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MUSKY RAT-KANGAROOS, *Hypsiprymnodon moschatus*: CURSORIAL FRUGIVORES IN AUSTRALIA'S WET-TROPICAL RAIN FORESTS.

Thesis submitted by
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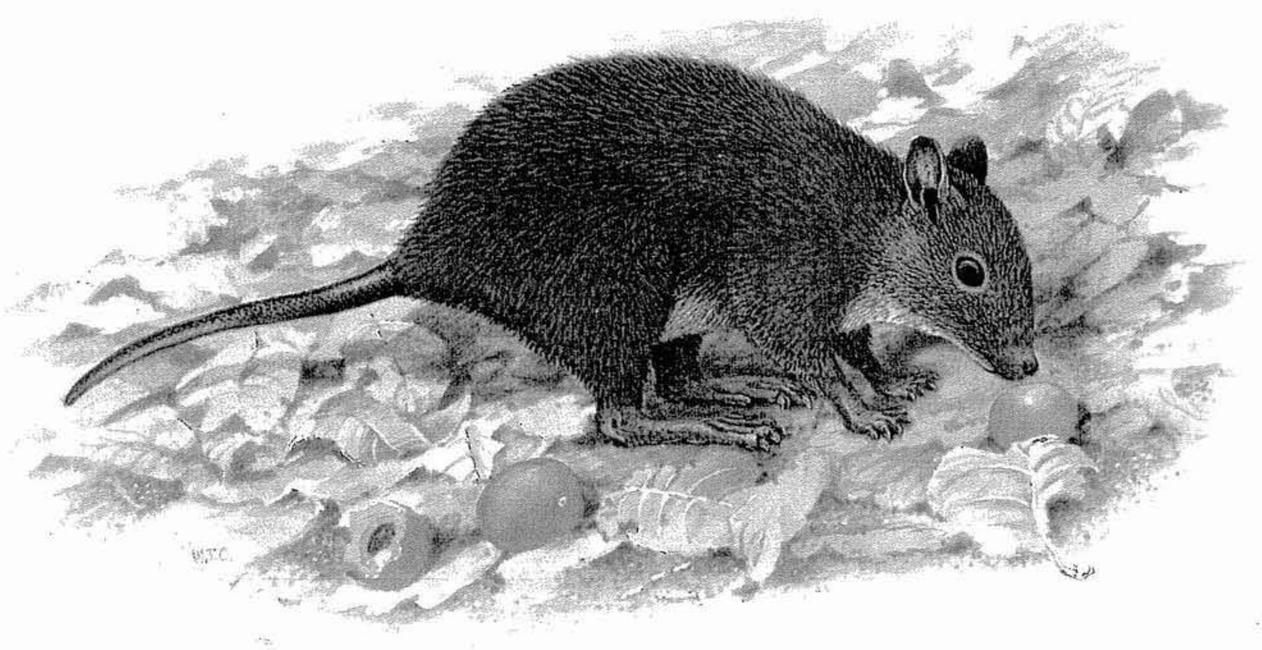
in May 1997

for the degree of Doctor of Philosophy
in the Departments of: Zoology and Tropical Ecology;
and Tropical Environment Studies and Geography,
James Cook University of North Queensland



Hypsiprymnodon moschatus
MUSKY RAT-KANGAROO

A Musky Rat-kangaroo inspecting the fruit of Baileyoxylon, *Baileyoxylon lanceolatum*.

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ABSTRACT

Musky Rat-kangaroos, *Hypsiprymnodon moschatus*, are the smallest member of the kangaroo family (Macropodoidea) and are restricted to Australia's tropical rain forest in north-east Queensland, where they are important dispersal agents for rain forest plants. This study was the first to examine their basic ecology in the field and initially aimed to determine their diet, reproduction, population size and movement patterns. After beginning field-work, I discovered that Musky Rat-kangaroos were primarily frugivorous and scatterhoarded fruits and seeds. Subsequently, the aims of my study focussed on their role as dispersal agents and what effects their caching behaviour had on the survival of the seeds they disperse.

The diet of Musky Rat-kangaroos was examined through direct observation, assessing teeth marks in fruit and by microscopic examination of faeces. They can be classified as frugivores on the basis that the fruits and seeds of at least 49 species accounted for the bulk of their diet throughout the year. However, they also consumed invertebrates and fungus which became more significant in their diet when fruit availability was low. Larger quantities of fungus were consumed during the Wet season (February to April) and invertebrates during the Cold season (May to July) than at other times of year. This shift in emphasis in their diet reflected the pattern of availability of ripe fruits. Ripe fruits were most abundant during the Dry and storm seasons (August to January), declined in the Wet season and reached their yearly minimum in the late Wet and early Cold season (April, May). Fruit biomass was at least 300 times higher during the peak than in the trough periods in the years examined, whereas invertebrate availability was stable in comparison.

Musky Rat-kangaroos were common on my study site, averaging 2.4/ha. They occupied small home ranges (males - 2.1 ha; females 1.4 ha) which overlapped extensively with other individuals of both genders. They were solitary and promiscuous and their seasonal reproductive pattern reflected the changes in availability of ripe fruits. Males underwent rapid expansion of their testes during the peak in fruit availability (September) and remained reproductive until fruit peak in fruit availability (September) and remained reproductive until fruit availability declined in March or April. Females evicted pouch young during peak fruit availability (October) and gave birth to one, two or three young at the end of the peak fruiting season (February to April). Both male reproductive seasonality and multiple young per litter are exceptional characteristics among macropodoids and probably result from Musky Rat-kangaroo's unique niche as the only frugivorous macropodoid.

Musky Rat-kangaroos dispersed the seeds of many of the fruits they consumed. They scatterhoarded 14% of the simulated fruits used in an experiment and moved 17% of them further than five metres from their source (up to 68m). The scatterhoarding behaviour of Musky Rat-kangaroos conferred several advantages to two tree species I examined experimentally. Firstly, burial removed their seeds from 100% predation (mostly by rats) suffered by seeds on the litter surface. Secondly, dispersal away from the parent plant aided the survival of one species due to escape from density- or distance-dependent mortality under the parent. Thirdly, 21% of seeds cached by Musky Rat-kangaroos were cached in canopy gaps, a microsite which often increases the vigour of seedlings. Musky Rat-kangaroos killed fewer seeds than many other frugivores sharing their habitat. Because of this, their scatterhoarding behaviour and the low diversity of frugivores in Australia, Musky Rat-kangaroos are clearly of great ecological significance in Australia's tropical rain forests.

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FOREWORD

This study was of a little known kangaroo in Australia's wet tropics. It required intensive fieldwork involving long hours in sometime difficult conditions. During the course of this study I simultaneously contracted infections of *Giardia lamblia*, an intestinal flagellate, and *Salmonella* sp. (similar to *S. typhae*). In combination, these organisms lead on to an ongoing and debilitating condition known as Ulcerative Colitis. In some of the following chapters I refer to "ill health" resulting in periods when monthly data were not collected. This was due to the condition described above. I am pleased to report that I am now completely recovered.

Technical Notes

Nomenclature follows: Gruson (1976) for birds outside Australia; recommendations of the Royal Australasian Ornithologists Union in Slater *et al.* (1995) for birds in Australia; MacDonald (1984a & b) for mammals outside Australia; the Australian Museum recommendations in Strahan (1995) for mammals in Australia; and Flannery (1995 a & b) for mammals in New Guinea and its neighbouring islands.

Two publications have already resulted from this study which are appended at the end of this thesis.

STATEMENT ON SOURCES

DECLARATION

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

.... 14/5/1997

Andrew James Dennis

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There are many people I wish to thank for their assistance and support during the process of completing this study. Foremost among them are Helene Marsh and John Winter who were exemplary supervisors, allowing me complete freedom to develop my work but always being available for assistance and advice when I asked for it. They were both careful and thorough in their comments on early drafts of this manuscript and Helene was particularly good at letting me know when I needed assistance with statistical analyses.

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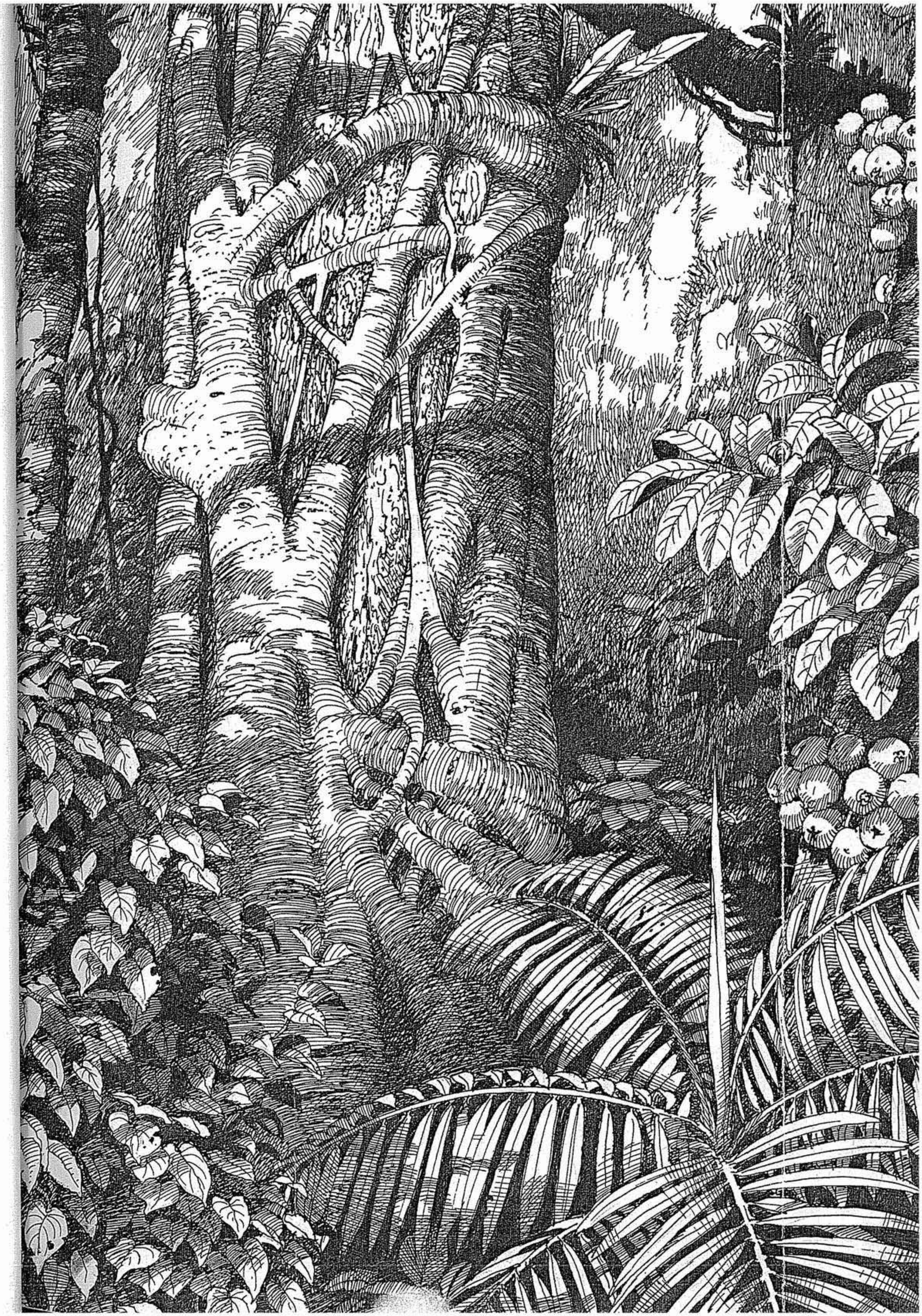
for sharing his observations on captive Musky Rat-kangaroos; Colin Mathews for help in sorting out various computer problems; Barbara Triggs for identifying the hairs in dingo scats for me; Diana House for assisting with typing references; Ian and Froone Bean for rainfall records; and V. English and Amy Jansen for temperature records.

David and Linda Joncour were neighbours to my study site and Dave was my frequent field companion, collecting and cleaning fruits, lugging traps and climbing trees (even though Hypsies are terrestrial). Dave also housed the control seeds for my experiment in his greenhouse and kindly demonstrated just how toxic the seeds of Fontain's Blushwood are. Thanks Dave. Linda was always ready with a hot cup of tea and a dry spot to sit when it was pouring rain. I'll never forget the pleasant surprises I would find on my car seat when I returned to get lunch after a wet and muddy morning in the field; a steaming hot bowl of Linda's pea and ham soup was a welcome treat on a cold wet day.

Stan Breeden, Bill and Wendy Cooper and Cliff and Dawn Frith were all inspirational support and made their extensive libraries available to me at various times. They also provided me with dry office space to use when times were tough (wet) and sharing stories on our respective projects was always encouraging.

Thanks also to my friends and fellow PhD students: Dr Frank Seebacher, Dr Amy Jansen, Eshana (Dr Elizabeth Bragg), Karl Vernes, Scott Burnett and Joan Bentrupperbaumer for sharing discussions, field work on our respective projects and good times; Amy Jansen for her constant support and collaborating on the litter fauna sampling; and the crew of JSAT (James Cook University Students on the Atherton Tableland) for many fruitful (and tea and cakeful) discussions.

I also thank Tony Annesley and Sue Bloomfield who were instrumental in supporting me through difficult periods of illness and getting me on the road to health. Finally, I wish to thank Diana for supporting me in so many ways and putting up with the intensity of the final stages of writing a thesis.



Chapter 1

GENERAL INTRODUCTION

AUSTRALIA'S SMALLEST KANGAROO

A member of the superfamily Macropodoidea which includes kangaroos, wallabies and rat-kangaroos, the Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, Ramsey, 1876 (Marsupialia, Potoroidae) is unique in many ways. It is by far the smallest Macropodoid weighing only 520g (±5.7g; mean ± SE; this study; N=127) which is a little more than half the weight of the next smallest in the group (Figure 1.1).

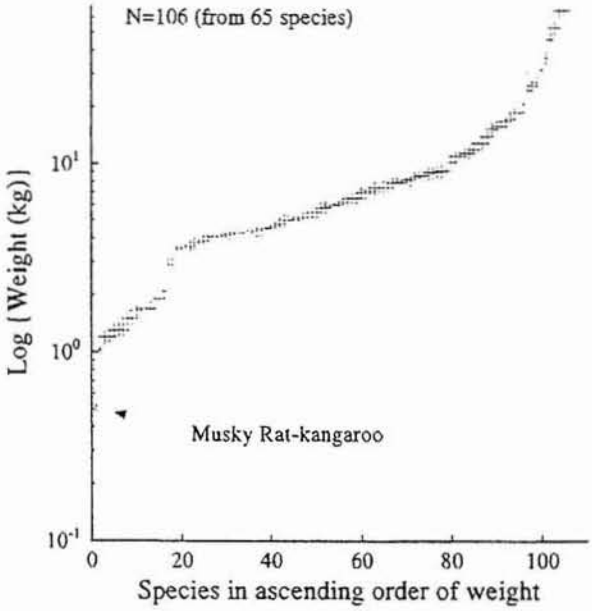


Figure 1.1 Distribution of weights in the Macropodoidea, ranging from 0.52kg to 66kg. Weights for each gender are listed separately for sexually dimorphic species.

Data Sources: (Flannery 1995a. Flannery 1995b. Flannery *et al.* 1996. Strahan 1995)

Kangaroos, wallabies and rat-kangaroos currently occupy all terrestrial habitats in Australia, New Guinea and some neighbouring islands (Hume *et al.* 1989) but are thought to have evolved in rain forest from an ancestor which they may have shared with the phalangerid possums (Archer 1985). Musky Rat-kangaroos retain many features likely to be similar to ancestral macropodoids, including their habitat: tropical rain forest. The oldest kangaroo fossils are found in mid-miocene deposits (15 million years old). Archer (1985) reconstructed an image of these animals based on fossil teeth and foot bones and estimated they were small (~500g) omnivores (likely to feed on insects and fruit) which had a quadrupedal running gait. Superficially, these ancestors were similar to Musky Rat-kangaroos which are the only extant macropodoids to locomote in this fashion (the others bound on their hindlegs when moving fast). Other features of Musky Rat-kangaroos unique among Macropodoidea include: an opposable first digit on the pes (Figure 1.2); a relatively simple digestive tract (see Chapter 3; Dawson 1989); retention of second incisors; and the regular birth of twins (see Chapter 6; Johnson and Strahan 1982).

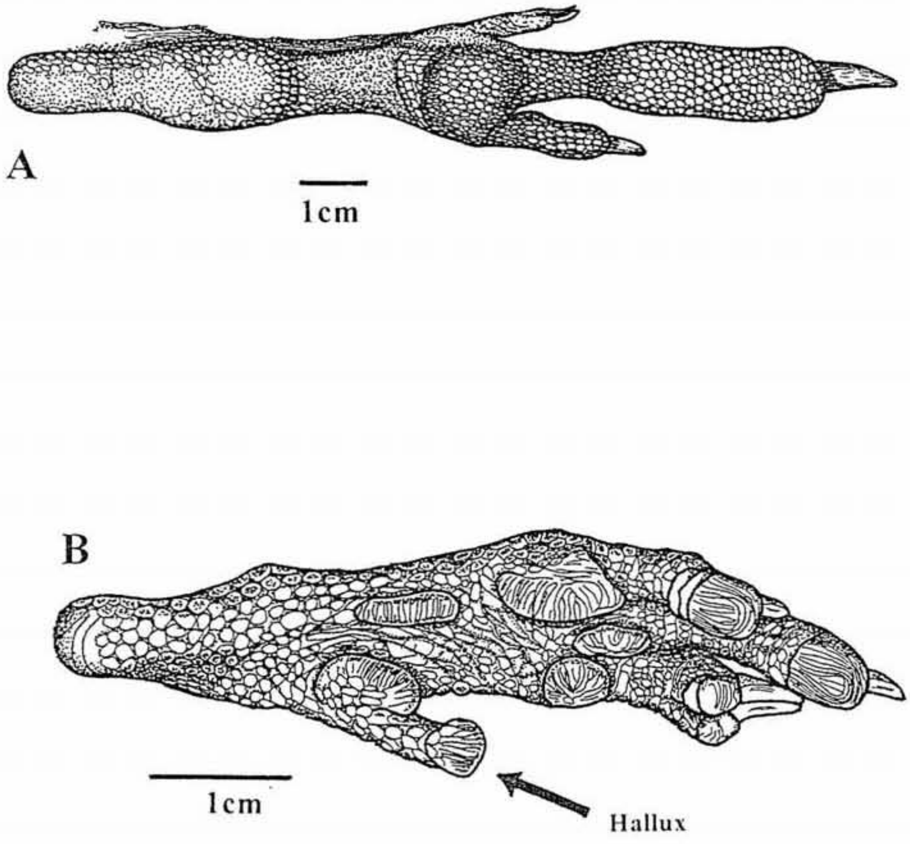


Figure 1.2 Pes of **A.** Rufous Bettong *Aepyprymnus rufescens*, more similar to the majority of Macropodoids and **B.** Musky Rat-kangaroo, note the hallux and the more similar toe lengths.

Several other features are common to Potoroids but not the Macropodids, these include: their general dentition; a prehensile tail; the regular use of a constructed nest; and a relatively omnivorous diet (Seebeck *et al.* 1989). The ten species of Potoroidae, which are all restricted to Australia, appear to be less specialised than macropodids. The retention of a prehensile tail (ancestral), small size (0.5 - 3.5kg) and relatively unspecialised dentition being some features in which they differ from the latter group (Hume *et al.* 1989; Seebeck *et al.* 1989; Seebeck and Rose 1989). While most potoroids are omnivorous, the majority have specialised to varying degrees on hypogeal fungi (Seebeck *et al.* 1989), another feature which sets Musky Rat-kangaroos, which do not eat hypogeal fungi, apart.

Prior to this study, only physical descriptions (Carlsson 1915; Heighway 1939; Johnson and Strahan 1982; Owen 1877; Owen 1878; Owen 1879; Ramsey 1876; Woods 1960), a few observations of wild behaviour (Breeden and Breeden 1970; Schurer 1985) and captive behaviour have been published on Musky Rat-kangaroos (Johnson and Strahan 1982). Little is known of its ecology or reproductive biology. Breeden and Breeden (1970) described its diurnal behaviour, observed it feeding on the seeds of the Candle-nut tree, *Aleurites mollucana*, and also noted that it fed on insects. Johnson's observations of a captive colony added much information to our knowledge of the Musky Rat Kangaroo's behaviour (Johnson *et al.* 1983a; Johnson *et al.* 1983b; Johnson and Strahan 1982). Johnson and Strahan (1982) confirmed that females normally rear two young simultaneously, a behaviour unknown in any other macropodoid, and confirmed its diet of fruit and litter fauna. Schurer (1985) summarised this information and added a few observations of wild animals. My own observations (Chapter 3) confirmed that fruits and seeds form the bulk of its diet, litter fauna are eaten year round and epigeal sporocarps of a few Agaric fungi are also consumed when available.

Because of the dearth of information on Musky Rat-kangaroos, this study was initially exploratory; developing trapping methods and examining basic aspects of their biology and ecology including: diet (Chapter 3); resources (Chapters 4 & 5); reproduction (Chapter 6); population size and movements (Chapter 7). As I gathered information on their diet and resources my main focus became their ecological roles as frugivores including: seed dispersal (Chapter 8); survival of dispersed seeds (Chapter 9); and relationships with other frugivores (Chapter 10). Thus, I review literature on frugivores and dispersal in the next section and focus most discussion and interpretation of data in the context of Musky Rat-kangaroos as frugivores. However, where I feel it is relevant I also discuss my data on Musky Rat-kangaroos in relation to other macropodoids (e.g. Chapters 3, 6 & 7).

TROPICAL RAIN FOREST FRUGIVORES AND THE DISPERSAL OF SEEDS

Exactly when animal dispersal of plant propagules began is lost somewhere in the depths of time with little chance of our scant fossil record ever revealing the beginnings of this important and long lasting association. However, it seems clear that this relationship evolved independently on a number of occasions: once with early amphibians, sauropods and fish and again with mammals and birds (see Tiffney 1986). Perhaps as early as the mid to late Devonian and early Carboniferous periods when ferns, horsetails and lycopods were producing large female spores or when gymnosperms, seed ferns and pro-gymnosperms began producing seeds (White 1986), amphibians, sauropods and fish may have begun ingesting plant reproductive parts and dispersing them through their faeces. Certainly by the Pennsylvanian, biotic dispersal seems to have been well established with reptiles consuming the propagules of seed ferns (van der Pijl 1972) including the large fleshy fruits of the medullosans (Tiffney 1986). These dispersal relationships declined and became extinct through the Permian and Triassic, probably due to the drying climate, and were replaced by fewer, less "specialised" relationships with herbivorous dinosaurs (Tiffney 1986). It was not until after the Cretaceous radiation of angiosperms that characters more obviously linked to biotic dispersal mechanisms again became more common. In the early Tertiary the dispersing animals were likely to have been birds and mammals, which were consuming fruits from families that still occur in present ecosystems (Tiffney 1986; van der Pijl 1972).

Whenever the origins, it seems clear that like many other associations such as the mycorrhizal association between plants and fungi, which date back to the dawn of plants' terrestrial existence (White 1986), the relationship between plant propagules and animal dispersers has been a long and fruitful one. In this section, I will briefly examine the different modes of dispersal used by plants, particularly in tropical rain forests, the consequences of being dispersed and the animals that do the dispersing; before going on briefly to examine the relationship between animals and the plants they disperse. I do this primarily to place this autecological study of Musky Rat-kangaroos into a broader community and ecosystem context to better understand the functional role played by Australia's smallest kangaroo.

Modes of Dispersal

Although the dispersal of seeds by animals may have evolved early in the history of seed dispersal, it is by no means the only mode of dispersal used by plants. In this section I will briefly outline the various modes of dispersal used by plants in an effort to place dispersal by animals in rain forests into a broader context. The following summary is derived from van der Pijl (1972) who provides a detailed account of the many aspects of each dispersal mode, and Howe and Smallwood (1982) who give a succinct general review.

Wind: Seeds dispersed by wind may be dust-like (as in the case of many orchids), variously winged or plumed (emergent trees) or attached to an entire plant or plant part that breaks off and rolls away (arid, semiarid or dune plants).

Water: Seeds dispersed in water may use hairs, small size or an unwettable seed coat to resist sinking or may use air spaces or oil to remain buoyant. Non-buoyant seeds may also be dispersed in floodwaters.

Self: Many pods are explosive (ballistic), often responding to a decrease in humidity which triggers the release of a ballistic mechanism which scatters seeds. Some desert plants have creeping diaspores.

No apparent adaptations: There are a few plants that have no apparent adaptations other than the release of seeds to the effect of gravity (Hart *et al.* 1989) (some of these may be subsequently dispersed by seed predators; for example see White 1994).

Animal: Animal-dispersed seeds may be equipped with hooks, spines or sticky substances for external attachment to animals or have fleshy pericarps or associated structures to attract animals to use them as a food source or decoration. There also appear to be some fruits that mimic the attractiveness of the fruits of other species without providing a nutritive reward. Animals may also act as accidental dispersal agents (e.g. Dung Beetles - Estrada and Coates-Estrada 1991). Animals involved in dispersal include worms and snails (minor), frogs (one account: Fiahlo 1990), ants, fish, reptiles, birds and mammals.

Dispersal in Tropical Rain forests

All of the modes of dispersal described above occur in tropical rain forests to varying degrees. The degree to which each occurs is probably dependent on environmental parameters such as rainfall and topography, biotic factors such as species composition of the stands and animal communities, and possibly historical climatic and biogeographic factors which may have determined the species composition of particular areas (see Webb and Tracey 1981). By far the most important dispersal mode (numerically) in tropical rain forests is animal dispersal (Table 1.1). Wind dispersal is also prominent, particularly in large canopy trees and epiphytes, as are dehiscent pods for trees in some areas (Foster 1982; White 1994; pers. obs.). In the following discussion all references to animal dispersal exclude epizoochorous dispersal (*sensu* van der Pijl 1972; for term definitions see Table 1.8).

Table 1.1 Examples of the prevalence of animal-dispersed propagules in tropical rain forests. Based on the percentage of rain forest plant species with adaptations for animal-dispersal.

Location	Subcanopy %	Canopy %	Total %	Reference
Colombia	94	79	89	Hilty 1980
Gabon			75 - 90[1]	White 1994
Panama (BCI)	87	78		Howe, Smallwood 1982
Panama (BCI)	89	75.5	72	Foster and Janson 1982
Borneo			35 - 40	Stapf, 1894[6]
Nigeria	71	46		Jones, 1956[6]
Australia				
Wet Tropics			84	Hyland 1982
Wet Tropics			81[2]	Cooper and Cooper 1994
Wet Tropics			75 - 95[3]	Webb and Tracey 1981
Mission Beach			70[4]	Jones and Crome 1990
Windsor Tableland			71[5]	Jones and Crome 1990

[1] Depending on inclusion of "other" category, many of which may be rodent dispersed.

[2] Based on a sample of 626 species.

[3] Depending on site.

[4] 64.5% of individuals

[5] 47% of individuals.

[6] in van der Pijl 1972

While animal dispersal predominates in tropical forests, other forms of dispersal dominate other biomes. There is a strong trend toward wind dispersal as habitats become drier, while beach strand and riparian communities have high proportions of water dispersed propagules (Howe and Smallwood 1982). The fact that animal dispersal in tropical rain forests is of such great importance suggests that it has the greatest selective advantages for a greater number of plants and that a large number of animals (employing many different styles of dispersal) are available for dispersal of seeds in tropical rain forests. Some of the reasons animal dispersal may be of importance to rain forest plants are outlined in the following section.

Consequences of Dispersal

Ecologists, recognising that plant propagules are dispersed by various means (see above; van der Pijl 1972; Howe and Smallwood 1982), have assumed for some decades that a plant gains advantages from being dispersed (van der Pijl 1972), specifically that dispersal increases its chances of having successful offspring. In recent years, dispersal by animals in tropical rain forests has been extensively studied and ecologists are beginning to get an understanding of some of the advantages of dispersal (Charles-Dominique 1993; Schupp 1993). Clearly, the issue is a complex one in which each species of plant and each dispersal agent shows different responses to dispersal or quality and effectiveness of dispersal (*sensu* McKey 1975; Table 1.8). When dealing with a system as diverse as a tropical rain forest the number of combinations of species and their effects is enormous and complex. Despite many researchers looking for generalised patterns that are applicable to rain forest trees (e.g. Denslow 1980; Howe 1989; Janzen 1970), no clear patterns are emerging and those that do often vary when studied for longer periods or in several places (for examples see Tables 1.2 - 1.3). However, there are several advantages to dispersal discussed at length in the literature which I discuss below.

Escape in Space and Time

The Escape Hypothesis

Janzen (1970) and Connell (1971) both developed theories to explain the diversity and spatial heterogeneity of tree species in tropical rain forests. Each suggested that mortality would be highest under parent crowns or at higher densities for both seeds (Janzen 1970) and seedlings (Connell 1971; Connell *et al.* 1984); mortality being due to distance and density responsive predators or pathogens. They assumed that dispersal of seeds away from this zone of higher mortality would benefit plants by a higher survival rate. This theory has become known as either the "Janzen-Connell model" or the "escape hypothesis" (Clark and Clark 1984; Howe and Smallwood 1982). Numerous subsequent studies have attempted to verify the existence of density- or distance-dependent mortality factors as processes which may lead to this effect. Many of these studies have clearly shown that these processes do occur and in many cases the agents of mortality have been elucidated (Table 1.2 end of Chapter). In fewer cases, studies have shown that these density- or distance-dependent effects are quite variable in space and time. Sometimes the effects occur at reduced rates in certain sites (De Steven and Putz 1984; Sork 1987; Lopes and Ferrari 1994), at different adult densities (Connell *et al.* 1984; Forget 1993; Schupp 1992), in different years when crops of fruit vary in size (Janzen 1972a), when analysed over longer time frames (Augspurger 1984; Terborgh *et al.* 1993) or when allospecifics produce large crops of fruit (Forget 1993). In addition, some of the studies listed in Table 1.2 (end of chapter) show less than 100% mortality under the parent. If the number of seeds falling under the parent is much higher than those dispersed, then there may ultimately be more recruitment under the parent than away so that in absolute numbers of surviving seedlings the escape advantage is not so important. In many other cases, it is clear that there are no density or distance effects. High seed and seedling densities occur beneath the parent crowns and recruitment occurs below the parents. In other cases, mortality is as high away from the parent as near (Table 1.3 end of chapter). In addition, there are a few species in most tropical countries which are not or are poorly dispersed and form monodominant stands recruiting under and close to parent trees to the point where they exclude other species (Hart *et al.* 1989).

Clearly, the escape process, with its two components (distance- and density-dependent mortality), is one factor at play in forest systems but not the only advantage to dispersal. Whether it will prove to be a major process leading to the diversity and spatial heterogeneity of tree species in tropical rain forests is yet to be proven (Clark and Clark 1984). For example, Hubbell (1980) demonstrated using a stochastic model that the escape process, even if universally effective would not maintain the diversity of trees found in tropical forests. Hubbell (1980) suggested that the variation in fruit crop sizes between years, localities, and age classes of trees, coupled with the variation in predator behaviour in different years and circumstances, makes any such mechanism unlikely to have a profound effect in the long term. More recently, Schupp (1992) demonstrated that *Faramea occidentalis*

(Rubiaceae), a subcanopy tree on Barro Colorado Island, Panama, that can show density- or distance-dependent mortality of seeds, does not show this effect when the density of mature conspecifics is high. The escape effect works at low adult densities for this species but as density increases the effect becomes less pronounced until at some point recruitment is more or equally likely under the parent tree than away. Clearly, the hypothesis does not account entirely for the diversity of tree species in tropical forests but, nonetheless, has been an important milestone in the development and progression of studies of frugivory and dispersal in the last three decades and elucidates one of the advantages to dispersal for certain species of tree in tropical rain forests (Tables 1.2 & 1.3 end of chapter).

Scatter and Clump Dispersal

Howe (1989) examined density-dependent effects differently and suggested that some species of plants are adapted to recruiting from high density clumps of seeds while others are not. Howe's (1989) thesis centres around two different animal dispersal modes. Some animals disperse seeds into faecal clumps with a high density of often mixed species, whereas other animals scatter seeds singly. Those seeds that are usually dispersed in clumps are expected to develop better resistance to density-dependent mortality factors, such as sibling competition, pathogen attack and seed predator attack. Those that are more often scattered do not suffer the same selective pressures but rather should be under pressure to be more attractive to animals that disperse seeds singly. This suggests that species whose seeds and seedlings germinate and grow under the parent tree are more likely to be dispersed by animals that leave seeds in large clumps or are not dispersed while those that suffer heavy mortality under their parent trees are likely to be species whose seeds are more often scatter dispersed.

The few studies that address these issues suggest that, as with predation under parent plants, the results are quite variable (see Hubbell 1980). Moore (1991) found that predation of seeds from clumps dispersed by Tooth-billed Bowerbirds, *Scenopoeetes dentirostris*, depended on the number of seeds in clumps and the combination of species in those clumps. For example, the only seeds which established well in clumps were Rose Satinash, *Syzygium johnsonii* (Myrtaceae), whose seeds are unprotected mechanically or chemically (opposite to Howe's 1989 prediction which suggests seeds that survive well in clumps will be heavily protected). They were deposited in clumps with seeds that were well protected mechanically but favoured by rodents which foraged the clumps. Similarly, Janzen (1986), using pseudo-defaecations of horse and cow dung, found that seed density, type of dung and habitat effected the predation rates of seeds by Spiny Pocket Mice, *Liomys salvini*. In addition, Spiney Pocket Mice preferred Guanacaste, *Enterolobium cyclocarpum*, (Leguminosae) seeds over others, which suggests that had these seeds not been present the other species may have suffered heavier predation. Lott *et al.* (1995) found that the seeds of Black Palms, *Normanbya normanbyi*, survived and germinated both in clusters and as singletons (albeit with lower predation as singletons) suggesting both dispersal fates were successful for this species.

Numerous other species of plants are clearly dispersed by both clump dispersing and scatter dispersing animals (e.g. Clark and Clark 1984; De Steven and Putz 1984; Forget 1993; Lott 1995; Schupp 1993; Terborgh *et al.* 1993) and in other cases the same animal will disperse seeds in both ways (e.g. Howe 1989; Janzen *et al.* 1976). Thus, the dichotomy of scatter- and clump-dispersal and the selective pressures each treatment may apply to plants is blurry at best. However, the issue does add yet another dimension and set of conditions which need to be examined when considering the issue of advantages to dispersal. Clearly some species will be better able to tolerate dispersal in clumps than others, even if they are not necessarily species with the characters predicted by the model (Moore 1991), and the species advantaged may vary in different years. This discussion raises the issue of quality of dispersal. What is high quality dispersal for one species of plant may be low quality dispersal for another or may become low quality dispersal under differing conditions. I will discuss these issues in a following section.

Escape in Time

Another aspect which has received little attention in the literature is escape in time. For many species, mortality is extremely high at the seed stage, often reaching 100%

or close to it (e.g. Clark and Clark 1984; Coates-Estrada and Estrada 1988; Harrington *et al.* 1997; Howe and Estabrooke 1977; Janzen 1970; Janzen 1972b). For many species, predation is as high away from the parent tree as under it (e.g. Connell 1971; Forget 1993; Harrington *et al.* 1997; Moore 1991; Terborgh *et al.* 1993; Willson 1988). Therefore, escape from seed predators may be more a function of time than of distance or density. That is, seeds need to escape for long enough to germinate and use up seed reserves so they become unpalatable to seed predators regardless of where they are. Many seeds which are dispersed to the litter surface will be found and consumed by predators and will only survive if buried by some means and therefore hidden from predators. In the case of scatterhoarding rodents, the seeds also need to remain unretrieved for long enough to germinate, which is known to occur at least some of the time (Forget 1990; Forget 1991). In the case of Rose Satinash, *Syzygium johnsonii*, which experiences >80% predation, escape in time may have been facilitated by the presence of more palatable species in dispersed clumps that were foraged through by seed-eating rats which left the majority of seeds of *Syzygium* to germinate (Moore 1991). Forget (1993) suggested that retrieval rates of seeds by rodents may vary in different years or times of year depending on the availability of fruits and seeds from allospecific plants. Thus, escape in time is yet another mechanism in which certain dispersal modes will benefit seed survival, allowing seedlings to recruit into the next life history phase and the next set of mortality factors. However, as with previously mentioned advantages to dispersal, this benefit is also highly variable in space and time.

Finding Suitable Sites

Another problem faced by trees is having their seeds placed in sites which are suited to germination. This simple problem encompasses several dimensions: colonisation; directed dispersal and, particularly in rain forest, finding suitable light environments. Each of these dimensions is overcome to greater or lesser degrees through dispersal of seeds by animals.

Colonisation

Long distance dispersal into new areas is a phenomenon which has occurred regularly but one which is probably unimportant to the evolution of dispersal (Dirzo and Dominguez 1986; Howe and Smallwood 1982). However, there has probably been no time when long distance dispersal across biogeographic discontinuities has been more efficiently accomplished than the present. This is entirely due to a supreme and efficient animal dispersal agent which is on one level quite selective in the species it disperses and on another the hapless tool of well adapted plants. The animal, of course, is Humans, *Homo sapiens*, and with regard to tropical rain forest species, the dispersal is of favoured timber, food, fibre, medicinal and decorative plants (anthropophytes of van der Pijl 1972). Once the plants cross oceans or normally dry barriers to dispersal, the more localised influences and benefits to dispersal are again at the forefront. Many of the species dispersed are chosen for traits other than ones that are evolved for dispersal. For example Impatiens, *Impatiens* spp., native to New Guinea, Asia and Africa (ballistic dispersal) are now naturalised in parts of Australia's tropical rain forests (pers. obs.) and have come here by virtue of their attractive flowers. However, many other species (e.g. *Calathea* spp.) arrive in tropical Australia but do not disperse beyond suburban gardens for lack of appropriate dispersal agents or self dispersal mechanisms (Horvitz 1981; Mabberley 1987). A large number of such plants are dispersed because of their fruits and can probably be considered pinnacles of success in the evolution of animal dispersed fruits. This particularly applies to those plants that are then dispersed in their new areas by wild animals. A good example is the invasion of rain forest understorey by exotic Coffee, *Coffea arabica*, plants in Australia. Their fruits are dispersed by many opportunistic and specialist frugivorous birds and once they are inside rain forest, frugivorous mammals also disperse their seeds (pers. obs.).

On a smaller scale, long distance dispersal to colonise new habitats is still important to rain forest plants, particularly with the fragmentation and clearfelling prevalent in rain forest areas. In tropical Australia, unused pastures are being colonised by weeds and rain forest plants (Willson and Crome 1989; pers. obs.) and many areas of sclerophyll forest, no longer subject to traditional burning practices, are being colonised by rain forest (Harrington and Sanderson 1994; pers. obs.). Willson and

Crome (1989) found that birds and bats dispersed seeds to over 100m from the forest edge with no difference in the number of seeds per trap with increasing distance, whereas wind dispersed seed numbers declined with distance. In addition, Willson and Crome (1989) found that vertebrate-dispersed seeds from 22 species of plants were more commonly deposited under existing plants that provided perches than in the open pasture. This allows plants from all successional stages a chance to germinate and form an epicentre for continued colonisation of more species. In the Peruvian Amazon, studies have highlighted the importance of colonisation dispersal in areas of forest strip-cut for timber (Gorchov *et al.* 1993) and on newly formed river bends (Foster *et al.* 1986). Gorchov *et al.* (1993) also found that bird and bat dispersal was the most important source of invading seeds and that bats gave a more evenly spread seed shadow of mostly pioneer species than birds. In their study of river bends on the Amazon, Foster *et al.* (1986) found that water-, bat- and wind-dispersed seeds were the first to establish. These were followed by bird-dispersed species and finally by mammal-dispersal (other than bats). Martinez-Ramos and Soto-Castro (1993) found that even in advanced stages of regeneration colonisation continues. In their study (Martinez-Ramos and Soto Castro 1993), new species were still appearing and were most likely dispersed by volant and non-volant mammals and birds. These studies serve to highlight the relevance of colonisation as an advantage of dispersal (long distance dispersal in particular).

Directed Dispersal

Dispersal in tropical rain forests is generally a very diffuse phenomenon (Herrera 1986), which is attributed to the unpredictability of germination sites in space and time (Herrera 1985). This differs from pollination, which has a predictable target and therefore provides more directed pressures to evolve close associations between plants and pollinators which may carry pollen to the appropriate place (Wheelwright and Orians 1982). Even so, most pollination systems are quite diffuse with at least several pollinators involved. In only few cases in tropical rain forest do plant groups require germination sites which are sufficiently narrow that they seem to have evolved close relationships with a narrow group of frugivores which disperse their seeds to those sites. The example is the association of Mistletoe (Loranthaceae) hemiparasites with Flowerpeckers (Dicaeidae; Indo-Malaysia and Australasia) and some Tanagers (Thraupidae; Neotropics), where the seeds need to be deposited on live branches to germinate successfully (Herrera 1985; Howe and Smallwood 1982; Snow 1971; but see "specialised verses generalised dispersal systems" below). An additional example of directed dispersal is that of strangler figs (Moraceae), seeds of which require placement in the tops of canopy trees. While many strangler figs are able to germinate and grow into trees after seeds are placed on the forest floor, most individuals encountered are those that have germinated in trees as epiphytes (pers. obs.; Irvine, A. pers. comm. April 1997). In Australasia, this service is probably provided by many of the volant frugivores, possums (Psuedocheiridae) and tree kangaroos (Macropodidae), which are known to eat fig fruits (Jones and Crome 1990; Flannery and Schouten 1994; Flannery *et al.* 1996; Cooper, W. T. pers. comm. 1996; pers. obs.). However, dispersal of fig seeds to canopy branches may also be performed by two Manucodes, *Manucodia* (Paradiseidae), which specialise on eating fig fruit (Beehler 1983) and Spotted Catbirds, *Ailuroedus melanotus*, which are known to cache fig fruit in epiphytes and branches high in the canopy (Frith, C. B. pers. comm. 1996). De Figueiredo (1993) suggests that Howler Monkeys, *Alouatta fusca*, may be important in dispersing strangler figs to appropriate microsites in Brazilian forests and shows that germination of their seeds is enhanced after passing through their guts. Although directed dispersal is a process rarely developed it is nonetheless an important advantage to dispersal for some species.

Light Environments

Numerous species of rain forest trees, particularly pioneers and canopy trees, require more light than is generally available in the forest understorey to germinate or grow into the canopy (Brokaw 1982b; Denslow 1980; Foster and Janson 1985). This need for specific microsite conditions means that dispersal of seeds to cover a wide area and encompass canopy gaps in time and/or space is an important advantage of dispersal for many rain forest plants. Here I use the phrase "canopy gap" in preference to "treefall gap" (*sensu* Brokaw 1982a) because smaller but still substantial gaps may be formed by falling branches, while rocks or earth movement can form much larger breaks in the canopy (pers. obs.).

Three degrees of gap-dependence, which are arbitrary divisions in a continuum, are generally recognised: large gap specialists; small gap specialists; and shade tolerant species (Denslow 1980; Foster and Janson 1985). Foster and Janson (1985) showed that species which are reliant on large gaps generally have smaller seeds than shade tolerant species or those that need small gaps. However, the reliability of their analysis was questioned by Kelly and Purvis (1995) because it did not account for phylogenetic constraints through relatedness of species within the data set. On re-analysis of Foster and Janson's data, Kelly and Purvis (1995) found that within taxonomic groups the data do not support the hypothesis that gap-dependent species have smaller seeds. Within some groups, those species requiring large gaps had larger seeds than those requiring small gaps or no gap at all. Taken together, I interpret these studies as suggesting that there is a prevalence amongst taxonomic groups with small seeds to be gap dependent. This may be based on the fact that, for many species, seedling vigour is greater in gaps than in the understorey (Augspurger 1983b; Augspurger and Kelly 1984; Dirzo and Dominguez 1986; Howe and Schupp 1985; Osunkoya *et al.* 1993; Osunkoya 1994; Sork 1987) and the effects of various mortality agents are diminished (including density-dependent mortality; Augspurger 1983b; Augspurger 1984; Augspurger and Kelly 1984; De Steven and Putz 1984; Fleming and Sosa 1994). These advantages would be greatest for species with small seeds which do not have the reserves to establish a seedling and recover from the attacks of herbivores and pathogens in a shaded environment. Larger seeds are most likely to provide seedlings with the reserves necessary to defend against and recover from such attacks. Clearly however, some species with small seeds are able to establish in the understorey or in small gaps (Foster and Janson 1995).

Although seedling vigour is often enhanced in canopy gaps, survival of seeds is not always higher in gaps than in the understorey. Several studies have shown that seed predation rates can be as high or higher in gaps than under the parent tree (Dirzo and Dominguez 1986; Schupp 1988; Schupp and Frost 1989). This diminishes the advantages to seeds which land directly into canopy gaps compared with those which land in the less heavily predated understorey, germinate and wait for a gap to form overhead. Alternatively, post-dispersal survivorship of seeds may be independent of microsite (Osunkoya 1994; Willson 1988), suggesting that seeds landing within gaps will have the advantage of more vigorous growth.

In some species, survival of seedlings in gaps is equal to or lower than survival in the understorey (Osunkoya *et al.* 1993; Schupp 1988). Despite this equal or higher seedling mortality, growth rates are still generally higher in gaps even if the adult is an understorey tree (e.g. Schupp 1988). Osunkoya *et al.* (1993) found, after controlling for herbivory, that the advantage of higher growth rates was proportionally greater for pioneer or early seral trees (which had small seeds) than for those associated with mature forest (which had larger seeds). However, when herbivory is present the advantages are diminished (Osunkoya *et al.* 1993; see also Coley 1982) and the rates of herbivory vary with different communities at different sites. Despite this, there are still clear advantages to growth in a canopy gap and for pioneer species disturbances such as canopy gaps are their only chance of germination and growth to the canopy.

Connell (1979) suggested that disturbance is an important factor maintaining the diversity of tree species in tropical rain forests. Given that the seeds of many pioneer species have light-controlled dormancy (e.g. Hopkins *et al.* 1990; Hopkins and Graham 1987; Vazquez-Yanes and Orosco-Segovia 1986) and can only germinate in substantial canopy gaps or larger disturbances, then Connell's model is at least partially correct. Without regular disturbances which create canopy gaps pioneer species would die out from the system. The monodominant stands described for many tropical forests (Hart *et al.* 1989) may be evidence of this. These stands comprise species with poor dispersal but low predation of seeds. Their shade tolerant seedlings are able to dominate areas which have had too few canopy gaps to allow other species to compete in space.

In mature forest on Barro Colorado Island (BCI), Panama, Brokaw (1982b) found that the frequency of treefalls in old forest was one per hectare every 5.3 years. Given that estimates of turn-over rates for one point in a forest range from less than one to several hundred years in various forests (114 for BCI; Brokaw 1982b and references therein) the advantages of an increased seed shadow through dispersal for pioneers is immediately evident. Many pioneers are widely used by frugivorous birds, bats and mammals, therefore ensuring a large seed shadow. In addition, many may lay dormant for periods greater than two years (Hopkins and Graham 1987) and may form the bulk of the seed bank in many rain forests (Alvarez-Buylla 1991; Hopkins *et al.* 1990). A continuum of strategies from pioneers to poorly-dispersed shade-tolerant plants allows a wide range of species to use gaps of various sizes and frequencies and possibly even partition large gaps (see Barton 1984).

The range of gap sizes useable by any one species may be quite broad and in some cases may be extended by the effects of dispersal agents. For example, Vazquez-Yanes and Orosco-Segovia (1986) found that ingestion of the seeds of *Cecropia obtusifolia* by monkeys increased the ability of these seeds to germinate in lower light conditions than without ingestion or after ingestion by bats. This may allow them, on occasions, to extend their niche to include gaps that would normally be too small to allow germination. In a study of long lived perennials in drier forest in Australia, Anderson (1989) found that microsites were by far the most important limiting factor for the recruitment of the four species he studied. Despite predation rates of around 95% there were still substantial soil seed banks but recruitment occurred only when rare microsites became available. Although extrapolation of this study to tropical rain forests is not wise, it highlights the possibility that one of the main advantages to dispersal for many rain forest trees may be the search for appropriate microsites in time and space.

Germination Enhancement

For some species of plant, seed germination may be enhanced by passage through the gut of an animal (e.g. Balasubranian and Bole 1993; Barnea *et al.* 1990; Fleming and Sosa 1994; Glyphis *et al.* 1981; Lieberman and Lieberman 1986; Rowell and Mitchell 1991; van der Pijl 1972) and in a few rare cases a mutual dependence has developed (Noble 1975; Rick and Bowman 1961; Temple 1977). The prevalence and importance of enhanced germination through treatment by animals is hard to determine, particularly in rain forest plants. After examining 85 plant-animal feeding combinations in a dry forest/grassland mosaic in Ghana, Lieberman and Lieberman (1986) found that 73% showed no significant effect on the proportion of seeds germinating. In only 12% did germination become more rapid after ingestion. Plant species was found to be a more important determinant of germination rate than the species of animal ingesting the seed. I was unable to find any similar comprehensive studies for rain forest species. However, several studies suggest that passage through the guts of animals may enhance germination ability of some species of rain forest plants (De Figueiredo 1993; Fleming and Sosa 1994; Vazquez-Yanes and Orosco-Segovia 1986). Whether this germination enhancement is of value to the species concerned is yet to be determined. Janzen (1983) suggests that passage through an animal's gut does not actively enhance germination. Rather the protective coat, whose purpose is to protect the seeds from digestion, is digested away . Given that, for many species, the seeds most likely to survive and germinate are those that are dispersed by animals (see above), a protective coat that inhibited germination for seeds that did not pass through vertebrate guts would pose little disadvantage.

In many cases, germination of seeds is little affected by ingestion (Barnea *et al.* 1990; Fleming and Sosa 1994; Glyphis *et al.* 1981; Lieberman and Lieberman 1986; Stocker and Irvine 1983). On occasion germination is retarded (Horn 1997). Changes in germination ability may result from the physical scarification or digestion of hard seed coats (e.g. Barnea *et al.* 1990; Janzen 1981), removal of inhibitors in the fruit pulp (Janzen 1983) or chemical changes in the seed coat (e.g. Vazquez-Yanes and Orosco-Segovia 1986). Some species of animals commonly digest seed coats completely, killing the seed in the process (Bodmer 1989; Bodmer 1990; Bodmer 1991; Janzen 1981). However, these same animals may act as dispersal agents to those seeds that survive passage through the gut (Bodmer 1991; Janzen 1981).

Clearly, the subject of germination enhancement as an advantage to dispersal is not fully understood. For some species, it may provide an advantage: for example the possible niche expansion for the seeds of *Cecropia obtusifolia* after ingestion by monkeys (Vazquez-Yanes and Orosco-Segovia 1986; see previous section). For others an advantage is questionable, as the function of inhibitors or hard seed coats may be to prevent germination until after dispersal or to protect seeds from digestion in the digestive tract of animals (Mckey 1975).

Genetic Advantages

To reduce the chances of inbreeding, it is advantageous to maintain a level of gene flow between populations (Ayala 1982). On Australia's Great Barrier Reef, where many organisms (corals and fish) have planktonic larvae, dispersal distances are regularly over hundreds or thousands of kilometres (Veron 1995). This means that for most widely dispersed species, entire regions act as a single population with little to no genetic variation (beyond the intrapopulation level) between widely separated reefs (Avise and Shapiro 1986; Planes *et al.* 1993; Shaklee 1984). Rain forest plants face very different dispersal problems. Lacking ocean currents for long distance dispersal they rely on wind, water, self or animals to carry propagules. This invariably results in much smaller units being identifiable as populations (Hamrick *et al.* 1993; Hamrich and Loveless 1986).

For rain forest trees, genetic neighbourhoods and variation between and within populations are determined by both pollen and seed dispersal with pollen dispersal often playing the major role (Hamrick *et al.* 1993; Hamrich and Loveless 1986; Howe 1989). However, seed dispersal modes certainly play a part in determining the distribution of adults that are within a breeding population (Gibson and Wheelwright 1995) and different modes of dispersal result in different patterns of related adult distributions (Howe 1989). In studies on Barro Colorado Island, Panama, Hamrick *et al.* (Hamrick *et al.* 1993; Hamrich and Loveless 1986) have found varying patterns of genetic structure for trees with different dispersal modes and different adult densities. It appears that little long-distance gene flow is occurring and tropical tree species form distinct genetic populations over small areas. Therefore, populations tend to inbreed and may, in the long term, respond to localised selective pressures causing even greater differences between populations (Ayala 1982). This may help to explain some of the great heterogeneity in plant attributes seen in different locations. However, without dispersal of propagules by animals, many species would have even more isolated populations, having lost a secondary but important mode of gene flow.

Animals that Disperse

Effectiveness of dispersers

Before examining the animals that disperse seeds in tropical rain forests around the world, I will introduce two related concepts: the effectiveness of dispersers (*sensu* Schupp 1993) and the nature of dispersal systems (*sensu* Howe 1993 - specialised or generalised).

Effectiveness

Schupp (1993) provides a recent review of the effectiveness concept and attempts to clarify terminology and outline important questions for future research. The concept of disperser "quality" (= effectiveness) was introduced by Mckey (1975) and subsequently considered by other researchers (Howe and Estabrooke 1977; Levey 1987; Snow 1981; Wheelwright and Orians 1982). Effectiveness has been the basis of various empirical studies (e.g. Becker and Wong 1985; Coates-Estrada and Estrada 1988; Howe and Primack 1975). The concept of disperser effectiveness attempts to relate the following variables to the overall impact on recruitment for the plant being visited (Mckey 1975; Schupp 1993): 1) the number of visits made; 2) the number of fruits ingested per visit; 3) the abundance of the frugivore; 4) the reliability of visitation; 5) the probability of dispersing a handled seed; 6) patterns of subsequent deposition (scattered, clumped, mixed species); and 7) how the seed is treated (killed/survived, altered germination). Aspects one to five relate to the quantity of seeds dispersed while aspects six and seven relate to quality of dispersal. Schupp (1993) found that the issue was extremely complex and that while a species may be an effective disperser for one plant it may not for another. In addition, in some cases quality was of greater importance than quantity of dispersal and in others quantity became the key factor determining effectiveness. Schupp (1993) also found that the number of visits by a disperser correlated best (but weakly) with the total number of seeds dispersed, rather than the number of seeds ingested per visit. This observation may provide a useful tool for estimating part of frugivore effectiveness in future studies. However, it seems clear that effectiveness will need to be examined at the level of the relationship between a species of frugivore or a coterie of frugivores and a species of plant. Trying to label a frugivore as effective will overlook the variability in its relationships with different species of plant.

Specialised verses Generalised Dispersal Systems

A related concept is that of specialised and generalised dispersal systems (*sensu* Howe 1993b). This is not to be confused with specialised and opportunistic frugivores (*sensu* Fleming *et al.* 1993; see also Snow 1971; Mckey 1975), although the two often refer to the same sets of relationships. The paradigm (see Howe 1993b) is that trees at one extreme produce relatively small but predictable numbers of nutritious fruits (high lipid and/or protein) over an extended season to attract a small number of quality dispersers, while at the other extreme trees produce a super-abundant crop of fruits with relatively poorer nutritive value (high sugar/water, lower protein/lipids) over a short period and attract a wide range of lower quality dispersers which in combination are abundant (Howe 1993b; Howe and Estabrooke 1977; Mckey 1975; Snow 1971; Snow 1981; Wheelwright and Orians 1982). What is often unclear (but see Mckey 1975) is that the frugivores (or coteries of frugivores) are effective dispersers at both ends of this continuum (see above) but that, in one strategy, quality is the most important aspect of effectiveness while in the other, quantity is the more important aspect. Charles-Dominique (1993) also uses the term specialised frugivores and contrasts it with non-specialised frugivores to differentiate those that feed from a limited (former) or broad (latter) range of fruit syndromes (see Table 1.8).

While these concepts provide important frameworks for future research aimed toward understanding the complexities of seed dispersal, circumstances in the wild are not so straightforward. An example which illustrates this point is the dispersal of mistletoe (Loranthaceae) by Mistletoebirds, *Dicaeum hirundinaceum*, and Spiny-cheeked Honeyeaters, *Acanthagenys rufogularis*, (Reid 1989). Flowerpeckers (*Dicaeum*) and mistletoes are often quoted as one of the exceptional mutualisms in seed dispersal relationships (Herrera 1985; Howe and Smallwood 1982; Mckey 1975; Snow 1971), in which mistletoes produce regular but small quantities of fruits and could be considered to have a specialised dispersal system. However, Reid (1989) found that although honeyeaters, which are nectar, insect and fruit generalists (Slater *et al.* 1995), were more wasteful by depositing a high proportion of seeds in inappropriate places, a few were deposited in extremely high quality sites. Mistletoebirds on the other hand, which are specialists on mistletoe fruit (Slater *et al.* 1995), were more reliable in depositing seeds on branches (suitable sites) but did not account for as many seeds as the honeyeaters (Reid 1989). Therefore, the higher quantity but lower quality dispersal by honeyeaters was more effective than the highly specialised dispersal by Mistletoe birds. This is contradictory to the expectations of generalised and specialised dispersal systems, which suggests that specialised birds will be the most effective dispersers and that specialised dispersal systems will entrain effective (specialist) dispersers (Howe 1993b). This apparent dichotomy may be due to Mistletoebirds becoming specialists on a generalist plant or Spiny-cheeked Honeyeaters displaying exceptional behaviour for a generalist. More generally the dichotomy may be due to the fact that there is always more than one way of solving the problem of dispersal with most apparent associations very diffuse. Wheelwright *et al.* (1984) mention another situation where a "high investment, high quality" fruit tree, *Ocotea tonduzii*, (Lauraceae) is dispersed by at least 18 species of birds including specialists and opportunists. Clearly, many more individual dispersal relationships need to be examined in detail before the relevance and applicability of these concepts can be determined. Despite this, there is weak evidence to support the general patterns described and they are useful concepts to consider when examining frugivores and dispersal systems.

The Frugivores - A Functional Classification

Most studies of frugivory focus on taxonomic differentiation between disperser groups (e.g. primates, birds, bats, ruminants etc. or subdivisions of these groups; Gautier-Hion 1980; Emmons *et al.* 1983; Coates-Estrada and Estrada 1986; Terborgh 1986; Fleming *et al.* 1987; Estrada *et al.* 1993). However, there are many circumstances in which taxonomic classification is not representative of a frugivore's comparative ecological role in disperser systems. I propose a broad functional classification based on animal movement patterns and microhabitat use (which affects the ultimate deposition pattern of seeds) while considering their level of frugivory and how seeds are treated in ecological space and time (Figure 1.3). It highlights the convergent roles played by different taxa in different countries. For example cassowaries (*Casuarius* spp.) are birds and are extremely important dispersal agents (Crome 1976; Stocker and Irvine 1983; Bentrupperbaumer, J. pers. comm. 1997). However, unlike other frugivorous birds they are large (~ 50kg), terrestrial and deposit large numbers of seeds in clumps. Thus from an ecological perspective, they have more in common with many forest ungulates than they do with other birds.

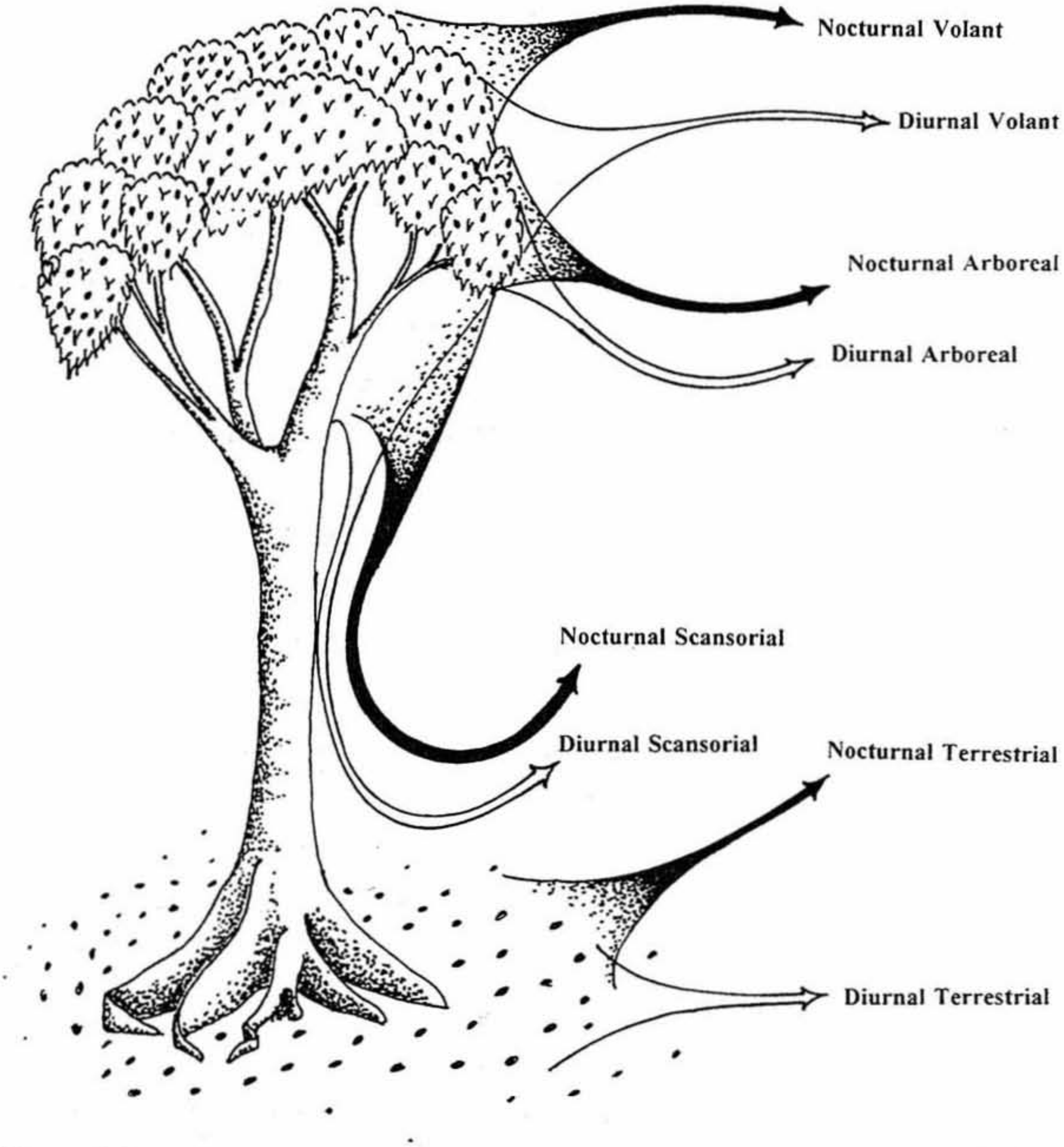


Figure 1.3 Broad categories for a functional classification of frugivores in tropical rain forests. Similar functional roles may be played by different taxonomic groups in different tropical countries. See Table 1.3 for details (end of chapter).

Similarly, Agoutis, Acouchies (Dasyproctidae) and small forest deer (Cephalophinae, Tragulidae) are all small, fast moving, terrestrial mammals which act as both seed predators and dispersers in different forests around the world and have much in common with Musky Rat-kangaroos (this study). I suggest that, as a group, their ecological parallels are sufficient for them all to be termed cursorial frugivores, a subdivision of terrestrial frugivores. Table 1.4 (end of chapter) outlines a functional classification that places animals of sometimes widely varying taxonomy into categories which display their functional similarities. The families included contain species which are primarily frugivorous, at least during the season of peak abundance.

Flying frugivores are categorised by size, which relates to the maximum seed size they are able to ingest and strength of flight. Large birds which fly above the canopy can potentially carry and scatter seeds over longer distances than those that habitually inhabit the understorey or remain primarily within the canopy. Smaller birds generally ingest smaller maximum fruit sizes and most commonly remain within the forest strata and probably do not disperse seeds far. Notable exceptions among the small birds are some of the tropical starlings (Sturnidae) which are strong fliers above the forest canopy. Some birds tend to be primarily seed predators and are therefore classified separately. One group, Columbidae, is often considered primarily granivorous (e.g. Fleming *et al.* 1987). However, some members are clearly not seed predators and subsist on the flesh of the fruits consumed (Crome 1975a; pers. obs.), although even primarily granivorous animals may be important dispersal agents (Gautier-Hion 1985; van der Pijl 1972).

Nocturnal frugivores that fly include bats and the Oilbird, *Steatornis caripensis*. Some bats and Oilbirds fly strongly over the canopy and carry fruit to individual feeding perches. Although the strong flying bats probably do not scatter seeds as widely as Oilbirds do, they do not have the regular feeding perches of some other bats which result in large clumps of seeds on the forest floor. Many species are insufficiently studied to be able to get a clear understanding of their roles. For example, within the diurnal arboreal primates, I was unable to determine how many regularly predated seeds (see Gautier-Hion 1993; Rowell and Mitchell 1991). Similarly, the dispersal roles of many arboreal frugivores active at night and scansorial frugivores are unclear at present. Crowned Pigeons (Gourinae), some Guans and Curassows (Cracidae) pose a special case. While they are not truly scansorial they are reported to feed both on the forest floor and in the canopy (Austin 1965), a characteristic of the other scansorial frugivores with which they have been placed.

Conspicuous by their absence from this classification are reptiles, fish and invertebrates. I was unable to unearth enough information on dispersal by these group in tropical rain forests to warrant their inclusion. However, they are probably important agents of dispersal for certain plants (see Fiahlo 1990; Horn 1997; Horvitz 1981). Although necessarily a preliminary grouping of frugivores, Table 1.4 lists the main groups of the world's bird and mammal frugivores that inhabit tropical rain forest which are likely to be important dispersal agents for at least some taxa of rain forest plants.

Communities and Coteries

Table 1.4 suggests that common functional groups occur in most tropical regions and that these roles may be played out by similar or different taxonomic groups. However, table 1.5 shows considerable taxonomic differences between regions with the Neotropics standing out as having the highest number of frugivore families and the least overlap with other regions (see also Fleming *et al.* 1987). I list 68 families of birds and mammals (34 each; includes two subfamilies of Cercopithecidae) which appear to be significant seed dispersers (references listed in Table 1.4). Table 1.5 outlines the total number of families in each region and the overlap in families between regions. The Neotropics has a total of 20 unique families (12 bird and eight mammal families), while the Ethiopian region has nine (two bird, seven mammal), and Indo-Malaya and Australasia five each (both with two bird and three mammal families; not shown in Table 1.5). The total number of families of frugivores in each region are 32 (Neotropics), 28 (Ethiopian), 29 (Indo-Malayan) and 19 (Australasian), with one mammal (Muridae) and two bird families (Columbidae and Psittacidae) occurring in all areas. Excluding the latter three families, the oldworld regions and Australasia have only four bird and two mammal families in common. The Ethiopian, Indo-Malayan and Neotropical forests have only one mammal and two bird families in common apart from the global groups mentioned above. The combination of Australasia, Indo-Malaysia and the Neotropics has no additional families in common.

Table 1.5 Total number of frugivore families in each region and percentage overlap between regions (derived from Table 1.3, end of chapter). Eth - Ethiopian, IM - Indo-Malayan, Aus - Australasian and Neo - Neotropical; B = Bird, M = Mammal; ( ) = Total percentage overlap.

		Eth	IM	Aus	Neo
Eth	B	11	9	6	3
	M	17	10	3	2
			(50)	(24)	(9)
IM	B		13	8	4
	M		16	4	4
				(33)	(15)
Aus	B			12	3
	M			7	1
					(9)
Neo	B				20
	M				12

These differences in taxa may have led to larger differences at a finer spatial scale, between the frugivore communities and how they interact in different tropical countries (e.g. Charles-Dominique 1993; Emmons *et al.* 1983; Fleming *et al.* 1987; Gautier-Hion 1985; Harrington *et al.* 1997; Terborgh 1986). For example, while various workers in the Neotropics have documented fruiting syndromes peculiar to a narrow range of specialised frugivores (e.g. Manakins and *Miconia* Snow 1965; Bats and *Piper* Fleming 1981), those in Africa have found no such close associations; fruit syndromes fitting into broad categories such as a bird/monkey syndrome and a ruminant/large rodent/elephant syndrome where broad ranges of species feed on each fruit type (Emmons *et al.* 1983; Gautier-Hion 1985; Gautier-Hion 1990). In addition, Snow (1965) and Fleming (1981) have hypothesised that specialised frugivory by bats or manakins on particular genera of plants have driven the different species within the plant genera *Piper* and *Miconia* to stagger their fruiting periods - suggesting coevolution between frugivores and fruit phenology. Attempts to verify this in forests at Makokou, Gabon, have not demonstrated that this phenomenon occurs (Gautier-Hion 1985). Many forests in Malesia, peninsula Malaysia, have an extremely irregular phenological pattern characterised by some years having mass-flowering and mast-fruiting throughout the forest and other years producing little or no flowers and fruit (Ashton *et al.* 1988). This may be a factor influencing the lower species diversity of frugivorous birds and primates in south-east Asia as compared to the Neotropics and Africa.

Another difference between regions is the prevalence of understorey trees as important fruit sources. Most of the "close mutualisms" reported for the Neotropics (see above) relate to understorey plants. Both African and Malaysian forests have fewer understorey fruit-bearing plants than the Neotropics (Francis 1990; Gautier-Hion 1985) which may be why close associations have not developed between frugivores and plants. Instead of taxon-specific associations and fruit characteristics, Gautier-Hion *et al.* (1985) suggest different feeding zone syndromes for fruit, with fruit fed on by primarily arboreal frugivores having one suite of characteristics and those fed on by terrestrial frugivores another. Clearly communities differ in many regards and many of the differences are only just becoming resolved, while in some places (e.g. Australasia) insufficient work has been carried out to make detailed community comparisons with other regions (but see Beehler and Pruett-Jones 1983).

On a smaller scale, individual trees may attract a range of frugivores from either restricted or various taxonomic groups (see references in Table 1.6). Although few thorough studies of frugivore visitation for species of plant in tropical rain forest exist, I have compiled a sample from the literature to give an indication of the variation in minimum coterie size at the species level. Many of the studies I have used, examined only one group of animals (e.g. birds) and therefore do not necessarily represent a total coterie. Table 1.6 lists the mean minimum coterie size for 73 tropical plants around the world. The Neotropics shows the greatest variation in coterie size which is partly due to some data being biased toward one taxonomic group (i.e. birds) but may also be due in part to the dichotomy of specialised and generalised dispersal systems (see above). A oneway Analysis of Variance on coterie size showed significant difference between regions. Pairwise comparisons showed that the Indo-Malayan region had significantly larger coterie sizes than the other regions (Table 1.7). This is probably due to the data coming from a single study of bird dispersal of the the fruits of 25 *Ficus* spp. on the Malaysian peninsula (Lambert 1989). It is well known that figs often support larger numbers and a higher diversity of frugivores than other plants (e.g. Terborgh 1986).

Table 1.6 Number of species in frugivore coteries feeding on the fruits of rain forest plants in different regions. # Species refers to the number of tree species examined. References are listed below.

Region	Mean	S.E.	Minium	Maximum	# Species
Ethiopian	5.5	1.26	1	9	6
Indo-Malay	20.4	1.16	6	34	25
Australasian	4.7	0.59	1	10	21
Neotropical	12.3	3.59	2	80	21
Total	12.3	1.4	1	80	73

[1] Birds and *Ficus* only.

[2] No comprehensive studies.

(Becker and Wong 1985, Chapman and Chapman 1996, Coates-Estrada 1986, Coates-Estrada and Estrada 1988, De Steven and Putz 1984, Gautier-Hion 1985, Harrington *et al.* 1997, Howe 1993a, Howe and Primack 1975, Howe and Schupp 1985, Lambert 1989, Levey 1990, Murray 1988, Pratt and Stiles 1985, Schupp 1988, Schupp 1990, Smythe 1989, Sork 1987, Wheelwright 1985)

Table 1.7 Oneway analysis of variance table for frugivore coterie size in tropical plants in four biogeographic regions.

Source of Variation	DF	Mean Square	F	P
Between Regions[1]	3	1036.6	10.01	<0.00001
Error	69	103.54		

[1] Tukey HSD test showed Indo-Malaya as significantly different.

In their work in Gabon, Gautier-Hion *et al.* (1985) list 122 plants and their dispersers, predators and neutral consumers. Only 17% were dispersed by less than two major taxonomic groups (e.g. monkeys, ruminants) which represent variable numbers of species. These data suggest that the majority of animal-dispersed plants are dispersed by a wide range of animals, often from widely different taxa and habits. At the same time, however, there is considerable variation in the size of coteries suggesting that several strategies may be used by different species of plant and that selective pressures exerted by frugivores on their food plants could be directional in some cases but not so in many.

Coevolution ?

Much of the foregoing discussion contains allusions to and raises the possibility of coevolution between dispersal agents and the plants they disperse. Literature on this subject is considerable and I will only outline the discussion here (see Charles-Dominique 1993; Herrera 1985; Herrera 1986; Howe 1984; Janzen 1983; Jordano 1995; Mckey 1975; Smith 1975; Snow 1965; Snow 1971; Temple 1977; Wheelwright 1988; Wheelwright and Orians 1982).

One subject often referred to and well accepted is that of fruit syndromes (definition Table 1.8). Some species have fruits that seem to be adapted to attracting certain groups of frugivores and these categories have been well described and are based on sensory and foraging/feeding capabilities of animals (van der Pijl 1972). The divisions are usually between bird and mammal dispersed fruits although specific adaptations for reptile and ant dispersal are also noted (van der Pijl 1972). Despite many trees being variously listed as dispersed by birds or mammals (for example see Foster and Janson 1985), very few have been demonstrated conclusively to be dispersed by only one group. In many instances researchers concentrate on one category of dispersers and too easily accept these generalised syndromes. In reality, it is hard to label fruits as being dispersed by only one group of animals although they can be classified as being at extremes or near the centre of a continuum (Jordano 1995). Gautier-Hion (1985) found more partitioning of fruit types within than between major groups of dispersers.

The implicit suggestion in most articles relating to fruit syndromes is that dispersers have exerted enough positive, selective pressure that appropriate traits have been developed and refined via disproportionate survival of individual plants gaining disproportionate attention from a particular group of dispersers. Jordano (1995) has recently analysed the contributions to different fruit syndromes which are due to phylogeny or ecological interactions. The most significant factor accounting for variation in fruit types is phylogenetic (61%) while the only factor which correlates with disperser type (after controlling for phylogenetic effects) is fruit diameter; most mammals being able to feed on larger fruit than most birds (see also Kelly 1995). Two other recent studies (Corlett 1996; Tamboia *et al.* 1996) found that physical and chemical traits were not correlated with animal choices of fruit. This suggests that the various fruiting syndromes displayed by plants are probably not adaptations to the current balance in their disperser coteries. One problem with Jordano's (1995) data set is that it includes significant numbers of plants from all regions of the world and, as discussed above, there are significant differences in community behaviour in different regions. It may be of value to analyse data exclusively from the Neotropics where the relationships between plants and their dispersal agents seem to be tighter.

Various other plant attributes are suggested to coevolve with frugivores. They are fruit size (Wheelwright 1993), crop size (Davidar and Morton 1986; Howe and Estabrooke 1977; Murray 1987) and phenology patterns (Fleming 1981; Snow 1965; Snow 1971). However, most authors concede that the selective pressures on these traits are diffuse at best (Murray 1987; Snow 1965; Wheelwright 1993) and are probably less important than pressures brought to bear by physical environmental parameters (such as disturbance) and interactions with animals and plants on other stages in their life history (Herrera 1985; Herrera 1986; Howe 1984). In extremely diverse communities such as tropical rain forests, Howe (1984) and Herrera (1986) suggest that any potential mutualisms developing will be diluted by the effects of the diverse array of other species which may be involved and the variation in interactions in different geographical areas. With even a small amount of gene flow occurring between populations that vary somewhat in species composition of dispersers, possible selective changes are again diluted (Wheelwright and Orians 1982). Perhaps the most important constraint on coevolution between plants and their dispersers is the usually huge difference in longevity. Most rain forest plants live much longer and have a much slower alternation of generations than animals and therefore are less able to respond to selective pressures (Herrera 1985; Herrera 1986; Tiffney 1986). In addition, over spans of geological time plants have been dispersed by widely different animal groups (Tiffney 1986). Thus, the most likely evolutionary interaction occurring is that animals are adapting behaviourally and ecologically to existing traits in plants that produce edible fruit.

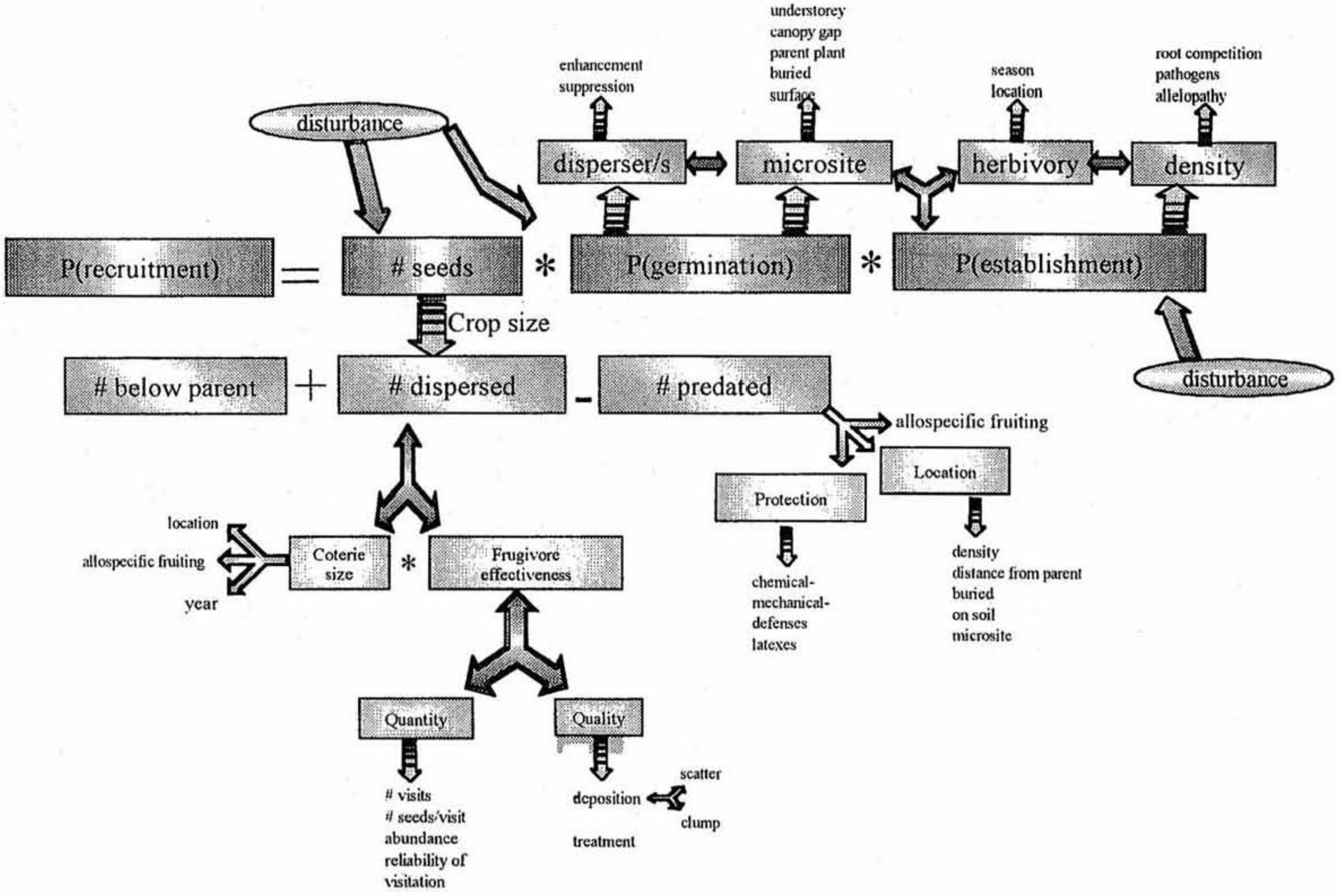
Summary of Introduction

The foregoing discussion serves to highlight the complexity and variability in tropical rain forest frugivores, their communities, the dispersal of seeds and its advantages. Figure 1.4 (next page) summarises what has been discussed above in the form of an equation and flow chart, simplifying much of the detail and complexity represented in each box.

The ultimate puzzle being examined by this type of research (above) is how young plants are recruited into tropical rain forest communities. In this context the dispersal of seeds by animals is only one aspect. However, it seems clear that animal-dispersal is important to the plants that invest heavily in the production of fruits and seeds that are attractive to animals. When one considers some of the difficulties that need to be overcome (described above) to recruit an offspring it is hardly surprising that the issue is so complex and involves so many interactions.

The reciprocal aspect of the story, only briefly mentioned above, is the impact of fruit on frugivore life histories, diversity and communities. These impacts can be due to the availability of fruits as a resouce to frugivores. Seasonality in fruit production being a main factor impacting the life history of frugivores.

Figure 1.4 Flow chart summarising the factors involved in the recruitment of an animal-dispersed rain forest plant after pollination, fruit set and pre-dispersal predation (see Table 1.8). P() - Probability of (.....).



This Study

Because so little was known about Musky Rat-kangaroo ecology, I began this study with few expectations about their behaviour. However, as I began making observations and collecting data, I realised that they were cursorial frugivores and dispersers of rain forest fruits (see "The Frugivores - a Functional Classification" above). At this point I began attempts to examine frugivory and dispersal for this species from two angles: the effects of fruits and their availability on Musky Rat-kangaroos; and the dispersal of seeds by Musky Rat-kangaroos and its effects on the plants dispersed. Firstly, I asked: What is the importance of fruit in their diet and what sizes of fruit are they able to use and disperse? As discussed above (in "Coevolution?") many frugivores are restricted to using particular fruit sizes which limits their capabilities as dispersers. I expected that Musky Rat-kangaroos, being cursorial frugivores with considerable dexterity, were not restricted to swallowing fruit whole and would therefore use a wide range of fruit sizes and syndromes (see Chapter 3: "The diet of Musky Rat-kangaroos").

The region I was working has a seasonal rainfall pattern and most areas in the seasonal tropics have marked times of peak fruit production (e.g. Crome 1975a; Foster 1982; Smythe 1970a). Because of this I set out to determine: What is the pattern of availability of fruit?; How does it vary seasonally and between years (Chapter 4: "Availability of fruits and seeds")?; and How does this variation effect the life history of Musky Rat-kangaroos? These questions relate to the possibility of coevolution between frugivores and their fruit resources ("Coevolution?" above) and to the structure and size of frugivore communities ("Communities and Coteries" above). With respect to the effects of fruit availability on life history I asked: What other resources do Musky Rat-kangaroos use, particularly during seasonal troughs in fruit production? Does the availability of these other resources impact life history attributes (Chapter 5: "Distribution and abundance of fauna in leaf litter")?; and How does the combined availability of these resources effect their reproduction (Chapter 6: "Life history and reproduction")?

I also examine the potential of Musky Rat-kangaroos as dispersal agents, addressing the following questions: What is the population density of Musky Rat-kangaroos?; and how far do they move (Chapter 7: "Population size and space use in Musky Rat-kangaroos")? These questions relate to the discussion of disperser effectiveness (above), more specifically the abundance of a disperser (part of the quantity aspect of effectiveness). To answer this question (Are they effective dispersal agents?) further, I examined how many seeds they dispersed, how far they dispersed them and where they were deposited (Chapter 8: "Seed dispersal by Musky Rat-kangaroos"). To determine if this was beneficial to the recruitment of the plants they dispersed, and therefore examine "advantages to dispersal" (see above), I conducted survival experiments for two species consumed and cached by Musky Rat-kangaroos. These species were also eaten by a range of other animals (Chapter 9: "Benefits to seed survival attributable to dispersal by Musky Rat-kangaroos"). Finally, to gain initial insight into how Musky Rat-kangaroos compare to part of the frugivore community using the area, I examined evidence on the impacts of other frugivores and the overlap in fruit species consumed by selected frugivore groups (Chapter 10: "Community relations between Musky Rat-kangaroos, their predators and other frugivores").

These questions and others in this thesis, all address aspects of my main question, which is: What is the functional role played by Musky Rat-kangaroos as frugivores in Australia's tropical rain forests. A question which arose from the more basic one of: How do Musky Rat-kangaroos relate to their environment? These general questions are discussed in my final chapter (Chapter 11: "Musky Rat-kangaroos: cursorial frugivores") where I will attempt to relate the findings of this study to aspects of frugivore functional roles, communities and advantages to dispersal in the context of the Australian and world arenas of frugivory and dispersal discussed above.

◆⁘◆

Table 1.2 Evidence that escape from disproportionate mortality under parent plants is important to some rain forest plants in different communities. **Agent** = mortality agent; **Life Stage** = life history stage affected; **Mortality%** = mortality rate under parent plant/ Mortality away from parent; **Dispersers** = animals or methods of dispersal known to remove propagules from parent.

Location	Plant Species	Agent	Life Stage	Mortality %	Dispersers	Reference
Mexico	*Cymbopetalum baillonii*	rodents ?	seed seedlings	100/30 >90/?	8 bird spp.	Coates-Estrada & Estrada 1988
Costa Rica	*Casearia nitida*	insects?	seeds	?	2 Toucans, 1 Flycatcher, 1 Tityra	Howe and Primack 1975
Costa Rica	*Casearia corymbosa*	?	seeds	100/?	?	Howe 1977
Costa Rica	*Andira inermis*	*Cleogonus* weevils	seeds	77 - 94/10-96	bat *Artebius jamaicensis*	Janzen *et al.* 1976
Costa Rica	*Welfia georgii*	Litterfall + ?	seedlings	?	?	Vandermeer 1977
Costa Rica	*Welfia georgii*	?	seeds	~ 90/~45	?	Schupp & Frost 1989
Costa Rica	*Sterculia apetala*	*Dysdercus fasciatus* Bug	seeds	100/0	Squirrel *Sciurus variegatoides*	Janzen 1972
Costa Rica	*Dipterix panamensis*	?herbivores or pathogens	seedlings	100/53-87	bat, agouti, squirrel, monkey	Clark & Clark 1984
Costa Rica	*Huberodenron allenii*	rodent	seeds	100/lower	wind	Janzen 1970

Table 1.2 (Cont...)

Location	Species	Agent	Life Stage	Mortality %	Dispersers	Reference
Panama	*Scheelia zonensis*	bruchid	seeds	60/10	?	Wright 1983
Panama	*Dipteryx panamensis*	?	seedlings	88/26-68	bat, monkey, coatimundi, paca	De Steven & Putz 1984
Panama	*Faramea occidentalis*	rodents	seeds	90/60	monkeys, Guan	Schupp 1988
Panama	*Platypodium elegans*	fungus rodents	seedlings seeds	35-81/? minor/?	wind	Augspurger 1983a
Panama	*Platypodium elegans*	fungus	seedlings	60-100/0-10	wind	Augspurger 1983b
Panama	*Platypodium elegans*	fungus	seedlings	100/65-95	wind	Augspurger 1984a (Note: seedling mortality is taken at one year from germination)
	Triplaris cumingiana	fungus	seedlings	90/70-93	wind	
	Lonchocarpus pentophyllus	fungus	seedlings	100/70-97	wind	
	Aspidosperma cruenta	fungus	seedlings	70/55-80	wind	
	Terminalia oblonga	fungus	seedlings	100/90-98	wind	
	Cavanillesia platanifolia	fungus	seedlings	100/98	wind	

Table 1.2 (Cont...)

Location	Species	Agent	Life Stage	Mortality %	Dispersers	Reference
Panama	*Platypodium elegans*	fungus	seedling	60-100/ 20-70	wind	Augspurger 1984b
Panama	*Virola nobilis*	2 beetles, Agouti, deer	seeds seedlings	98/85-90 97/89-95	birds, monkeys	Howe 1993
Panama	*Virola surinamensis*	weevil, Agouti	seeds seedlings	98/85-90 96-98/83-86	birds, monkey	Howe *et al.* 1985
Peru	*Astrocaryum macrocalyx*	Bruchid	seeds	97/91	Capuchin, Agouti	Terborgh *et al.* 1993
Uganda	*Balanites wilsoniana*	squirrel	seeds	5/0	?	Chapman & Chapman 1996
	Mimusops bagshawei	rodents ?	seeds seedlings	100/90 32/5	monkeys, ape, bird	
	Uvariopsis congensis	?	seedlings	12/10	monkeys	
	Psuedospondias microcarpa	?	seedlings	26/3	monkeys	
Malaysia	*Aglaia* sp.	rodents, beetle ?	seeds seedlings	>?/<? 78/24-67	hornbill, squirrel	Becker & Wong 1985
Australia	*Normanbya normanbyi*	pigs, earwig	seeds	25-45/4-18	Cassowary, MRK	Lott *et al.* 1995

Table 1.2 (cont....)

Location	Species	Agent	Life Stage	Mortality %	Dispersers	Reference
Australia	*Planchonella* sp. nov.	insects ?	seedlings	51-70/14-42	birds	Connell 1971
Australia	*Litsea connorsii*	rats	seeds	74/58	birds	Moore 1991

Table 1.3 Studies which found that escape from mortality under parent plants is not important to some species. **Life Stage** = life history stage studied.

Location	Species	Life Stage	Dispersers	Reference
Uganda	*Uvariopsis congenensis*	seedlings	monkeys	Chapman & Chapman 1996
	Psuedospondias excelsa	seedlings	apes, monkeys	
	Mimusops bagshawei	seedlings	ape, monkeys, bird	
Puerto Rico	*Euterpe globosa*	seeds/seedlings	?	Janzen 1972a
Panama	*Tabebuia rosea*	seedlings	wind	Augpsurger 1984 (Note: mortality at 1 year)
	Ceiba pentandra	seedlings	wind	
Panama	*Faramea occidentalis*	seedlings	monkeys, guans	Schupp 1988
Panama	*Scheelea zonensis*	seeds/seedlings	?	Wright 1983
Panama	*Dipteryx panamensis*	seedlings	bat	De Steven & Putz 1984
		seeds	Agouti	Forget 1993

Table 1.3 (cont...)

Location	Species	Life Stage	Dispersers	Reference
Brazil	*Eschweilera albiflora*	seedlings	monkeys	Lopes & Ferrari 1994
Peru	*Bertholettia excelsa*	seeds	agoutis	Terborgh *et al.* 1993 (dispersal in these species seems poor)
	Calatola venzuelana	seeds	monkeys, birds	
	Dipteryx micrantha	seeds	bats	
	Hymenaea courbaril	seeds	rodents	
Australia	*Cryptocarya corrugata*	seeds	birds, cassowary	Connell 1970
Australia	*Eugenia brachyandra*	seeds seedlings	?	Connell 1979
Australia	44 species	seedlings	-	Connell *et al.* 1984
Australia	*Normanbya normanbyi*	seedlings	-	Lott *et al.* 1995
Australia	*Syzygium johnsonii*	seeds	birds, cassowary	Moore 1991
	Acronychia acronychioides	seeds	birds, bats	
	Cryptocarya densiflora	seeds	birds.	
	Elaeocarpus largiflorens	seeds	birds, cassowary	
	Endiandra dielsiana	seeds	birds, cassowary	
Tropics	10+ species	seeds/seedlings	poor dispersal	Hart *et. al.* 1989

Table 1.4 A functional classification of rain forest frugivores based on where and when they are active within the forest strata and how they treat seeds.This classification includes birds and mammals that are primarily frugivorous. Where a family has species covering more than one size class or category it is listed for all size classes ad categories it fits. Classification follows Gruson, 1976 #193 for birds and Macdonald, 1984 #195 for mammals. Region = Biogeographic region: Eth-Ethiopian; IM-Indo Malayan; Aus-Australiasian; Neo-Neotropics. #sp = estimate of the number of species fitting the category - "/" unknown proportion of species. References used are listed as below.

Movement	Activity	Characteristics	Description	Region	#sp	Families
Volant	Diurnal	Large (>~350mm), above canopy	Large birds which tend to be strong flyers above the forest canopy and may scatter seeds long distances. Capable of swallowing large seeds.	Eth	2	Columbidae
					20	Bucerotidae
				IM	/39	Columbidae
					17	Bucerotidae
				Aus	/39	Columbidae
					2	Bucerotidae
					1	Cracticidae
				Neo	?	Columbidae
					/22	Icteridae
		Large (>~350mm), within canopy	Large birds which tend to fly from tree to tree within the canopy or lower strata. Shorter dispersal potential. Capable of swallowing large seeds.	Eth	17	Musophagidae
					3	Trogonidae
				IM	11	Trogonidae
				Aus	/42	Paradisaeidae
					1+	Cuculidae
				Neo	20	Trogonidae
					/38	Ramphastidae
					/79	Cotingidae
					/34	Cracidae
					?	Cuculidae, Corvidae,
					?	Momotidae

Table 1.4 (Cont...)

Movement	Activity	Characteristics	Description	Region	#sp	Families
Volant	Diurnal	Small (<~350mm), above canopy	Small birds which sometimes have strong flight above the canopy. May scatter seeds long distances. Generally take small fruits.	Eth	?	Sturnidae, Oriolidae?
				IM	?	Sturnidae, Oriolidae?
				Aus	?	Sturnidae, Oriolidae?
				Neo	1	Campephagidae
					/22	Icteridae
		Small (<~350mm), within canopy	Small birds which tend to forage and remain within the canopy or lower strata. Short diatance dispersal. Generally take small fruit	Eth	38	Capitonidae
					2	Philepittidae
					?	Pycnonotidae
					18	Zosteropidae
					/8	Oriolidae
				IM	/39	Columbidae
					26	Capitonidae
					?	Picnonotidae
					3	Eurylaimidae
					14	Chloropsidae
					32	Dicaeidae
					20	Zosteropidae
					?	Meliphagidae
					?	Oriolidae
				Aus	/39	Columbidae
					16	Dicaeidae
					19	Zosteropidae
					?	Meliphagidae
					/11	Oriolidae
					12	Ptilinorhynchidae
					/42	Paradisaeidae

Table 1.4 (Cont...)

Movement	Activity	Characteristics	Description	Region	#sp	Families
Volant	Diurnal	Small (<~350mm), within canopy	Small birds which tend to forage and remain within the canopy or lower strata. Short distance dispersal. Generally take small fruit.	Neo	13	Capitonidae
					/38	Ramphastidae
					?	Tyrannidae
					/79	Cotingidae
					50	Pipridae
					3	Ptilogonatidae
					/22	Icteridae
					?	Muscicapidae
					?	Vireonidae
		Mostly predators or poor dispersers	Birds which feed on fruit but generally are seed predators or consume only flesh and do not carry seeds. May disperse some species, particularly with small hard seeds.	Eth	?	Psittacidae, Columbidae
				IM	?	Psittacidae, Columbidae
				Aus	?	Psittacidae, Columbidae
					4	Cacatuidae
				Neo	?	Psittacidae, Columbidae
					190	Emberizidae
Volant	Nocturnal	Strong flying above canopy	Birds and bats that scatter disperse seeds (over long distances in the case of the Oilbird *Steatornis caripensis*). Lack regular feeding perches.	Eth	/26	Pteropodidae
				IM	/66	Pteropodidae
				Aus	/21	Pteropodidae
				Neo	1	Steatornithidae
					/96	Phyllostomatidae
		Within forest or short distances above	Fly inside forest and usually have regular feeding stations. Therefore disperse seeds to dense clumps.	Eth	/26	Pteropodidae
				IM	/66	Pteropodidae
				Aus	/21	Pteropodidae
				Neo	/96	Phyllostomatidae

Table 1.4 (Cont...)

Movement	Activity	Characteristics	Description	Region	#sp	Families
Arboreal	Diurnal	Move through canopy from tree to tree.	Primates which feed in the canopy and generally ingest seeds whole, dispersing them as clumps in defaecations. Some members (except perhaps Hylobatidae) act primarily as seed predators or usually ingest only the flesh of fruits and drop the seeds, therefore may be considered a separate functional group but are not separated here.	Eth	/17	Cercopithecinae
					1+	Colubinae
					/15	Lemuridae
				IM	/8	Cercopithecinae
					/14	Colobinae
					9	Hylobatidae
					1	Pongidae
				Neo	/21	Callitrichidae
					/30	Cebidae
Arboreal	Nocturnal	Move through canopy from tree to tree	Generally small mammals which feed partially or almost exclusively on fruit. Likely to be short range dispersal.	Eth	8	Lorisidae
					1	Daubentonidae
					1	Anomaluridae
				IM	1-2	Lorisidae
				Aus	6+	Phalangeridae
					1+	Psuedocheiridae
				Neo	3+	Didelphidae
					2	Procyonidae
Scansorial	Diurnal	Forage both in canopy and on ground	Wide range of body sizes in mammals that are partially or almost wholly frugivorous. Includes some birds which are not truly scansorial but forage both in the canopy and on the ground. Likely to be short range dispersal.	Eth	2	Pongidae
					1+	Lemuridae
				IM	/14	Colobinae
					1+	Tupaiidae
				Aus	4	Columbidae
					4+	Ptilinorhynchidae
				Neo	3	Procyonidae
					/34	Cracidae

Table 1.4 (Cont...)

Movement	Activity	Characteristics	Description	Region	#sp	Families
Scansorial	Diurnal	Forage both in canopy and on ground	Mostly seed predators but may disperse some seeds through caching.	Eth	9+	Sciuridae
				IM	12+	Sciuridae
				Neo	?	Sciuridae
	Nocturnal	Forage both in canopy and on the ground	Mammals of varying size and mostly unkown dispersal efficiency. Most are primarily frugivorous.	Eth	2	Viverridae
				IM	9	Viverridae
				Aus	1	Viverridae
					3+	Phalangeridae
				Neo	1	Procyonidae
			Mostly seed predators but may disperse some species through caching.	Eth	?	Muridae
				IM	?	Muridae
				Aus	?	Muridae
				Neo	?	Muridae
Terresrial	Diurnal/ Nocturnal	Large (>20kg), some may feed night and/or day.	Large animals which forage for fallen fruit by day or night (Cassowaries are strictly diurnal). Includes some primarily browsing animals that eat sigificant quantities of fruit and digest some.	Eth	1	Hippopotamidae
					1	Elephantidae
					1	Hominidae
				IM	1	Elephantidae
					1	Tapiridae
					2	Ursidae
					1	Hominidae
				Aus	3	Casuaridae
					1	Hominidae
				Neo	2	Tapiridae
					1	Hominidae

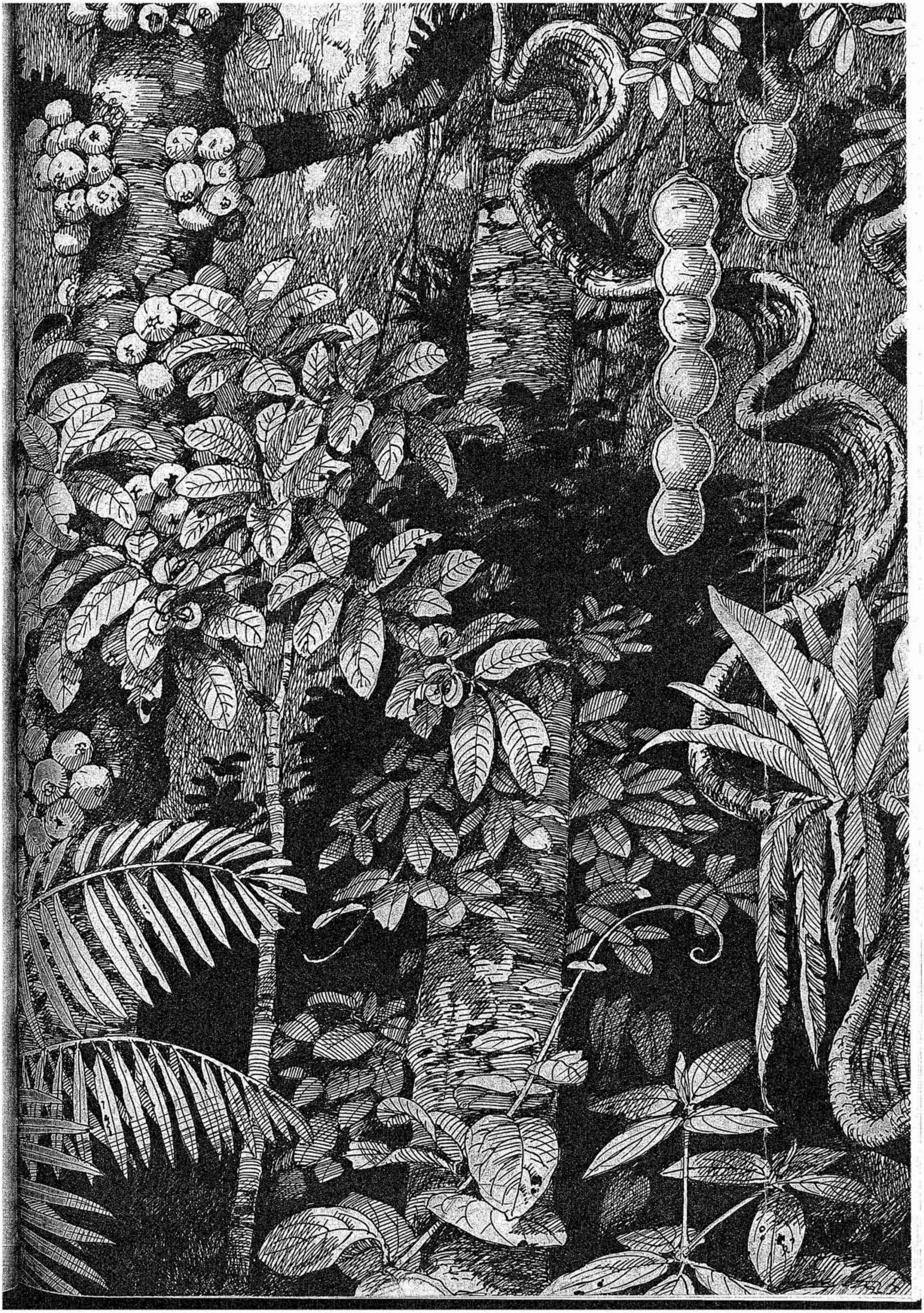
Table 1.4 (Cont...)

Movement	Activity	Characteristics	Description	Region	#sp	Families
Terrestrial	Diurnal or Nocturnal	Small (5-19kg), often omnivores	Small forest deer which eat varying proportions of fruit and probably digest many seeds but disperse some.	Eth	1	Tragulidae
					4	Cephalophinae
					1+	Histricidae
				IM	3	Cervidae
				Neo	4	Cervidae
					?	Psophiidae
	Diurnal Nocturnal or Both	Primarily predators	Generally crush or gnaw seeds. Wide range of body sizes. Ground squirrels and peccaries are diurnal, most murids nocturnal and most pigs active at any time. Are sometimes important dispersal agents as well as predators.	Eth	2	Sciuridae
					?	Muridae
					1	Hystrichidae
				IM	3	Suidae
					?	Muridae
					2+	Sciuridae
				Aus	1	Suidae
					?	Muridae
				Neo	2	Tayassuidae
					?	Muridae
					?	Sciuridae
					?	Tinamidae. Phasianidae
	Diurnal	Small (<5kg) cursorial frugivores, partial seed predators	Small, fast moving mammals which are partial seed predators but also disperse many seeds. Many cache seeds.	Eth	1	Cephalophinae
					1+	Macroscelididae
				IM	3	Tragulidae
				Aus	1	Potoroidae*
				Neo	13	Dasyproctidae

Sources: Austin 1965; Gruson 1976; Clutton-Brock and Harvey 1977; Gautier-Hion *et al.* 1980; Snow 1981; Emmons *et al.* 1983; Terborgh 1983; Macdonald 1984a & b; Coates-Estrada and Estrada 1986; Terborgh 1986; Fleming *et al.* 1987; Smythe 1989; Bodmer 1990; Rowell and Mitchell 1991; Charles-Dominique 1993; Flannery and Schouten 1994; Medellin 1994; Mittermeier *et al.* 1994; Strahan 1995; Flannery 1995; * present study.

Table 1.8 Definitions for some terms used in this chapter.

Term	Definition
BCI	Abbreviation for Barro Colorado Island, Panama.
Coterie	A group of animals/people, in this context it refers to a group of frugivores that all feed on the fruits of the same species of plant in the same area.
Effectiveness	A term which applies to the ability of frugivores to successfully disperse seeds (see quantity and quality; discussed in detail in the section on "Effectiveness").
Epizoochorous	Propagules which adhere to the outside of an animal.
Fruit Syndrome	A system of categorising fruits based on their physical and ecological characteristics. Relates particularly to characteristics which might attract the animals that are percieved as being their primary dispersal agents.
MRK	Abbreviation for Musky Rat-kangaroo.
Pre-dispersal Predation	Seed predation which occurs before a fruit/seed is separated from the plant.
Quality	Aspect of disperser effectiveness - how well it treats and handles seeds.
Quantity	Aspect of disperser effectiveness - how many seeds an animal dispersers, how often it visits a fruiting tree and the abundance of the animal are all aspects relating to quantity.
Seed Shadow	Pattern of deposition of seeds from a plant resulting from the activity of dispersal agents including: animals, wind, gravity, water etc.



Chapter 2

STUDY SITE AND CLIMATE

Tropical rain forest in Australia currently covers a small area relative to most other tropical countries (10,515 km^2; Winter *et al.* 1987b) and extends in patches from the tip of Cape York Peninsula to Mt Spec near Townsville (Figure 2.1). The largest area (now 7910 km^2; Winter *et al.* 1987b) is between Cooktown and Townsville and it is within this block that my study was conducted. Approximately one third of what existed prior to the European invasion has been cleared, mostly on the flat lowlands and tablelands with more nutrient rich soils (Winter *et al.* 1987a). Australian rain forests are often considered to be of great scientific interest due to their large number of endemic plants and animals, many of which have primitive characteristics. They are also considered to be the habitats from which all of the dry and cold adapted species in Australia originated, when the Australian plate was covered in extensive rain forest (Winter *et al.* 1987a).

My study site was in complex mesophyll vine forest (type 1b; Tracey 1982) on basalt derived soil at an average elevation of 740m (range 720 - 760m). It was inland of Queensland's highest mountain (Bartle Frere: reaching 1622 m a.s.l.) on the eastern side of the Atherton Tableland (145°44'43"E, 17°22'38"S) and was within the 94 000 ha Wooroonooran National Park, which is part of the largest continuous block of rain forest in Australia (Figure 2.1). Prior to its listing as National Park in 1992, the area was part of a State Forest system (SF 310, Gadgarra) and was last selectively logged during the mid-1970's. It is now part of the Wet Tropics World Heritage Area.

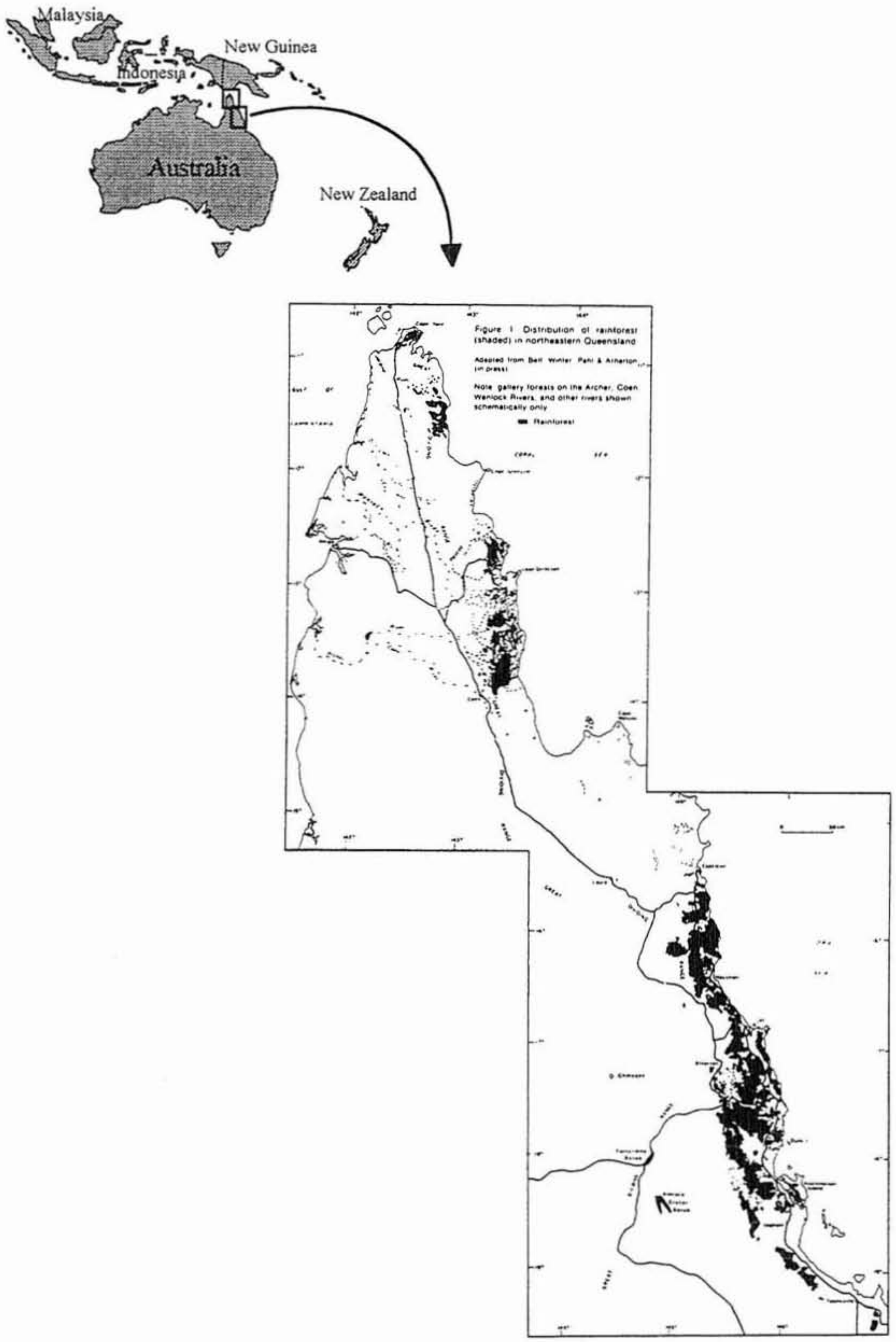


Figure 13.1 Distribution of rainforest in north-eastern Queensland (adapted from Bell, Winter, Pahl and Atherton, in press)

Note: Gallery forests on the Archer, Coen, Wenlock and other rivers shown schematically only

Figure 2.1 Map showing the distribution of tropical rain forest in Australia and indicating the general region of this study. Adapted from Winter *et al.* (1987).

Forest and Topography

The forest is tall (canopy 30 - 40 m; emergents 50 - 60 m) with high species diversity (up to 200 tree species and hundreds of other plants on my 9 ha site; Irvine, A. pers. comm. 1990; Plate 1). It supports the numerous plant growth forms typical of tropical rain forests, including: epiphytes; hemi-epiphytes; lianes; vines; tree ferns; gingers; aroids; palms; climbing palms; pandanus; cycads; ferns and; strangler figs. Many trees have buttresses and one species, Watergums, *Syzygium gustavioides*, have flying buttresses (Plate 2). Both buttresses and flying buttresses are significant to the Musky Rat Kangaroo (see Chapter 7).

The understorey density varies with the degree of closure of the canopy and ranges from extremely dense thickets of regrowth (sometimes including the exotic weed, *Lantana camara*) where past logging or cyclone disturbance has broken the canopy, to a very open understorey of scattered saplings or understorey plants below undisturbed forest canopy (Plate 3).

Approximately one third of the site (32%; Figure 2.2) is fairly level ground, the remainder slopes away into a perennial stream with three main tributaries, one with smaller branches (Plate 4). Several old snig tracks (roads used to extract one or more trees for timber) traverse the site and are generally characterised by a dense growth of saplings.

Figure 2.2 Map of study site showing: areas of differing topography; the forest edge; and the placement of grid points. Topographic areas are: **S** - slope; **MS** - moist slope (generally leading into or surrounding a gully); **G** - gully; **R** - ridge; **F** - flat; and **MF** - moist flat.

Grid, Traps and Transects

I established a 300 x 300m grid on the site with the assistance of a qualified surveyor. Pegs were placed at 25 m intervals and colour coded for ease of recognition from a distance. Each peg also carried a written indication of its position. I mapped the site according to its topographical features using grid markers as reference points (Figure 2.2, 2.3).

Fence traps and a set of transects were central to much of my data collection. I display their configuration here (Figure 2.3). Details of the methodology surrounding each are described in the relevent chapters (Fence traps - Chapters 6&7; Transects - Chapters 3, 4&10). Data on diet (Chapter 3) and food availability (Chapter 4) were collected along seven transects placed systematically along grid lines (Figure 2.3). The transects were cut for ease of walking with minimal removal of vegetation.

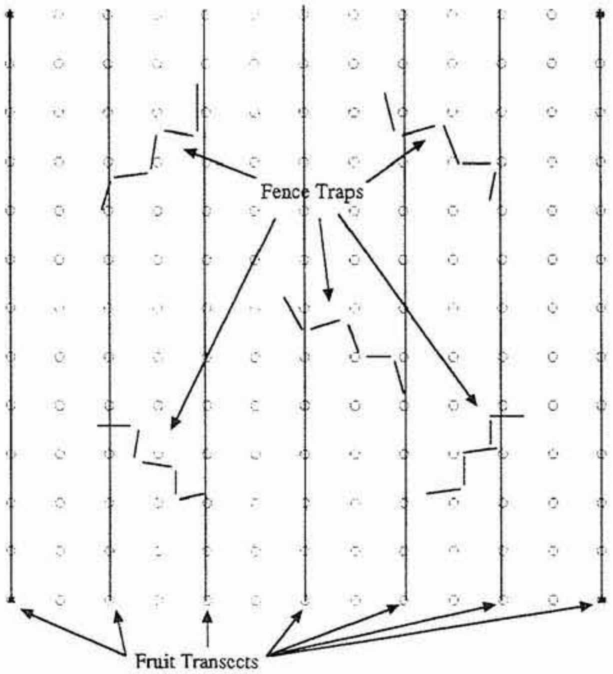


Figure 2.3 Study site grid showing placement of fence traps (Chapters 6 & 7) and transect lines (Chapters 3, 4 & 10).

Climate

Rainfall records from a farm 1km from the site (I. and F. Bean, Gourka Rd) show that over the 11 years from 1984 to 1994 the mean yearly total was 3187 mm (± 173 SE; range 2128 - 4072). A highly seasonal pattern was evident (Figure 2.4). Usually there were three very wet months in each year (February, March and April), five wet months (January, May, June, July and December) and four dry months (August to November).

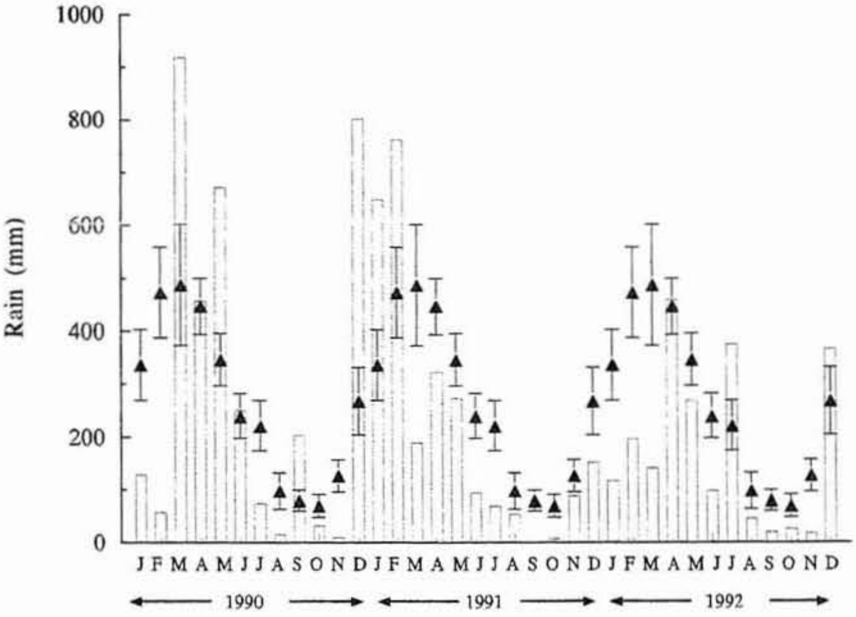


Figure 2.4 Rainfall during my study (bars: 1990, 1991 and 1992) and the mean monthly rainfall over 11 years from 1984 to 1994 (± SE).

Rain fell in several different patterns: as storms; as continuous monsoonal rains; and as continuous orographic drizzle. Each of these patterns, in combination with monthly rainfall totals, can result in a different number of cloudy days per month. The number of cloudy days per month may impact on the timing of ripe fruit production and is therefore displayed here (Figure 2.5) and used in an analysis in Chapter 3.

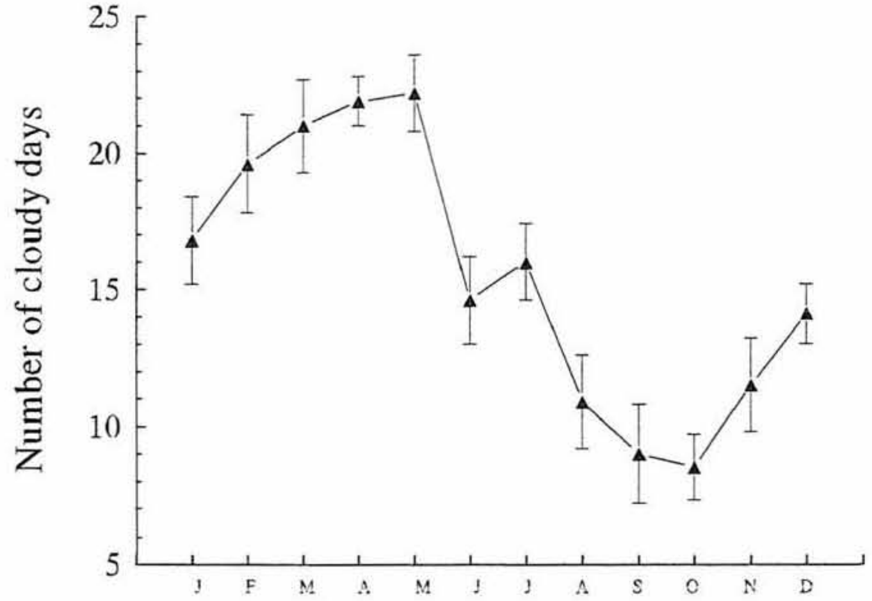


Figure 2.5 Mean number of cloudy days per month (± SE) at my study site. Data for 11 years from 1984 to 1994.

I have used temperature data from Malanda, 13km west of the study site, to show seasonal fluctuations. Records were collected at 0600 hrs daily (excluding Sundays) by V. English, using a maximum/minimum thermometer. Data recorded under the the rainforest canopy two kilometres from the study site (collected haphazardly 3 - 13 times per month by A. Jansen, using a maximum/minimum thermometer) were compared to the Malanda records. Temperatures under the canopy fluctuated in a similar pattern (Correlation $R = 0.98$, $Pr < 0.0001$) but did not reach the extremes that temperatures in Malanda did. Because the data from Malanda are more complete and differences between the forest records and those in Malanda are minimal, I have chosen to display the Malanda data here (Figure 2.6) and use it in analyses in Chapter 5.

Mean monthly maximum temperatures ranged from 29°C between November and January each year to 19°C in July. Minimums ranged from around 20°C in the warmer season to around 10°C in the Cold season (Figure 2.6).

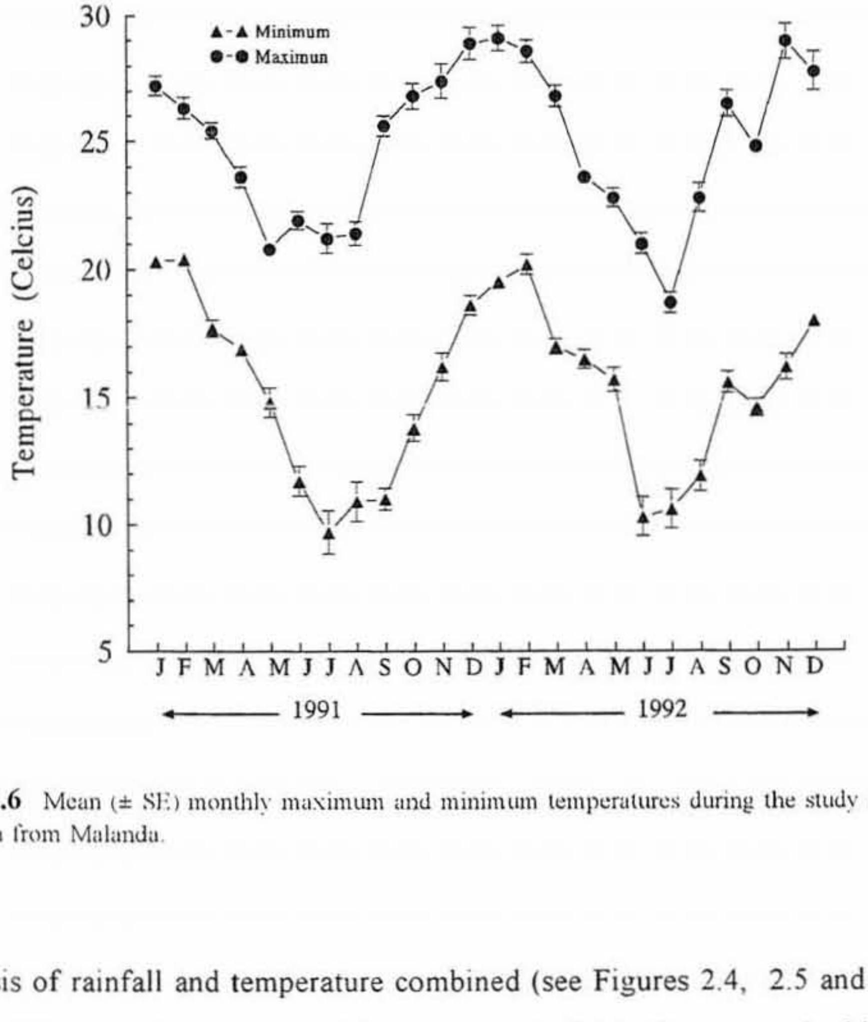


Figure 2.6 Mean (± SE) monthly maximum and minimum temperatures during the study (1991 and 1992). Data from Malanda.

On the basis of rainfall and temperature combined (see Figures 2.4, 2.5 and 2.6), I have divided the year into seasons which are meaningful in the area and which do not correspond with the usual temperate seasons (Table 2.1). The Storm season, November to January, is characterised by increasing frequency of storms and high temperatures. The Wet season, February to April, has high monsoonal rainfall and warm temperatures. The Cold season, May to July, has persistant rainfall of orographic origin with low temperatures. While the Dry season, August to October has low rainfall with increasingly warm temperatures.

Table 2.1 Seasons and their climatic parameters for the region of my study. These seasons will be used to discuss the timing of various occurances in subsequent chapters and analyses.

Season	Months	Mean Rainfall	Mean # Rainy Days	Temperature Max	Temperature Min
Storm	Nov	126	11.5	28.2	16.2
	Dec	267.6	14.1	28.4	18.3
	Jan	336.3	16.8	28.1	19.9
Wet	Feb	473.5	19.6	27.4	20.3
	Mar	487.3	21	26.1	17.3
	Apr	446.6	21.9	23.6	16.6
Cold	May	346.5	22.2	21.8	15.3
	Jun	239.3	14.6	21.5	11
	Jul	221.6	16	20	10.2
Dry	Aug	97	10.9	22.1	11.4
	Sep	79.3	9	26.1	13.3
	Oct	68.6	8.5	25.8	14.2

Although these seasons reflect the conditions at my study site better than those based on the temperate model (i.e. Winter, Spring, Summer, Autumn), what actually occurs in any one year is quite variable. During the three years displayed in Figure 2.4, 1990 had a late wet season (Monsoon rains from March to May) while the following one was early (December to February). Subsequent to the wet season, rainfall in 1991 was continuously below average. Nineteen ninety two was the driest year in the 11 year period from 1984 to 1994 with most months being below average.

◆ ⁂ ◆

Plate 1 Complex mesophyll vine-forest on my study site.

Plate 2 Flying buttresses on a Watergum, *Syzygium gustavioides*, often used as shelter and foraging sites by Musky Rat-kangaroos.

Plate 3 Area of study site with a closed canopy and open understorey.

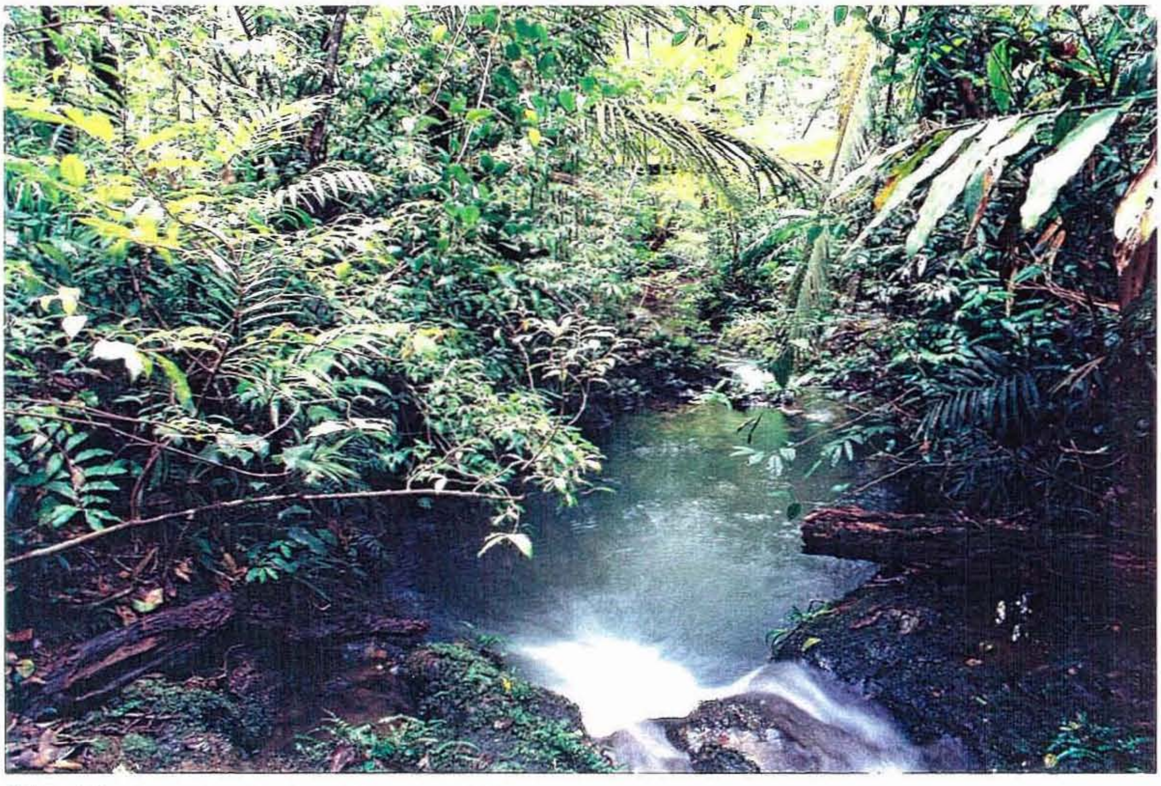


Plate 4 Area of study site with a perennial stream.