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Seed dispersal by male Tooth-billed Bowerbirds, *Scenopoeetes dentirostris* (Ptilonorhynchidae), in north-east Queensland rainforests: Processes and Consequences.

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in December, 1991

for the degree of Doctor of Philosophy
in the Department of Zoology at James Cook University
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ABSTRACT

The seed dispersal service of male Tooth-billed Bowerbirds (*Scenopoeetes dentirostris*), hereafter Tooth-bills, was investigated from June 1987 to December 1989, in upland rainforest near Paluma, North-east Queensland. Male Tooth-bills form "exploded leks" during the display season from September to January. Within leks, males establish traditional court sites on the forest floor. Males return to the same court site each display season, with some males known to attend the same court site for 13 years. If a male is displaced or lost from a court site, another male will establish at that site, maintaining lek cohesion. Leks and court sites within are therefore spatially and temporally stable.

Spatial distributions of male Tooth-bills and canopy gaps were examined in two 10ha sites, one logged and the other unlogged. Leks were positioned along ridge lines or on hill tops. Within leks, males were spaced regularly at about 50m intervals. Canopy gaps were randomly distributed across both sites, and were more abundant in the unlogged site. Three of 32 male Tooth-bills continued to maintain courts within or immediately adjacent to canopy gaps.

Fruiting phenologies were monitored at both sites using both fruit fall traps and transect walks. Male Tooth-bill display occurred during the first peak of fleshy fruit production from September to December. The number of species fruiting and the abundance of fruits produced varied between seasons and sites. A total of 61 plant species were deposited on the forest floor during the study.

Detailed observations on the behaviour and movement of four male Tooth-bills were made over the 1989 display season using radio-tracking and observations from hides. Males spent 50% of daylight hours calling from favoured song posts 1-6m above the court. The remaining period was spent actively foraging for fruits, collecting leaves for the court or interacting with other Tooth-bills. The median duration of bouts away from the courts was 12.4mins, while the median duration of bouts at the court was 6.2 mins. The median distance of foraging bouts away from the court ranged from 40-86m, with maximums ranging from 311-391m. The mean home range of males over the display season was 9.6ha. Analysis and modelling of foraging behaviour sequences suggest that more seeds were deposited within the court area (68%) than would be expected from time spent at the court (46%).

Male Tooth-bill diet was monitored using fruit fall traps beneath the favoured perches of ten birds. Over three display seasons, 51 species of fleshy fruited plant species were consumed and deposited in large seed piles beneath favoured calling perches. Of these, 40 species were large fruits containing large seeds (>4mm). Five families comprised 95% of the large fruit recorded in the diet. These were (in decreasing importance) the Elaeocarpaceae, Lauraceae, Symplocaceae, Myrtaceae and Rutaceae. Members of the Moraceae were also well represented in the diet. Gut treatment by male Tooth-bills was gentle, to the extent that members of the Rutaceae passed through the gut unchanged with the pericarp still intact. Seeds of all other species passed through the digestive system undamaged and with the pericarp variously digested.

Germination trials were conducted on 36 plant species consumed by male Tooth-bills. Of these, 53% of species germinated with varying success, with members of the Loganiaceae, Myrtaceae and Lauraceae exhibiting the highest germination success. Comparisons of germination response were also made between bird dispersed and non-bird dispersed seeds. In a comparison of nine plant species, male Tooth-bill dispersal enhanced germination in seven species and shortened the germination time in six species. Examination of the germination response of seed passing through Cassowaries (*Casuarius casuarius*) and Shining Starlings (*Aplonis metallica*) provided similar results. Fast germinating seeds, produced in the late dry season, may benefit most from seed dispersal by male Tooth-bills, and seeds with extended dormancy may benefit least.

Seeds and seedlings deposited in clumps require the ability to survive density dependent mortality. Experiments were conducted to compare seed predation in Tooth-bill seed clumps with other microsites on the forest floor. Experiments tested the effects of seed species, density, microsite and year on seed predation intensity. *Litsea connonsii* and *Acronychia acronychiodes* seeds were predated heavily while most other species were rarely predated. Predation of *Litsea* seeds was greatly reduced when seeds occurred at lower densities. Seed predation intensity of *Litsea* seeds also varied dramatically between years, with high seed predation in 1988 and significantly less seed predation in 1990. Reduction in seed predation coincided with a decline in rodent seed predator numbers. Seeds in Tooth-bill seed piles were predated with similar intensity to other sites on the forest floor.

Experiments were also conducted to compare seedling survival in Tooth-bill seedling clumps with other microsites on the forest floor. Microsite had no significant effect on seedling survival for either *Acmena resa* or *Syzygium johnsonii*. Seedlings grew very little in the first year of life. Seedling density had a significant positive effect on seedling growth in height, but a significant negative effect on growth in number of leaves. The only seedlings to gain leaves in the first year of life were those in canopy gaps.

Beneath the closed canopy, seedlings of *Acmena resa* and *Guioa acutifolia* persisted as bouquets of seedlings within Tooth-bill seed piles for four years after deposition. Shade tolerant *Chionanthus axillaris* saplings were more abundant in Tooth-bill court areas than in random sites within the forest, also suggesting effective recruitment within these areas.

These data suggest that clump dispersal of seeds by male Tooth-bills is an effective mode of seed dispersal for a number of plant species within tropical rainforests. Mechanisms of recruitment are discussed in relation to fluctuations of fruit production, seed predators and the availability of safe sites for germination. Advantages to the plants and birds are also discussed. This study consummates a link between a known seed disperser and the fate of seeds dispersed, a connection not previously reported for tropical rainforests.

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"The observer new to the scene would perhaps be first struck by the varied yet symmetrical trunks, which ... give an impression similar to that produced by the columns of an enormous building. Overhead, at a height, perhaps, of a hundred feet, is an almost unbroken canopy of foliage ... so dense that ... the intense tropical sunlight only penetrates to the ground subdued and broken into scattered fragments. There is a weird gloom and a solemn silence, which combine to produce a sense of the vast-the primeval-almost of the infinite. It is a world in which man seems an intruder, and where he feels overwhelmed by the contemplation of the ever-acting forces, which, from the simple elements of the atmosphere, build up the great mass of vegetation which overshadows, and almost seems to oppress the earth."

A. R. Wallace

"Tropical nature and other essays"
Macmillian and Co. 1878.

Chapter One

GENERAL INTRODUCTION

1.1 INTRODUCTION

Some 300 million years ago, primitive cycads bore fleshy fruits, speculated to be dispersed by dinosaurs (Sporne 1965). Today, possums disperse the seeds of the *Macrozamia* (Burbidge and Whelan 1982). The players may have changed, but the game remains the same.

With the adaptive radiation of modern Angiosperms over the last 125 million years, an enormous diversity of fleshy fruits has evolved in concert with an equally diverse array of frugivores. Fleshy fruits have become variously modified for dispersal by birds, bats, monkeys, ungulates, reptiles and fish (Van der Pijl 1972). The magnitude of the relationship between fruit and frugivores is nowhere more evident than in tropical rainforests (Snow 1971, 1981, Wheelwright 1988).

In studies of seed dispersal by vertebrates a high degree of mutualism between plant and frugivore is often assumed but seldom demonstrated. Studies of frugivory detail diet selection, fruit handling, and very occasionally seed shadows produced by the frugivore (Martin 1985, Murray 1987, 1988, Howe 1989). However, the fate of seeds dispersed by frugivores and the success of the resulting seedlings has rarely been documented (Janzen 1983, Howe and Smallwood 1982, Martin 1985, Howe 1989, 1990). Similarly, from the plant perspective, plant demographers detail adult and juvenile tree distributions with little attention to the patterns of seed dispersal and seed and seedling mortality (Becker and Wong 1985, Dirzo and Dominguez 1986, Howe 1986, 1989, 1990). Thus the link between frugivores and the patterns of adult tree dispersion remain a mystery.

The problems in identifying the links between seed disperser and plant species are largely pragmatic. A tropical rainforest tree may produce 10^{6-9}seeds in its life time (Harper 1977). If on average each plant during the course of its life leaves one descendent (Harper 1977), then the chances of defining the circumstances that enabled recruitment of any one individual are intractable. When seed production is countered by mortality at every life stage: seed, germination, establishment, seedling and sapling, then the relevance of the fate of a single seed seems questionable at best.

In order to determine the effectiveness of a seed disperser in a system as complex as a tropical rainforest, ecologists must search for dispersers that provide predictable seed dispersal services in time and space. The male Tooth-billed Bowerbird (*Scenopoeetes dentirostris*) hereafter male Tooth-bill, in upland rainforests of north eastern Australia, is one example. Each year males return to traditional court sites to display, depositing large seed clumps beneath favoured calling perches. Clump dispersal of rainforest seeds has been viewed as an ineffective mode of seed dispersal in tropical rainforests (Wheelwright 1983, Howe 1983, 1986, Wheelwright and Orians 1982), but this remains untested.

1.2 SEED DISPERSAL: THE PROCESSES

1.2.1 A brief history of seed dispersal ecology

Plant-avian frugivore interactions have been documented since the times of the early natural historians. Darwin (1859 p 116) commented "..as the mistletoe is disseminated by birds, its existence depends on birds". Schuster (1930) first attempted to synthesise the widely scattered literature on European plant-avian frugivore interactions, listing which birds fed on what fruits. Ridley (1930) detailed seed dispersal commenting on distances, with emphasis on long distance seed dispersal over 100's to 1000's of kilometres. Finally, Snow (1971) attempted to assimilate frugivory and seed dispersal data into a workable co-evolutionary and ecological framework. He suggested that adaptive strategies of fruit production, presentation and nutritional reward by plants, were designed to attract the greatest number and variety of dispersers possible. McKey (1975) refined Snows' framework, proposing the notion that plants were divided into a continuum of strategies designed to attract different quality dispersers. At one extreme, plants produce enormous numbers of small, nutritionally poor fruits ("generalist" fruits) that attract a wide range of "poor quality" dispersers. At the other extreme, plants produce small numbers of large highly nutritious fruits ("specialist" fruits), which in turn are dispersed by a few species of "high quality" "specialist" dispersers (McKey 1975).

With this foundation, a seed dispersal research boom ensued. Between 1973 and 1982 seed-dispersal was viewed from both theoretical (Morton 1973, Howe and Estabrook 1977, Howe 1979, Thompson and Willson 1978, Fleming 1979, Howe and Smallwood 1982) and empirical (Smith 1975, Howe 1977, McDiarmid *et al.* 1977, Thompson and Willson 1978, Howe and De Steven 1979, Howe and Vande Kerckhove 1979, Howe 1980, Howe 1981, Snow 1981) perspectives. These studies refined many hypotheses, and evaluated some predictions (Wheelwright and Orians 1982). However, most of these studies continued to emphasise diet selection, frugivore visitation rates and removal rates, and fruit handling, with little concern for the possible advantages to a parent plant that are actually conferred by seed dispersal (Howe and Smallwood 1982). Consequently, most studies continued to focus on McKey's notion that frugivores differ in behavioural and ecological traits that affect their suitability as seed dispersers. The underlying premise was that natural selection should lead to mutualism in which an individual plant species should develop a tight association with an effective disperser (Howe 1977) or a small number of obligate frugivores (Howe and Primack 1975, McKey 1975, Howe and Estabrook 1977). Of the enormous number of possible plant-animal disperser interactions known, examples of mutualisms, where a so called "specialist" disperser provided a seed dispersal service that enhanced the survival and recruitment of a specific plant species were rare. They included: mistletoes and mistletoe birds (Docters Van Leeuwen 1954, Davidar 1983, Reid 1989), Galapagos tortoises and tomatoes (Rick and Bowman 1961) dodos and tambalacoque trees (Temple 1977), jays and acorns (Chettleburgh, 1952), emu and the nitre bush (Nobel 1975), aardvarks and aardvark cucumbers (Patterson 1975) and rhinoceros and *Trewia* fruits (Dinerstein and Wemmer 1988).

McKey's dichotomy, a giant step forward in 1975 and of immense historical importance through its role in stimulating thought on patterns in plant frugivore interactions, has since been discarded as a useful framework for either empiracle or theoretical studies (Wheelwright and Orians 1982). So called "specialised" frugivores (*sensu* McKey 1975) have been found to have broad diets, including: the Oilbird (Snow, 1962c, 1979), the Bearded Bellbird and other Cotingas (Snow, 1970, 1972, 1977, Snow 1973), Fruit Pigeons (Crome 1975, Frith *et al.* 1976), Manakins (Snow 1962a, 1962b, Worthington 1982), the Southern Cassowary (Stocker and Irvine 1982) and the Resplendent Quetzal (Wheelwright 1983). Equally, so called "specialised" high reward fruits of some Lauraceae may have their seeds dispersed by as many as 17 bird species from eight families (Wheelwright 1983). The lack of tight mutualisms in the world of tropical plant-seed-disperser associations seems largely due to the nature of seed dispersal. Seed dispersers are prepaid for their dispersal service and so the directions of the service are impossible to control. The result is a myriad of loose associations (Wheelwright and Orians 1982).

From 1982 to 1991 the emphasis shifted from examining the component parts of frugivory and seed dispersal to bridging the gap between the process of seed dispersal and evaluating the possible advantages conferred to the plant. Howe and Smallwood (1982) suggested that advantages conferred to the plant by seed dispersal included: (1) Escape from density and or distance responsive mortality agents near the parent plant (The "escape hypothesis", Janzen 1970, Connell 1971). (2) The widespread dissemination and colonisation of unstable or ephemeral microhabitats and (3) directed dispersal, that is, non-random seed movement to specific microsites (e.g. canopy gaps). Although the above possibilities were not mutually exclusive, they did provided a testable framework that would allow the determination of advantages conferred to the plant.

The "escape hypothesis" has been shown to be of differing importance to different rainforest plant species. Some plant species suffer intense seed and seedling mortality beneath parent crowns (Augspurger 1983a, 1983b, 1984, Augspurger and Kelly 1984, Becker and Wong 1985, Clark and Clark 1984, DeSteven and Putz 1984, Howe 1983, 1986b, Howe et al. 1985, Wright 1983), while others do not, that is, some seedlings survive beneath the parent crown (Howe 1980,1989, Schupp 1988a, 1988b) (The "Hubbell effect" Hubbell 1980).

Murray (1988) provided the first data that evaluated the effectiveness of seed dispersal by three legitimate seed dispersers: Black-faced Solitares, Black and Yellow Silky Flycatchers and Prong-billed Barbets, on three gap dependent plant species. Murray developed a model that used data on: seed shadows generated by the dispersers, germination requirements, seed dormancy and the forest dynamic processes to estimate the reproductive success, that is, total offspring produced during an individual plants lifetime. His results showed that seed dispersal by any of the three legitimate dispersers increased reproductive output by 16-36 times, even without seed dormancy. In so doing, Murray provided the first empiracle evidence to show the reproductive benefits conferred to a plant by seed dispersal.

More recently Howe (1989), in a speculative paper suggested that the variation in responses of different plant species to density and distance dependent mortality near the parent tree (the "escape hypothesis"), meant that some plant species were pre-adapted to differing modes of seed dispersal. Howe hypothesised that historically, species deposited in clumps would suffer much greater predation than those whose seeds were scattered. As a consequence, natural selection for mechanical and or chemical defences should be greater in clump-dispersed species, that is plants species whose fruits were regularly consumed by large frugivores and deposited in clumps, than plant species whose fruits were consumed by small frugivores who scatter seeds.

The shift in direction since 1982, demonstrates a greater understanding of the processes operating. The fact that seed dispersers are pre-paid for their dispersal service means that plants have little or no control over the "quality" of the disperser (Wheelwright and Orians 1982). Instead, plants are reliant on the attentions of a great many disperser species each providing a differing dispersal service. It is these loose associations and their diversity that provide an enormous array of seed dispersal possibilities for each plant each fruiting season. Each plant species has a discrete number of microsites "safe sites" available within its surrounds each fruiting season. The resultant seed shadows produced by a suite of seed dispersers over a fruiting season will increase the probability of seeds being deposited within these sites. Variation in crop size, numbers of seed dispersers and the number of available microsites each year will determine the number of potential recruits each year. The advantage conferred by seed dispersers, will thus be dependent on the likelihood of seed dispersers hitting these specific sites, and some species, as a consequence of their behaviour and gut treatment, may provide greater chances than others within an ecosystem. Its is these subtle relationships that will most likely give insights into the benefits of seed dispersal by animals.

1.2.2 Patterns of seed dispersal: scattered or clumped

Howe (1989) reviewed patterns of dispersal, dividing dispersers into two opposing syndromes, scattered and clumped seed dispersers. Scatter dispersers deposit bulky seeds singly or in small groups and tend to be smaller frugivorous birds and bats, ranging in size from 10-500 grams (Howe 1977, 1980, 1981, 1983 1989, Morrison 1978a, 1978b, Howe and Vande Kerckhove 1979, Fleming 1981, 1985, 1988, Heithaus 1982, Charles-Dominique 1986). Clump dispersers generally exceed 3kg in weight, provide larger dispersal distances, and may retain seeds in the gut for several days. These larger mammals and birds (11-7,500 kgs, eg. elephants) can consume many seeds in a sitting, digesting some and depositing the remainder in large clumps (Nobel 1975, Alexandre 1978, Janzen 1981, 1982a, Stocker and Irvine 1983, Dinerstein and Wemmer 1988, Howe 1989). Within clumps, several to thousands of seeds may be deposited. These clumps in turn may be processed by rodents (Janzen 1982b, 1986) which may then provide secondary seed dispersal.

Clump dispersal is not restricted to the larger seed dispersers. Annually, many smaller dispersers generate high density clumps of seeds as a consequence of breeding or social behaviour. Smaller birds and bats deposit large seed piles beneath favoured roosts (Heithaus *et al.* 1975, Fleming 1981, 1985, 1988), display perches (Snow 1970, 1972, 1973, 1977) and nests (Snow 1962c, Wheelwright 1983).

1.2.3 Predictable seed dispersal in time and space.

Of the 200 genera of specialist avian frugivores described by Snow (1981), the males of four families, the birds of paradise (Paradisaeidae) and bowerbirds (Ptilonorhynchidae) of Australasia, and the cotingas (Cotingidae) and manakins (Pipridae) of the Neotropics, may provide predictable clump seed dispersal services in time and space. By predictable, I mean, birds maintain specific sites within the forest, that they return to year after year. These sites are often referred to as traditional display sites (Gilliard 1969, Snow 1982). It is these display sites that hold the history of the recruitments patterns of plants dispersed by these birds.

1.2.3.1 Polygamy, leks and frugivory

Most fruit eating birds of the world are monogamous (Beehler 1983, Beehler and Pruett-Jones 1983). A number of bird groups, however, have developed polygamous, promiscuous mating systems where males are no longer needed at the nest and are free to devote most of their time to attracting mates (Snow 1982). Within these groups, competition between males is intense, and in many cases it has led to the evolution of extravagant ornamentation, elaborate courtship displays and male dispersion patterns ranging from widely-spaced solitary individuals to spatially clumped individuals in communal leks (Snow 1982, Beehler 1983, Beehler and Pruett-Jones 1983). The vast majority of the polygamous arena-displaying birds are almost entirely frugivorous and restricted to tropical rainforests (Snow 1976, Beehler 1983). Conspicuous amongst these are the Neotropical cotingas (Snow 1970, 1972, 1973, 1977) and manakins (Snow 1962a, 1962b, Lill 1974a, 1974b, 1976, Foster 1977b, Worthington 1982), and the Australasian birds of paradise (Gilliard 1969, Cooper and Forshaw 1977, Beehler and Pruett-Jones 1983, Beehler *et al.* 1986) and bowerbirds (Marshall 1954, Gilliard 1969, Pruett-Jones and Pruett-Jones 1982, Frith and Frith 1985a, Crome and Moore 1989).

1.2.3.2 Spatial dispersion patterns

Leks are defined as aggregations of males where inter-male distance within a clump is substantially less than inter-clump distances (Bradbury 1981). A further refinement of this general definition includes: (i) true leks, where inter-male distances may be less than 10m, and displaying males have both visual and vocal contact (Pitelka *et al.* 1974, Wiley 1974, Payne and Payne 1977, Myers 1979, Bradbury 1981, Beehler and Pruett-Jones 1983), and (ii) exploded leks, where inter-male distances may be 30-100m and displaying males are in vocal contact only (LeCroy 1981). Genera and species exhibiting lek and exploded lek dispersion are detailed in Table 1.1.

A number of hypotheses have been suggested to explain the development of lek dispersion patterns among polygamous bird species. These include: (i) predator avoidance (Wiley 1974, Wittenberger 1978, Bradbury 1981), (ii) increased stimulus to females (Bradbury 1981), (iii) the ability of aggregated males to signal more females (Snow 1962a), (iv) social dispersion (Wiley 1974, Bradbury 1981) and (v) population density (Snow 1973) (see Beehler and Foster, 1988, for a complete review).

Beehler and Pruett-Jones (1983) in a comparison of nine polygamous species of birds of paradise, found a significant relationship between male dispersion and diet. Obligate insectivores defended exclusive territories, while obligate frugivores formed leks. This suggests that an important factor influencing the evolution of lek behaviour in polygamous tropical passerines is also due in part to fruit-eating. Beehler and Pruett-Jones gave no explanation as to how, or why obligate frugivory could assist in lek maintenance, but I suggest the following: (i) for a male to be effective within a lek (i.e attempt to maximise copulations), time at the lek must be maximised, (ii) time away from the lek feeding must therefore be minimised, (iii) fruits are abundant, conspicuous and easy "prey" by comparison to insects (Snow 1981), thereby minimising feeding times and maximising the time they are available to display.

1.2.3.3 Temporal dispersion and Site fidelity

The Cotingas, whether in leks or exploded leks, tend to persist at known sites from year to year, as long as the bird and the surrounding forest remain intact (Snow 1982). The Golden-collared Manakin (*Manacus vitellinus*) has been observed to use the same lek site on Barro Colorado Island since 1935, some 47 years (Chapman 1935, Worthington 1982). Within lek systems, some male Tooth-bills (*Scenopoeetes dentirostris*), have been recorded using the same court site for 13 years (Frith and Frith unpub.). Although much of the data is scant and anecdotal, it suggests that leks and exploded leks are traditional sites persisting in time and space (Table 1.1).

Researchers have been attracted to the bird families listed above because of their spectacular plumage and breeding behaviour, rather than the dispersal service they may provide to plants by their use of traditional sites. Whether or not these services are beneficial to seeds dispersed is unknown, but because display sites are traditional, a record of seed dispersal effectiveness, or otherwise may be encapsulated within these sites.

TABLE 1.1 Spatial dispersion, diet and display site constancy, for male lek and exploded lek displaying tropical rainforest birds.

Species and common name	# males[1]	IMD[2]	Diet[3]	Years[4]	Display[5]	Source
A. Species known to have exploded lek breeding systems						
Family Cotingidae						
Lipaugus vociferans Screaming Piha	4-30	40-60	F/I	*	SC/P	Snow (1982)
Cephalopterus glabricollis Bare-necked Umbrellabird	4	?	F	*	SC/P/R	Snow (1982)
Procnias averano Bearded Bellbird	3-4	100	F	*	E/P/V	Snow (1982)
P. nudicollis Bare-throated Bellbird	?	?	F	*	E/P/V	Snow (1982)
P. alba White Bellbird	?	?	F	*	E/P/V	Snow (1982)
P. tricarunculata Three-wattled Bellbird	?	?	F	*	E/P/V	Snow (1982)
Family Paradisaeidae						
Parotia wahnesi Wahnes' Parotia	?	?	?	*	G/C	Gilliard (1969)
P. sefilata Western Parotia	?	?	F	*	G/C	Gilliard (1969)
P. helenae	?	?	?	*	G/C	Gilliard (1969)
P. carolae Carola's Parotia	?	?	F	*	G/C	Gilliard (1969)
P. lawesii Lawes' Parotia	25	77[1] 5-350	95F	*	G/C	Beehler and Pruett-Jones (1983)
Pteridphora alberti	?	400	80F	*	C/P	Gilliard (1969)
Circinurus regius	?	50?	F	*	C/P	Gilliard (1969)
Paradisea decora Goldie's Bird of Paradise	?	?	F	*	E/P	Gilliard (1969)
Family Ptilonorhynchidae						
Scenopoeetes dentirostris Tooth-billed Bowerbird	30+	44-49	99F	13	C/G/R	Frith and Frith (unpub.), Crome and Moore (1989)
Archboldia papuensis Archbolds' Bowerbird	?	?	F	*	B/G	Gilliard (1969)
Amblyornis flavifrons Golden-fronted Bowerbird	?	?	F	*	B/G	Gilliard (1969)
A. macgregoriae McGregors'Bowerbird	42	75- 348	F	*	B/G	Pruett-Jones and Pruett-Jones (1982)
A. subalaris Streaked Bowerbird	?	?	F	*	B/G	Gilliard (1969)
A. inornatus Vogelkop Bowerbird	?	?	F	*	B/G	Gilliard (1969)
Prionodura newtonia Golden Bowerbird	20	200	95F	13	B/G	Frith and Frith (pers. comm.)
Sericulus aureus Golden Regent Bowerbird	?	?	F/I	*	?	Gilliard (1969)
S. bakeri Adelbert Regent Bowerbird	?	?	F/I	*	?	Gilliard (1969)

Species and common name	# males[1]	IMD[2]	Diet[3]	Years[4]	Display[5]	Source
S. chrysocephalus Australian Regent Bowerbird	?	?	F/I	*	?	Gilliard (1969)
Ptilonoryhnchus violaceous Satin Bowerbird	4	70	95F	*	B/G	Gilliard (1969)
B. Species known to have true lek breeding systems						
Family Cotingidae						
Phoenicircus nigricollis Red Cotinga	12	?	F	*	E/P	Snow (1982)
Tijuca atra Black and gold Cotinga *T. condita* Grey-winged Cotinga	1-3	0-10	F	*	E/P	Snow (1982)
Pyroderus scutatus Red-ruffed Fruit-crow	<=10	3m	F/I	*	SC/P	Snow (1982)
Perissocephalus tricolor Calfbird, Capuchinbird	4	0.15-15	F/I	*	SC/P	Snow (1982)
Rupicola rupicola Guianan Cock-of-the-Rock	5-10 to 55	1-10	F	*	G/C	Snow (1982), Trail (1985)
R. peruviana Andean Cock-of-the-Rock	6	6-9	F	*	SC/P	Snow (1982)
Family Pipridae						
Manacus vitellinus Golden-collared Manakin	?	?	F	47	SC/P	Worthington (1982), Chapman (1935),
P. mentalis ignifera Red-capped Manakin	?	?	F	*	SC/P	Worthington (1982)
M. manacus White-bearded Manakin	6-60	0.1-1	F	10	G/C	Snow (1962b), Lill (1974a,1974b)
P. erythrocephala Golden-headed Manakin	?	?	?	*	?	Lill (1976)
Family Paradisaeidae						
Semioptera wallacei Wallace's Standard Wing	?	?	75F	*	?	Cooper and Forshaw (1977)
Astrapia stephaniae Stephanie's Astrapia	?	?	85F	*	E/P	Schodde (1976)
Paradisaea apoda Greater Bird of Paradise	?	?	?	*	E/P	Gilliard (1969)
P. raggiana Raggiana Bird of Paradise	4-6	?	90F	*	E/P	Beehler (1983), Beehler and Pruett-Jones (1983)
P. minor Lesser Bird of Paradise	?	?	?F	*	R/P	Beehler and Pruett-Jones (1983)
P. rubra Red Bird of Paradise	?	?	?F?I	*	E/P	Gilliard (1969)
P. guiliemi Emperor Bird of Paradise	?	?	?F	*	E/P	Cooper and Forshaw (1977)

[1] #males: Number of males in an aggregation, [2] IMD: Inter-male distance within a display site (m), [3] Diet:(x) percentage of F=Fruit, I=Insects, [4] Years=number of years display site known to be active: (*) Anecdotal evidence of traditional site use. [5] Display: Display area, G=Ground, SC=Subcanopy, C=Canopy, E=Emergent,/ P=Song Perch, B=Bower, C=court,/ R=Ridge, H=Hilltop, V=Valley, ?=Unknown

1.3 SEED DISPERSAL: THE CONSEQUENCES

> " A plant population that is found growing at a point in time and space is the consequence of a catena of past events. The climate and substrate provide the scenery and the stage for a cast of plant and animal players to come and go. The cast is large and many members play no part, remaining dormant. The remainder act out a tragedy dominated by hazard, struggle and death in which there are few survivors."
>
> Harper (1977)

These words describe better than most, the complex interplay between a plant community and its biotic and abiotic environment. A seed dispersal event determines the site at which a plant must germinate, establish, grow and ultimately all going well, reproduce. The potential mortality factors from seed to adult are vast, with biotic factors including, seed and seedling predation, pathogens, intracohort competition, interspecific competition and allelopathy to name a few. Compounding these are the ever present random abiotic factors including disturbance, physical damage, light, microhabitat, micronutrients and water availability. All these differ in importance in time and space, but the cumulative effects determine the survivors.

1.3.1 Survival in clumps: the debate

Twenty years ago, Janzen (1970) and Connell (1971) proposed that density and/or distance dependent mortality beneath the parent tree would be extreme relative to areas beyond the parent crown. They proposed that density dependent agents including host specific seed and seedling predators and pathogens would result in disproportionately high mortality beneath the parent crown. Similarly, distance responsive agents might search immediately beneath the parent crown ignoring seeds and seedlings only metres away (Janzen 1970). The Janzen-Connell model or "escape hypothesis" became a paradigm with almost no empirical evidence to support it and suggested that seed dispersal in clumps was ineffective (Howe and Smallwood 1982, Clark and Clark 1984, Howe 1989).

Hubbell (1980), disputed the model, pointing out that even extremely low survival beneath the parent tree would still result in a greater proportion of recruits due to the greater initial progeny densities within these sites.

Clark and Clark (1984), evaluated the Janzen/Connell model in a review of 24 data sets on tropical woody plants. They found that most studies demonstrated evidence of density and/or distance dependent progeny mortality about the parent tree. They also found some evidence for the minimum critical distance effect (i.e. total mortality within some critical distance of the parent tree). However, in most studies it was not possible to rule out the influence of either allelopathy or intracohort competition, as distinct from the predators or pathogens central to the Janzen/Connell model (Clark and Clark 1984).

1.3.2 Patterns of seed dispersal, consequences and Howe's model

Patterns of seed dispersal vary in a continuum from seeds scattered as single isolated individuals to dense seed clumps. Howe (1989), hypothesised that different plant species should have evolved different seed and seedling demographic traits determined by their predominant mode of seed dispersal. Howe (1989) proposed that scatter-dispersed plant species would recruit as isolated individuals, and were unlikely to evolve exceptional resistance to herbivores, pathogens or other sources of density dependent seed or seedling mortality. Conversely, clump-dispersed plant species, would tend to germinate and grow in high densities and as a consequence are likely to have evolved chemical and/or mechanical defences against density dependent mortality agents.

Howe further suggested that population and genetic attributes should reflect this dichotomy in conditions of recruitment. He predicted that scatter-dispersed species would rarely survive as seedlings in clumps, beneath frugivore roosts or beneath the parent tree, and that seed dispersal to light gaps or other specific microsites would be necessary. As a result, adults and juveniles would be outbred, exist at low densities in loose aggregations or be randomly distributed. In contrast, clump-dispersed species should be adapted for survival as seedlings in high densities beneath the parent tree or in faecal clumps, and adult and juveniles should be inbred, common, and highly aggregated.

1.3.3 Survival in clumps: the evidence

In a review of 83 individual test cases, including: seeds, seedlings and saplings stages, evidence of disproportionate mortality and total mortality within clumps was evaluated (Table 1.2). In their review of mortality about adult trees, Clark and Clark (1984) separated the effects of distance and density dependent mortality. The problem with this is that the two are not mutually exclusive (Harper 1977, Clark and Clark 1984). Further, the relative affects of distance and/or density dependant mortality agents, such as seed predators or pathogens, are difficult to isolate from allelopathy or intra-cohort competition (Clark and Clark, 1984). Harper (1977) commented that " Neither plants nor animals react to their populations, but to the effects of the number and proximity of their neighbours. The term "density" is an abstraction removed from the level of cause and effect". In this review, the mechanisms of mortality are not evaluated, instead I ask the question, is there any evidence of disproportionate mortality, or total mortality in clumps relative to areas outside these circumstances?

I have classified three clump types: (i) parent tree clumps, for seeds and seedlings present in high densities beneath the parent tree, (ii) animal dispersed clumps, where seeds and seedling are in dense animal dispersed faecal clumps, or caches and (iii) artificial or man made clumps. Even though these clumps differ in magnitude, they are subject to the same effects relative to scattered seeds and seedlings on the forest floor. An animal dispersed clump is subject to the ravages of intracohort competition, and density dependent mortality agents. In addition a parent tree clump is subject to distance responsive agents and allelopathy. Other factors of note, are that animal dispersed clumps contain seed with testa variously scarified and the pericarp variously removed. Clumps beneath the parent tree, in contrast, may contain both intact fruits and ingested seed.

Table 1.2 summarises evidence of disproportionate mortality and total mortality in clumps (equivalent to minimum critical distance (Clark and Clark 1984)) for the early life stages of tropical woody plants.

TABLE 1.2: Evidence of disproportionate mortality and total mortality of seeds, seedlings and saplings in clumps in tropical forests.

Reference	Species	Reg[1]	Type[2]	Gro[3]	Dis4	CL[5]	DS[6]	MA[7]	EDD[8] /TM[9]
	SEEDS								
Janzen (1970)	*Huberodendron allennii*	Neo	Wet	T	?	P	?	?	+/?
Connell (1971)	*Cryptocarya corrugata*	Aus	Wet	T	B	P	S	?	?/?
Janzen (1972b)	*Sterculia apeltata*	Neo	Dry	T	?	P	S	?	?/-
Wilson and Janzen (1972)	*Sheelea rostrata*	Neo	Dry	P	M	P	S	I	+/-
Janzen (1975 in Connell, 1979)	*Spondias mombin*	Neo	Dry	T	?	P	?	?	-/-
Janzen *et al.*(1976)	*Andira inermis*	Neo	Dry	T	M	P/C	S	I	+/+
Silander (1978)	*Cassia biflora*	Neo	Dry	S	?	P	?	?	-/?
Howe (1980)	*Tetragastris panamensis*	Neo	Wet	T	M	P	C	?	-/-
Boucher (1981)	*Quercus oleoides*	Neo	Dry	T	M	P	?	A	+/-
Janzen (1982b)	*Enterolobium cyclocarpum*	Neo	Dry	T	M	C	?	M	+/-
Howe (1983)	*Virola surinamensis*	Neo	Mst	T	B	C	S	I	+/+
Wright (1983)	*Scheela zoenensis*	Neo	Mst	P	M	P	S	I	+/-
Becker and Wong (1985)	*Aglaia sp.*	Mal	Wet	T	B	P	S	?	+/+
Howe *et al.*(1985)	*Tetragastris panamensis*	Neo	Mst	T	M	P	C	?	-/-
Howe (1986)	*Virola surinamensis*	Neo	Mst	T	B	C	S	I	+/+
Schupp (1988a)	*Faramia occidentalis*	Neo	Wet	T	M	P	C	M	-/-
Schupp (1988b)	*Faramia occidentalis*	Neo	Wet	T	M	P	C	M	-/-
Howe (1989)	*Tetragastris panamensis*	Neo	Mst	T	M	P	C	?	-/-
Kitajima and Augspurger (1989)	*Tachigalia versicolor*	Neo	Wet	T		?	?	?	?/?
Schupp and Frost (1989)	*Welfia georgii*	Neo	Mst	P	M	P	S	M	+/-
Howe (1990)	*Virola surinamensis*	Neo	Mst	T	B	P/C	S	M/I	+/+
	Tetragastris panamensis	Neo	Mst	T	M	P/C	C	?	-/-
	SEEDLINGS								
Connell (1971)	Many species	Aus	Wet	T	?	P	?	?	+/?
	Planchonella sp.	Aus	Wet	T	M	P	S	M	-/-
	Eugenia brachyandra	Aus	Wet	T	B	P	C	?	+/-
Janzen (1971)	*Dioclea megacarpa*	Neo	Dry	T	?	P	?	I	+/+
Janzen (1972a)	*Euterpe megacarpa*	Neo	Wet	T	?	P	?	I	?/-

Reference	Species	Reg^1	Type^2	Gro^3	Dis^4	CL^5	DS^6	MA^7	EDD^8 /TM^9
Howe and Primack (1975)	*Caesaria nitida*	Neo	Wet	T	?	P	S	?	+/-
Howe (1977)	*Caesaria corymbosa*	Neo	Wet	T	?	P	S	?	+/+
Vandermeer (1977)	*Welfia georgii*	Neo	Wet	P	M	P	S	L	+/?
Connell (1979)	*Eugenia brachyandra*	Aus	Wet	T	B	P	?	?	-/-
Chan (1980)	*Shorea spp.*	Mal	Wet	T	W	P	S	?	+/?
Denslow (1980a)	*Bombacaceae*	Neo	Wet	T	?	P	S	?	+/+
Howe (1980)	*Tetragastris panamensis*	Neo	Mst	T	M	P/C	C	?	-/-
Clark and Clark (1981)	*Bursera graveolens*	Neo	Dry	S	?	P	?	?	+/-
Augspurger (1983a)	*Platypodium elegans*	Neo	Mst	T	W	P	S	?	+/+
Augspurger (1983b)	*Platypodium elegans*	Neo	Mst	T	W	P	S	?	+/+
Davidar (1983)	*Loranthaceae*	Neo	Mst	P	B	C	C	?	+/-
Howe (1983)	*Virola surinamensis*	Neo	Mst	T	B	C	S	M/I	+/+
Wright (1983)	*Scheela zonnensis*	Neo	Mst	P	M	P	S	?	?/-
Augspurger (1984)	*Triplaris cumingiana*	Neo	Wet	T	W	P	S	?	-/-
	Lochnocarpus pentaphyllus					P	S	P	+/+
	Aspidosperma cruenta					P	S	?	-/-
	Cordia alliodora					P	S	?	-/-
	Terminalia oblonga					P	S	P	+/+
	Platypodium elegans					P	S	P	+/+
	Cavanillesia platanifolia					P	S	P	+/+
	Tabebuia rosea					P	S	?	-/-
	Ceiba pentandra					P	S	?	-/-
Augspurger and Kelly (1984)	*Platypodium elegans*	Neo	Wet	T	W	C	S	P	+/+
	Lafoensia punicifolia					C	S	P	+/+
	Pseudobombax septenatum					C	S	P	+/+
	Triplaris cumingiana					C	S	P	+/+
	Luehea seemannii					C	S	P	+/+
	Tababuea rosea					C	S	P	+/+
	Cordia alliodora					C	S	?	-/-
	Aspidosperma cruenata					C	S	?	-/-
	Terminalia oblonga					C	S	?	-/-
	Terminalia amazonica					C	S	?	-/-
	Ochroma pyramidale					C	S	?	-/-
	Cochlospermum vitifolium					C	S	?	-/-
	Ceiba pentandra					C	S	?	-/-
Clark and Clark (1984)	*Dipteryx panamensis*	Neo	Mst	T	M	P	S	M	+/+
De Steven and Putz (1984)	*Dipteryx panamensis*	Neo	Mst	T	M	P	S	M	+/-

Reference	Species	Reg[1]	Type[2]	Gro[3]	Dis4	CL[5]	DS[6]	MA[7]	EDD[8] /TM[9]
Becker and Wong (1985)	*Aglaia sp.*	Mal	Wet	T	B	P	S	?	+/+
Howe *et al.*(1985)	*Virola surinamesis*	Neo	Mst	T	B	P/C	S	I/M	+/+
Sork (1985)	*Gustavia superba*	Neo	Mst	T	M	A	C	M	-/-
Howe (1986)	*Virola surinamensis*	Neo	Mst	T	B	P/C	S	I/M	+/+
Clark and Clark (1987)	*Dipteryx panamensis*	Mal	Mst	T	M	P	S	M	+/+
Sork (1987)	*Gustavia superba*	Neo	Mst	T	M	P	C	M	?/?
Schupp (1988a)	*Faramia occidentalis*	Neo	Wet	T	M	P	C	M	+/-
Schupp (1988b)	*Faramia occidentalis*	Neo	Wet	T	M	P	C	M	-/-
Howe (1989)	*Tetragastris panamensis*	Neo	Mst	T	M	P	C	?	-/-
Kitajima and Augspurger (1989)	*Tachigalia versicolor*	Neo	Mst	T	?	P	?	?	-/-
Reid (1989)	Loranthaceae	Aus	Dry	P	B	C	C	?	+/-
Howe (1990)	*Virola surinamensis*	Neo	Mst	T	B	C,P	S	M	+/+
	Tetragatris panamensis	Neo	Mst	T	M	C,P	C	?	-/-
Dinerstein and Wemmer (1988)	*Trewia nudiflora*	Mal	Dry	T	M	C	C	?	+/-
	SAPLINGS								
Hubbell (1979)	Many tree species	Neo	Mst	T	?	P	?	?	?/-
Connell et al. (1984)	Many tree species	Aus	Wet	T	?	P	?	?	-/-
Hubbell and Foster (1986)	Many tree species	Neo	Mst	T	?	P	?	?	-/-
Hubbell and Foster (1990)	Many tree species	Neo	Mst	T	?	P	?	?	+/-

CODES:
[1]Reg= Biogeographic region: Neo=Neotropics, Aus=Australasian, Mal=Malaysian
[2]Type = Forest Type: Wet, Mst=Moist, Dry
[3]Gro = Growth Form: T=Tree, S=Shrub, V=Vine, P=Parasite
[4]Dis = Seed Dispersal: W=Wind, B=Bird, M=Mammal
[5]CL= Clump Type: P=Parent tree clump, C=Animal dispersed, A=Artificial
[6]MA = Mortality Agent: I=Insect infestation, R=Rodent, A=Animals, P= Pathogens, L=Litter-fall, ?=Unknown
[7]EDD = Evidence of disproportionate mortality in clumps: (+)=yes, (-)=No, (?)=Unknown
[8]TM = Evidence of total mortality in a clump: (+)=yes, (-)=No, (?)=Unknown

1.3.3.1 Seeds

At the seed stage, 50% of cases demonstrated disproportionate mortality in clumps, 36.4% demonstrated no response, while the remainder are questionable (Table 1.2, 1.3 below). Mammalian seed predators (Janzen 1982a, Howe 1986, 1989, Schupp and Frost 1989) and weevil infestations (bruchidae), (Wilson and Janzen 1972, Janzen 1976, Howe 1983, 1986, 1990) were extremely effective mortality agents in a number of studies. The influence of pathogens on seeds has not been assessed and may also be high (Augspurger 1990).

1.3.3.2 Seedlings

At the seedling stage 61.4% of cases showed disproportionate mortality in clumps, 33.3% no clear response, while the remaining 5.3% are unknown (Tables 1.2 and 1.3). At the establishment and seedling stage, plant pathogens are extremely effective mortality agents (Augspurger 1983a, 1983b, 1984, Augspurger and Kelly 1984). Some evidence also exists for mortality by mammalian herbivores (Sork 1985, 1987, Schupp 1988a, 1988b, Howe 1990) and insect herbivores (Janzen 1971, 1972b, Howe 1983, Howe *et al.* 1985).

TABLE 1.3: Summary of density dependent and total mortality of seeds seedlings and saplings in clumps. Codes (+)= positive evidence, (-)=No evidence, (?)=Unknown.

	Density dependent mortality			Total mortality in clumps			
Stage	(+)	(-)	(?)	(+)	(-)	(?)	Total
Seed	11	8	3	5	13	4	22
	(50)	(36.4)	(13.6)	(22.7)	(59.1)	(18.2)	
Seedling	35	19	3	22	30	5	57
	(61.4)	(33.8)	(5.3)	(38.6)	(52.6)	(8.7)	
Sapling	1	2	1	4	0	0	4
	(25)	(50)	(25)	(100)	(0)	(0)	
Total	47	29	7	31	43	9	83

1.3.3.3 Saplings

Disproportionate mortality of saplings in clumps (i.e. evidence of density dependent mortality), has been identified for saplings, but responses were variable between locations and census dates (Hubbell and Foster 1990).

1.3.3.4 Consistent responses within a species

Some responses observed were consistent within a species. *Virola surinamensis* and *Platypodium elegans* suffered consistent density dependent mortality and total mortality within clumps between years and sites (Howe 1983, 1986, 1990). Similarly, *Tetragastris panamensis* suffered less mortality, and consistently survived in clumps (Howe 1980, 1990). These examples support Howe's predictions for dispersal syndromes outlined earlier, with *Platypodium* and *Virola* exhibiting responses expected of members of the scatter-dispersal syndrome, and *Tetragastris* exhibiting responses expected of a member of the clump dispersal syndrome (Howe 1989).

1.3.3.5 Inconsistent responses within a species

Some mortality responses, however, are inconsistent within a species. *Gustavia superba* suffered heavy mortality in some sites and not in others (Sork 1987). Similarly, *Faramia occidentalis* suffered dramatically different mortality levels between years due to differences in community fruit production, and generalist predators being distracted by other plant species (Schupp 1988a 1988b).

1.3.3.6 Total mortality in clumps

Finally, disproportionate mortality in clumps, does not necessarily result in 100% mortality within a clump. Within the Loranthaceae, density dependent mortality of seeds and seedlings occurs, but Mistletoes still festoon trees (Davidar 1983, Reid 1989). In some rainforest species conspecific juveniles tolerate conditions beneath the parent crown, and may invade the canopy by tree-by-tree replacement (Hart *et al.* 1989, Connell and Lowman 1989). Though mortality in clumps may be high, the survival of a single individual within a clump may be equivalent to effective dispersal both in clumps and beneath adult conspecifics.

1.3.4 Abiotic factors: Density independent

Compounding any disproportionate mortality in clumps by density and/or distance responsive biotic mortality agents are an enormous diversity of density independent abiotic factors, outlined below.

1.3.4.1 Small-scale disturbances

Small-scale disturbances that result in the significant mortality of seedlings may include litterfall (Vandermeer 1977, Brokaw 1985, Lieberman *et al.* 1985, Clark and Clark 1987), branchfall and treefall (Uhl 1982, Kiew 1986, Aide 1987, Martinez-Ramos *et al.* 1988), and trampling and uprooting by understorey vertebrates (Clark and Clark 1989, Clark 1990).

1.3.4.2 Light gaps

As a consequence of leaf, branch and tree-fall, holes occur in the rainforest canopy allowing light to penetrate to the forest floor. Light is probably the single most important factor affecting the long term survival and growth of seedlings (Denslow 1987). On average, the rainforest floor receives only 1-2% incident sunlight (Chazdon and Fetcher 1984). The light regime in which a seedling survives and grows is dependent on its species specific shade tolerance, with tolerance ranging from shade tolerant plants, which survive beneath the canopy, to big gap or pioneer species which only grow in large light gaps (Denslow 1980b, 1987). Estimates of forest turnover rates (the mean time between successive gaps) ranges from 80-136 years, resulting in 0.7-1.2% of a forest area being converted to canopy gaps annually (Hartshorn 1978, Brokaw 1982). Gaps generally form at random spatially, and this means that at any point in time only a very small component of the forest is floor provides a suitable light environment for recruitment and growth. Closure rate of gaps vary with gap size. In large canopy gaps formed by treefalls, gaps close by both ingrowth from the canopy margins, and upward growth from the saplings below (Denslow 1987). This means that within primary forests, seedlings and saplings may require more than one gap formation event to reach the canopy.

1.3.4.3 Soil nutrients

Within treefall gaps, there are differences in soil nutrients. In general, nitrates and phosphates are lower in the root zone than in the crown and bole zones (Vitousek and Denslow 1986). Similarly, species specific gap zone preferences have been exhibited by a number of plant species (Barton 1984, Brandani *et al.* 1988). Thus even in small canopy gap areas, suitable recruitment "safe sites" for some species may be restricted to even smaller areas, like a canopy gap.

1.3.4.4 Major disturbances

Major disturbances to tropical rainforest system can occur in the form of (i) cyclones, where extensive canopy openings may be formed (Crow 1980, Hopkins and Graham 1987), (ii) smaller windstorms where large multiple tree, treefall gaps form (Foster and Brokaw 1982), (iii) floods, such as the flooded forests of the Amazon basin (Pires and Prance 1985, Goulding 1988), (iv) droughts and fire associated with El Nino, (Sanford *et al.* 1985, Beaman *et al.* 1985), or (v) landslides, as documented in Panama (Garwood *et al.* 1979).

The abiotic factors detailed above include only a subset of those available. But what this brief review emphasises is the diversity and variation in potential mortality factors affecting every life stage of a rainforest plant. The significance of this enormous variability is discussed below.

1.4 DISCUSSION

1.4.1 The noise inherent in the system.

Patterns of progeny mortality in clumps in tropical rainforests are enormously variable. Howe's (1989) model of seed dispersal syndromes is supported by some of the evidence, with consistent mortality in clumps for *Platypodium* and *Virola* (scatter dispersal syndrome), and consistent survival in clumps for *Tetragastris* (clump dispersal syndrome). However, other species, such as *Gustavia superba* and *Faramia occidentalis*, exhibit different responses between sites and years. The inherent noise within the system may mean that given the right circumstances, even scatter-dispersed species may survive in clumps. Disproportionately high mortality in clumps certainly occurs, but in many cases, total loss does not follow (*sensu* Hubbell effect).

This tendency for extremely low survival in clumps is still effective survival. The circumstances described here for seeds in animal dispersed clumps is equivalent to that described by Hubbell (1980) for parent trees. Importing large numbers of seeds to a specific site on the forest floor is equivalent to large seed input beneath a parent tree. With proportionally high numbers of seeds to start with, even with high losses, recruitment within these sites may still be higher than elsewhere.

The major factor limiting recruitment in tropical rainforest is the availability of "safe sites" light gaps (Denslow 1980b, 1987). Although in reality a continuum, regeneration strategies of rainforest trees can be placed in three general categories: (i) shade intolerant, large-gap specialists or pioneer species whose seeds germinate in high temperature and high light conditions of large gaps, (ii) small gap specialists whose seeds germinate in the shade but require the presence of a gap for growth into the canopy, and (iii) shade tolerant, understorey specialists that survive in the absence of a canopy gap, and germinate and grow to reproductive size through sun fleck activity (Denslow 1980b). Annually seeds of many plant species are broadcast in a complex mosaic across the forest floor, and each year, most die (Cook 1979). The availability of canopy gaps to enable the germination, survival or growth of those seeds, seedlings and saplings below is the primary driving force of rainforest dynamics. Seed dispersal merely increases a plants chances of hitting a safe site in a constantly changing mosaic.

1.4.2 Bird/Plant interactions

The evolution of lek breeding systems by some frugivorous bird species, that persist in time and space, has profound ramifications on plant species dispersed. This behaviour results in an enormous numbers of seeds being deposited in clumps at very specific focal sites year after year. Given this, there are a number of seed and seedling recruitment scenarios for any plant species deposited in these sites: (i) if seed and seedling mortality is density dependent, and total mortality occurs within these sites, then no recruitment will occur, (ii) if seed and seedling mortality is density independent, then some plant species may establish and flourish at these sites. Even with density dependent mortality, some individuals may still survive (*sensu* the Hubbell effect; Hubbell 1979).

Secondary seed dispersal is also possible. Many of these lek breeding birds locate their display sites at the tops of ridges. In heavy rains, common in tropical rainforests, it is possible and probable that sheet runoff from ridges results in the dispersal of many seeds from clumps down slopes. This may counter some density dependent losses. Similarly many rodent seed predators work these seed piles, and may scatter hoard seeds which may also result in recruitment.

The persistence of the leks themselves implies dependence on the plants. In order for lek breeding males to achieve reproductive success they must persist at lek sites. This may only be possible by the close proximity of an abundant and nutritious food supply, fleshy fruits. To maximise display times, males must minimise feeding times. Some male manakins have been recorded spending only 8-10% of daylight hours foraging, with some forays less than one minute (Snow 1962a, 1962b, Foster 1977b, Worthington 1982). By consistently freighting preferred food plant species to lek sites, birds may increase the abundance of a selected food plant in the immediate area. The benefit of this dispersal system to the lek is not immediate but long term. The obvious long term benefit of this would be to decrease male foraging time, and increase lek cohesion. The persistence of lek sites may provide some evidence that bird/plant interactions in tropical rainforests are more than loose associations (Wheelwright and Orians 1982). The above scenario is only speculative and, in the absence of data, it is impossible to evaluate the effectiveness of lek breeding birds as seed dispersers. This is one of the areas that will be investigated in this study.

1.5 AIMS OF THIS STUDY

The primary aim of this study was to evaluate the effectiveness of clump seed dispersal by male Tooth-bills and attempt to bridge the gap between seed dispersal and potential advantages or disadvantages conferred to plants consumed. The study was conducted in two sections detailing the processes of seed dispersal (the bird perspective) and then examining the consequences of these processes (the plant perspective). Patterns of survival and recruitment within clumps was then compared with current models: The Janzen (1970)/Connell (1979) or "escape hypothesis", the Hubbell (1979) model and the Howe (1989) model.

The processes of seed dispersal by male Tooth-bills explored three areas:

i) What fruits were available to avian seed dispersers and when were they available (phenologies)?
ii) What was the seed dispersal service provided by birds (seed dispersal)?
iii) What fruits do the birds choose from the suite that was available (diet)?

The consequences of seed dispersal by male Tooth-bills examined the following areas:

i) Were the seeds deposited by the birds viable and did ingestion inhibit or enhance germination responses (germination)?
ii) Once deposited by the bird, how did survival within the faecal clumps compare with other microsites on the forest floor (seed predation)?

iii) Of the plant species dispersed by the bird, which germinated, established and grew, and how did survival and growth in faecal clumps compare with other microsites on the forest floor?
iv) What plant species established within these sites as seedlings and saplings and what were the recruitment patterns of these species?

1.6 THESIS OUTLINE

The thesis can be divided into the two main areas of investigation: (i) the processes of seed dispersal by male Tooth-bills, and (ii) the consequences for the plant species being dispersed.

1.6.1 The processes of seed dispersal (The bird perspective)

Chapter Two describes (i) climate, study sites, forest type, (ii) details the behaviour, ecology and distribution of male Tooth-bills, and (iii) the distributions of canopy gaps, and how they relate to Tooth-bill court sites. These parameters provide the temporal and spatial framework of the study.

Chapter Three describes the fruiting phenology of the forest, detailing temporal variation in fleshy fruit abundance and avian seed dispersal.

Chapter Four examines the seed dispersal process of male Tooth-bills, detailing the nature of foraging bouts, and the patterns of seed deposition of the plants consumed.

Chapter Five details the diet of male Tooth-bills, or seeds dispersed over three display seasons, and compares fruit availability with fruit consumed.

1.6.2 The consequences of seed dispersal (The plant perspective)

Chapter Six enumerates the germination response of plant species consumed and dispersed by male Tooth-bills.

Chapter Seven examines patterns of seed predation for seeds deposited near Tooth-bill courts compared to other microsites on the forest floor.

Chapter Eight examines seedling growth and survival and seedling and sapling composition in and about male Tooth-bill courts, to assess their effectiveness as seed dispersers, and to determine the possible recruitment processes at these microsites.

Finally, Chapter Nine, the general discussion, assesses the overall effectiveness of clump seed dispersal by male Tooth-bills and examines the recruitment patterns observed, comparing them with current models detailing recruitment in clumps.

Chapter Two

CLIMATE, STUDY SITE, SPECIES AND DISTRIBUTIONS OF TOOTH-BILLS AND CANOPY GAPS

2.1 CLIMATE

The study site at Paluma, in the Mount Spec region, is located at the southern end of Australia's Wet Tropics. The area is isolated from the main forest block to the north by the Herbert River gorge and drier forest areas of Mount Fox and the Coen Ranges. Rainforest dominates the cap of the ranges from an elevation of 400m to 1000m.

Rainfall data for the area was obtained from a meteorological sub-station located 7km SE of the study area in the Paluma township. Rainfall and temperature data were also obtained from (Anon 1990, Tracey 1982). The area is highly seasonal, characterised by a distinct warm wet and cool dry seasons (Fig 2.1a,b). Temperatures above 800m remain mild, rarely exceeding 30°C or falling below 10°C (Fig 2.1a). Average annual rainfall, obtained from 32 years of records was 3169 mm, with 73% of rain falling during the wet season from December to March (Tracey 1982), (Fig 2.1b). The average number of rain days per year was 81. Rainforests above 800m were also subject to additional moisture input from cloud mists. Seasonal fluctuations in rainfall between years are detailed in Chapter Three (Fig 3.1).

2.2 STUDY SITES, VEGETATION AND LOGGING HISTORY

This study was conducted in State Forest 268, in an area of simple notophyll vine forest (SNVF) (Tracey 1982) at an elevation of 875m near the township of Paluma, North

Queensland (19°00'S, 146°10'E) (Fig 2.2). Two 10ha sites were chosen (one logged and the other unlogged), within a 50ha grided site established for avian ecological studies by Cliff and Dawn Frith (pers. comm.) (Fig 2.2).

Simple notophyll vine forest (SNVF), is the dominant forest type occurring on granitic soils at elevations from 400-1000m (Tracey 1982). The canopy surface is relatively even, from 24-33m, with occasional emergents of *Cardwellia sublimis*, *Planchonella euphlebia*, *Acmena resa* and *Syzygium wesa* (Power 1987, pers. obs.). Emergents often support the strangler fig, *Ficus destruens*, particularly *Acmena resa* and *Syzygium wesa* (Tracey 1982, pers. obs.). This forest type is classified as "pole forest" as girth sizes, with the exception of emergents, tend to be uniform and plant species with plank buttresses are rare (Tracey 1982).

Most of the 50ha grid was logged 30 years ago, with the exception of the 10 hectare unlogged site (Frith and Frith pers. comm.). Visible evidence of logging includes the presence of large pioneer species such as *Alphitonia petrei* within the forest and a dense understorey growth of saplings and smaller trees (pers. obs.). Favoured timber trees removed from the logged site included, *Cardwellia sublimis* (Northern Silky Oak) and *Flindersia pimenteliana* (Maple Silkwood) (Frith and Frith pers. comm.). Both of these are wind dispersed species.

Fig 2.1a

Mean monthly temperature range for Paluma (mean minimum to mean maximum)

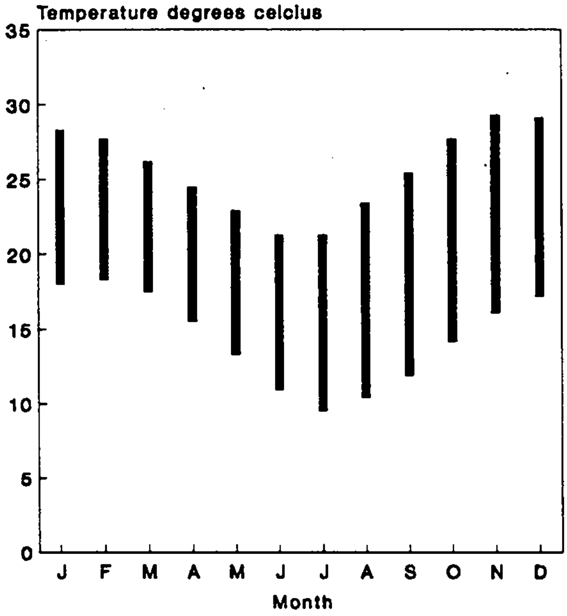
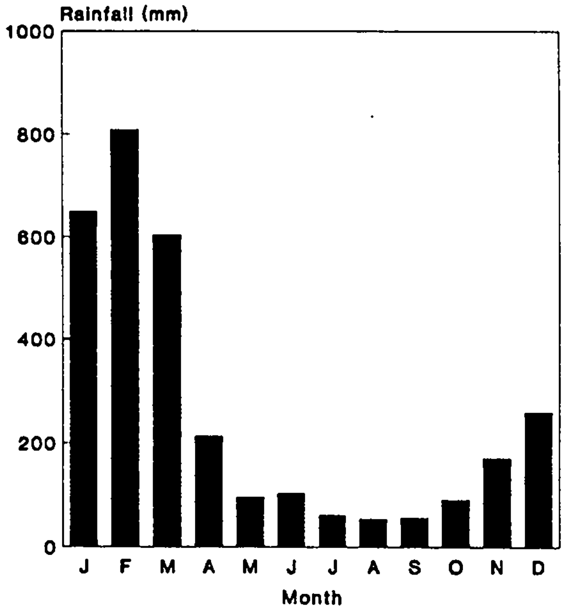


Fig 2.1b

Mean monthly rainfall for Paluma

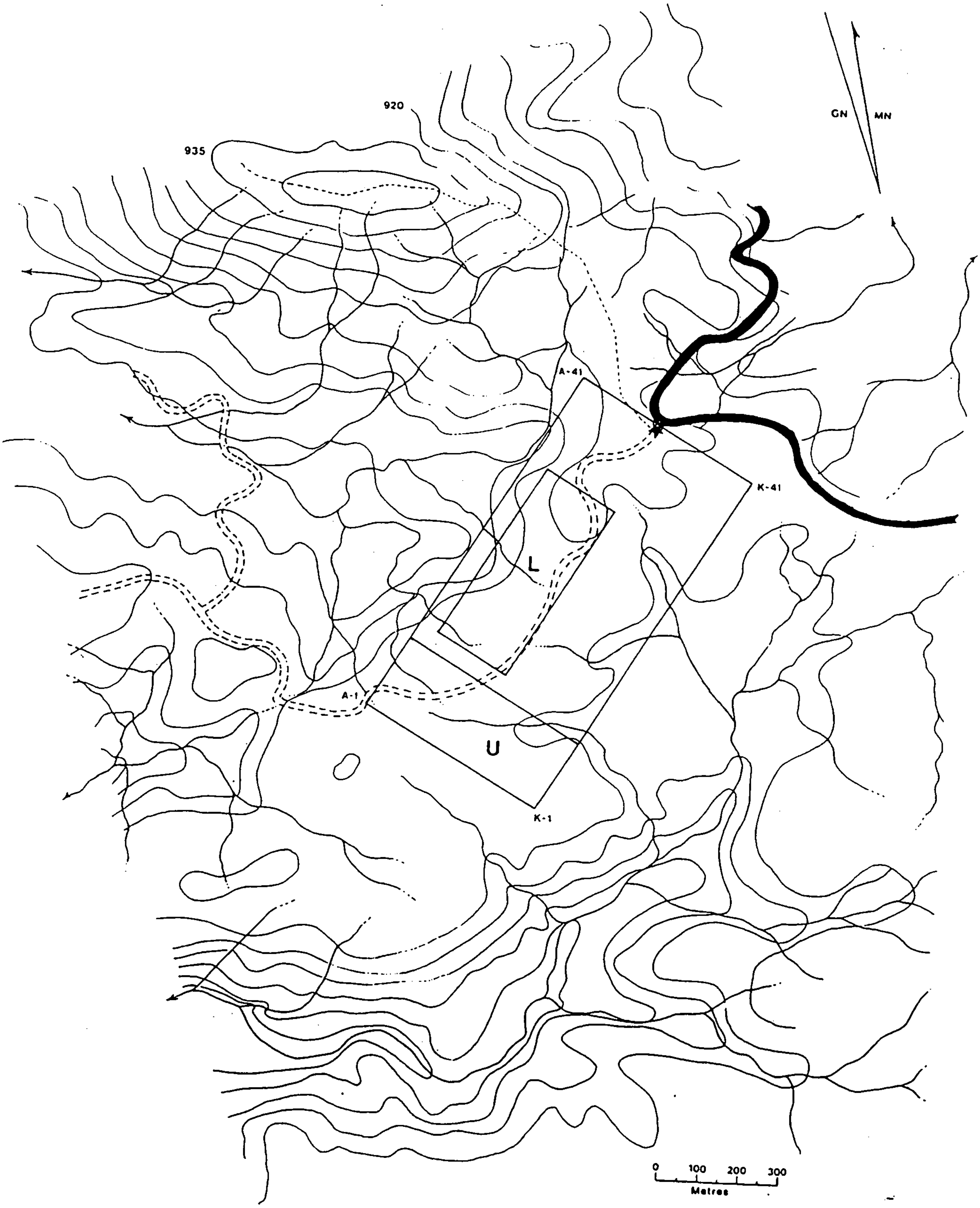


Mean annual rainfall was 3169mm,
mean number of days rain was 81,
from 32 yrs of data (Anon 1977).

Fig 2.2

Location of study area and study sites, logged (L) and unlogged (U), within a 50ha grided site.

Information obtained from: 1:50,000 Topographic Survey Map "Mount Spec" Sheet 8160 (3), Clapham junction turn-off at (*) Site grid reference E-F, 41, Map grid coordinates 12200,99650, contours approximately 15m.



2.3 LEGITIMATE AVIAN SEED DISPERSERS

"Legitimate" avian seed dispersers are those bird species that consume fleshy fruits whole and subsequently deposit the seeds unharmed, either through regurgitation or having passed through the gut (Murray 1988). Within the Paluma study site, a suite of 12 legitimate seed dispersers were observed during this study (Table 2.1). Most of these species were obligate frugivores whose diet was comprised almost entirely of fleshy fruits. Other bird species such as Honeyeaters also consume fleshy fruits, however, fleshy fruits are a minor component of their diet and seeds tend to be discarded before swallowing the fruit pulp (Moore pers. obs.).

The legitimate frugivores described below provide very different dispersal services. The Southern Cassowary, weighing 50-60kgs consumes large quantities of fruit from the forest floor and deposits the seeds in large fecal clumps (Table 2.1). Cassowaries were transient visitors to the study site. The fruit pigeons, range in size from the Topknot pigeon 518g to the Red-crowned pigeon 112g. All pigeon species were nomadic or migratory, usually arriving at the study site during periods of fruit abundance and absent during periods of fruit scarcity as observed in other areas (Crome 1975, Innis 1989). Fruit pigeons would tend to broadcast seeds over large areas, particularly the Topknot pigeons which were seen in flocks of 20-50. Members of the Paradisidae were all of similar size ranging from 100-200g and were resident within the study site during the breeding season, September to January and tended to be transient outside these periods. Male Tooth-bills were consistently the most conspicuous frugivore present in the study site during the breeding season. Male Tooth-bills deposit seeds in piles beneath favoured perches during the breeding season, as do male Golden bowerbirds. The females of these species and both sexes of the spotted cat bird and Victoria's riflebird broadcast seeds over their foraging range. Mistletoe birds were transient, and were present within the study site while mistletoes were fruiting.

TABLE 2.1 Legitimate avian seed dispersers observed within the Mt Spec study site during the three years of study. [1]Presence refers to the consistency with which a species occupied the study site: (1) Resident during the breeding season, transient outside the breeding season, (2) Transient, migratory or nomadic. [2]Abundance refers to the abundance of a species within the study site between September and January: (R) rarely sighted, (P) present, (A) abundant.

Species	Source	Weight (g)	Breeding Season	[1]Presence	[2]Abundance
Tooth-billed bowerbird *Scenopoeetes dentirostris*	1	155	Sept-Jan	1	A
Golden bowerbird *Prionodura newtonia*	3	100	Sept-Jan	1	P
Spotted catbird *Ailuroedus melanotus*	3	160	Sept-Jan	1	P
Victoria's riflebird *Ptiloris victoriae*	3	150	Sept-Jan	1	P
Purple-crowned pigeon *Ptilinopus superbus*	2	122	Nov-Dec	2	R
Red-crowned pigeon *Ptilonopus regina*	2	112	Sept-Dec	2	R
Wompoo pigeon *Ptilonopus magnificus*	2	328	Aug-Oct	2	P-A
Topknot pigeon *Lopholaimus antarcticus*	2	518	Sept-Dec	2	R-A
Brown pigeon *Macropygia amboinensis*	2	183	July-Jan	2	P
White-headed pigeon *Columba leucomela*	2	426	Oct-Dec	2	R
Southern Cassowary *Casuarius casuarius*	3	5000	Jun-Oct	2	R
Mistletoe bird *Dicaeum hirundinaceum*	3	20	Oct-Mar	2	P

Source (1) Frith and Frith pers comm, (2) Crome 1975, (3) Readers digest complete book of birds

2.4 MALE TOOTH-BILLS

The Tooth-billed Bowerbird (*Scenopoeetes dentirostris*) is one of four bowerbirds (Family Ptilonorhynchidae) found in upland rainforests between Townsville and Cooktown. It is a uniparental species, that is, males are promiscuous and females alone tend the nest (Frith and Frith 1985). The male Tooth-bill is a robust bird approximately 260mm in length, olive-brown above and mottled brown below (Plate 1). Displaying males at the Paluma study site weighed a mean of 155.5g (SE=1.911g, range=142.5g - 167.7g, n=16; Frith and Frith unpub.).

During the display season (October to December) males aggregate along ridge tops and form "exploded arenas" (Gilliard 1969) or exploded leks (Frith and Frith unpub., Crome and Moore 1989). They establish and maintain a cleared court of 1-3m in diameter (elliptical in shape Table 2.2) on the forest floor, littered with pale upturned leaves (Plate 2). The male calls from favoured song-perches within a 4m radius and 1-6m above the court for most of the display season (Table 2.2). Court sites are traditional, and some males have been found to return to the same court site for 13 years in succession (Frith and Frith unpub.). Within the study site, 11 of 24 colour-banded males were still active in their 13th breeding season. Estimated annual survival rate was high at 88%, with the mean life expectancy after banding of 8.4 years. No further sightings of 13 of 24 colour-banded males were made after they ceased to maintain their courts (Frith and Frith unpub.). The courts of displaced or lost males were taken over by new individuals (Frith and Frith unpub.).

Crome and Moore (1989) also found male Tooth-bills to exhibit high court fidelity on the Mt Windsor Tableland, north-west of Mossman. They found 83 to 95% of court sites were in identical positions within the forest from year to year and 61% of courts were maintained for the duration of their observations (4 years). Male Tooth-bills, however, were displaced from court sites as a result of logging activities on the Mt Windsor Tableland (Crome and Moore 1989).

TABLE 2.2: Characteristics of male Tooth-bill courts and seed piles. Number of seed piles and distance from the court, indicate the location and number of favoured song perches.

Measure/ parameter	Mean	SE	range	n
Court length	1.9	0.06	0.8-3.3	35
Court width	1.4	0.06	0.7-2.3	35
Number of seed piles	2.0	0.20	1-7	35
Distance of seed piles from the court	1.47	0.12	0-4	35

PLATE 1: Male Tooth-billed Bowerbird (*Scenopoeetes dentirostris*) calling from a favoured perch above the court (Photo courtesy of Roy Mackay, Paluma).

PLATE 2: Male Tooth-billed Bowerbird display court, usually 1.5 - 2.5m in diameter, cleared of leaf litter and debris and decorated with pale upturned leaves of *Polyscias* and *Endiandra spp.*

2.5 DISTRIBUTIONS OF MALE TOOTH-BILLS AND CANOPY GAPS

The male Tooth-bill courts and canopy gaps were mapped in the two 10ha sites (logged and unlogged) prior to and during the 1988 display season. Each site was searched systematically for courts during the peak display season, and bearings and distances were taken from grid coordinates to allow the courts to be mapped onto the study grid. Gap locations were also mapped prior to the display season by systematically searching the study site and the area of each gap was calculated as outlined below.

A canopy gap was defined as a hole in the canopy extending to within 2m of the forest floor (Brokaw 1982). Canopy gap areas were measured by staking the gap centre and measuring the distance to the perimeter of the gap on the 8 cardinal points of the compass. The gap edge was determined by establishing a vertical line between the gap edge at canopy level and forest floor using an inclinometer. Canopy gap areas were determined by plotting gaps to scale on a map and measuring areas using a digitising pad and Sigmascan (V3.9).

Nearest neighbour distances between male Tooth-bill courts were obtained from measures of projections on maps using a digitising pad and Sigmascan (V3.9). Additional measures of seed and seedling clump proximity with respect to the court centre were also taken.

2.5.1 Male Tooth-bill distributions

Male Tooth-bills were regularly distributed at both sites, with neighbouring birds in audible but not visual contact with one another. Mean nearest neighbour distances were 63.1m in the logged site (SE=5.6m, range 38.4 - 126.6m, n=15) and 58.5m in the unlogged site (SE=6.7, range=31.5 - 121.4, n=17) (Fig 2.3a,b). The mean distances between courts at the two sites were not significantly different (Independent T test, T=0.514, p=0.612). The two study sites chosen did not include all the courts of individuals within the lek.

2.5.2 Canopy gap distributions

Canopy gaps were more prevalent in the unlogged (n=30) than logged site (n=5) (Fig 2.3a,b). Canopy gap areas differed between sites, with a mean of 67.1m^2 in the unlogged site (SE=5.6, range=21.5 - 162.3) and a mean of 195.2m^2 in the logged site (SE=122.6, range=34.0 - 683.0). These differences were significant (Independent T test, T=-2.619, p=0.013). Canopy gap availability at both sites was 194m^2/ha for the logged site, and 98m^2/ha for the unlogged site. Most canopy gaps were formed by single large tree fall events, with the exception of the very large canopy gap (Gap 100, 683m2, Fig 2.3b) which was formed by a multiple tree fall event caused by wind shear associated with cyclone "Althea" in 1974 (Frith and Frith pers comm).

2.5.3 Interactions between male Tooth-bills and canopy gaps

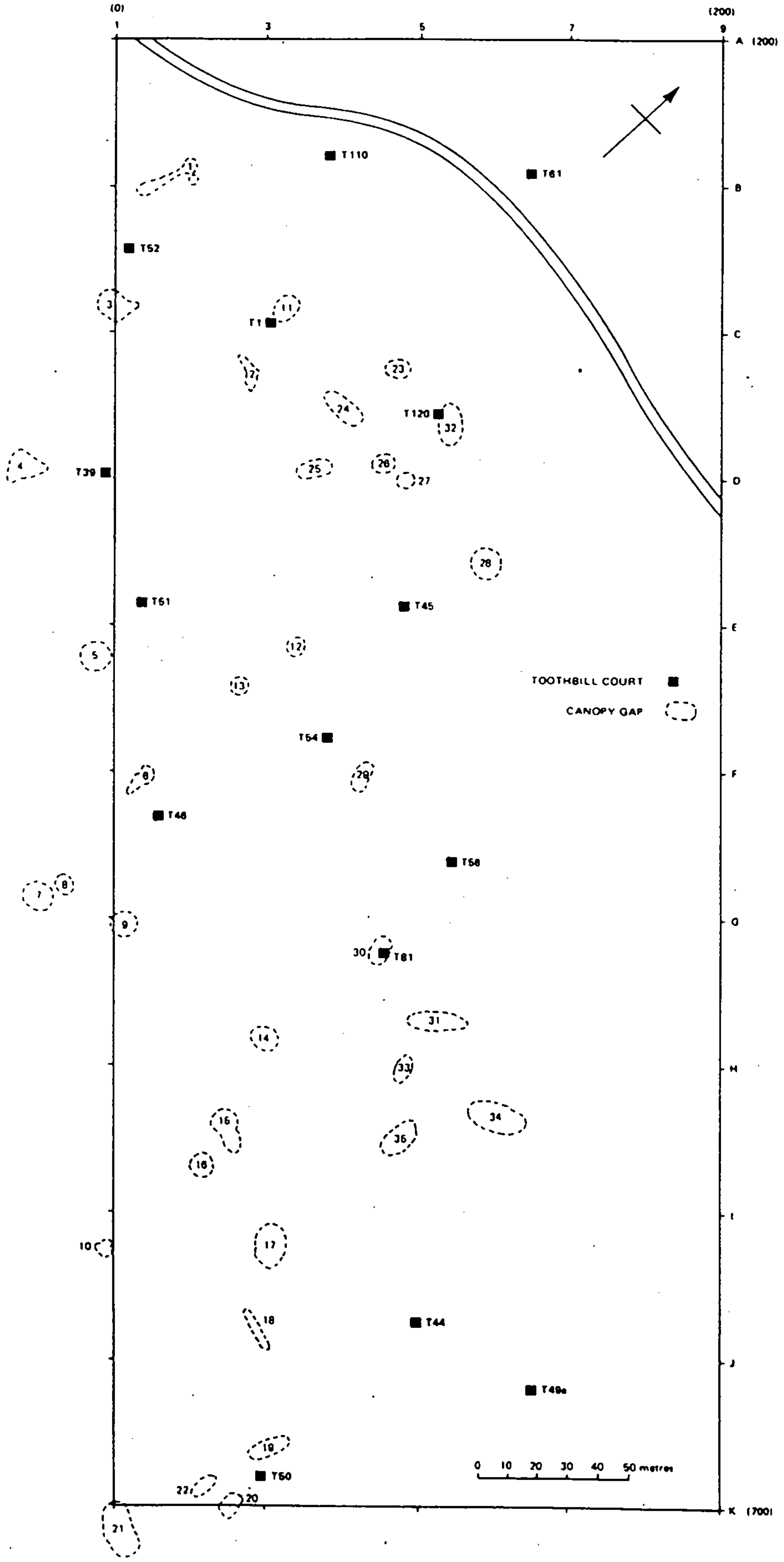
Mean nearest neighbour distances between court sites in this study (58-63m), are slightly larger than those obtained by Crome and Moore (1989) (43-50m). The dispersion of males however, is similar with males spaced regularly along ridge tops (Crome and Moore 1989).

Male Tooth-bills maintain consistent distributions within leks over many years. Eleven of 24 colour banded males maintained the same court sites within a lek over 10 seasons (Frith and Frith unpub.). Further, if males were displaced or lost from a court site, a new male would arrive to take its place, maintaining lek integrity (Frith and Frith unpub.). Traditional sites such as these should therefore persist as long as the forest remains intact (Snow 1982).

Three of the 32 mapped courts of male Tooth-bills were maintained within or immediately adjacent to canopy gaps. This results in seeds being freighted directly to canopy gap areas, providing directed dispersal for gap-dependant species (Howe and Smallwood, 1982). Almost all rainforest plant species are gap dependent in varying degrees (Denslow 1980b). Shade tolerant tree species can survive beneath the canopy, but require canopy gaps to establish within the canopy. Shade intolerant tree species require transportation directly to canopy gaps, or for a canopy gap to form before seed reserves are consumed by seedlings (Murray 1988).

By maintaining traditional court sites on the forest floor male Tooth-bills provide three potential avenues of recruitment for seedlings of rainforests tree species: (i) shade tolerant seedlings can exist beneath the canopy in Tooth-bill court areas, and establish with the eventual formation of a canopy gap, (ii) shade intolerant plant species can be transported directly to a canopy gap site through "directed dispersal" as was evident for three of 32 birds, or (iii) pioneer species will be stored in the soil seed bank until gap formation. All three scenarios will be examined in later chapters.

Fig 2.3a Distribution of male Tooth-billed Bowerbird court sites and canopy gaps in 10ha unlogged site along a ridge line near Paluma, North Queensland.



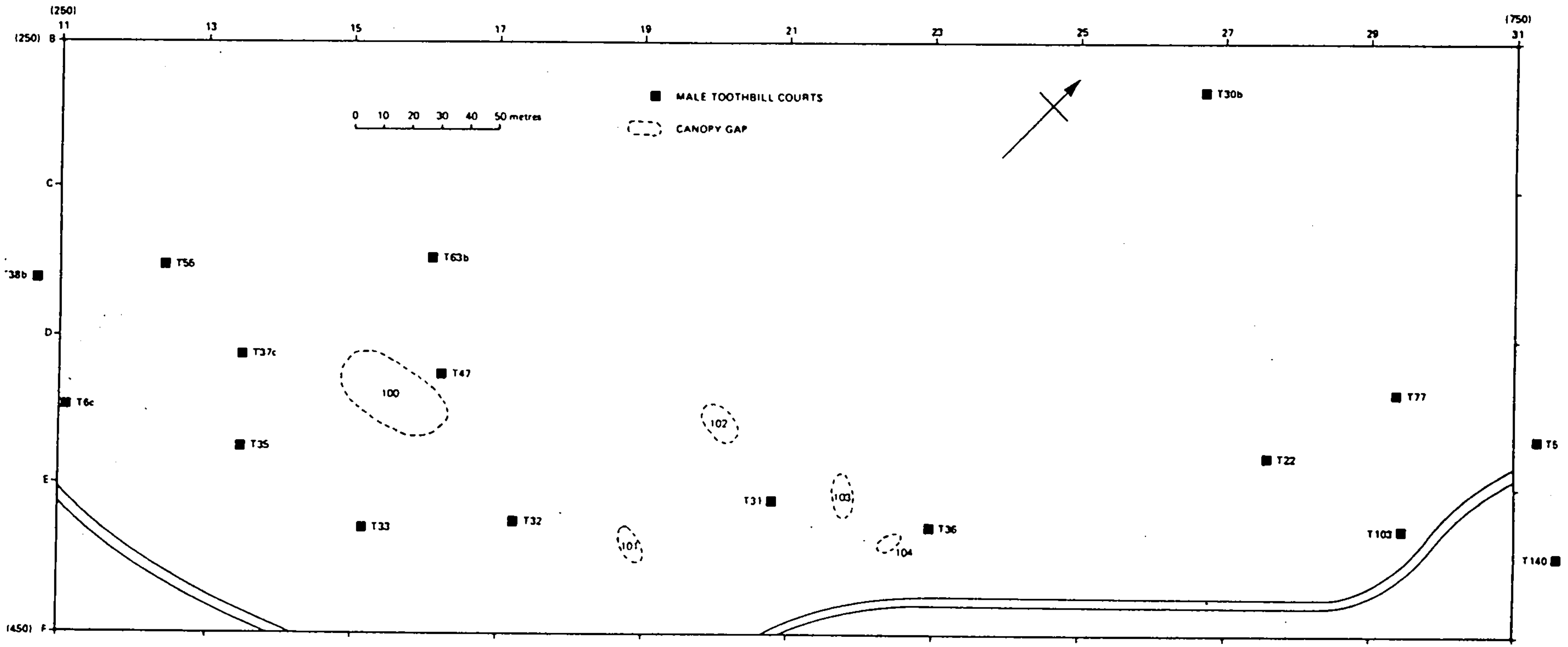


Fig 2.3b Distribution of male Tooth-billed Bowerbird court sites and canopy gaps in a 10ha logged site along a ridge line in 10ha logged site near Paluma, North Queensland.

Chapter Three

FRUITING PHENOLOGIES

3.1 INTRODUCTION

Phenological patterns of Australian rainforests are poorly understood (Hopkins and Graham 1989). They have been monitored in association with populations of frugivorous pigeons (Crome 1975), insects (Lowman 1982, Frith and Frith 1985b) and seasonal water availability (Hopkins and Graham 1989). Australia's wet tropics are seasonal with distinct hot wet and cool dry seasons. Peaks in fruit production generally occur over the late dry, early wet season and occasionally extend to the late wet season, December to March, (Crome 1975, Frith and Frith 1985b, Hopkins and Graham 1989).

In tropical forest communities, peak avian frugivore abundance generally occurs during periods of peak fruit abundance (Crome 1975, Howe and Estabrook 1977, Levey 1988, Snow 1971). A concomitant increase in dispersal of rainforest seed by frugivores might therefore be expected. For individual plant species, frugivore visitation and absolute fruit removal, increases with increasing crop size, both in tropical (Coates-Estrada and Morton 1988, Howe and DeSteven 1979, Howe and Vande Kerckhove 1979, Howe 1980, 1981, Murray 1987) and temperate systems (Davidar and Morton 1986, Denslow 1987, Moore and Willson 1982, Stapanian 1982). However, the relationship between crop size and subsequent effective dispersal by frugivores is variable. In some cases, increased crop size results in an increase in the number of seeds removed from a tree (Howe 1977, 1981, Howe and Vande Kerckhove 1979). In other examples however, the converse is true. Although the number of frugivores may increase, a large fruit crop can often result in sedentary behaviour by frugivores, so less seeds are effectively removed from the tree (Howe 1977, 1980, 1981, Howe and Vande Kerckhove 1979, Pratt and Stiles 1983).

The primary aims of this component of the study were threefold: (1) to describe the pattern of fruiting phenology for the study area, (2) to describe the changes in abundance of dispersed seeds by avian frugivores relative to fruit availability, (3) to obtain a species list of fruits available for consumption by male Tooth-bills.

3.2 METHODS

3.2.1 Study sites, climate, vegetation and logging history

Study sites, climate, vegetation and logging history are detailed in Chapter Two.

3.2.2 Monitoring of fruit and seed fall patterns

Fruit and seed fall patterns were monitored each month, where possible, from June 1987 to December 1989, as an index of fruit and seed production and fruiting phenology within the habitat. Two methods were used: (i) fruit fall traps (a quantitative method), and (ii) transect walks (a qualitative method).

A great variety of fruits and seeds rain down from the canopy each year. To avoid confusion, the following terms were used to define broad fruit and seed classifications: "Fleshy fruit fall" refers to all fleshy fruits that fall to the forest floor intact, that is, the pericarp or aril still envelops the seed, "Bird dispersed seed" refers to fleshy fruits that have been consumed by any legitimate avian frugivore and have passed through the gut undamaged, leaving a clean seed free of pericarp or aril, and "Wind dispersed seed" refers to dry seeds with paper wings that are dispersed by the wind.

3.2.2.1 Fruit and seed fall traps

A total of 21 fruit fall traps were distributed along three 300m transect lines at 50m intervals at both sites (Fig 3.1). Fruit fall traps were 66cm diameter wire hoops covered with a fine knit terylene mesh, giving a capture area of $0.25m^2$. Each trap was suspended 75cm above the ground on a sapling tripod. For each site a total area of $5.25m^2$ was sampled.

Material accumulated in traps was collected monthly and sorted in the field. The following information was recorded:

i) Species (where possible, or the fruit and seed were returned to the lab for later identification),

ii) number of individuals,

iii) condition, which included:

I. Fleshy fruited species may reach the forest floor as:

(a) aborted immature fruit,

(b) mature fruit (fully formed fruit and seed with pericarp intact),

(c) damaged fruit, where fruit/seed is damaged or scarred from vertebrate predation, and testing,

(d) bird dispersed seed, where frugivorous birds have consumed the seed and removed pericarp through digestion (clean seed).

II. Wind dispersed species also reached the forest floor as:

(a) aborted immature capsules,

(b) mature capsules (where capsules were beginning to open to release seed),

(c) predated capsules, where Sulphur Crested Cockatoos (*Cacatua galerita*) and other seed predators had partially devoured or damaged capsules (pers. obs.), and

(d) as wind dispersed seed, where capsules had effectively released seed.

Most fleshy fruited plant species collected produced fruits containing a single seed, however, some species produced fruits containing multiple seeds. To standardise the dispersal units between species, for both fruit and seed fall, the total number of seeds/species was divided by the mean number of seeds/fruit for that species. This prevented over-estimating bird dispersed seed relative to fruit fall. Where possible, 20 fruits of each species was dissected and number of seeds counted to calculate the mean number of seeds/fruit for that species (Appendix 3.1).

Fruits containing numerous tiny seeds, such as: Figs, *Ficus spp.*, False Figs, *Timonius spp.*, and Acacias, *Acacia spp.*, were excluded from the data. These species were excluded from the data set for largely pragmatic reasons. As all sorting was conducted at the fruit trap site in the field, attempting to count potentially thousands of tiny seeds was intractable. Instead, a broad abundance estimate was used.

3.2.2.2 General transect walks

General transect walks were also conducted while sampling fruit fall traps. A species list was obtained from fruit and seed fall events that occurred within three 300m, 2m wide transects that extending the length of both sites (Fig 3.1). This provided a more realistic picture of the diversity of fruit and seed fall than would have been obtained from the small area sampled by the fruit-fall traps alone.

Figure 3.1

Distribution of fruiting phenology transect lines and fruit fall traps across logged and unlogged study sites

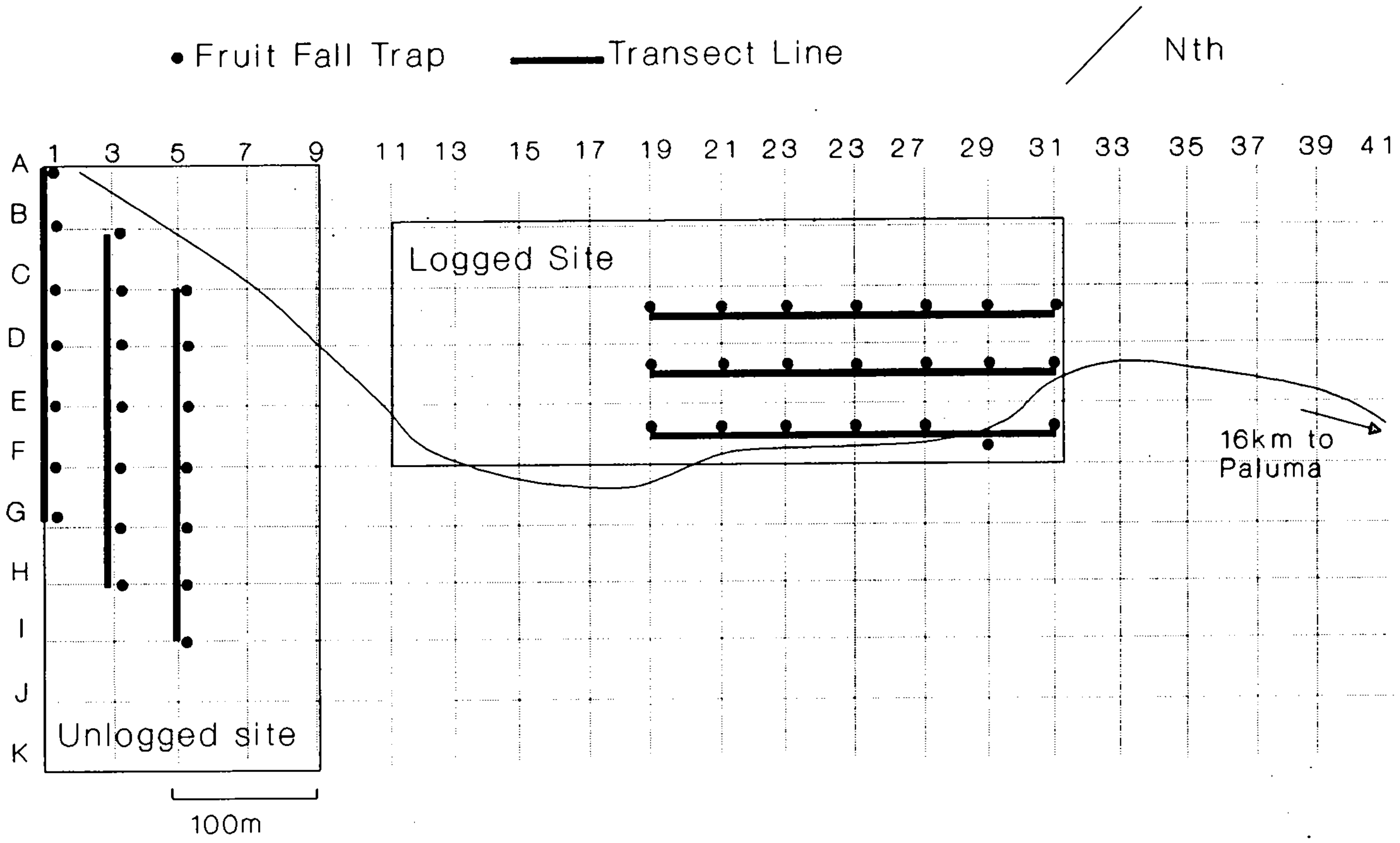
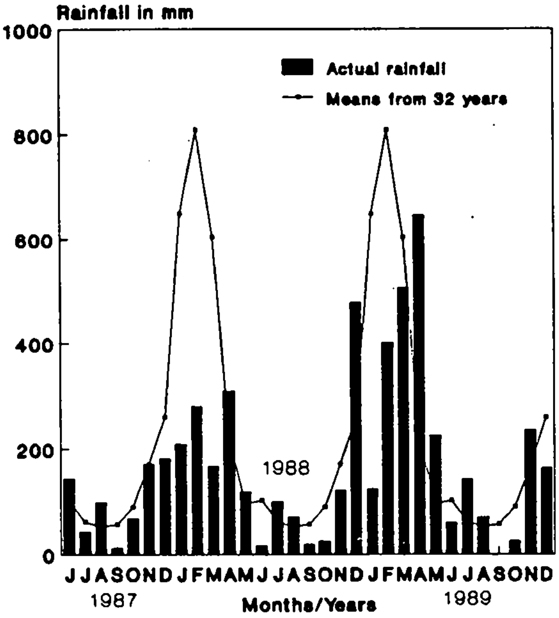


Fig 3.2

Paluma rainfall data from June 1987 to December 1989



3.3 RESULTS

3.3.1 Climate

The study area is characterised by a warm wet season, December to March, and a cooler dry season, April to November. During this study, the wet seasons produced less rain than expected from the average obtained from 32 years of rainfall data (Anon 1990) (Fig 3.2). The total wet season rainfall in 1987-88 and 1988-89 was 837mm and 1511mm which represents 36% and 65% of the average respectively (Fig 3.2).

3.3.2 Fruiting Phenologies

3.3.2.1 Comparison of phenologies at each site from fruit fall traps and transect walks

The fruit and seed from 64 rainforest plant species was deposited on the forest floor during this study. More species produced fruit and seed in the logged site (56) than the unlogged site (47) (Table 3.1). 53 fleshy fruited plant species produced fruit in the logged site, and 47 in the unlogged site (Table 3.1). At both sites, three wind dispersed species produced seed (Table 3.1). More plant species were detected using fruit fall traps (54) than were observed during transect walks transect walks (45) (Table 3.1) as fruit fall traps collected those species that were small and or difficult to see on the ground. Whereas, transect walks enabled the detection of large conspicuous species that were rare. By combining the results of both techniques a greater number of rare or inconspicuous species were recorded.

Fruit and seed fall was higher in the logged than in the unlogged site. The total number of fruit and seeds collected in fruit fall traps was 866 for the logged site and 603 for the unlogged site. The fruit fall traps in the logged site collected a greater proportion of fleshy fruits (both fallen fruits and bird dispersed seed) (68.1%) than those in the unlogged site (48.9%) (Table 3.1). Conversely, there was a greater proportion of wind dispersed seeds collected by traps in the unlogged site (16.1%) than by those in the logged site (3.1%) (Table 3.1). The proportion of bird dispersed seed collected in the traps set under Tooth-bill perches was marginally higher in the unlogged site (35%) than in the logged site (28.8%) (Table 3.1).

Although some of the differences in the data from the fruit-fall traps in the logged and unlogged sites seem large, none were statistically significant. This may be due to the high degree of spatial patchiness of fruit and seed fall (revealed by the high variation in fruit collected between traps at each site) and the small area sampled by traps (5.25m^2/site). Comparisons between sites for different seed dispersal types collected in fruit fall traps (One Way Analyses of Variance) were non-significant for: i) fleshy fruit fall (F=3.19, df=1,42, p=0.0813), ii) bird dispersed seed fall (F=0.88, df=1,42 p=0.3541), iii) wind dispersed seed fall (F=2.40, df=1,42, p=0.1291), and iv) total fruit and seed fall from all sources (F=2.60, df=1,42, p=0.1141).

TABLE 3.1: Total number of large seeded mature fruit/seed collected in fruit fall traps and the total fruit/seed fall events found on transect walks within the logged and unlogged site at Paluma from November 1987 to December 1989.

	Fruit Fall Traps			Transect walks	
Dispersal Type	[1]No. Species	[2]No. Ind	[3] %	No. Species	Total Species
Logged Site					
Fleshy fruit fall	44	590	68.1	35	53
Bird dispersed	44	249	28.8		
Wind dispersed	3	27	3.1	3	3
Total	47	866		38	56
Unlogged Site					
Fleshy Fruit fall	38	295	48.9	30	44
Bird dispersed	38	211	35.0		
Wind dispersed	3	97	16.1	3	3
Total	41	603		33	47
TOTAL (Both sites)	54	1469		45	64

[1]No. species = number of species; [2]No. Ind. = number of individual seeds or fruits; [3] % = percentage of total fruits and seeds.

Fig 3.3a
Seasonal variation in the number of fruiting species (Logged site)

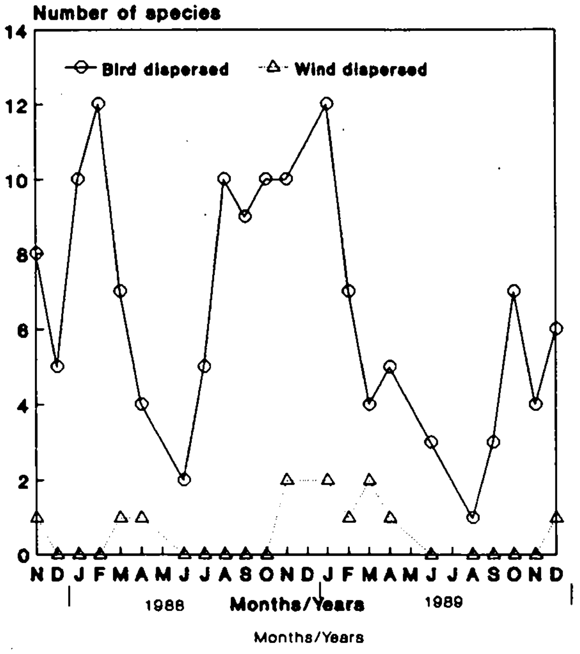
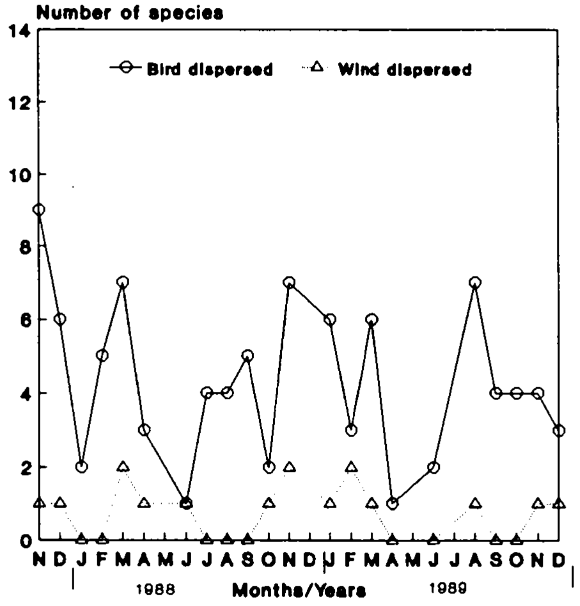


Fig 3.3b
Seasonal variation in the number of fruiting species (Unlogged Site)



Combined fruitfall traps and transect walk data

3.3.2.2 Seasonality of fruiting species

The number of plant species producing mature fleshy fruits varied between sites and seasons (Fig 3.3a,b). More species of fleshy fruits were produced in the logged site than the unlogged site (Fig 3.3a,b). More plant species produced fleshy fruits in the late dry season to wet season (August to March) than at all other times of the year for both sites. Over the same period (August to December), at both sites, wind dispersed plant species also tended to shed mature seed (Fig 3.3a,b).

3.3.2.3 Seasonality of fruit production

In this study, only one complete fruiting season (April-April) was obtained for fruit fall trap data, (1988-89). For the 1987-88 season the latter half was monitored, and for the 1989-90 season the earlier half was monitored.

Total fleshy fruit production (fleshy fruit fall + bird dispersed seed) varied between sites and seasons, but indicated bimodal fruit production extending from the late dry season to the late wet season, September to April (Fig 3.4a,b). The 1987-88 season showed a bimodal peak in fleshy fruit production extending from November to March (Fig 3.4a,b). The 1988-89 season also showed bimodal peaks in fruiting. In the logged site, fruiting peaks were broad and commenced in July and then tailed off in April (Fig 3.4a). Whereas in the unlogged site, fruiting peaks were more acute and were observed in September and March (Fig 3.4b). Finally, the 1989-90 season was extremely poor with very little fruit produced at either site (Figs 3.4a,b).

Wind dispersed seed was less abundant than fleshy fruit/seed and small, bimodal peaks were observed in November and February at both sites (Figs 3.4a,b).

Fig 3.4a
Seasonal variation in fruit and seed fall for the Logged site.

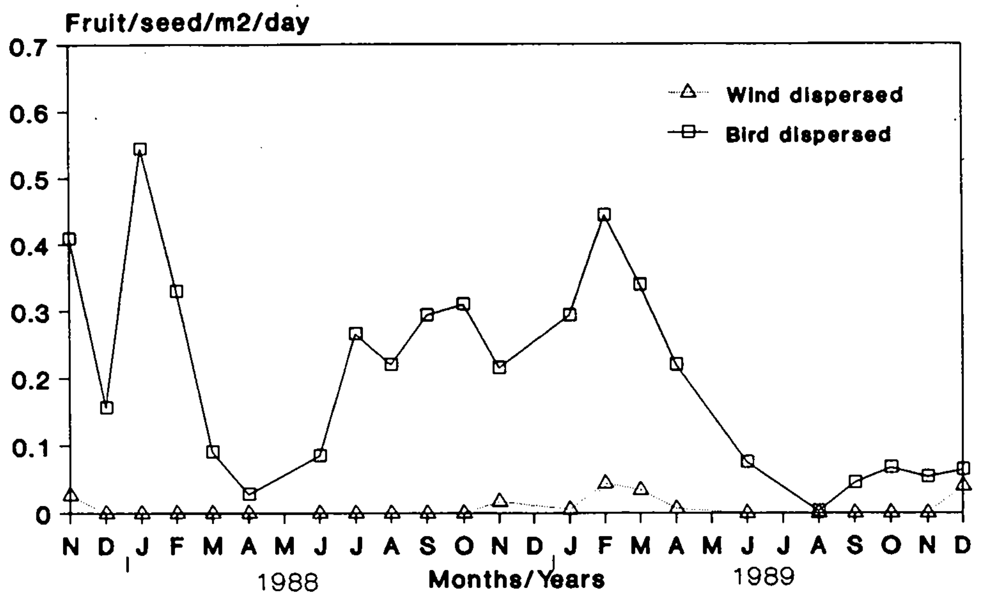
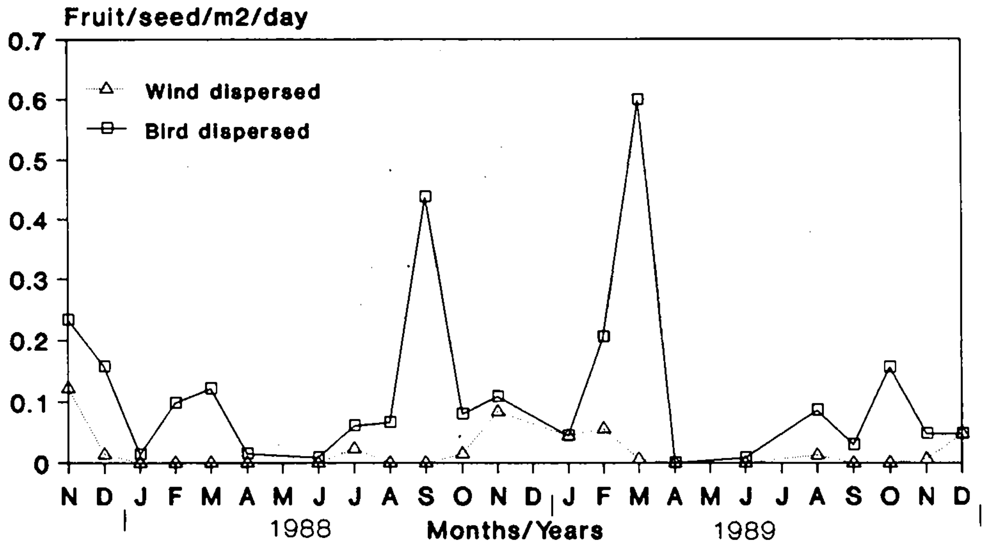


Fig 3.4b
Seasonal variation in fruit and seed fall for the Unlogged Site



Bird dispersed, refers to total fleshy fruit production, both bird dispersed seeds and fleshy fruit fall

Fig 3.5a Logged Site
Seasonal variation in fleshy fruit production and bird dispersed seed

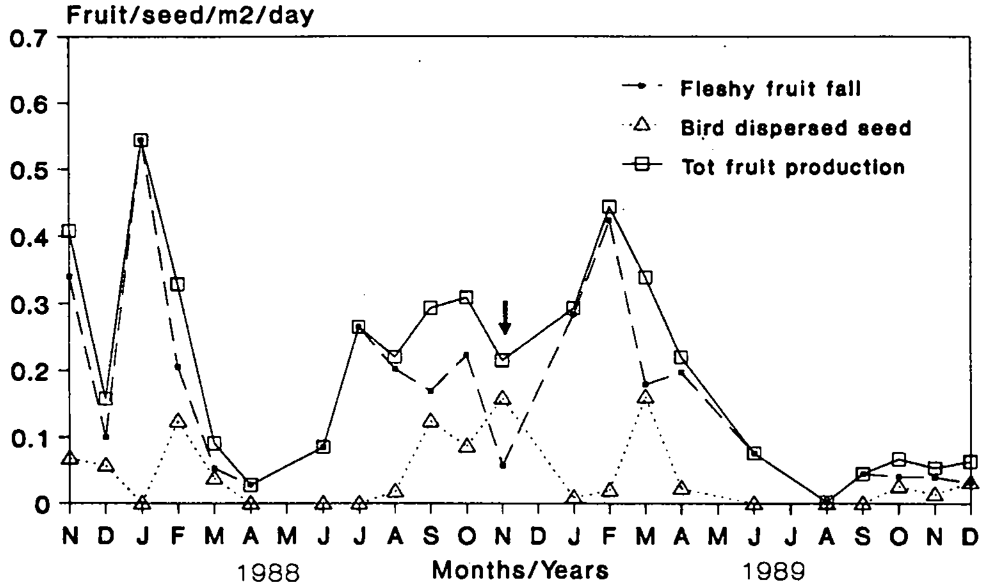
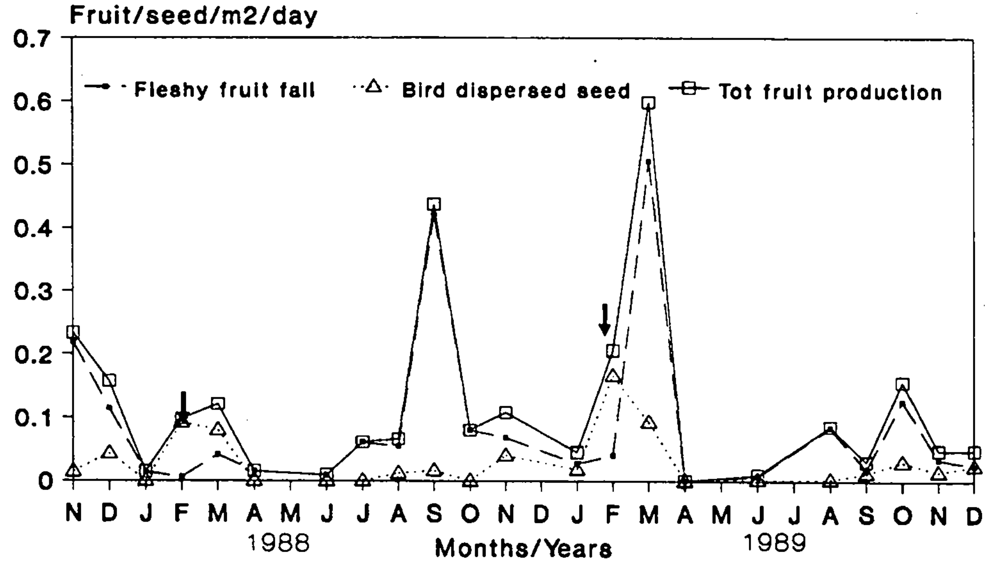


Fig 3.5b Unlogged Site
Seasonal variation in fleshy fruit production and bird dispersed seed



Arrows depict periods where avian seed dispersal exceeds fleshy fruit fall

3.3.2.4 The relationship between fleshy fruit production and avian seed dispersal

Results from fruit fall trap data indicated that peaks in bird dispersed seed roughly tracked peaks in fleshy fruit production (Fig 3.5a,b). Two distinctive peaks in bird dispersed seed occurred; the first during the late dry and early wet season (September to November), and the second during the wet season in February (Fig 3.5a,b). In some instances, bird dispersed seed exceeded fleshy fruit fall, that is, more fruit was being dispersed than was falling to the ground. This may indicate the most effective periods of seed dispersal by avian frugivores (Fig 3.5a,b). Conversely, during the periods of low fleshy fruit fall, bird dispersed seed was virtually absent (Fig 3.5a,b).

3.3.3 Summary of results

i) The seeds and fruits of 64 plant species were collected from fruit fall traps and general transect walks between June 1987 and December 1989. Of these, 61 plant species produced bird dispersed fleshy fruits and three plant species produced wind dispersed seeds.

ii) The logged site produced a greater diversity and abundance of fleshy fruits than the unlogged site. In contrast, the unlogged site produced a greater abundance of wind dispersed seed. These differences did not, however, achieve statistical significance.

iii) Fleshy fruit and wind dispersed seed production fluctuated seasonally and varied in magnitude between years and sites. Fleshy fruit production showed bimodal peaks extending from September - March. Smaller bimodal peaks in wind dispersed seed also occurred, but these were shorter in duration and occurred later in the season, during November to February.

iv) Bird dispersed seed tracked fleshy fruit production. In some instances bird dispersed seed exceeded fruit fall, indicating periods of effective avian seed dispersal, that is, more seeds were dispersed by birds than were falling to the ground beneath a parent tree. These periods were most conspicuous in November and February.

3.4 DISCUSSION

3.4.1 The effect of site on fruit production

Differences between the two sites in fleshy fruit fall, bird dispersed seed, wind dispersed seed and total fleshy fruit production proved non-significant for fruit fall trap data. The magnitude of differences observed between sites for transect walk data disagreed with these findings. The small area sampled by fruit fall traps (5.25m^2/site) relative to transect walks (1800m^2/site), and the extreme patchiness of fruit and seed fall, suggest that transect walk data is a more reliable estimate of the magnitude of fruit and seed production. With this in mind, the logged site produced more fleshy fruits and the unlogged site more wind dispersed seed. The two wind dispersed species, Northern Silky Oak (*Cardwellia sublimis*) and Maple Silkwood (*Flindersia pimenteliana*), were extracted from the logged site 30 years previously, resulting in disturbance to the logged site (Frith and Frith pers. comm.). Disturbed areas are usually colonised by secondary growth or pioneer species, which produce large crops of medium sized fruits (Frankie *et al.* 1974, Wheelwright *et al.* 1984, Martin 1985, Levey 1988). The prominence of secondary growth species in areas of logging disturbance may explain the higher levels of fleshy fruit production at this site. In contrast, the higher production of wind dispersed seed in the unlogged site is probably due to the retention of these species which were extracted from the logged site.

3.4.2 Seasonality of fruiting

Bimodal peaks in fleshy fruit production occurred between September and March, coinciding with the late dry season to late wet season. Hopkins and Graham (1989) also found bimodal fruiting peaks in lowland complex mesophyll rainforest at Downey Creek, 250km north of Paluma. However, their peaks occurred between October and April. Seasonal forests of the Neotropics also demonstrate similar trends in fruit production, with peaks in fruit production occurring prior to and near the end of the wet season (Frankie *et al.* 1974, Foster, 1982).

The magnitude of fleshy fruit production varied between years and sites. Consistent with this, enormous inter-annual variability in fruit and seed production has been noted in many tropical rainforest studies (Crome 1975, Foster 1982, Worthington 1982, Wheelwright 1983, Denslow *et al.* 1986, Ashton *et al.* 1988).

3.4.3 Fleshy fruit production and avian seed dispersal

Peaks in fleshy fruit production were tracked by peaks in bird dispersed seed. The peaks in bird dispersed seed probably resulted from an influx of avian frugivores during this period. Three guilds of avian frugivores (residents, transient and migrants) frequent the Paluma range over the period of fleshy fruit production and these vary in abundance between years.

Residents were those bird species that are present throughout the year. Many of the frugivorous species at Paluma time their breeding seasons to coincide with the peak in fleshy fruit abundance from September to December (Frith and Frith pers. comm.). Similar patterns have also been observed for other tropical frugivores (Crome 1975, Snow 1982). Outside the breeding season, male Tooth-bills are inconspicuous members of the frugivore community. However, during the breeding season the males descend to the forest floor and establish courts and display in exploded leks. During this time the Golden Bowerbird also attended traditional bower sites.

Transients were those bird species that arrived intermittently, and varied in attendance from year to year depending on the magnitude of fleshy fruit production. Cassowaries (*Casuarius casuarius*) were present at the study site in the 1987-88 and 1988-89 seasons, during the periods of peak fruit production, but absent in the 1989-90 season, an extremely poor fruiting season (pers. obs.). Similarly, Top Knot pigeons (*Lopholaimus antarcticus*) and other frugivorous pigeon species were present in the 1987-88 season. During the 1988-1989 season they were present in enormous numbers and bred locally. However, in other years they were virtually absent (pers. obs.).

Migrants were those bird species that migrate from Papua New Guinea to breed during good fruiting years. The Shining Starling (*Aplonis metallica*) which forms large nesting colonies on the seaward edge of the Paluma Range, were present during the 1987-88 and 1988-89 seasons, but absent during the poor fruiting year (1989-90) (pers. obs.).

In some instances avian seed dispersal exceeded fruit fall, indicating periods of effective seed dispersal by the frugivore community. These periods occurred during the peaks in fleshy fruit abundance (September-November, February) and coincided with the peak breeding activities of the resident birds and the influx of transient frugivores (pers. obs.).

In all years, the resident frugivores provided a consistent seed dispersal service, even when fruit production was low. During mast years, or years of high fruit production, large numbers of transient frugivores arrived to feed. Once the fruit resource was depleted, the transient species moved on and only returned if another large pulse of fruit production occurred. The enormous intra and inter-annual variation in fruit production and the transient nature of many frugivore species observed during this study may be evidence that they are exploiting a recource that is patchy in time and space.

Chapter Four

SEED DISPERSAL

4.1 INTRODUCTION

The study of seed dispersal is a vague and poorly defined area of ecology with interpretation of patterns relying primarily on qualitative investigations (refer to Chapter One). Estimates of the size and shape of an area where seeds have been dispersed (seed shadow), by frugivores have been given by a number of authors (for example: Smith 1975, Brunner 1976, Bullock 1978, Foster 1978, Janzen 1978, Lieberman *et al.* 1979, Thompson 1980). However, the complete picture of seed source, disperser and subsequent sites of deposition is largely unknown (Murray 1988).

Among avian frugivores, variation in behaviour can produce enormous differences in the patterns of seeds deposition. This results in considerable differences in the quality of the seed dispersal service provided (Murray 1988). Seed dispersal patterns produced by avian frugivores vary from those that deposit seeds in a single area, usually relating to a regular perching site (clump dispersers) to those that deposit seeds in a random manner (scatter dispersers). Murray (1988) described the seed dispersal patterns of three species of birds based on the distance travelled after fruit consumption relative to gut retention times. He found the birds (*Phanoptila melanoxantha*- the Black and Yellow Silky flycatcher; *Semnornis frantzii*- the Pronged-billed barbet; *Myadestes melanops*- the Black-faced solitaire) produce extensive seed shadows for the small seeded plant species examined. All the plant species in Murray's study were dependent on gaps for successful germination. The three birds examined by Murray may be considered scatter dispersers (Howe 1989). The foraging behaviour and seed shadows of birds that deposit seeds in clumps is virtually unknown.

The primary aim of this section of the study was to examine a known clump disperser, the male Tooth-bill, over the display season, and attempt to identify the seed shadow produced and the seed dispersal service it provides.

4.2 METHODS

4.2.1 Radio-tracking

Four male Tooth-bills, known to be long term residents of the study site (Frith and Frith pers. comm.), were radio-tracked for three periods during the display season of October to December, 1989. The radio-tracking periods covered the early (17 - 27/10), middle (16 - 26/11/89) and late (12 - 22/12/89) display season. Short periods of radio tracking were also undertaken at night (2000 -2100h) to determine roosting sites of male Tooth-bills relative to their court sites.

Male Tooth-bills were each caught in mist nets at their court sites, colour banded, measured, weighed and fitted with a 4g BIOTRACK single stage transmitter (SS-1) using a tail mount (Kenward 1978). A small amount of coloured paint was placed on the underside tips of the outer tail feathers to assist in the visual identification of radio-tagged birds in the canopy. The birds were then released near their court site. Radio tracking was initiated on the day following capture to allow sufficient time for each bird to adjust to the transmitter.

Each tracking day was divided into four 3h periods: 0600 - 0900h, 0900 - 1200h, 1200 - 1500h and 1500 - 1800h. Tracking was maintained until data for each of the four birds was collected for each of the four time periods. Two birds were randomly selected for each tracking period, and two tracking periods were completed each day. Monitoring of birds included two components as described below.

4.2.2.1 Observations at the court

A hide was placed 6m from each Tooth-bill court to monitor all bird activity associated with the court. The hides were established 2 weeks prior to capture to allow the birds time to acclimate to the hides. The observer remained within the hide during each monitoring period and all behaviour, locations, departure and return times and flight directions were noted. Behaviour and location codes are presented in Appendices 4.1 (behaviour) and 4.2 (locations). The observer within the hide was in radio contact with the radio-tracking team, as described below.

4.2.2.2 Observations away from the court

The radio tracking team remained approximately 30m from the court to avoid disturbing the bird at the court and other birds in the area. The observer in the hide would alert the radio-tracking team as soon as the bird left the court. The tracking team consisted of an individual with the radio-tracking equipment who followed the track of the bird and an observer with binoculars who recorded the final destination of the bird. The purpose of the bird's movements was inferred from the characteristics of its destination or from direct observation of its behaviour.

Birds were tracked using a TELONICS (U.S.A.) TR-2 receiver. To improve reception at close range and direction finding ability, an enhanced manual gain control was fitted to the receiver. A three element, folding hand held Yagi antenna (CUSTOM ELECTRONICS, U.S.A) was used for direction finding. A small single earphone was used for surveillance to ensure that observer noise was kept to a minimum. The earphone assisted in communication between observer and tracker which was necessary as most forays resulted in a dash of up to 400m to locate the feeding destination. Signal strength and consistency was used as a guide to bird activity, and, if the bird could not be sighted, its position was determined by triangulation. If the signal was strong and consistent, this usually meant the bird was stationary. A bearing was then taken from a known site on the grid (i.e a grid reference point, or known flagged tree), and a second bearing taken approximately 50m from the first (i.e. the next major grid reference point) to obtain a fix. To test the accuracy of this method calibration transmitters were placed in trees and the resulting fixes were found to be within 5m of the actual transmitter position. A highly variable signal, in both strength and consistency, indicated the bird was moving. In these cases the signal was followed until a strong and consistent signal was obtained and the process was then repeated. If feeding or foraging, a strong variable signal was obtained as the bird would change its orientation moving between branches, and the sound of falling debris or fruit was a good indicator of approximate bird location within the canopy above. If interacting with other individuals, then male Tooth-bill calls and chase flights were often heard above.

Once the bird had been followed to a destination, the destination tree was tagged and the bird's activities within that tree or at that specific site were recorded (Appendices 4.1 and 4.2). At a later date details of all destination trees were taken including: species name, diameter at breast height (dbh), tree type (feed tree, leaf tree or unknown), tree height (sub-canopy, canopy and emergent), and fruit volume produced (very small, small, intermediate, large and very large).

Male Tooth-bills are well camouflaged and rely on cryptic habits to avoid predation by remaining motionless when calling at their display courts (Frith and Frith pers. comm.). Consequently, when an observer is attempting to follow a well camouflaged bird that prefers to feed and move in the rainforest canopy, it is often difficult or impossible to establish its final destination and activities, leaving the reason for many forays by a bird as unknown, and destinations as approximate areas.

4.2.2 Estimators used in home range analysis

A great variety of home range estimators are available for home range analysis, for example, Minimum Convex Polygon (Mohr 1947), Kernel (Worton 1989), and Anderson (Anderson 1982). Following animals using focal animal sampling, that is following the animal on foot, results in autocorrelation of locations (i.e. non-independent fixes). This is thought to be a significant problem deciding the correct analysis for radio-tracking data. In a number of recent studies, however, it was found that home range estimates based on independent versus non independent locations were statistically indistinguishable (Anderson and Rongstad 1989, Gese *et al.* 1990). As most of the fixes collected in this study were non-random the Minimum Convex Polygon estimator was used to estimate home range size. This method is sufficiently robust to deal with non-independence of locations, if a problem exists, and allows direct comparison between most studies. The "Ranges IV" computer package (Robert Kenward; Institute of Terrestrial Ecology, Wareham, United Kingdom) was used to estimate home range areas.

4.3 RESULTS

4.3.1 Estimates of home range size

Pooling all fixes for each of the four birds over the 1989-90 display season resulted in a mean home range of 9.5ha for male Tooth-bills (range=6.9-12.5ha, SE=1.2, n=4; Fig 4.1). In a three way fixed-factor Analysis of Variance examining the effect of month, time of day and bird on home range estimate there were no significant differences (Table 4.1). As noted earlier, values obtained using the Minimum Convex Polygon method are used in all subsequent discussions of these results.

TABLE 4.1: Three-way fixed factor Analysis of Variance examining the effect of month, time period and bird on home range estimates for male Tooth-billed Bowerbirds (Minimum Convex Polygon).

Treatment	df	F	p
Month	2	1.43	0.269
Time period	3	1.26	0.320
Bird	3	2.31	0.115
Month x Time period	6	0.22	0.965
Time period x Bird	9	0.36	0.938
Month x Time period x Bird	16		
Total	39		

The home ranges of different birds overlapped; the extent of overlap ranged from 22.6% to 79.6% with a mean of 50.4% (SE= 5.3, n=12: Fig 4.2). There was a significant difference in the amount of overlap observed between individual birds and their nearest neighbours (One way Analysis of Variance using arcsin square root transformed proportions; df=3,8 F=6.36 p=0.0164; Table 4.2).

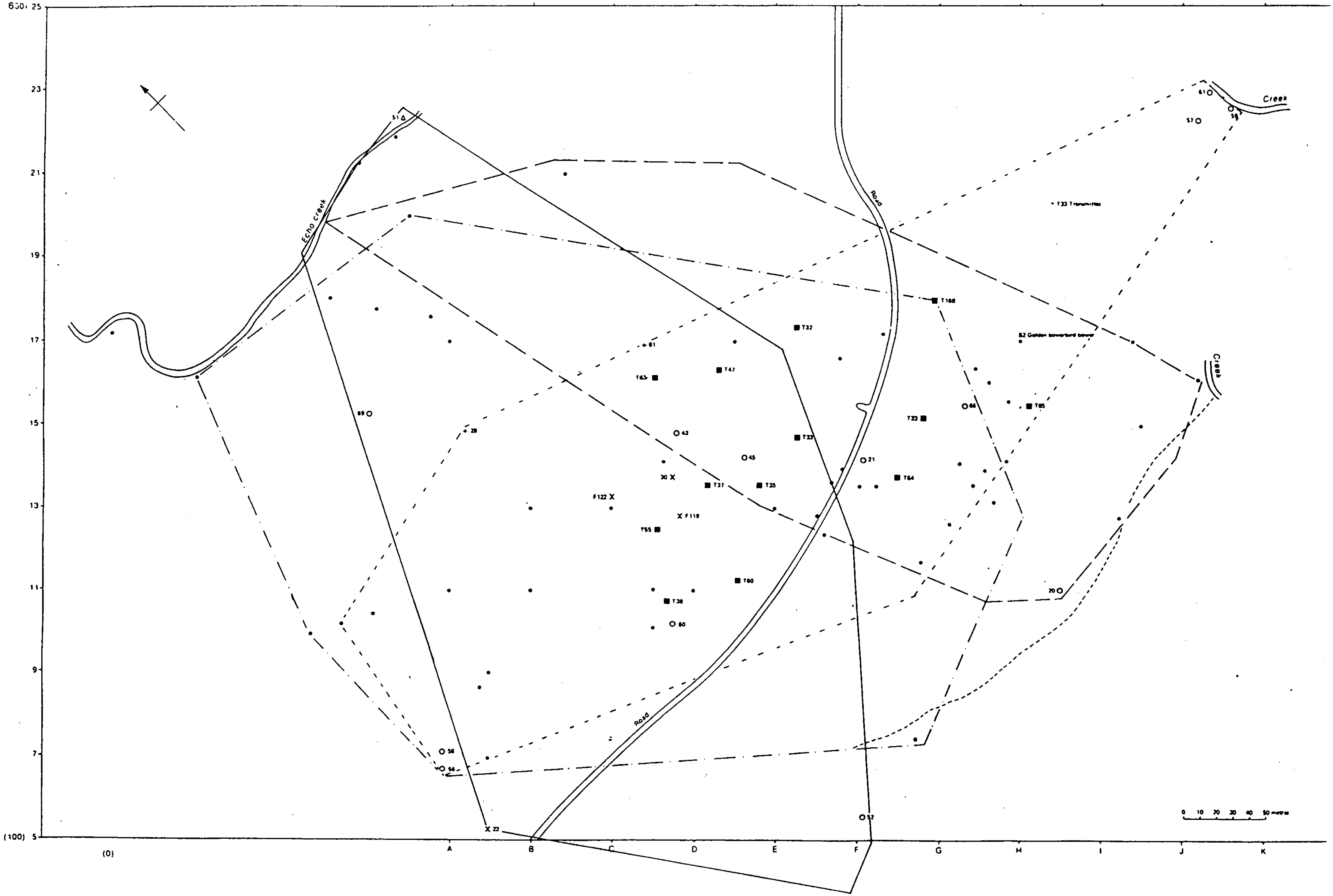
TABLE 4.2: Percent overlap of the home ranges of the four radio-tagged male Tooth-billed Bowerbirds.

Bird ID number	23	33	35	37
23	100	56.0	32.4	45.1
33	30.7	100	64.8	54.7
35	22.6	79.6	100	47.7
37	36.6	78.6	56.2	100

Fig 4.1: Minimum Convex Polygon home range areas for four male Tooth-bills in adjacent courts during the 1989 display season.

Codes:

Male Tooth-bill courts
Male Tooth-bill (T23)
Male Tooth-bill (T33)
Male Tooth-bill (T35)
Male Tooth-bill (T37)
Elaeocarpus foveolatus food trees
Cryptocarya corrugata food trees
Beilshmiedia obtusifolia food trees
Ficus destreuns food tree
Sightings in the canopy of trees



600 25
23
21
19
17
15
13
11
9
7
(100) 5
(0)
A
B
C
D
E
F
G
H
I
J
K
Echo creek
Creek
Creek
Road
Road
51
61
57
58
T33 Transmitter
B2 Golden bowerbird bower
T168
T32
61
T63
T47
T85
T23
66
69
28
43
45
T33
21
T64
30
T37
T35
F122
F119
T55
T60
T38
60
20
58
56
22
52
0 10 20 30 40 50 metres

4.3.2 Pattern of time/space utilisation

Within their home ranges the use of time and space by each bird (Figs 4.2a,b,c,d) and by all birds together (Fig 4.3) was estimated. The distances between the home court and each fix away from the court were determined for each bird using the computer package Ranges IV. The cumulative times in seconds for each fix were summed and plotted in 10m intervals from the home court. The cumulative times were then expressed as percentages of the total observation time.

Three of the male Tooth-bills spent approximately 50% of their time within the home court area. One male (T33) spent less than 40% of its time in the home court, however this male was unique in that he established a second court 40m from the original during the first month of observation (Fig 4.2b). This may have resulted from disturbance during the initial capture phase. In a Three Way Fixed Factor Analysis of Variance examining the effects of month, time period, and bird on the proportion of time spent by a male at the home court, there were no significant differences (Table 4.3).

TABLE 4.3: Three-way fixed factor Analysis of Variance examining the effect of month, time period and bird on proportion of time spent at the home court (using arcsin square root transformed proportion data).

Source	df	F	p
Month	2	0.51	0.6091
Time period	3	0.12	0.9494
Bird	3	1.06	0.3918
Month x Time period	6	0.21	0.9700
Time period x Bird	9	0.21	0.9885
Month x Time period x Bird	16		
TOTAL	39		

Results of the night radio-tracking revealed that male Tooth-bills roost above their home courts. This suggests that 75% of each 24h period is spent in direct association with the court.

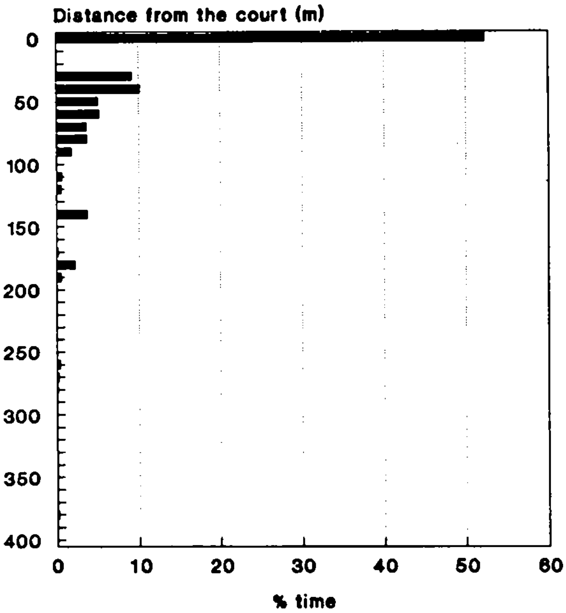
The median distance from the home court for all types of movement recorded ranged from 40-86m (Table 4.4). The three most common types of movement recorded were foraging, leaf collection and interactions with conspecifics. Male Tooth-bills were observed interacting with males in adjacent courts, often stealing leaves for their own display courts. The mean distance between courts was 52.6m (SE=1.9, n=56), which falls within the range of median distances moved by all males. This indicates that forays into neighbouring courts may be an important component of social interaction and breeding success between male Tooth-bills.

TABLE 4.4: Descriptive statistics for all movements away from the home court (distance in m) for male Tooth-billed Bowerbirds during the 1989-90 display season.

Bird number	(n)	median	minimum	maximum
23	202	50.6	27.2	384.8
33	148	58.6	13.9	370.7
35	122	86.4	14.3	311.3
37	164	40.4	8.2	391.4
TOT	636	59.4	8.2	391.4

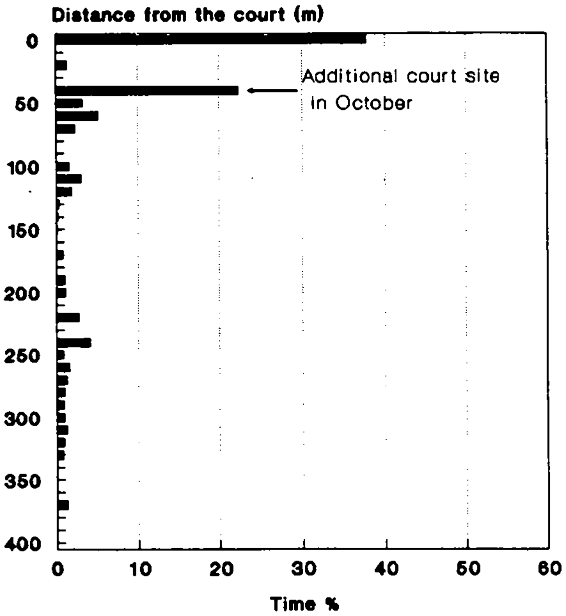
The maximum dispersal distances ranged from 311-391m (Table 4.4, Figs 4.2a,b,c,d and 4.3). The greatest distances recorded occurred when males flew to a creek to bath and preen, usually in the middle of the day. The courts were located on ridges and hilltops where water was scarce during most of the display period. The nearest standing water was located in gullies more than 300m from the courts (Fig 4.1).

Fig 4.2a
Time/space use by male Tooth-bill (T23) about the court



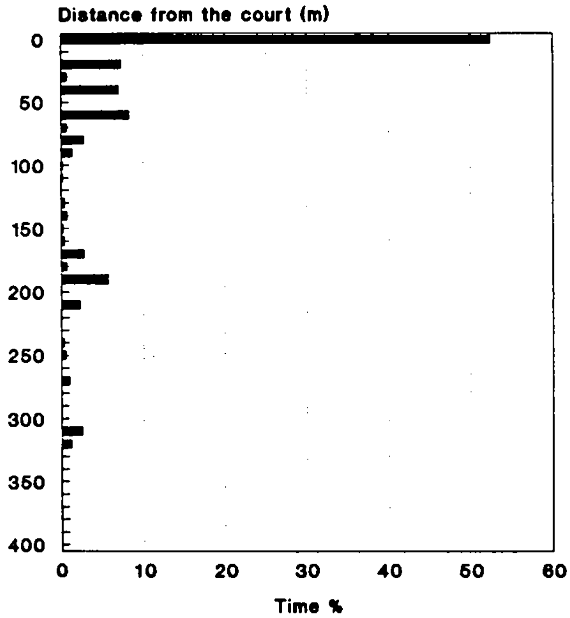
(36 hrs of observations)

Fig 4.2b
Time/space use by male Tooth-bill (T33) about the court



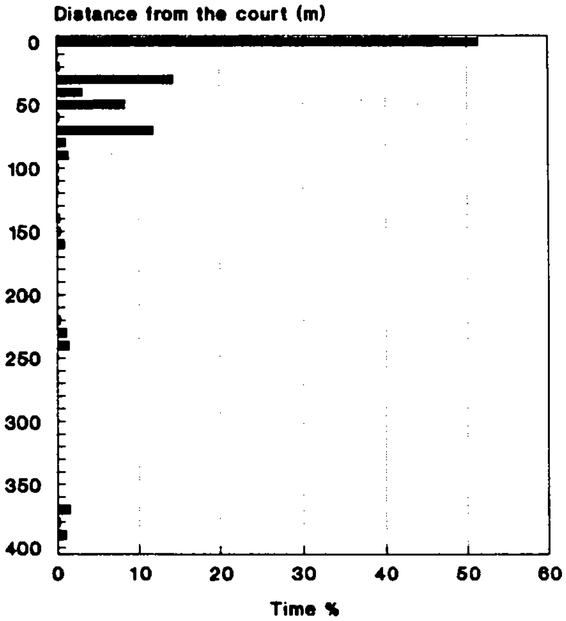
(24hrs observations)

Fig 4.2c
Time/space use by male Tooth-bill (T35) about the court



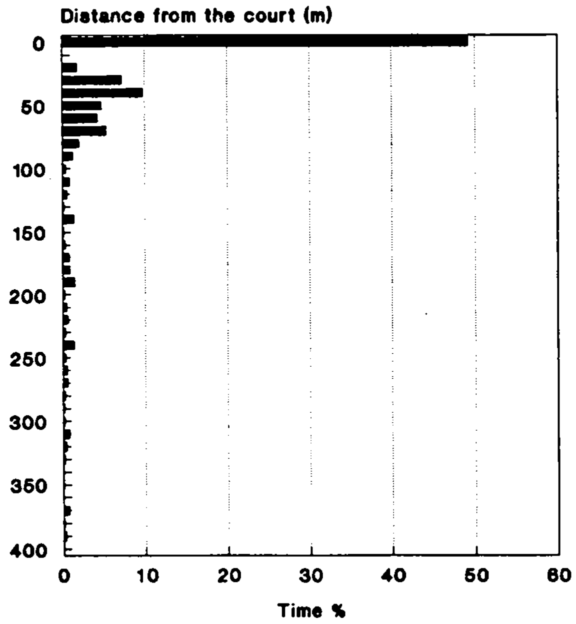
(24 hrs observations)

Fig 4.2d
Time/space use by male Tooth-bill (T37) about the court



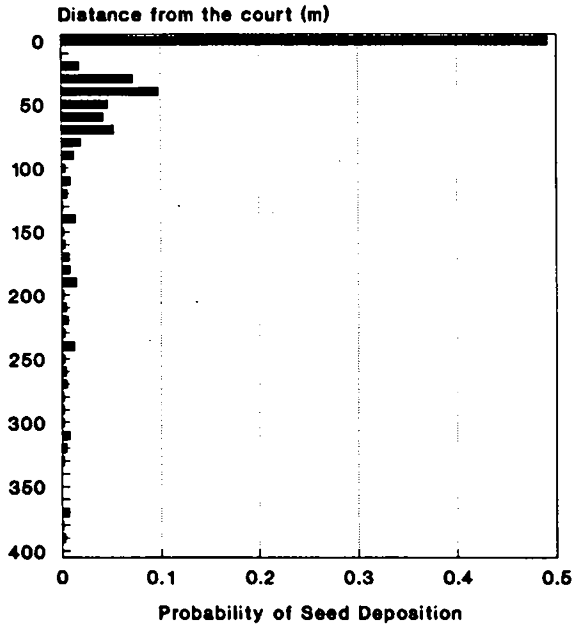
(36 hrs of observations)

Fig 4.3
Time/space use by male Tooth-billed Bowerbirds about the court



Pooled data from 120hrs observations of four males

Fig 4.4
Probability of seed deposition with distance from a male Tooth-bill court



Seed deposition probabilities based on constant seed deposition rates (MODEL 1)

4.3.3 Model I; Potential patterns of seed deposition estimated from total time spent at the court

Figure 4.4 displays estimates of the probabilities of a seed being deposited at specific distances from the court of a displaying male Tooth-bills, assuming that seeds are deposited at constant rates during daylight hours and are not deposited at night (Model I). Model I is a compilation of all timed male Tooth-bill data outlined in Fig 4.3. The model is probably better described as the probability of the bird being at a certain distance from the home court over the display season. This simplistic model suggests that at least half of the seeds from fruits consumed by each bird will be deposited in the area of the court. This model can be further refined, as described in Model II following.

4.3.4 Model II; Potential patterns of seed deposition estimated from behaviour patterns and gut retention times

Model I does not take into account the idiosyncrasies of bird behaviour. In Model II, I attempt to define a more precise picture of the seed deposition patterns by male Tooth-bills by breaking seed dispersal into its individual components:

(i) foraging behaviour,
(ii) post feeding behaviour,
(iii) individual times at and away from the court (bouts),
(iv) gut retention times.

I then compare the predicted proportions of seeds deposited using Model I with that of Model II to determine the influence of behaviour on seed deposition patterns.

4.3.4.1 Foraging behaviour and the duration of foraging bouts

Units used in model II were bouts of time at and away from the court. Bouts of time away from the court were divisible into feeding and non-feeding. The shortest foraging bout observed was 2.4 min in duration. It is likely that this represented a minimum time for successful foraging for fruits away from the court, given the poor fruiting season. Movement away from the court was therefore assigned to two categories, relating to the behaviour of the bird while it was absent from the court: (i) interaction bouts, which were short departures from the court with no time for feeding, usually leaf stealing from a neighbours court (< 2.4 min duration) and, (ii) foraging bouts, which involved longer departures from the court that include foraging (>2.4 min duration).

Establishing a final destination using radio-assisted surveillance usually resulted in the observer reaching a destination some time after the bird. This problem increased the further the bird travelled from the court. Therefore, all visiting times associated with individual fixes represent minimum feeding times (Table 4.5).

Of the 636 fixes obtained away from the home-courts for the four birds, 128 fixes were confirmed to be to 14 known food trees. The species and number of known food trees were as follows: 12 *Eleocarpus foveolatus*, 1 *Bielschmedia obtusifolia* and 1 *Cryptocarya corrugata* (Table 4.5).

The distances from courts to food trees, established from known male Tooth-bill, food tree interactions, ranged from 19 to 391m, with a median dispersal distance of 31.4m (Table 4.6). Birds fed high in the canopy and swallowed fruit whole. Radio-tagged individuals were readily identified by the antenna extending beyond the tail and by the presence of paint beneath the outer tail feathers.

TABLE 4.5: Visit times and distances to the home courts of male Tooth-bills to three species of known feed trees (*Eleocarpus foveolatus, Bielschmedia obtusifolia, Cryptocarya corrugata*).

Tree no.	Species	C[1]	DBH (cm)	fixes[2]	total visits to tree (min)	mean (min)[3]	SD	nv[4]	distance (m)[5]
20	*E. foveolatus*	L	32	16	60.5	3.8	3.2	1	133.5
21	*E. foveolatus*	L	38	12	25.8	2.2	1.9	2	43.2
28	*B. obtusifolia*	L	30	6	49.5	8.3	6.3	2	162.7
43	*E. foveolatus*	L	25	2	5.8	2.9	0.5	1	59.4
45	*E. foveolatus*	L	25	34	275.8	8.1	10.5	3	26.0
51	*C. corrugata*	I	38	1	0.9	0.9		1	309.7
52	*E. foveolatus*	I	33	1	1.2	1.2		1	209.3
56	*E. foveolatus*	L	85	2	9.5	4.8	5.1	2	265.4
57	*E. foveolatus*	L	58	5	25.4	5.1	3.3	1	371.1
58	*E. foveolatus*	I	30	4	22.1	5.5	3.1	2	242.7
59	*E. foveolatus*	I	48	1	12.4	12.4		1	391.4
60	*E. foveolatus*	L	30	4	23.1	5.8	5.2	2	99.0
61	*E. foveolatus*	I	45	1	2.3	2.3		1	386.8
66	*E. foveolatus*	L	38	39	196.8	5.1	4.8	2	29.2
TOTALS				128	710.9	5.6	6.7	4	84.5

[1]C=Crop size: (I) Intermediate, (L) Large,
[2]Fixes= Number of fixes; [3]mean= mean duration of visits (mins),
[4]nv=Number of visitors to tree, [5]distance= mean distance from known food trees to home courts of visitors.

TABLE 4.6: Descriptive statistics for dispersal distances between known food trees and home courts over the display season, for male Tooth-bills, based on individual fixes.

Bird number	Number of fixes	Median distance (m)	Minimum	Maximum
23	58	27.2	27.2	133.5
33	20	42.4	35.1	295.1
35	20	19.2	19.2	309.7
37	30	119.6	27.8	391.4
TOTAL	128	31.5	19.2	391.4

The 128 fixes to known food trees resulted from 66 individual foraging bouts away from courts. In any one foraging bout, a number of fixes were often obtained. A foraging bout was therefore defined as, the accumulation of fixes (movements) obtained between the time a bird departed the court until its return. These bouts were used as the best estimates of feeding duration.

Table 4.7 presents descriptive statistics for foraging times for male Tooth-bills. The distributions of times was strongly skewed to the left, that is, short foraging bouts were more frequent than longer bouts. Thus food trees closer to the home court were visited more frequently than those further away (Fig. 4.5). Some trees were clearly more favoured than others, and again these proved to be trees closer to the home court (Table 4.7). There was a significant correlation between distance and foraging time ($r=0.3257$ $df=64$ $p>0.0076$) indicating the obvious association in the greater the distance to a known feed tree the longer the foraging time.

TABLE 4.7: Descriptive statistics for foraging times (min), for male Tooth-bills over the display season, based on known foraging bouts to food trees.

Bird number	number of foraging bouts	Median foraging time (min)	Minimum foraging time (min)	Maximum foraging time (min)
23	22	16.8	2.4	50.0
33	14	16.9	3.5	65.3
35	12	11.3	3.0	74.6
37	18	23.6	3.7	55.9
TOT	66	18.2	2.4	74.6

4.3.4.2 Post foraging behaviour

Post foraging behaviour is an essential component of seed dispersal, as what the bird does after feeding determines where the seeds will be deposited and how effective the bird will be as a disperser. If a bird exhibits sedentary behaviour after feeding, and remains in that tree to digest fruits consumed, then seeds may be deposited beneath the tree of origin (ineffective dispersal). In contrast, birds that quickly depart a feed tree once fruits are consumed will remove seeds from the parent tree (effective dispersal). Of the foraging bouts observed at known food trees, 85.5% resulted in direct return flights back to the court post feeding. Return flight times were readily determined since departure from the food tree was recognised by signal loss and or visual observation, and subsequent arrival back at the court was registered by the observer at the court.

4.3.4.3 Pattern of all bouts at and away from the court

The distribution of all bouts away from the court in time are shown in Fig 4.6 (median=12.4min, range=0.1-90.8min, n=225). This illustrates that male Tooth-bills make many more short forays (<15 mins) from the court than long forays.

After returning from a foraging bout, males would either remain silent above the court or begin calling, displaying or maintaining the court by arranging leaves. The distribution of durations of all bouts at the courts is shown in Fig 4.7, (median=6.2, range=0.07-119.4min, n=234). This similarly, illustrates that more short bouts (< 10 mins) occur at the court than long.

TABLE 4.8: Results of three Way Fixed Factor Analysis of Variance examining the effect of month, time period and bird on the frequency of bouts at and away from the court.

Source	df	F	p
Month	2	0.58	0.569
Time period	3	1.76	0.194
Bird	3	1.14	0.364
Month x Time period	6	0.31	0.923
Time period x Bird	9	0.58	0.795
Month x Time period x Bird	16		
TOTAL	39		

There were no significant effects of month, time period or bird on the frequency of bouts at and away from the court for male Tooth-bills over the display season (Table 4.8). This suggests that the frequency of movement to and from the court changed little over the season.

4.3.4.4 Estimated gut retention times

During 120 hours of observation, male Tooth-bills were never once observed regurgitating seeds, either at the court or throughout their foraging range. Similarly, Cliff and Dawn Frith who have observed Tooth-bills for countless hours at court sites, nests and feeding in the canopy, have never once observed a bird regurgitating seeds (Frith and Frith 1985a, Frith and Frith pers comm). In all instances seeds were defecated, which means that seeds take some time to pass through the gut.

It was not possible to obtain gut retention times for male Tooth-bills. Retention times were therefore estimated from data presented by Murray (1988). In the three bird species examined by Murray, gut retention times were enormously variable for the small seeded (1-3mm) plant species examined. For one small seeded plant species consumed, (*Phytolacca rivinoides*), times ranged from 12-28min for *Phanoptila melanoxantha* (the Black and Yellow Silky flycatcher), 4-63min for *Myadestes melanops* (the Black-faced solitaire) and 15-81min for *Semnornis frantzii* (the Prong-billed barbet).

Male Tooth-bills are at least four times the weight of the bird species examined by Murray, and fed on large seeded species (5-20mm). Given that large seeded species are voided more quickly than small seeded species (Levey 1986a, 1987), the shortest gut retention estimates were used to estimate male Tooth-bill gut retention rates. This corresponded to Murray's data for *Myadestes melanops* consuming *Witheringia solanacea*. The hypothetical gut retention times for male Tooth-bills, based on this data, are presented in Fig 4.8. Based on these hypothetical times, the majority of seeds are deposited within 30min of digestion.

4.3.4.5 Assumptions and calculations for Model II

Model II estimated the probability of seed being deposited at the court, using data on bouts at and away from the court, non-sedentary post-feeding behaviour and hypothetical gut retention times. Probabilities were calculated using a program written in Basic and is based on the following assumptions and calculations (Appendix 4.3) (Lokkers pers. comm.). Firstly, the model assumes that seeds are consumed at the mid point of each foraging bout then sums the probabilities of seed deposition for each subsequent 5 min block for that bout. It then continues to sum these probabilities for each 5 min block during the subsequent bout at the court for the same gut retention cycle. It continues the cycle until the cumulative probability is equal to one. With each subsequent foraging bout, the process is repeated.

In this model, seeds from more than one foraging bout may be present in the gut simultaneously. In these instances probabilities of seed deposition were calculated based on the rule that either A or B or both can occur where,

$$Pr(A \text{ or } B)=Pr(A)+Pr(B)-Pr(A \text{ and } B).$$

In instances where observation periods change (i.e. 0600-0900h to 0900-1200h), the final seed deposition probability obtained from the previous observation period is used as the starting point for the next observation period. That is, by 0900h the bird is more likely to have some seeds in the gut than no seeds, whereas first thing in the morning (0600h; pre-feeding) it is likely to have no seeds in the gut. For each 3h observation period, the cumulative probabilities (expressed as a percentage of seeds deposited) for each bout at and away from the court are presented and used in the remaining calculations.

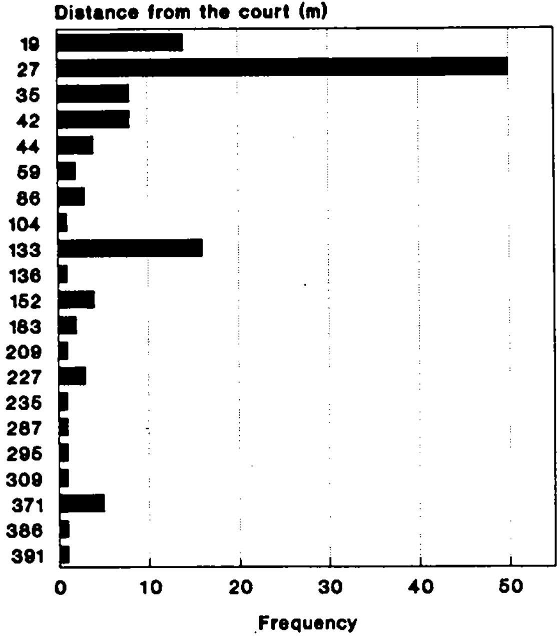
4.3.5 Comparison of the probability of seeds being deposited at the court for Model I and Model II

If the hypothetical gut retention times (Section 4.3.4.4) are superimposed over the birds behaviour even at the most simple level (in this case time intervals or bouts at or away from the court), then Model II better estimates the probabilities of seeds being deposited at or away from the court than those derived from Model I (which uses total proportions of time at the court, Section 4.3.3).

Using Model I and assuming constant seed deposition rates, 46.4% of seeds were deposited at the court (SE=2.3, range=7.6-91.1%, n=40). Using Model II and assuming variable deposition rates based on hypothetical gut retention times, 68.13% of seeds were deposited at the court (SE=1.5 range=46.7-94.3% n=40). Thus Model II predicts more deposition in the court site than Model I. This suggests that bird behaviour and digestion are of considerable importance in determining patterns of seed dispersal by avian frugivores. Although these estimates could be improved with more a accurate understanding of gut retention times, this basic conclusion is unlikely to change: that is, that a disproportionately large number of seeds consumed by the birds will be deposited back at the court.

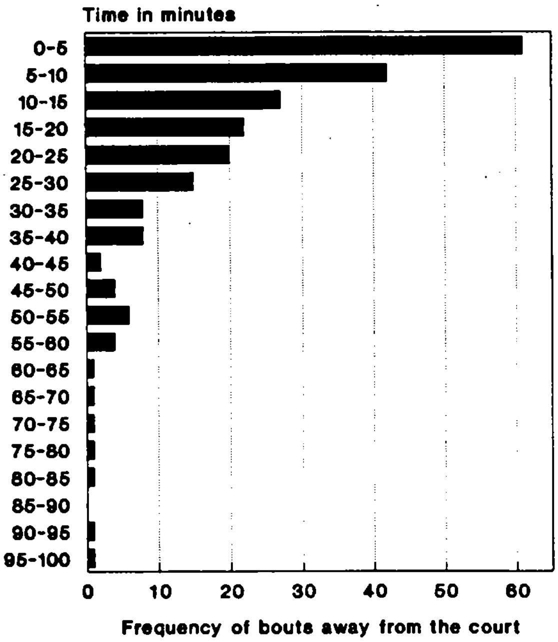
Fig 4.5

Effect of distance on the frequency of visits to known feed trees by male Tooth-billed Bowerbirds



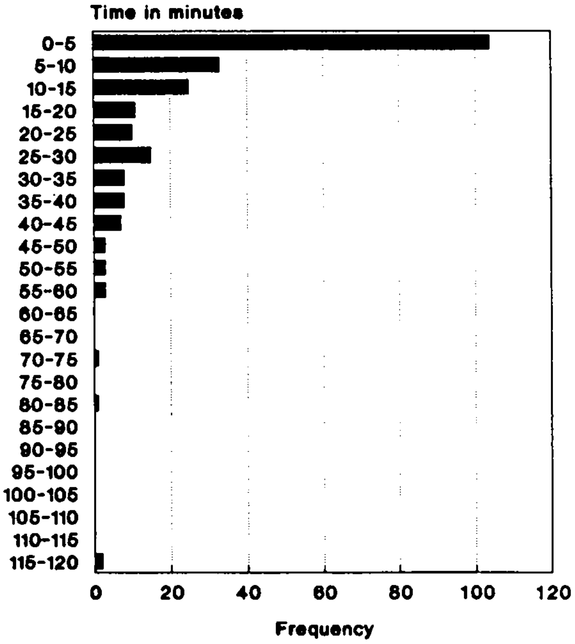
(n=128 fixes)

Fig 4.6
Time frequency of bouts away from the court by male Tooth-billed Bowerbirds



(n=226 bouts obtained from 4 males)

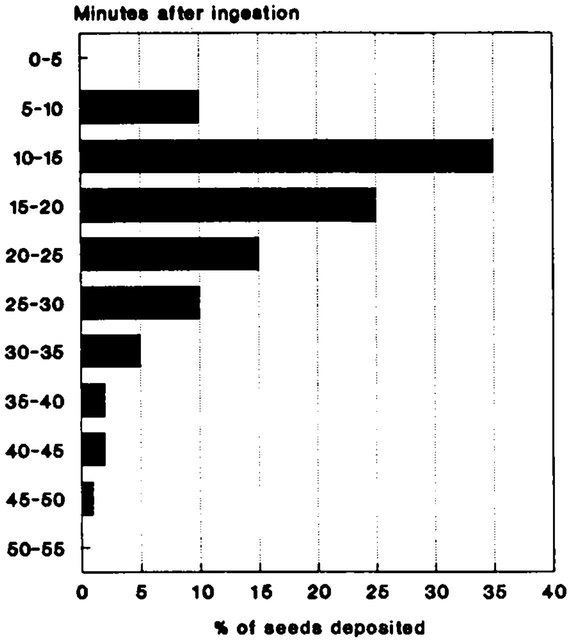
Fig 4.7
Time frequency of bouts at the court by male Tooth-billed Bowerbirds



(n=234 bouts obtained from four males)

Fig 4.8

Hypothetical gut retention times for male Tooth-billed Bowerbirds.



(Modified from Murray 1988)

4.3.6 Summary of Results

Timed movements, foraging behaviour and home ranges of four, adjacent male Tooth-bills within an exploded lek was investigated over the 1989-90 display season.

i) Displaying male Tooth-bills had a mean home range area of 9.5ha. The ranges of individual birds overlapped other males by up to 50%.

ii) The birds spent 50% of daylight hours within the home court area. Much of this time was spent calling from a single song post. Males also roosted above their courts.

ii) Foraging bouts were generally short, with a median duration of 12.4 mins (range 0.1- 90.7 mins, n=225).

iv) Bouts at the court were also short, with a median duration of 6.2mins (range 0.1-119.4mins, n=234).

v) Median foraging distances away from the court ranged from 40-86m for the four birds, with maxima of 311-391m.

vi) Probabilities of seed being deposited at specific distances away from the home court were calculated assuming constant seed deposition rates (Model I). Model I predicted that 46% of seeds consumed was deposited at the court. A second model, detailing actual foraging bouts at and away from the court and hypothetical gut retention times suggests that 68% of seeds would be deposited at the court (Model II). This model assumed variable seed deposition rates.

vii) Radio tracking and behaviour observations were recorded during a poor fruiting season (1989-90; refer to Chapter Two).

4.4 DISCUSSION

4.4.1 Dispersal Distances

The seed dispersal service provided by male Tooth-bills resembled that provided by the species examined by Murray (1988). Similarities, included dispersal distances from the parent tree, seed consumption and seed deposition (i.e fruits were swallowed whole and deposited in a viable state away from the feed tree). The patterns of dispersal and bird behaviour were, however, different.

The median dispersal distances for male Tooth-bills over the display season ranged from 40-86m. Murray (1988), obtained similar median dispersal distances ranging from 35-60m for nine bird species/plant species combinations. The comparable distances calculated by Murray (1988) and this study suggest similarities in the spatial distribution of fruiting trees within his study area and those in the present study. Also, none of the birds examined in the present study and in Murray's study exhibited sedentary post-feeding behaviour (i.e. feeding at trees with large crops and then remaining in the same tree to digest the food). Both studies indicate that frugivores effectively move seeds beyond the parent crown and beyond the influence of distance responsive mortality agents for seeds and seedlings associated with parent trees (Howe 1989).

Maximum dispersal distances for this study exceeded 390m, while those obtained by Murray exceeded 500m. Estimates provided by other studies for the dispersal of large seeded species (5-20mm) are based on few visual observations of behaviour and are biased toward short dispersal distances (Murray, 1988). Murray (1988) commented that this bias not withstanding, "it is unlikely that large seeds are dispersed as far as much smaller seeds", on the basis that (i) large seeds are voided more rapidly than small seeds (Levey 1986a, 1987, Murray 1988) and (ii) frugivores with large crops tend to exhibit more sedentary behaviour such that they fly short distances after a large feed and tend to sit and process the seeds before flying to a new resource or returning to the same resource (Pratt and Stiles 1983).

The assumptions described above for the dispersal pattern of large fruits by avian frugivores disagree with the results of this study. Male Tooth-bills were consuming mostly large seeded species (40 of the 51 species consumed contained large seeds of 5-20mm: refer to Chapter Five) and dispersal distances were not greatly dissimilar from those recorded by Murray for small-seeded fruit species. Further, despite crop size, male Tooth-bills made rapid return flights to the court at the end of feeding bouts rather than displaying sedentary behaviour at the fruiting tree. The potentially large dispersal distances for male Tooth-bills appears to be the product of a number of factors.

Firstly, over the display season male Tooth-bills, as with other lek-breeding bird species, need to stay in close proximity to their court if they are to successfully display and attract females to mate (Snow 1962a, 1962b, Lill 1974a, 1974b). Thus, irrespective of the size of the meal eaten or the distance travelled to the food source, males return directly to the court to defend it from leaf stealing rivals and to call and display. In effect, male Tooth-bills attempt to minimise time away from the court foraging, and maximise time at the court calling and displaying. In so doing, male Tooth-bills will invariably disperse seeds away from the parent tree at which they feed.

Secondly, male Tooth-bills could be classified as an intermediate sized disperser, ranging in weight from 142-168g (Chapter Two, Section 2.3). They are four times as large as the dispersers examined by Murray and their ability to carry a larger load is therefore proportionally greater. Furthermore, in most cases the seed load was carried more than 100m uphill from the creeks to the ridge-tops where the courts were located.

Finally, the major reason for the potentially short median dispersal distances for male Tooth-bills is not because of quick voiding times combined with sedentary behaviour, as suggested by Murray (1988) and others. Rather, they are a result of behavioural constraints imposed by their breeding system. Similarly, the greatest dispersal distances recorded (>390m) resulted from the bird's need for water. None of the observed movements of the Tooth-bills away from their courts appeared to be the result of random movement patterns.

4.4.2 Patterns of dispersal.

The foraging behaviour of the three frugivorous species examined by Murray (1988) alternated between brief episodes of rapid movement, followed by relatively long stationary periods of 7-12 mins, while the bird was presumably feeding. These data correspond with observations of feeding behaviour in captive birds. In these trials, the birds were observed to feed and then perch virtually motionless for approximately 10 min before moving about the cage in search of more fruit (Murray 1988). Male Tooth-bills displayed a similar type of feeding behaviour. Each of the birds radio-tracked was observed to move rapidly to and from the feeding sites, spending a median time of 12 min feeding. However, the Tooth-bills differed in that they were not observed flying to another tree to feed (random movement), rather, the birds were observed returning to a fixed site in the forest in which many seeds were deposited (non random movement). In this respect, male Tooth-bills provide a totally different dispersal service to those species examined by Murray (1988). Male Tooth-bills were non-random, clump dispersers, whereas the species examined by Murray were random, scatter dispersers.

During the display season, when bird behaviour is directed toward breeding, seed dispersal patterns may differ greatly from patterns observed at other times of the year. When a male Tooth-bill is not compelled to remain within the court area, behaviour and subsequent pattern of seed dispersal may be similar to those described by Murray (1988). If this is the case, male Tooth-bills may alternate seasonally from non random, clump dispersers to random scatter dispersers and hence vary the type of seed dispersal service they offer to rainforest plants, depending on the abundance of fleshy fruits.

4.4.3 Elements of non random movement; safe sites.

An elusive concept presented by Howe and Smallwood (1982) is that of "directed dispersal", where a frugivore takes seeds to a specific non-random site, where seed and seedling survival and growth are high. Harper (1977) called these "safe sites", where seed survival, germination, establishment and growth are capable of being fulfilled. To date, the only example of directed dispersal even vaguely associated with rainforests is Flower-peckers (Dicaidae) dispersing Mistletoes (Loranthaceae) (Davidar 1983). This group of parasitic plants is restricted to the canopy and are therefore not typical of the reproductive strategies of most rainforest trees. However, while the concept of directed dispersal has yet to be observed for rainforest trees, there are sites within the rainforest that are more favourable to plant growth which may be considered "safe sites".

The successful dispersal of many rainforest plant species generally requires dispersal to light gaps. Directed dispersal to gaps has been suggested by movement of frugivores to fruiting herbs and shrubs within gaps (Blake and Hoppes 1986, Levey 1986b), however data obtained by Murray (1988) for gap dependent plants refutes this.

Male Tooth-bills return to the same site on the forest floor year after year to establish their courts, and some birds have returned to the same site for 13 years (see Section 2.3) (Frith and Frith unpub.). These sites move very little between years. In the event of a tree fall, males will release the original court site for that year, establishing an alternative court at the gap edge. In the subsequent year however, males will often return to the original court site (Frith and Frith pers. comm.). This extremely high site fidelity amongst male Tooth-bills results in seeds being deposited in very specific sites on the forest floor sites over the peak fruiting period every year. Of 32 known birds on the Paluma site, three birds had courts in or associated with light gaps (see Chapter Two, Section 2.4.3). This meant that not only were male Tooth-bills involved in non-random dispersal of seed to very specific sites on the forest floor, but 8% of the population were also depositing seeds into light gap areas, evidence for "directed dispersal".

4.4.4 Comparison of the two models for estimating seed dispersal.

The seed dispersal Models I and II presented in this study describe different possibilities for the patterns of seed deposition by male Tooth-bills. Model I, based on the proportion of time spent at and away from the court, and assuming constant deposition rates, results in 46.4% of seeds consumed being deposited at the court. Model II, which is based on actual bird behaviour (bouts at and away from the court) assuming variable deposition rates (based on hypothetical gut retention times), results in a much greater proportion of seeds being deposited at the court (68.1%). Clearly, the tendency for male Tooth-bills to return quickly to the court after feeding and then spending a considerable amount of time at the court, results in far greater seed deposition at the court than would be expected otherwise. With the lack of accurate gut retention data for male Tooth-bills, this is a best guess scenario.

4.4.5 Ecological consequences of seed dispersal by male Tooth-bills

Regardless of the actual proportion of seeds deposited, male Tooth-bills deposit large quantities of seeds of different plant species at a specific site on the forest floor at a specific time of year, (corresponding with the peak fruiting season, and immediately prior to the wet season) for the duration of their reproductive lives. These sites are no longer exposed to effects of the parent tree, such as allelopathy (Connell 1971), but are still exposed to density-dependent mortality (Janzen 1970).

Howe (1989) suggested that a basic dichotomy exists between plant species that is based on their mode of dispersal. He suggests clump dispersed plant species should be adapted for survival in dense aggregations. If this is the case, then clump dispersed species should receive some advantage in being dispersed by male Tooth-bills. The ecological consequences of this dispersal service to the dominant plants consumed by Tooth-bills will be further discussed in Chapters Six, Seven and Eight.

Chapter Five

SEEDS DISPERSED

5.1 INTRODUCTION

Frugivorous birds play a major role as seed dispersers for the propagules of many rainforest plant species. Different bird species provide different dispersal services, and the manner in which they consume fruits, digest and subsequently move and deposit seeds largely determines the fate of seeds and thus the effectiveness of the dispersal agent (Murray 1988).

Most studies view seeds dispersed by avian frugivores from the bird perspective, that is the diet of the bird. Comprehensive diet studies have been limited to a handful of frugivores including: the Oilbird (Snow 1962c, 1979), the Bearded Bellbird and other Cotingas (Snow 1970, 1972, 1977, Snow 1973), Fruit Pigeons (Crome 1975, Frith *et al.* 1976, Innis 1989), Manakins (Snow 1962a, 1962b, Worthington 1982), the Southern Cassowary (Stocker and Irvine 1983) and the Resplendent Quetzal (Wheelwright 1983). Most other studies are largely anecdotal, with short term information on feeding records, gut contents or droppings.

From the diet data available, avian frugivores were broadly classified into those that feed almost entirely on fruits, obligate frugivores, including: the Oilbird, Fruit Pigeons, Cotingas and Toucans, and those species that consume fruits opportunistically, such as: Flycatchers, Thrushes and Finches. Within these two broad groups, the former is likely to contain the greatest proportion of "legitimate frugivores" which include those species that swallow fruits whole and subsequently void viable seeds having only digested the pericarp or other soft parts. Whereas the latter group is more likely to contain those species that discard seeds before swallowing the fruit pulp, or destroy seeds in the gut (Snow 1981, Murray 1988).

The diet of frugivorous birds also defines the suite of plant species dispersed. In situations where birds freight seeds to a specific focal site, the frugivore determines the potential composition of plant recruits for that site. The male Tooth-bill is a legitimate frugivore, feeding almost entirely on fleshy fruits (Frith and Frith pers. comm.). During the display season, male Tooth-bills freight large numbers of seeds to their court sites. The primary aims of this component of the study were to (1) document the suite of large seeded plant species dispersed to court sites by Tooth-bills over the display season, (2) to define the treatment fruits and seeds received having passed through the Tooth-bill gut, and (3) comment on the prospects of recruitment for the different plant species dispersed.

5.2 METHODS

Seeds deposited by male Tooth-bills were monitored over three display seasons; 1987-88, 1988-89 and 1989-90. In the first two seasons, five males were selected from two adjacent 10ha sites, one logged and the other unlogged. Males were not selected at random, rather those males that exhibited high perch fidelity were chosen (i.e. their droppings fell in one or two distinct piles adjacent to the court). A dropping trap (66cm in diameter- giving an area of 250cm^2) was used to collect defecated seeds. The trap was placed in an area adjacent to the court 2 to 3 weeks prior to the establishment of court sites to ensure the birds would not move in response to an unfamiliar object. Once the birds had established their courts, the trap was placed under the perch most frequently used by each bird. In some instances birds were unsettled by the traps and moved to a new perch, in which case the trap was shifted beneath the new perch and so on until the bird accepted the trap.

Seeds deposited in each trap were collected weekly or in some cases fortnightly, and all samples were placed in plastic bags to avoid seed desiccation. Samples were classified into three types:

i) complete, where large deposits of seed were collected from the trap and no subsidiary seed piles were observed on the ground in the court.

ii) partial, where small deposits of seed were collected from the trap and subsidiary seed piles were observed on the ground in the court, indicating the bird was using more than one perch

iii) incomplete, where no seeds were deposited in the trap and one or more seed piles were observed on the ground in the court indicating the bird had moved its perch. In these cases

seeds were collected from the ground.
Only complete samples (i) were used for analysis.

Samples were sorted through a series of graded sieves, providing three size classes of seed:
i) Class one, large seeds (>4mm),
ii) Class two, intermediate to small seeds (2-4mm)
iii) Class three, very small seeds (<2mm).
All seeds in size classes one and two were sorted, identified to species and counted. In addition, levels of fruit/seed digestion and rodent damage was also noted.

Large to small seeds (seed size classes one and two) were examined in detail (Table 5.1 and 5.2), whereas very small seeded species (seed size class three) were largely excluded from detailed examination (Table 5.2).

Very small seeded species were excluded for a number of reasons: Firstly, processing and separating enormous numbers of very tiny seeds, given the already vast number of larger seeds that needed to be sorted, was viewed as an ineffective use of time. Secondly, Figs within the study site were exclusively hemiepiphitic forms (pers. obs.). This means that effective germination and establishment can only occur within the rainforest canopy. As Tooth-bills disperse seeds from the canopy to the forest floor, they provide ineffective seed dispersal for these species and thus exclude these species by default from further examination. Thirdly, both *Ficus destruens* and *F. watkinsiana* seeds were present in the diet of Tooth-bills and in seed fall traps during the 1987-88 display season. Separating and subsequently counting the seeds of these two species proved intractable. Finally, attempting to approximate numbers of seeds per fruits also proved inaccurate as numbers of seeds in each fruit was enormously variable.

Digestion of the fruit/seed in each sample by the Tooth-bills was classified as:
i) complete, where all pericarp and associated flesh was digested from the seed
ii) partial, where various amounts of pericarp and flesh remained attached to the seed
iii) no digestion, where the pericarp of the seed was little modified from digestion.

Seeds were occasionally preyed upon by rodents after being deposited by male Tooth-bills. Seeds were scored for this type of activity with (i) no damage, where seeds were undamaged, and (ii) damaged, where rodent teeth marks were obvious on the seed.

All numbers presented within the text refer to numbers of seeds (the plant perspective) rather than numbers of fruits (the bird perspective) unless otherwise specified. Relative proportion, by volume, was used to provide a descriptive overview of the relative abundance of very small seeded plant species deposited within Tooth-bill courts. The volume of very small seeded species within each sample was estimated using the following categories: 0, 0-25%, 25-50%, 50-75%, and >75%.

For each species collected a reference sample was taken and preserved in 70% alcohol. A list of the species collected is given in Appendix 6.1. A second sample was taken, where possible, for subsequent germination trials (see Chapter Six) and to aid identification.

Due to the time constraints imposed by the radio tracking component of this study the amount of time spent directed to seed collection and sorting was limited in the third season (1989-90; see Chapter Four). Instead, droppings were collected daily from beneath the perches of the four males being radio-tracked. All four males were dominant birds within the logged site. The accumulated droppings of other Tooth-bills were collected, where possible, between radio-tracking periods.

5.3 RESULTS

5.3.1 Total numbers of species and individuals

A total of 51 plant species were deposited by male Tooth-bills at court sites over the three display seasons from 1987 to 1989 (seeds >=2mm 23647, fruits 21754), (Tables 5.1 and 5.2).

Of the seeds deposited, 40 were large seeded species (>4mm, 20771 seeds, 20536 fruits), six were intermediate to small species (2-4mm, 2876 seeds, 1218 fruits) and three were very small seeded species (<2mm, unknown number of seeds and fruits), (Table 5.1 and 5.2).

Some 40 species bore fruits containing a single seed, eight species contained 2-5 seeds and the remaining three species contained greater than 100 seeds (Table 5.1 and 5.2). Three of the species placed in the single seed category: *Acronychia acronychiodes*, *Acronychia vestida* and *Halfordia scleroxyla* (Rutaceae), have four seeds contained in a solid woody capsule within each fruit. In all instances, the woody capsules passed through the Tooth-bill gut as a single undamaged unit, retaining the seeds within. The single woody unit was therefore referred to as a single seed.

TABLE 5.1: Summary of all large seeds (>4mm) deposited by male Tooth-bills over three seasons at the unlogged and logged sites (Paluma).

Family and species	Spp id#	Display season and site					TOTAL Seeds (Fruits)
		1987		1988		1989	
		Logged	Unlogged	Logged	Unlogged	Logged	
Family Elaeocarpaceae							
Elaeocarpus foveolatus	6	2415	594	17	835	1888	5749
Elaeocarpus largiflorens	14	466	165	725	578	7	1941
Elaeocarpus elliffi	157					151	151
Sloanea langii	16	33		22			55
Sloanea macbrydei	40	2		2			4
Elaeocarpus grandis'							
Family Lauraceae							
Litsea connonsii	20	6	532	942	676	1	2157
Endiandra dielsiana	25	11	5	488	1623		2127
Cryptocarya densiflora	5	489	362	793	430		2074
Cryptocarya leucophylla	13	52	73	77	20	4	226
Endiandra hypotephyra	119			25	163	17	205
Endiandra wolfei	114			4	63		67
Cryptocarya corrugata	102			13	9	24	46
Bielschmedia obtusifolia	117			1	35	2	38
Bielschmiedia collina	28	10	1			3	14
Unknown	161					7	7
Family Symplocaceae							
Symplocus cochinchinensis (?)	23	1409	311		31		1751
Family Myrtaceae							
Syzygium johnsonii	106			968	519		1487
Syzygium wesa	98			62	108		170
Syzygium sp	32	2					2
Syzygium papyraceum	43			1			1
Family Rutaceae							
Acronychia acronychiodes	1	47	928	26	308	94	1403
Acronychia vestida	2		1				1
Halfordia scleroxyla'	3						
Family Vitaceae							
Cissus hypoglauca	8	24 (8)	33 (11)	30 (10)	251 (84)	2 (1)	340 (114)
Family Apocynaceae							
Alyxia spicata	7	61	207	4	30	6	308

Family and species	Spp id#	Display season and site					TOTAL Seeds (Fruits)
		1987		1988		1989	
		Logged	Unlogged	Logged	Unlogged	Logged	
Family Smilacaceae							
Smilax glycophylla	26	25	44	9	14		92
Family Podocarpaceae							
Podocarpus elatus	129				72		72
Family Sapindaceae							
Henslowia sp	44				33		33
Guioa montana	48				11		11
Family Meliaceae							
Synoum muelleri	35	30					30
Myrcinaceae							
Amesa sp	9	12	4				16
Family Sapotaceae							
Planchonella euphlebia (3-5)	22	1 (1)	6 (2)	2 (1)	1 (1)	1 (1)	11 (6)
Eleagnaceae							
Eleagnus triflora	17	4	1	1		1	7
Icacinaceae							
Apodytes sp	138				1		1
Unidentified							
Unknown	29	30		19	8		57
Unknown	118			6	41		47
Unknown	112			13	27		40
Unknown	39	7	4		1		12
Unknown	120			4	7		11
Unknown (3-5)	143				6 (2)		6 (2)
Unknown	125				1		1
Number of species at each site for each year		21	17	25	29	15	
Total number of species for each year		**22**		**33**		**15**	**40**
Number of seeds at each site for each year		5136 (5120)	3271 (3245)	4254 (4233)	5902 (5731)	2208 (2207)	
Total number of seeds for each year		**8407 (8365)**		**10156 (9964)**		**2208 (2207)**	**20771 (20536)**

[1] Species collected from Tooth-bill courts outside the two study sites (logged and unlogged) in logged forest during 1988. These species were excluded from counts of species and number of seeds in both study sites.

TABLE 5.2: Summary of all intermediate to small seeds deposited by male Tooth-billed Bowerbirds for three seasons, at the logged and unlogged site and outside the study area.

(FAMILY[1]) and species	Spp id#	Display season and site					TOTAL SEEDS
		1987		1988		1989	
		Logged	Unlogged	Logged	Unlogged	Logged	
Small seeded species between 2-4mm in size eaten by male Tooth-bills							
(LO) *Fagraea gracilipes*	4	1(1)	1(1)	155 (39)	898 (225)	29(8)	1084(274)
(AR) *Polyscias australiana*	18	647 (324)	3(2)	117 (59)		275 (138)	1042(523)
(PI) *Piper caninum*	21	169	120		1		290
(RH) *Alphitonia petreyi*	57			239 (80)			239(80)
(AQ) *Sphenostemon lobosporus*	30	2(1)	41(9)	1(1)	99(20)		143(31)
(?) Unknown	124			76(19)	2(1)		78(20)
Very small seeded species <2mm in size eaten by male Tooth-bills							
(RU) *Timonius timon*	33	6.6	4.4	3.1	0.65		
(MO) *Ficus destruens*	34	41.4	25	8.8	21.4	12.2	
(MO) *Ficus watkinsiana*	19	*	*				
Number of species eaten		7	7	7	6	3	9
Number of seeds eaten		819 (495)	165 (132)	588 (198)	1000 (247)	304 (146)	2876 (1218)

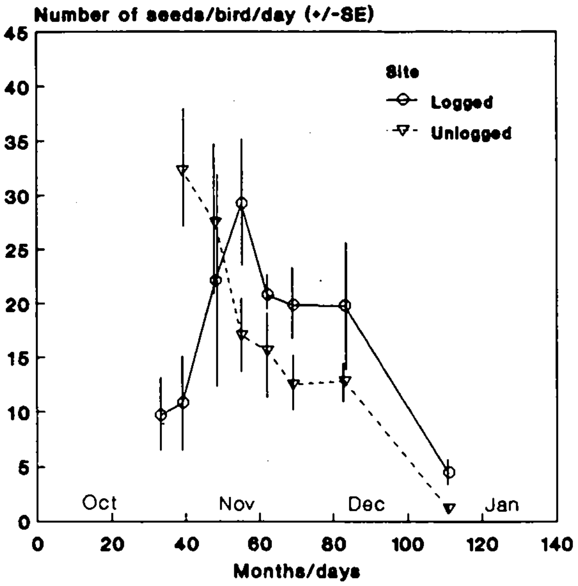
[1] Key to families: LO= Loganiaceae ; AR= Araliaceae ; PI= Piperaceae ; RH= Rhamnaceae ; RU= Rubiaceae ; AQ Aquifoliaceae ; MO= Moraceae

5.3.2 Variation in the mean number of seeds deposited.

Only complete samples and large seeded species were used to examine trends in the mean number of seeds deposited/bird/day. The mean number of large seeds deposited daily by each bird was 14.02 seeds/bird/day (SE=0.67, range=0.01-44.00). The number of seeds deposited at the court by male Tooth-bills was distinctly seasonal. At the start of the display season, seed deposition was low as males spent little time at the court. As the season progressed, seed deposition increased as males became more engrossed with calling and display activities and thus spent more time on favoured perches at the court. Seed deposition then decreased at the end of the display season as display behaviour gradually diminished (Figs 5.1-5.3).

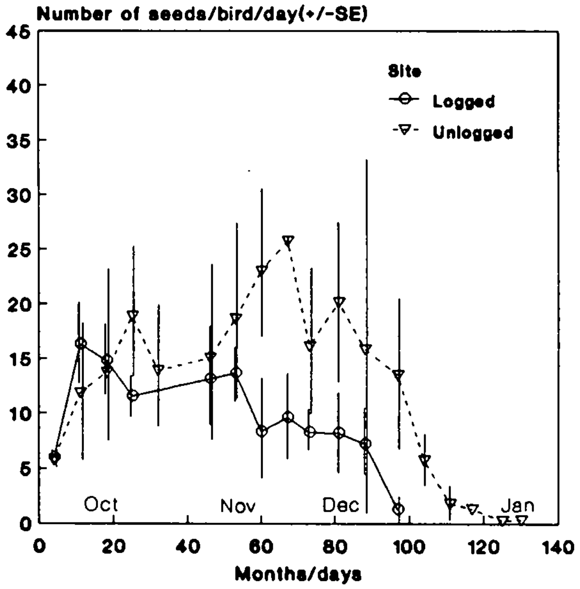
Seed deposition varied between seasons and sites in both duration and form. The 1987 display season extended over 12 weeks. During this time seed deposition peaked in the unlogged site 2 weeks earlier than the logged site (Fig 5.1). The 1988 season differed markedly, with the logged site peaking in the first 2 weeks of the display season and then tailing off to completion at 13 weeks (Fig 5.2). In the unlogged site the display season lasted 19 weeks and the amount of seed deposited by the birds peaked twice. The first peak was at 4 weeks and the second later in the season at 10 weeks (Fig 5.2). During the 1989 display season only the logged site was sampled. The number of species deposited by Tooth-bills in the logged site during the 1989-90 season (18 species), was considerably lower than the preceding two seasons (87-88, 28 species, 88-89 32 species).

Fig 5.1
Seed deposition by male Tooth-billed Bowerbirds over the 1987-88 season.



X axis starts on the 25th of September and finishes on the 5th of February in following year

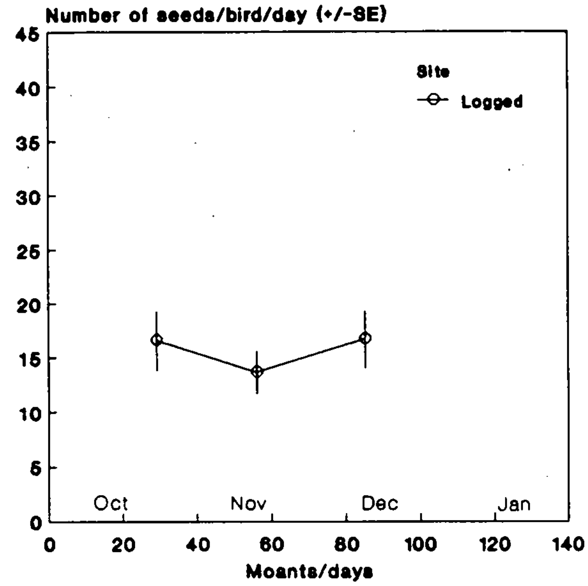
Fig 5.2
Seed deposition by male Tooth-billed Bowerbirds over the 1988-89 season.



X axis starts on the 25th of September and finishes on the 5th of February in following year

Fig 5.3

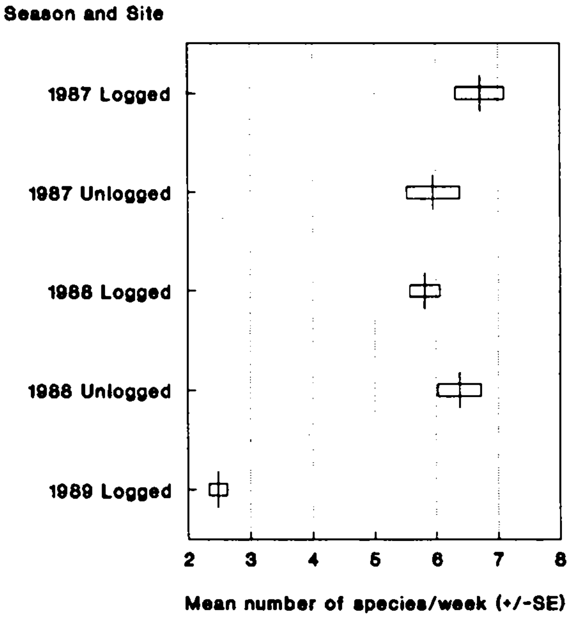
Seed deposition by male Tooth-billed Bowerbirds over the 1989-90 season.



X axis starts on the 26th of September and finishes on the 5th of February in following year

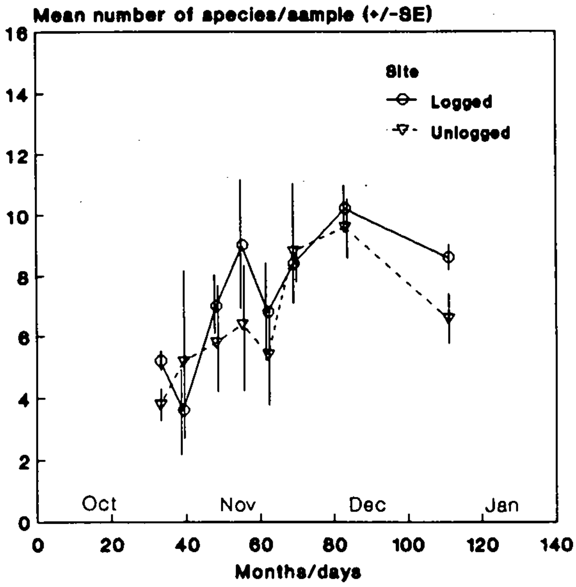
Fig 5.4

Variation in the mean number of species deposited by male Tooth-bills.



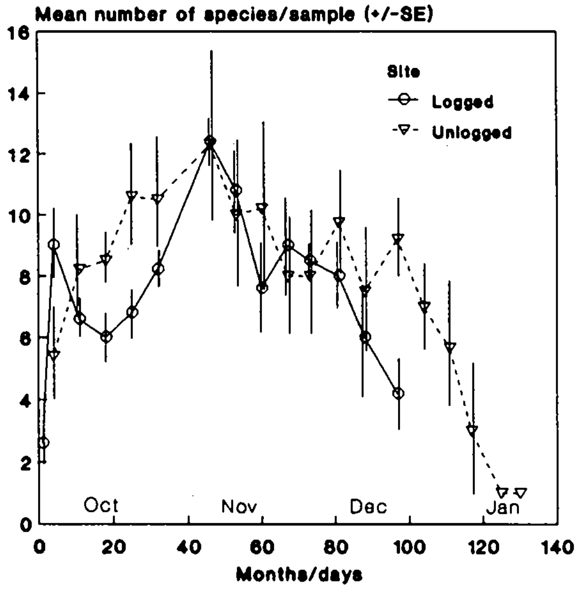
NB: Means obtained from weekly samples over 1987-1989 display seasons

Fig 5.5
Mean number of species deposited by male Tooth-bills over the 1987-88 season



X axis starts on the 25th of September and finishes on the 5th of February in following year

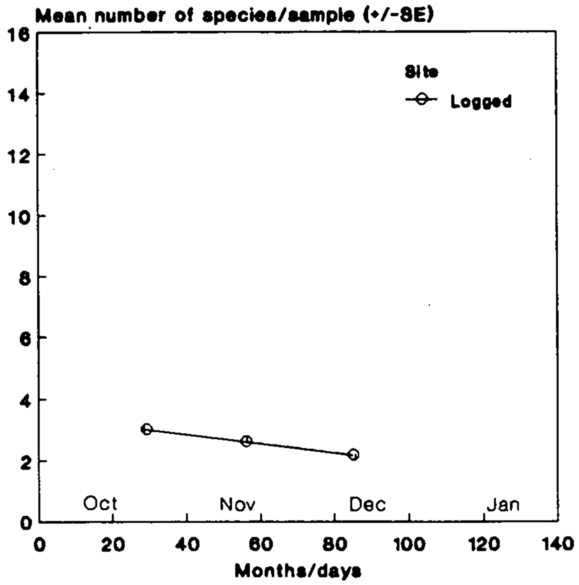
Fig 5.6
Mean number of species deposited by male Tooth-bills over the 1988-89 season



X axis starts on the 25th of September and finishes on the 5th of February in following year

Fig 5.7

Mean number of species deposited by male Tooth-bills over the 1989-90 season



X axis starts on the 26th of September and finishes on the 5th of February in following year

5.3.4 Diet composition; large seeded species, figs and false figs

Over the three seasons, eight fleshy fruited plant species accounted for 90% of the 20,803 large seeds deposited by male Tooth-bills (Table 5.1), with two species of Elaeocarpaceae (37%), three species of Lauraceae (30.6%), and one species of Symplocaceae (8.4%), Myrtaceae (7.2)% and Rutaceae (6.8%).

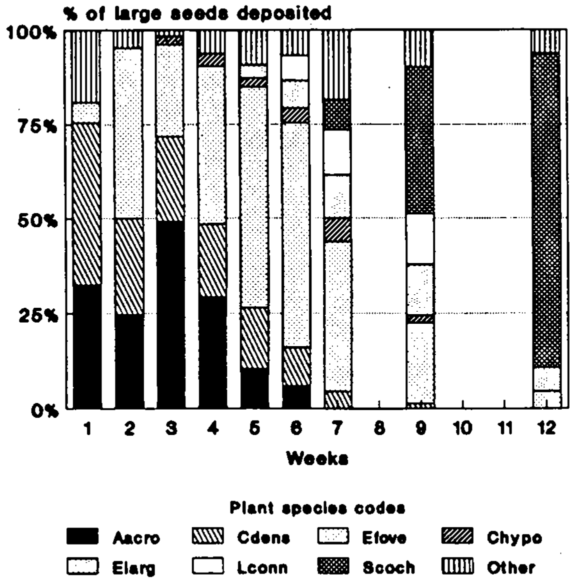
Early in the 1987 display season, *Acronychia acronychiodes* and *Cryptocarya densiflora* were major components of the droppings of male Tooth-bills. As these species declined in abundance, the birds switched to *Elaeocarpus foveolatus*, which was replaced by *Symplocus cochinchinensis* towards the end of the display season (Fig 5.8).

During the 1988 display season, the seeds deposited by male Tooth-bills were dominated by *Syzygium johnsonii* and *Litsea connonsi* early in the season and replaced mid season by *Cryptocarya densiflora*, *Elaeocarpus largiflorens* and *Endiandra dielsiana*. The latter species, together with *Elaeocarpus foveolatus*, were important components of the droppings until the end of the display season.

The most abundant species in the seeds deposited by male Tooth-bills during the 1989 season were *Acronychia acronychiodes* and *Elaeocarpus foveolatus*. The latter species was dominant in the droppings during the entire display season (Fig 5.10).

Figs (*Ficus destruens*, *F. watkinsiana*) and false figs (*Timonius timon*) were both important components of the seeds deposited by male Tooth-bills. In all seasons and sites figs always exceeded 10% of the volume of each sample (Fig 5.11). In 1987, the proportion of figs and false figs accounted for an average of 48% of the volume of each sample in the logged site.

Figure 5.8
Male Tooth-bill diet over the 1987-88 display season.



Plant codes and species:

Aacro - *Acronychia acronychiodes* **(Rutaceae)**

Cdens - *Cryptocarya densiflora* **(Lauraceae)**

Efove - *Elaeocarpus foveolatus* **(Elaeocarpaceae)**

Chypo - *Cissus hypoglauca* **(Vitaceae)**

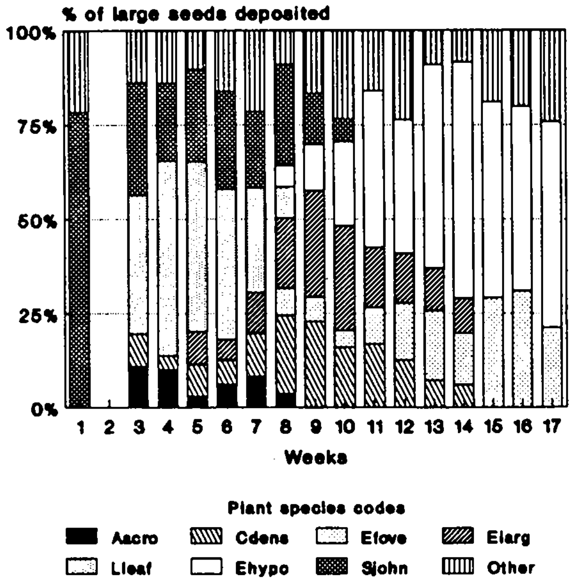
Elarg - *Elaeocarpus largiflorens* **(Elaeocarpaceae)**

Lconn - *Litsea connonsii* **(Lauraceae)**

Scoch - *Symplocus cochinchinensis* **(Symplocaceae)**

Other - Remaining species

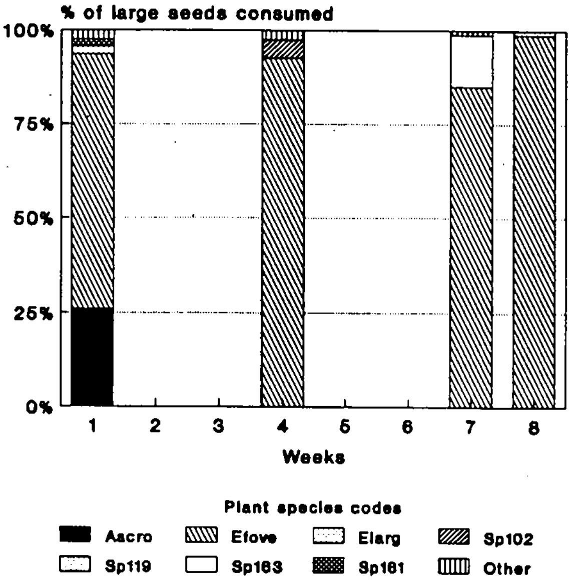
Figure 5.9
Male Tooth-bill diet over the 1988-89 display season.



Plant codes and species:

Aacro - *Acronychia acronychiodes* **(Rutaceae)**
Cdens - *Cryptocarya densiflora* **(Lauraceae)**
Efove - *Elaeocarpus foveolatus* **(Elaeocarpaceae)**
Elarg - *Elaeocarpus largiflorens* **(Elaeocarpaceae)**
Lconn - *Litsea connonsii* **(Lauraceae)**
Ediel - *Endiandra dielsiana* **(Lauraceae)**
Sjohn - *Syzygium johnsonii* (Myrtaceae)
Other - **Remaining species**

Figure 5.10
Male Tooth-bill diet over the 1989-90 display season.



Plant codes, species and families:

Aacro - *Acronychia acronychiodes* **(Rutaceae)**

Efove - *Elaeocarpus foveolatus* **(Elaeocarpaceae)**

Elarg - *Elaeocarpus largiflorens* **(Elaeocarpaceae)**

Sp102 - *Cryptocarya corrugata* **(Lauraceae)**

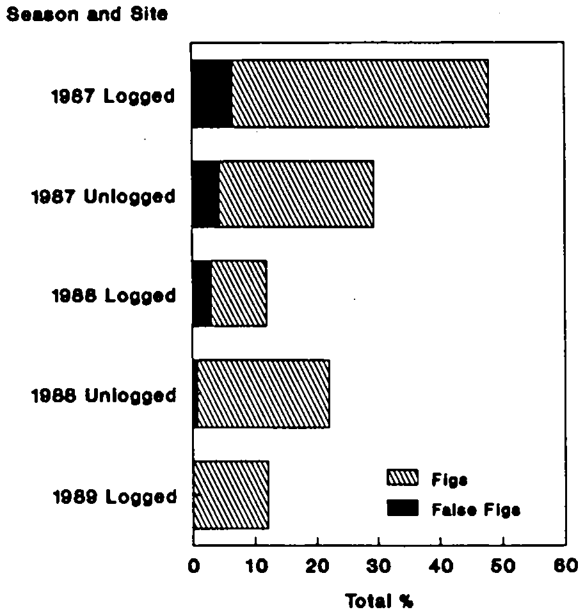
Sp119 - *Endiandra hypotephyra* **(Lauraceae)**

Sp157 - *Elaeocarpus elliffi* **(Elaeocarpaceae)**

Sp161 - **(Lauraceae)**

Other - **Other plant species**

Fig 5.11
Percentage of Figs and False Figs in male Tooth-bill diet



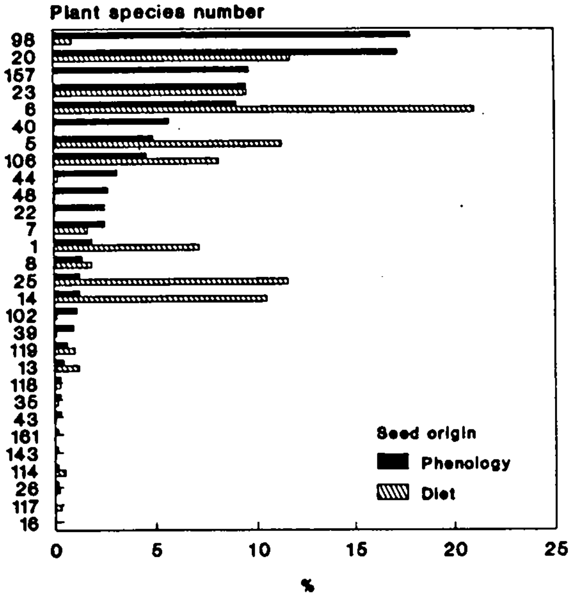
False Figs (*Timonius timon*)
Figs (Ficus destruens, F. watkinsiana)

5.3.5 Fruiting Phenology and Diet.

The male Tooth-bill display season corresponded to the late dry, early wet season peak in fleshy fruit production in each of the years examined (refer to Chapter Three).

Of the 40 large seeded species present in the diet over the display season, 29 were present in the fruit and seed fall traps used in the phenology component of this study (Chapter Three). The proportions of large-seeded species in the diet did not reflect the proportions present in the habitat (Fig 5.12). Male Tooth-bills consumed a greater proportion of six tree species than were represented in the habitat, including: *Elaeocarpus foveolatus*, *Cryptocarya densiflora*, *Syzygium johnsonii*, *Acronychia acronychiodes*, *Endiandra dielsiana*, and *Elaeocarpus largiflorens* (Figs 5.12 and 5.13). They consumed a lesser proportion of six tree species than were represented in the habitat, including: *Syzygium wesa*, *Elaeocarpus elliffi*, *Sloanea macbrydii*, *Henslowia sp.*, *Guioa montana*, and *Planchonella euphlebia* (Figs 5.12 and 5.13). And consumed three species which were represented in approximately equal proportions in both the diet and habitat, including: *Symplocus cochinchinensis*, *Alyxia spicata*, and *Cissus hypoglauca* (Figs 5.12 and 5.13). Even though the proportions of dominant species within phenology fruit fall traps differed between sites, similar trends in preferences were evident at both sites (Fig 5.13 and 5.14).

Fig 5.12
Fruiting phenology/diet comparison
for male Tooth-bills



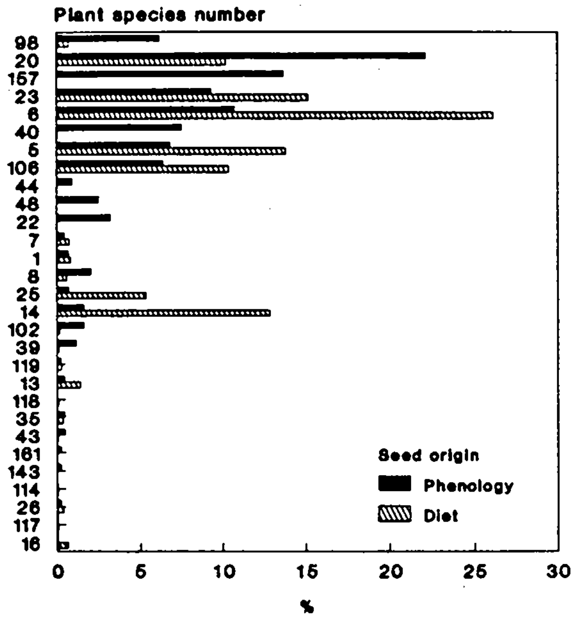
NB: Pooled data from both sites for
large seeded plant species
No of seeds:Phenology (632), Diet(18346)

Number/Plant species:

98	*Syzygium wesa*
20	*Litsea connonsii*
157	*Elaeocarpus elliffi*
23	*Symplocus cochinchinensis*
6	*Elaeocarpus foveolatus*
40	*Sloanea macbrydei*
5	*Cryptocarya densiflora*
106	*Syzygium johnsonii*
44	*Henslowia sp*
48	*Guioa sp*
22	*Planchonella euphlebia*
7	*Alyxia spicata*
1	*Acronychia acronychiodes*
8	*Cissus hypoglauca*
25	*Endiandra dielsiana*
14	*Elaeocarpus largiflorens*
102	*Cryptocarya corrugata*
39	Brain nut
119	*Endiandra hypotephyra*
13	*Cryptocarya leucophylla*
118	White Litsea
35	*Synoum muelleri*
43	*Syzygium papyraceum*
161	Unknown (Lauraceae)
143	*Drypetes australasica*
114	*Endiandra wolfei*
26	*Smilax glycophylla*
117	*Bielschiedia obtusifolia*
16	*Sloanea langii*

Fig 5.13

Fruiting phenology/diet comparison for male Tooth-bills in the Logged Site.

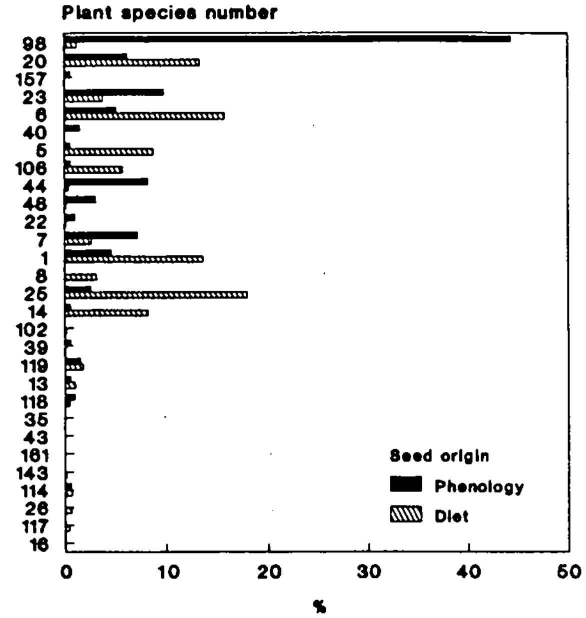


NB: For large seeded species only
No. seeds: Phenology (438) Diet (9296)

Number/Plant species:

98	*Syzygium wesa*
20	*Litsea connonsii*
157	*Elaeocarpus elliffi*
23	*Symplocus cochinchinensis*
6	*Elaeocarpus foveolatus*
40	*Sloanea macbrydei*
5	*Cryptocarya densiflora*
106	*Syzygium johnsonii*
44	*Henslowia sp*
48	*Guioa sp*
22	*Planchonella euphlebia*
7	*Alyxia spicata*
1	*Acronychia acronychiodes*
8	*Cissus hypoglauca*
25	*Endiandra dielsiana*
14	*Elaeocarpus largiflorens*
102	*Cryptocarya corrugata*
39	Brain nut
119	*Endiandra hypotephyra*
13	*Cryptocarya leucophylla*
118	White Litsea
35	*Synoum muelleri*
43	*Syzygium papyraceum*
161	Unknown (Lauraceae)
143	*Drypetes australasica*
114	*Endiandra wolfei*
26	*Smilax glycophylla*
117	*Bielschiedia obtusifolia*
16	*Sloanea langii*

Fig 5.14
Fruiting Phenology/diet comparison for male Tooth-bills in the unlogged site.



NB: For large seeded species only
No. Seeds: Phenology (194) Diet (9050)

Number/Plant species:

98	*Syzygium wesa*
20	*Litsea connonsii*
157	*Elaeocarpus elliffi*
23	*Symplocus cochinchinensis*
6	*Elaeocarpus foveolatus*
40	*Sloanea macbrydei*
5	*Cryptocarya densiflora*
106	*Syzygium johnsonii*
44	*Henslowia sp*
48	*Guioa sp*
22	*Planchonella euphlebia*
7	*Alyxia spicata*
1	*Acronychia acronychiodes*
8	*Cissus hypoglauca*
25	*Endiandra dielsiana*
14	*Elaeocarpus largiflorens*
102	*Cryptocarya corrugata*
39	Brain nut
119	*Endiandra hypotephyra*
13	*Cryptocarya leucophylla*
118	White Litsea
35	*Synoum muelleri*
43	*Syzygium papyraceum*
161	Unknown (Lauraceae)
143	*Drypetes australasica*
114	*Endiandra wolfei*
26	*Smilax glycophylla*
117	*Bielschiedia obtusifolia*
16	*Sloanea langii*

5.3.6 Digestion

Of the 51 species consumed, 21 species passed through the gut of male Tooth-bills exhibiting only partial digestion of the pericarp surrounding the seeds (Table 5.3). Species that were partially digested having passed through the gut of a male Tooth-billed Bowerbirds were:

i) More than 50% of the fruits of *Acronychia acronychiodes*, *Syzygium wesa*, Species 29, and *Podocarpus elatus*

ii) More than 21% of the fruits of *Elaeocarpus foveolatus*, *Elaeocarpus largiflorens* and *Alyxia spicata*

iii) Less than 16% of the remaining 16 species (Table 5.3).

The partial digestion of the fruits listed above was consistent between sites and years. *Acronychia acronychiodes* had consistently high levels of partial digestion between years (>90%) whereas both *Elaeocarpus* species displayed considerable fluctuations between years (Table 5.3).

TABLE 5.3: The number and proportions of partially digested fruits within the diet of male Tooth-billed Bowerbird, for all species with greater than 20 seeds.

(**Family**[1]) and Species	spp id#	No. and prop[2]	Display season and site					TOTAL
			1987		1988		1989	
			Logged	Unlogged	Logged	Unlogged	Logged	
Species that were a major component of the diet								
(**RU**) *Acronychia acronychiodes*	1	n	47	928	26	308	94	1468
		%	100	99.1	100	100	94.6	98.3
(**MY**) *Syzygium wesa*	98	n	-	-	62	108	-	170
		%	-	-	72.6	86.1	-	81.7
Unknown	29	n	30	-	19	8	-	57
		%	60	-	89.4	62.5	-	70.2
(**PO**) *Podocarpus elatus*	129	n	-	-	-	72	-	72
		%	-	-	-	59.7	-	59.7
(**EL**) *Elaeocarpus largiflorens*	14	n	466	165	725	578	-	1941
		%	50.6	93.9	12.0	14.4	-	28.9
(**EL**) *Elaeocarpus foveolatus*	6	n	2415	594	17	835	1888	5760
		%	47.2	57.2	11.8	12.1	2.3	28.4
(**AP**) *Alyxia spicata*	7	n	61	207	-	-	-	311
		%	29.5	22.7	-	-	-	21.5
Species that were a minor component of the diet								
(**LO**) *Fagraea gracilipes*	4	n	1	-	155	898	29	1094
		%	100	-	0.6	5.7	48.3	7.0
(**LA**) *Cryptocarya densiflora*	5	n	489	362	793	430	-	2159
		%	18.6	16.3	3.7	5.3	-	9.8
(**VI**) *Cissus hypoglauca*	8	n	-	33	-	251	-	340
		%	-	15.1	-	1.5	-	2.7
(**LA**) *Cryptocarya leucophylla*	13	n	52	-	-	20	-	226
		%	11.5	-	-	20.0	-	4.4
(**AR**) *Polyscias australiana*	18	n	-	-	117	-	-	1052
		%	-	-	3.4	-	-	0.4
(**LA**) *Litsea connonsi*	20	n	6	-	942	676	-	2157
		%	16.6	-	1.8	1.3	-	1.3
(**SY**) *Symplocus cochinchinensis*	23	n	1409	-	-	-	-	1751
		%	0.9	-	-	-	-	0.7

(Family[1]**)** and Species	spp id#	No. and prop[2]	Display season and site					TOTAL
			1987		1988		1989	
			Logged	Unlogged	Logged	Unlogged	Logged	
(LA) *Endiandra dielsiana*	25	n	-	-	488	1623	-	2127
		%	-	-	2.0	2.0	-	2.0
(SA) *Henslowia sp*	44	n	-	-	-	33	-	33
		%	-	-	-	15.1	-	15.2
(LA) *Cryptocarya corrugata*	102	n	-	-	13	9	-	46
		%	-	-	7.6	11.1	-	4.3
(MY) *Syzygium johnsonii*	106	n	-	-	968	519	-	1487
		%	-	-	8.6		-	7.3
Unknown	112	n	-	-	13	27	-	40
		%	-	-	38.5	3.7	-	15.0
(LA) *Endiandra wolfei*	114	n	-	-	-	63	-	67
		%	-	-	-	7.9	-	7.5
(LA) *Endiandra hypotephyra*	119	n	-	-	25	163	-	205
		%	-	-	28.0	9.2	-	10.7
(EL) *Elaeocarpus elliffi*	157	n	-	-	-	-	151	151
		%	-	-	-	-	5.9	5.9

[1] Key to families: RU=Rutaceae, MY=Myrtaceae, PO= Podocarpaceae, EL= Elaeocarpaceae, AP= Aponcynaceae, LO= Loganiaceae, LA= Lauraceae, VI= Vitaceae, EU= Euphorbiaceae, SY=Symplocaceae; 2 No. and prop: n= total number of seeds, %= proportion of seeds partially digested;

5.3.7 Seed Predation

Even though seed deposition traps were suspended above the forest floor (45cm), seeds deposited in traps were occasionally predated by rodent seed predators. A total of 11 species experienced rodent seed predation within the fruit traps. Of these, five species experienced greater than 10% seed predation, including: *Elaeocarpus elleffi* (59%), *Symplocus cochinchinensis* (25.6%), *Acronychia acronychiodes* (23.2%), *Elaeocarpus foveolatus* (11.3%), *Elaeocarpus largiflorens* (10.6%) while the remaining six species experienced less than 10% (Table 5.4). There was little difference between sites within years, but substantial differences between years (Table 5.4). In 1987, 19.4% of those species preferred by rodents were consumed while in 1988 less than half this number were consumed (6.4%). In 1989 it increased to 15.3%, however, values obtained in this year were not equivalent to the previous years as much of the seed collected was taken from the ground, presumably where rodents would have had unlimited access.

TABLE 5.4: Rodent seed predation, NB: 1989 collections were from ground collections rather than trap collections.

Plant species (and id number)	No. and prop[1]	Display season and site					TOTAL
		1987		1988		1989	
		Logged	Unlogged	Logged	Unlogged	Logged	
Acronychia acronychiodes (1)	n	-	928	-	308	-	1468
	%	-	31.9%	-	13.3%	-	23.2%
Elaeocarpus foveolatus (6)	n	2415	594	17	835	1888	5760
	%	15.6%	4.2%	11.7%	2.6%	11.8%	11.3%
Alyxia spicata (7)	n	-	-	-	30	-	311
	%	-	-	-	3.3%	-	0.3%
Cissus hypoglauca (8)	n	-	-	-	251	-	340
	%	-	-	-	0.7%	-	0.6%
Cryptocarya leucophylla (13)	n	52	-	77	-	-	226
	%	9.6%	-	1.2%	-	-	2.7%
Elaeocarpus largiflorens (14)	n	466	-	725	578	-	1941
	%	10.3%	-	12.4%	11.6%	-	10.6%
Litsea connonsii (20)	n	-	-	942	676	-	2157
	%	-	-	6.3%	12.9%	-	6.8%
Symplocus cochinchinensis (23)	n	1578	311	-	31	-	1920
	%	28.7%	9.0%	-	32.2%	-	25.6%
Endiandra dielsiana (25)	n	-	-	488	1623	-	2127
	%	-	-	3.6%	1.2%	-	1.8%
Bielschmiedia obtusifolia (117)	n	-	-	-	35	-	38
	%	-	-	-	5.7%	-	5.3%
Unknown (118)	n	-	-	6	-	-	47
	%	-	-	16.0%	-	-	2.1%
Elaeocarpus elliffi (157)	n	-	-	-	-	151	151
	%	-	-	-	-	59.6%	59.6%
TOTAL	N	4511	1833	2255	4367	2039	16607
	%	19.6%	19.0%	7.6%	5.8%	15.3%	11.9%

[1] No. and prop: n= total number of seeds, %= proportion of seeds partially digested.

5.4 DISCUSSION

5.4.1 Legitimate frugivores and diet

Male birds that use traditional display arenas are confined to small areas associated with successfully attracting mates over the display season (Snow 1982). This generally restricts their feeding to short out and back forays from a specific site, rather than free ranging over the habitat. Male Tooth-bills in this study deposited the seeds of 51 plant species in their courts. Some 40 of these were large single seeded fruits and 33% of these species were members of the Lauraceae. Similarly, Snow (1970), with a comparable study in the Neotropics, with a similar exploded lek species, over a similar time frame, found that displaying Bearded Bellbirds (*Procnias averano*) deposited the seeds of 45 plant species in their courts and 33% of these species were also members of the Lauraceae. An interesting coincidence.

The major life-history events of Quetzals coincide with the fruiting of Lauraceae, with breeding occurring over the peak fruiting season (Wheelwright 1983). Similarly, the display and breeding season of Tooth-billed Bowerbirds coincided strongly with the fruiting season of the Lauraceae, which was confined to the period from October to February.

Wheelwright (1983) found that Quetzals do not eat fruits in proportion to their availability in the habitat. Male Tooth-bills were also found to consume certain species ahead of others. This was reflected in the marked differences in proportions of the dominant species present in the habitat compared to those deposited within court areas. Members of the Lauraceae and *Elaeocarpus foveolatus* were the most preferred species.

Male Tooth-bills were restricted to a small area on ridges by virtue of their breeding behaviour. Favoured fruiting trees close to the courts were exploited more heavily than those further away (refer to Chapter Four). In the 1989 season, male Tooth-bills were so effective in their foraging of *Elaeocarpus foveolatus* that enormous quantities were found in and around Tooth-bill courts, but virtually no material was found deposited beneath known fruiting trees. Male Tooth-bills were never observed foraging for fruits on the ground. This meant as fruit were ripening they were picked off, never having the opportunity to fall to the forest floor. Consequently, the birds were extremely effective dispersers, as they were not only regular visitors to specific favoured trees (McKey 1975), but virtually all fruits were dispersed away from the parent tree and deposited in a viable condition at court sites (Howe and Smallwood 1982).

In contrast, most *Syzygium wesa* fruits fell to the forest floor beneath the parent tree and became a major component in the diet of the ground feeding Cassowary (pers. obs.). Even though *Syzygium wesa* fruits were enormously abundant on the tree, they were largely ignored by male Tooth-bills. The reasons for this observed avoidance are unknown, but it seems likely that sufficient favoured species were available to allow the avoidance of this non-preferred species.

Another of the features of a legitimate frugivore, as defined by Snow (1981), is a predictably gentle digestion. The consistently low levels of digestion (i.e. pericarp intact) experienced by *Acronychia acronychiodes* and other species certainly support this, however, in some species there were dramatic differences in the levels of digestion from year to year. If we assume that digestion in a Tooth-bills' gut is constant for a given plant species from year to year, then marked fluctuations in the level of digestion for the favoured *Elaeocarpus* species suggest other factors, were operating to produce differences in the digestion levels between years. If unripe fruit maintain the pericarp through the digestive process then the high levels of partially digested fruit deposited in 1987, relative to 1988, may be the end result of the birds taking more unripe fruit, possibly due to reduced fruit availability.

The Bearded Bell Bird (Snow 1970), and the Black and White Manakin (Snow 1962a) display all year round and their displays are only reduced during moult, or during times of fruit scarcity. This is primarily due to the constant availability of fruits in second growth forest of the Neotropics, where these species occur (Snow 1962a, 1970). Male Tooth-bill display was restricted to the period from September to December, which coincides with the end of the dry season peak in fruiting. Predictability in the availability of food resources is a major factor determining the duration and maintenance of bird display systems (Worthington 1982). The energetic costs imposed by maintaining a fixed display site mean that ritualised traditional display systems can only occur in areas or times of high fruit availability (Snow 1962a, 1962b, Worthington 1982). Once fruit availability falls to a level where time spent foraging compromises the ability of a male to maintain the display sites, then the display system is likely to break down. The duration of the display season for male Tooth-bills varied between years according to the availability of fruits.

Wheelwright (1983), in his examination of Quetzals, stated that seed dissemination was poor and estimated that 60-90% of all seeds dropped by Quetzals fell beneath or within 100m of parent trees. But what constitutes an effective dispersal distance? or a safe site? The assumption that a short dispersal distance means ineffective dispersal is unsubstantiated (Howe 1989). The assumption that being deposited in piles is ineffective dispersal is equally unsubstantiated (Howe 1989). Without rigorous field experimentation to examine the effects of dispersal distance and seed density on subsequent seed survival or establishment responses, it is impossible to realistically assess the "effectiveness" of the dispersal agent. Janzen (1970) and Connell (1971) suggested that seed dissemination over even short distances from the parent plants may dramatically increase the probabilities of seed and seedling survival. The question of what constitutes effective dispersal, however, still remains largely unassessed. It may be that 5m beyond the parent crown is a "safe site". These questions, examining the consequences of dispersal are addressed in detail in Chapters Six to Nine.

Chapter Six

GERMINATION

6.1 INTRODUCTION

The effectiveness of a seed disperser depends on where and in what condition the disperser deposits the seed. In the first review of seed dispersal (that is, the consumption, ingestion and subsequent deposition of seeds), Ridley (1930) concluded that the process resulted in some if not all seeds being deposited unharmed. It was later suggested that seed dispersal actually "enhanced" germination (Van der Pijl 1972). Seed dispersal, has subsequently been found to have a wide range of effects on germination (Lieberman and Lieberman 1986).

Germination success of many plant species is enhanced by gut treatment, for example; Mistletoe birds and Mistletoes (Davidar 1983), Galapagos tortoises and tomatoes (Rick and Bowman 1961), Emus and the Nitre bush (Nobel 1975), Cucumber Aardvarks and Aardvark cucumbers (Patterson 1975).

At the community level, determining the effects of seed dispersal on germination often produces varying results. Ingestion has no effect on germination success in 73% of 85 plant-animal disperser combinations from the Accra plains in Ghana (Lieberman and Lieberman 1986). Many other studies have demonstrated similar varying germination responses to ingestion (Lieberman *et al.* 1979, Agami and Waisel 1986, Lieberman and Lieberman 1986, Barnea *et al.* 1990).

In tropical rainforests, frugivores feed on a wide range of plant species (Crome 1975, Gautier-Hion *et al.* 1980, 1985, Snow 1981). Similarly, fruits are fed on by a wide range of frugivores (Howe 1977, Howe and DeSteven 1979, Bonaccorso *et al.* 1980, Snow 1981, Wheelwright *et al.* 1984). Given the complex nature of plant-frugivore interactions in tropical rainforests, the development of mutual dependence between a plant species and a specific disperser seems remote. A suite of dispersers for any given plant species is more likely to be the norm (Wheelwright *et al.* 1984). The effectiveness of dispersers within this suite will, in part, be determined by the germination success they impart to the plant.

The aim of this section of the study was to assess the effects of ingestion by three legitimate frugivores: male Tooth-bills, Shining Starlings and the Australian Cassowary, on the germination responses of the seeds they consume.

6.2 METHODS

6.2.1 Climate data and collection sites

The Paluma site is described as simple notophyll vine forest, the most extensive mountain forest type occurring between 400 - 1000m on the granitic ranges between Cooktown and Townsville (Tracey 1982). The Mission Beach Site is described as Type 2a Mesophyll vine forest, and comprises most of the remaining rainforests below 400m on soils of low to medium fertility (Tracey 1982).

Climate data were obtained from the meteorological station closest to each site. Mean monthly temperature and rainfall data were taken from 32 years of data for Paluma and 48 years of data for Innisfail (Anon 1990).

Full details of the Paluma study site and climate are presented in Chapter Two (Sections 2.1 and 2.2).

6.2.2 Seed dispersers

The characteristics of male Tooth-bills are detailed in Chapter Two (Section 2.3).
The Australian Cassowary (*Casuarius casuarius*), is a large flightless, frugivorous bird, with adult females attaining 60kg in weight. Cassowaries are reasonably common in remaining

lowland rainforests north of Ingham. They are less common in the upland rainforests, where rainforest fruits tend to be smaller, producing sub-optimal habitat for the Cassowary. Cassowaries are the largest extant seed disperser in north Queensland rainforests, depositing large dung piles on the forest floor containing up to 1kg of seeds and fruit fragments (Stocker and Irvine 1983). A total of 70 species of plant have been found to germinate within these piles (Stocker and Irvine 1983).

The Shining Starling (*Aplonis metallica*) is a migrant, moving south from New Guinea in July to September to breed in northern Australia (Pizzey 1980). Shining Starlings are highly social birds, travelling in large flocks and establishing colonies in tall isolated trees within rainforests (Pizzey 1980). Nesting sites are most common in the lowlands, but extend to an altitude of 600m. Beneath nest trees, enormous numbers of seeds are deposited (pers. obs.).

6.2.3 Seed and fruit collection

Seeds dispersed by male Tooth-bills, Shining Starlings and Cassowaries were collected from the two study sites described in Section 6.2.1. Seeds were collected from the droppings of all three dispersers at the Paluma site, but only Cassowary droppings were collected from the Mission Beach site.

Tooth-bill dispersed seeds were obtained from seed deposition traps beneath the favoured perches of 10 displaying males over the display season (September to January; refer to Chapter Five, Section 5.2). Shining Starling dispersed seed was collected from October to February from large shade cloth traps (2m x 5m) set beneath two small breeding colonies, containing 20 and 30 breeding pairs respectively. Fresh Cassowary droppings were collected opportunistically from the Paluma site from September to February, and at the Mission Beach site from March to September.

Intact fleshy fruits (non dispersed) were obtained opportunistically from the ground beneath fruiting trees at both sites to compare germination between dispersed and non-dispersed seeds. All fruits and seeds collected were placed in plastic bags to avoid desiccation, as drying can destroy seed viability in some rainforest species (Jackes pers. comm.). Fruits and seeds were washed through graded sieves (>20mm, 4-20mm, 2-4mm, <2mm), and sorted into taxa. Samples of the seeds and fruits were then preserved in vials containing 70% alcohol for identification and reference. All specimens collected were lodged in the Herbarium of the Botany Department, James Cook University (see Appendix 6.1). Fleshy fruits obtained beneath fruiting trees were identified from both adult and juvenile material (Hyland 1982, Jackes 1990). The seed for which no parent tree material was available were identified from seeds or germinated seedlings where possible. Only undamaged seed and unblemished fruits (i.e. seeds with no sign of insect infestation or rodent tooth marks) were used in germination trials .

6.2.4 Germination trials

The number of seeds or fruits used in any trial was dependent on seed and fruit availability. Where possible, three to four replicates of 20 very large seeded species or 30 large to small seeded species were placed in flat plastic trays containing three parts washed river sand to one part peat. In instances where only a few seeds were available, seeds were placed in mixed plantings until the full complement of 20 or 30 seeds was met. Very small seeds, such as Figs (*Ficus spp.*) and False Figs (*Timonius spp.*), were placed in petri dishes on filter paper, with 100 seeds in three replicates for each treatment.

The major parameters recorded for each collection and trial included:
i) Date of collection,
ii) Species, or species number where no identification was possible (see Appendix 6.1),
iii) Dispersal treatment,
    (a) no dispersal, (pericarp intact),
    (b) Tooth-bill dispersed,
    (c) Shining Starling dispersed and
    (d) Cassowary dispersed,
iv) Seed size, based on the dimension of their smallest diameter,
    (a) very small (< 2mm),
    (b) small-intermediate (2-4mm),

(c) large (4-20mm), and finally
(d) very large (>20mm).

All germination trials were conducted within a green house that had a roof of 50% shade cloth. Trials were commenced within a week of seed/fruit collection so that the planting date approximated dispersal date. All seeds were buried until covered by soil, and watered to saturation whenever necessary. Trials were monitored at 1-4 day intervals during the first 6 weeks and at 7-10 day intervals after this period until the termination of the trials. The number of germinating seeds was noted during each monitoring period. Trials were terminated after 2-3 months if no new germinants had appeared or when seeds were found to have rotted.

Successful germination was defined as the effective emergence of cotyledons, radicle or any other seed part above the substrate. Two measures of germination performance were obtained:

i) Percent germination, or the total number of germinants (g) expressed as a percentage of the total number of seeds sown (n) for that trial.
ii) Time to 50% germination of all germinants (THG), calculated as the time taken in days from the day of sowing until g/2 was reached.
Time to 50% germination has been adopted by many authors for defining germination response time within a seed lot (Sonia and Heslehurst 1978, Turnbull and Martenz 1982). In circumstances where most germinants appeared simultaneously, the germination time (THG) was given as the first sampling period in which germinants were observed.

6.2.5 Comparison of germination responses for dispersed and non dispersed seed.

When comparing the germination of dispersed seeds with non-dispersed seed a wide range of responses are possible. These fall into three broad groupings:

i) Group 1, where non-dispersed seed did not germinate and dispersed seed did (Fig 6.1a).
ii) Group 2, where both non-dispersed and dispersed seed germinated. The germination responses of this group were characterised by a wide range of germination scenarios (Fig

6.1b).

iii) Group 3, where non-dispersed seed did germinate and dispersed seed did not (the opposite of Group 1.

iv) Group 4 or no response, was characterised by those species which did not germinate, indicating either some other mechanism may be required to stimulate germination, the seeds had a particularly long period of dormancy, or the seeds were not viable.

In attempting to classify whether a germination response to dispersal was positive, negative or neutral, the following criteria were used:

i) Positive responses were those where consumption by a disperser resulted in enhanced germination, that is, a greater percentage germination was attained/seed lot by a species having passed through a disperser relative to non-dispersed seed. A positive response in seed dormancy was difficult to assess accurately, but it was assumed that germination was stimulated by the arrival of the wet season, thus shortened dormancy should be an advantage in maximising growth time over the initial wet season, and minimising the time the seed is available to seed predators and pathogens (Garwood 1983, Ng 1980). Thus, a positive dormancy response result indicated the dormancy period of the seed was shortened as a consequence of dispersal.

ii) A neutral response was one where there was no difference in either the percent of seeds germinating or dormancy duration between dispersed and non-dispersed seed.

iii) A negative response was one where the percent of seeds germinating was reduced and the dormancy period was lengthened as a consequence of dispersal.

6.2.6 Methodological limitations

Natural germination conditions cannot be reproduced in a greenhouse beneath 50% shade cloth. However, as all material was subject to the same light regime, growth conditions were constant for all species examined. Trials were regularly watered, and no attempt was made to simulate natural precipitation regimes. The Paluma region experiences a distinct dry season, and the lack of an extended dry period due to continuous watering may have affected seed dormancy and viability in some species.

Fig 6.1a
Germination response group (1)

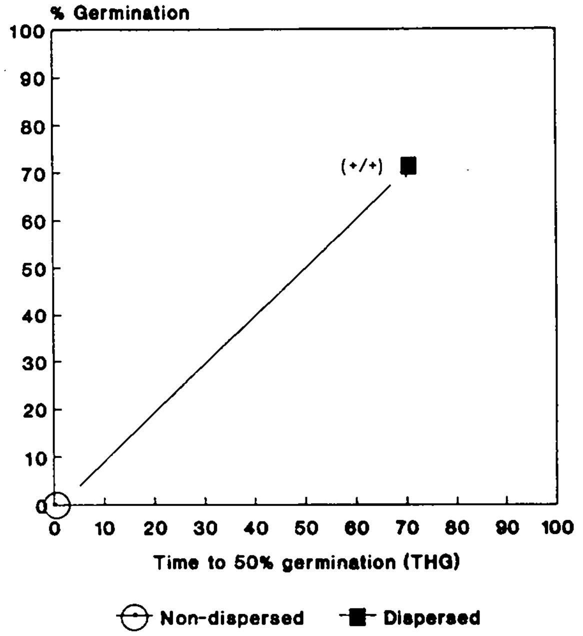
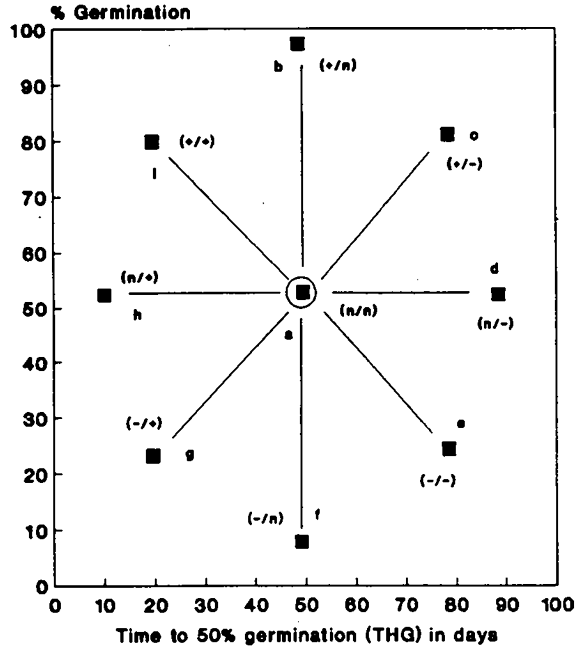


Fig 6.1b
Germination response group (2)



Germination response group (1) illustrated above, demonstrates a positive germination response for a plant whose seeds have been ingested by a seed disperser. Ingested seed germinates, whereas non-ingested seed does not germinate.

Germination response is guauged on two levels of performance: % germination (G) and dormancy (D) defined as time to 50% germination by seeds in each trial.

Germination responses are categorised as positive (+) , neutral (n) or negative (-) (see section 6.2.3), depending on the magnitude and direction of germination response by ingested seed relative to non-ingested seed.

Germination response group (2) is where dispersed and non-dispersed seeds both germinate, and contains a continuum o germination response types. All responses detailed in this figure show response direction from non-dispersed to dispersed seeds, where:

2a Dormancy and % germination are the same
2b % germination increases but dormancy remains the same
2c % germination increases but dormancy increases
2d % germination is the same but dormancy increases
2e % germination decreases and dormancy increases
2f % germination decreases but dormancy is the same
2g % germination decreases but dormancy decreases
2h % germination is the same but dormancy decreases
2i % germination increases and dormancy decreases

Response codes are the same as Fig 6.1a

6.3 RESULTS

6.3.1 Site Characteristics

The seasonal trends in temperature and rainfall were similar at both sites, with a distinct warm wet season from January to March, and a cool to hot dry season from April to November. Paluma was cooler than Mission Beach, and received more rain earlier in the wet season. However, Mission Beach (3,592mm/annum) received more rain during the dry season than Paluma (3,015mm/annum) (Fig 6.2).

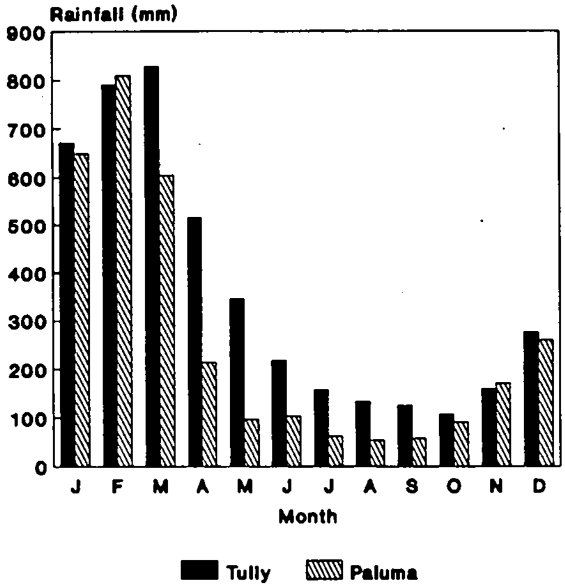
6.3.2 The effect of seed dispersal treatment

There were three major differences in the patterns of fruit consumption by the three frugivores examined. Firstly, both male Tooth-bills and Cassowaries consumed fruits and seeds with the seeds passing in droppings. However, at 75g, Shining Starlings were half the size of male Tooth-bills and often regurgitated large seeds, such as *Myristica insipida* and some members of the Lauraceae (pers. obs.). Secondly, Cassowaries fed on all the fruits consumed by the other two bird species, but due to size constraints the two other disperser species could not feed on many of the very large fruits available to Cassowaries. Finally, gut retention times were shortest for Shining Starlings, as seeds were often regurgitated, and longer for male Tooth-bills, as the seeds were only passed in the droppings (pers. obs.). Cassowaries had the longest gut retention times and could take up to 12 hours to pass seed in their droppings (pers. obs.).

A total of 355 germination trials were conducted on 114 rainforest plant species (Appendix 6.1). The effect of dispersal treatment on the germination success (i.e. germination or no germination) of the plant species consumed by the three dispersers resulted in 61% of plant species germinating after passing through Cassowaries and 53% each for Tooth-bills, Shining Starlings and non-dispersed seeds (Table 6.1).

Fig 6.2

Mean monthly rainfall averaged over 48 years for Tully and 32 years for Paluma.



Total annual rainfall, Tully 4321
and Paluma 3169mm (Tracey 1982).

TABLE 6.1: Results of the initial germination trials (114 plant species) used in the avian dispersed versus non-dispersal treatments.

Dispersal treatment	Successful Germination			Unsuccessful Germination		Totals	
	No sp. %tot	No seeds	n germ % germ	No sp. % tot	No seeds	sp.	No. seeds
No-dispersal	16 53.3%	1161	185 15.9%	14 46.7%	809	30	1970
Tooth-bill Bowerbird	19 52.8%	3221	681 21.1%	17 47.2%	582	36	3803
Shining Starling	18 52.9%	1972	396 20.1%	16 47.1%	358	34	2330
Cassowary	27 61.4%	2701	559 20.7%	17 38.6%	325	44	3026
TOTAL	80	9055	1821	64	2074	144	11129

Germination success (% germination) was enormously variable between plant species for all seed dispersal treatments. All plant species examined are listed in descending order of germination success in Appendix 6.2. Within each seed dispersal treatment, some plant species germinated better than others. The most successful plant species, (i.e. germination success >50% with >20 seeds) within each seed dispersal treatment are presented in Table 6.2. Seed dormancy over all plant species was also enormously variable, with the THG (Time to 50% germination) days ranging from 4 to 473 days.

The plant species with the greatest germination success after passing through male Tooth-billed Bowerbirds were, *Fagraea gracilippes*, *Litsea connonsii*, *Syzygium johnsonii* and *Syzygium wesa* (Table 6.2). These species were all large seeded (4-20mm; see Section 6.2.4), dispersed from September to November, and had short seed dormancies (THG mean days=36.1, SE=6.8)

The plant species with the greatest germination success having passed through Shining Starlings were, *Omalanthus novaehollandia*, *Endiandra dielsiana*, *Litsea connonsii* and *Elaeagnus triflora* (Table 6.2). These species were also large seeded (with the exception of *Omalanthus novaehollandia* which had intermediate sized seeds- 2-4mm) and dispersed from October to December. These species also had short seed dormancies (THG mean days=25.7, SE=6.2).

The plant species with the greatest germination success having passed through Cassowaries were, *Randia fitzlanni*, *Endiandra sankeyana*, *Endiandra montana*, *Syzygium forte*, *Syzygium wesa*, *Syzygium kuranda*, *Syzygium papyraceum*, *Cryptocarya grandis* and *Acmena hemilampra* and *Prunus turnerana* (Table 6.2). These species were obtained from both the Paluma and Mission Beach sites, were large to very large seeded (5>20mm), were dispersed from July to October, and had a long seed dormancy (THG mean days=69.10, SE=8.1).

Among the non-dispersed seeds, *Synoum muelleri* did best with 82% germination. This species was large seeded, dispersed in November, and had a very short germination time at 11 days THG (Appendix 6.2).

Only species that were collected in sufficient numbers as intact fruits (non-dispersed) and from bird droppings (bird dispersed) were used for comparisons of the effect of seed dispersal on germination responses.

6.3.3 The effect of Dispersal vs No-dispersal

Only 24 of the original 114 plant species collected were able to be used for further comparisons between dispersed and non-dispersed seeds. From this sub-set, only six plant species provided sufficient seeds and fruits for quantitative comparison of dispersed and non-dispersed seed. The remainder providing less conclusive qualitative responses, or no response (Table 6.3).

TABLE 6.2: Characteristics of the avian dispersed plant species that germinated successfully (>50% germination success) from 355 germination trials, using 114 plant species (see Appendix 6.2).

Disperser/plant species (Family[1])	Spp ID#	Number of seeds	Germination (%)	THG[2] (days)	Month dispersed	seed size
Tooth-billed Bowerbirds						
Fagraea gracilipes (Lo)	4	35	83	17	November	Large
Litsea connonsii (La)	20	90	76	36	October	Large
Syzygium johnsonii (My)	106	44	68	44	October	Large
Syzygium wesa (My)	98	30	54	48	October	Large
Shining Starlings						
Omalanthus novaehollandia (Eu)	147	100	99	11	February	Interm
Endiandra dielsiana (La)	25	90	97	36	October	Large
Litsea connonsii (La)	20	90	76	36	October	Large
Eleagnus triflora (Eg)	17	90	63	20	November	Large
Cassowaries						
Randia fitzlanni	1022	100	98	76	June	Large
Endiandra sankeyana (La)	1036	22	95	105	August	Very Large
Endiandra montana (La)	1004	46	81	76	June	Very Large
Syzygium forte (My)	1028	24	73	18	February	Very Large
Syzygium wesa (My)	98	90	72	71	October	Large
Syzygium kuranda (My)	1023	60	68	72	June-July	Very Large
Syzygium papyraceum (My)	43	90	61	38	December	Very Large
Cryptocarya grandis (La)	1025	30	57	61	June	Large
Acmena hemilampra (My)	1002	60	55	76	August	Large
Prunus turnerana (Ro)	1050	26	54	98	September	Very Large

[1] For plant families: (My) Myrtaceae, (La) Lauraceae, (Lo) Loganiaceae, (Ro) Rosaceae, (Eg) Eleagnaceae, (Eu) Euphorbiaceae; [2] (THG) Time to 50% germination.

TABLE 6.3: Comparison of the germination responses of the 24 plant species collected in sufficient numbers to allow direct comparisons of non-dispersed seed (pericarp intact) and bird dispersed seed, in descending order of germination success.

TREATMENT		NON-DISPERSED			BIRD DISPERSED			
SEED DISPERSER/ Plant species (Family¹)	Spp id#²	N	% GERM	THG DAYS	N	% GERM	THG DAYS	RESPONSE (G/D)³
TOOTH-BILLED BOWERBIRD								
Fagraea gracilipes (Lo)	4	30	0	--	35	82.9	17	1a(+/+)
Litsea connonsii (La)	20	90	0	--	90	75.6	35.7	1a(+/+)
Syzygium johnsonii (My)	106	90	12.2	61.3	90	67.8	44	2i(+/+)
Syzygium wesa (My)	98	90	0	--	28	53.6	48	1a(+/+)
Cryptocarya densiflora (La)	5	164	0	--	74	16.5	127	1a(+/+)
Ficus destruens (Mo)	34	300	1.33	24	366	4.27	32	2c(+/-)
Elaeocarpus largiflorens (El)	14	90	0	--	60	3.33	28	1a(+/+)
Acronychia acronychiodes (Ru)	1	110	0	--	67	0	--	3(0/0)
Planchonella euphlebia (Sa)	22	5	20.0	84	6	0	--	1a(-/-)
SHINING STARLINGS								
Endiandra dielsiana (La)	25	6	0	--	90	96.7	36	1a(+/+)
Piper caninum (Pi)	21	9	44.4	53	150	14.2	49	2g(-/+)
Ficus destruens (Mo)	34	100	0	--	999	1.40	72	1a(+/+)
CASSOWARY								
Endiandra montana (La)	1004	3	100	59	46	81.4	76	2e(-/-)
Syzygium wesa (My)	98	90	0	--	90	72.2	71	1a(+/+)
Syzygium kuranda (My)	1023	60	71.7	102	60	68.3	72	2f(n/+)
Syzygium papyraceum (My)	43	90	7.8	38.5	90	61.1	38	2b(+/n)
Cryptocarya grandis (La)	1025	3	66.7	98	30	56.7	61	2g(-/+)
Cryptocarya oblata (La)	1031	4	100.0	112	2	50.0	109	2g(-/-)
Melia azedarach (Me)	1001	15	0	--	15	40.0	95	1a(+/+)
Elaeocarpus angustifolius (El)	1000	80	0	--	80	33.8	473	1a(+/+)
Halfordia scleroxyla (Ru)	3	188	0	--	30	3.33	62	1a(+/+)
Acronychia acronychiodes (Ru)	1	110	0	--	180	0	--	3(0/0)
Syzygium alliiligneum(My)	1003	14	78.6	76	3	0	--	1b(-/-)
Lepidozamia sp(Za)	1026	6	0	--	1	0	--	3(0/0)

[1] Plant Families: (El) Elaeocarpaceae, (La) Lauraceae, (Lo) Loganiaceae, (Mo) Moraceae, (My) Myrtaceae, (Me) Meliaceae, (Pi) Piperaceae, (Ru) Rutaceae, (Sa) Sapotaceae, (Za) Zamiaceae.

[2] Spp id#= (<999)=Plants collected from Paluma, (>999)=Plants collected from Mission Beach

[3] Response: Germination response in (G)=% germination and (D)=dormancy (see Fig 6.1). Criteria for +/- does not indicate statistical significance, merely an observed difference. Samples sizes were too small for meaningful statistical analysis.

6.3.3.1 Percent germination

For the 24 disperser/plant species interactions tested, 58.3% yielded a positive germination response, that is, more seeds germinated after passing through a disperser than not (enhanced germination). For the remainder of species examined, 4.2% exhibited a neutral response (no difference), 25% a negative response (less seeds germinating after passing through a disperser), and 12.5% no response (no germination) (Table 6.4). Tooth-billed Bowerbirds provided the most positive comparisons with 78% (nine species), Shining Starlings next with 67% (two species) and Cassowaries, the least with 41.6% (12 species) (Table 6.4).

TABLE 6.4: Summary of the effect of dispersal on germination responses of the 24 plant species used in the disperser/plant interactions. For definitions see both Table 6.3 and text. (Relevant codes from Table 6.3: For Total (G/D) or amalgamation of both % germination and dormancy, Positive responses= ++,+n,n+, Neutral = nn,+-,-+, and Negatives responses = --,n-,-n).

Response	Dispersal	Germination (G)	Dormancy (D)	Total G/D)
POSITIVE				
	TOTAL	(14) 58.3%	(15) 62.5%	(14) 58.3%
	Tooth-bills	(7) 77.7%	(6) 66.7%	(6) 66.7%
	Shining Starlings	(2) 66.7%	(3) 100%	(2) 66.7%
	Cassowaries	(5) 41.6%	(6) 50%	(6) 50%
NEUTRAL				
	TOTAL	(1) 4.2%	(1) 4.2%	(3) 12.5%
	Tooth-bills	--- ---	--- ---	(1) 11.1%
	Shining Starlings	--- ---	--- ---	(1) 33.3%
	Cassowaries	(1) 8.3%	(1) 8.3%	(1) 8.3%
NEGATIVE				
	TOTAL	(6) 25%	(5) 20.8%	(4) 16.7%
	Tooth-bills	(1) 11.1%	(2) 22.2%	(1) 11.1%
	Shining Starlings	(1) 33.3%	--- ---	--- ---
	Cassowaries	(4) 33.3%	(3) 25%	(3) 25%
NO RESPONSE				
	TOTAL	(3) 12.5%	(3) 12.5%	(3) 12.5%
	Tooth-bills	(1) 11.1%	(1) 11.1%	(1) 11.1%
	Shining Starlings	--- ---	--- ---	--- ---
	Cassowaries	(2) 16.6%	(2) 16.6%	(2) 16.6%
		24	24	24

6.3.3.2 Dormancy

The effect of passing through the digestive tract of a frugivore on the period of seed dormancy produced a positive response (reduced the period of dormancy) in 62.5% of the 24 plant species examined. A neutral response was observed in 4.2% of bird/plant species comparisons, 20.8% of comparisons produced a negative response (increased dormancy) and 12.5% of comparisons displayed no response having been dispersed by a frugivore (Table 6.4). Shining Starlings provided the most positive comparisons with 100% (three species) of the seeds dispersed by these frugivores displaying a decreased period of dormancy. Tooth-billed Bowerbirds were next with 67% (nine species) positive comparisons and Cassowaries least with only 50% (12 species) of the seeds examined having a shorter dormancy period after passing through their gut.

6.3.3.3 Total germination response

Combining the results of Sections 6.3.3.1 (germination) and 6.3.3.2 (dormancy), 58.3% of the 24 bird/plant species comparisons yielded positive germination and dormancy responses, 12.5% neutral responses, 16.7% negative responses and 12.5% no response (Table 6.4). Both Tooth-bills and Shining Starlings provided the most positive responses with 66.7% (nine and three species respectively) and Cassowaries the least with 50% (12 species).

The six species with sufficient material for quantitative assessment all demonstrated enhanced or positive germination in responses to consumption by an avian frugivore. *Litsea connonsii*, *Syzygium wesa* and *Elaeocarpus angustifolius* exhibited enhanced germination, with positive responses in both germination and dormancy (Fig 6.3a). *Syzygium papyraceum* exhibited enhanced germination success, but neutral dormancy. *Syzygium kuranda* exhibited neutral success, but enhanced dormancy. *Syzygium johnsonii* exhibited both enhanced germination success and dormancy (Table 6.3, Fig 6.3b).

Fig 6.3a Germination responses

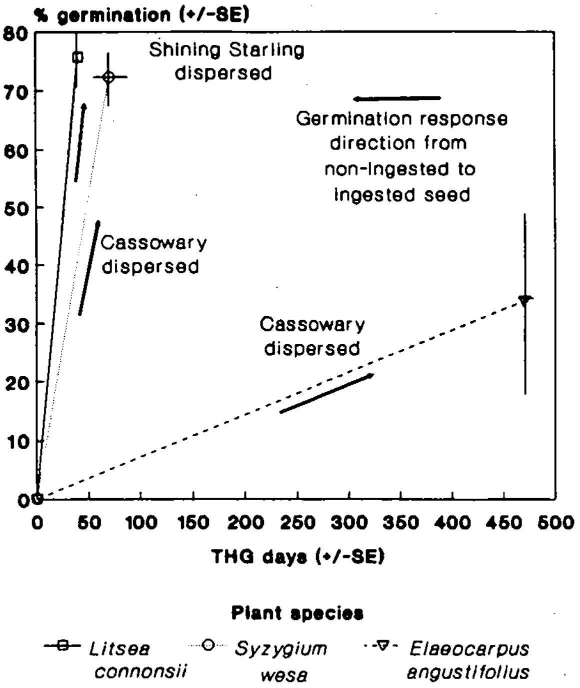
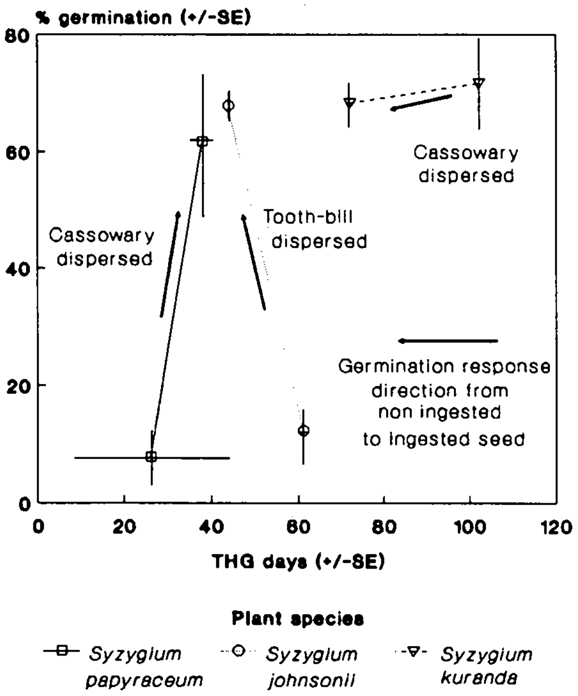


Fig 6.3b Germination Response



6.3.4 Summary of results

i) More than 52% of the 114 plant species in the four seed dispersal treatments (bird dispersed and non-dispersed) germinated.

ii) Of the 24 plant/specialist frugivores comparisons examined, 58% resulted in enhanced germination of the plant species, and 62% of seeds displayed enhanced dormancy (i.e. decreased dormancy).

iii) In nine male Tooth-bill/plant species comparisons, male Tooth-billed Bowerbirds provided 78% enhanced germination, and 67% enhanced dormancy for the seeds of the plant species they deposited.

iv) In three Shining Starling/plant species comparisons, Shining Starlings provided 67% enhanced germination and 100% enhanced dormancy for the seeds of the plant species they ingested.

v) In 12 Cassowary/plant species comparisons, Cassowaries provided 42% enhanced germination and 50% enhanced dormancy for the seeds of the plant species they deposited.

6.4 DISCUSSION

6.4.1 Community effects of seed dispersal

The critical finding of this study was that 58% of 24 plant species exhibited enhanced germination and 62% faster germination periods having passed through the gut of a legitimate frugivore. These findings contrast strongly with those of Lieberman and Lieberman (1986) who found ingestion by frugivores did not affect germination success in 73% of the seeds they examined and only 12% of seeds had a significantly faster germination.

A number of fundamental differences exist between the two studies that may explain the differences in results. Firstly, Lieberman and Lieberman's study was conducted on 85 plant/animal species pairs from the dry forests of Ghana, whereas, this study was conducted on 24 plant/animal species from the rainforests of Australia's wet tropics. Secondly, Lieberman and Lieberman used six species of fruit eaters (three birds, two bats and a monkey) whereas this study used three legitimate avian frugivores (Snow 1981). Finally, Lieberman and Lieberman artificially fed fruits to each frugivore. In contrast, the frugivores in this study selected their own fruit from those available in the wild. The differences in the results of these two studies suggest that the dispersal service provided by frugivores may vary considerably between plant-animal communities, or between legitimate and "other" frugivores. In addition, the fruits offered to frugivores in captive feeding trials may not correspond to their preferred diets in the wild, and the results of such trials may therefore underestimate the dispersal service offered by these animals.

Lieberman and Lieberman concluded from their study that the assemblage of plants they examined was not dependent upon animals for successful germination of their seeds. In contrast, this present study suggests more than 50% of plant species examined may attain some advantage having their seeds dispersed by a legitimate frugivore. The advantages identified included enhanced germination success and a faster germination (decreased period of dormancy). The advantage of enhanced germination to the plant is obvious, by increasing the number of seeds that successfully germinate the reproductive success of the plant is increased. However, the advantage of decreased dormancy (that is, faster time to germination) is somewhat obscure. Presumably the plant developed a dormancy period of a certain duration in response to specific environmental cues. The possible reasons for decreased dormancy in avian dispersed seeds are discussed below.

6.4.2 Advantages of faster germination (decreased dormancy)

The peak time for germination in seasonal tropical rainforests is the early wet season (Garwood 1983). This presumably maximises the length of the first growing season for seedlings trying to establish and enables the development of a substantial root system to assist in surviving the dry season (Frankie *et al.* 1974, Garwood 1983). Shortening the period of seed dormancy in seasonal tropical rainforests may maximise the growth potential of seedlings over their first wet season (Ng 1978). A shorter period of seed dormancy for the seed may also reduce the time that the seed is available to predators (Ng 1980, Vaquez-Yanez & Segovia 1984).

At the Paluma study site, male Tooth-bills were actively displaying from September to January. Shining Starlings were also active over this period, but their breeding season started one month later, in October and finished in February. The breeding of both species is effectively geared to the period of peak fleshy fruit production, which occurs in the late dry season, early wet season (see Chapter Three). Fruiting in the Lauraceae and Myrtaceae occurred late in the dry season and both families were prevalent in the diet of male Tooth-bills and Shining Starlings (see Chapter Five). At the Paluma study site, the Myrtaceae and Lauraceae exhibited a naturally high germination success and relatively short seed dormancies of 30-60 days (Ng 1980).

Given the above information, seed dispersal by a legitimate frugivore may provide an advantage to the plant by maximising the growth potential of its seedlings. However, there is a trade-off for these plants in being dispersed by frugivores. Many of the seeds dispersed by male Tooth-bills and Shining Starlings were deposited in seed piles where they could be exposed to density dependent seed predators and pathogens (Howe 1989; see Chapter Seven). However, as mentioned above, shortened germination time may also reduce the time seeds are available these predators. This suggests that the dispersal service offered by male Tooth-bills and Shining Starlings may greatly benefit the fastest germinating species, which fruit in the late dry early wet season.

6.4.3 Other germination strategies

At the Paluma study site, members of the Rutaceae, such as *Acronychia acronychiodes* and *Halfordia scleroxyla*, and the Elaeocarpaceae, such as *Elaeocarpus largiflorens* and *E. foveolatus*, fruit in the late dry season and the seeds enter an extended dormancy. Despite using large numbers of seeds, members of both families were particularly difficult to germinate. The difficulties in germinating these two plant groups have also been experienced by other workers (Stocker and Irvine 1983). By depositing seeds in piles, as the disperser species were observed doing, the plant species with extended seed dormancies may be exposed to greater seed predation than those species with a short seed dormancy. Whilst some species may be disadvantaged by the increased incidence of rodent predation at the court/deposition site, other species may require this secondary dispersal phase for successful germination. For the latter species, dispersal by frugivores may be an important component of the germination process.

6.4.4 Cassowaries

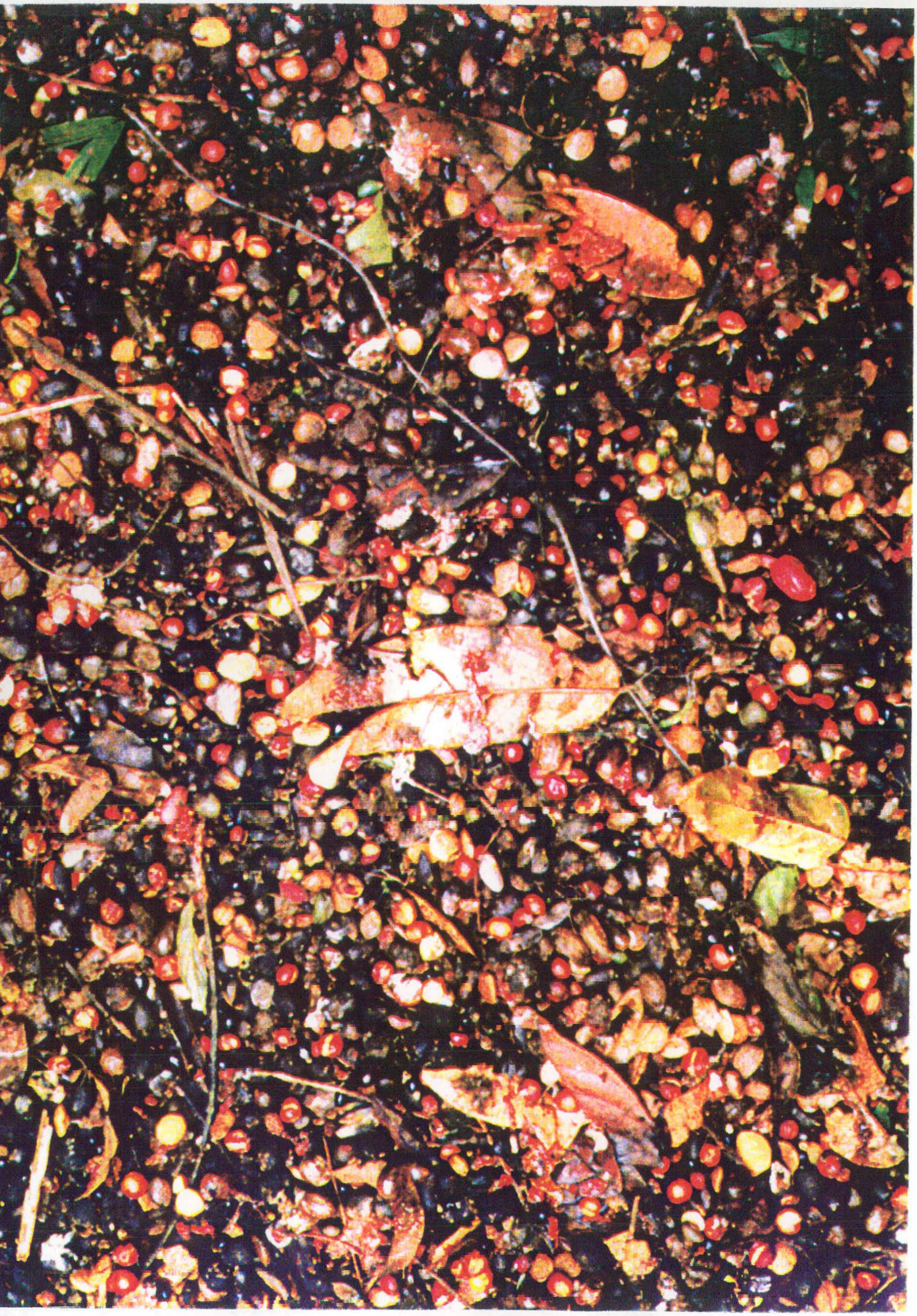
Cassowaries differed from the dispersers examined in the study as well as many others, in being the only disperser that consumed very large fruits (Stocker and Irvine 1983). Fruit bats (*Pteropus spp.* and *Dobsonia spp.*) also consume and carry large fruits, but they do not pass the seed through their gut.

The plant community at Paluma that produced fleshy fruits, was structured for small to intermediate sized frugivores, with 93% of the plant species producing small to large fruits (4-20mm). Cassowaries were transitory feeders at the Paluma site, only visiting during the peak periods of fruit production in September to January (pers. obs.). Only 7% of plant species at Paluma produced very large fruits (>20mm) and the site may be considered sub-optimal habitat for Cassowaries (Crome 1976, 1990).

In contrast, at Mission Beach where Cassowary numbers are high, 46% of the plant species examined produced very large fruits and seeds (>20mm). These very large fruits are produced over much of the dry season from July to November (Crome 1975). As Cassowaries are resident in the Mission Beach area they are available all year round to disperse fruits and seeds are deposited in piles (Crome 1976). Overall, the very large seeded plant species examined from Mission Beach had a higher germination success and longer seed dormancies than those plant species examined at Paluma. The longer seed dormancies exhibited reflect the time of dispersal prior to the wet season (Garwood 1983). Very large seeded species may contain large quantities of secondary compounds that can assist in defence against density dependent seed predators and pathogens (Howe 1989). Clearly, the plant species of the Mission Beach rainforests are geared for a different dispersal service than those at Paluma, and these differences are reflected in fruit and seed size, the timing of fruit production and the dormancy strategies used.

Tropical rainforests are the centre of fleshy fruit and frugivore diversity, yet the few detailed studies examining the affects of seed dispersal on germination responses of fleshy fruits come from temperate or drier and potentially less diverse systems (Lieberman and Lieberman 1986). Even though a large proportion of the data in this study is qualitative, it suggests that numerous positive germination responses from plant-disperser interactions exist within tropical rainforests. Clearly more detailed studies at the community level are required to elucidate the complex relationships between plants and animals in tropical ecosystems.

Plate 3: Seeds deposited beneath a Shining Starling (*Aplonis metallica*) colony, Mission Beach, Queensland.



Chapter Seven

SEED PREDATION

7.1 INTRODUCTION

Seeds of most rainforest tree species fall in a leptokurtic distribution away from the parent tree, that is, seeds are most dense beneath the parent tree and decrease in density with increasing distance from the parent (Howe and Smallwood 1982). Janzen (1970) and Connell (1971) produced a model to explain high local diversity in rainforest tree communities. They proposed that beneath the parent tree, density and its effects on mortality would be extreme relative to areas beyond the parent crown. They suggested that density dependent agents, including host specific seed and seedling predators and pathogens, would result in disproportionately high mortality beneath the parent crown. Similarly, distance responsive agents might search immediately beneath the parent crown ignoring seeds and seedlings only metres away (Janzen 1970). The Janzen-Connell model or "escape hypothesis" became a paradigm, even though it had almost no empirical evidence to support it (Howe and Smallwood 1982, Clark and Clark 1984).

Hubbell (1980), disputed the model, pointing out that even extremely low survival beneath the parent tree could still result in most recruits surviving due to their greater initial progeny densities within these sites. Evidence to support the Janzen-Connell model is variable. In a review of 24 data sets, Clark and Clark (1984) found that: (i) in relation to density dependent mortality, 29% of studies gave strong evidence and 33% weak evidence; (ii) in relation to distance dependent mortality, 33% had strong evidence and 62.5% weak evidence; and (iii) in relation to the minimum critical distance effect (i.e. total mortality beneath the parent tree) 17% had strong evidence and 29% had weak evidence. Connell (1984), in an independent review, came to similar conclusions. Clearly there is evidence to support and refute both the Janzen-Connell and Hubbell models.

Howe (1989) proposed that some of the variability in evidence for the Janzen-Connell model may be due to differences between plant species in their seed dispersal syndrome, which was defined as a constellation of traits associated with some ecological process. Howe suggested that because many tree species are scatter-dispersed by birds, bats or other small frugivores and deposit seeds singly or in pairs, these scatter-dispersed species (members of the scatter-dispersed syndrome) normally recruit as isolated individuals and should have evolved little resistance to density dependent mortality agents. Conversely, clump-dispersed species are deposited by larger frugivores in dense seed clumps (members of the clump-dispersed syndrome). These species will tend to germinate in dense groups and should have evolved defences against density dependent mortality agents. If Howe is correct, then scatter-dispersed species may be prone to density dependent seed predation and are likely to fit the Janzen-Connell model. In contrast, clump-dispersed species will be less affected in a density dependent agents and will conform to Hubbell's model (1980). As yet, quantitative estimates of seed and seedling mortality in animal dispersed seed clumps are scarce and there are virtually none for scatter dispersed seed (Howe 1989).

All the above hypotheses have one thing in common, they all attempt to provide a mechanism to "explain" patterns of recruitment for rainforest trees. The underlying difficulty is that patterns of recruitment in tropical rainforests are extremely variable in time and space with no one theory/hypothesis providing a full explanation, or alternatively considering full range of patterns that exist in nature. Simply, in this study, I propose to examine patterns of seed predation in seed clumps on the forest floor and then attempt to examine how these patterns support or otherwise the hypotheses outlined above. Finally I hope to provide a theoretical framework which covers the range of responses found both here and elsewhere.

The primary aim of this chapter was to test the response of seed predators to seeds dispersed in clumps on the forest floor, which in turn would shed light on the effectiveness of clump seed dispersal for dominant plant species consumed by male Tooth-bills. Patterns of rodent seed predation for seeds of a number of rainforest tree species were examined over a range of microsites, densities, species combinations, nights and years in north-east Queensland rainforests.

7.2 METHODS

Details of the Paluma study site can be found in Chapter Two. Plant species deposited (diet) and germination responses are examined in Chapters Five and Six, respectively.

7.2.1 Plant species and rodent seed predators

Enormous variation in fruit and seed availability occurred within seasons and between years (see Chapter Three). Therefore, seed predation patterns for the dominant plant species dispersed by male Tooth-bills were examined over the display season. The tree species examined were: *Litsea connonsii, Syzygium johnsonii, Acronychia acronychiodes, Cryptocarya densiflora, Endiandra dielsiana* and *Elaeocarpus largiflorens*. Seed characteristics of each species are described in Table 7.1. For the remainder of this chapter, plant species will be referred to by generic name only.

Rodent abundance was monitored in an adjacent site from June 1987 to December 1989 as part of a separate study (Watt unpub.). Animals were trapped on a 100 x 100m trapping grid with two Elliot (Type A) traps spaced every 20m. Trapping was undertaken at least every two months for 3-5 days to give a total of 4067 trap nights[1]. The species and number of captured rodents that may be predators of seed are given in Table 7.2.

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[1] 1 trap night=1 trap opened over one trapping night

TABLE 7.1: Seed characteristics of plant species used in seed predation experiments.

Species	Family	seed length	seed breadth	test	germination	comments
Litsea connonsii	Lauraceae	13.6 (0.283)	8.6 (0.187)	soft	36 days	spicy odour
Syzygium johnsonii	Myrtaceae	6[1]	7[1]	soft	44 days	
Acronychia acronychiodes	Rutaceae	11.7 (0.212)	11.9 (0.202)	hard	extended dormancy	citrus odour
Cryptocarya densiflora	Lauraceae	12.0 (0.306)	16.5 (0.319)	intermediate	unknown dormancy?	spicy odour
Elaeocarpus largiflorens	Elaeocarpaceae	14.2 (0.277)	8.8 (0.186)	hard	extended dormancy	
Endiandra dielsiana	Lauraceae	21.7 (0.673)	10.2 (0.244)	intermediate	36 days	

[1] Measurements obtained from Hyland 1983: Seed dimensions are given in mm and values enclosed in brackets give the SE of seed dimensions (n=20).

TABLE 7.2: Characteristics of rodent seed predators within the Paluma study site. Data obtained from 4067 traps nights in and adjacent study site (Watt unpub.).

Species	Sub family[1]	Weight[2] (g)	Total number caught	Percentage of total catch
Uromys caudimaculatus	Hydromyinae	250-700	64	13.3
Rattus fuscipes	Murinae	70-200	339	70.3
Melomys cervinipes	Hydromyinae	40-100	79	16.4

[1] Strahan, R. "The Australian Museum Complete Book of Australian Mammals" Angus and Robertson. 1983.
[2] Watt (unpub.)

Bird dispersed seed was collected from dropping traps (refer to Chapter Five) set beneath the favoured perches of ten male Tooth-bills and also a Shining Starling colony (*Aplonis metallica*) of approximately 60 adult birds. Bird dispersed seed was allowed to accumulate over a week and then collected. All material collected from the traps was washed, sorted and prepared for experiments. Numbers of seeds of each species used were dependent on the availability of different species at the time of experimentation (see Table 7.3a-d).

Natural and experimental seed units were defined as: (1) seed piles, which are the large seed piles deposited beneath the favoured perch of a male Tooth-bill, (2) clumps, referring to a discrete pile where all seeds are in direct contact with one another and (3) patches, where seeds are dispersed randomly over 0.5m^2.

TABLE 7.3: Experimental designs for the four seed predation experiments.

a. Experiment One: examined the effect of species, and clump composition on seed predation patterns adjacent to male Tooth-bill seed piles. Dispersed seeds of four plant species were used (L=*Litsea connonsii*, S=*Syzygium johnsonii*, A=*Acronychia acronychiodes*, C=*Cryptocarya densiflora*). 30 seeds of three species were allocated to each replicate and the experiment repeated over two nights (4-6/10/1988).

Night	Male Tooth-bill Bowerbird court				
	1	2	3	4	5
1	30 L	30 L	30 L	30 L	30 L
	30 S	30 S	30 S	30 S	30 S
	30 C	30 A	30 A	30 C	30 C
2	30 L	30 L	30 L	30 L	30 L
	30 S	30 S	30 S	30 S	30 S
	30 C	30 C	30 C	30 A	30 A

Total seeds in Experiment One: *Litsea connonsii*=300, *Syzygium johnsonii*=300, *Acronychia acronychiodes*=120, *Cryptocarya densiflora*=180

b. Experiment Two: examined the effect of microsite, species and night on seed predation patterns for mixed scattered seed piles. Dispersed seeds of two plant species (L=*Litsea connonsii*, S=*Syzygium johnsonii*) were used. 30 seeds of each species were placed in seed pairs, and the experiment was repeated over three nights (12-15/10/1988).

Replicate	Microsite (see Table 7.4 for definitions)				
	BSB	PTL	PTS	RBC	GAP
1	30 S	30 S	30 S	30 S	30 S
	30 L	30 L	30 L	30 L	30 L
2	30 S	30 S	30 S	30 S	30 S
	30 L	30 L	30 L	30 L	30 L
3	30 S	30 S	30 S	30 S	30 S
	30 L	30 L	30 L	30 L	30 L
4	30 S	30 S	30 S	30 S	30 S
	30 L	30 L	30 L	30 L	30 L
5	30 S	30 S	30 S	30 S	30 S
	30 L	30 L	30 L	30 L	30 L

Total seeds used in Experiment Two: *Litsea connonsii*=2250, *Syzygium johnsonii*=2250

c. Experiment Three: examined the effect of microsite and night on seed predation patterns for single species, clumped seed piles (*Litsea connonsii*). 30 seeds were placed in each replicate, and the experiment was repeated over three nights (22-24/10/1988).

Replicate	Microsite (See Table 7.4 for definitions)			
	BSB	PTL	RBC	GAP
1	30 L	30 L	30 L	30 L
2	30 L	30 L	30 L	30 L
3	30 L	30 L	30 L	30 L
4	30 L	30 L	30 L	30 L
5	30 L	30 L	30 L	30 L

Total seeds used in Experiment Three: *Litsea connonsii*=1800

d. Experiment Four: examined the effect of microsite and species on seed predation patterns for mixed clumped seed piles. Dispersed seeds of two plant species, El=*Elaeocarpus largiflorens* and Ed=*Endiandra dielsiana* were used. Microsites are defined in Table 7.4. 30 seeds of each species were placed in a pile, and monitored over one night (7/1/1989).

Microsite Replicate	Microsite (see Table 7.4 for definitions)				
	BSB	RNL	RAL	GNL	GAL
1	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed
2	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed
3	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed
4	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed	30 El 30 Ed

Total seeds used in Experiment Four: *Elaeocarpus largiflorens*=1200, *Endiandra dielsiana*=1200

7.2.2 Experiment One: Seed preferences of rodents for clumped mixed seed located near Tooth-bill courts.

Experiment One examined seed preferences by rodents feeding on seeds in Tooth-bill seed piles early in the display season. Five Tooth-bill courts with distinctive seed piles were chosen, and sets of mixed seed clumps were placed in a cleared area within a 1m radius of the court seed pile. *Litsea* and *Syzygium* were most abundant and *Acronychia* and *Cryptocarya* least abundant at the time of experimentation. Each seed pile contained three species of the four available and 30 seeds of these species. The most abundant species, *Litsea* and *Syzygium*, were used in all five replicates, and the less common species, *Acronychia* and *Cryptocarya*, were randomly assigned to a seed pile, with two and three replicates respectively.

The experiment was repeated over two nights. Seed piles were placed out in the late afternoon of day one, and all piles were checked early in the morning of day two and the number of seeds predated and form of predation was recorded. All piles were replaced with new seed the subsequent afternoon and the entire procedure repeated on day three. The experimental design is detailed in Table 7.3a.

7.2.3 Experiment Two: The effect of microsite on seed predation intensity for scattered mixed seed.

The effectiveness of a seed dispersal system is in part dependent on how seed predators respond to patterns and densities of seed deposited. Experiment Two examined the effect of microsite, species and night on post dispersal seed predation for scattered mixed seed patches. Two species were chosen for this experiment, *Litsea* and *Syzygium*. as they were the most abundant species at the time of experimentation. Using the Janzen-Connell model, it was predicted that both species would be predated in a density dependent manner and would suffer greater mortality in high risk areas such as beneath a parent tree or near bird dispersed clumps (see Table 7.4).

All canopy gaps (GAP), Tooth-bill courts (BSB) and dominant fruiting trees (BPL, BPS) were mapped in two 10 hectare sites. Five random locations were chosen across both sites and these were defined as random beneath canopy sites (RBC). The nearest Tooth-bill court, large gap, and fruiting tree of both plant species were then chosen (Table 7.4). Each microsite unit was at least 20m from the influence of any other microsite.

A $0.25m^2$ quadrat was placed in the centre of each of the five microsites (see Table 7.4). Each quadrat was then further divided into 100 5cm x 5cm subunits by nylon fishing line. Three of the subunits in each line of ten were then randomly selected for placement of each seed pair (one seed of each species), giving a total of 30 randomly placed seed pairs per quadrat. Seed predation was monitored as outlined in Section 7.2.2 with the experiment repeated over three nights. The experimental design is detailed in Table 7.3b.

TABLE 7.4 : Microsite codes, definitions, descriptions and selection criteria. Both BPT and BSB are high seed density microsite, and therefore "high risk" areas subject to density dependent seed predation. Conversely, GAP and RBC are low seed density and therefore "low risk areas" (According to the Janzen-Connell Model).

Code	Definition	Description	Selection criteria
BPT	Beneath parent tree	. Area of high fruit and seed fall directly beneath parent crown, . High seed/fruit densities . single species	A random compass bearing was taken, and quadrat placed at a distance half the radius of the parent crown, placing the quadrat in the centre of the parent tree seed bed.
BPL	*Litsea connonsii*		
BPS	*Syzygium johnsonii*		
BSB	Bird dispersed seed bed	. Seed pile beneath the favoured display perch of male Tooth-bill . High seed density . multiple species	Quadrat was placed within a 1 m radius of Tooth-bill seed pile, on a random compass bearing.
GAP	Canopy gap	. Area where a major tree fall event forms a large gap in the canopy . High light conditions . Low seed density	Quadrat was placed in the centre of the canopy gap.
GNTF	Near log fall		Immediately adjacent to a log fall
GATF	Away from log fall		3m from log fall
RBC	Random area beneath canopy	. Random area beneath the canopy . Low light conditions . Low seed density	Random sites were chosen as specific grid coordinates on site maps. These acted as foci for the selection of other microsites, and were at least 20m from the influence of other microsites.
RNTF	Near log fall		Immediately adjacent old log fall
RATF	Away from log fall		3m from log old fall

7.2.4 Experiment Three: The effect of microsite on seed predation intensity for clumped *Litsea* seeds (1988).

Experiment Three was a repeat of Experiment Two using *Litsea* seeds only. Seeds were placed in clumps rather than in the scattered random patches. This is more indicative of how the seeds would be deposited by male Tooth-bills. It was predicted that seed predation patterns would be similar to those proposed in Experiment Two, but with greater mortality due to the ease with which seed predators could process clumps. The experimental design is detailed in Table 7.3c and microsite definition in Table 7.4. Again, this experiment was repeated over three nights and monitored as described in Section 7.2.2.

7.2.5 Experiment Four: The effect of microsite on seed predation intensity for clumped mixed seed.

By the 7/1/89, most Tooth-bill males had finished displaying and were no longer depositing seeds in piles. All courts had been processed by rodents to varying degrees. Experiment Four examined the effect of microsite and species on seed predation after the display season. *Endiandra* and *Elaeocarpus* were the only species available in sufficient quantity over this period to conduct experiments.

Microsites differed from those defined in Experiments Two and Three, as no parent tree microsites could be found. Avian frugivores had been so effective in their removal of fruit from parent trees that no seeds or fruit were deposited on the ground beneath the parent, rather all seeds were in Tooth-bill seed piles or other bird dispersed units.

The experimental design for Experiment Four is outlined in Table 7.3d. Microsites included: bird dispersed seed beds (BSB), Gaps near tree falls (GNTF), gaps away from tree falls (GATF), beneath canopy near rotting logs (RNTF), and beneath canopy away from rotting logs (RATF) (see Table 7.4 for explanations). Seed was only available for one night's trial.

7.2.6 Experiment Five: The effect of microsite on seed predation intensity for clumped *Litsea* seeds (1990).

Experiment Five repeated Experiment Three during the 1990 Tooth-bill display season. This experiment tested whether seed predation patterns were consistent between years. The experimental design is outlined in Table 7.3c.

7.2.7 Analytical Methods

In all trials, all seeds removed (assumed eaten elsewhere), or damaged (rodent tooth marks or seed fragments found *in situ*) were recorded as predated.

The proportion of seeds predated were arcsine square root transformed (Zar 1974). Transformed data were tested for normality using Wilk-Shapiro / Rankit plots. Seed predation experiments were analysed using Mixed Model Analysis of Variance (Statistix version 3.0). The models used in the analyses varied according to the seed treatments and the availability of seeds, and the tree species fruiting at the time of the experiment. All the models are outlined in detail in Tables 7.5- 7.10. Fixed factors in the analysis included all main effects and interaction terms involving only the main effects. Random factors (error terms) included replicates within main effects and their interactions (Tables 7.5-7.10). By incorporating random effects into the model, the most appropriate error term was used in calculating the F statistic, reducing the problem of pseudoreplication.

7.3 RESULTS

7.3.1 Rodent seed predators

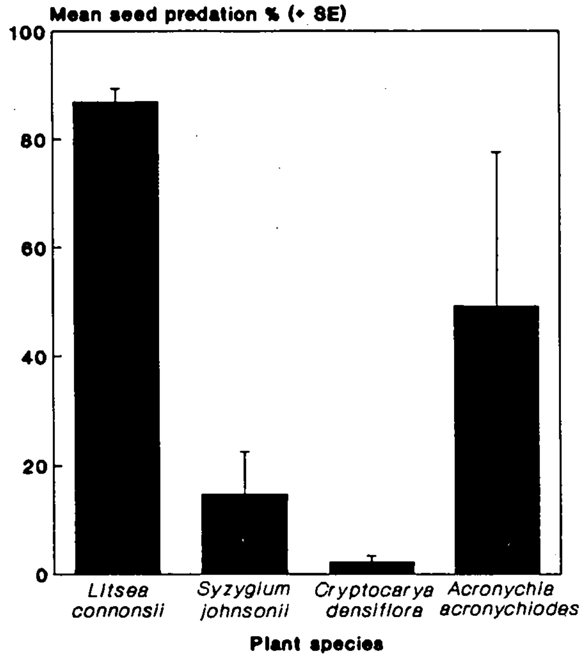
A total of 482 Murid rodents were caught from 4067 trap nights in an adjacent study site (Watt, unpub.). Of these, 70.3% were the intermediate sized *Rattus fuscipes* (70-200g), 16.4% the smaller *Melomys cervinipes* (40-100g) and 13.5% the large *Uromys caudimaculatus* (250-700g). The size of the traps used may have resulted in the exclusion of some *Uromys*.

7.3.2 Experiment One: Seed preferences of rodents for clumped mixed seed located near Tooth-bill courts.

The rodent community preferred *Litsea* seed (88%), followed by *Acronichia* (50%), with the remaining species *Syzygium* and *Cryptocarya* only occasionally damaged or removed (1-15%) (Fig 7.1). There were no significant differences in the number of seeds removed from each seed clump over successive nights (X^2=2.471, df=4, p=0.6498). This implied that seed predators consistently returned to a known food source. The number of seeds predated in clumps containing *Cryptocarya* was significantly lower than for other clumps (X^2=12.39, df=4, p=0.015). Seed predation in clumps containing *Acronychia* was highly variable with some clumps predated heavily and others largely ignored (X^2=48.16, df=2, p=0.0000). There were major differences in the levels of seed predation between clumps of differing seed composition, with clumps including *Acronychia* being predated much more heavily than clumps including *Cryptocarya* (X^2=69.34, df=2, p<0.000).

Figure 7.1

Rodent seed preferences in seed clumps near male Tooth-bill seed piles.



7.3.3 Experiment Two: The effect of microsite on seed predation intensity for scattered mixed seed.

In the scattered seed trial, *Litsea* seeds were predated more frequently than *Syzygium* seeds (Fig 7.2a). Seed predation was highest in high risk microsites (i.e. beneath parent tree -BPL and bird dispersed seed beds-BSB) and least in the remaining low risk microsites (i.e GAP,BPS,RBC), (Fig 7.2a). These differences were not, however, statistically significant. In a Mixed Model Analysis of Variance examining the effect of species, microsite and night on seed predation, species had significant effect on seed predation, but all remaining factors and interaction terms did not (Table 7.5). There was an increase in predation of *Litsea* seeds over successive nights from 18% to 33%, suggesting that rodents were searching more thoroughly over successive nights, however, this increase did not prove significant (Fig 7.2b). More than 70% of the scattered seed patches were discovered by seed predators in all microsites, with the exception of RBC microsites where slightly more than 40% of seed patches were discovered (Fig 7.2c).

TABLE 7.5: Experiment Two- Mixed Model Analysis of Variance, examining the effect of microsite, species and night on rodent seed predation for scattered mixed patches.

Source	df	MS	F	P
microsite[1]	4	0.3139	1.30	0.3041
ss(microsite)[2]	20	0.2416		
plant species [1]	1	2.6157	39.56	0.0000
plant species * microsite[1]	4	0.1007	1.52	0.2334
ss(plant species * microsite)[2]	20	0.0613		
night[1]	2	0.1810	2.09	0.1371
night * microsite[1]	8	0.1545	1.78	0.1093
replicate(night * microsite)[2]	40	0.0866		
plant species * night[1]	2	0.0387	1.07	0.3523
plant species * night * microsite[1]	8	0.0356	0.99	0.4614
replicate(plant species * night * microsite)[2]	40	0.0361		
TOTAL	149			

[1]= fixed and [2]= random factors

Figure 7.2b

Increase in seed predation for scattered seed patches over three nights

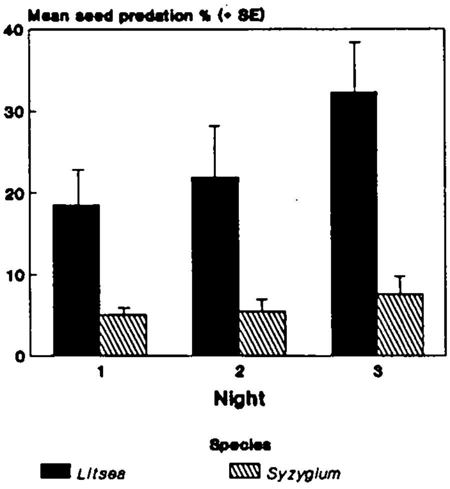


Figure 7.2c

The effect of microsite on the chance of encountering a scattered seed patch.

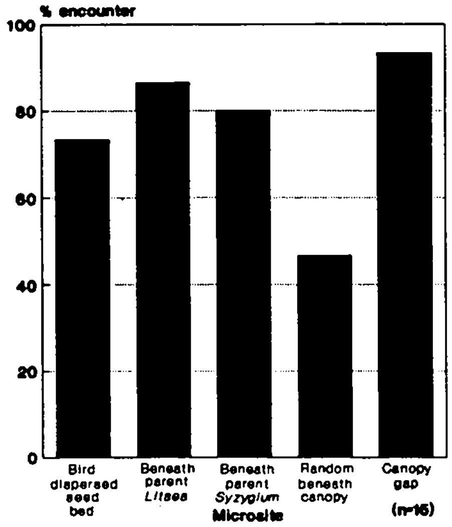
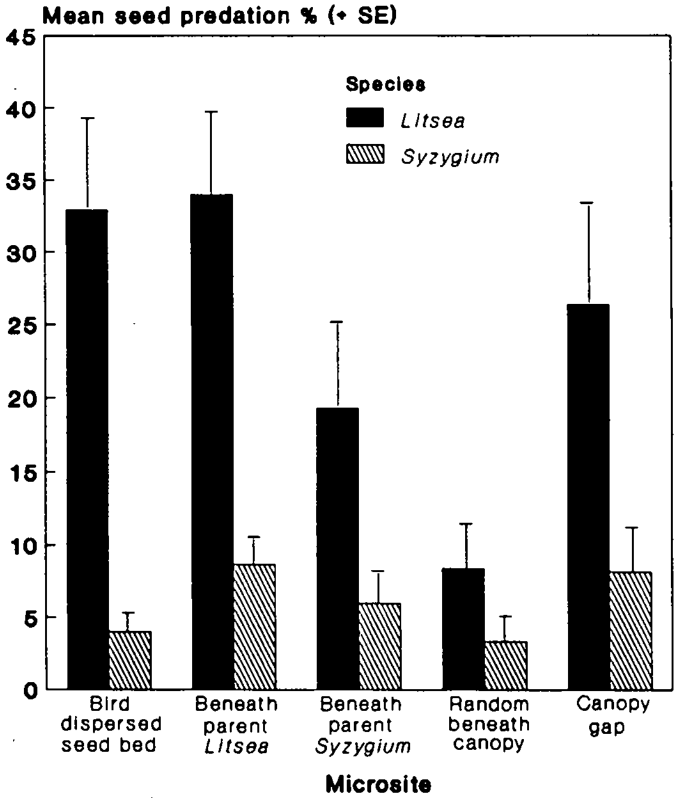


Figure 7.2a

The effect of microsite and species on seed predation for scattered seed mixed seed patches



7.3.4 Experiment Three: The effect of microsite on seed predation intensity for clumped *Litsea* seeds (1988).

When Experiment Two was repeated with *Litsea* only and the seeds deposited in discrete clumps rather than scattered, predation was far greater (total removed: clumped 59.7%, scattered 25.4%). Seed predation was marginally higher in high risk microsites (i.e. BPL and BSB), than in other sites (Fig 7.3a). These differences were not statistically significant. In a Mixed Model Analysis of Variance examining the effect of microsite and night on seed predation, there were no significant effects (Table 7.6).

TABLE 7.6: Experiment Three- Mixed Model Analysis of Variance, examining the effect of microsite and night on rodent seed predation for clumps containing *Litsea connonsii.*

Source	df	MS	F	P
microsite[1]	3	0.4581	0.94	0.4460
ss(microsite)[2]	16	0.4891		
night[1]	2	0.1404	0.46	0.6350
night * microsite[1]	6	0.1382	0.45	0.8370
ss(night * microsite)[2]	32	0.3046		
TOTAL	59			

[1]= fixed and [2]= random factors;

Unlike scattered seed, the proportion of clumped seeds predated did not increase consistently over subsequent nights, but rather remained high throughout the experiment (>50%) (Fig 7.3b).

The chance of encountering *Litsea* seeds in clumps was also slightly higher in high risk microsites (Fig 7.3c). This suggests that discrete clumps of seeds of a favoured species will be subject to high seed predation intensity irrespective of microsite or night.

Figure 7.3b
The effect of night on seed predation for *Litsea* seed clumps

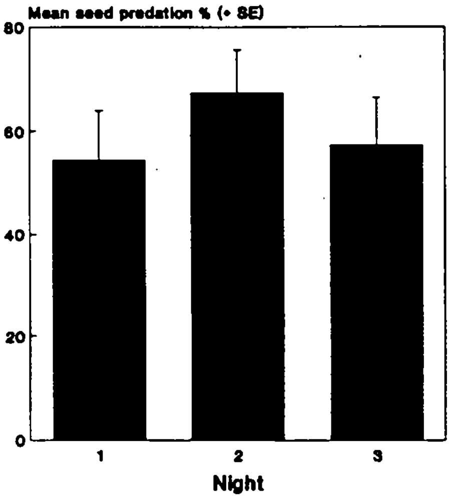


Figure 7.3c
The effect of microsite on the encounter of *Litsea* seed clumps by rodents.

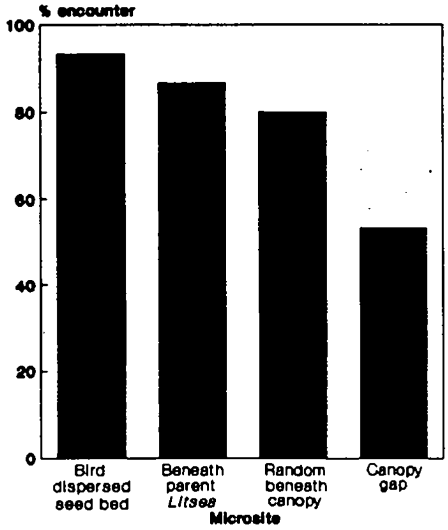
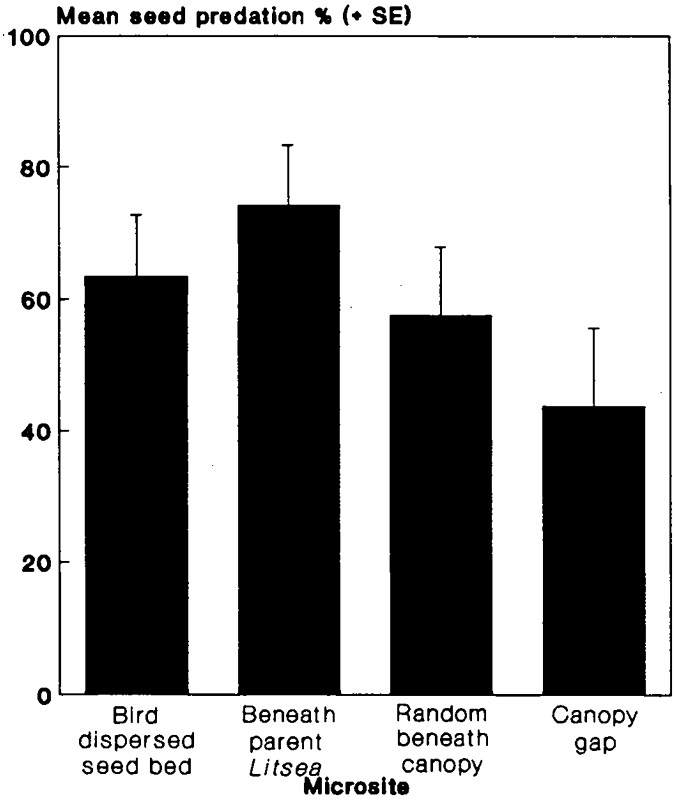


Figure 7.3a
The effect of microsite on seed predation for *Litsea* clumped patches.



7.3.5 Experiment Four: The effect of microsite on seed predation intensity for clumped mixed seed.

Seed predation intensity was extremely low at all microsites (< 8%). *Elaeocarpus* was predated more than *Endiandra*, and patches in gaps away from tree falls (GATF) had the highest seed predation for both species (Fig 7.4a). The chance of a predator encountering a clump was similar between microsites (50-75%) (Fig 7.4b). In a Mixed Model Analysis of Variance examining the effect of species and microsite on seed predation, there were no significant effects (Table 7.7).

TABLE 7.7: Experiment Four- Mixed Model Analysis of Variance, examining the effect of microsite and species on rodent seed predation for mixed clumps containing *Endiandra dielsiana* and *Elaeocarpus largiflorens*.

SOURCE	df	MS	F	P
microsite[1]	4	0.0093	0.28	0.8884
ss(microsite)[2]	15	0.0336		
plant species[1]	1	0.0296	1.41	0.2539
plant species * microsite[1]	4	0.0015	0.07	0.9898
ss(plant species * microsite)[2]	15	0.0021		
TOTAL	39			

[1]= fixed and [2]= random factors

The seeds of *Elaeocarpus* deposited in bird dispersed seed piles were ignored over the period of greatest seed abundance (September to March). These seeds remained dormant (refer to Chapter Six) and were heavily predated during the period of seed scarcity (April to August) later in the year. *Endiandra* suffered heavy losses from fungal pathogens (i.e. the seeds went slimy and rotted).

Figure 7.4a
The effect of microsite and species on seed predation for clumped patches.

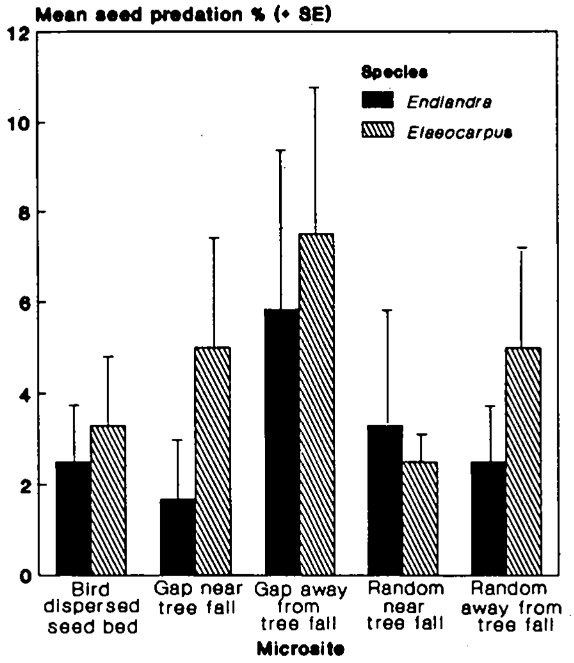
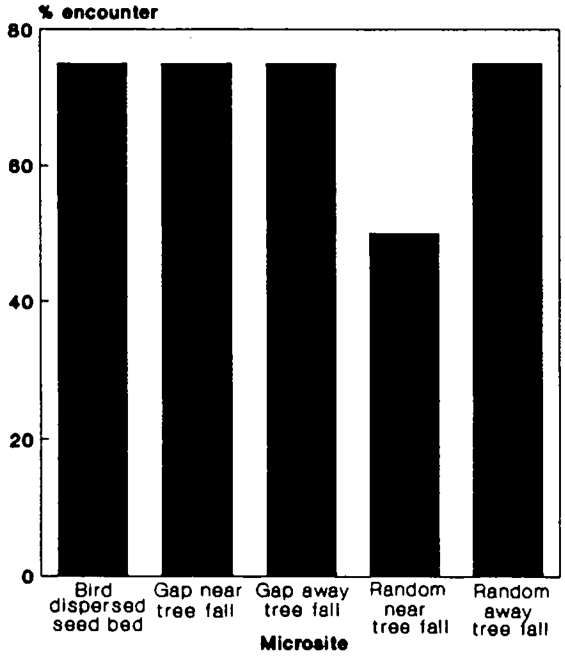


Figure 7.4b
Encounter of *Endiandra* and *Elaeocarpus* seeds in clumps by rodent seed predators



7.3.6 Experiment Five: The effect of microsite on seed predation intensity for clumped *Litsea* seeds (1990).

When Experiment Three was repeated two years later, results differed from those of 1988 (Section 7.3.4). Overall, *Litsea* seeds suffered less than 1/12 the previous predation levels (total percentage predated: 1988=60.9%, 1990=4.7%; Fig 7.5). A Mixed Model Analysis of Variance examining the effect of microsite and night on seed predation, revealed no significant effects (Table 7.8).

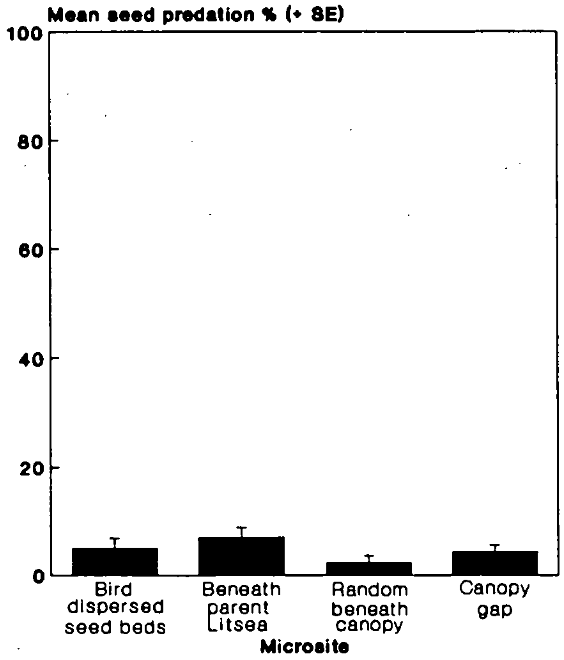
TABLE 7.8: Experiment Five- Mixed Model Analysis of Variance, examining the effect of microsite and night on rodent seed predation for clumps containing *Litsea connonsii.*

Source	df	MS	F	P
micrositeⁱ	3	0.0374	1.77	0.1942
ss(microsite)²	16	0.0212		
night¹	1	0.0043	0.17	0.6838
night * microsite¹	3	0.0021	0.08	0.9678
ss(night * microsite)²	16	0.0255		
TOTAL	39			

¹= fixed and ²= random factors

Figure 7.5

The effect of microsite on seed predation of *Litsea* seed clumps (1990)



7.3.7 Scattered vs clumped seed

Data from Experiment Two (scattered seed) was compared to Experiment Three (clumped seed) for *Litsea* only. In a Mixed Model Analysis of Variance examining the effects of microsite, patch type (scatter/clumped) and night on seed predation, patch type had a significant effect on seed predation (Table 7.9, Fig 7.6). This suggests that patch density is an important factor affecting seed predation intensity.

TABLE 7.9: Comparison between *Litsea connonsii* predated in clumps and scattered patches (Experiments Two and Three). Mixed Model Analysis of Variance, examining the effects of microsite, and night on rodent seed predation for clumped and scattered patches.

Source	df	MS	F	P
microsite[1]	3	0.5911	1.07	0.3902
ss(microsite)[2]	16	0.5532		
seed patch [1]	1	6.2139	29.21	0.0001
seed patch * microsite[1]	3	0.3201	1.50	0.2513
ss(seed patch * microsite)[2]	16	0.2127		
night[1]	2	0.1249	0.62	0.5424
night * microsite[1]	6	0.1594	0.80	0.5803
replicate(night * microsite)[2]	32	0.2004		
seed patch * night[1]	2	0.0605	0.33	0.7198
seed patch * night * microsite[1]	6	0.1128	0.57	0.7530
replicate(seed patch * night * microsite)[2]	32	0.1988		
TOTAL	119			

[1]= fixed and [2]= random factors

Fig 7.6
Seed predation intensity for scattered and clumped *Litsea* seeds

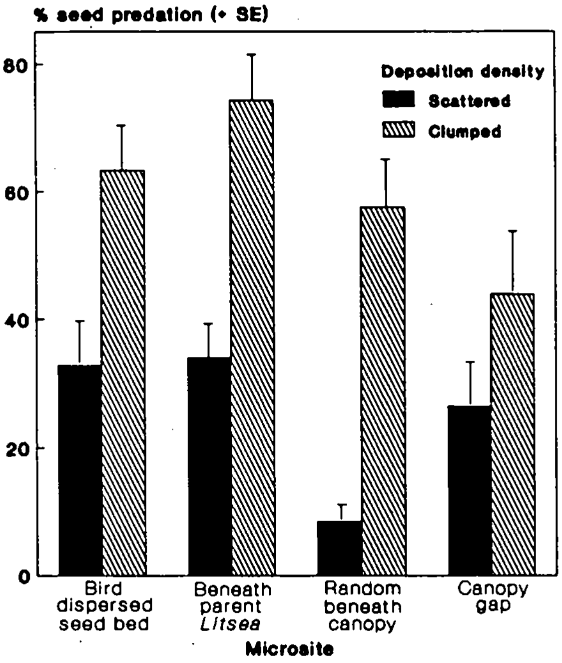
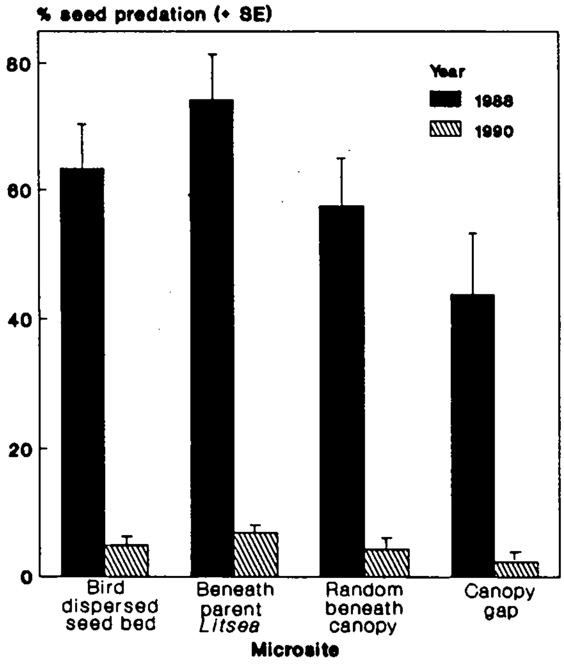


Fig 7.7
Seed predation intensity for clumped *Litsea* seeds in 1988 and 1990



7.3.8 The effect of year

Data from Experiment Three (Section 7.3.4) for *Litsea* seed clumps (1988) was compared with Experiment Five (1990) (Section 3.3.6). In a Mixed Model Analysis of Variance examining the effects of microsite, year and night on seed predation, only year had a significant effect (Table 7.10, Fig 7.7). This confirms that patterns of seed predation may vary enormously from year to year. Similarly rodent populations, measured from trapping success[2], fluctuated dramatically from year to year (Fig 7.8).

TABLE 7.10: Comparison between *Litsea connonsii* predated in clumps (Experiments Three and Five) for 1988 and 1990. Mixed Model Analysis of Variance, examining the effects of microsite, year and night on rodent seed predation for clumps.

Source	df	MS	F	P
microsite[1]	3	0.3293	1.28	0.3136
ss(microsite)[2]	16	0.2564		
year [1]	1	10.838	35.91	0.0000
year * microsite[1]	3	0.1261	0.42	0.7426
ss(year * microsite)[2]	16	0.3018		
night[1]	1	0.1774	1.67	0.2142
night * microsite[1]	3	0.0081	0.08	0.9720
replicate(night * microsite)[2]	16	0.1060		
year * night[1]	1	0.1075	0.81	0.3812
year * night * microsite[1]	3	0.0210	0.16	0.9225
replicate(year * night * microsite)[2]	16	0.1325		
TOTAL	79			

[1]= fixed and [2]= random factors

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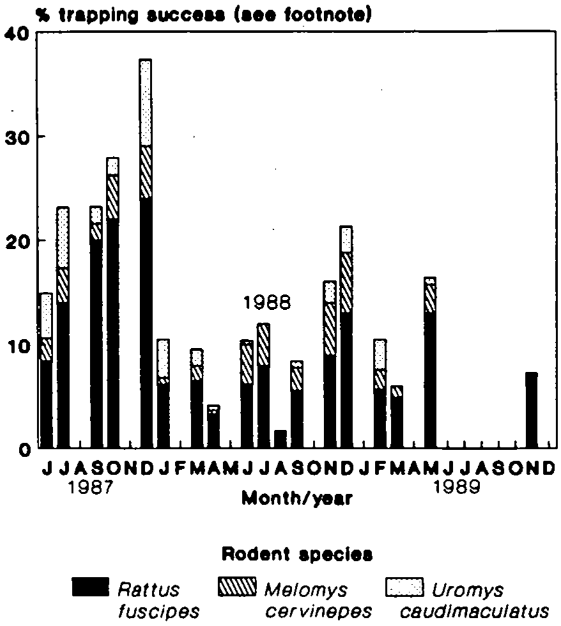
[2] Trapping success= (number of animals caught/number of traps set) x 100

Fig 7.8

Trapping success of rodents at the Paluma study site, 1987-1989



7.3.9 Summary of Results

Table 7.11 summarises the results of each of the experiments.

TABLE 7.11: Summary of Findings for Experiments One to Five and comparisons between experiments

Factor	Results of Experiment[1]					Comments
	Exp 1 C+m	Exp 2 S+m	Exp 3 C+s	Exp 4 C+m	Exp 5 C+s	
plant species	*	*		ns		Some species are preferred
microsite	ns	ns	ns	ns	ns	No evidence of density dependence
night	ns	ns	ns	ns	ns	No evidence of differences between nights
patch (clump/scatter)		*	*			Evidence of density dependent mortality
year			*		*	Evidence of switching from density dependence to density independence between years, windows of recruitment.

[1] Codes used: Exp 1-5 refers to Experiments One to Five; S=scattered seed, C=clumped seed, m=mixed species, s=single species; *=significant effect at α= 0.05, ns=not significant at α=0.05

The seed predation patterns observed were as follows:

i) Plant species had a significant effect on seed predation intensity, with *Litsea* clearly being preferred over other plant species in the 1988 display season (Section 7.3.2 and 7.3.3).

ii) There was no evidence to suggest that microsite had a significant effect on seed predation, as seed predation intensities in high risk microsites were not significantly different from low risk microsites in any experiments. This may indicate that the seed densities used were inappropriate to detect microsite effects (Section 7.3.3-8, Table 7.11).

iii) Night had no significant effect on seed predation for seeds in clumps, that is, predation intensity was similar over successive nights. This implies that the chance of finding a seed clump was similar each night. Seed predation intensity did increase over successive nights from 18-33% for scattered *Litsea*, suggesting that rodents searched patches more thoroughly over successive nights, but this increase did not prove statistically significant (Sections 7.3.3-8 Table 7.11).

iv) Seed predation intensity for *Litsea* was significantly lower for scattered than clumped patches. This suggests that increased scattering results in decreased predation intensity for this species (i.e. it may be predated in a density dependent manner) (Section 7.3.7, Table 7.11).

v) Seed predation intensity for *Litsea* was significantly lower in 1990 than 1988, illustrating enormous variation in seed predation between years. This corresponds to the marked fluctuations in rodent seed predators between years in an adjacent site (Section 7.3.8, Table 7.11).

vi) The low intensity of rodent seed predation on many of the species examined suggests that they escape seed predation from rodents. Other sources of mortality need to be investigated for these species.

7.4 DISCUSSION

7.4.1 Species effects

Litsea connonsii was favoured by rodent seed predators above all other species examined in this study, with predation levels as high as 88%. The predation intensity of the remaining five species ranged from 3% to 49% which were substantially lower than the predation levels for *Litsea* even in the so called "high risk" areas or when deposited in "high risk" piles.

Variability in seed predation between species, is a common phenomenon (Harper 1977, Clark and Clark 1984, De Steven and Putz 1984, Howe *et al.* 1985, Howe 1986). In Costa Rican montane forests, Wheelwright (1985) found 95% rodent seed predation for a Laurel species over a few days. Willson (1988) examined rodent seed predation in a number of north Queensland rainforest sites and found predation levels for different species ranging from 6-92%. Clearly rodents can be extremely effective seed predators when targeting specific plant species, but the response is enormously variable between different plant species.

Given *Litsea* was the species most preferred by rodents, the location and manner of seed deposition was particularly relevant for this species. No significant trends were demonstrated in rodent seed predation for the other species examined.

7.4.2 Microsite effects

The prediction that seed deposited in "high risk" microsites, (i.e beneath parent trees and in bird dispersed seed beds) are more prone to seed predation than other microsites due to seed predation, was not supported in any experiments. Seed predation intensity was marginally greater in high risk microsites for *Litsea* in 1988 only.

Most rodents locate seeds by olfaction (Price and Jenkins 1986). The olfactory conspicuousness of a seed affects encounter rates by determining how close a rodent must approach the seed before detection. Odour concentrations provide cues to seed identity, location and densities (Price and Jenkins 1986). *Litsea* seeds were particularly conspicuous, with a rich aromatic cinnamon smell. In the high seed densities used in the experiments in this study, *Litsea* would probably have been discovered wherever it was, masking potential microsite effects.

The effect of microsite on seed predation by rodents is variable. Some studies have demonstrated density dependent rodent seed predation, with greater seed predation intensity beneath parent trees than outside the parent crown (Wright 1983, Clark and Clark 1984, De Steven and Putz 1984, Howe 1983, Howe *et al.* 1985, Howe 1986, Schupp 1988a, 1988b). However, other studies have been less conclusive (Howe 1980, 1989).

Seed predation of animal dispersed seed piles is similarly variable. Janzen *et al.* (1976) examined the bat dispersed tree *Andira inermis* and found 10% weevil predation for scattered seed, 30% for seed beneath bat roosts and 60% for seed beneath parent trees. Howe (1983, 1986) found catastrophic weevil infestations in *Virola* seed piles under Kinkajou (*Potos flavus*) nests. Davidar (1983) and Reid (1989) both found density dependent mortality of mistletoe seeds. Janzen (1982b) found that seeds in dung piles were more easily located by spiny tailed mice (*Heteromys sp.*) than seeds without dung. Conversely, Stiles (1980) found that seeds in bird faeces were less attractive to *Peromyscus* mice than those in fruit or clean on litter.

In this study, gap microsite seed predation was almost as high as microsites considered as "high risk" in the scattered seed trial for *Litsea*. Schupp (1988b) examining post dispersal seed survival for the subcanopy tree *Faramea occidentalis* found that seed predation within tree fall gaps was indistinguishable from predation beneath parent trees. Schupp concluded that tree falls and vine tangles provide suitable den sites for rodents resulting in greater rodent activity near these sites. In contrast Willson (1988) found that different microsites had little consistent influence on short term seed predation for scattered seed located along transects which also included gap microsites. Clearly, the predation by rodents of seed in different microsites varies enormously.

7.4.3 Night effect

In the mixed scattered seed trial (Experiment Two), there was an increase in seed predation of *Litsea* over successive nights from 18-33%, however, these results did not achieve statistical significance. The increase may be due to rodents learning the whereabouts of reliable seed resources and searching more thoroughly over successive nights.

7.4.4 Scattered vs clumped

Clumped *Litsea* seed was more heavily predated than scattered seed. Conversely, with the exception of *Acronychia*, seeds of most other species were minimally predated even in clumps. Price and Jenkins (1986) confirm that rodents preferentially harvest seeds from dense patches, however, it is not known to what extent this is a function of clumped seed being more conspicuous or more likely to be harvested once encountered. Whatever the cause, seed removal rates increase with increasing seed density (Heithaus 1981, Sork 1983, Stapanian and Smith 1978).

7.4.5 Year effects

Seed predation intensity for *Litsea connonsii* varied dramatically between years, with 61% predation in 1988 and only 5% in 1990. The dramatic reduction in predation observed is probably due to an apparent decline in the abundance of rodent seed predators.

Hubbell (1980) suggested that the interaction between a tree species, its dispersers and seed predators leads to high variation in the effectiveness of dispersers and intensity of seed predation, from tree to tree and year to year. The main factor contributing to this variance is high variation in seed production between trees and years. Dramatic variation in seed predation intensity between years, due to fluctuations in seed predator numbers, may provide windows of recruitment for those species normally decimated by seed predators.

7.4.6 Variation within the system

Of the species examined, *Litsea* was preferred by rodents and when deposited in clumps experienced high seed predation intensity no matter where it was deposited. When deposited in scattered patches there was a four fold decrease in seed predation intensity, but no microsite effect. Seed densities used in these experiments were large enough to attract seed predators irrespective of microsite, possibly masking density dependent microsite effects.

Given the high probability of discovery and consumption of *Litsea* seeds in 1988, this species would have benefited from being scatter-dispersed in far lower densities than those examined, and was unlikely to recruit beneath parent trees or in dense feacal clumps. Conversely, with the low seed predation intensities in 1990, *Litsea* survived in faecal clumps. Clearly survival in feacal clumps is variable between years.

The remaining species, with the exception of *Acronychia*, suffered little rodent seed predation at any microsite, even though deposited in clumps in "high risk" areas. These species were then likely to recruit both beneath parent trees and also in other dense patches. However, this is an overly simplistic view of processes operating, as this study deals only with short term rodent seed predation and provides no estimates of mortality by other agents such as: plant pathogens, allelopathy, herbivores or other processes which may act in a density dependent manner. Different levels of rodent seed predation were observed between plant species in 1988, however, since these differences were not observed in 1990, it may be misleading to generalise from the 1988 results.

The long term processes also complicate the picture. For example, *Elaeocarpus* entered seed dormancy (refer to Chapter Six). This species was not palatable to the rodent community and escaped predation in seed piles over the period of fruit/seed abundance. However, *Elaeocarpus* was heavily predated in subsequent months during the period of fruit/seed scarcity (April-August). This may be due to the leaching of secondary compound defences over time, or decreased discrimination with increased rodent hunger. *Cryptocarya* was decimated by bruchid beetle larvae prior to germination. *Endiandra* on the other hand was not predated heavily by seed predators, but experienced almost 100% loss due to fungal pathogens. Clearly jumping to conclusions about the fates of seeds on the basis of short-term susceptibility to rodent seed predation is misleading unless losses from other sources are known.

Of the dominant species examined, only *Syzygium* successfully established in any numbers beneath parent trees or in clumped patches (refer to Chapter Eight). In the case of *Syzygium*, escape from seed predators may have been achieved by being worthless in the presence of other favoured available species, or escaping by rapid germination before being considered palatable by rodents.

One interesting observation was that the most heavily defended seeds were preyed upon by rodents with the greatest intensity. *Planchonella euphlebia* was mechanically the best defended seed within the study site, having an extremely hard and thick test, but beneath the parent tree all seeds were destroyed by rodents. Similarly those seeds discovered in rodent caches were also decimated (pers. obs.). In upland rainforests to the north of Paluma, *Athertonia sp.*, *Endiandra palmerstonii*, *Beilschmiedia bancroftii*, *Pouteria castanospora* and a number of other Lauraceous "walnuts" are all 'ironclad', but are nonetheless destroyed by rodents to an extraordinary extent (Harrington pers. comm.).

7.4.7 The role of clump dispersal by male Tooth-bills.

The dispersal service offered by male Tooth-bills over the display season was of absolutely no advantage to *Litsea*, in 1988 or to those species that suffered from high density dependent mortality due to other factors. It was, however, effective for *Syzygium*, which survived and germinated effectively in faecal clumps and beneath the parent tree.

Clump-dispersal may act as a filter, enabling some species to pass through to germination, but impeding the progress of others. This filtering process varies between species, but also within species between years. *Litsea* did not survive to germinate in clumps in 1988, but did in 1990. Fluctuations in fruit and seed production between and within plant species and years, may drive fluctuations in the importance of dispersers and mortality agents. This suggests that even species "normally" predated in a density dependent manner may on occasion escape seed predation in clumps. On these occasions windows of recruitment to seedling stage in clumps are likely for those species that are normally heavily preyed upon.

Plate 4: Seedlings beneath an *Acmena resa* parent tree, Paluma Range, Queensland.

Chapter Eight

SEEDLING GROWTH AND SURVIVAL

8.1 INTRODUCTION

Janzen (1970) and Connell (1971) proposed that host specific predators and pathogens would operate in a density and or distance responsive manner resulting in disproportionately high mortality beneath the parent tree. Hubbell (1979) disputed this model and argued that even extremely low survival beneath the parent tree would still result in a greater numbers of recruits beneath the parent due to greater initial progeny densities within these sites. A number of reviews have examined support for the Janzen-Connell Model and found the evidence ambiguous, with some species fitting the model, and some not (Howe and Smallwood 1982, Clark and Clark 1984, Connell 1984, Howe 1989).

Howe (1989) suggested that seed dispersal syndromes may be linked to seed and seedling demography, and that this may, in part, account for some of the ambiguity observed. Howe proposed that scatter-dispersed species normally recruit as isolated individuals, and were unlikely to evolve resistance against density-dependent seed and seedling mortality agents, consistent with the Janzen/Connell model. In contrast, clump-dispersed species normally recruit in dense aggregations, and were therefore likely to have evolved mechanisms of resistance against density-dependent mortality agents, consistent with the Hubbell model (Howe 1989) (refer to Chapter One: Section 1.3.4).

A number of authors have detailed seedling mortality about parent trees (Augspurger 1983a, 1983b, Clark and Clark 1984) (refer to Chapter One). However, quantitative estimates of seedling mortality and growth within animal dispersed clumps are rare (Howe 1989). The primary aim of this study was therefore to provide quantitative estimates of seedling establishment, growth and survival within Tooth-bill dispersed clumps relative to other microsites on the forest floor. In effect to test the null hypothesis that: growth and survival in Tooth-bill dispersed clumps is ineffective relative to other microsites. In addition, recruitment history in around Tooth-bill courts was assessed by examining sapling composition.

8.2 METHODS

Three field experiments were conducted examining seedling survival and growth in clumps. Two species of Myrtaceae were used, *Acmena resa* and *Syzygium johnsonii*. The seedlings of both these species established beneath the parent tree and in bird dispersed clumps.

8.2.1 Plant species

Acmena resa is one of the largest tree species within the forest examined, attaining heights of 30m and a DBH to 80cm. It is often an emergent canopy species. *Acmena* produces white fruits of 12-16mm in diameter, with a single seed 9-13mm in diameter (Hyland 1983). Seeds germinate in 30-40 days (Hyland 1983). Large specimens often support the strangler fig, *Ficus destruens*. The fruiting of *Acmena* occurred late in 1986 (Power pers. comm.). Over the four years of this study *Acmena* did not flower or set fruit. The seedling beds resulting from the 1986 fruiting were extensive and abundant implying some degree of masting. Field experiments were conducted on the post wet season seedling distribution of this species. Sampling commenced in June 1987 and terminated June 1988 for Experiments One and Two.

Syzygium johnsonii is a less abundant canopy tree species, attaining heights to 25m with a DBH of less than 40cm. It produces watery purple fruits of 20 by 15mm, with a single seed 6-7mm in diameter. Seeds germinate in 30-50 days (Hyland 1983, pers. obs.). Fruiting occurred in November 1987 and large numbers of seeds were dispersed by male Tooth-bills to court areas. Dispersed seeds were collected from Tooth-bill seed piles (refer to Chapter Five), and germinated in the glass house before reintroduction to the field during the wet season (February 1988) for field experimentation (Experiment Three). The fruit fall and resultant seedling densities beneath the parent tree were far less for *Syzygium* than for

Acmena. Field sampling for was *Syzygium* commenced in February 1988 and terminated February 1989.

Throughout the remainder of this chapter, both species will be referred to by their generic name only.

8.2.2 Experiment One: The effect of seedling density on seedling growth and survival for *Acmena*

Experiment One examined the effect of seedling density on the recruitment of *Acmena* seedlings about the parent tree and tested the null hypothesis that seedling density has no effect on seedling growth and survival (i.e. the Janzen/Connell model).

Three parent trees were chosen at random. Three concentric zones were defined based on seedling densities radiating from the parent tree: (1) High density, beneath the parent crown, (H= >400 seedlings/m^2), (2) Intermediate density, at the crown periphery, (I= 100-20 seedlings/m^2) and (3) Low density, away from the parent crown, (L= <10 seedlings/m^2).

TABLE 8.1 Observed mortality agents and definitions: (1) density dependent (2) density independent.

Code:	Mortality agent	Definition
1	Unknown	. Seedling dying, cause undefined
2	Uprooted[1,2]	. Seedling displaced by animal diggings
3	Fungal infection[1]	. Stem brown to black and slimy . Leaves lose lustre and droop, browning in advanced cases
4	Wilting[2]	. Stem retains normal texture . Leaves collapse completely
5	Grazing, unknown[1]	. Chunks of leaf removed, or whole leaves
6	Grazing, leaf miner[1]	. Transparent wiggly lines on leaf surface, indicating the presence of a leaf miner within
7	Leaf/Branch fall[2]	. Seedlings smothered or flattened by fallen leaves or branch fall.

The area about each parent tree was divided into the eight cardinal points of the compass and a wedge between points was randomly chosen. Each wedge extended 20m from the base of the tree, and 100 seedlings were individually tagged, with a plastic bread tag, within each density zone (Table 8.2a). The density zones varied in width with each tree, as parent crown dimensions and seedling densities varied both within and between trees.

Experiment One commenced in June 1987, immediately after the wet season. The fate of all tagged seedlings was monitored on five sampling occasions over twelve months noting, presence/absence, height in mm, number of leaves, and condition. Condition included: (i) Undefined (ii) Uprooted, (iii) fungal infection, (iv) wilting, (v) grazing from unknown causes, (vi) grazing from leaf miners and (vii) leaf and branch fall (see Table 8.1 for definitions).

The penultimate cause of mortality for any seedling was not able to be determined, as sampling occasions were too infrequent. Instead, evidence of potential mortality agents acting on the remaining seedlings adjacent to those that suffered mortality were used as an indicator of possible cause of mortality.

8.2.3 Experiment Two: The effect of microsite and density on seedling growth and survival for *Acmena.*

Experiment Two examined the effect of microsite and density on the recruitment of *Acmena* seedlings and tested he null hypothesis that: seedling microsite and density have no effect on seedling growth and survival, either in parent tree and/or bird dispersed seed beds (i.e. the Janzen/Connell model).

Two microsites were selected, parent tree (BPC) and bird dispersed seedling clumps (TBC). Bird dispersed seedling clumps were a much reduced and isolated example of parent tree clumps. Microsites were further divided into two densities high (H) and low (L). Four parent trees were chosen at random (BPC), and the Tooth-bill courts closest to these selected for the experiment (TBC). For high density subsites within each of the two microsites (H), a $0.5m^2$ quadrat was randomly placed beneath the parent crown or directly over the bird dispersed seedling clump, and 30 seedlings were tagged within each quadrat. For the low density subsite (L) within the parent tree microsite, a 3m radius quadrat was placed in the outer margin of the intermediate zone (I; defined in Experiment One). For the equivalent Tooth-bill seedling low density subsite, a 3m radius quadrat was placed directly over the bird dispersed seed pile quadrat. Again 30 seedlings were tagged within each of these, but tagged seedlings were at least 0.5m from the high density clump. This resulted in two microsites (BPC and TBC), and two densities within each microsite (H and L). Four replicates of each microsite/density combination were used, and 30 seedlings tagged within each replicate (Table 8.2b). Seedlings were then monitored as for experiment one.

TABLE 8.2 Experimental design for seedling survival and growth experiments

a. Experiment One: The effect of seedling density zone on seedling growth and survival about parent tree *Acmena*. Dense seedlings beds surrounding three parent trees were used, and 100 seedlings tagged in each density treatment. Seedlings were sampled on five occasions over 12 months. (n=900 seedlings)

Seedling Density	Parent Tree		
	1	2	3
High (H)	100	100	100
Intermediate (I)	100	100	100
Low (L)	100	100	100

b. Experiment Two: The effect of microsite and seedling density on seedling growth and survival for *Acmena*. Both microsites contained two densities and four replicates within each containing 30 seedlings.
Seedlings were sampled on five occasions over 12 months. (n=480 seedlings)

Replicate	Microsite and density of seedlings			
	Beneath Parent tree clump		Tooth-bill seedling clump	
	High (H)	Low (L)	High (H)	Low (L)
1	30	30	30	30
2	30	30	30	30
3	30	30	30	30
4	30	30	30	30

c. Experiment Three: The effect of microsite on seedling growth and survival for *Syzygium*. Microsite definition is detailed in (Table 8.3). Five replicates of each microsite were used and 30 seedlings tagged in each. Seedlings were sampled on five occasions over 12 months. (n=750 seedlings)

Replicate	Microsite				
	Beneath Parent tree clump (BPC)	Tooth-bill clump (TBC)	Canopy gap centre (GCE)	Canopy gap edge (GED)	Random beneath canopy (RBC)
1	30	30	30	30	30
2	30	30	30	30	30
3	30	30	30	30	30
4	30	30	30	30	30
5	30	30	30	30	30

8.2.4 Experiment Three: The effect of microsite on seedling growth and survival for *Syzygium*

Experiment Three examined the effect of microsite on the growth and survival of *Syzygium* seedlings, and tested the null hypothesis that: microsite has no effect on seedling growth and survival (i.e. the Janzen/Connell model).

Seedlings were germinated in a glasshouse from the droppings of male Tooth-bills (refer to Chapter Six). Healthy seedlings were transplanted into the field and distributed amongst five microsites with five replicates of 30 seedlings in each. Microsites were:
i) Tooth-bill dispersed seedling clumps (TBC),
ii) Beneath parent crown seedling clumps (BPC),
iii) Canopy gap centre (GCE),
iv) Canopy gap edge (GED), and
v) At random beneath the canopy (RBC) (Table 8.2c).

Five grid co-ordinates were selected randomly over the length of the 50ha study area. Grid coordinates were chosen as RBC microsites. The nearest BPC, TBC, GCE and GED microsites to the RBC grid coordinates were then chosen, with a minimum distance of 30m between each condition (Table 8.3). A 0.5m^2 quadrat was placed at the core of each microsite, and seedlings were planted and tagged. Seedlings were then monitored as for previous experiments.

Four spot light readings were taken at seedling level from the corners of each quadrat between 1000h and 1400h at the beginning of the study using a LICOR Quantum light meter, to obtain estimates of light conditions experienced by the seedlings.

TABLE 8.3 Microsite codes, definitions, descriptions, predicted mortality agents, risk of mortality and growth and selection criteria. Predictions of mortality agents and risk of mortality are consistent with the Janzen/Connell model (Howe 1989).

Code	Definition	Description	Predicted mortality agents, Risk of mortality and growth	Selection criteria
BPC	Beneath parent tree	. Area of high fruit and seed fall directly beneath parent crown, . High seedling densities . single species . low light	. Density dependent, distance dependent and density independent mortality agents . High risk of mortality . Low potential for growth	A random compass bearing was taken, and quadrat placed at a distance half the radius of the parent crown, placing the quadrat in the centre of the parent tree seed bed.
TBC	Bird dispersed seed bed	. Seed pile beneath the favoured display perch of Male Tooth-bills . High seedling density . multiple species .Low light	. Density dependent and density independent mortality agents . High risk of mortality . Low potential for growth.	Quadrat was placed within a 1 m radius of Tooth-bill seedling clump, on a random compass bearing.
GCE	Canopy gap centre	. centre of a major tree fall event, canopy opening . Low seedling density . High light	. Density independent mortality agents, . Low risk of mortality . High potential for growth	(GCE) Quadrat was placed in the centre of the canopy gap.
GED	Canopy gap edge	. Edge of a major tree fall event, canopy opening . Low seedling density .Intermediate light	. Density independent mortality agents, . Low risk of mortality . Intermediate potential for growth	(GED) a random bearing was taken from the centre and Quadrat placed at the edge of a canopy gap.
RBC	Random beneath canopy	. Random area beneath the closed canopy . Low seedling density . Low light	. Density independent mortality agents, . Low risk of mortality . Intermediate potential for growth	Random sites were chosen as specific grid coordinates on site maps. These acted as foci for the selection of other microsites, and were at least 30m from the influence of other microsites.

8.2.5 Sapling composition

The distribution of different plant families in and around Tooth-bill courts and at random sites beneath the canopy was also investigated. Cuttings were taken from all individual saplings 0.5 to 2.0m in height, within a 5m radius of three Tooth-bill courts and three random sites and all material was returned to the lab for counts and identification.

8.2.6 Assumptions

Seedlings are subject to both density and distance dependent mortality. Beneath the parent tree, both distance and density dependent mortality agents can operate. In Experiment One, the effects of density were confounded by distance effects. However, in Experiment Two and Three the effects could be separated based on the following assumptions:

i) Both density and distance dependent mortality agents can operate beneath the parent tree.
ii) Only density dependent mortality agents operate within Tooth-bill seedling clumps (TBC).
iii) High density microsites (H) should be subject to greater density dependent mortality than low density microsites (L).
iv) Neither density or distance dependent mortality agents operate in gap centre (GCE), gap edge (GED) or random beneath (RBC) microsites.

In Experiments Two and Three, if parent tree clumps were observed to suffer significantly higher mortality than Tooth-bill clumps, then there was significant distance dependent mortality. If high density sites (H), suffered significantly greater mortality than low density sites (L), there was significant density dependent mortality. Similarly in Experiment Three if both (BPT) and (TBC) were significantly different from other microsites (GCE, GED, RBC) then there was significant density dependent mortality. Finally, if there were no significant differences between microsites, neither distance or density dependent mortality agents were effective.

8.2.7 Analytical methods

Two measures of seedling performance, proportion surviving, and growth (height in mm) were analysed using Repeated Measures Analysis of Variance for all three experiments. At the termination of all experiments, after 12 months, contrasts were performed on all three measures of seedling performance: final proportion surviving, final height in mm and change in the number of leaves (number of leaves T5-T1), and significant effects determined. All survival data was transformed using Arcsine square root(proportion) transform and growth data was un-transformed. Models used are outlined below.

8.2.7.1 Experiment One

For proportion surviving, three treatment groups were analysed: Density (H,I,L) were crossed with tree (1,2,3), with no replication, with repeated measures over four times (Table 8.2a). For growth (height in mm), for four treatment groups were analysed: Seedlings were nested in density (H,I,L) which was crossed with tree (1,2,3), with repeated measures over four times (Table 8.2a).

8.2.7.2 Experiment Two

Proportion surviving was analysed for three treatment groups: replicate was nested within density (H,L) which was crossed with microsite (BPC, TBC), and measures were repeated over four times (Table 8.2b). For growth (height in mm), four treatment groups were analysed: Seedlings were nested in replicate which was nested in density (H,L) which was crossed with microsite (BPC, TBC), and measures were repeated measures over four times (Table 8.2b).

8.2.7.3 Experiment Three

For proportion surviving two treatment groups were analysed: replicate was nested within microsite (BPC, TBC, RBC, GED, GCE) and measures were repeated over four times (Table 8.2c). For growth (height in mm), three treatment groups were analysed: seedlings were nested in replicate which was nested within microsite (BPC,TBC,RBC,GED,GCE) and measures were repeated over four times. Contrasts were performed between levels of major treatments, for all measures at the termination of all three experiments where Repeated measures analyses proved significant.

8.3 RESULTS

8.3.1 Experiment One: The effect of seedling density on seedling survival for *Acmena.*

Seedlings abundances showed a skewed distribution, with the highest seedling densities beneath the parent crown, and decreasing density away from the parent tree. Seedling densities and width of crown varied between trees (Fig 8.1a).

8.3.1.1 The effect of seedling density on the survival of *Acmena* seedlings.

For between treatment effects, density, had no significant effect on seedling survival (Table 8.4). Within treatment effects, time had a significant and expected effect, that is, seedling survival decreased over time (Table 8.4). However, there was no significant time by density effect on seedling survival, that is, seedling survival did not differ significantly between seedling density treatments (Table 8.4, Fig 8.1c).

TABLE 8.4 Experiment One: Survival. The effect of seedling density, tree and time on seedling survival, for *Acmena*. Repeated measures Analysis of Variance was performed on Arcsin square root transformed proportion survival data. Univariate between effects average over time, whereas, multivariate within effects test effect of time on major treatments. For multivariate tests, Wilk's Lambda statistic was used. Contrasts were not performed as there were no significant effects.

Treatment	df	MS	F	p
Between effects				
Seedling density	2	0.04	0.26	0.786
Tree	2	0.34	2.19	0.228
Seedling density x Tree	4	0.15		
Within effects		Wilks Lambda		
Time	1,4	0.0008	281.76	0.045
Time x Seedling density	2,8	0.01	1.97	0.379
Time x Tree	2,8	0.04	0.98	0.595

8.3.1.2 The effect of seedling density on the growth of *Acmena* seedlings.

From an original 900 tagged seedlings, 192 surviving individuals were used in growth analyses. For between treatments effects, density had a significant effect on growth (height in mm), with increased seedling height in high seedling density (Table 8.5a, Fig 8.2a). For within treatment effects, time, time by density, time by tree and time by density by tree all had significant effects on seedling growth in height (Table 8.5a). Seedlings in the lower densities tended to shrink, those in high densities grew, and all grew after the wet season (Fig 8.2a).

TABLE 8.5a Experiment One: Growth (height in mm). The effect of seedling density, tree and time, on *Acmena* seedling growth (height in mm). 192 of 900 seedlings were used in analyses. Repeated Measures Analysis of Variance was performed on un-transformed data. Univariate tests examined between effects. Multivariate tests examined within effects, and Wilk's Lambda statistic was used.

Treatment	df	MS	F	p
Between				
Seedling density	2	8039.42	16.24	<0.001
Tree	2	726.04	1.47	0.233
Seedling density x Tree	4	910.88	1.84	0.123
Se(Seedling density x Tree)	183	495.14		
Within		Wilks Lambda		
Time	4,180	0.738	15.90	<0.001
Time x Seedling density	8,360	0.814	4.86	<0.001
Time x Tree	8,362	0.848	3.84	<0.001
Time x Seedling density x Tree	16,550	0.811	2.44	0.001

Contrasts at the termination of the study between the three densities for growth in height proved significant between high and intermediate, and high and low densities (Fig 8.2b, Table 8.5b). Seedlings grew differently in different densities, but those in high densities were tall at the outset, and grew taller than those at low and intermediate densities (Fig 8.2b).

Fig 8.1a
Seedling distribution around three *Acmena resa* parent trees

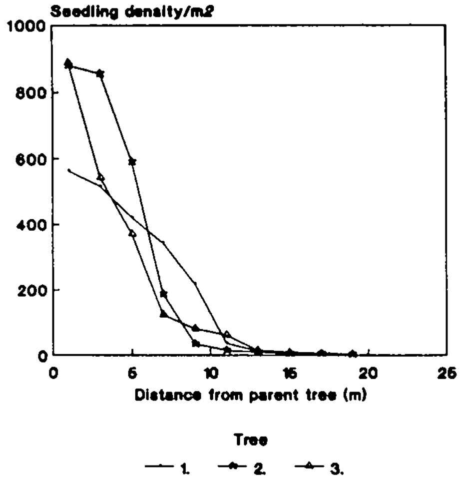


Fig 8.1c
The effect of density on seedling survival for *Acmena resa* at (12 months)

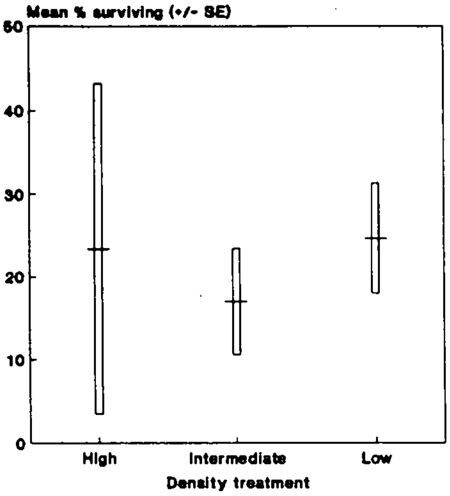


Fig 8.1b
The effect of seedling density on seedling survival for *Acmena resa*

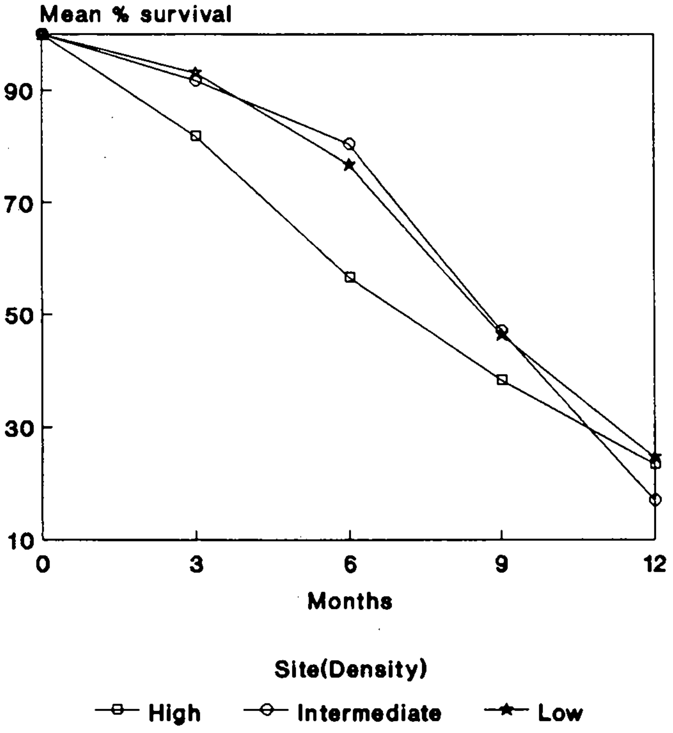


Fig 8.2b

Effect of density on final seedling heights for *Acmena resa* (12 months)

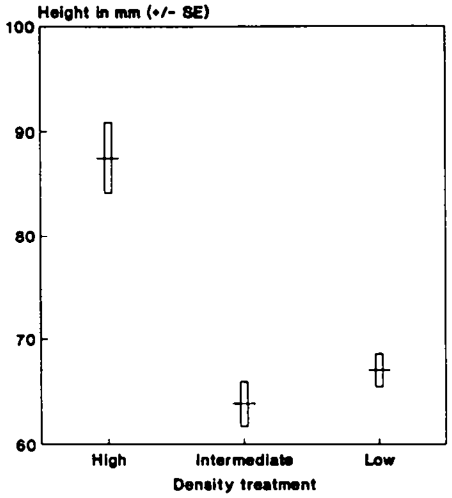
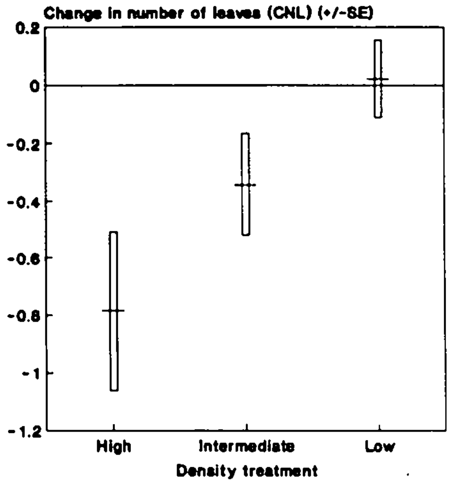


Fig 8.2c

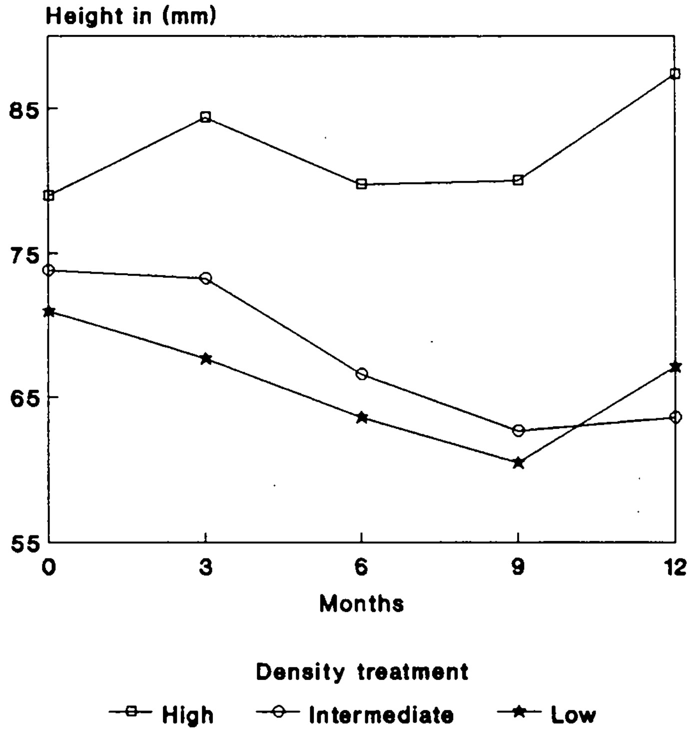
Effect of density on number of leaves for *Acmena resa* seedlings (12 months)



CNL = Number of leaves at 12 months minus the number of leaves at time 0

Fig 8.2a

Effect of density on growth (height in mm) for *Acmena resa* seedlings



192 of 900 individuals used

TABLE 8.5b Analysis of Variance testing the effect of density and tree on *Acmena* seedling growth (height in mm) at the termination of the experiment. Contrasts between levels within density were performed.

Treatment	df	MS	F	p
Seedling density	2	3183.90	19.37	<0.001
Tree	2	246.33	1.50	0.226
Seedling density x Tree	4	719.19	4.37	0.002
Se(Seedling density x Tree)	186	164.39		
Contrasts				
H vs I	1	5986.61	36.42	0.000*
L vs I	1	245.40	1.49	0.223
H vs L	1	5113.53	31.10	0.000*

Conversely, seedling density treatment had a significant and negative effect on the change in number of leaves, with seedlings in high densities losing most leaves and those in low densities, maintaining their leaves (Table 8.5c, Fig 8.2c). Contrasts between levels within density proved significant for low vs intermediate and low vs high density (Table 8.5c).

TABLE 8.5c Experiment One: Growth (Change in the number of leaves). Analysis of variance testing the effect of density and tree on *Acmena* seedling growth (Change in the number of leaves). Contrast were performed on levels within density.

Treatment	df	MS	F	p
Seedling density	2	4.57	3.99	0.020
Tree	2	3.24	2.82	0.062
Seedling density x Tree	4	1.24	1.09	0.364
Se(Seedling density x Tree)	186	1.15		
Contrasts				
H vs I	1	2.08	1.82	0.179
L vs I	1	3.16	2.76	0.098
H vs L	1	7.97	6.96	0.009

8.3.1.3 Experiment One: Potential factors affecting the growth and survival of *Acmena* seedlings

Of the potential causes of mortality observed, grazing in different forms accounted for 69%, leaf and branch fall 19%, wilting 9% and the remaining 3% was attributable to other factors including uprooting and fungal infections. Whether these factors caused the ultimate demise of the seedlings was unknown, but they may have assisted in the process. The incidence of mortality agents increased in the seedling beds over time to 47% of surviving individuals (Fig 8.3a). Density treatment appeared to have little effect on the incidence of the various mortality factors (Fig 8.3b). High leaf loss in high seedling density treatments was not supported by a concomitant increase in the evidence of grazing in the high seedling densities (Fig 8.3b).

8.3.2 Experiment Two: The effect of microsite and seedling density on the survival and growth of *Acmena* seedlings.

This experiment expanded on the first, testing whether: (i) high density seedling beds, either parent tree or bird dispersed, had any effect on seedling survival and growth, and (ii) whether differences in seedling density about these sites, similarly had any effect on seedling survival and growth for *Acmena* seedlings. This experiment allowed for the separation of density and distance dependent effects.

8.3.2.1 The effect of microsite and seedling density on the survival of *Acmena* seedlings.

There were no significant treatment effects on survival (Table 8.6, Fig 8.4a). Within treatments, there were also no significant effects, with the exception of time (Table 8.6, Fig 8.4a). Variation in seedling survival was far greater beneath parent trees (Fig 8.4b).

Fig 8.3a

Incidence of mortality factors affecting *Acmena resa* seedlings over time

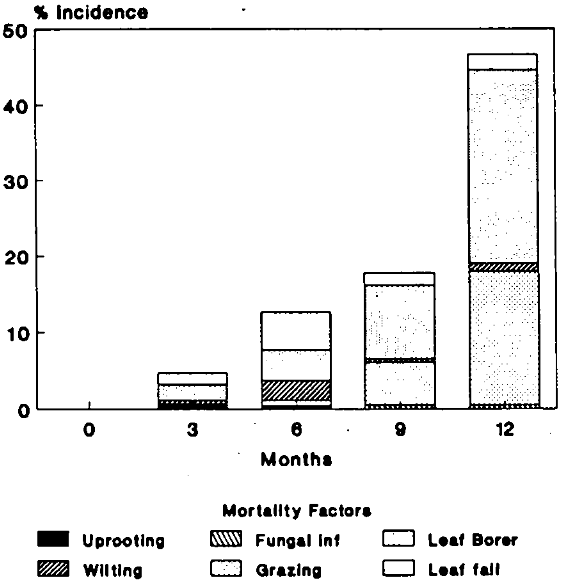


Fig 8.3b

Effect of density on the incidence of mortality agents: *Acmena resa* seedlings

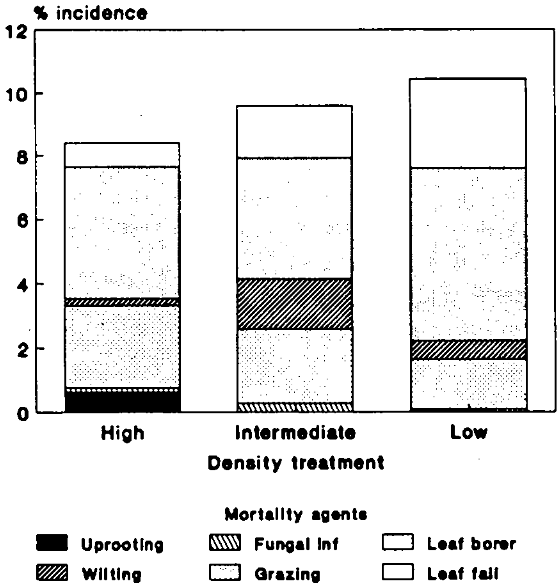


Fig 8.4a

Effect of microsite and density on seedling survival for *Acmena resa*

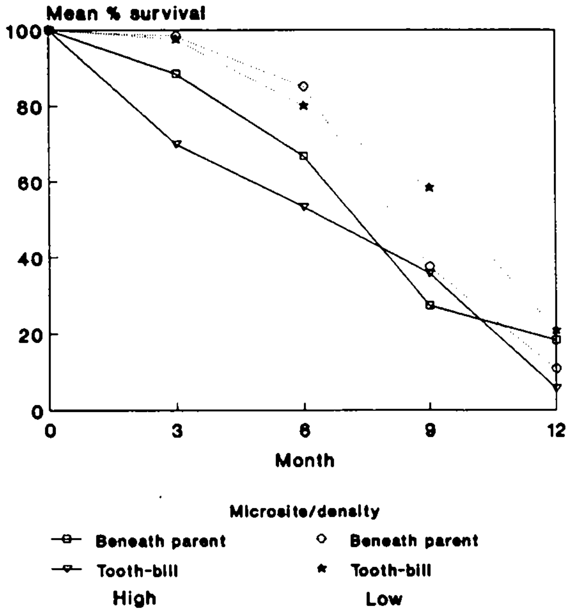


Fig 8.4b

The effect of microsite and density on survival for *Acmena resa* (12 months)

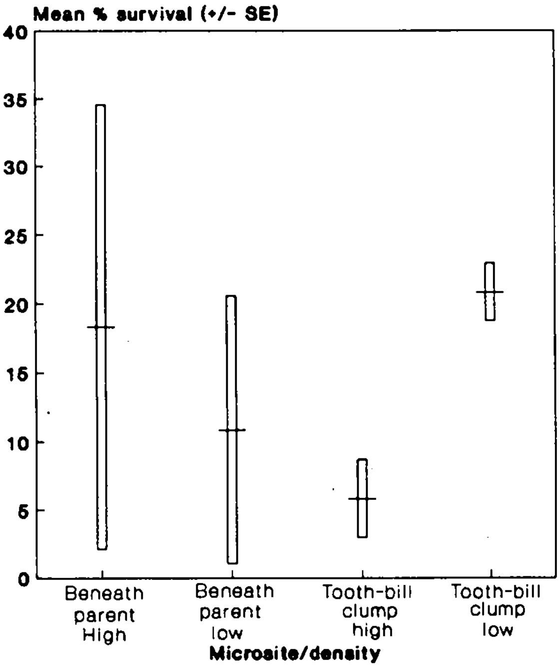


TABLE 8.6 Experiment Two: Survival. The effect of microsite, seedling density, and time on seedling survival, for *Acmena*. Repeated measures Analysis of Variance was performed on Arcsin square root transformed proportion survival data. Univariate between effects average over time, whereas, multivariate within effects test effect of time on major treatments. For multivariate tests, Wilk's Lambda statistic was used. Contrasts were not performed as there were no significant effects.

Treatment	df	MS	F	p
Between effects				
Microsite	1	0.06	0.26	0.616
Seedling density	1	0.82	3.50	0.085
Microsite x Seedling density	1	0.16	0.68	0.425
Rep(Microsite x Seedling density)	12	0.23		
Within effects		Wilks Lambda		
Time	3,10	0.07	46.29	<0.001
Time x Microsite	3,10	0.79	0.85	0.497
Time x Seedling density	3,10	0.68	1.54	0.264
Time x Rep(Microsite x Seedling density)	3,10	0.777	0.95	0.452

8.3.2.1 The effect of microsite and seedling density on the growth of *Acmena* seedlings.

Only 64 surviving individuals of the 480 tagged seedlings were used in growth analyses. Density and the interaction between replicate within microsite by density, had a significant effect on growth in height (Table 8.7a). Seedlings growing in high seedling densities confirmed previous findings, with taller seedlings in higher seedling densities (Fig 8.5a). Within treatments, time and time by density had a significant effect on seedling growth in height (Table 8.7a). Seedlings tended to shrink prior to the wet season, and grow in the period after the wet season, with individuals in high density microsites tending to grow as fast or faster than those in low density microsites (Fig 8.5a). For contrasts performed between density and microsite levels at the termination of the experiment, high vs low bird dispersed treatments proved significant, (Table 8.7b, Fig 8.5b).

TABLE 8.7a Experiment Two: Growth (height in mm). The effect of microsite, density and time, on *Acmena* seedling growth (height in mm). 192 of 900 seedlings were used in analyses. Repeated Measures Analysis of Variance was performed on un-transformed data. Univariate tests examined between effects. Multivariate tests examined within effects, and Wilk's Lambda statistic was used. 64 surviving seedlings of 480 were used in analyses

Treatment	df	MS	F	P
Between effects				
Microsite	1	98.14	0.27	0.605
Seedling density	1	3562.38	9.80	0.003
Microsite x Seedling density	1	450.06	1.24	0.271
Rep(Microsite x Seedling density)	7	1797.16	4.95	0.000
Se(Rep(Microsite x Seedling density))	53	363.42		
Within effects				
Time	4,50	0.62	7.578	0.000
Time x Microsite	4,50	0.83	2.466	0.057
Time x Seedling density	4,50	0.78	3.463	0.014
Time x Microsite x Seedling density	4,50	0.94	0.784	0.541
Time x Rep(Microsite x Seedling density)	28,182	0.47	1.507	0.058

TABLE 8.7b: Analysis of Variance testing the effect of density and tree on *Acmena* seedling growth (height in mm) at the termination of the experiment. Contrasts between levels within density were performed. 67 surviving seedlings of 480 were used in analyses.

Treatment	df	MS	F	p
Microsite	1	335.78	2.55	0.116
Seedling density	1	2430.17	18.46	<0.001
Microsite * Seedling density	1	141.38	1.07	0.304
Rep(Microsite * Seedling density)	7	620.30	4.71	<0.001
Se(Rep(Microsite * Seedling density))	56	131.65		
Contrasts				
HP vs HB	1	447.77	3.40	0.070
LP vs LB	1	22.50	0.17	0.681
HP vs LP	1	501.37	3.81	0.056
HB vs LB	1	2414.45	18.34	0.000

There were significant effects of density, and replicate within microsite by density, on change in the number of leaves (Table 8.7c, Fig 8.5c). Contrasts between individual treatments proved significant between high and low density bird dispersed clump microsites, but proved non-significant between densities in the parent tree microsites (Table 8.7c, Fig 8.5c).

TABLE 8.7c Experiment Two: Growth (change in the number of leaves). Analysis of Variance testing the effect of density and tree on *Acmena* seedling growth (height in mm) at the termination of the experiment. Contrasts between levels within density were performed.

Treatment	df	MS	F	p
Microsite	1	0.45	0.56	0.456
Seedling density	1	4.17	5.24	0.026
Microsite * Seedling density	1	1.86	2.34	0.132
Rep(Microsite * Seedling density)	7	3.95	4.96	0.000
Se(Rep(Microsite * Seedling density))	56	0.79		
Contrasts				
HP vs HB	1	2.05	2.57	0.114
LP vs LB	1	0.23	0.29	0.589
HP vs LP	1	0.11	0.14	0.705
HB vs LB	1	7.31	9.17	0.004

8.3.2.3 Factors affecting growth and mortality of *Acmena* seedlings

Grazing in different forms accounted for 57.5%, leaf and branch fall 13.5%, wilting 17% and uprooting, the remaining 12% incidence of possible mortality. The percentage of remaining seedlings affected by these factors increased over the course of the study to 57% (Fig 8.6a). Seedlings growing in bird dispersed microsites were subject to a greater incidence of leaf fall than beneath parent tree microsites, whereas beneath parent low densities suffered greater incidence of wilt (Fig 8.6b).

Fig 8.5b
Effect of microsite and density on seedling growth for *Acmena resa* after 12 months

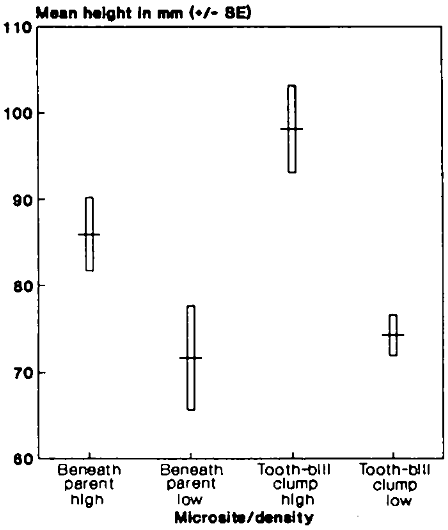


Fig 8.5c
Effect of microsite and density on number of leaves for *Acmena resa* after 12 months

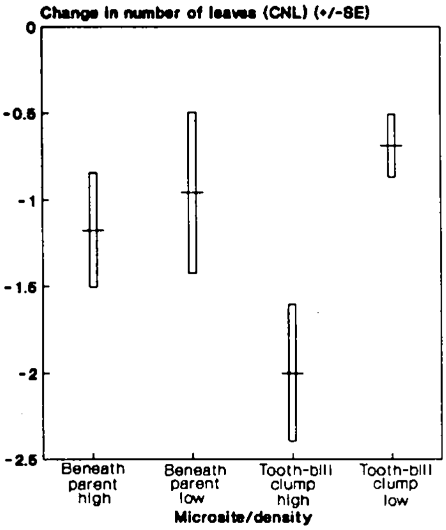


Fig 8.5a
The effect of microsite and density on seedling growth for *Acmena resa*

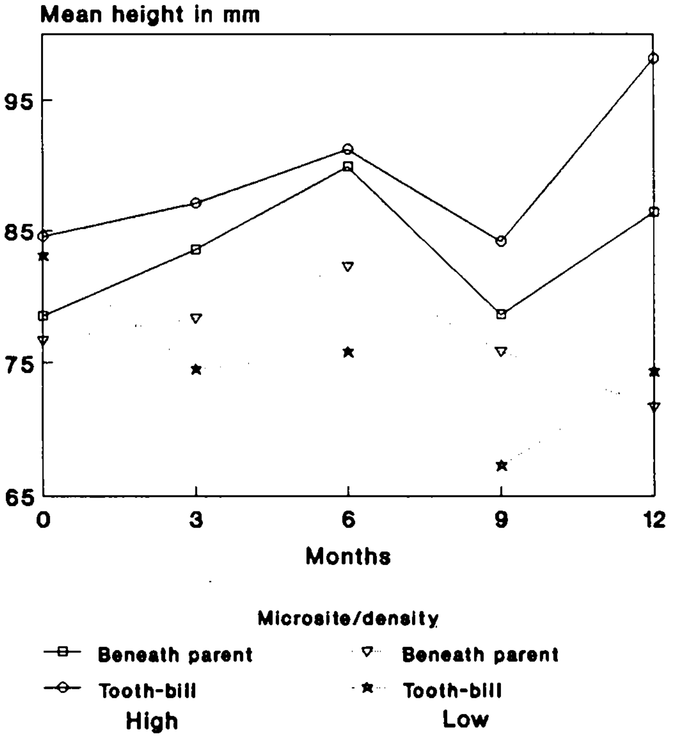


Fig 8.6a

Effect of time on the incidence of mortality agents on *Acmena resa*

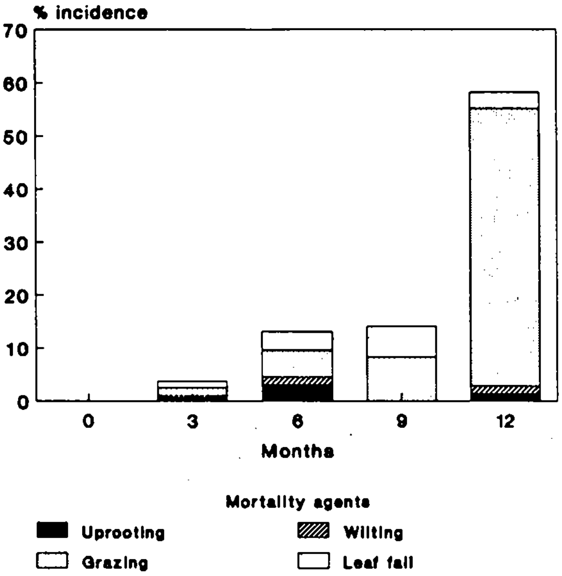
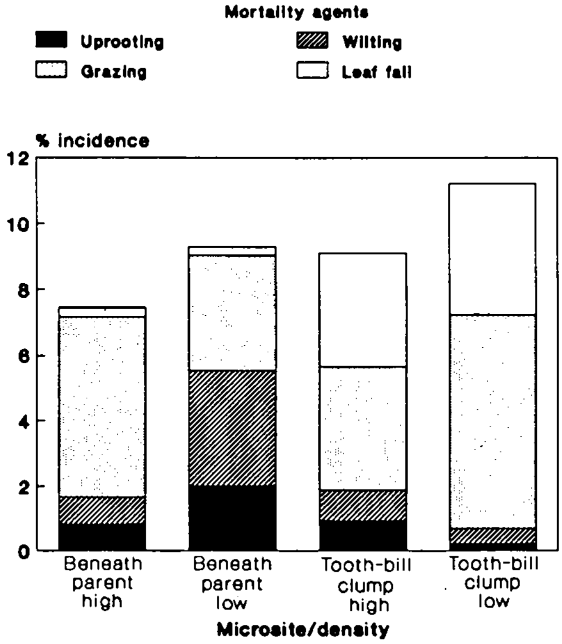


Fig 8.6b

Effect of microsite and density on incidence of mortality agents on *Acmena resa* seedlings



8.3.3 Experiment Three: The effect of microsite on the survival and growth of *Syzygium* seedlings.

Experiment three examined the effect of microsite on seedling growth and survival testing the hypothesis: if density and or distance responsive mortality is weak or non-existent for members of the clump dispersal syndrome, then mortality should be similar, irrespective of microsite. The exception was light gaps, where survival and growth may have been enhanced.

8.3.3.1 The effect of microsite on the survival of *Syzygium* seedlings.

Seedlings in gap microsites survived better than those beneath the parent tree. Those beneath the parent tree survived better than those in Tooth-bill clumps, and both survived better than seedlings in clumps at random beneath the canopy (Fig 8.7a). Microsite had a significant effect on survival, with most microsites similar (22-39% survival), but random sites experienced high mortality (4% survival) (Table 8.8a, Fig 8.7a). Within treatments, there was a significant time effect, but no significant time by microsite effect on seedling survival (Table 8.5a, Fig 8.9a). Contrasts between microsites and grouped microsites confirmed these findings, with significant differences between random microsites and both major groupings, gap (GCE, GED) and clump (BPC, TBC) microsites (Table 8.8b, Fig 8.7b).

TABLE 8.8a Experiment Three: Survival. The effect of microsite and time on seedling survival, for *Syzygium*. Repeated measures Analysis of Variance was performed on Arcsin square root transformed proportion survival data. Univariate between effects average over time, whereas, multivariate within effects test effect of time on major treatments. For multivariate tests, Wilk's Lambda statistic was used.

Treatment	df	MS	F	P
Between effects				
Microsite	4	0.82	3.13	0.0376
Rep(Microsite)	20	0.26		
Within effects				
Time	3,18	0.04	124.8990	0.0001
Time x Microsite	12,48	0.38	1.7449	0.0864

Fig 8.7b
Effect of microsite on the survival of *Syzygium johnsonii* seedlings (12 months)

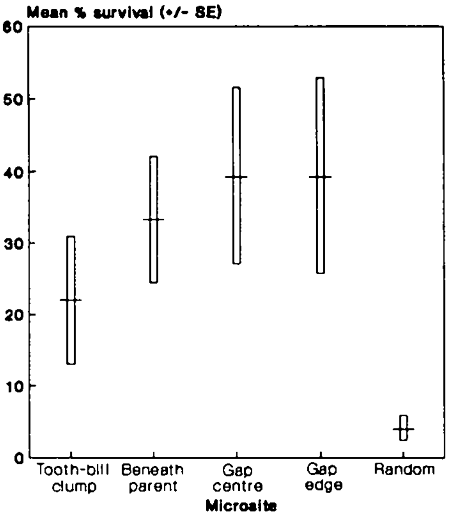


Fig 8.7c
Light levels within each microsite treatment for *Syzygium johnsonii*

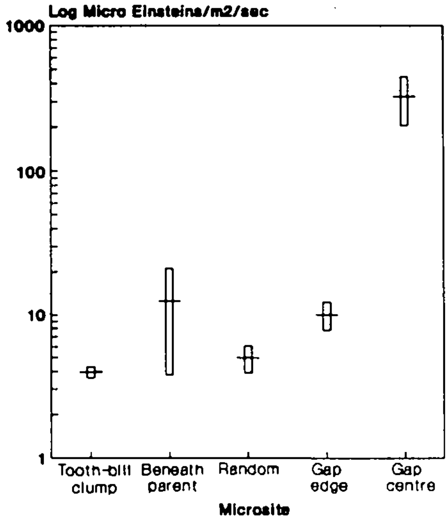


Fig 8.7a
The effect of microsite on seedling survival for *Syzygium johnsonii*

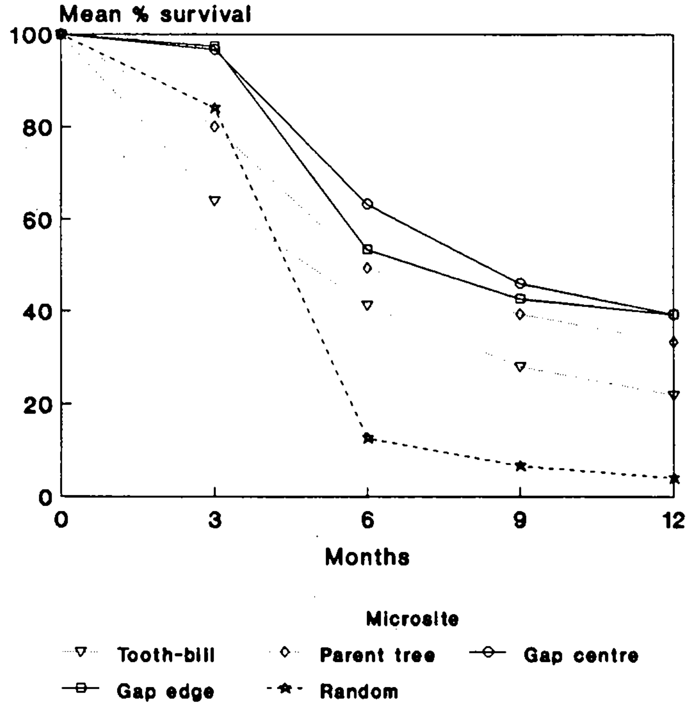


TABLE 8.8b: Analysis of Variance testing the effect of microsite on *Syzygium* seedling survival at the termination of the experiment. Contrasts between levels within microsite were performed. Contrast comparisons, levels within microsite include: (Microsite) microsite, (L1) tooth-bill clumps, (L2) beneath parent clumps, (H1) gap centre, (H2) gap edge, (M) random beneath canopy, (L) pooled L1 and L2, and (H) pooled H1 and H2.

Treatment	df	MS	F	P
Microsite	4	0.23	2.88	0.049
Rep(Microsite)	20	0.07		
Contrasts				
L1 vs L2	1	0.07	0.91	0.3513
H1 vs H2	1	0.00	0.00	0.9532
H vs L	1	0.11	1.46	0.2406
M vs L	1	0.40	5.13	0.0348
M vs H	1	0.84	10.58	0.0040

8.3.3.2 The effect of microsite on the growth of *Syzygium* seedlings.

It was predicted that seedlings in gap centre (GCE) and gap edge (GED) microsites should grow best, whereas seedlings in bird dispersed (BDS), beneath parent crown (BPC) and random microsites (RBC=control) should grow least.

Microsite had significant effect on light levels (One Way Analysis of Variance Log(light); df=4,95, F=6.83, p <0.001), with highest light levels in the gap centre (GCE) microsites (Fig 8.7c). Only 206 surviving individuals of the 750 initially tagged were used in growth analyses. Unlike the previous experiments, taller seedlings did not occur in high density seedling microsites, as seedlings were initially grown in a greenhouse. As predicted, surviving seedlings were tallest in gap microsites and shortest in sites beneath the canopy (Fig 8.8a). Microsite had no significant effect on growth in height, but replicate within microsite did, that is, there was high variation between replicates within microsites (Table 8.9a). Within treatments, all proved significant, that is they grew the pattern of growth differed among treatments (Table 8.9a, Fig 8.8a).

TABLE 8.9a Experiment Three: Growth (height in mm). The effect of microsite and time, on *Syzygium* seedling growth (height in mm). 206 of 750 observations used in analyses. Repeated Measures Analysis of Variance was performed on untransformed data. Univariate tests examined between effects. Multivariate tests examined within effects, and Wilk's Lambda statistic was used.

Treatment	df	MS	F	P
Between				
Microsite	4	559.28	0.61	0.6558
Rep(Microsite)	16	1887.80	2.06	0.0118
Se(Rep(Microsite))	185	916.48		
Within		Wilks Lambda		
Time	4,182	0.81	10.602	0.0001
Time x Microsite	16,556	0.77	3.021	0.0001
Time x Rep(Microsite)	64,715	0.59	1.5630	0.0043

Differences in heights between different microsites at the end of the experiment were compared using contrasts (Table 8.9b). The differences between high density clump microsites, and gap microsites proved non-significant, but there was a weak significant difference between pooled gap and random microsites (Table 8.9b, Fig 8.8b).

TABLE 8.9b: Analysis of Variance testing the effect of microsite on *Syzygium* seedling growth (height in mm) at the termination of the experiment. Contrasts between levels within microsite were performed. Levels within microsite included: (L1) tooth-bill clumps, (L2) beneath parent clumps, (H1) gap centre, (H2) gap edge, (M) random beneath canopy, (L) pooled L1 and L2, and (H) pooled H1 and H2.

Treatment	df	MS	F	p
Microsite	4	430.04	1.56	0.186
Rep(Microsite)	16	393.66	1.43	
Se(Rep(Microsite)	185	274.96		
Contrasts				
L1 vs L2	1	5.74	0.02	0.8852
H1 vs H2	1	242.70	0.88	0.3487
H vs L	1	858.00	3.12	0.0790
M vs L	1	300.23	1.09	0.2974
M vs H	1	1032.38	3.75	0.0542

Fig 8.8b

Effect of microsite on height of *Syzygium johnsonii* seedlings (12 months)

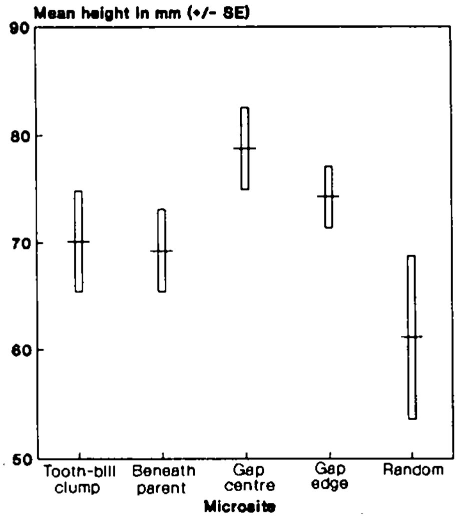


Fig 8.8c

Effect of microsite on change in number of leaves for *Syzygium johnsonii* (12 months)

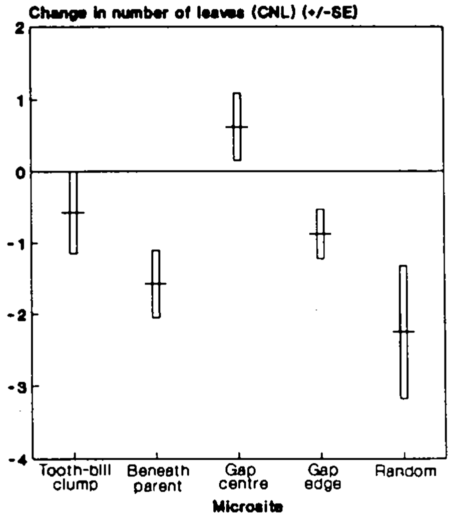
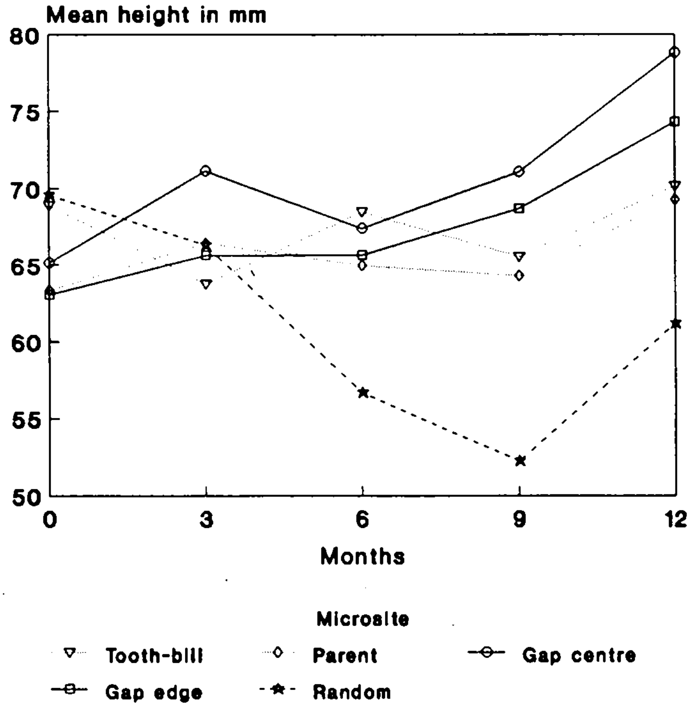


Fig 8.8a

Effect of microsite on growth (ht in mm) for *Syzygium johnsonii* seedlings



Both microsite and replicate within microsite had a significant effect on changes in the number of leaves (Table 8.9c, Fig 8.8c). Seedlings in gap centre microsites gained leaves, whereas seedlings in all other microsites lost leaves. Contrasts between individual microsites and grouped microsites proved significant for gap centre vs gap edge, gap vs clumps and gap vs random (Table 8.9c, Fig 8.8c). Seedlings in gap centre microsites grew significantly more leaves than all other microsites.

TABLE 8.9c Experiment Three: Growth (change in the number of leaves). Analysis of variance testing the effect of microsite on *Syzygium* seedling growth (change in the number of leaves T5-T1) at the termination of the experiment. Contrasts between levels within microsite were performed. Levels within microsite included: (L1) tooth-bill clumps, (L2) beneath parent clumps, (H1) gap centre, (H2) gap edge, (M) random beneath canopy, (L) pooled L1 and L2, and (H) pooled H1 and H2. Univariate tests on the change in the number of leaves.

Treatment	df	MS	F	p
Microsite	4	14.95	3.65	0.0069
Rep(Microsite)	16	10.35	2.53	0.0015
Se(Rep(Microsite))	185	4.09		
Contrasts				
L1 vs L2	1	7.42	1.81	0.1796
H1 vs H2	1	26.94	6.58	0.0111
H vs L	1	16.52	4.04	0.0459
M vs L	1	5.65	1.38	0.2415
M vs H	1	19.63	4.80	0.0298

8.3.3.3 Factors affecting survival and growth for *Syzygium* seedlings.

Grazing in different forms accounted for 38% of mortality amongst the seedlings, with leaf and branch fall 31%, wilting 25% and other factors including uprooting and fungal infections the remaining 6%. The percentage of remaining seedlings affected by these factors increased over the course of the study to 11%, far less than the incidence of potential mortality factors for *Acmena* (47-58%) (Fig 8.9a). Seedlings growing in gap microsites suffered greater wilting than other sites, and seedlings in bird dispersed microsites proved undamaged (Fig 8.9b).

Fig 8.9a
Effect of time on the incidence of mortality agents on *Syzygium* seedlings

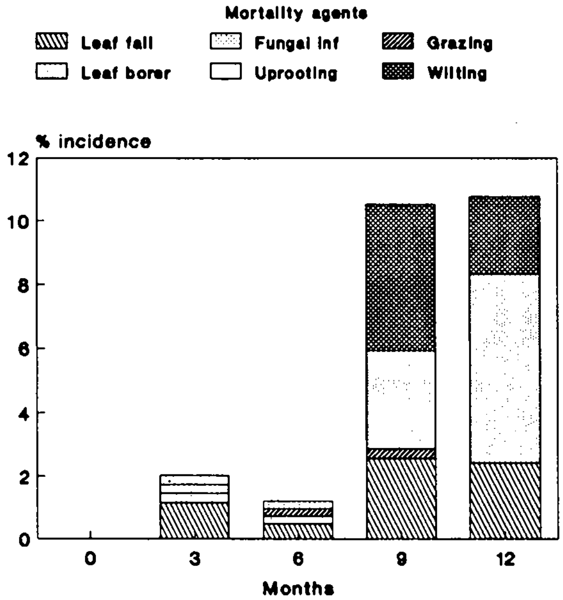
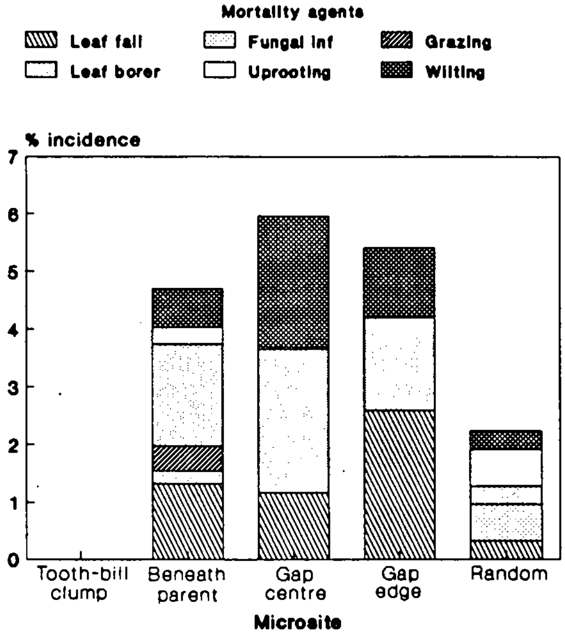


Fig 8.9b
Effect of microsite on incidence of mortality agents on *Syzygium* seedlings



8.3.4 Saplings

Individuals belonging to five families had sufficient saplings for analysis. Sapling composition differed significantly between Tooth-bill court areas and random areas ($X^2 = 64.45$, df=4, p < 0.001). The frequency of individuals of four families were distributed similarly between both Tooth-bill and random sites, but individuals of the family Oleaeceae *Chionanthus axillaris* were well represented within Tooth-bill court areas but virtually absent from random sites (Table 8.10).

TABLE 8.10 Sapling composition in Tooth-bill court areas and at random beneath the canopy. Contingency table for the frequency of saplings of bird dispersed families
for families totalling > 5 individuals, (Chi square=64.45, df=4, p=0.0000).

	Tooth-bill		Random		N
Family	Obs	Exp	Obs	Exp	
Oleaceae	88	55.34	2	34.66	90
Lauraceae	70	82.39	64	51.61	134
Myrtaceae	76	89.77	70	56.23	146
Euphorbiaceae	20	26.44	23	16.56	43
Rutaceae	27	27.05	17	16.95	44
N		281		176	457

8.3.5 Summary of results

A summary of the experimental results is presented in Table 8.11.

i) There was little evidence of density dependent mortality of seedlings for either *Acmena* or *Syzygium* (Table 8.11).

ii) Seedling density had a significant effect on seedling growth in height, with taller seedlings found in higher densities (Table 8.11).

iii) Seedling density, had a variable and generally negative effect on the number of leaves, with most seedlings losing leaves at higher seedling densities (Table 8.11).

iv) The only seedlings to gain leaves were those in gap centre microsites (Table 8.11).

v) The total incidence of mortality agents ranged from 11% for *Syzygium* to 57% for *Acmena.*

vi) Saplings of *Chionanthus axillaris* (Oleaceae) were better represented in Tooth-bill areas than at random beneath the canopy (Section 8.3.4).

TABLE 8.11 Summary of findings in relation to predictions from the Janzen/Connell model. Table codes: Density dependent mortality (DED), Distance dependent mortality (DID), Density independent mortality (DIN); (*) Significant effects (-) non-significant effects (?) Unknown effects; Responses for Survival (Surv)=final % surviving, Growth in height mm, and number of leaves, (Gr ht, Gr nl) % increase (+) or % decrease (-). Values obtained from overall means, and differences between the start and finish of experiments (T5-T1). Seedling densities (H) High, (I) Intermediate, (L) Low.

Microsite/ Major Parameters	Factors	Beneath parent canopy (BPC)	Tooth-bill seedling clump (TBC)	Random beneath canopy (RBC)	Gap edge (GED)	Gap centre
Characteristics of the Janzen/Connell model (Summary of Table 8.3)						
Factors affecting survival	DED	(*)	(*)	-----	-----	-----
	DID	(*)	------	-----	-----	-----
	DIN	(?)	(?)	(?)	(?)	(?)
Risk of mortality		High	High	Low	Low	Low
Predicted growth		Low	Low	Low	Interm	High
Evidence from seedling survival and growth at the termination of experiments after one year.						
Experiment One: *Acmena*	Surv H	23%				
	I	17%				
	L	25%				
	Gr ht H	+10.7%				
	I	-13.8%				
	L	-5.4%				
	Gr nl H	-33.3%				
	I	-14.8%				
	L	0%				
Experiment Two: *Acmena*	Surv H	18.3%	5.8%			
	L	10.8%	20.8%			
	Gr ht H	+10.1%	+16.2%			
	L	-6.6%	-10.6%			
	Gr nl H	-44.4%	-15.1%			
	L	-40.9%	-21.4%			
Experiment Three: *Syzygium*	Surv	33%	22%	4%	39%	39%
	Gr ht	+5.8%	+1.8%	-12.1%	+17.9%	+20.9%
	Gr nl	-35.5%	-13.6%	-32.3%	-10.8%	+7.9%

8.4 DISCUSSION

8.4.1 Seedling survival

There was no evidence of density dependent mortality of seedlings around parent trees or in bird dispersed seedling clumps for either *Acmena* or *Syzygium* over the first year of life. This was also supported by the similar percentage incidence of the different mortality factors between microsites and densities. These findings contrast strongly with those of other studies, where density and distance dependent mortality were significant (Augspurger 1983a, 1983b, Augspurger and Kelly 1984, Howe 1989).

Similar seedling attrition over all treatments, 30-59% over the three experiments, suggests density independent factors consistent with all treatments were responsible for most seedling demise. Clark and Clark (1984) in Costa Rican forests, found that 82% of seedling models were destroyed by density independent physical damage; flattened, uprooted or broken off at the stem. Clearly, physical damage alone has the potential to provide strong density independent mortality of seedlings in some tropical forests, and this may also hold true for the forest examined in this study.

8.4.2 Growth (Height in mm)

Seedlings grew very little over the first 12 months of life, with a maximum increase of 21% of the original seedling height. These results are consistent with other studies (Turner 1990). Seedlings grew taller in high seedling densities than in low seedling densities. Intracohort competition amongst seedlings for light may account for taller seedlings in high densities.

In Experiment Three, seedlings grew taller in gap microsites, (low density, high light), than high density seedling microsites (high density, low light), while those seedlings in random sites, (low density, low light) grew least. High light conditions afford the best growth conditions for seedlings (Denslow 1987). High seedling densities in low light conditions seem to afford better conditions for establishment and initial seedling growth than low density, low light conditions. How this is accomplished is unknown, but one possibility is that high seedling densities may provide a more moist microclimate, as well as intra-cohort competition for the limited light available. Mulch produced by dead seedlings in the case of parent tree microsites, or bird faeces and dead seedlings, in the case of bird dispersed clumps, may also assist by reducing ground water loss over the drier months, and also providing nutrients.

8.4.3 Change in number of leaves

The loss of leaves by many of the seedlings towards the end of the experiments seems to conflict with the trends in height mentioned previously. Seedling density had a negative effect on growth in number of leaves. Even though seedlings grew tallest in high density seedling beds, they also lost most leaves. Moreover, leaf loss was not supported by a concomitant increase in the incidence of herbivory, or other leaf loss agents, with increased high seedling densities. Leaf loss experienced in the high seedling densities may indicate differences in partitioning of seed reserves into growth in height, or increase in the number of leaves. Alternatively, leaf loss may be a precursor to seedling mortality. However, the experiments were too short to divulge whether there was sufficient loss of photosynthetic material to cause the ultimate demise of the seedlings.

Light availability determines the survival and growth of both species in the long term. With the consumption of seed reserves, seedlings become more dependent on available light for survival (Denslow 1987). Similarly in the continuum from shade tolerance to shade intolerance, seedlings also become increasingly dependent on light availability (Denslow 1980b). It is important to note that the only seedlings to gain leaves over all three experiments, were *Syzygium* seedlings in gap centre microsites. This suggests that both species were shade intolerant, and light gap dependent. If leaf loss reflects mortality for seedlings in low light conditions beneath the canopy, then almost all seedlings beneath the canopy will die, with the exception of those in areas of high sunfleck activity. This means that both species were dependent on being dispersed to a canopy gap, or having a canopy gap form in the first year of life whilst seedling reserves were still available. Suitable "safe sites" for survival and growth of both species is thus limited to suitable light gaps.

8.4.4 Mechanisms

The patterns of seedling survival in this study, that is, consistent attrition across all treatments, suggests that most mortality was density independent and that density dependent mortality agents were weak or ineffective.

A number of mechanisms have been posed to explain the enormous variation in patterns of seedling survival in clumps. Howe (1989) suggested that members of the clump dispersal syndrome should produce seeds and seedlings well defended by allelo-chemicals, lignification or mechanical protection against a variety of density dependent mortality agents, and this enables recruitment in clumps. These mechanisms imply that clump species should exhibit little or no damage from herbivores, as seedlings are well protected. Both species examined in this study were subject to a variety of herbivores, both leaf miners and grazers, but the incidence of herbivory did not appear to be related to density. That is, seedlings in different densities had equal chance of herbivory. The fact that both species were readily grazed suggests that neither species contained sufficient secondary compounds, allelo-chemicals or lignification to impede herbivory.

The density independent patterns of seedling attrition observed in this study, may also be due to the complex interplay between shade tolerance, seed reserves and light availability. Once a shade intolerant seedling has used its seed reserves in low light conditions, it is effectively starving and therefore more susceptible to disease, predation and an early death (Augspurger 1983a). For seedlings beneath a closed canopy, this would create a prolonged die-off independent of seedling density.

Another possible mechanism of density independent seedling attrition is the seasonal patterns of rainfall, and the potential for mortality through drought stress. During the late dry season, neutral and even negative growth was observed in some seedlings which may have resulted from water loss through drought stress (Woodrow pers. comm.). However, an increase in the incidence of wilt over this same period among the seedlings in all experiments was not observed. It is possible, however, that a major wilt event may have occurred during the intervals between sampling.

8.4.5 The Role of male Tooth-bills as dispersal agents

For both tree species examined, patterns of seedling mortality seemed little affected by site of deposition, with the exception of random microsites where mortality was higher. What this means from a dispersal perspective is that deposition in bird dispersed clumps will give seedlings of these tree species as good if not a better chance of survival than random microsites on the forests floor during the first year of life. However, the long-term survival of seedlings, will depend on a number of factors, such as: i) If seedlings are deposited beneath the canopy, then species with high shade tolerance will likely survive, whereas those with low shade tolerance will not (Denslow 1980b), and ii) Species with low shade tolerance will depend on being transported to a canopy gap, or having a canopy gap form prior to loss of seed reserves (Howe 1989). Seedlings of *Acmena resa* and *Guioa actifolia* were observed within 58 Tooth-bill seedling clumps in the 1986-87 wet season and were still persisting in the 1990-91 wet season (pers. obs.). This implies that shade tolerant seedlings can and do persist beneath the canopy within these clumps.

The sapling species composition within Tooth-bill court areas differed from random areas beneath the canopy. *Chionanthus axillaris* saplings flourished beneath the canopy in Tooth-bill court areas and were virtual absence from others sites. This suggests that *Chionanthus* was effectively dispersed by male Tooth-bills to court sites, where its shade tolerance may have enabled it to survive and grow.

Although most male Tooth-bills maintain court sites beneath the canopy, some maintain courts within canopy gaps. Because male Tooth-bills use traditional court sites, they return to the same site on the forest floor each year. If a large tree fall event occurs at a court site, males will still tend to occupy these areas. Of the 32 male Tooth-bills examined, three maintained courts within canopy gap areas and thus provided effective and directed dispersal for seeds to a canopy gap, the growth area of the rainforest (Denslow 1980b). Consequently, the seedlings of some rainforest tree species flourished in Tooth-bill seed piles at these court sites.

8.4.6 Experimental Limitations

The experiments in this component of the study suffered from a number of limitations. Firstly, experiments were too short to validate the fate of seedlings given high leaf loss. Secondly, sampling periods were inadequate to sample a number of critical phases in the seedling life history, namely, use of seedling reserves and possible drought stress at the end of the dry season. Finally, the incidence of potential mortality factors was noted only in surviving individuals. Closer monitoring may have enabled determination of actual mortality for individual seedlings. Further, incidence does not allude to the severity of a given event, and a classification of severity may have assisted in isolating true causes of mortality.

Chapter Nine

GENERAL DISCUSSION

9.1 INTRODUCTION

Each chapter has been discussed independently (see discussions of previous chapters). All the important results from each chapter are summarised in Table 9.1 and will now be discussed in the relation to current seed dispersal theory and patterns of lek maintenance and dispersion.

TABLE 9.1: Summary of results

Chapter: **Area of study**	**Summary of results:**
Chapter Two: Distributions	(1) Male Tooth-bills were distributed as an "exploded lek" across ridge tops in primary and secondary forests. (2) Males return to the same court site year after year, and are known to persist at traditional display sites for at least 13 years. (3) If displaced or lost from a court site, a new male replaces that individual at that site (4) Canopy gaps are more abundant, and smaller in unlogged sites, than logged sites.
Chapter Three: Fruiting Phenologies	(1) The logged site produced a greater abundance and diversity of fleshy fruits than the unlogged site. (2) Fleshy fruit production varied in magnitude and duration and between sites and years. (3) Peaks in fleshy fruit production were tracked by peaks in bird dispersed seed, indicating period of effective seed dispersal.
Chapter Four: Seed Dispersal	(1) Displaying male Tooth-bills had a mean home range of 9.5ha overlapping other males by 50%. (2) 50% of daylight hours were spent calling from a sub-canopy song perch above the display court. Males also roosted above the court site. (3) Median duration of foraging bouts was 12.4mins with a range from 0.1 to 90.7mins (n=225). (4) Median duration of bouts at the court was 6.2mins, with a range of 0.1 to 119.4mins (n=234) (5) Median distance of foraging bouts away from the court ranged from 40-86m, with maximums of 311-391m (6) Two models determining the probability of seeds being deposited at the court predict between 50-68% of seeds consumed will be deposited at the court. (7) Birds were observed in a very poor fruiting season.
Chapter Five: Diet	(1) Male Tooth-bills consumed 51 fleshy fruited plant species over three seasons, 40 of which were large, single seeded species. (2) Timing and persistence at the court varied between sites and seasons and may reflect fleshy fruit production. (3) Proportions of fleshy fruited plant species in the diet, did not reflect proportions available in the habitat, that is, birds fed selectively. (4) Seeds were deposited unharmed in piles, with pericarp of some fruits only partially digested (gentle digestion).
Chapter Six: Germination	(1) In glasshouse trials, greater than 52% of (36) plant species germinated, having passed through a male Tooth-bill. (2) Large fast germinating plant species had greatest germination success (2) For nine plant species male Tooth-bills enhanced the germination of 7, and shortened dormancy of 6. (3) Only three plant species were observed to germinate, and establish within Tooth-bill seed piles, *Acmena resa*, *Syzygium johnsonii* (Myrtaceae) and *Guoia acutifolia* (Sapindaceae).
Chapter Seven: Seed predation	(1) Plant species had a significant effect on seed predation intensity (2) Microsite, had no significant effect on seed predation intensity, mortality was similar on the forests floor, no matter where seed was deposited. (3) Rodent favoured *Litsea connonsii* was predated in a density dependent manner in 1988, but ignored in 1990. (4) The rodent seed predator population also declined over a similar period.
Chapter Eight: Seedling Survival	(1) There was no evidence of density dependent seedling mortality for either *Acmena resa* or *Syzygium johnsonii* over the period examined. (2) Seedling density had a significant positive affect on seedling growth in height, but a significant negative affect on leaf gain in shaded microsites. (3) The only seedlings to gain leaves in the first 12 months of life were those in canopy gap microsites. (4) *Acmena resa* and *Goiua acutifolia* seedlings persisted in Tooth-bill seed piles from the 1986-87 to the 1990-91 wet season and beyond. (5) *Chionanthus axillaris* (Oleaceae) saplings were better represented in Tooth-bill areas than at random beneath the canopy

9.2 THE PLANT PERSPECTIVE

9.2.1 The role of male Tooth-bills as seed dispersers

Howe and Smallwood (1982), proposed three alternative hypotheses to explain the ecological and evolutionary advantages of seed dispersal to a plant. These include: (i) the "escape hypothesis", where dispersal results in decreased density and or distance dependent mortality of seeds and seedlings near the parent plant, (ii) The "colonisation hypothesis", where widespread dispersal allows the colonisation of ephemeral or spatially unpredictable patches of disturbed habitat, and (iii) the "directed dispersal hypothesis", where seed dispersal is non-random to sites where seed and seedling survival and growth are high. These hypotheses are not mutually exclusive, and may differ in importance from one plant population to another.

Murray (1988) suggested that of these hypotheses, the colonisation hypothesis was the most important within tropical rainforests, with most plant species requiring canopy disturbances such as tree falls for effective recruitment (Whitmore 1978, Hartshorn 1978, Brokaw 1985, Denslow 1980b, 1987). Almost all rainforest plant species are in some sense gap-dependent (Denslow 1987). Gap-dependency varies in a continuum from those plant species that are highly shade tolerant, and survive beneath a closed canopy as seedlings until a gap forms, to those that are shade intolerant and require direct dispersal to a canopy gap (pioneer species) (Denslow 1980b, 1987, Ng 1978, Garwood 1982, 1983, Foster and Janson 1985). Recruitment direct to canopy gaps is therefore important for pioneer species, but of less importance to shade tolerant species.

Results obtained in this study show that male Tooth-bills provide a distinct dispersal service, namely the deposition of viable seeds in piles, generally away from the parent tree beneath the canopy, but occasionally in tree-fall gaps. The effectiveness of this dispersal service is discussed in relation to the hypotheses outlined above (sensu Howe and Smallwood 1982).

9.2.1.1 Colonisation, and directed dispersal hypotheses

Large canopy gaps are essential for the germination and establishment of pioneer species (Denslow 1980b, 1987). Evidence for "directed dispersal" of seeds to canopy gaps was proposed by Blake and Hoppes (1986) and Levey (1986b), based on the observations that: (i) herbs and shrubs (pioneer species) were more concentrated within gaps than the surrounding understorey, and (ii) mist net captures of birds, that is, more birds in gaps than within the rainforest, often reflects this concentration.

In this study, three of 32 male Tooth-bills maintained court sites within canopy gaps. Thus, these three males dispersed large numbers of seeds directly to gap sites, providing some evidence of "directed dispersal" (*sensu* Howe and Smallwood 1982). Equally, these three birds also provide evidence to support the "colonisation" hypothesis (*sensu* Howe and Smallwood 1982), as male Tooth-bills freighted viable seeds directly to these growth areas of the forest. Although the fate of seeds dispersed by male Tooth-bills to canopy gaps was not monitored, the prevalence of two pioneer species within the diet of Tooth-bills, *Polyscias australiana* and *P. murrayi*, certainly suggests that some pioneer species were being dispersed to favoured areas of recruitment. In addition, *Acmena* and *Syzygium* seedlings grew best within these gap sites (see Chapter Eight) and certainly flourished in the bird dispersed clumps associated with these three birds (pers. obs.). Thus, although some male Tooth-bills did demonstrate effective directed dispersal to gaps sites, the bulk, 91% , did not.

9.2.1.2 The escape hypothesis

Seed shadows surrounding a parent tree tend to be highly leptokurtic, with most seeds deposited beneath the parent and seed numbers rapidly decreasing with increased distance away from the parent (Harper 1977, Fleming and Heithaus 1981, Augspurger 1983a, 1983b). Each seed disperser that feeds upon a tree creates its own unique seed shadow. Murray (1988), defined the seed shadows produced by three Neotropical avian frugivores, *Myadestes melanops*, *Phainoptila melanoxantha* and *Semnornis frantzii*. These were the first seed shadows to be estimated for wild frugivores, and demonstrated that a large proportion of seeds were moved considerable distances from the parent plant. For the nine bird species/plant species combinations examined, the median dispersal distance ranged from 35-60m , with a maximum dispersal distance exceeding 500m (Murray 1988).

Unlike the bird species examined by Murray, male Tooth-bills are constrained to traditional court sites during the display season. As a result, most forays are limited to short feeding or leaf collecting bouts, occasional interactions with other individuals within the lek, or occasional long forays to bathe in a creek (see Chapter Four). On the completion of any bout away from the court, males return rapidly to their courts and commence calling. This behaviour results in seeds being transported away from the parent tree and directly to court sites. For the four male Tooth-bills examined in this study, the median dispersal distance away from a food tree was 40-86m, with a maximum dispersal distances of 311-391m. These distances are similar to those recorded by Murray (1988), even though the behaviour of the birds was completely different.

As a consequence of their behaviour male Tooth-bills move seeds considerable distances from parent trees, thus allowing seeds to escape the ravages of density and or distance dependent mortality beneath the parent. It might then be said that some plants gain an advantage from the dispersal service provided by male Tooth-bills by escaping high mortality beneath the parent (i.e. the "escape hypothesis"). Or do they? Of the total seeds consumed by male Tooth-bills, 46-68% end up in seed piles beneath favoured calling perches. The end result is that seeds are again deposited in high density seed clumps, which may result in seeds being taken out of the frying pan, and placing the into the fire. The seeds have escaped potential density and or distance responsive mortality agents beneath the parent, only to be ravaged by potential density responsive mortality agents in dense seed piles. The potential risk of mortality in these clumps is discussed in Chapter Seven; Section 7.4, Chapter Eight; Section 8.4 and Chapter Nine; Section 9.3.

9.2.2 Germination in clumps: legitimate frugivores, large seeded fruits and "safe sites"

Legitimate frugivores often consume large seeded fruits (Snow, 1970, McKey 1975, Snow 1981, Snow 1982, Wheelwright 1983, Wheelwright *et al.* 1984). Rainforest plant species with large seeds tend to: (i) germinate in response to rain rather than canopy gap openings (Garwood 1983, Foster and Janson 1985, Sork 1985, Denslow 1987), (ii) have short seed dormancies (<4 months) (Ng 1978, Garwood 1983,), and (iii) have higher seedling shade tolerance (Ng 1978, Becker and Wong 1985). As a result, these large seeded species readily germinate beneath a closed canopy and often survive as suppressed seedlings or saplings, until gap formation (Denslow 1987).

Most male Tooth-bills dispersed seeds to sites beneath a closed canopy. Most, 40 of 51 species consumed by male Tooth-bills containing a large single seed (refer to Chapter Five). It seems reasonable then to assume that most plant species dispersed by male Tooth-bills are likely to germinate and establish beneath the canopy within these court sites. The plant species that germinated most successfully after passing through the gut of a male Tooth-bill were species with large seeds and short dormancies (see Chapter Six). Dormancies of some large seeded species were further decreased having passed through the gut of a male Tooth-bill (see Chapter Six). The plant species that germinated and established effectively in Tooth-bill seed piles also produced shade tolerant seedlings. *Acmena resa* and *Guoia acutifolia* were present as dense seedling clumps beneath the canopy for at least four years, after establishing from Tooth-bill seed piles. *Chionathus axillaris* (Oleaceae) saplings were also more prevalent in Tooth-bill court areas than at random beneath the canopy, indicating another shade tolerant plant species that may have established from Tooth-bill seed piles. Clearly then, male Tooth-bill seed piles are suitable "safe sites" for the germination and establishment of some large seeded plant species.

9.2.3 Seeds and seedlings in clumps: risk of mortality and current models of recruitment

The "escape hypothesis" (Howe and Smallwood 1982) also known as the Janzen/Connell model (Janzen 1970, Connell 1971), has been variously tested, reviewed, supported and refuted for the last 20 years (refer to Chapter One; Section 1.3.2). For some plant species the escape hypothesis holds true with all progeny deposited beneath the parent crown facing certain death (Augspurger 1983a, 1983b, Howe 1977, 1983, 1986, 1990). However, its is now well established that the offspring of other plant species happily survive beneath the parent crown (Janzen *et al.* 1976, Howe 1980, Howe *et al.* 1985, Sork 1985, 1987). Equally, some plant species also survive in animal dispersed clumps (Janzen *et al.* 1976, Davidar 1983, Sork 1985, 1987, Reid 1989, Dinerstein and Wemmer 1988, Howe 1989).

A number of hypotheses have been proposed to explain why the seeds and seedlings of some plant species survive beneath a parent crown, while other do not. Howe (1989) suggested that seed dispersal syndromes may provide one explanation for the dichotomy/continuum observed in seed and seedling mortality patterns. Howe proposed that scatter-dispersed species would normally recruit as isolated individuals and were therefore unlikely to evolve resistance against density-dependent seed and seedling mortality agents. In contrast, clump-dispersed species would normally recruit in dense aggregations, and were therefore likely to evolve resistance against density-dependent mortality agents (see Chapter One, Section 1.3.2). Male Tooth-bills deposit most of the seeds they consume in clumps beneath favoured calling perches. The fact that *Acmena resa* and *Guoia acutifolia* seedlings survived and flourished within Tooth-bill dispersed clumps and that *Chionanthus axillaris* saplings also flourished at these sites, suggests that these species may be members of the clump dispersal syndrome. However, this is only one possible explanation and as yet unfounded (see Chapter Seven, Section 7.4 and Chapter Eight, Section 8.4).

9.2.4 Hubbells hypothesis and windows of recruitment

Hubbell (1980), proposed that high variation in seed production between and within plant species and years, results in high temporal and spatial variation in the effectiveness of seed dispersers and seed predators. A consequence of this is that no single spacing rule (Janzen/Connell model, Hubbell model) operates on all adults of a given plant species at the same time, nor is the rule the same at a given tree from one year to the next.

Results of this study support Hubbell's hypothesis. High variation in fruit production and seed dispersal were certainly evident between sites and years (see Chapter Three). Seed predation also varied enormously between years with *Litsea connonsii* seeds predated heavily in 1988, but left largely untouched in 1990. The observed variation in seed predation between years may have been due to a reduction in the number of rodent seed predators (see Chapter Seven). Further evidence to support Hubbell's lottery hypothesis was that species recruitment in seedling piles was not consistent from year to year.

The traditional use of court sites by male Tooth-bills and deposition each year of large mixed seed piles beneath favoured perches, means that a history of differential plant recruitment events is encapsulated within each court site. If a shade tolerant plant species produces fruits every other year, and successfully germinates and establishes in the seed piles of male Tooth-bills, then there should be evidence of different age stands of seedlings and saplings of that plant species about male Tooth-bill courts. This would be the type of recruitment profile expected from the Howe (1989) model. However, this was not the case. Instead, different plant species recruited in these seed piles in different years, and in some years no recruitment occurred. In effect, recruitment each year is a lottery, dependent on a specific suite of biotic and abiotic conditions unique for each plant species.

Over three seasons of this study, male Tooth-bills consumed 51 fleshy fruited plant species. Of these, most species (50) were lost in the seed phase through either seed predation by rodents, infestation by bruchid beetle larvae, infection by pathogens, or as a result of inappropriate ques for germination, such as poor rainfall or a late wet season. The three seasons observed were distinctive in having wet seasons with far less than the average rainfall for the area, (36% and 65%) (see Chapter Three). This may have impeded the germination of many species within the seed clumps. The final result of the lottery for the three seasons observed, was that only *Syzygium johnsonii* established in seed piles in the 1988-89 wet season.

Prior to 1986, *Chionanthus axillaris* established in and around Tooth-bill seed piles. In the 1986-87 wet season, *Guoia acutifolia* and *Acmena resa* established in Tooth-bill seed piles and persisted through the 1990-91 season and perhaps beyond. These patterns suggest that recruitment windows which differ in time and space occur at these sites, and that what is a "safe site" for a given plant species one year, may not be the next.

The findings of this study, although preliminary, have profound ramifications on all current models suggested to explain patterns of seed and seedling mortality. What I would like to propose is a windows of recruitment/lottery model, based on the hypotheses posed by Hubbell (1980). This model does not deny that the other mechanisms exist but rather suggests that plant production, seed dispersers, seed and seedling predators and pathogen fluctuations are sufficiently great to result in shifts from one pattern of mortality (Janzen/Connell model) to another (Hubbell model) from one year to the next. This means that windows of recruitment occur when the right combination of fruit production, predator and pathogen numbers exist, in concert with the appropriate abiotic conditions. In effect the model describes recruitment as a lottery of chance events (Hubbell and Foster 1986, 1990).

9.3 THE BIRD PERSPECTIVE

9.3.1 Speculation: fleshy fruits, traditional site use, male dispersion and the potential for coevolution

The plant/frugivore interaction has been discussed from the plant perspective for this study, but what of the bird perspective or the potential for coevolution between birds and plants? Evidence of close mutualism between plants and avian frugivores has been largely discounted, with most viewed as diffuse associations (Wheelwright and Orians 1982, Herrera 1986). However, the evolution of polygamous lek breeding systems in some rainforest bird families, and differing patterns of dispersion between species seems intimately tied to the fleshy fruits upon which they feed. Beehler and Pruett-Jones (1983) found a significant positive correlation between diet and dispersion in a study of nine species of Bird of Paradise which fed on insects and fruits. They found that only those species with diets containing more than 80% fruit had a clumped male dispersion pattern over the display season (i.e exploded leks and leks). From this they concluded that the shift from territoriality to non-territoriality (lek dispersion systems), was causally related to the composition of the bird diet. Consistent with this, male Tooth-bills are polygamous, displaying in an "exploded lek" and feed almost exclusively on fleshy fruits (see Chapters Two to Four).

9.3.1.1 Dispersion and habitat

Factors other than diet have also been proposed to explain male dispersion patterns in promiscuous bird species. These include: predation (Wiley 1974, Wittenberger 1978) and habitat limitation with respect to display sites (Snow 1974, Gullion 1976). True lek spacing patterns have not yet been confirmed for any species of Bird of Paradise existing in primary forests, which usually exhibit either dispersed, non-territorial or exploded lek patterns of male dispersion (Beehler and Pruett-Jones 1983).

True lek species, *Paradisaea spp.*, are typically birds of second growth forests or forest edges. Occupation of second growth forests by true lek breeding birds has also been observed for Manakins (Snow 1962a, 1962b, Lill 1974a, 1974b, Worthington 1982). Beehler and Pruett-Jones (1983) suggest that the restriction of lek dispersion to second growth forest results from the abundance and diversity of avian predators within this habitat type (the predation hypothesis). I refute their argument, and suggest that the prevalence of true lek species in second growth forests is again largely the result of a fruit diet, specifically levels of fruit production.

The development of lek breeding systems imposes very specific pressures on a habitat. Maintenance of high concentrations of sedentary fruit feeding birds requires a consistently high availability of fruits. Also, a polygamous mating system tends to minimise feeding time, because of the time needed for elaborate courtship displays, (Snow 1962a, 1962b, 1971, Snow 1970, 1972, 1973, 1977, Lill 1974a, 1974b, Foster 1977b, Beehler 1983). This places additional pressures on the fruit resources due to intense localised feeding patterns necessary to maintain the lek.

Plants of second growth forests are often fleshy fruited, and usually characterised by rapid growth, early reproductive maturity, and high fecundity (Harper 1977). This results in the annual production of copious quantities of fleshy fruits, which in many cases have extended fruiting seasons with some species fruiting all year round (Martin 1985, Flemming 1985, Charles-Domonique 1986, Hopkins 1990). Second growth forests, therefore, provide consistent high fruit production to meet the demands of high densities of displaying males. For these reasons, I feel the diet hypothesis is again the most appropriate to explain the presence of true lek species in second growth forests.

9.3.1.2 Duration of display

Variation in the duration of display seasons for lek breeding birds is also intimately tied to fleshy fruit production. When fruits are abundant, lek displaying Manakins spend less than 8-11% of their daylight hours feeding (Snow 1962a, 1962b, Foster 1977b). Manakins found in second growth forests, display for most of the year, and only suspend display during periods of food shortage or during moult (Snow 1962a, 1962b, Lill 1974a, 1974b, Foster 1977b, Worthington 1982). During this study, male Tooth-bills were observed to spend 50% of daylight hours foraging. The extended foraging times observed for male Tooth-bills were the product of a particularly poor fruiting season in the year of observation, and lek maintenance under these conditions was probably borderline. Male Tooth-bills displayed during the first peak in fleshy fruit production, from September to January. Display season duration seems closely linked to the duration of fruit production. In years of extended fruit production, display seasons are prolonged, whereas in poor, short fruiting seasons, display seasons are reduced (see Chapter Five).

Both dispersion and duration of lek breeding systems for tropical rainforest birds seems intimately linked to fleshy fruit production. Lek dispersion systems in primary forests tend to range from exploded leks to non-territoriality, whereas true leks systems are restricted to more productive second growth forests. Similarly, if fruit resources drop beneath a threshold at which leks cannot be maintained, then the lek breaks down (Worthington 1982). Therefore fruit production characteristics of a forest are likely to determine the development and maintenance of lek breeding systems.

9.3.1.3 Evidence from a survivor

Chionanthus axillaris saplings were found within Tooth-bill court areas, but were virtually absent in neighbouring random sites beneath the canopy. This suggests that *Chionanthus* was dispersed to these areas by male Tooth-bills, where it germinated and established and grew. *Chionanthus* is a member of the Oleaceae, a family known to have the highest lipid content of all known fruit, (olives, 68%) (Snow 1962c). What this means from an energetic standpoint, is that fruiting of this plant species results in a highly nutritious food source. Consumption of this species would probably maximise the time a male Tooth-bill spents at the court, by minimising the number of fruits that needed to be consumed, which in turn would maximise the reproductive potential of male Tooth-bills.

What are the long term consequences of male Tooth-bills depositing seeds at court sites? Male Tooth-bills consuming and depositing favoured plant species within court sites obtain the immediate nutritional benefit from that plant. However, there are also a number of long term benefits. Firstly, if leks are stable over hundreds of years, and windows of recruitment do occur, then the resulting plant community in and around court sites may differ in composition from the surrounding forest area. Secondly, by increasing the compliment of preferred plants in these areas, a concomitant increase in lek cohesion, or lek size may result. Thirdly the reproductive success of the lek as a whole may also be directly related to the amount of time spent by males within lek sites, which again is probably dependent on the proximity, production and quality of food species in and around a lek area. Future investigations examining the energetics of fruit production, lek stability and success, may unravel coevolutionary trends never before considered.

9.4 DO MALE TOOTH-BILLS PROVIDE AN EFFECTIVE SEED DISPERSAL SERVICE?

This thesis set out to evaluate the effectiveness of clump seed dispersal by male Tooth-bills to the plants consumed, but the re-occurring problem remains, what is "effective" seed dispersal? At what life history stage do we arbitrarily decide a bird has done its job effectively? Is it: (i) if a plant survives gut passage and is moved from its seed source, (ii) if it germinates and establishes in the site of deposition, (iii) if seedlings survive beyond seed reserves or (iv) if saplings survive to potentially become adults? Clearly, each stage is a differing level of effectiveness.

If survival is essentially a lottery, then a sapling derived from a faecal clump, constitutes effective seed dispersal. Given that 99.99% of propagules produced by most rainforest plants are doomed to failure, then a seed that has survived to become a sapling has struck the jackpot. So, do male Tooth-bills provide an "effective" seed dispersal service? I think the answer to this question is yes they do. The real effectiveness of this service however is not detectable in the time scale of a three year study. The windows of recruitment model provides the most likely scenario to explain the patterns of recruitment observed. It also emphasises the time scale rainforest tree recruitment processes operate at relative to time scales of research. Studies producing dichotomous theories based on one off observations on seed and seedling mortality patterns can produce misleading and contradictory results. Long term monitoring of processes is essential to understanding mechanisms of recruitment for rainforest trees and the advantages of seed dispersal services by avian frugivores.

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APPENDICES

Appendix 3.1: Fruiting phenologies for logged and unlogged sites within the "Friths Grid", Paluma, from September 1987 to December 1989. Information from all sources, (i.e. fruitfall traps and transect walks) are presented.

Species (Family)	Sp No	Dispersal	# of seeds/ fruit	1987	1988	1989
Plant species				J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S O N D
Acronychia acronychiodes (Rutaceae)	1	Bird	1	* * *	* * * *	* * * *
Halfordia scleroxyla (Rutaceae)	3	Bird	1	* * *	* * *	* * *
Fagraea gracilipes (Loganiaceae)	4	Bird	4-5	* * *	* * *	* * *
Cryptocarya densiflora (Lauraceae)	5	Bird	1	* * *	* * *	
Elaeocarpus foveolatus (Elaeocarpaceae)	6	Bird	1	*	* *	* * * *
Alyxia spicata (Apocynaceae)	7	Bird	1	* *	* * * * * * * *	* * * * * * * *
Cissus hypoglauca (Vitaceae)	8	Bird	2-4		* * *	*
Cryptocarya leucophylla (Lauraceae)	13	Bird	1	*		
Elaeocarpus largilorens (Elaeocarpaceae)	14	Bird	1	* *	* *	* *
Sloanea langii (Elaeocarpaceae)	16	Bird	2	* * *	* * *	
Polyscias autraliana (Araliaceae)	18	Bird	2		* *	*
Litsea connonsii (Lauraceae)	20	Bird	1	* *	* *	
Piper caninum (Piperaceae)	21	Bird	1		* *	*
Planchonella euphlebia (Sapotaceae)	22	Bird?	4-5		* * * *	* * * *
Symplocus cochinchinensis (Symplocaeae)	23	Bird	1	* *	* *	
Endiandra dielsiana (Lauraceae)	25	Bird	1		*	
Smilax glycophylla (Smilacaceae)	26	Bird	1			* *
Bielschmiedia collina (Lauraceae)	28	Bird	1		* *	* *
Unknown	29	Bird	1		*	*
Sphenostemon lobosporous (Aquifoliaceae)	30	Bird	5	*	* * * * *	* * * *
Syzygium sp (Myrtaceae)	32	Bird	1		* * *	
Timonius timon (Rubiaceae)	33	Bird	100's	* *		
Ficus destruens (Moraceae)	34	Bird	100's	* *	* * * *	* * *
Synoum muelleri (Meliaceae)	35	Bird	4	* *		* *

Species (Family)	Sp No	Dispersal	# of seeds/ fruit	1987	1988	1989
Plant species				J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S O N D
Cardwellia sublimis (Proteaceae)	38	Wind	10-20		* *	
Unknown	39	Bird	1	* * *		
Sloanea macbrydei (Elaeocarpaceae)	40	Bird	2	* * *		
Prumnopitys amosa (Podocarpaceae)	42	Bird	1	* * * *	*	
Syzygium papyraceum (Myrtaceae)	43	Bird	1		* * *	
Henslowia sp (Santalaceae)	44	Bird	1	* *		* *
Unknown (Sapindaceae)	45	Bird	2	*		
Jagera discolor (Sapindaceae)	46	Bird	2	* *		
Guioa montana (Sapindaceae)	48	Bird	2	* *		
Flindersia pimenteliana (Rutaceae)	50	Wind	10	* *	* *	* *
Ardisea brevipedata (Myrtaceae)	52	Bird	1		* *	* *
Dendrotrophe various (Santalaceae)	55	Bird	1		* * *	
Darlingia darlingiana (Proteaceae)	56	Wind	2		* *	* *
Alphitonia petreyi (Rhamnaceae)	57	Bird	1	* *	* * * * * * *	* * *
Maesa dependens (Myrsinaceae)	62	Bird	1		*	
Unknown	66	Bird	1	* *	* *	*
Archontophoenix alexandrae (Aracaceae)	73	Bird	1	*		
Calamus australis (Aracaceae)	75	Bird	1	*		
Acacia aulacocarpa (Mimosaceae)	78	Dehiscent	20		* *	
Acacia melanoxylum (Mimosaceae)	79	Dehiscent	20		*	
Unknown	82	Bird	4		*	
Pittosporum revolutum (Pittosporaceae)	92	Bird	10	*	*	
Unknown	93	Bird	1		*	
Unknown	94	Bird	1		*	
Syzygium wesa (Myrtaceae)	98	Bird	1		* * *	
Unknown	101	Bird	1	*		
Cryptocarya corrugata (Lauraceae)	102	Bird	1	*	* *	
Syzygium johnsonii (Myrtaceae)	106	Bird	1		* *	
Endiandra sp (Lauraceae)	107	Bird	1		*	
Cryptocarya sp (Lauraceae)	108	Bird	1			*

Species (Family)	Sp No	Dispe rsal	# of seeds/ fruit	1987	1988	1989
Plant species				J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S O N D
Psychotria sp (Rubiaceae)	109	Bird	1		* * * *	* * *
Cryptocarya sp (Lauraceae)	113	Bird	1		*	
Endiandra wolfei (Lauraceae)	114	Bird	1		* *	
Unknown	123	Bird	1		*	
Apodytes sp (Icacinaceae)	126	Bird	1		*	
Guioa montana (Sapindaceae)	127	Bird	1		* *	
Alphitonia whiteii (Rhamnaceae)	141	Bird	1		*	
Drypetes australasica (Euphorbiaceae)	143	Bird	1		*	*
Polyscias murrayii (Araliaceae)	146	Bird	2			
Elaeocarpus elliffi (ELaeocarpaceae)	157	Bird	1			* * *
Acmena resa (Myrtaceae)	160	Bird	1			
Unknown (Lauraceae)	161	Bird	1			*
Piper novaehollandia (Piperaceae)	164	Bird	1			* *

Appendix 4.1

SUMMARY OF BEHAVIOUR CODES: All recorded summarised/revised (7/2/91).

CODE	DEFINITION
1	PERCHING - Unknown Silent (Combined codes 1,2,5)
3	PERCHING - Calling
6	MAINTENANCE - Court
10	INTERACTION - Unknown (Combined codes 10,12,13,14,16) Chasing, male? female? unknown, inspecting rival?
11	INTERACTION - Leaf Stealing
15	INTERACTION - Display
20	FORAGING- Unknown (Combined codes 20,30) Departure flight unknown subsequent behaviour, assumed foraging.
21	FORAGING- Fruit/leaves/shoots (Combined codes 21,22) recognised feeding
23	FORAGING - Leaf Collecting
24	FORAGING- Water Bathing/Drinking
25	FORAGING - Known area UNKNOWN OBJECTIVE
31	FLIGHT - Return
32	FLUSHED - DISTURBANCE

Appendix 4.2

SUMMARY OF LOCATION CODES:

CODE	DEFINITION
1	HOME COURT - Low Perch
2	HOME COURT - High Perch, Not visible (Combined codes 2,3)
4	ALTERNATE COURT - Low Perch
5	ALTERNATE COURT - High Perch, not visible (Combined codes 5,6)
7	ADJACENT COURT - (Neighbours court area)
11	LEAF TREE - (Subcanopy)
12	CANOPY-EMERGENT (Combined codes 8,9,12,13,15,16,21,22)
14	SUBCANOPY (Combined codes 10,14,17,23)
18	CREEK / WATER COURSE
20	LOCATION UNDEFINED - (All approximate areas)

Appendix 4.3

Basic programme to calculate percentage of seeds consumed deposited at the court, vs away from the court. Written by Conn Lockkers, Zoology Department, James Cook University. (1990)

```
REM Time in minutes
REM Input seed deposition cycle probabilities
DATA 0,0.1,0.35,0.25,0.15,0.1,0.5,0.02,0.02,0.01,0
Dim seed (10),M(100),S(2)
? "  Bird#  Month  bout  length  % in   % out"
For I=0 to 10
Read seed(I):next I
REM Input data file
Open "I",#1,"C:\data\brt\timbud.txt"
Open "O",#2,"Shit.out"
REM Read next data line
10 BNOP=BNO:MTHP=MTH:TPP=TP
IF EOF(1) THEN GOTO 30
INPUT#1,BNO,MTH,TP,BOUT,LOCA
BOUT=BOUT/60
IF TIME=0 THEN GOTO 20
IF TPP=TP THEN GOTO 20
30 NTP=N-NP
            PRINT#2,BNOP;MTHP;TPP;NTP;
            PRINT#2,USING "###.###";SSIN;SOUT
NP=N
IF EOF(1) THEN END
SSIN=O:SOUT=O
IF (MTH=MTHP AND BNOP=BNO) THEN GOTO 20
FOR I=1 TO N
M(I)=0:NEXT I
TIME=0:N=0:NP=0:S(1)=0:S(2)=0:TEND=0
20 IF LOCA=1 THEN GOSUB 100 ELSE GOSUB 200
GOTO 50
? "      "BNO;"     ";MTH;
PRINT USING "######.###";BOUT;S(1);S(2)
50 SSIN=SSIN+S(1):SOUT=SOUT+S(2)
S(1)=0:S(2)=0
GOTO 10
REM INSIDE COURT
100 TEND=TIME+(INT(BOUT/5))
GOSUB 300
RETURN
REM OUTSIDE COURT
200 TEND=TIME+(INT(BOUT/5))
IF BOUT<2.4 THEN GOTO 210
N=N+1
m(N)=CINT((TEND-TIME)/2)+TIME
210 GOSUB 300
RETURN
REM CALCULATE % SEED DROP PER INTERVAL
300 FOR I=1 TO N
INTER=TIME-M(I)
IF INTER<11 THEN S(LOCA)=S(LOCA)+SEED(INTER)
NEXT I
TIME=TIME+1
IF TIME<TEND THEN GOTO 300
RETURN
```

Appendix 6.1

Comparison of germination responses of non-dispersed seeds (pericarp intact) and bird dispersed seed, in descending order of germination success. Seed disperser treatments include:(1) male Tooth-billed Bowerbirds, Shining Starlings and Cassowaries.

TREATMENT: DISPERSAL AGENT:		NON-DISPERSED			BIRD DISPERSED			
Disperser/ Plant species	Sp No.	seeds (n)	% GERM	THG DAYS	seeds (n)	% GERM	THG DAYS	RESPONSE TYPE
TOOTH-BILLS								
Fagraea gracilipes	4	30	0	--	35	82.9	17	1
Litsea connonsii	20	90	0	--	90	75.6	35.7	1
Cissus hypoglauca	8				10	70.0	4	
Syzygium johnsonii	106	90	12.2	61.3	90	67.8	44	2i
Syzygium wesa	98	90	0	--	28	53.6	48	1
Bielschmiedia obtusifolia	117				6	50.0	55	
Cryptocarya corrugata	102				2	50.0	33	
Cryptocarya leucophylla	13				31	42.3	28	
Unknown	107				85	40.8	49	
Alyxia spicata	7				100	27.7	90	
Eleagnus triflora	17				30	23.3	46	
Cryptocarya densiflora	5	164	0	--	74	16.5	127	1
Endiandra hypotephra	119				16	12.5	68	
Smilax glcophylla	26				10	10.0	205	
Ficus destruens	34	300	1.33	24	366	4.27	32	2c
Elaeocarpus largiflorens	14	90	0	--	60	3.33	28	1
Elaeocarpus foveolatus	6				30	3.33	164	
Polyscias australiana	18				41	2.44	8	
Unknown	49				90	1.11	15	
Symplocus cochinchinensis	23				120	0	--	
Unknown	100				100	0	--	
Timonius timon	33				90	0	--	
Acronychia acronychiodes	1	110	0	--	67	0	--	3
Sphenostemon lobosporus	30				49	0	--	
Acroychia vestida	2				40	0	--	
Unknown	124				22	0	--	
Unknown	29				19	0	--	

TREATMENT: DISPERSAL AGENT:		NON-DISPERSED			BIRD DISPERSED			
Disperser/ Plant species	Sp No.	seeds (n)	% GERM	THG DAYS	seeds (n)	% GERM	THG DAYS	RESPONSE TYPE
Unknown	122				17	0	--	
Canarium muelleri	133				13	0	--	
Unknown	118				10	0	--	
Unknown	37				10	0	--	
Planchonella euphlebia	22	5	20.0	84	6	0	--	
Endiandra dielsiana	25				6	0	--	
Henslowia sp	44				6	0	--	
Guioa montana	127				5	0	--	
Unknown	113				2	0	--	
SHINING STARLINGS								
Omalanthus novaehollandia	147				100	99.0	11	
Endiandra dielsiana	25	6	0	--	90	96.7	36	1
Litsea connonsii	20				90	75.6	36	
Eleagnus triflora	17				90	63.3	20	
Unknown	111				8	62.5	37	
Unknown	145				2	50.0	11	
Unknown	132				36	35.0	26	
Cryptocarya leucophylla	135				50	33.5	73	
Apodytes sp	138				26	30.8	292	
Endiandra wolfei	114				38	20.8	112	
Unknown	116				47	18.9	59	
Piper caninum	21	9	44.4	53	150	14.2	49	2g
Unknown	134				18	11.1	67	
Unknown	149				20	10.0	25	
Canarium muelleri	133				12	8.33	249	
Myristica insipida	110				90	5.56	39	
Unknown	137				28	3.57	46	
Ficus destruens	34	100	0	--	999	1.40	72	1
Palm	131				60	0	--	
Unknown	136				48	0	--	
Polyscias murrayii	146				30	0	--	
Synima cordierorum	130				30	0	--	
Unknown	154				30	0	--	
Synoum sp	155				30	0	--	
Unknown	144				30	0	--	
Unknown	156				30	0	--	
Unknown	140				18	0	--	
Unknown	65				12	0	--	

TREATMENT: DISPERSAL AGENT:		NON-DISPERSED			BIRD DISPERSED			
Disperser/ Plant species	Sp No.	seeds (n)	% GERM	THG DAYS	seeds (n)	% GERM	THG DAYS	RESPONSE TYPE
Ripogonum sp	148				11	0	--	
Synoum sp	142				9	0	--	
Unknown	151				7	0	--	
Guioa montana	48				6	0	--	
Apodytes sp	126				5	0	--	
Unknown	123				2	0	--	
CASSOWARY								
Unknown	1011				6	100.0	76	
Endiandra sankeyana	1027				3	100.0	91	
Randia fitzlanni	1022				100	98.0	76	
Endiandra sankeyana	1036				22	95.0	105	
Endiandra montana	1004	3	100	59	46	81.4	76	2e
Syzygium cormiflorum	1037				4	75.0	65	
Syzygium forte	1028				24	73.3	18	
Syzygium wesa	98	90	0	--	90	72.2	71	1
Syzygium kuranda	1023	60	71.7	102	60	68.3	72	2f
Unknown	1016				3	66.7	155	
Syzygium papyraceum	43	90	7.8	38.5	90	61.1	38	2b
Syzygium cormiforum	1047				10	60.0	67	
Cryptocarya grandis	1025	3	66.7	98	30	56.7	61	2g
Acmena hemilampra	1002				60	55.0	76	
Prunus turnerana	1050				26	53.8	98	
Cryptocarya oblata	1031	4	100.0	112	2	50.0	109	2g
Melia azedarach	1001	15	0	--	15	40.0	95	1
Archontophoenix alexandrae	1014				91	38.0	81	
Endiandra dielsiana	1040				8	37.5	109	
Elaeocarpus augustifolius	1000	80	0	--	80	33.8	473	1
Planchonella brownlessiana	1041				10	30.0	67	
Podocarpus elatus	129				90	28.9	66	
Chionanthus ramiflorus	1044				40	23.3	83	
Unknown	1013				35	22.9	91	
Ptychosperma elegans	1008				7	14.3	141	
Unknown	1017				36	8.33	174	
Halfordia scleroxyla	3	188	0	--	30	3.33	62	1
Acronychia acronychiodes	1	110	0	--	180	0	--	3
Unknown	1024				50	0	--	
Elaeocarpus largiflorens	14				30	0	--	
Elaeocarpus foveolatus	1007				24	0	--	

TREATMENT: DISPERSAL AGENT:		NON-DISPERSED			BIRD DISPERSED			
Disperser/ Plant species	Sp No.	seeds (n)	% GERM	THG DAYS	seeds (n)	% GERM	THG DAYS	RESPONSE TYPE
Acronychia acidula	1006				18	0	--	
Unknown	1042				4	0	--	
Unknown	1018				4	0	--	
Syzygium alliiligneum	1003	14	78.6	76	3	0	--	
Unknown	1039				2	0	--	
Unknown	1009				2	0	--	
Cryptocarya corrugata	115				2	0	--	
Unknown	1010				1	0	--	
Unknown	1015				1	0	--	
Musa sp	1005				1	0	--	
Unknown	113				1	0	--	
Lepidozamia hopei	1026	6	0	--	1	0	--	3
Unknown	1012				1	0	--	
Syzyguim cormiflorum	1030	1	100	76				
Cardwellia sublimis	38	14	100	30				
Synoum muelleri	35	22	81.8	16				
Darlingia darlingiana	56	7	71.4	35				
Bowenia spectabilis	1035	3	33.3	156				
Prumnopitys amosa	42	30	0	--				
Delarbrea michieana	1033	1	0	--				
Unknown	1034	1	0	--	1	0	--	

Appendix 6.2

Complete reference collection material obtained by Geoff Moore from June 1987 to December 1989 at Paluma and Mission Beach study sites. Material was collected from: (1) Monthly fruit phenology traps and transect walks, (2) Diet collections for a variety of avian frugivores: (i) Seedfall traps set beneath male Tooth-billed Bowerbirds, (ii) seed fall traps set beneath shining starlings, (iii) cassowary droppings.

All material was identified where possible from (Hyland 1982), and (Jackes 1990). Additional confirmation of species identification was obtained from Bemie Hyland (CSIRO) (pers. comm.), Tony Irvine (CSIRO) (26/4/91) (pers. comm.) and Betsy Jackes (JCU) (pers. comm.)

All reference collection material is available in the James Cook University Herbarium (Geoff Moore reference collection), and includes:(i) seeds and fruits preserved in alcohol, (ii) pressed seedlings and adult material, (iii) photocopied seedlings and adult plant material, (iv) photographed seed material.

Spno.	SPNO/Species	Family
1	*Acronychia acronychiodes*	Rutaceae
2	*Acronychia vestida*	Rutaceae
3	*Halfordia scleroxyla*	Ruteacae
4	*Fagraea gracilipes*	Loganiaceae
5	*Cryptocarya densiflora*	Lauraceae
6	*Elaeocarpus foveolatus*	Elaeocarpaceae
7	*Alyxia spicata*	Apocynaceae
8	*Cissus hypoglauca*	Vitaceae
9	*Amesa sp*	Myrsinaceae
10	Unknown	
11	Palmae	
13	*Cryptocarya leucophylla*	Lauraceae
14	*Elaeocarpus largiflorens*	Elaeocarpaceae
16	*Sloanea langii*	Elaeocarpaceae
17	*Eleagnus triflora*	Eleagnaceae
18	*Polyscias australiana,*	Araliaceae
19	*Ficus watkinsiana*	Moraceae
20	*Litsea connonsii*	Lauraceae
21	*Piper novaehollandia*	Piperaceae
22	*Planchonella euphlebia*	Sapotaceae
23	*Symplocus cochinchinensis*	Symplocaceae
25	*Endiandra dielsiana*	Lauraceae
26	*Smilax glycophylla*	Smilacaceae
28	*Bielschmedia collina*	Lauraceae
29	Unknown	Unknown
30	*Sphenostemon lobosporus*	Aquifoliaceae
32	*Syzygium sp*	Myrtaceae

Spno.	SPNO/Species	Family
33	*Timonius timon*	Rubiaceae
34	*Ficus destruens*	Moraceae
35	*Synoum muelleri*	Meliaceae
38	*Cardwellia sublimis*	Proteaceae
39	Unknown	Unknown
40	*Sloanea macbrydii*	Elaeocarpaceae
42	*Prumnopitys amosa*	Podocarpaceae
43	*Syzygium papyraceum*	Myrtaceae
44	*Henslowia sp.*	Santalaceae
45	Unknown	Sapindaceae
46	*Jagera discolor*	Sapindaceae
48	*Guoia montana*	Sapindaceae
50	*Flindersia pimenteliana*	Rutaceae
51	*Canthium odoratum*	Myrsinaceae
52	*Ardisia brevipedata*	Myrsinaceae
53	*Neolitsea dealbata*	Lauraceae
54	*Glochidion sp.*	Euphorbiaceae
55	*Dentrotrophe various*	
56	*Darlingia darlingiana*	Proteaceae
57	*Alphitonia petreyi*	Rhamnaceae
62	*Maesa dependens*	Mysinaceae
66	Unknown	
73	*Archontophoenix alexandra*	Araceae
75	*Calamas australis*	Araceae
78	*Acacia aulacocarpa*	Mimosaceae
79	*Acacia melanoxylum*	Mimosaceae
92	*Pittosporum revolutum*	Pittosporaceae
93	Unknown	Unknown
94	Unknown	Unknown
97	*Mishocarpus sp.*	Sapindaceae
98	*Syzygium wesa*	Myrtaceae
102	*Cryptocarya corrugata*	Lauraceae
106	*Syzygium johnsonii*	Myrtaceae
109	Unknown	Unknown
110	*Myristica insipida*	Myristicaceae
111	Unknown	Unknown
112	Unknown	Unknown
114	*Endiandra wolfei.*	Lauraceae
115	*Cryptocarya corrugata*	Lauraceae
116	Vine	Unknown

Spno.	SPNO/Species	Family
117	*Bielscmedia obtusifolia*	Lauraceae
118	Unknown	Unknown
119	*Endiandra hypotepyra*	Lauraceae
120	Unknown	Unknown
123	Unknown	Unknown
124	Unknown	Sapindaceae
125	Unknown	Unknown
126	*Apodytes sp.*	Icacinaceae
127	*Guioa montana*	Sapindaceae
128	Unknown	Unknown
129	*Podocarpus elatus*	Podocarpaceae
130	*Synima cordierorum*	Sapindaceae
131	Palm	Arecaeae
132	Unknown	Unknown
133	*Canarium muelleri*	Burseraceae
134	Unknown	Unknown
135	*Cryptocarya leucophylla*	Lauraceae
136	Unknown	Unknown
137	Unknown	Unknown
138	*Apodytes sp.*	Icacinaceae
139	Palm	Arecaceae
140	Unknown	Unknown
141	*Alphitonia whiteii*	Rhamnaceae
142	*Synoum sp.*	Meliaceae
143	*Drypetes australasica*	Euphorbiaceae
144	Unknown	Unknown
145	Unknown	Unknown
146	*Polyscias murrayii*	Araliaceae
147	*Omalanthus novaehollandia*	Euphorbiaceae
148	Unknown	Unknown
149	Unknown	Unknown
150	Unknown	Unknown
151	Unknown	Unknown
152	Unknown	Sapindaceae
154	Unknown	Unknown
155	*Synoum sp*	Meliaceae
157	*Elaeocarpus elliffi*	Elaeocarpaceae
158	*Elaeocarpus sp*	Elaeocarpaceae
159	*Elaeocarpus angustifolius*	Elaeocarpaceae
160	*Acmena resa*	Myrtaceae

Spno.	SPNO/Species	Family
161	*Lauraceae*	Lauraceae
164	*Piper caninum*	Piperaceae
165	Unknown	Unknown

Spno.	SPNO/Species	Family
	MISSION BEACH SPECIES	
1000	*Elaeocarpus angustifolius*	Elaeocarpaceae
1001	*Melia azedarach*	Meliaccae
1002	*Acmena hemilampra*	Myrtaceae
1003	*Syzygium alliiligneum*	Myrtaceae
1004	*Endiandra montana*	Lauraceae
1005	*Musa sp.*	Unknown
1006	*Acronichia acidula*	Rutaceae
1007	*Elaeocarpus foveolatus*	Elaeocarpaceae
1008	*Ptychosperma elegans*	Unknown
1009	Unknown	Unknown
1010	Unknown	Unknown
1011	Unknown	Unknown
1012	Unknown	Unknown
1013	Unknown	Unknown
1014	*Archontophoenix alexandrae*	Aracaceae
1015	*Litsea leefeana*	Lauraceae
1016	Unknown	Unknown
1017	Unknown	Unknown
1018	Unknown	Unknown
1019	Unknown	Unknown
1020	Unknown	Unknown
1021	Unknown	Unknown
1022	*Randia fitzlanni*	Rubiaceae
1023	*Syzygium kuranda*	Myrtaceae
1024	Unknown	Unknown
1025	*Cryptocarya grandis*	Lauraceae
1026	*Lepidozamia hopei*	Zamiaceae
1027	*Endiandra sankeyana*	Lauraceae
1028	*Syzygium forte*	Myrtaceae
1029	*Castanospermum australe*	Fabaceae
1030	*Syzygium cormiflorum*	Myrtaceae
1031	*Cryptocarya.oblata*	Lauraceae
1032	Unknown	Unknown
1033	*Delarbrea michieana*	(Araliaceae)
1034	Unknown	Unknown
1035	*Bowenia spectabilis*	Zamiaceae
1036	*Endiandra sankeyana*	Unknown
1037	*Syzygium cormiflorum*	Myrtaceae
1038	*Acronychia accidula*	Rutaceae

Spno.	SPNO/Species	Family
1039	Unknown	Unknown
1040	*Endiandra dielsiana*	Lauraceae
1041	*PLanchonella brownlessiana*	Sapotaceae
1042	Unknown	Unknown
1043	*Canarium austyralianum*	Burseraceae
1044	*Chionanthus ramiflorus*	Oleaceae
1045	*Litsea leefeana*	Lauraceae
1046	*Myristica insipida*	Myristicacaea
1047	*Syzygium cormiflorum*	Myrtaceae
1048	Unknown	Unknown
1049	*Calamas sp.*	Aracaceae
1050	*Prunus turnerana*	Rosaceae
1051	Unknown	Unknown