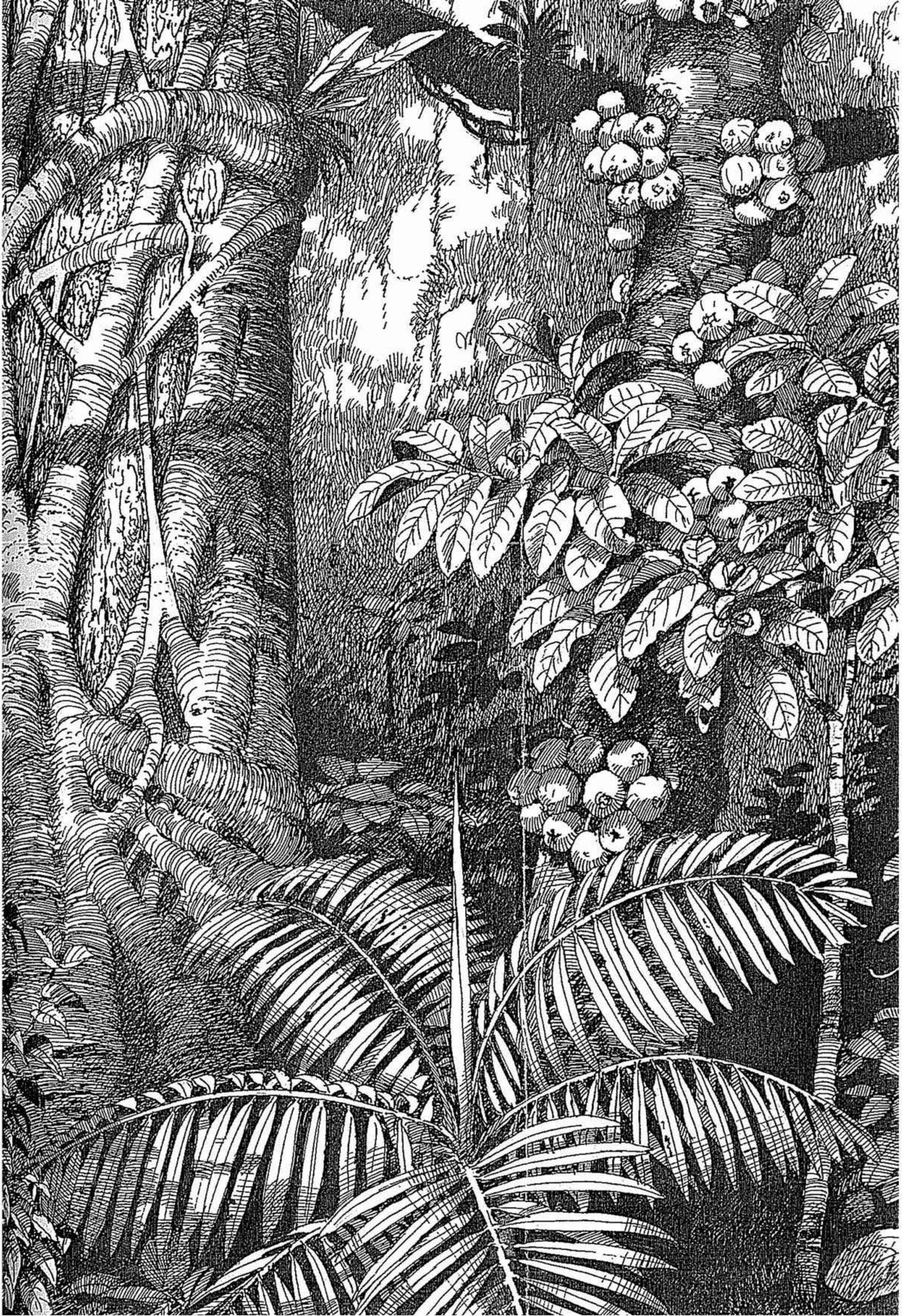
In addition, caching rates probably have both temporal and spatial variation. In temperate regions animals tend to cache food prior to winter (Smith and Reichman 1984). Seasonality of caching behaviour has not been widely explored in the tropics. Most studies have revolved around the fruit of a single species of plant and not explored the behaviour of the animal at all times of year (Emmons 1980; Forget 1990; Goldberg 1994; but see Forget 1993). However, most rain forests show seasonality in fruit production (Foster 1977; Levey 1988; Marinho-Filho 1991;

Smythe 1970a; Terborgh 1986) as do the wet tropics of Australia (Crome 1975a; Moore 1991; Chapter 4). It is therefore reasonable to expect a greater rate of caching prior to the season of fewer fruit. This would normally be toward the latter part of the fruiting peak (December, January, February; Chapter 4). My spool and line tracking experiments were conducted in the early to middle part of the peak (September, October, November) a period when caching rates would be expected to be lower.

Forget (1993) found that scatterhoarding rates of Agoutis was greater during mid and late fruiting periods for *Dipterix panamensis*, a tropical canopy tree which fruits prior to the peak in overall fruit abundance. Agoutis scatterhoarded from 8% to 26% of the *D. panamensis* fruits they handled. In this study, Musky Rat-kangaroos scatterhoarded 25% of the simulated fruits they handled, a percentage comparable to the upper end of the range for Agoutis.

The proportion of fruits handled by frugivores tends to vary with the number of fruits available on the forest floor. During lean times a higher proportion of the available fruits are taken by terrestrial frugivores (Zhang and Wang 1995). I expect that most fruits that are handled by Musky Rat-kangaroos during lean months are either eaten entirely or cached. Because of this change in behaviour, there was little or no evidence of Musky Rat-kangaroos handling fruits when few were available (see Figures 8.3 and 8.4) and therefore, I was unable to calculate how many were cached or dispersed. Caching experiments using simulated fruits at all times of year would address this issue at least for species whose seeds are not consumed.

Despite the various assumptions addressed above, I believe it is reasonable to use the available data to estimate the potential dispersal capabilities of Musky Rat-kangaroos. Future work addressing some of these issues will refine the estimates. Future research also needs to determine what proportion of dispersed and/or cached seeds are found and eaten and whether the scatter hoarding behaviour of Musky Rat-kangaroo increases the survival rates of seeds to germination and whether the seedlings are advantaged. Some of these issues are addressed in Chapter 9.



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Chapter 9

BENEFITS TO SEED SURVIVAL ATTRIBUTABLE TO DISPERSAL BY MUSKY RAT-KANGAROOS

INTRODUCTION

Dispersal of propagules away from the parent has been demonstrated to be advantageous for many tree species (Augspurger 1983a; Coates-Estrada and Estrada 1988; Dirzo and Dominguez 1986; Howe and Schupp 1985; Janzen 1972b; Webb and Willson 1985). Seed survival rates tend to be lowest under the parent tree for many species. This is due to higher levels of seed predation by mammals and insects (Coates-Estrada and Estrada 1988; Dirzo and Dominguez 1986; Howe and Schupp 1985; Janzen 1972b; Webb and Willson 1985) and seedling mortality due to fungal pathogens (Augspurger 1983a) and unkown factors (Becker and Wong 1985) under the parent tree. Many other tree species have defensive and competitive mechanisms which allow them to survive in high density situations both under the parent tree and away from it (Howe 1989). Therefore, advantages from dispersal for density independent species are due mostly to seeds being spread to more favorable growth sites.

More studies have examined seedling establishment than the post-dispersal mortality of seeds (Whelan *et al.* 1991) and therefore do not elucidate the mechanisms by which the original distribution of seeds come about. Most studies which have examined post dispersal predation/survival of seeds have done so for clumps of seeds on the surface of the forest floor (Howe and Schupp 1985; Janzen 1972b; Osunkoya 1994; Whelan *et al.* 1991). These studies imitate large animals that deposit seeds in clumps. In Australia, only cassowaries, Tooth-billed Bowerbirds, *Scenopoeetes* *dentirostris*, and Metallic Starlings, *Aplonis metallica*, are known to deposit seeds in large clumps (Moore 1991; Stocker and Irvine 1983). Few studies have examined the effects of scatter dispersal of seeds. Smythe (1989) examined the effects of seed burial by Agoutis, which scatterhoard, and their potential for benefits to the seeds dispersed. He suggests that the Palm, *Astrocaryum standleyanum*, is unlikely to recruit new members into the population without Agoutis scatterhoarding its seeds. Howe (1993a) examined the scatter dispersal of a Panamanian canopy tree, *Virola noblis*, which is dispersed primarily by avian frugivores. He found that initial seed mortality due to insects and mammals was strongly density or distance dependent, while seedling mortality was density or distance independent. Therefore, the interaction between initial seed dispersal and predation sets the scene for later survival and growth of seedlings and ultimately the spatial and temporal dynamics of the adult population.

Musky Rat-kangaroos scatter disperse the propagules of many species of tree (Chapters 3 and 8), some of which are clearly able to survive and germinate beneath their parent (e.g. Boonjie Blush Walnut, *Beilschmiedia volckii*; unpublished observation: Irvine, A. pers. comm.1995), while others appear not to survive under their parent (e.g. Fontain's Blushwood, *Fontainea picrosperma*; unpublished observation). In this chapter, I compare the fates of seeds in two species of rainforest tree, Baileyoxylon, *Baileyoxylon lanceolatum*, and Fontain's Blushwood, *Fontainea picrosperma*, which are handled and dispersed in several ways by Musky Rat-kangaroos. Seedling establishment rates under the parent tree appear to be low or zero for both of them. Musky Rat-kangaroos eat the flesh and/or seeds of both species. Fruits whose seeds were not eaten were handled in several ways: 1) eaten *in situ* and seed dropped; 2) dispersed and seeds left on the forest floor; and 3) seeds scatterhoarded both under the parent tree and away from it (Chapter 8; unpublished observation). I also examine the impacts of mammalian seed predators compared to seed mortality caused by other agents and find that dispersal by Musky Rat-kangaroos enhances the survival of both species.

METHODS

Seed Survival Experiment

I designed and implemented a seed survival experiment to determine if the scatterhoarding behaviour of Musky Rat-kangaroos provided direct benefits to the species of plants whose fruits were cached.

I chose two species of trees whose fruits and seeds were frequently eaten by Musky Rat-kangaroos, White-tailed Rats, species of *Rattus* and Fawn Footed Melomys. They were Baileyoxylon, *Baileyoxylon lanceolatum*, and Fontain's Blushwood, *Fontainea picrosperma*, (hereafter referred to as *Baileyoxylon* and *Fontainea* in this chapter). For each species I had four replicate trees. At each tree, seeds were placed into one of four treatments:

1) on the surface of the litter and attached to a convenient sapling or root using a 20cm length of thin fencing wire (**Surface**);
2) buried 2cm into the soil and wired as above (**Buried**);
3) housed in a 0.5cm² wire-mesh cage on the litter surface and wired to a support (**Caged on Surface**);
4) buried 2cm into the soil in a wire-mesh cage as above (**Caged and Buried**);

Seeds in each treatment were placed at zero, 10 and 20 m from each parent tree. I chose 10m and 20m to represent the distance seeds are cached by Musky Rat-kangaroos. The mean distance cached is 17m (± 2.7 SE; Chapter 8) and the mean distance seeds were carried without caching was 15.2m (± 2.9m SE; Chapter 8). Five seeds were placed at each 10 and 20m distance. The total results of the experiment at these distances were combined for the analyses to determine the effects of the various treatments on scattered seeds. Figure 9.1 shows graphically the treatment design and Table 9.1 shows the numbers of seeds placed in each treatment and distance from each parent tree for each species of tree. The number of seeds I used for each species was determined by their availability at the time of setting up the experiment.

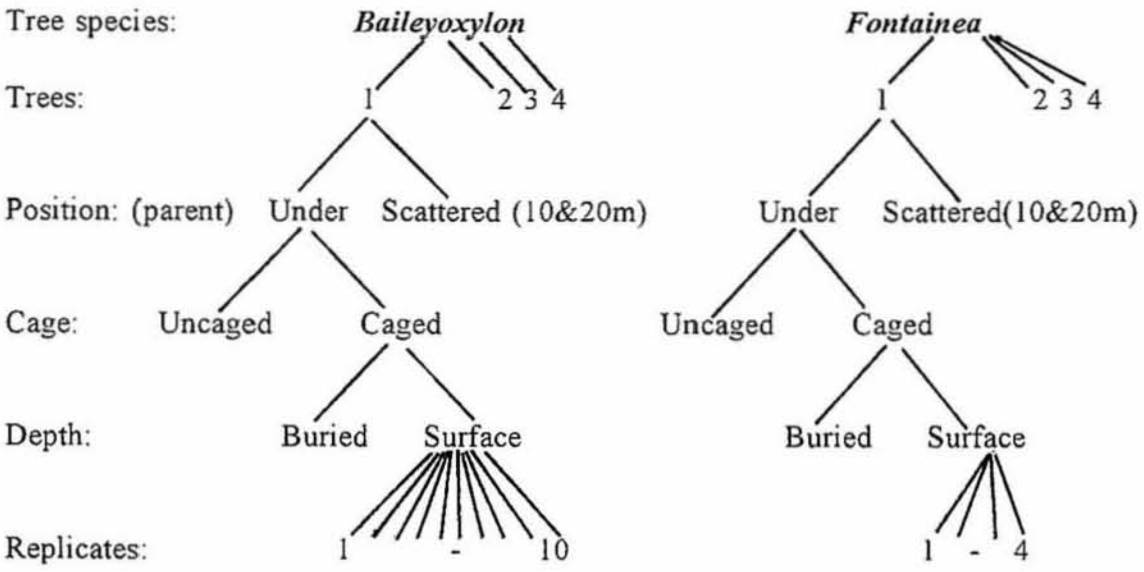

Figure 9.1 Diagramatic representation of seedling survival experiment. Note that the results of the treatments at the two distances (10 and 20m) from the parent tree have been combined to represent scatterhoarding behaviour of Musky Rat-kangaroos. Each treatment in each level is equally replicated at the subsequent level for each species.

Table 9.1 Summary of seed survival experiment showing numbers of seeds placed in each treatment at each distance for each of four *Baileyoxylon* and four *Fontainea* trees. Note that the results of the treatments at the two distances (10 and 20m) from the parent tree have been combined to represent scatterhoarding behaviour of Musky Rat-kangaroos.

Treatment	Distance (m)	*Baileyoxylon*	*Fontainea*
Surface	0	10	4
	10	5	2
	20	5	2
Buried	0	10	4
	10	5	2
	20	5	2
Caged on Surface	0	10	4
	10	5	2
	20	5	2
Caged and Buried	0	10	4
	10	5	2
	20	5	2
Totals			
Under Parent Tree		40	16
Scattered		40	16
Grand Total (4 trees)		320	128

Each treatment was chosen to represent a naturally occuring fate for a seed which has been handled by a Musky Rat-kangaroo. Those on the surface and under the parent tree represent a fruit whose flesh was eaten *in situ* and the seed dropped and also those that were not eaten or handled at all. Those buried under the parent tree represent seeds cached without removal. Those scattered (i.e. at 10 or 20m from the parent tree) and on the surface represent fruits carried from the parent tree which had their flesh devoured and seed dropped. Those scattered and buried replicate the scatterhoarding behaviour of Musky Rat-kangaroos.

I used wire-mesh cages to control for the effects of mammal predation and assess other mortality factors affecting seed survival, for example invertebrate and/or fungal attack.

Control Seeds

Simultaeneous to the placement of seeds in the forest, I planted 80 seeds of *Baileyoxylon* and 40 seeds of *Fontainea* in seedling trays in a green house on private property within 1km of the experimental sites. The seeds were in commercial potting mix, inaccessible to seed predators and not exposed to litter fungi. Half the seeds were treated with wire glued to them (as in the experiment) and the other half were untreated. This was to test whether gluing wire to the seed coat affected their germination potential.

When the majority of control seeds had germinated, the experiment in the forest was assessed for the final time. The experiment was left in place for three months. Seeds which had not germinated in either the experimental plots or the greenhouse were removed and their viability was determined by cutting the seed to see if the tissue remained alive.

Analysis

Survival Experiment

The results were analysed, using Analysis of Variance, separately for each species because the number of replicate seeds was different in each case. I used the sum of the number of seeds remaining viable and the number of seeds which had germinated as the dependent variable in one set of analyses and the number of seeds germinated in a second set of analyses. The initial models included four main effects: 1)Tree - each of the four individuals; 2) Position - under the parent tree or scattered; 3) Depth - surface or buried; and 4) Cage - caged or uncaged. I included all two and three-way interactions with the four-way interaction as the error term. I then re-ran the models in stages after eliminating non-significant interactions from each level in stages. By pooling non-significant interactions the specific error term for the random factor (Tree) was pooled into the error in each analysis resulting in a final model with only the overall error term included.

Predicting Survival

I used logistic regression to calculate the probability of a seed surviving (to three months or germination) in each treatment. I used data for uncaged seeds only in this analysis as caged seeds were not relevent to real life and were used to assess the impacts of mammal predation. I then developed a model based on the proportion of seeds scatterhoarded during the spool and line tracking of fruit experiment (Chapter 8) and the probability of survival for buried and/or scattered and buried seeds from the survival experiment. The model was then used to calculate the number of seeds surviving to germination from a crop of given size.

RESULTS

Control Seeds

Ninety four percent of *Baileyoxylon* seeds in the control plantings had germinated after three months. None of the *Fontainea* seeds had, even though 30% of those in the field experiments germinated after three months.

Treatment with wire had little impact on the germinability or survival of seeds in both species over three months. However, for both species there was more mortality for those treated with wire (Table 9.2). Even if the difference between treatments is a real effect, it is not relevant to the interpretation of survival data in the experiment as mortality agents for nearly all uncaged seeds were identified.

Table 9.2 Number of seeds dead and number germinated and/or viable after three months for *Baileyoxylon* and *Fontainea* treated with wire and not treated.

Treatment	*Baileyoxylon*		*Fontainea*	
	Alive	Dead	Alive	Dead
Wire	36	4	17	3
No Wire	39	1	19	1

Seed Survival Experiment

Uncaged seeds of both *Baileyoxylon* and *Fontainea* in the survival experiment were heavily predated by mammals. One hundred percent of uncaged seeds on the surface of the ground were eaten (Figure 9.2), the majority being eaten in the first two weeks. Most had rat and a few had Musky Rat-kangaroo teeth marks in them indicating that predation by mammals is the most significant mortality factor that these species face. In addition, one cage on the surface of the litter for each species was broken into and had seeds eaten by White-tailed Rats. The effects of Musky Rat-kangaroo dispersal and caching behaviour on seed survival varied with the species. Therefore, I examine each separately.

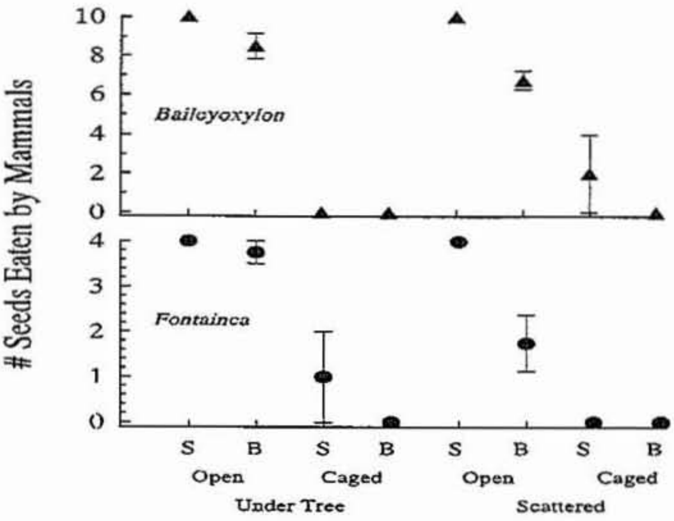

Figure 9.2 Number of seeds (mean ± SE) consumed by mammals during seed predation experiment. Open = without cage. S - on surface; B - buried.

Survival of *Baileyoxylon lanceolatum*

For *Baileyoxylon*, the two factors most important in explaining the variation in survival rates of seeds were cage (caged or uncaged) and depth (surface or buried; Table 9.3; Figure 9.3). As discussed above, caged seeds were not subjected to the high rates of predation by mammals facing unprotected seeds (Figure 9.2).

Table 9.3 Analysis of Variance table from seed survival experiment for *Baileyoxylon*. Final model after step-down model reduction. Full model in Appendix 3). Adjusted R-squared = 0.72.

Source of Variation[1]	DF	Mean Square	F	P
Tree[2]	3	0.19	0.93	0.44
Position[3]	1	0.22	1.1	0.305
Depth[3]	1	5.81	29.09	**0.0001**
Cage[3]	1	10.3	51.6	**0.0001**
Error	25	0.20		

1. Dependent variable - seeds still viable plus those germinated.
2. Random factor.
3. Fixed factor.

Those seeds that were buried without cages had higher survival rates both under the parent tree and away from it than those that were on the surface (Figure 9.3). This suggests that burial is an effective means of hiding seeds from mammal predators. In addition, caged seeds on the surface of the litter had a lower survival rate than those which were buried in cages (Figure 9.3). This was due to Hemipterans (Pentatomoidea) which I saw piercing the testas of caged seeds on the ground surface with their proboscis. Apart from digesting some of the seed reserves they probably also facilitated penetration by fungal pathogens. None of the mortality factors affecting *Baileyoxylon* varied with position. That is, there were no density dependent mortality factors associated with the parent tree.

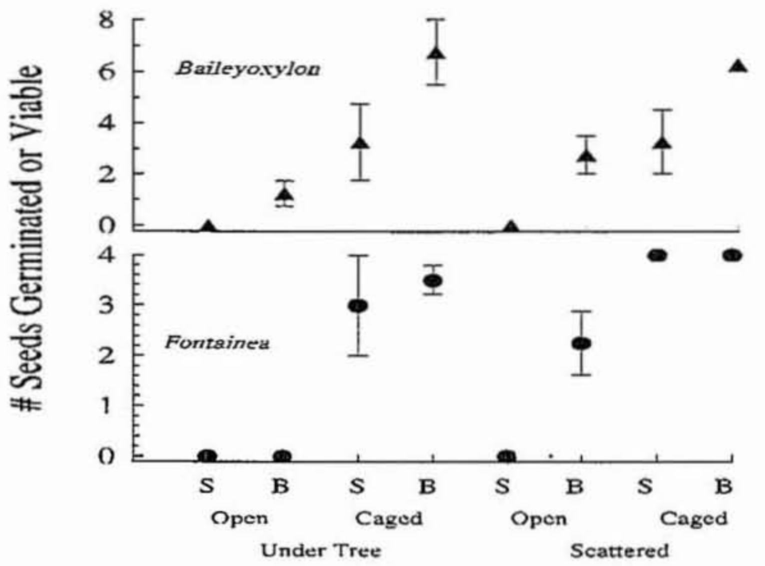

Figure 9.3 Number of seeds remaining viable or germinated (mean ± SE) after three months. Open - without cage. S - On surface; B - Buried.

Survival of *Fontainea picrosperma*

Analysis of the seed survival data for *Fontainea* showed a significant three way interaction between: position in relation to the parent tree; whether the seeds were on the surface of the litter or buried; and whether they were caged or uncaged (Table 9.4; Figure 9.3). Scattered seeds, both caged and uncaged, survived better than those under the parent tree. Those that were uncaged and buried survived well away from the parent tree but not under it. The survival of all caged seeds, particularly those on the surface of the litter, was poorer under the parent tree.

Table 9.4 Analysis of Variance table from seed survival experiment for *Fontainea*. Final model after step-down model reduction. See appendix 3 for full model. Adjusted R-squared = 0.9.

Source of Variation[1]	DF	Mean Square	F	P
Tree[2]	3	0.04	0.69	0.573
Position[3]	1	1.34	22.14	**0.001**
Depth[3]	1	1.00	16.52	**0.002**
Cage[3]	1	11.51	189.83	**0.0001**
Tree*Position	3	0.19	3.12	0.066
Tree*Cage	3	0.19	3.12	0.066
Position*Depth	1	0.35	5.74	**0.034**
Depth*Cage	1	0.35	5.74	**0.034**
Position*Depth*Cage	1	1.00	16.52	**0.002**
Error	12	0.06		

1. Dependent variable - seeds still viable plus those germinated.

2. Random factor.

3. Fixed factor.

Several factors were identified which created this pattern. Firstly, the flesh and seeds from the fruit of *Fontainea* were eaten by Fawn-footed Melomys which buried seeds in large numbers under the parent tree. As crops of *Fontainea* finished falling, Melomys searched thoroughly under parent trees and recovered and ate all seeds. Scattering and burying seeds reduced the rate at which Melomys found them. In addition, *Fontainea* are small understorey trees which had large numbers of fruits in their crops during the study. This created a high density of seeds beneath each tree. The higher mortality rate of caged seeds under parent trees appeared to be due to fungal attack. On cutting the seeds to check their viability, I found that the contents were liquified and rotted.

Germination of *Baileyoxylon lanceolatum*

An examination of *Baileyoxylon* seeds which germinated shows a different pattern to that for the combination of germinated and viable seeds. A three way interaction between position, depth and cage status was significant (Table 9.5; Figure 9.4).

Table 9.5 Analysis of Variance table from seed survival experiment for *Baileyoxylon*. Final model after step-down model reduction. See Appendix 3 for full model. Adjusted R-squared = 0.71.

Source of Variation[1]	DF	Mean Square	F	P
Tree[2]	3	0.26	1.67	0.204
Position[3]	1	0.14	0.86	0.364
Depth[3]	1	3.58	22.75	**0.0001**
Cage[3]	1	7.13	45.26	**0.0001**
Depth*Cage	1	0.83	5.29	**0.032**
Position*Depth*Cage	1	0.81	5.13	**0.034**
Error	21	0.16		

1. Dependent variable - germinated seeds.

2. Random factor.

3. Fixed factor.

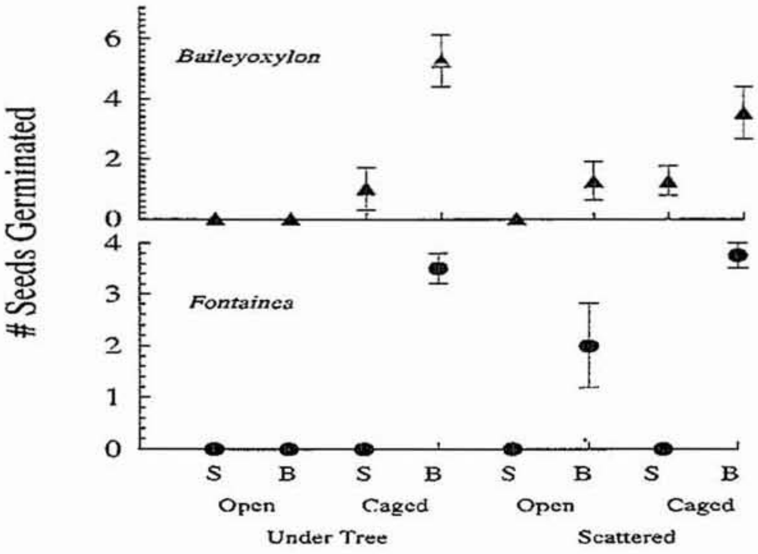

Figure 9.4 Number of germinated seeds (mean ± SE) from seed survival experiment. Open - not in a cage. S - On surface; B - Buried.

In this case, some of the uncaged seeds that were buried away from the parent tree (scatterhoarding by Musky Rat-kangaroos) germinated. Whereas no uncaged and buried seeds under the parent tree germinated. Of those that were caged, a larger number of buried seeds germinated, although more under the parent tree than away from it.

Germination of *Fontainea picrosperma*

Only 30% of the seeds of *Fontainea* germinated. Most of these were those that were caged and buried (Figure 9.4). In addition, a number of seeds that were scattered and buried without cages also germinated. No seeds left on the surface germinated and only those buried and caged germinated from those left under the parent trees (Figure 9.4). Again an Analysis of Variance showed a significant three way interaction between position, depth and cage status (Table 9.6).

Table 9.6 Analysis of variancetable from seed survival experiment for *Fontainea*. Final model after step-down model reduction. See Appendix 3 for full model. Adjusted R-squared = 0.88.

Source of Variation[1]	DF	Mean Square	F	P
Tree[2]	3	0.05	0.72	0.552
Position[3]	1	0.51	8.00	**0.010**
Depth[3]	1	8.01	126.33	**0.0001**
Cage[3]	1	2.2	34.76	**0.0001**
Position*Depth	3	0.51	8.00	**0.010**
Position*Cage	1	0.40	6.33	**0.020**
Depth*Cage	1	2.20	34.76	**0.0001**
Position*Depth*Cage	1	0.40	6.33	**0.020**
Error	21	0.06		

1. Dependent variable - germinated seeds.

2. Random factor.

3. Fixed factor.

Predicting Seed Survival

In the previous section I demonstrated that scatterhoarding (with or without removal from the parent tree) increased the chances of survival for *Baileyoxylon* seeds (Figure 9.3) for at least three months or to germination (Figure 9.4). *Fontainea* differed in that only scatterhoarding away from the parent tree increased the survival of seeds (Figure 9.3) for at least three months or to germination (Figure 9.4). By using logistic regression analysis (Boxes 9.1 & 9.2) I was then able to predict the probability of a seed surviving in each treatment in the seedling survival experiment and derive confidence intervals to give some measure of the possible variation. I used only the data for uncaged seeds as caged seeds were to control for predation and are not relevent to real life.

Box 9.1 Results of logistic regression analyses for *Baileyoxylon*.

Table 9.7 Summary of logistic regression analysis using backward elimination for seed survival experiment on *Baileyoxylon*. The response variable is dead or alive. Model one, the full model, is followed by models which have had variables removed but still adequately explain the data. When the model deviance is significantly different from the previous model [Pr(Chi)], the model is rejected as not explaining the data adequately. Model 5 adequately explains the data.

Predictor Variables	Resid.Dev	DF	Deviance	DF	Pr(Chi)
Model 1					
Tree, Position, Depth, Tree*Position, Tree*Depth Position*Depth Tree*Position*Depth	69.95	7	n.a.		
Model 2					
- Tree*Position*Depth	69.95	10	0.0006	3	0.999
Model 3					
- Tree*Position. Tree*Depth. Position*Depth	76.54	17	6.593	7	0.472
Model 4					
- Tree	77.19	20	0.653	3	0.884
Model 5					
- Position	80.067	21	2.87	1	0.090
Model 6					
+ Position - Depth	101.471	21	24.27	1	**0.000**
Model 8					
μ	104.027	31			

Table 9.8 Parameter estimates for the logistic regression model for *Baileyoxylon*. Model 5 (Table 9.7).

Variable	B	SE	Wald	DF	Sig	R	Exp(B)
Depth	-4.9083	15.1399	0.1051	1	0.7458	0.0	0.0074
Constant	-6.2946	15.1399	0.1729	1	0.6776		

Box 9.2 Results of logistic regression analyses for *Fontainea*.

Table 9.9 Summary of logistic regression analysis using backward elimination for seed survival experiment with *Fontainea*. The response variable is dead or alive. Model one, the full model, is followed by model in which variables have been removed but still adequately explain the data. When the model deviance is significantly different from the previous model [Pr(Chi)] it is rejected as not explaining the data adequately. Model 4 adequately explains the data.

Predictor Variables	Resid.Dev	DF	Deviance	DF	Pr(Chi)
Model 1					
Tree, Position, Depth, Tree*Position, Tree*Depth Position*Depth Tree*Position*Depth	15.59	3	n.a.		
Model 2					
- Tree*Position*Depth	15.59	6	0.00008	3	0.999
Model 3					
- Tree*Position, Tree*Depth, Position*Depth	15.59	13	0.0002	7	1.0
Model 4					
- Tree	21.931	16	6.34	3	0.096
Model 5					
- Position	38.025	17	16.094	1	**0.000**
Model 6					
+ Position - Depth	38.025	17	16.094	1	**0.000**
Model 7					
µ	51.9803	31			

Table 9.10 Parameter estimates for the logistic regression model for *Fontainea*. Model 4 (Table 9.9).

Variable	B	SE	Wald	DF	Sig	R	Exp(B)
Position	-5.7522	34.7125	0.0275	1	0.8684	0.0	0.0032
Depth	-5.7522	34.7125	0.0275	1	0.8684	0.0	0.0032
Constant	-11.253	49.0893	0.0525	1	0.8187		

To calculate the probability of a seed surviving in one of the treatments used in the experiment, I used the following equation (Norusis 1993):

$\text{Prob} = 1/1+e^{-Z}$ **Equation 9.1**

Where

$Z = B_0 + B_1X_1 + B_2X_2 + \ldots + B_pX_p$ **Equation 9.2**

B is the coefficient taken from the parameter estimate table in the logistic regression and X is the parameter coding value from the logistic regression. For example for a *Baileyoxylon* seed that has been buried:

$$Z = -6.2946 + -4.9083 \times -1 = -1.3863$$

$$1+e^{-z} = 5.000023$$

Probability $1/5.000023 = 0.20$

For *Baileyoxylon*, the probability of a seed surviving in each treatment is shown in Table 9.11.

Table 9.11 Probability of survival of *Baileyoxylon* seeds in each of four seed fates. Obs - observed survival rate. Est - estimated probability of survival with 95% confidence intervals in parentheses.

	Under Parent Tree	Scattered	Marginal Total
Surface	Obs. 0/40 = 0 Est. 0.00001 (0 - 0.0009)	0/40 = 0 0.00001 (0 - 0.0009)	0.0 0.00001
Buried	Obs. 5/40 = 0.125 Est. 0.2 (0.03 - 0.37)	11/40 = 0.275 0.2 (0.3 - 0.37)	0.2 0.2
Marginal Total	Obs. 0.0625 Est. 0.1	0.1375 0.1	0.1 0.1

For *Fontainea*, the probability of a seed surviving in each treatment is shown in Table 9.12.

Table 9.12 Probability of survival of *Fontainea* seeds in each of four seed fates. Obs - observed survival rate. Est - estimated probability of survival with 95% confidence intervals in parentheses.

	Under Parent Tree	Scattered	Marginal Total
Surface	Obs. 0/16 = 0 Est. 0.0	0/16 = 0 0.00001 (0 - 0.001)	0.0 0.000005
Buried	Obs. 0/16 = 0 Est. 0.00001 (0 - 0.001)	9/16 = 0.563 0.563 (0.32 - 0.81)	0.282 0.282
Marginal Total	Obs. 0.0 Est. 0.000005	0.282 0.282	0.141 0.141

In Chapter 8, I showed how many simulated fruits were handled by Musky Rat-kangaroos and the way in which the fruits were handled. Fourteen percent of the total number of fruits placed out were scatterhoarded and 12% of the total were scatterhoarded away from the parent tree (Figure 8.1). Assuming that Musky Rat-kangaroos handle fruits of *Baileyoxylon* and *Fontainea* in a similar manner to which they handled simulated fruits, it is possible to calculate the number seeds which are likely to survive for three months or to germination.

If we assume a crop size of 100 fruits of *Baileyoxylon* then 14% of those are likely to be scatterhoarded by Musky Rat-kangaroos. The probability of one of those fruits surviving is 0.2. Therefore, about three seeds from a crop of 100 are likely to survive for three months or to germination. Writing this as an equation:

$\# \text{ Surviving} = S \times C \times P_s$ **Equation 9.3**

$100 \times 0.14 \times 0.2 = 2.8$ (95% CI = 0.42 - 5.2)

Where: S = crop size; C = caching rate (Figure 8.1); and P_s = estimated probability of a scatterhoarded seed surviving (Table 9.11).

From a crop of 100 *Fontainea*, the number of seeds likely to survive to three months or germination is about seven. Calculated as:

$\# \text{ Surviving} = S \times C_a \times P_{sa}$ **Equation 9.3a**

$100 \times 0.12 \times 0.56 = 6.72$ (95% CI = 3.8 - 9.7)

The subscript $_a$ is added to C and P_s to denote seeds scatterhoarded away from the parent tree (Table 9.12).

This model would benefit from the inclusion of two more factors. A time factor, to determine the number of seeds surviving or germinated after different periods of time and a recovery rate factor:

$\# \text{ Surviving} = S \times C \times P_{st} \times (1-R)$ **Equation 9.4**

Where: P_{st} is the probability of a scatterhoarded seed being alive at time t; and R is the estimated rate of seed recovery by Musky Rat-kangaroos.

Although I checked the status of seeds at different intervals during the seed survival experiment I was unable to determine if they were viable without destroying them. Therefore, I cannot be certain when seeds died, except when they were eaten by mammals. All mammal predation occurred within the first month of the experiment.

The recovery rate factor is difficult to determine. It would require being able to mark and observe the caches of Musky Rat-kangaroos. This may be possible in captivity but is unlikely to reflect wild behaviour because of the limited space for caching and searching.

Simulated fruits which were relocated by Musky Rat-kangaroos were found in the first three days subsequent to being cached (Chapter 8). Beyond that time they were not touched during two weeks of observation (N = 18; Chapter 8). The proportion of seeds cached in Figure 8.1 is the end fate of seeds after three days. Some of these were relocated, had their flesh eaten and were re-cached (Table 8.2). This suggests that the data on caching rates already includes information about initial retrieval rates. Therefore, only estimation of longer term retrieval rates is needed for the model.

In addition, there were no obvious environmental cues to determine the location of caches (Chapter 8; cf White-tailed Rats; Goldberg 1994). Therefore, Musky Rat-kangaroos may rely on random search effort and odour for relocating caches. Given that 76% of uncaged *Baileyoxylon* seeds and 69% of uncaged *Fontainea* seeds that I cached were eaten, random search seems to be a profitable method of locating caches.

DISCUSSION

Post-dispersal predation of the seeds of *Baileyoxylon* and *Fontainea* by mammals was high (Figure 9.2), particularly for seeds on the surface of the litter. In addition, other factors, such as predation by bugs (Pentatomoidea) and possibly fungus, killed seeds. Scatterhoarding successfully removed a proportion of seeds from these mortality factors (Figures 9.3; Tables 9.3 and 9.4).

The seeds of each species of plant showed differing survival rates with regard to distance from the parent tree. Some uncaged seeds of *Baileyoxylon* survived both under and away from the parent tree if they were buried (Figure 9.3). For *Fontainea* only seeds buried away from the parent tree survived (Figure 9.3). I attributed this to greater density-dependent mortality under *Fontainea* trees due to Fawn-footed Melomys. Therefore, Musky Rat-kangaroos remove seeds from predation by rats, hemipterans, conspecifics and possibly mortality due to fungi. Burying seeds also aided germination in both species (Figure 9.4). For *Fontainea*, only seeds that were buried germinated.

These results are similar to those found by Smythe (1989) for scatterhoarding of Palm seeds *(Astrocaryum standleyanum)* by Agoutis. However, one major difference exists. *Astrocaryum standleyanum* seeds germinated equally well on the surface of the litter or buried. In other cases, burial by hoarding animals is known to influence the germination of seeds. Vander Wall (1993) developed a model for the interaction between germination and the depth seeds of Bitterbrush, *Purshia tridentata*, were buried by scatterhoarding Chipmunks, *Tamias amoenus*. Bitterbrush seeds buried at 20mm depth had the greatest germination success. Chipmunks buried seeds between five and 20mm and the probability of retrieval of artificial caches decreased dramatically with depth. It seems likely, given the increase in germination success, that a similar pattern may occur with seeds of *Baileyoxylon* and *Fontainea* which are scatterhoarded by Musky Rat-kangaroos.

Dispersal without burial was of little consequence to the seeds of *Baileyoxylon* and *Fontainea* (Figure 9.2) due to 100% predation of seeds on the litter surface. This suggests that dispersal by bats and birds, which scatter seeds onto the forest floor, is of much lower value to the plants than scatterhoarding. However, the factor of retrieval rate of scatterhoards still needs to be accounted for (Equation 9.4). Even so, the advantages of scatterhoarding are likely to be greater than dispersal onto the forest floor. I suggest that *Baileyoxylon* and *Fontainea* are adapted to dispersal by scatterhoarding, whereas plants adapted to scatter dispersal on the forest floor have higher levels of chemical or physical defenses in their seeds to deter seed predators. Howe (1993) examined mortality factors surrounding a Panamanian canopy tree, *Virola noblis*, which is dispersed primarily by avian frugivores which leave seeds on the litter surface. Insect and mammal predation of seeds is significant and density or distance dependent. Seeds are dispersed greater distances for *V. noblis* than seeds of *Baileyoxylon* and *Fontainea* in this study. However, survival rates were still higher for seeds of *V. noblis* at distances comparable to those in this study. This suggests that the importance of burial varies with the density of terrestrial predators and the distance from the parent tree.

Osunkoya (1994) found differential survival rates for seeds placed on the forest floor in two sites on the Atherton Tableland depending on the species and the location. The location effect seemed to relate to a higher density of rats at the site with lower survival rate. Survival of some species, presumably those more palatable to rats, was zero where rats were abundant. Other species, such as Blackbean, *Castenospermum australe*, Candlenut, *Aleurites mollucana* and Silver Quandong, *Elaeocarpus angustifolia*, which have high toxicity or extremely thick seed coats, survived better (15 - 40% survival). Species with high rates of mammal predation are likely to benefit most from scatterhoarding by Musky Rat-kangaroos, while those which are predated little by rats will benefit by both scatterhoarding and dispersal onto the forest floor.

Predicting Seed Survivial

The scatterhoarding behaviour of Musky Rat-kangaroos affords seeds that are not relocated by the cacher a higher probability of survival than those that are not cached (Tables 9.11 and 9.12). From a crop of 100 seeds of *Baileyoxylon* I predicted that three seeds would survive for at least three months or to germination. For *Fontainea* I predicted seven seeds would survive. In contrast, Forget (1993) in his studies of Agoutis caching *Dipterix panamensis* seeds, found that all were refound from two experiments and 2% survived for at least a month in a third experiment. However, no seeds or seedings survived beyond three months. This highlights the need to determine the recovery rate of cached seeds. The probability of a seed surviving estimated in this study applies directly to those that are not refound by the animal that cached them. More accurate estimation of the number of seeds to survive from a crop of given size requires a measure of how many are relocated.

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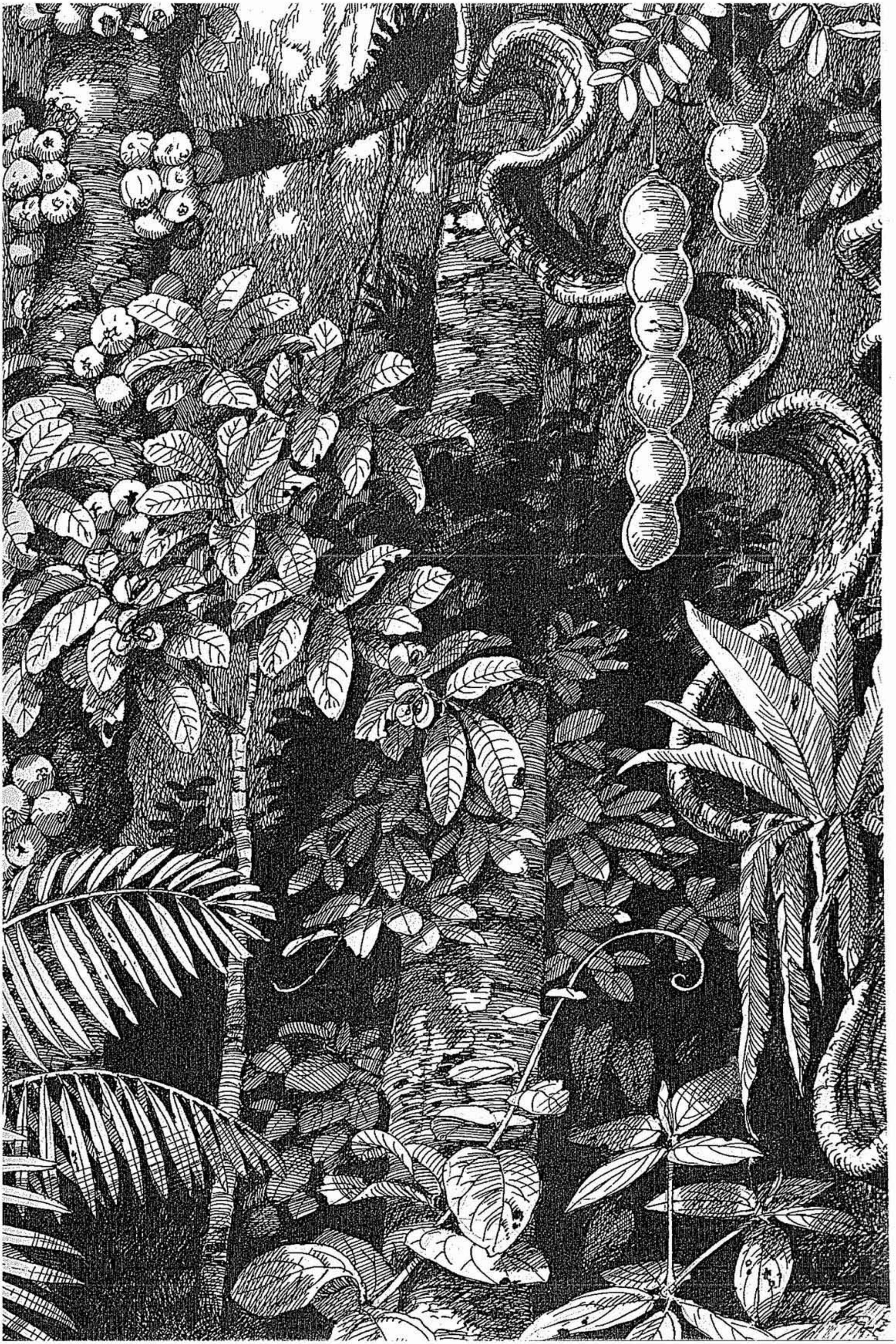

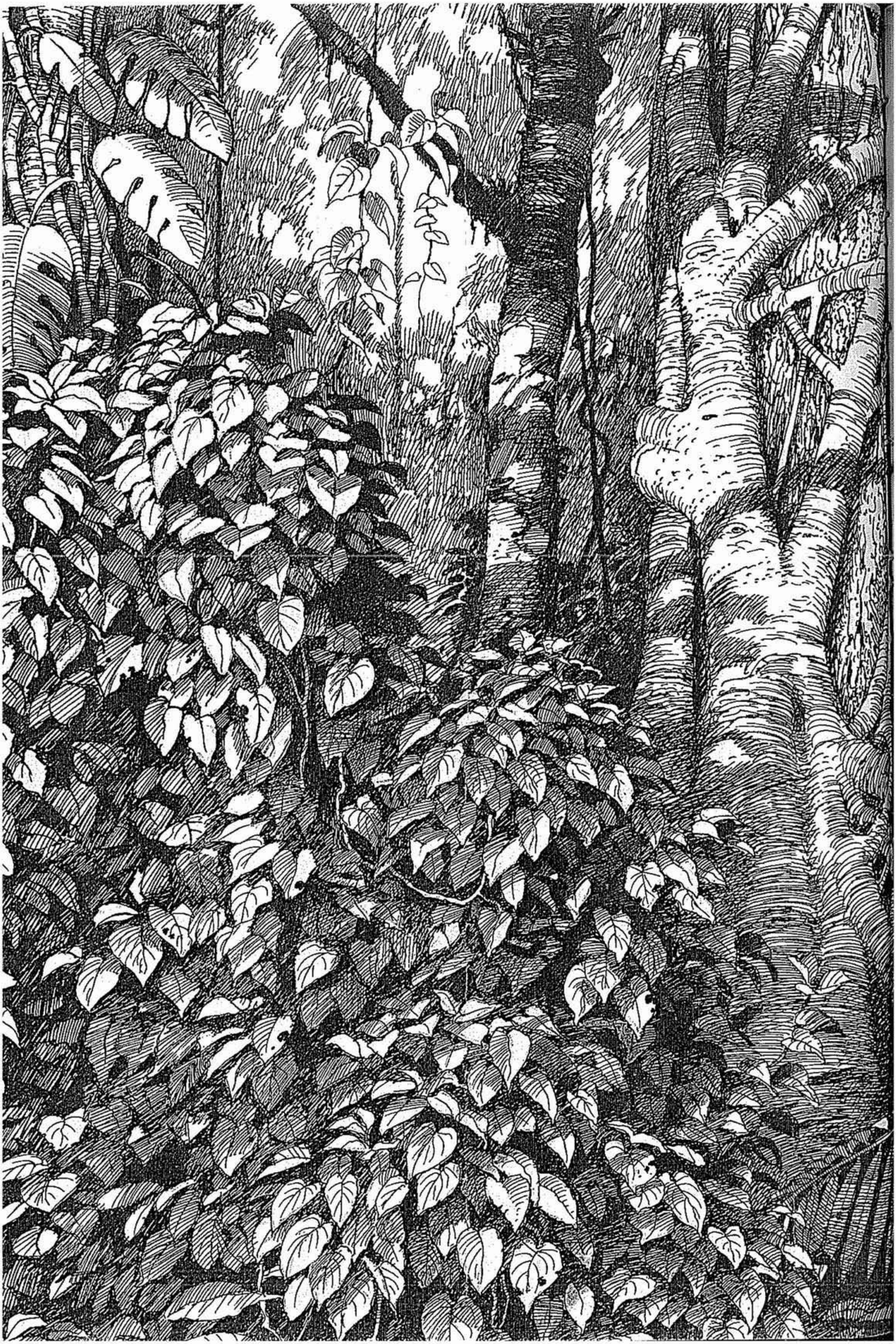

Chapter 10

COMMUNITY RELATIONS BETWEEN MUSKY RAT-KANGAROOS, THEIR PREDATORS AND OTHER FRUGIVORES

INTRODUCTION

Many authors refer to fruits whose size, shape, colour and smell suggest that they are designed to be attractive to a particular subset of frugivores and classify them as "bird fruit", "mammal fruit" and others (Foster and Janson 1985; Jordano 1995; van der Pijl 1972). For example "bird fruits" are expected to have bright and contrasting colours, soft digestible flesh when ripe, are often dehiscent and remain attached to the tree after ripening. In addition, they do not smell and the seed/s is/are protected from digestion (van der Pijl 1972). I demonstrated in Chapter 3 that Musky Rat-kangaroos consume fruits of many size classes, colours and in the form of arillate seeds in dehiscent pods and drupes. Therefore, they consumed fruits that fit into several fruit syndromes. In this chapter, I will explore which other frugivores also feed on the fruits eaten by Musky Rat-kangaroos.

Dispersal agents and the plants they disperse never operate in isolation in a system (Herrera 1986). This is particularly true in tropical rain forests. Many interactions between frugivores, seed predators and a plant species occur simultaeneously. Because of this, I consider it important to examine Musky Rat-kangaroos in the context of other frugivores and seed predators operating on my study site. My data on feeding by other frugivores are restricted to species which consume parts of fruits or somehow leave evidence of their feeding on the forest floor. The data I use are derived from fruit transects (see Chapter 4), therefore, excluding most frugivores that swallow fruits whole and scatter seeds singly through the forest, such as fruit pigeons (Columbidae). However, most terrestrial feeding frugivores (including scansorial groups; bowerbirds, White-tailed Rats) and one arboreal group (Parrots) are represented. In addition, I examine the occurrence of Musky Rat-kangaroo remains in the diet of Dingoes *Canis familiaris dingo* and list observations of other predators which consume Musky Rat-kangaroos to give an indication of their place in the system as a whole.

In this chapter I demonstrate that Musky Rat-kangaroos are important members of the frugivore community. While the community shows a high degree of overlap in species preferred and eaten, there is also significant partitioning, particularly amongst species whose feeding zones are similar. Musky Rat-kangaroos also represent an important food source for at least eight predator species.

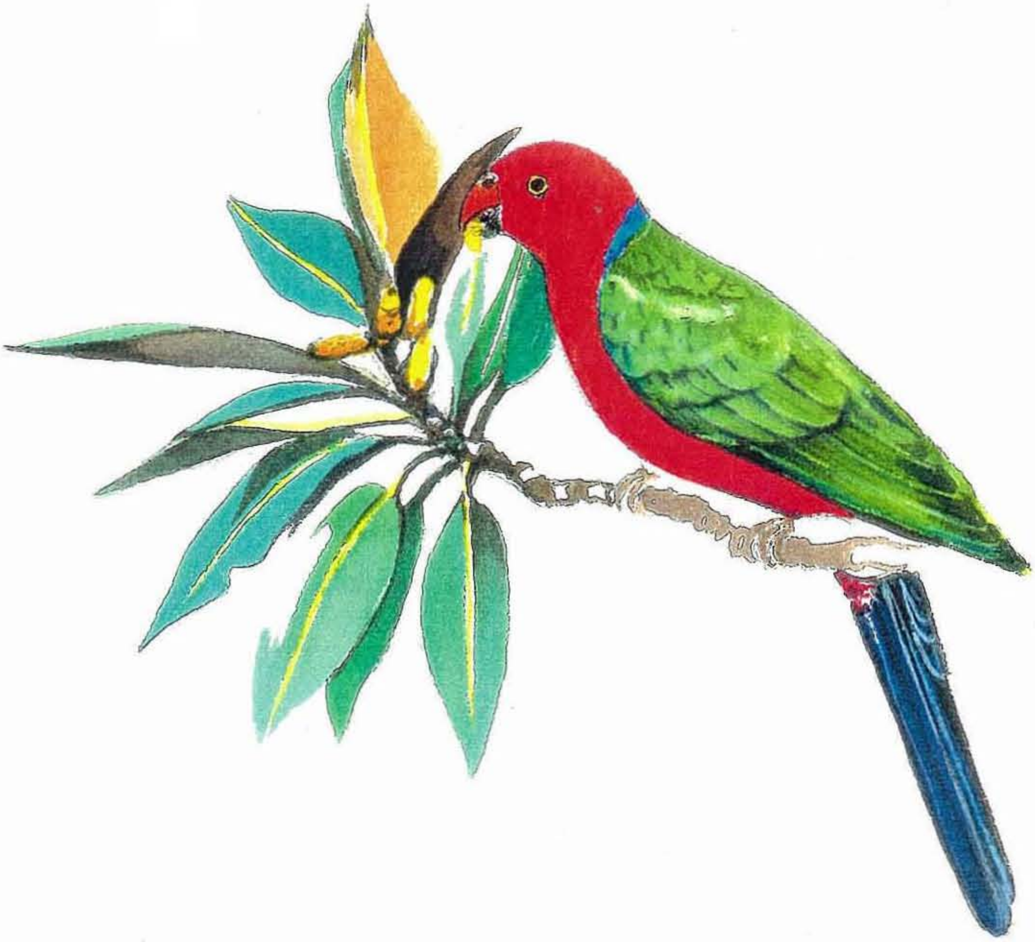

Plate 10 King Parrot, *Alisterus scapulatus*, feeding on a Banana Fig, *Ficus pleurocarpa*.

METHODS

Frugivores

I determined which animals were eating fruits and seeds along fruit transects using a reference collection of bite marks in fruits as detailed in Chapter 3. The fruit transects, which were usually sampled monthly, are described in Chapter 4. Comparison of the impacts of different groups of frugivores on fruits are for the total number of fruits and plant species sampled from October 1990 to December 1992. The names of frugivores used in this chapter follow the categories described in Chapter 3:

MRK	- Musky Rat-kangaroo;
Uromys	- White-tailed Rat *Uromys caudimaculatus* (largest rat)
Rats	- Bush Rat *Rattus fuscipes*, *Rattus leucopus*, Fawn-footed Melomys *Melomys cervinipes*, Masked White-tailed Rat *Uromys hadrourus*;
Parrot	- King Parrot *Alisterus scapularis*, Sulphur-crested Cockatoo *Cacatua galerita*, Crimson Rosella *Platycercus elegans*
Bowerbird	- Mostly Spotted Carbird *Ailuroedes melanotis* and Tooth-billed Bowerbird *Scenopoectes dentirostris*, but also includes Eastern Whipbird *Psophodes olivaceous* which is mostly searching for invertebrates in fruit;
Pig	- Feral Pig *Sus scrofa*;
Maggot	- Various Dipteran larvae infecting fruits;
Others	- Cassowary *Casuarius casuarius*, Insects (other than Maggots).

Determining Seed Predation

In this chapter, I differentiate between fruit consumption and seed predation. While Musky Rat-kangaroos consume the seeds of only 11% of the fruits they eat, when they do consume a seed they kill it by chewing the endosperm and embryo. White-tailed Rats, rats, parrots and pigs also kill seeds by chewing them but occasionally eat only the flesh leaving the seed intact. Maggots, Cassowaries and insects tend to leave most seeds intact, either swallowing fruits and defaecating the seeds whole (Cassowaries) or eating only the flesh (insects and maggots). Bowerbirds often swallow small fruits whole and defaecate the seeds intact but will also gouge sections out of large fruits, sometimes destroying the seed in the process. Seed predation is based on the nubers of fruits or seeds which were destroyed by chewing or gouging by each of the frugivore groups. Data for bowerbirds represents only the large fruits they consume and not the small fruits they eat whole.

Predators

I collected Dingo faeces in each month from February 1990 until January 1991 along 4km of gravel road which ran adjacent to the rain forest in which my study site was situated. Different numbers of scats were found in different months (range 1 - 7; total = 45). I have not examined any seasonal changes in the diet or Dingoes because of the unequal number of samples and the positive correlation between number of prey species and number of scats. Prey species were identified by Barbara Triggs (Dead Finish, Genoa, Victoria) using microscopic examination of hairs in the scats.

RESULTS

Frugivores

I examined 30,815 fruits along transects for bite marks. Nineteen percent had evidence of frugivore attack. In 67% of cases I was able to identify the animal which had fed on the fruit; most were eaten by one of seven animals or animal groups (Figure 10.1).

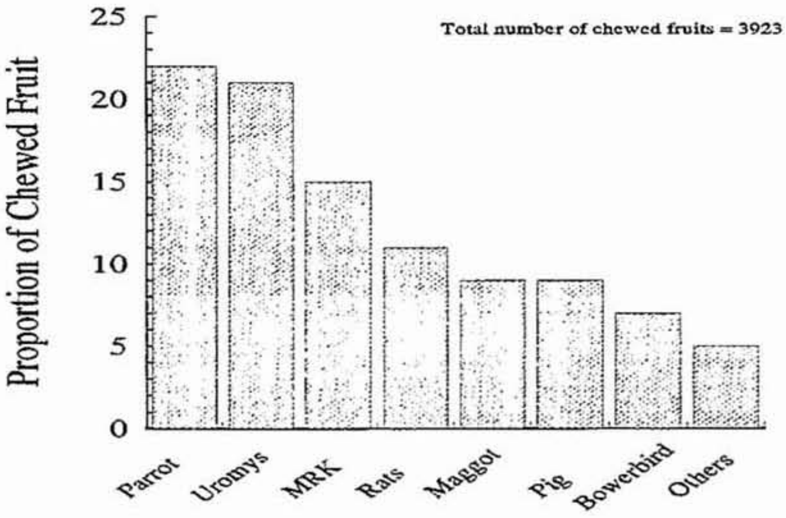

Figure 10.1 Proportion of fruits of known frugivore attack accounted for by each animal or animal group.

Maggot attack was restricted to large numbers of one species, Rose Walnut, *Endiandra monothyra*. Maggots ate most of the flesh but left the seed. Pigs consumed an entire crop of Black Walnut, *Endiandra palmerstonii*, flesh and seeds, but did not attack other species on my study site. Cassowaries, long recognised as significant frugivores and dispersal agents, accounted for very few fruits along the transects. This is probably due to their low density (relative to the other frugivores) and habit of dispensing seeds and fruits in clumps, only a few of which landed on transects. The other five groups of animals (parrots, White-tailed Rats, Musky Rat-kangaroos, rats and bowerbirds) ate a broader range of species along my transects and will be discussed further.

Seed Predation

The five frugivore groups which consumed the most fruits all killed the seeds of a number of the species they consumed (Figure 10.2). At one extreme White-tailed Rats consumed the seeds of 95% of species while Musky Rat-kangaroos and Bowerbirds consumed the seeds of only 50% of species.

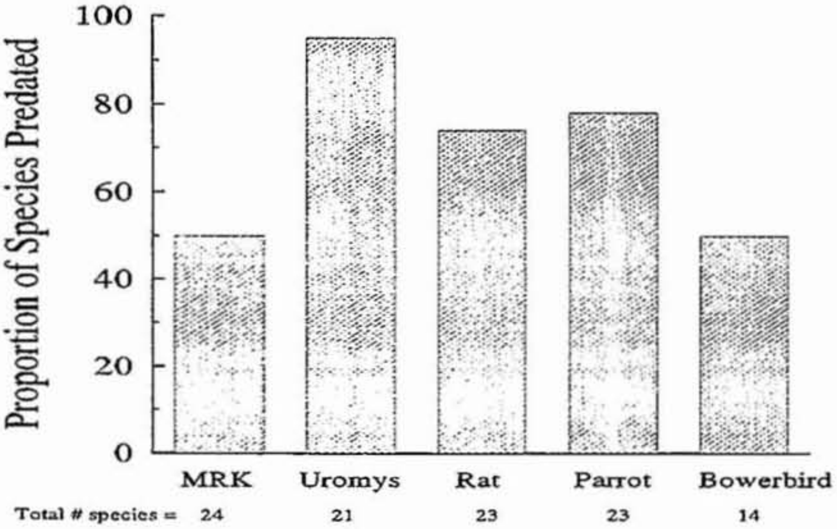

Figure 10.2 Proportion of species consumed by each frugivore group whose seeds are eaten, at least some of the time.

For each group of frugivores, the proportion of fruits handled whose seeds were killed is shown in Figure 10.3. White-tailed Rats, rats and parrots were major seed predators, whereas bowerbirds and Musky Rat-kangaroos were less predatory. Musky Rat-kangaroos ate only 11% of the seeds they handled.

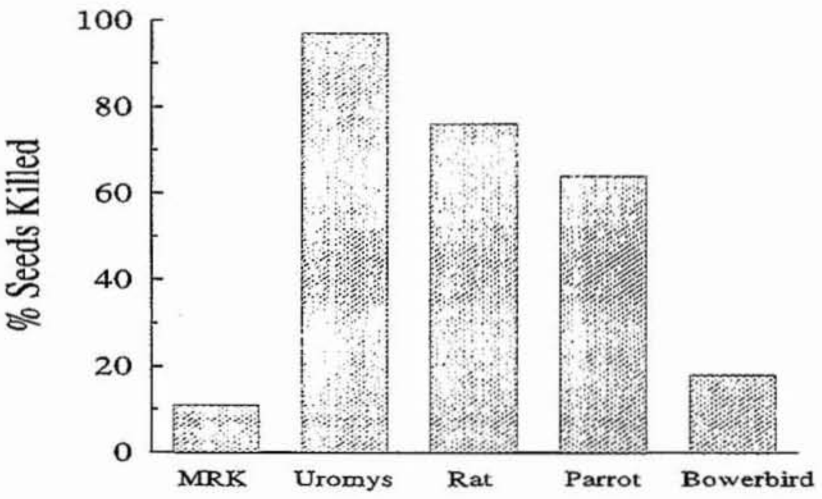

Figure 10.3 Proportion of fruits consumed and whose seeds were killed by each animal group.

Figure 10.4 gives a detailed breakdown of the proportion of seeds killed in each species of plant for each frugivore group. In some cases, seed predation data includes seeds that had been cached. This is particularly so for Austrobaileya, *Austrobaileya scandens*, (#2) which has 4 - 12 seeds per fruit and is regularly cached by Musky Rat-kangaroos. Figure 10.4 shows there are a few species which are heavily predated by several groups of frugivores (e.g. Fontain's Blushwood, *Fontainea picrosperma* - #5 and Mountain Mangosteen, *Garcinia gibbseae* - #16) and others which escape predation entirely (e.g.Boonjie Blush Walnut, *Beilschmiedia volckii* - #12). Figure 10.4 also shows that parrots, White-tailed Rats and rats kill a high proportion of seeds from a larger number of species than do Musky Rat-kangaroos and bowerbirds. In addition, Musky Rat-kangaroos and bowerbirds are significant predators for a limited number of species.

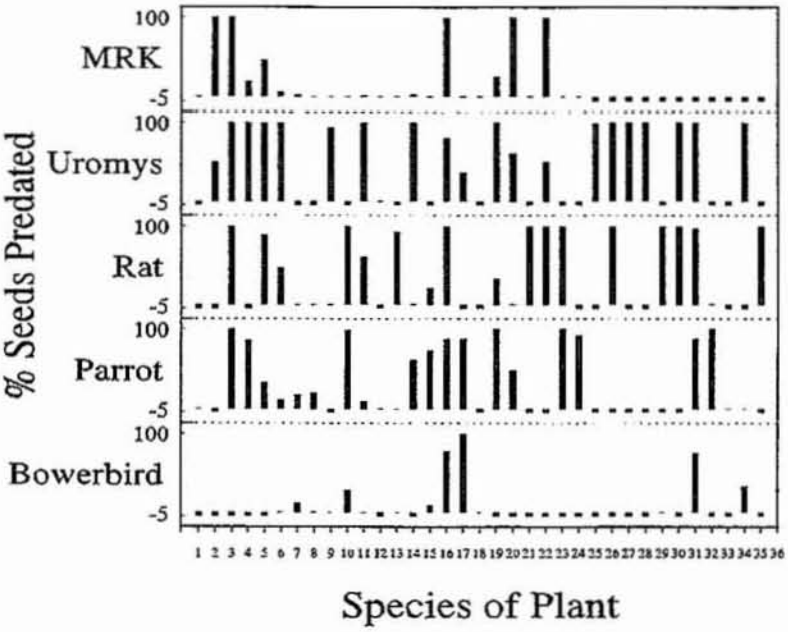

Figure 10.4 Predation rates on seeds for each species of plant and each frugivore group. -5 means neither the fruits or seeds were eaten.

List of plant species for Figures 10.4 and 10.5.

1. *Castenosperma alphandii*
2. *Austrobaileya scandens*
3. *Syzygium gustavioides*
4. *Neimeyera prunifera*
5. *Fontainea picrosperma*
6. *Prunus turnerana*
7. *Beilschmiedia tooram*
8. *Endiandra sankeyana*
9. *Oraniopsis appendiculata*
10. *Ficus pleurosperma*
11. *Cryptocarya oblata*
12. *Beilschmiedia volckii*
13. *Elaeocarpus angustifolia*
14. *Syzygium papyraceum*
15. *Endiandra monothyra*
16. *Garcinia gibbseae*
17. *Siphonodon membranaceum*
18. *Diploglottis bracteata*
19. *Endiandra insignis*
20. *Faradaya splendida*
21. *Myristica insipida*
22. *Baileyoxylon lanceolatum*
23. *Cinnamomum laubatii*
24. *Beilschmiedia recurva*
25. *Athertonia diversifolia*
26. *Pouteria castenospora*
27. *Endiandra palmerstonii*
28. *Calamus moti*
29. *Austromyrtus dallachiana*
30. *Pittosporum rubiginosum*
31. *Irvingbaileya australis*
32. *Pothos longipes*
33. *Halfordia scleroxylla*
34. *Niesosperma poweri*
35. *Aglaia australiensis*
36. *Syzygium trachyphloium*
37. *Tetrasynandra lasciflora*
38. *Triunia erythrocarpa*

Despite the large number of frugivores, both individuals and species, feeding on fruits on my study site, direct competition was limited. Figure 10.5 which uses electivity indices (see Chapter 3; Vanderploeg and Scavia 1979), shows the rates at which fruits were sought by each group of frugivores in relation to each species of plant.

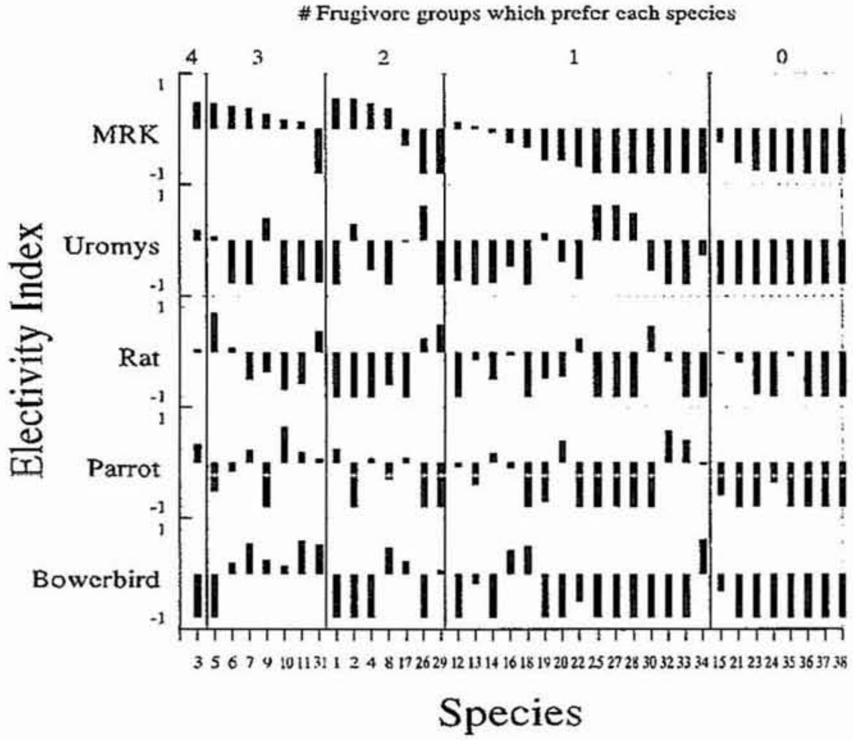

Figure 10.5 Electivity indices for the fruits of 38 species of plants for 5 frugivore groups. -1 = not selected. +1 = maximum selection for.

There is no species of fruit for which all five frugivore groups showed positive preference. In 24% of species three frugivore groups had positive preferences, while in 21% two frugivore groups had a positive preference for the same species. A large number were positively selected by only one frugivore group (29%), while many (26%) were not positively selected by any of the frugivores. Parrots and Bowerbirds overlapped most extensively with Musky Rat-kangaroo preferences (six species overlapping each), while White-tailed Rats had positive indices in common with Musky Rat-kangaroos in four cases and rats in two. For only two species favoured by Musky Rat-kangaroos did they not share a positive index with another frugivore group (Boonjie Blush Walnut, *Beilschmiedia volckii* - #12; Silver Quandong, *Elaeocarpus angustifolia* - #13). Frugivores other than Musky Rat-kangaroos overlapped in species preferences less with other groups than with Musky Rat-kangaroos, although Parrots and Bowerbird had common positive preferences for six species. These data suggest that Musky Rat-kangaroos are the least selective of the frugivores examined.

Three species were not recorded as being eaten by the groups examined due to limitations in the sampling method. Two species (*T. lasciflora* - #37 and *S. trachyphloium* - #36) had very small fruits which were consumed whole by birds (other than parrots; direct observation) and in one case (*S. trachyphloium*) by Musky Rat-kangaroos (see Appendix 1) and therefore no evidence of feeding was found on the transects. The third species (*Triunia erythrocarpa*), known to be eaten by Musky Rat-kangaroos (Appendix 1), did not fall frequently within my transects and no evidence of feeding on this species was recorded within the transects.

Table 10.1 Percentage overlap in fruits favoured, eaten or not eaten by Musky Rat-kangaroos and other frugivore groups. Percentages are out of 14 species favoured (Electivity index >0), 10 species eaten (Electivity index <0) and 11 species not eaten by Musky Rat-kangaroos.

		Musky Rat-kangaroos		
		Favoured	Eaten	Not eaten
Favoured	*Uromys*	29	10	36
	Rats	21	10	36
	Parrots	50	20	27
	Bowerbirds	43	30	27
Eaten	*Uromys*	36	40	27
	Rats	50	60	18
	Parrots	36	40	9
	Bowerbirds	7	20	0
Not Eaten	*Uromys*	36	50	36
	Rats	29	40	45
	Parrots	14	40	64
	Bowerbirds	50	50	73

Table 10.1 summarises dietary overlap between frugivore groups and Musky Rat-kangaroos based on the categories of favoured, eaten and not eaten derived from positive or negative values on the electivity indices and absence from the diet. This

shows a reasonably even spread of percentage overlap in species that are favoured, eaten or not eaten by each frugivore and Musky Rat-kangaroos. While the potential for competition exists there appears to be significant partitioning of resources. The most significant overlap in fruits favoured by Musky Rat-kangaroos is with parrots and bowerbirds both of which forage primarily in the canopy (although bowerbirds also feed on the ground) and therefore are spatially separated from competition. In addition, the foraging of birds in the canopy often dislodges fruits and makes them available to terrestrial frugivores, suggesting that the overlap in preferred species between bowerbirds parrots and Musky Rat-kangaroos may actually be advantageous to Musky Rat-kangaroos.

Predators

Analysis of hair in 45 Dingo scats showed that Dingoes are predators on Musky Rat-kangaroos (Figure 10.6; next page). Musky Rat-kangaroo remains were found in 11% of the 45 scats (8.6% of prey occurrences). All scats containing Musky Rat-kangaroo remains were found in March, April and May (1990), soon after young Musky Rat-kangaroos had become independent (Chapter 6). I suspect the majority of animals killed were subadult.

Other predators consuming Musky Rat-kangaroos included Amethyst Pythons, *Morelia amythestina*, Grey Goshawks, *Accipiter novaehollandiae*, Rufous Owls, *Ninox rufa*, Lesser Sooty Owls, *Tito multipunctata*, Spotted Tailed Quolls, *Dasyurus maculatus*, Domestic Cats, *Felis catus* and farm dogs, *Canis familiaris*. I witnessed two occasions when Grey Goshawks were feeding on the remains of Musky Rat-kangaroos (one adult and one subadult) on my study site. A resident Amethyst Python ate an adult Musky Rat-kangaroo which was wearing a radio-collar.

Scott Burnett (pers. comm. June 1996), in his study of predators in the wet tropics of Australia, found that Musky Rat-kangaroos were one of the most significant items in the diet of Spotted Tailed Quolls, accounting for 11.4% to 37% of prey occurrences in scats from different areas. In addition, Burnett found subadult Musky Rat-kangaroo remains were a common component of pellets under roosts of Lesser Sooty

Owls and less often, Rufous Owls. I witnessed five farm dogs, hunting as a pack, kill an adult Musky Rat-kangaroo but only witnessed them hunting on two occasions. A single domestic cat killed three adult Musky Rat-kangaroos in one year in an area where Musky Rat-kangaroos are not abundant (Rowles, P. pers. comm. 1991). Clearly Musky Rat-kangaroos are an important food resource for many predators in tropical rain forests in Australia.

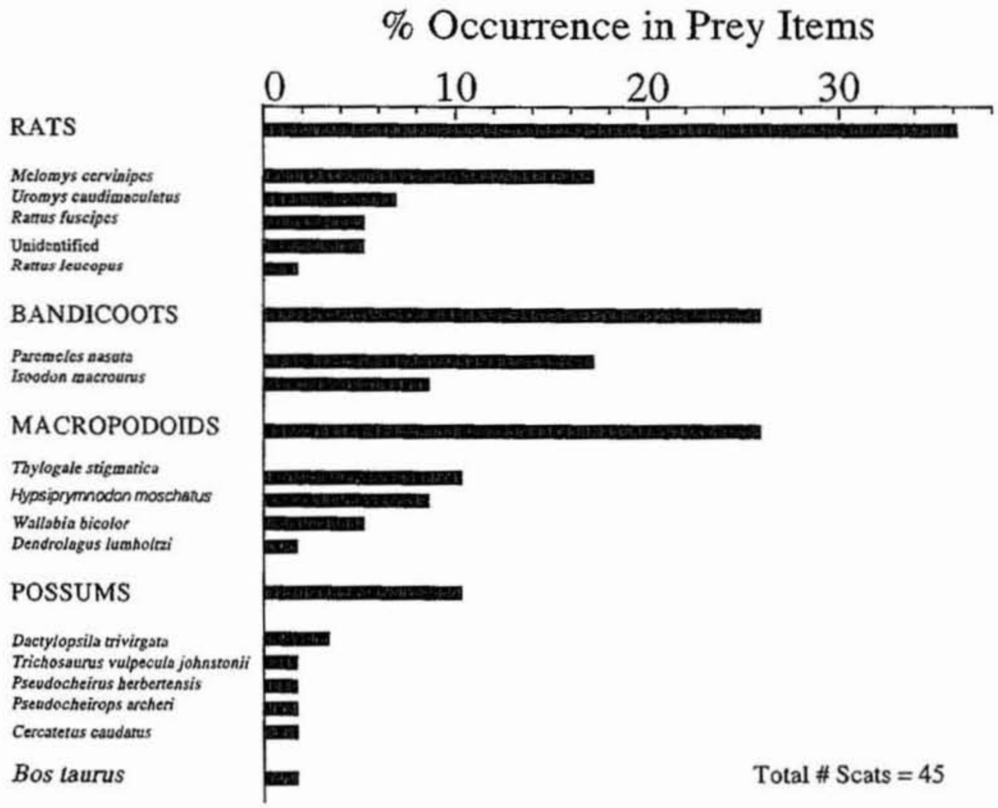

Figure 10.6 Frequency of occurrence of different species of prey in the scats of Dingoes near to my study site.

DISCUSSION

Frugivores

Compared to other frugivores active in the area, Musky Rat-kangaroos appear to be significant consumers of fruit (see Figure 10.1). They are less predatory than many other frugivores, consuming the seeds of only 11% of the fruits they handle compared to over 60% for White-tailed Rats, rats and parrots (Figure 10.3). They also appear less predatory than some other cursorial frugivores which eat considerable quantities of seed (e.g. Acouchies and Agoutis, Smythe 1986; Dubost 1988).

In addition to those mentioned above, many other frugivorous birds occurred on my study site, including: fruit pigeons (Columbidae; six species); Victoria's Riflebirds *Ptiloris victoriae*; and Pied Currawongs *Strepera graculina* (pers. obs.). These species, and Bowerbirds and Cassowaries, tend to swallow fruit whole and defaecate or regurgitate intact seeds (although Brown Cuckoo-doves *Macropygia amboinensis* are known to digest the majority of seeds they eat; Jansen, A. pers. comm.1994; Irvine, A. pers. comm. April 1997). Even so, the germination of seeds from Cassowary droppings, which often contain fruits with their flesh still intact, is poor for some species (24.5% of species showed <3% germination; Stocker and Irvine 1983). This may be due to partial digestion during passage through the gut of a Cassowary or perhaps inherently poor germination of the seeds of those species. No tests have been done to confirm either possibility. Similarly no studies have been conducted to examine the germination of fruits after passage through the other frugivorous birds of the area. Musky Rat-kangaroos, like these avian frugivores, handle most seeds gently and are probably comparable to them with respect to disperser quality (see Chapter 1). For species whose seeds are eaten by rats, Musky Rat-kangaroos may be higher quality dispersal agents due to their habit of scatterhoarding resulting in better deposition patterns for the seeds (see Chapter 9).

Musky Rat-kangaroos were significant predators on the seeds of five species of plant (Figure 10.4). However, they regularly cached three of these: Austrobaileya *Austrobaileya scandens*; Baileyoxylon *Baileyoxylon lanceolatum*; and Watergum

Syzygium gustavioides, and therefore probably acted as dispersal agents as well as predators (see Chapters 8 & 9). In addition, they regularly chewed the very large seeds of Watergums (size class 5; Chapter 3) but rarely killed them, eating only a small amount of the endosperm and leaving the embryo intact and still able to germinate. While the few October Vine *Faradaya splendida* fruits that fell on transects had their seeds partially consumed, several large crops fell nearby and were mostly ignored by Musky Rat-kangaroos. This suggests that October Vines generally escape the depredations of Musky Rat-kangaroos and that their high ranking on the predation index was due to a small sample size. Finally, Mountain Mangosteens, which were heavily predated by all frugivores, have seeds housed in numerous chambers (5 - 9) whose surrounding flesh exuded sticky, yellow latex. All predators left fruit with one or more chambers intact, presumably being put off by excess latex. While Musky Rat-kangaroos may be significant predators for a range of rain forest plant seeds, they are probably important dispersal agents for those seeds as well. This pattern is recognised for many other seed predators, Agoutis being a good example (Smythe 1989).

The overlap in fruits eaten and favoured by Musky Rat-kangaroos, White-tailed Rats, rats, bowerbirds and parrots was considerable (Figure 10.5; Table 10.1). However, there was also clear partitioning of species. No species was favoured by all groups. Those favoured, eaten and not eaten were fairly evenly divided among the groups. The largest overlap being between birds and Musky Rat-kangaroos. These findings are similar to those of Gautier-Hion *et al.* (1980), who found considerable overlap in the species of fruits consumed by ruminants, squirrels and primates.The diet of squirrels overlapped more extensively with those of primates and ruminants than the diet of either primates or ruminants did among the three groups examined. In addition, a considerable proportion of the diets of primates and ruminants consisted of species unique to each group (Gautier-Hion *et al.*1980). In comparison, much less specificity occurred in my study, which may be due to sampling factors, such as the difference in area sampled (a much larger area in Gautier-Hion *et al.*'s 1980 study) or the difference engendered by the inclusion of birds in my study. Alternatively, Australian frugivores may be less selective than those in Gabon, possibly due to a less diverse community existing in Australia.

Despite the resource partitioning amongst the frugivores I examined, there was still considerable overlap in fruits favoured. For arboreal and terrestrial frugivores this overlap probably does not translate into potential competition due to their different feeding zones. However, in the case of terrestrial frugivores, dietary overlap may result in direct competition for fruits, particularly during periods of fruit shortage. Smythe (1986), in his review of terrestrial frugivores in the Neotropics, suggests that competition for fruits may be a factor leading to the evolution of hoarding behaviour (see also Smith and Reichman 1984). The hoarding behaviour of Musky Rat-kangaroos and White-tailed Rats may be due to interspecific competition for resources as well as intraspecific competition. In Chapter 8, I highlighted the difference in cache sites between White-tailed Rats and Musky Rat-kangaroos and Goldberg (1994) recorded that White-tailed Rats recovered mock caches at a rate similar to their own. Together these data suggest that caching may be more effective at concealing fruit from interspecific competitors than intraspecific competitors.

Predators

Dingoes *Canis familiaris dingo*, commonly eat a high proportion of macropodoids, often 30 - 60% (Brown and Triggs 1989; Lunney *et al.* 1990; Triggs *et al.* 1984). The appearance of Musky Rat-kangaroos in their diet is therefore unremarkable. However, what does seem remarkable, is the diversity of predators which consume Musky Rat-kangaroos, at least eight species. Given the abundance of Musky Rat-kangaroos, they probably play an important role in supporting this diverse array of predators. Smythe (1978) found that Agoutis were also important prey items, particularly in sustaining the population of male Coatis during the period of few fruit. Clearly, Musky Rat-kangaroos are ecologically important animals, both in terms of their role as frugivores and dispersal agents and as food for predators.

◆ ⁂ ◆