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Vertical Distribution, Resource and Space Use in a Tropical Rainforest Small Mammal Community

Thesis submitted by

Romina RADER BSc(Hons) UNSW

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for the research Degree of Master of Science
in Zoology and Tropical Ecology
within the School of Tropical Biology and
Cooperative Research Centre for Tropical Rainforest Ecology and Management
James Cook University
Australia

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ABSTRACT

Mammal assemblages of rainforest communities are commonly vertically stratified. This can be driven by competition for or access to resources in the upper canopy layers of the forest. Arboreal mammals comprise a substantial proportion of tropical mammal communities and yet are difficult to census due to their inaccessibility and often, cryptic and nocturnal behaviour. Nonetheless they require attention to ensure they are appropriately managed. This study found the rodent community of Cape Tribulation to be vertically stratified with *Pogonomys mollipilosus* found only in the upper canopy layers and *Rattus leucopus* on the ground. *Melomys cervinipes* and *Uromys caudimaculatus* were found at all four height layers. Fruit and flower resource abundance were not significantly correlated with total rodent captures, however arboreal captures of *M. cervinipes* and *P. mollipilosus* were correlated with the number of individual flowering canopy trees.

The consumption of fruits by vertebrates and invertebrates may be both advantageous and detrimental to seeds. The consumption of *Acmena graveolens* fruit pulp by rodents and beetle presence, increases the germination success of *A. graveolens* seeds. Germination success is also higher as seed size increases and seed size influences the amount of pulp remaining on seeds. In this study, both vertebrate and invertebrate interaction with the fruit appears advantageous.

Nesting and resource availability were identified as two mechanisms driving arboreal activity of *M. cer*vinipes, a scansorial rainforest rodent. Home range size does not significantly differ between the sexes. The number of canopy trees increased linearly with area size for the 95% harmonic mean area but the average number of canopy trees remained the same regardless of area for core home range areas.

The salient points of this study are as follows:

1. Arboreal trapping is an important part of biodiversity assessment of forest-dwelling small mammal communities
2. Removal of pulp by rodents and beetle presence enhances germination success of *A. graveolens* seeds
3. The number of canopy trees influences core home range size of *M. cervinipes*

Understanding the full extent of rodent resource use, including fruit consumption, is important to increase our knowledge and understanding of community dynamics, the associated impacts upon seed survival and in the long term, the structuring of plant communities and maintenance of diversity in tropical rainforests.

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CHAPTER 1: GENERAL INTRODUCTION

1. **Objectives of this study**

My interest in examining space and resource use by rodents developed from many observations of several different species coexisting in the rainforests at Cape Tribulation. I found little information available about the vertical dimension of habitat but some speculation in the literature regarding competition among these species (Wood 1971; Laurance 1994; Heinsohn and Heinsohn 1999). I was interested in finding out how these rodents used all levels of the canopy and whether they were segregated according to habitat preferences in space or time.

The literature suggests two of the four rodents present on site are scansorial to varying degrees, namely *Melomys cervinipes* (Wood 1971) and *Uromys caudimaculatus* (Moore 1995); *Pogonomys mollipilosus* (Winter and Whitford 1995) is arboreal and *Rattus leucopus* (Leung 1999) is terrestrial. Competition and niche partitioning have most often been documented primarily at ground level in the literature so quantifying space use according to height level was an important advance in our understanding.

This led to the formation of four hypotheses:

My first hypothesis (chapter 3):

1. Rodent abundance is linked to resource (fruit/flower) abundance (as revealed by trap success).

My investigation of the abundance and vertical distribution of all four rodents further developed my interest in the extent and scale of space use by arboreal/scansorial mammals. *M. cervinipes* was the most common species trapped at all levels and therefore an ideal species to test further hypotheses. Individuals were often trapped in the same areas and seemed to be more common in and around canopy trees. These observations led to the second area of study - *M. cervinipes* home range and its relationship with food resources (Chapter 5).

While conducting trapping to investigate vertical space use (Chapter 3), I often observed *M. cervinipes* feeding on *Acmena graveolens* fruit pulp, most frequently on the ground, but also while fruits were still attached to the tree. On further investigation I found that two other rodents, *U. caudimaculatus* and *R. leucopus* also feed on these fruits. *A. graveolens* is a common canopy tree at the site and produces fruit in abundance between May-September. Fruits are variable in size but all have a thin layer of pulp and a large seed. The rodents ate only the fruit pulp and left the seed behind intact. Beetles were also always present in the pulp of fallen *A. graveolens* fruits.

This developed my interest in the role of rodents in the ecosystem and the effect of beetle presence. These ideas culminated in the final three hypotheses (chapter 4):

4. Rodent pulp consumption enhances the germination success of *A. graveolens*
5. Beetle presence reduces the germination success of *A. gravoelens*
6. Smaller seeds have a higher germination success than larger seeds (due to rodent preference)

1.2 BACKGROUND: A REVIEW OF THE LITERATURE

Why study canopy mammals?

Species diversity is the most basic unit of informed decision-making in the biodiversity planning process and is essential in order to define conservation priorities (Fallding *et al*. 2001). Accurately estimating diversity and abundance is therefore a fundamental part of this process. Arboreal and scansorial mammals are frequently ignored as they are rarely captured in ground traps and canopy trapping is logistically difficult. The literature suggests estimates of diversity and richness of species may be inaccurate or non-existent when tree-climbing mammals are present (Chapter 2). Determining which species use the canopy and to what extent they do so is therefore important when making predictions or assumptions about the community dynamics of any tropical mammal assemblage (Kays and Allison 2001).

Resource use and home range are two factors which influence the density of arboreal/scansorial mammals in any given area. These factors are consequently an important consideration when attempting to determine a species' presence or quantify patterns of habitat use.

The importance of quantifying resource use in arboreal rainforest mammal communities

In tropical rainforest areas, dominant canopy trees provide year round resources (Emmons 1995). The canopy in particular is the primary production layer of most forests and therefore contains most of the resources including fruit, flowers and leaves (Emmons 1995). This, coupled with the complexity of vertical strata, increases the number and type of available microhabitats in rainforests (Meserve 1977). Rainforest mammals have radiated to fill many niches, particularly those lineages able to climb trees and have first choice of resources.

In addition, segregation along the vertical dimension may reduce interspecific competition by resource partitioning (Cunha and Vieira 2002). This favours coexistence (Smith and Speller 1970; Meserve 1977; Barry *et al*. 1984) in addition to other advantages such as protection of juveniles from predation (Ren *et al*. 2001). As a result, arboreal mammal species diversity is comparatively rich with between 60-80% of tropical mammal communities being arboreal/scansorial (Kays and Allison 2001).

Home range size

Estimating an animal’s home range and habitat preferences is important both for addressing specific land management issues including reserve planning and design, as well as the determination of species interactions, competition and community dynamics (Chapter 5).

Home range size and use by a particular species is important to land managers as it allows wildlife needs to be integrated into planning protocols. For instance, nesting/roost trees with specific characteristics (tree hollows, branch orientation), favoured food items and sheltering sites (Fallding *et al*. 2001) may be limiting factors governing an animal's distribution in a certain area. Understanding the use of space for all fundamental activities (feeding, nesting, reproduction etc.) is essential when devising any planning regime for reserve design and for assessing the potential impacts of urban development, logging or agriculture (see Kremen *et al*. 1995; Fallding *et al.* 2001).

Resource availability (Lindstedt *et al*. 1986; McLoughlin and Ferguson 2000), quality (Ferguson and Mcloughlan 2000) and availability of nesting sites (Milner and Harris 1999) can govern spatial use and determine home range size Dominant individuals often occupy the most productive areas (Mcloughlin and Ferguson 2000) and those animals occupying less productive areas tend to have larger home ranges (Soutiere 1979; Smith and Schaefer 2002) to gain the required resources.

Calculating a scansorial/arboreal animal's home range is therefore dependent upon many interrelated factors which are not often easy to identify or quantify.

For instance in arboreal/scansorial mammals that use the canopy extensively, home range size includes a vertical dimension, however this space is difficult to ascertain. Some studies have attempted to characterize vertical space use by measuring branch diameters and inclines (Harney and Dueser 1987; Reagan 1992; Cunha and Vieira 2002), distance traveled up tree trunks (Bright and Morris 1991) and volume around trap stations (Meserve 1977). However, to account for total vertical space use, surface areas of enormously variable structures such as branches, trunks, vine, liana and leaf pathways would require the input of sophisticated modelling techniques which were beyond the scope of this study.

Canopy mammal frugivory and its impacts upon seed germination success and dispersal

For the seeds of vertebrate dispersed plants, several events can influence or limit the recruitment process including fruit removal or primary dispersal, seed dissemination, post-dispersal seed predation, potentially secondary dispersal and seedling establishment. At any point throughout this process (and assuming all seeds are viable), vertebrate/invertebrate interaction can enhance or reduce germination success (Wenny 2000), depending on the method of consumption. For instance, consumption may result in passing, spitting or regurgitating viable seeds due to the removal of pulp (Traveset and Willson 1997; Wenny 2000). Conversely, consumption may involve seed maceration and therefore a reduction in the overall number of viable seeds (DeSteven and Putz 1984; Howe *et al*. 1985, Chapman 1989, Peres *et al*. 1997).

Differences in foraging behaviour (Cruz 1981; Santana and Milligan 1984; Trainer and Will 1984), fruit removal rates (Bronstein and Hoffman 1987; Englund 1993), seed handling techniques (Janzen 1983; Corlett and Lucas 1990), size of seeds (Kelrick *et al*. 1986; Alcantara *et al*. 2000) and the presence/absence of invertebrates (Manzur and Courtney 1984; Redford *et al*. 1984; Knight 1987), can result in varying germination rates.

It is well known that the seeds of some species have a greater chance of germination success if pulp fruit is removed from seeds (Traveset and Willson 1997; Wenny 2000 and references therein). This is most likely because germination inhibitors present in fruit pulp (such as invertebrates and fungal spores) are removed when pulp is eaten, and/or mechanical or chemical scarification of the seed coat is sometimes necessary before the seed will germinate (Traveset and Willson 1997). The manual removal of fruit pulp results in a seed cleaned of its pulp, presumably analogous to the passing of a seed through an organisms' gut. Invertebrates (beetles in particular) can be both advantageous and detrimental to seed survivorship (Manzur and Courtney 1984; Redford *et al*. 1984; Jordano 1987; Knight 1987). Detrimental effects involve the degradation of the seed or fruit pulp, rendering it unattractive to vertebrate pulp consumers that might otherwise disperse the seed (Janzen 1983; Manzur and

Courtney 1984; Jordano 1987; Knight 1987). Invertebrate infestation can also be advantageous to a seed by increasing the protein, lipid or other nutrient content of the fruit, thereby making it attractive to potential vertebrate consumers/dispersers (Redford *et al*. 1984).

Seed size can govern both disperser access (Theimer 2001; Alcantara *et al*. 2000; Parciak 2002) and exposure to consumers (Kelrick *et al*. 1986; Kollman *et al*. 1998), thereby affecting a seeds' chance of recruiting into the next stages of its life cycle (Alcantara *et al*. 2000). Although often considered detrimental to seed survivorship, rodents also disperse many large fruits and nuts, thereby increasing the likelihood of seeds surviving to the next stage of their life cycle (Forget 1993, 1994; Brewer and Rejmanek 1999; Theimer 2001).

In conclusion, understanding the full extent of rodent resource and space use is important to increase our knowledge and understanding of community dynamics and to contribute to the database from which planning and management regimes are developed. Rodent consumption and dispersal of fruits may also impact upon seed survival and in the long term, the structuring of plant communities and the maintenance of diversity in tropical rainforests.

CHAPTER 2: BIODIVERSITY ASSESSMENT: THE IMPORTANCE OF CANOPY CENSUS

ABSTRACT

The availability and accuracy of data relating to the present status and distribution of a particular species is pivotal when management plans and frameworks are produced. This ensures that informed decision-making and the appropriate allocation of money and resources are possible. Arboreal mammals are difficult to census due to their inaccessibility and often, cryptic and nocturnal behaviour. Nonetheless they comprise a substantial proportion of tropical mammal communities and therefore require further attention to ensure they are appropriately surveyed. I suggest that the census of arboreal mammals is an important part of biodiversity assessment of forest-dwelling small mammal communities.

Key words: canopy trapping, vertical distribution, biodiversity, mammals

The importance of comprehensive fauna surveys

Not all ecosystems can be protected and this results in the need to determine conservation priorities (Burgman and Lindenmayer 1998). It is difficult to know what to protect, or how to protect it, if we are ignorant of the identity and ecological characteristics of biota (Burgman and Lindenmayer 1998). Strategies for conservation are developed on the basis of data on biological diversity, as well as information concerning threatened, endangered or endemic species (Rojas 1995). Incomplete or misleading information on species distribution and abundance distorts this process so that other comparatively less rich ecosystems may be protected at the expense of the richer but poorly surveyed ones.

‘Species richness’ and ‘species diversity’ are useful indicators of mammalian biodiversity in a given ecosystem (Wilson *et al*. 1996). Census of mammalian faunas generally involves determining species richness and relative abundance. However, in tropical mammal communities between 50 and 80% of the mammals are arboreal (Kays and Allison, 2001).

There is a marked difference between ground and canopy capture rates for several scansorial/arboreal species (Table 1,2).

TABLE 1: Small mammal and bat abundance in studies utilizing both terrestrial and arboreal trapping techniques.

Species	Common name	Total terrestrial captures (0-1m)	Total arboreal captures (>1m)	Reference
Pogonomys mollipilosus	Prehensile-tailed rat	0	41	This study (Chapter 3)
Glaucomys volans	Flying squirrel	1	37	Sawyer and Rose 1985; Risch and Brady 1996
Caluromys philander	Woolly opossum	3	56	Malcolm 1991
Oecomys Concolor	Rice rat	0	6	Viera 1998
Peromyscus leucopus	Deer mouse	229	94	Harney and Dueser 1987
Peromyscus maniculatus	Deer mouse	78	62	Harney and Dueser 1987
Rhipidomys mastacalis	Climbing rat	1	8	Malcolm 1991
Oryzomys bicolor	Rice rat	0	10	Malcolm 1991
Micoureus cinereus		0	11	Passamani 1995
Muscardinus avellanarius	Common dormouse	0%	100%	Tattersall and Whitbread 1994
Cynopterus brachyotis[a]		6	29	Zubaid 1994
Cynopterus horsfieldi[a]		3	18	Zubaid 1994
Artibeus concolor[a]		25	161	Bernard 2001

[a] terrestrial and arboreal captures considered to be 0-3m, and above 3m respectively for all bats.

In practical management terms, failure to trap in the canopy may result in underestimates of the population size of scansorial/arboreal species leading to the conclusion that some species may be rare when in fact they are only rare on the ground. In addition, population dynamics of coexisting species may not be as they appear. For example, Malcolm (1995) reports that the abundance of

Proechimys sp. was thought to be 10 times that of *Caluromys philander* until canopy trapping demonstrated equivalent abundance of the two species. A lack of arboreal trapping may also completely exclude the census of wholly arboreal species. Up to four species (out of fifteen) would not have been recorded at rainforest sites in Brazil and Panama, had Malcolm (1991) foregone canopy trapping. Thus, inappropriate conservation status and hence management priorities may be applied to particular species or sites.

TABLE 2: Small mammal and bat species diversity in studies utilizing both terrestrial and arboreal trapping techniques (a=dry season, b=wet season)

Terrestrial species richness (0-1m)	Arboreal species richness (>1m)	Exclusively arboreal species richness	Reference
Small mammals			
6	9	3	Viera 1998
11	9	4	Malcolm 1991
8a	10a	6a	Woodman *et al*. 1995
10b	10b	3b	Woodman *et al*. 1995
8	7	1	Passamani 1995
2	3	1	Tattersall and Whitbread 1994
Bats*			
8	11	3	Francis 1994
36	36	15	Bernard 2001
5	6	1	Zubaid 1994

* terrestrial and arboreal captures considered to be 0-3m, and above 3m respectively for all bats.

Different traps and heights yield different results

It is widely accepted that results of mammal census studies vary considerably depending on the type of trap set eg. pitfall, live or snap traps (Weiner and Smith 1972; Mengak and Guynn 1987; Slade *et al*. 1993). It is surprising therefore that the trapping success and diversity at different heights has been rarely addressed (Risch and Brady 1996). In addition, those studies that do include ‘arboreal’ trap stations often only census from 1 to 4 metres (Meserve 1977; Holbrook 1979; Harney and Dueser 1987), thereby restricting the study to mammals found in the understorey. Only a handful of published studies have sampled subcanopy and canopy mammals by setting traps above 15 metres (Malcolm 1991; Mcclearn *et al*. 1994; Passamani 1995; Viera 1998), probably because canopy trapping is logistically difficult and/or other survey methods can be used, including spotlighting (Davey 1990; Goldingay and Sharp 2004), stag watching (Smith *et al*. 1989; van der Ree and Richard 2002) and provision and checking of nest boxes (Bowen and Goldingay 2000). This has resulted in a lack of standardization and few comparable results with respect to heights, method used, trapping design and capture rates.

Management implications

One of the many obstacles to biodiversity conservation is a lack of specific information with regard to the ecological requirements of flora/fauna (Fallding *et al*. 2001). This includes baseline data on the presence and status of species, as well as an assessment of changes in ecosystem structure and function (Kremen *et al*. 1995). Availability of these specifics to the planning process ensures that capital and resources are not wasted on surveys, which offer a limited perspective of an ecosystem that is not necessarily comprehensive or adequate. This knowledge is also important in assessing resilience and response to disturbance during ongoing monitoring and therefore essential to adaptive management practices (Fallding *et al*. 2001).

Species diversity is the most basic unit of informed decision-making in the biodiversity planning process and is essential in order to define conservation priorities (Fallding *et al*. 2001). Number of species, distribution, abundance and conservation status are often used in environmental impact assessments to evaluate priorities in planning, zoning and management. Changes in the perception of a species' status would require a restructure of conservation and management priorities. For example *Pogonomys mollipilosus*, an arboreal rodent was considered uncommon due to its failure to be trapped in thousands of terrestrial trap-nights (Winter and Whitford 1995), until the results of this study (Chapter 3) suggest it is relatively common if canopy trapping is undertaken.

Understanding the full extent of biodiversity in any given ecosystem is essential before conservation priorities and planning protocols are established. If particular ecosystems or habitats are poorly sampled, fundamental errors may be made at this primary step of the conservation/planning process, i.e. number and abundance of species. In forest-dwelling small mammal communities, a census of arboreal mammals should be included, to ensure biodiversity is adequately surveyed.

CHAPTER 3: DOES RESOURCE AVAILABILITY GOVERN VERTICAL STRATIFICATION OF RODENTS IN AUSTRALIAN LOWLAND TROPICAL RAINFOREST?

Abstract

Mammal assemblages of rainforest communities are commonly vertically stratified. This can be driven by competition for or access to resources in the upper canopy layers of the forest. This study investigated the extent of vertical stratification in a tropical rainforest rodent community and whether any structure was driven by resource abundance. The rodent community was vertically stratified with *Pogonomys mollipilosus* found only in the upper canopy layers and *Rattus leucopus* on the ground layer. *Melomys cervinipes* and *Uromys caudimaculatus* were found at all four height layers. Fruit and flower resource abundance were not significantly correlated with total rodent captures, however arboreal captures of *M. cervinipes* and *P. mollipilosus* were correlated with the number of individual flowering canopy trees. Arboreal behaviour is probably driven by the advantages of first access to food resources, the availability of abundant resources and ultimately reduced competition in the upper strata.

Introduction

Tropical rainforests are complex three-dimensional habitats containing diverse assemblages of biota utilizing different height strata (Woodman *et al*. 1995). Between 50 and 80% of species in tropical mammal communities are arboreal (Kays and Allison 2001), so the mammal fauna is particularly well adapted to the three dimensional nature of rainforests. Vertical stratification of mammal fauna is common in tropical rainforests, with some obligate canopy users and others found as temporary visitors. For instance, 70 % (12 of 17 species) of mammals in Brazilian forest were captured in arboreal traps while the remaining 30% were confined to the ground and/or understorey (Fonseca and Kierulff 1989; Stallings 1989). The small mammal fauna of Peruvian lowland rain forest is similarly stratified, with half the species captured exclusively on the ground and the other half exclusively above the ground (Woodman *et al*. 1995).

Availability of, and access to resources can drive canopy use (Jekanoski and Kaufman 1995). Mammals that are highly "canopy dependent" include many folivores and frugivores that are restricted to the upper strata by diet (Emmons 1995). Transitory arboreal behaviour allows use of diverse food resources as well as means of travel (August 1983). For example, Jekanoski and Kaufman (1995) found that two species of seed-eating rodents regularly foraged in the canopy only when seeds were unavailable at ground level.   Consequently, arboreality increases the ecological flexibility of a species (Layne 1970), allowing individuals to have first preference to canopy resources, before they become available to ground competitors, as well as exploit above-ground nest and refuge sites (Emmons 1995). This increased efficiency in resource use thus allows individuals to exploit a wider range of environments than a non-arboreal species (Layne 1970).

Intra- and interspecific social interactions including competition (Meserve 1977) and predator avoidance (Ren *et al*. 2001), can also be among the main driving forces behind arboreal behaviour (Holbrook 1979). Vertical stratification may reduce interspecific competition and increase the possible number of coexisting species (Schoener 1974; Cameron and Kincaid 1982; Barry *et al*. 1984). In cricetid rodents competition is reduced through use of the vertical dimension, with food resources being obtained exclusively or partially from the canopy levels of the forest (Smith and Speller 1970; Meserve 1977; Passamani 1995).

The Australian wet tropical rainforest rodent community includes four ecologically-similar sympatric species that vary in life history and arboreality. The Fawn-footed Melomys, *Melomys cervinipes,* and Prehensile-tailed rat, *Pogonomys mollipilosus,* are the smallest of the rodent community. *M. cervinipes* (45-110 g) is partly arboreal (Wood 1971; Heinsohn and Heinsohn 1999) and *P. mollipilosus* (42-83 g), is considered arboreal and has not been trapped in any published study prior to this one (Winter and Whitford 1995). The white-tailed rat, *Uromys caudimaculatus* (900g)*,* is one of the largest of Australia's rodents and is partly arboreal (Moore 1995). The Cape York rat, *Rattus leucopus,* is a medium-sized (65-220g) terrestrial species that breeds all year round (Leung 1999). Although predominately terrestrial, it can access the understorey to some degree by climbing fallen logs and thick vines which are in contact with the ground. This species is difficult to distinguish in the field from *Rattus fuscipes*, which occurs in similar habitats (Vazquez-Dominguez *et al*. 2001). However, based on the mammary formula (Covacevich and Easton 1974) of a subset of individuals captured, the lack of morphological variation in the individuals captured (pers. obs.) and the unlikely occurrence of overlap between the two species (Laurance 1994), all *Rattus* captures in this study were classified as *R. leucopus.*

All these rodents are considered to be predominantly frugivores/granivores, probably with other items seasonally available such as insects and fungi. This study considers the vertical stratification of rodent frugivore and granivore distributions in Australian lowland wet tropical rainforest.

Methods

Study site

This study was conducted at the Australian Canopy Crane Research Facility, 140km north of Cairns at Cape Tribulation, North Queensland (16° 17’ S, 145° 29’ E). The vegetation at the site is complex mesophyll vine forest, Regional Ecosystem 7.8.2 (Sattler and Williams 1999) with an average annual rainfall of about 3500 millimetres (Australian Bureau of Meteorology). The site adjoins the Daintree National Park, a large protected area of World Heritage-listed Rainforest spanning over 100,000 hectares.

Vertical stratification of small mammals

Small mammal trapping was conducted at each of four height strata for 5 nights each month from May 2002 to April 2003. The strata trapped were the ground layer (0 metres), understorey layer (1-3 metres), sub-canopy layer (10-15 metres) and canopy layer (25-30 metres). Thirty Elliott (300 x 100 x100 mm) and five cage (500 x 150 x 150 mm) traps were set at each height. Above-ground traps were set on timber platforms fixed with wire to tree branches or the sides of tree trunks, and covered with a plastic sheet. Trap stations were positioned on radial lines within the circular area accessible by the crane. Canopy and sub-canopy traps were accessed using the Australian canopy crane and understorey and ground traps were accessed on foot. Traps were set at dusk and checked at dawn. The traps were baited with a mixture of rolled oats, peanut butter, honey and pistacchio essence. After removal from the trap, animals were sexed and tagged, with a passive induced transponder tag (LifeChip, Destron-Fearing) implanted subcutaneously and suprascapularly, then released at the trap site.

The relationship between rodent species abundance and height was analysed with Chi-square tests of significance. Expected values were generated assuming a uniform distribution across the strata.

The relationship between arboreal behaviour and resource abundance

Each of the four species of rodent present at the site is partially frugivorous (Harrison 1961; Moore 1995; Winter and Whitford 1995; Leung 1999). To determine the relationship between rodent abundance and aspects of resource abundance, the abundance of fruits and flowers within a 125 m^3 (5 x 5 x 5 m) volume centred at each trap site was estimated according to an index from 0 (absent) to 5 (the most abundant observed in the first month). The variation in the index was documented with photographs that were used as a reference throughout the study to ensure continuity between observer estimates. Monthly rodent captures at each trap site were compared with monthly resource index estimates using a non-parametric correlation (Spearman's rank correlation, Sokal and Rohlf 1995).

The influence of canopy tree flowering phenology on arboreal rodent captures

Six of the ten dominant canopy trees at the site have edible flowers and/or fruits and/or seeds (Cooper and Cooper 1994). The intensity of flowering or fruiting for each of these tree species was recorded monthly at each trap site using the index described above. This was then correlated as above with monthly arboreal captures of *Melomys cervinipes* and *Pogonomys mollipilosus*, the two primary canopy-using rodents.

Results

Vertical stratification of small mammals

Seven species of small mammal were captured in this study (Table 1). Three of the seven small mammal species, the long-tailed pygmy possum (*Cercartetus caudatus*: Burramyidae), northern brown bandicoot (*Isoodon macrourus*: Peramelidae) and yellow-footed Antechinus (*Antechinus flavipes rubeculus*:

Dasyuridae) were in low abundance and have not been included in statistical analyses. The remaining four species used in this study are the white-tailed rat (*Uromys caudimaculatus*: Muridae*),* fawn-footed Melomys (*Melomys cervinipes*: Muridae), Cape York rat (*Rattus leucopus*: Muridae) and the prehensile-tailed rat (*Pogonomys mollipilosus*: Muridae).

Table 1: Small mammal species trapped in mesophyl vine forest at the Australian Canopy Crane Site, Cape Tribulation.

Species	**Strata where captured**	**Number of individuals**	**Number of captures**
Fawn-footed Melomys (*Melomys cervinipes*)	ground (0m) understorey (1-3m) subcanopy (10-15m) canopy (25-30m)	99	446
Giant white-tailed rat (*Uromys caudimaculatus*)	ground (0m) understorey (1-3m) subcanopy (10-15m) canopy (25-30m)	19	74
Cape York rat (*Rattus leucopus*)	ground (0m) understorey (1-3m)	110	512
Prehensile-tailed rat (*Pogonomys mollipilosus*)	subcanopy (10-15m) canopy (25-30m) understorey (1-3m)	19	52
Long-tailed pygmy possum (*Cercatetus caudatus*)	subcanopy (10-15m) canopy (25-30m)	3	8
Northern brown bandicoot (*Isoodon macrourus*)	ground (0m)	6	16
Yellow-footed Antechinus (*Antechinus flavipes rubeculus*)	ground (0m) understorey (1-3m)	12	37

The fawn-footed Melomys and giant white-tailed rat were trapped in all four strata but were significantly more abundant at the understorey (1-3m) level ($\aleph^{2}=111.647$, $P<0.0001$, Figure 1; $\aleph^{2}=10.973$, $P=0.012$, Figure 1). The Cape York rat was only trapped in the two lowest strata, ground and understorey with significantly more captures at ground level ($\aleph^{2}=53.070$, $P<0.0001$, Figure 1). The prehensile-tailed rat was was trapped almost exclusively in the top two canopy layers with only a single understorey capture ($\aleph^{2}=23.115$, $P<0.0001$, Figure 1).

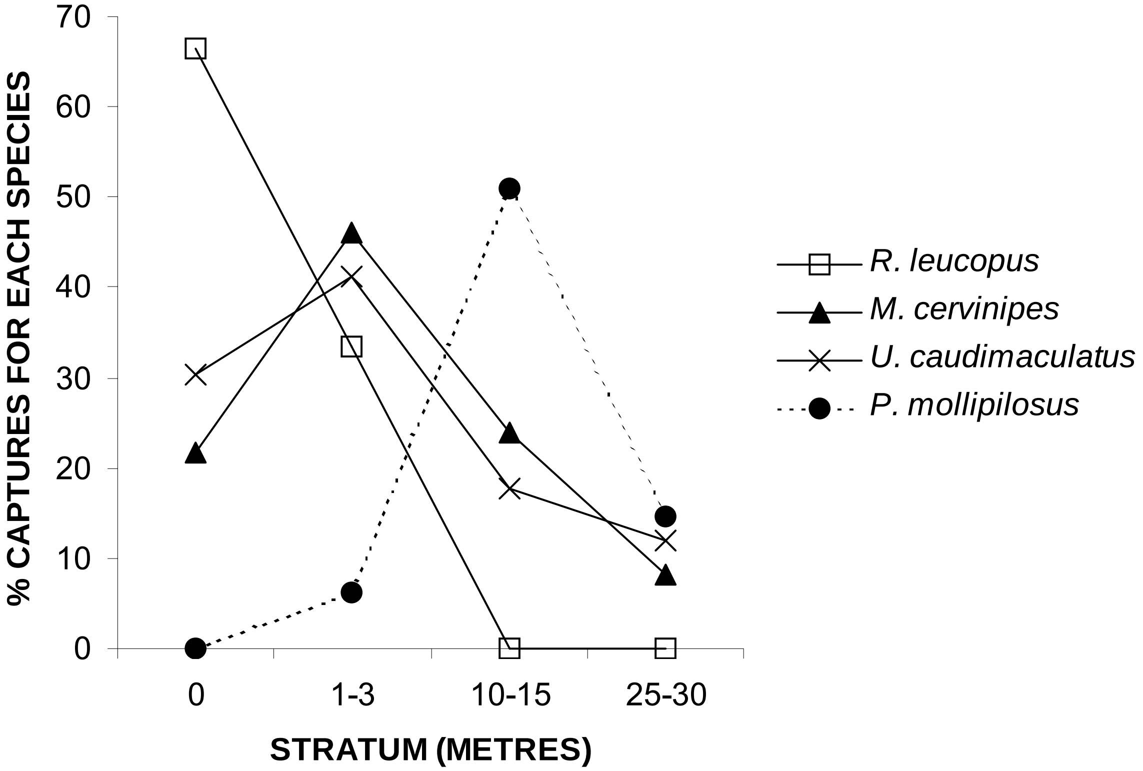

Figure 1: The relative distribution (%) of captures for each species across four height stratum in mesophyll vine forest at the Australian Canopy Crane Site, Cape Tribulation.

R. leucopus and *M. cervinipes* captures were positively correlated both on the ground and above the ground (ground level: correlation coefficient 0.581, *P*=0.023; understorey level: correlation coefficient 0.693, *P*=0.004).

The relationship between arboreal behaviour and resource abundance

There was no significant correlation between the combined abundance of all rodent species at individual traps and the amount of foliage, flowers, and fruit around those individual traps (Table 2). However, when arboreal captures of only *M.cervinipes* and *P. mollipilosus* alone were considered, there was a significant correlation between arboreal captures of *M. cervinipes* and the flowering canopy trees species *Syzigium sayeri, Acmena graveolens*, and *Argyrodendron perelatum* (Table 3). There was also a significant correlation between *P. mollipilosus* captures and the flowering canopy trees *Syzigium sayeri, Argyrodendron perelatum* and *Castanospermum australe* (Table 3).

Table 2: The relationship between small mammal captures and resource indices.

	Rodent captures	
Resource index All layers	Correlation coefficient	P-value
Foliage	-0.037	0.814
Flowers	-0.208	0.516
Ripe fruit	0.540	0.167
Flowers	-0.417	0.410

Table 3: The relationship between canopy tree species flowering at the time and arboreal captures of *P. mollipilosus* and *M. cervinipes*

	P. mollipilosus		*M. cervinipes*	
	Correlation coefficient	P-value	Correlation coefficient	P-value
Syzigium sayeri	0.796**	0.002	0.611*	0.035
Syzigium gustavioides	0.421	0.173	0.203	0.528
Acmena graveolens	0.439	0.153	0.743**	0.006
Argyrodendron perelatum	0.710**	0.01	0.684*	0.014
Castanospermum australe	0.900**	<0.001	0.447	0.145
Elaeocarpus angustifolius	0.174	0.589	0.426	0.168

* correlation is significant at the 0.05 level

** correlation is significant at the 0.01 level

Discussion

Vertical stratification of small mammals

In this study, several mammal species coexisted at different height strata (Figure 1). The canopy-dwelling fauna consisted of four species, *M. cervinipes, U. caudimaculatus, P. mollipilosus* and *C. caudatus*. Of these, the former two used all four strata (including ground) but were caught in highest numbers in the understorey and therefore considered to be scansorial. The later two species seem to be ‘obligate’ or exclusive canopy dwellers, being captured primarily in the subcanopy/canopy layers. The ground layer was inhabited by three wholly terrestrial species in addition to the above temporary canopy users.

The relationship between arboreal behaviour and resource abundance

Two possible mechanisms, influencing canopy use include access to abundant seasonal resources (Emmons 1995) and/or competition (Meserve 1977). The significant correlation between fawn-footed Melomys and prehensile-tailed rat captures and the flowering of several dominant canopy tree species (Table 3), suggests resource use may partly explain strata preference. The lack of correlation between total resource indices and total rodent numbers (Table 2) may be because different species responded to the resources in different ways. The resource index estimated in this study combined all fruiting and flowering vines/shrubs/trees at each trap location. Thus, if the fruits/flowers of some abundant tree species were not used, their contribution to the index could mask effects of other species. The fruits/seeds of the six dominant canopy tree species at this site (Table 3), are known to be food resources for a number of rodent species (pers. obs.; Cooper and Cooper 1994) but whether they are key resources in the diets of specific species remains unknown until more detailed diet studies are carried out. However, the correlations between captures of *P. mollipilosus* and *M. cervinipes* and flowering of *S. sayeri, C. australe* and *A. graveolens*, suggests that they are food species.

Resource partitioning and habitat segregation among similar species may facilitate coexistence and maintain diversity in ecological communities (Schoener 1974, Pacala and Roughgarden 1982). The resulting microhabitat differences are the principal means of competitive avoidance for many cricetid and heteromyid rodents (M'Closkey 1976; Price 1978). Habitats with high structural heterogeneity, such as rainforests present greater opportunities for microhabitat selection (Malcolm 1995). Consequently, tropical rainforest communities often contain many sympatric species, due to the diversity and abundance of resources and nesting/refuge sites (Fleming 1973; August 1983; Dickman *et al*. 1983; Emmons 1995).

The most diverse rainforest mammal assemblages of Peru, Gabon and Borneo are comprised of 30-80 non-flying mammal species, of which over half are arboreal (Emmons 1995). The number of coexisting mammal species at the Cape Tribulation study site totals 12 species of which 60-70 % are arboreal. The Murid rodent species alone at the study site comprise a rich assemblage (Emmons 1995), with 3-4 rodent species coexisting in each height strata. The abundance of arboreal mammals in tropical rainforest communities is most likely because structural complexity in rainforests is particularly pronounced in the vertical dimension (August 1983; Malcolm 1995), not only by the presence of large canopy trees providing ground to canopy access, but also via the myriad of vines and lianas which provide arboreal platforms and pathways, increasing the usable surface areas for non-volant canopy-dwelling fauna (Montgomery and Sunquist 1978; Emmons 1995).

Competition?

In this study the vertical dimension is partially divided between these species. However, there is also spatial overlap and all the species have similar, fairly catholic diets (Harrison 1961; Moore 1995; Winter and Whitford 1995; Leung 1999). This suggests that there is the potential for competitive interactions among these rodents. However, this study did not specifically set out to examine the role of competition between the rodent species.

By obtaining food resources from the canopy levels of the forest, competition at ground level could be reduced (Smith and Speller 1970; Meserve 1977; Passamani 1995). The four resident rodent species in this study could encounter competition both on the ground (from northern brown bandicoots, musky rat kangaroos, yellow-footed Antechinus and pigs) and in the canopy (long-tailed pygmy possum, striped possum), as all these species' diets and/or nesting areas overlap, at least broadly. However, by using above ground resources the white-tailed rat and fawn-footed Melomys and prehensile-tailed rat have certain advantages. These three rodents have first access to fruit and flower resources that are inaccessible to ground-dwelling competitors until they fall to the ground. This access to resources before ground-dwelling frugivores can access them, may be particularly important when resources are in low abundance. Consequently canopy access may translate to an increased efficiency in finding those limited resources.

P. mollipilosus is a rodent that is little known as it has not been trapped prior to this study despite the effort of thousands of trap-nights (Whitford and Winter 1995). The results of this study suggest it is an obligate canopy dweller. Nest sites were not determined in this study, but information from individuals found in Australia (Whitford and Winter 1995) and New Guinea (Dwyer 1975) suggests that it feeds on canopy resources but nests in ground burrows. Its ability to access ground level resources, yet use of canopy resources, also suggests a possible competitive advantage of canopy resource use.

There has been some speculation as to whether interspecific competition exists between populations of the similar-sized *Rattus sp.* and *M. cervinipes (*Wood 1971; Laurance 1994; Heinsohn and Heinsohn 1999*)*. Heinsohn and Heinsohn (1999) suggest the competitive relationship may be negatively driven by *M. cervinipes*. Laurance (1994) suggests *Rattus sp*. are the more competitive. The limited findings of this study do not support the suggestion of competition. In fact, the total number of *R. leucopus* and *M. cervinipes* captures were positively correlated (ground level: correlation coefficient 0.581, P=0.023; understorey level: correlation coefficient 0.693, P=0.004). However, the results of this study do elucidate spatial patterns of habitat use influencing abundance estimates. Mean monthly captures of *R. leucopus* are much higher than mean monthly captures of *M. cervinipes* when ground data only are considered (Figure 1) suggesting *R. leucopus* is the more abundant rodent. However, arboreal trapping records reveal that *M. cervinipes* is not less abundant, but moves upwards to utilize the canopy layers, a resource *R. leucopus* is unable to access. If abundances are determined for ground layers only, this pattern is not evident.

In conclusion, vertical stratification is evident in the rodent fauna of the Australian lowland Wet Tropics. The exact mechanisms underlying the use of the vertical strata remain unclear, however, seasonal canopy use suggests a greater efficiency and/or reduced competition in the upper rainforest strata, thereby facilitating the coexistence of at least four sympatric species.

CHAPTER 4: A PLANT- ANIMAL INTERACTION INVOLVING RODENTS, BEETLES AND AN AUSTRALIAN RAINFOREST FRUIT (*Acmena graveolens)*

Abstract:

The consumption of fruits by vertebrates and invertebrates may be both advantageous or detrimental to the survival of the seeds they contain. This study investigated the interaction between rodent pulp consumption, presence of beetle larvae and fruit size, and their effect on the germination success of *Acmena graveolens* seeds, a tropical rainforest canopy tree found in northern Australia. As fruit size increased, germination success and the amount of pulp remaining on the fruits was greater. Of those fruits undamaged by beetle larvae, germination success was highest when most of the pulp was removed, and decreased as rodent pulp consumption decreased. The reverse was true for fruits with beetle larval damage present. In this study, both vertebrate and invertebrate fruit consumers have complicated, but potentially advantageous effects on germination.

Key words: recruitment success, rodent predation, small mammals, plant-animal interactions

Introduction

Spatial and temporal patterns of seed predation and dispersal influence recruitment and distributions of tree species, patterns of plant diversity and community structure (Janzen 1970; Howe and Smallwood 1982; Traveset and Willson 1997; Kollman *et al*. 1998; Cypher and Cypher 1999; Brewer and Rejmanek 1999; Adler 2000; LoGiudice and Ostfield 2002). Animals play an important role in seed predation and dispersal by influencing the number and viability of seeds entering into the seed dispersal process (Ballardie and Whelan 1986; Whelan *et al*. 1991; Forget 1993; Ostfield *et al*. 1997; Silvius and Fragoso 2002). Consequently, understanding the factors influencing the number of seeds entering the dispersal process is of fundamental importance in describing the major ecological forces that structure and maintain diversity in tropical forest communities as well as some aspects of the evolution of plants (Janzen 1971; Schupp 1988; Willson and Whelan 1990).

Both vertebrates and invertebrates can be fruit consumers. Separation of the impacts of vertebrates and invertebrates may be important since these animals may differ in both the temporal and spatial scales of their effects as well as the consequences of their foraging as predation or dispersal (Hulme 1997).

Invertebrates (beetles in particular) can be both advantageous and detrimental to seed survivorship and dispersal (Manzur and Courtney 1984; Redford *et al*.

1984; Jordano 1987; Knight 1987). Detrimental effects involve directly causing damage and mortality (DeSteven and Putz 1984; Howe *et al*. 1985; Chapman 1989; Peres *et al*. 1997) as well as less direct effects such as the degradation of the seed or fruit pulp, rendering it unattractive to vertebrate pulp consumers that might otherwise disperse the seed (Manzur and Courtney 1984; Jordano 1987; Knight 1987). Invertebrate infestation can also be advantageous to a seed by increasing the protein, lipid or other nutrient content of the fruit, thereby making it attractive to potential vertebrate consumers and dispersers (Redford *et al*. 1984).

Similarly, consumption of fruits by vertebrates may be both advantageous and detrimental to seeds, depending on the method of consumption. Vertebrates may either consume whole fruits or remove pulp without ingesting the seed (Silvius and Fragoso 2002). Of those that consume whole fruits, advantages include increased germination success and dispersal. Increased germination success is a result of chemical scarification in the stomach, with seeds passed in excrement or by regurgitation (Traveset and Willson 1997; Wenny 2000). Detrimental effects include seed mortality (Whelan *et al*. 1991; Forget 1993; LoGiudice and Ostfield 2002).

Fruit consumers as well as ‘pulp consumers’ can act as seed dispersers, by caching, spitting or carrying seeds to another location (Corlett and Lucas 1990; Forget 1993; Theimer 2001; Balcomb and Chapman 2003; Dominy and Duncan 2003; Dennis 2003). Despite not actually damaging or dispersing seeds, pulp-consuming rodents in tropical forests could have substantial impact on seed survivorship and/or dispersal. By removing pulp, rodents may remove chemical, invertebrate or fungal inhibitors, thereby speeding germination (e.g. Traveset and Willson 1997). The manual removal of fruit pulp results in a seed cleaned of its pulp, partially analogous to the passing of a seed through an organisms' gut, and may have similar effects. Conversely, their interaction may reduce the attractiveness of pulp to other potential fruit consumers or dispersers (Manzur and Courtney 1984; Jordano 1987; Knight 1987), thereby reducing germination or dispersal success.

The fate of rodent dispersed seeds can vary with a number of seed features, including size, thickness of endocarp/exocarp, nutrient content and toxicity (Rosenzweig and Sterner 1970; Kelrick *et al*. 1986; Jansen *et al.* 2000). Seed size is a phenotypic trait that can both govern disperser access (Alcantara *et al*. 2000; Theimer 2001; Parciak 2002) and exposure to predators (Kelrick *et al*. 1986; Kollman *et al*. 1998), thereby affecting a seeds' chance of being recruited into the next stages of its life cycle (Alcantara *et al*. 2000). Both large seeds and vertebrate frugivore's are particularly common in the tropics compared with other latitudes (Moles and Westoby 2003). Seed-caching rodents disperse many large fruits and nuts (Forget 1993, 1998; Brewer and Rejmanek 1999) and a large seed size may have evolved, at least in part, to facilitate this mode of dispersal (Vander Wall 2003).

This study investigated the interaction between the following variables, and their effect on the germination success of *Acmena graveolens* seeds:

(1) the degree of pulp removed by rodents
(2) the presence/absence of beetles
(3) seed size

Methods

Site and species characteristics

This study took place from May 2002 to April 2003 at the Australian Canopy Crane Research Facility, 140km north of Cairns at Cape Tribulation, North Queensland (16° 17’ S, 145° 29’ E). The site is part of Australia’s Wet Tropics World Heritage Area and adjoins the Daintree National Park. The forest type is described as Regional Ecosystem 7.8.2- complex mesophyl vine forest (Sattler and Williams 1999). The area has an average annual rainfall of about 3500 mm (Australian Bureau of Meteorology)

The study species, *Acmena graveolens,* is a common, large-seeded canopy tree that grows up to 35 metres tall and fruits between May and September. The pink fruits range in size from 20-60mm, have a solitary seed and are consumed by both vertebrates and invertebrates (Cooper and Cooper 1994).

Pulp removal by rodents and beetles and its effect on germination success

To examine the effects of pulp removal by rodents and beetles, I collected 640 fruits from 10 individual *A. graveolens* trees. Fruits were divided into four categories based on the amount of pulp remaining on the seed after removal by rodents: 1 = *little* (<25% fruit pulp), 2= *some* (25-50% fruit pulp), 3 = *moderate* (50-75% fruit pulp), 4= *high* (75-100% fruit pulp). Fruits in categories 1-3 were collected around the base of several fruiting *A. graveolens* trees. Fruits in category 4 were picked from the tree's canopy using the Australian canopy crane for access. Fruits were also divided into three size classes. Fruits were considered "small" if length along longest axis was less than 20 mm, "medium" if length was 21-30 mm and "large" if greater than 31 mm. The fruit pulp layer in this species is less than 2mm, so the size differences between the classes were not due to differential removal of pulp.

I placed fruit in each of four wire cages that contained leaf litter gathered from under the closest *A. graveolens* tree. Each cage contained 40 fruits from a single pulp category and about thirteen fruits from each size class. The cage prevented further rodent consumption and the addition of leaf litter was to allow natural decay processes. The four cages corresponding with the four levels of remaining pulp, were placed beneath fruiting *A. gravoelens* trees at four replicate sites for 8 weeks (16 cages overall).

After the 8-week period under the parent tree, each fruit was examined for the presence of beetle/invertebrate holes and then transferred to individual pots in a greenhouse. After 2 weeks, one month, two months, three months and six months, a census of seedlings was conducted to determine the proportion of each treatment that had germinated, however only germination success at 6 months was used for this study. After 6 months ungerminated fruits were removed and examined. All fruits which had not germinated after six months had either rotted or disintegrated and were therefore considered unviable. The two beetle species present in the fruits were identified to genus and species level, respectively, by P. Grimbacher of Griffith University (Lawrence *et al*. 1999) and matched with specimens in the CRC Rainforest Wet Tropics Beetle Reference Collection at James Cook University, Cairns.

The effect of seed size on germination success

To examine the effects of seed size on germination success I selected 50 fruits from each of four sites and from each pulp category and combined them into one sample. I ensured an equal distribution of pulp categories in each size class. The germination success of the two hundred fruits was then calculated as above.

Identification of fruit pulp consumers

To confirm that rodents were actually the main consumers of *A. graveolens* fruit pulp, an infrared/motion sensor camera was placed in front of 20 fruits, beside a fruiting *A. graveolens* tree for four weeks over June and July. In addition, I observed and recorded fruit consumers for three hours each night for two weeks, under two individual fruiting *A. graveolens* trees.

Pulp removal and seed size under natural conditions

To ascertain the end-point of rodent consumption, i.e., the amount of pulp remaining on fruits under natural conditions, 20-30 control fruits (with 100% pulp) were positioned outside the wire cages at each of the four sites. Each fruit was pegged *in situ* under the parent tree using tent pegs and labels and given an identification number. At the end of the 8-week period, the amount of pulp remaining on each fruit was recorded. The natural distribution of size classes was also determined by collecting all fallen fruits under two trees (n=176) and recording the frequency of fruits in the three seed size classes listed above.

Statistical Analysis

Heirarchical loglinear analysis was used to determine if there were interactions between pulp categories, presence of beetle holes, seed size and germination success (after 6 months), for each treatment.

Chi square tests of significance were then used to test for differences in germination success within pulp, beetle attack and size categories, assuming an equal germination success across all categories in the absence of experimental effects. Similarly, Chi square tests of significance were used to test for: differences in pulp remaining within beetle attack, size, and germination success; differences in beetle attack within size, germination success and pulp and differences in size within germination success, pulp and beetle attack. The statistical package used was SPSS version 12 (SPSS 2000).

Results

Pulp removal by rodents, the presence of beetle holes and their effect on germination success

There was a statistically significant interaction between the amount of pulp remaining, the presence of beetle holes and germination success (Table 1). The presence/absence of beetle holes influenced the germination success of seeds across the different pulp categories.

Of those fruits without beetle holes, germination success was highest at high levels of rodent consumption (i.e. little <25% pulp remaining on seed), and dropped as rodent consumption decreased (i.e. large amount of pulp remaining) (LR Chisquare change =12.6, df=3, *P*=0.005; Figure 1). Within fruits with beetle holes the reverse was true. In that category germination success was low for those fruits with little pulp remaining and increased as the amount of pulp remaining increased. However pulp removal alone, considered irrespective of beetle larval presence did not influence germination success ($\aleph^2$=1.400, df =3, *P*=0.705).

Independent of germination success and size, the presence of beetle holes was related to the amount of pulp remaining on the fruit ($\aleph^2$=26.377, df =3, *P*=<0.001).

Fruits with little pulp (<25%) were equally likely to be found with beetle holes as without, yet as the amount of pulp remaining increased (>25%) more fruits were found with beetle holes than without.

Table 1: The interaction between pulp removal, presence of beetle holes, seed size, amount of pulp remaining and germination success using Hierarchical Loglinear Analysis. (Signficance level reduced to 0.025 to minimize type II error). Significant interactions marked with asterisk(*).

Effect	DF	L.R. Chisquare change	*P*-value
Beetle holes		N/A	
Germination success		N/A	
Amount of pulp remaining		N/A	
Seed size		N/A	
Pulp *germination success		N/A	
Beetle holes * germination success		N/A	
Beetle holes*pulp remaining		N/A	
Beetle holes*seed size	2	16.672	< 0.001*
Pulp remaining *seed size	6	46.053	< 0.001*
Germination success*seed size	2	28.020	<0.001*
Beetle holes*germination success*seed size	2	0.034	0.9833
Pulp remaining*germination success*seed size	6	7.629	0.2665
Pulp remaining*beetle holes*seed size	6	12.564	0.05
Pulp remaining*beetle holes*germination success	3	12.600	0.005*
Pulp remaining* beetle holes* germination success* seed size	6	1.351	0.9688

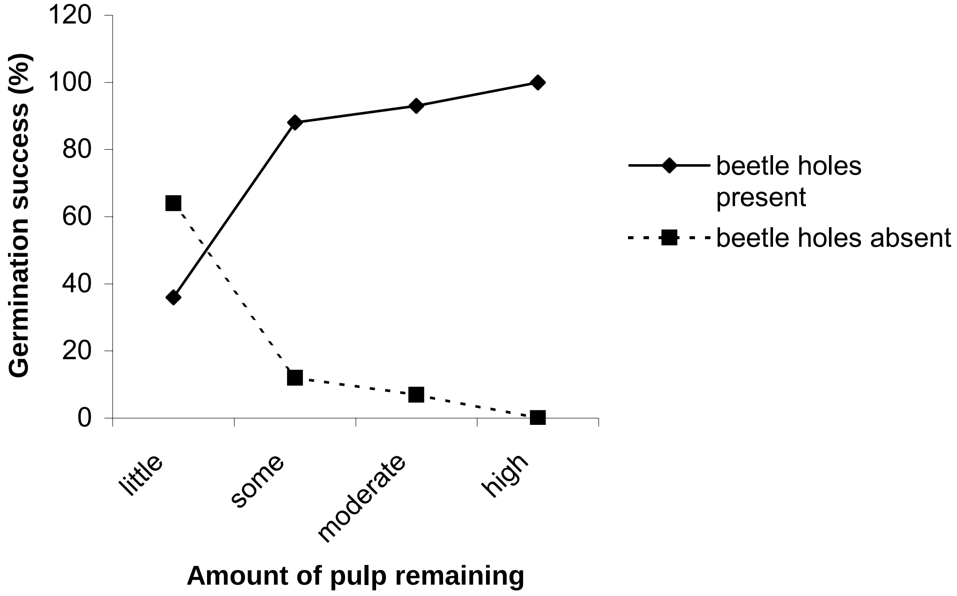

Figure 1: The influence of pulp remaining and beetle holes on germination success of *A. graveolens* seeds (LR Chisquare change =12.6, df=3, *P*=0.005)

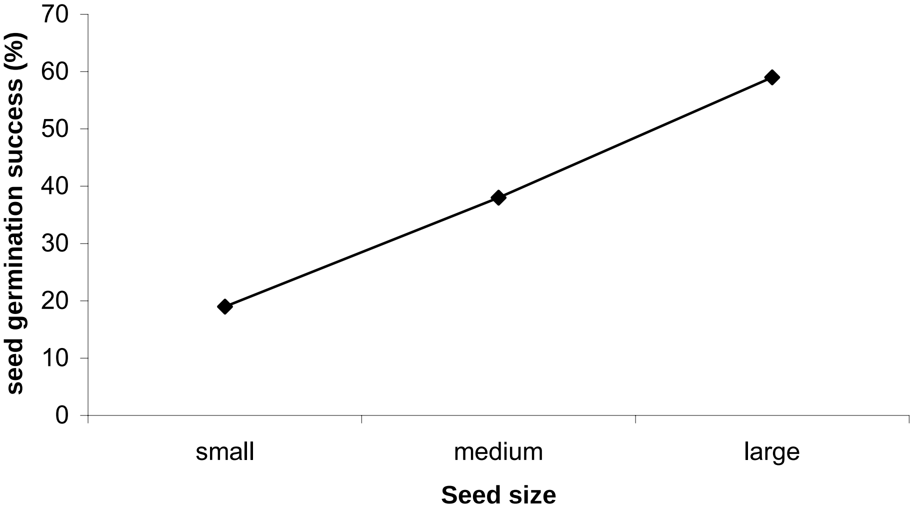

Figure 2: The effect of seed size on germination success (LR Chisquare change =28.020, df=2, *P*<0.001)

Independent of size neither beetle holes (small seeds $\aleph^2=0.175$, df =1, $P=0.449$; medium seeds $\aleph^2=0.186$, df =1, $P=0.387$; large seeds $\aleph^2=1.852$, df =1, $P=0.121$) nor pulp remaining (small seeds $\aleph^2=5.967$, df =3, $P=0.113$; medium seeds $\aleph^2=5.593$, df =3, $P=0.133$; large seeds $\aleph^2=1.400$, df =3, $P=0.705$) influenced germination success.

The effect of seed size on germination success, pulp remaining and the proportion of seeds with beetle holes

The proportion of seeds that germinated increased with increasing seed size (LR Chisquare change =28.020, df=2, $P<0.001$, Figure 2). In addition, the number of seeds with beetle holes was significantly influenced by seed size. A majority of large seeds (>70%) were found with beetle holes present whereas few small seeds (19%) had beetle holes (LR Chisquare change =16.672, df=2, $P<0.001$, Figure 3).

In all size classes, fruits with <25% pulp remaining comprised the greatest proportion of fruits. Few small seeds (8%) were found with > 25% fruit pulp. Conversely, many (60%) large seeds were found with >25% pulp remaining ($P=0.001$, Figure 4).

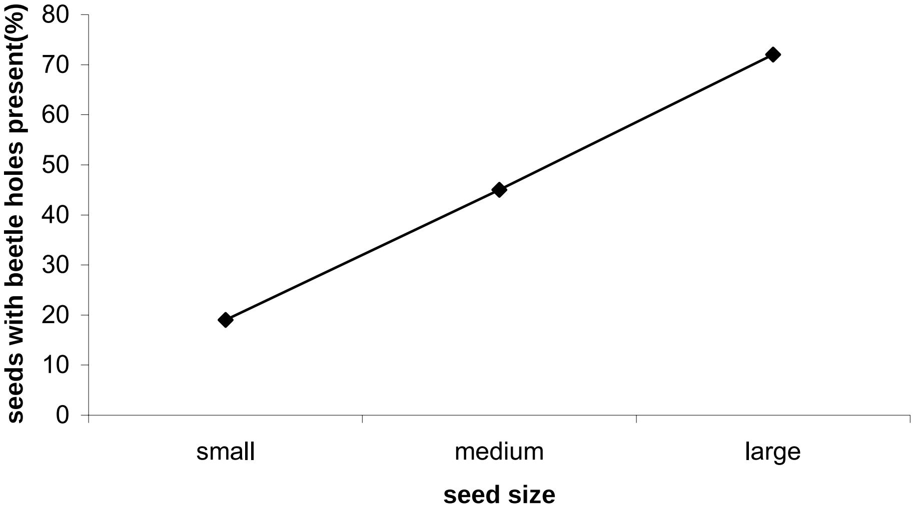

Figure 3: The influence of seed size on the number of seeds with beetle holes (LR Chisquare change =16.672, df=2, *P*<0.001).

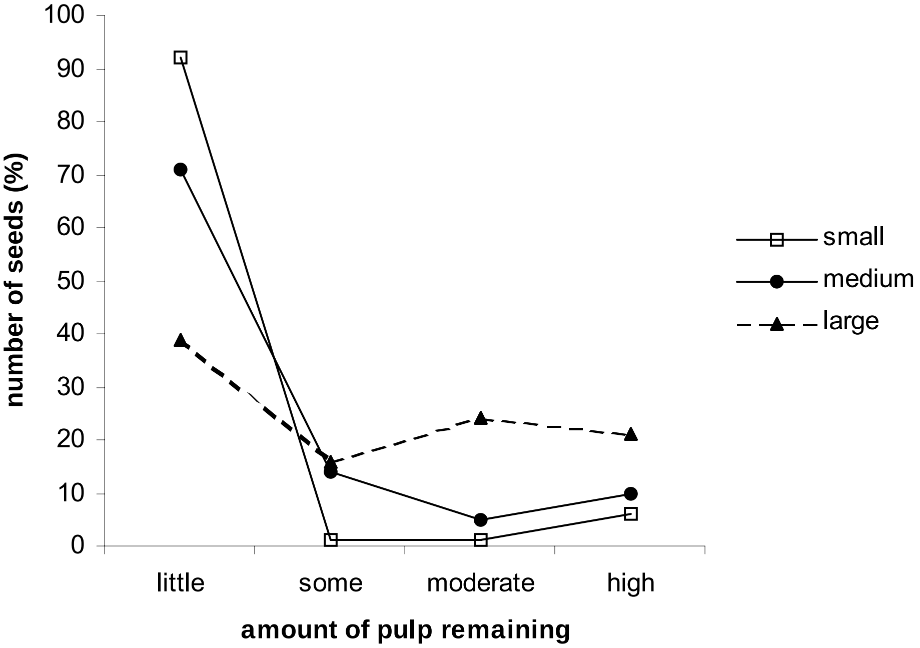

Figure 4: The influence of seed size on the amount of pulp remaining (LR Chisquare change =46.053, df=6, *P*<0.001)

Identification of pulp consumers

Infrared camera pictures and onsite observations in the canopy and ground suggest that two rodents, the fawn-footed Melomys (*Melomys cervinipes),* and the white-tailed rat *(Uromys caudimaculatus)* and a bat (*Pteropus conspicillatus)* were the main pulp consumers of *A. graveolens* fruits in the canopy. At ground level, *M. cervinipes, U. caudimaculatus* and *Rattus leucopus* were the major consumers with less frequent sightings of *Casuarius casuarius, Sus scrofa* and *Isoodon macrourus* (Table 2). The two beetles present were identified as *Epuraea ocularis* and *Brachypeplus sp*., both in the family Nitidulidae (P. Grimbacher pers. comm.; Lawrence *et al*. 1999).

Table 2: Observation records of fruit consumers
PO = personal observation, C = camera

Species recorded	Common name	Total # visits Ground	Total # visits Canopy	Method observed
Melomys cervinipes	Mosaic-tailed mouse	23	4	PO/C
Uromys caudimaculatus	White-tailed rat	6	1	PO/C
Rattus leucopus	Cape York rat	22	0	PO/C
Pteropus conspicillatus	Spectacled flying fox	0	3	PO
Casuarius casuarius	Southern cassowary	2		PO/C
Sus scrofa	Pig	3		C
Isoodon macrourus	Northern Bandicoot	2		PO/C

*a visit was defined as an individual visit to the observation area. Different individuals could not be differentiated so after leaving the observation area, the same animal could have returned more than once.

Pulp remaining and seed size under natural conditions

Over 50% of seeds had little pulp remaining (category 1). This class was significantly more abundant under natural conditions than those with higher fruit pulp (χ^2=82.51, DF=3, *P*<0.001). Very few seeds (8%) remained in category 4 (75-100% pulp remaining) under natural conditions. The most abundant size class under natural conditions was medium (Table 3)

Table 3: The distribution of fruit pulp and fruit size categories under natural conditions

Control factors	% fruits	χ^2	DF	*P*
Pulp remaining		82.51	3	<0.001
1, little (<25%)	51			
2, some (25-50%)	22			
3, moderate (50-75%)	19			
4, high (75-100)	8			
Seed size		79.86	2	<0.001
1 small (<1.5-2.0cm)	15			
2 medium (2.1-3cm)	55			
3 large (3.1+cm)	30			

Discussion

The interaction between pulp remaining, presence of beetle holes and germination success of A. graveolens seeds.

This study has shown that the interaction between the presence of beetle larvae (and/or possibly other invertebrates) and the degree of pulp remaining (due to rodent consumption) can influence germination success, without requiring the mechanism of increasing attraction to vertebrate frugivores as suggested in the literature (Redford *et al*. 1984). Beetle presence, resulted in higher germination success, but depended on the level of rodent consumption (Figure 1) so both rodents and beetles were necessary to influence germination success.

Seeds with <25% pulp remaining had a higher germination success than those with >25% pulp remaining, when beetle holes were absent. This may be explained by the presence of a natural germination inhibitor that prevents germination until the pulp is removed, thereby increasing the chances that the fruit has been dispersed first (Izhaki and Safriel 1990; Barnea *et al*. 1991; Witmer and Cheke 1991). By eating the fruit pulp, rodents may be removing the fruit's inhibitor and allowing it to germinate.

This interaction between the effects of rodent consumption and beetles may be due to differences in the scale and method of consumption, ultimately resulting in more efficient pulp removal when the effect of their consumption is combined. Individually, rodents may not remove enough flesh or remove it coarsely leaving the finer scale removal to beetles. As beetles have much smaller mouthparts, perhaps they can more effectively remove the pulp closer to the seed than rodents. Without rodents however, beetles may not be able to penetrate pulp and/or remove enough of the pulp to influence germination success. Separating the consumption methods and impacts of rodents and beetles would be required to answer these questions. This would involve further experimental analysis and was beyond the scope of this study.

However, in fruits with beetle holes there was the opposite effect. Seeds with >25% pulp remaining had a higher germination success than those with <25% pulp remaining. Although this relationship appears to have an opposite effect to rodent predation, it may in fact be similar. Although beetles were observed on fruits when flesh was intact, the experiment proceeded without further investigation or monitoring until germination occurred. When fruits were placed in categories of pulp remaining, many of the fruits with beetle holes had active beetles and larvae when placed in the greenhouse. The beetles may have continued eating the pulp while the experiment proceeded, regardless of their labeled pulp categories. This may have resulted in high germination rates for fruits, which, although categorized as having large amounts of pulp, actually had very little remaining. Unlike other invertebrates, the beetle larvae found in the *A.*

graveolens fruit do not burrow into the seed and appear to eat/reside in the pulp only (pers. obs) and so are unlikely to directly reduce seed viability.

The effect of seed size

Germination success of *A. graveolens* increases with increasing seed size (Figure 2). This may be due to larger seeds having greater capacity to deal with temperature and moisture stresses, with greater reserves to resist poor conditions (Foster 1986; Howe 1990).

In addition, the foraging strategies of rodents may also influence the higher germination success of larger seeds due to pulp preferences (Sultan 1996; Milberg *et al*. 1998). There is a substantial range of fruit sizes, so rodents can choose the size they prefer. This would presumably reflect a differential competency in handling and processing pulp from different size fruits (Gautier-Hion *et al*. 1980; Brewer 2001; Parciak 2002; Alcantara and Rey 2003; Vander Wall 2003) or fruit size availability (Julien-Laferriere 1993,1999; Brewer 2001; Alcantara and Rey 2003). If this is the case, different rodents may preferentially select a particular size classes of fruits. The pulp of this size class will be eaten and those fruits will either have a greater chance of germination success (due to pulp removal) or enter into the dispersal process (if the preferred size is carried away or cached).

Large seeds also had the highest amount of pulp remaining (Figure 4) and the highest proportion of beetle holes (Figure 3). Beetle preference for larger seeds may result from increased habitat or food resources due to increased pulp. However, beetle presence may also deter rodents as larger seeds were the least consumed.

Although large fruits had the highest germination success, medium-sized fruits were the most abundant size class present under natural conditions (Table 2). One suggestion for this anomaly is that pulp consumers (as opposed to ‘dispersers’) are the preferred handler due to the ubiquity and abundance of medium-sized rodents (this study, chapter 3) as opposed to the larger dispersers such as the white-tailed rat (*Uromys caudimaculatus)* or Southern Cassowary (*Casuarius casuarius*).

Conversely, a high abundance of medium sized fruits may benefit the tree by satiating the highly abundant medium-sized pulp eaters, leaving the larger fruits (with higher germination success) to be dispersed by the larger, more reliable dispersers (LoGuidice and Ostfield 2002). For instance the large rodent (900+grams) *Uromys caudimaculatus* is known to carry away and cache large seeded fruits (Theimer 2001) and the southern cassowary is also known to be a disperser (Stocker and Irvine 1983). Variation in size may therefore be a limiting factor influencing the number of seeds that germinate. This is supported by the result that small and medium seeds have the least pulp remaining and large seeds were the most numerous category with the most pulp remaining, possibly as they are more difficult to process and least preferred by the most abundant, medium sized rodents.

The identification of pulp consumers

The most common pulp consumers observed were the medium sized rodents, *M. cervinipes* and *R. leucopus*. Observation revealed rodents removing flesh by holding fruit in their forepaws. Of all rodents observed, none ate all the pulp of one fruit in a sitting. Frequent disturbance by other sounds or animals in the forest resulted in rodents spending little time with each fruit handled, dropping it and running at the slightest disturbance. *U. caudimaculatus* was observed handling the fruits in a similar way, however fewer were observed, probably due to their lower abundance. *A. graveolens* fruits were eaten by *C. casuarius* and the seeds were passed with no remaining pulp (pers. obs.).

Pulp removal under natural conditions

Fruits with little remaining pulp were by far the most abundant and those with high levels of remaining pulp the least abundant under natural conditions (χ_2=82.51, DF=3, P<0.0001). This indicates that rodent consumption of fruit pulp is the predominant fate of *A. graveolens* fruits. In the absence of beetles, germination success is highest when fruits have *little* pulp remaining, so the most common overall effect of the rodents is to enhance seed recruitment to seedling stage.

In conclusion, rodent pulp consumption improves the germination success of *A. graveolens* fruits. The presence of beetles further improves germination success. This is contrary to theoretical expectation as both rodents and beetles (with few exceptions) are traditionally considered to be seed predators.

CHAPTER 5: HOME RANGE, RESOURCE AND SPACE USE BY A TROPICAL RAINFOREST RODENT, *Melomys cervinipes*

Abstract

This study investigated the extent of arboreal activity, resource use and home range size of a tropical Australian rodent, *Melomys cervinipes*. Nesting and food resource availability were identified as two mechanisms driving arboreal activity. In seven of the eight *M. cervinipes,* nest sites were central to their range. Home range size did not significantly differ between the sexes with an average size of 0.42 +/- 0.06 ha (95% harmonic mean area) and 0.091 +/- 0.074 ha (core 65% harmonic mean area). *M. cervinipes* did not maintain exclusive home ranges and overlapped with both other focal individuals and other individuals not fitted with tracking devices. There was a relationship between the core range of *M. cervinipes* and individual trees of the dominant canopy species at the site. *M. cervinipes* core ranges included 1.96+/- 0.27 individual trees of those canopy species independent of the area of that core range, whereas the number of individual trees within their total range was proportional to the size of that range. This suggests that *M. cervinipes* set the core of their range to include a specific level of canopy fruiting/flowering resources regardless of the size required to achieve that level, but that their overall range is merely a representative sample of trees from the site. This is not surprising considering *M. cervinipes* captures are correlated with the number of individual flowering *Syzigium sayeri* and *Acmena graveolens* trees (Chapter 3).

Introduction

Many factors influence the size and shape of an animal's home range including climate, food, population density, body size and social organization (Harestad and Bunnell 1979; Tait and Krebs1981; Lindstedt *et al*. 1986). In addition to these general trends, local variations in home range size may be present between and within populations of species. Between species, home range size is governed primarily by body size (Calder 1984; McLoughlin and Ferguson 2000). Within species, habitat quality and food availability can exert a strong influence (Mcloughlin and Ferguson 2000) in addition to sex, social factors and density (Tait and Krebs 1981; McLoughlin and Ferguson 2000).

Habitat quality and food availability can also drive canopy use (Emmons 1995) which in turn, increases an animals usable home range area. The diversity of arboreal and scansorial vertebrates in tropical forests (Kays and Allison 2001) is testament to the high abundance of canopy resources (Emmons 1995). High habitat complexity and heterogeneity in the vertical strata increase microhabitat availability (Malcolm 1995), allowing increased overlap and reduced competition (Schoener 1974; Cameron and Kincaid 1982; Barry *et al*. 1984). Quantifying the extent of arboreal behaviour is therefore important not only for determining home range but also when investigating resource use and/or competition.

The fawn-footed Melomys (*Melomys cervinipes)* is a medium sized (45-110g) murid rodent found in closed forests along the east coast of Australia from central

New South Wales to Cape York Peninsula (Watts and Aslin, 1981). Being an omnivore (Wood 1971), its diet consists of fruits, insects and flowers, however the source of these items is unclear. *M. cervinipes* is semi-arboreal and abundant in the forest canopy (Wood 1971). Arboreal captures have been correlated with the number of flowering *Syzigium sayeri* and *Acmena graveolens* trees (Chapter 3).

Considering resource availability (Lindstedt *et al*. 1986; McLoughlin and Ferguson 2000) and quality (Ferguson and Mcloughlan 2000) can govern spatial use and determine home range size, any conservation planning with respect to reserve diversity, selection or size must account for resource and space use both on the ground and in the vertical dimension. *M. cervinipes* is an ideal model species to explore space and resource use by small mammals because it is common, tree-dwelling and uses canopy resources.

The objectives of this chapter are to consider:

1. The extent and purpose of *M. cervinipes* arboreal activity
2. *M. cervinipes* home range size and whether this differs according to sex, body weight or resource availability
3. The influence of canopy tree diversity on home range area selection

Methods

Extent and purpose of arboreal behaviour and home range using radio-telemetry

Five male and three female *M. cervinipes* were captured using folding Aluminium Elliott traps then fitted with radio-collars weighing approximately 3.0 grams (Titley Electronics, Ballina, Australia). Collared individuals were released at the site of their capture in late morning or early afternoon and then radio-located for the first time at 18:00 on the following day. Individuals were tracked for approximately 25 days with an average of four fixes each night. Nest sites were recorded once each day for the 25-day period. Total sightings ranged from 52-75. Care was taken not to approach too closely (5m) to the radio-collared animals when they were active at night as they are readily disturbed and will run ahead of the observer for as long as followed. The position of each animal was located by triangulation (Saltz, 1994) and the point was recorded using the crane positioning system (degrees, metres) or by tree number on the ground. All trees on the study site (1.4ha) above 10cm diameter at breast height were previously mapped and uniquely identified according to the same crane positioning system (Frieberg 2000).

Home ranges were calculated using the harmonic mean method (Dixon and Chapman 1980) using the computer software RANGES VI (Kenward and Hodder 1995). Core centers of activity were determined by calculating home range sizes from 20-95% harmonic mean and estimating the proportional change for each 5% increment. Core ranges were defined as the isopleth where the incremental proportion increase in range size was minimized (Johnson 1991), i.e. 65% harmonic mean (Figure 1).

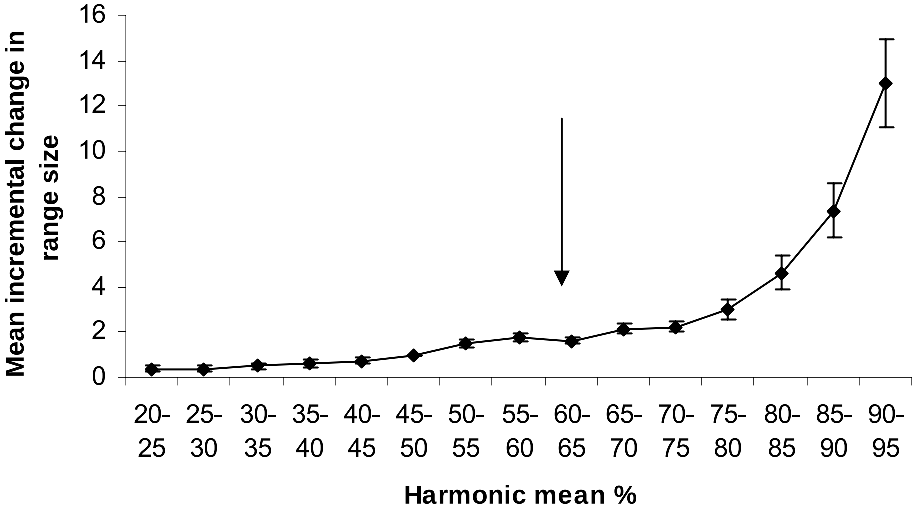

Figure 1: Plot of harmonic mean (%) versus home range area. Harmonic mean (HM) areas were averaged for the 8 individual animals (+SE). The "core" area was considered the 65% harmonic mean as indicated by the arrow.

To determine the number of observations required to define home range size, the cumulative home range area was calculated for randomly selected subsets of locations and plotted against the number of locations. The number of sightings required to fully define the home range was determined from the curves asymptote according to the method of Harris *et al*. (1990).

The influence of sex, weight and resource availability on home range size

The core (65%) and total (95% harmonic mean) home ranges of the eight radio tagged individuals were mapped on the site and the tree species and abundance within the ranges determined.

Canopy tree species diversity index

A tree species diversity index was calculated for each individual home range using Simpson's index of diversity, $D = N (N-1)/\sum n(n-1)$, where N = total number of individuals of all tree species and n = total number of individuals of a particular species.

Results

The extent of arboreal activity

The amount of time spent above ground was highly variable between individuals, ranging from 30-90% of observations occurring aboveground (from 1 to 30 metres, Figure 2).

The purpose of arboreal activity

Nest location

During the tracking session, individuals used 1-2 nest sites (Table 1). Three individuals (616, 524, 545) used two nests. The remaining individuals used only one nest. Both males and females used more than one nest, the second of which was located above-ground. Three of the eight individuals had nests exclusively in the canopy, two nested in the understorey at 0.8 metres and the remaining three on the ground. All individuals had a preferred nest where they were recorded most frequently. Nest sites did not change and individuals were located in their nests in the same location everyday.

All individual nests were sited centrally within that animal's 95% harmonic mean isopleth with the exception of individual 524, whose nests were located on the periphery.

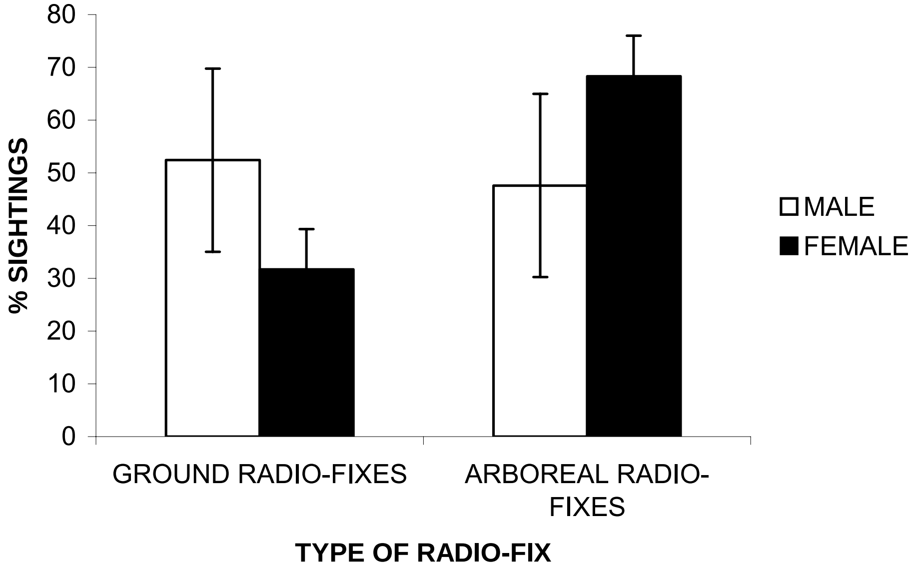

Figure 2: Proportion of time *M. cervinipes* spent both on ground and in canopy for radiotagged period of 4 weeks.

Table 1: Number of nests used by radiotagged individuals, type of nest and height above ground

Individual ID (sex)	Number of nests	Height above ground (m)	Nest description
564 (F)	1	0m	In rock crevice/burrow under ferns
616 (F)	2	0, 14.4m	Nest 1 in buttress roots; nest 2 in dead leaves in tree crown
602 (F)	1	16.6m	In ball of dead leaves in canopy
656 (M)	1	0.8m	In *Calamus sp.*
588 (M)	1	0m	Within buttress roots
634 (M)	1	0	Under woody debris next to buttress roots
524 (M)	2	0, 15m	Nest 1 in rock crevice, nest 2 in basket fern in subcanopy
545 (M)	2	0, 0.7m	Nest 1 in burrow under log; nest 2 within *Calamus sp.*

M. cervinipes were observed feeding in the canopy on 6 occasions throughout the duration of the study (Table 2)

Estimation of home range size and the influence of sex, body weight and resource availability

Overall home range size was estimated using the 95% harmonic mean isopleth. The core area of activity was determined as the 65% harmonic mean isopleth (Figure 1- minimal change from 60-65% isopleth). Core ranges of the focal individuals overlapped (Figure 3), and there were other incidental sightings of un-collared *M. cervinipes* within the area thoughout the study. Six of the eight individuals had only one core area. Two individuals, ID 524 and 545 had two and four core areas respectively (Figure 3).

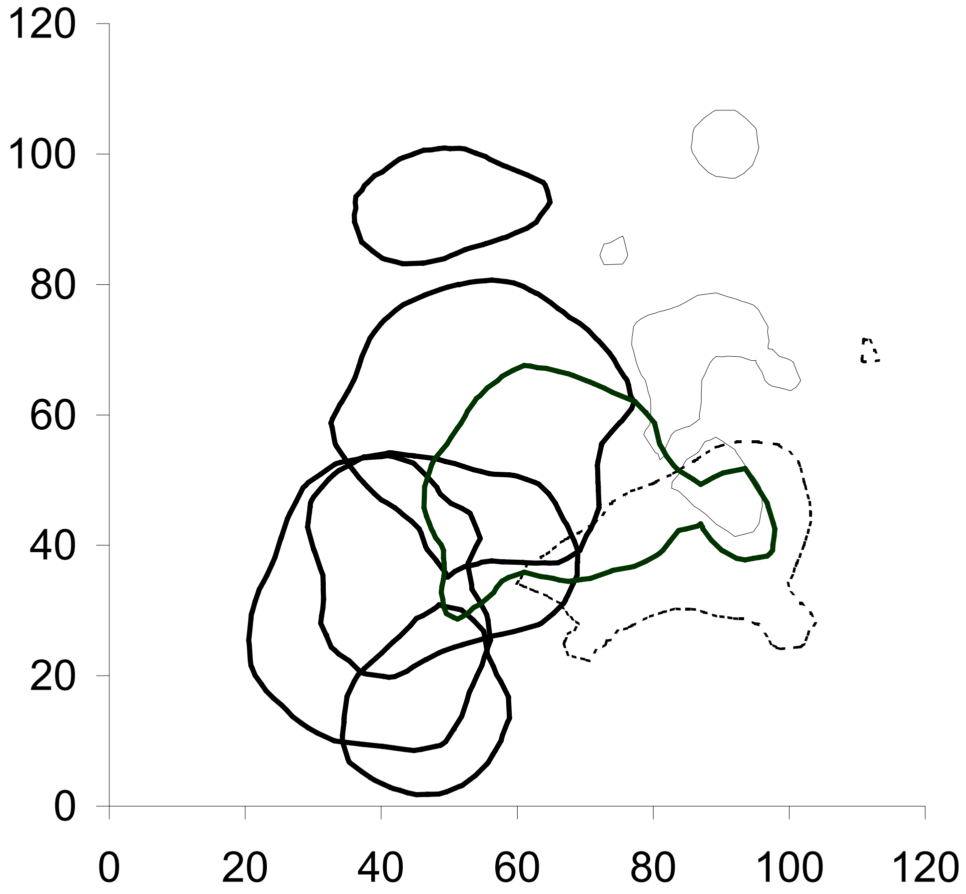

Figure 3: Spatial representation of core (65% HM) home ranges of 8 individuals. Two individuals, ID 524 and 545 (illustrated with fine and dotted lines) had two and four core areas respectively. All other individuals had only one core area (coarse black outline). Spatial organization of core areas for the 8 study animals on a 120 x 120 grid.

Sex and body weight

Male and female range sizes (95% harmonic mean) did not differ significantly (*t* = -0.572, *df* = 6, *P* = 0.973, Table 3). Average home range size was 0.421 (±0.061 SE) ha for 95%harmonic mean and 0.091ha (±0.074 SE) for the core

(65%) harmonic mean. Home range size was not significantly correlated with body weight both for 95% (correlation coefficient = 0.097; *P*=0.820) or 65% harmonic mean area (correlation coefficient = 0.591; *P* =0.123).

Table 2: Observations of *M. cervinipes* feeding activities between May 2002-June 2003. note: On two occasions it was difficult to determine if *M. cervinipes* was consuming flowers or insects.

Height	No. occasions	Resource
15m	2	*Acmena graveolens* fruit pulp
14,17m	2	*Eleocarpus augustifolias* fruits
19m	1	Syzigium sayeri flowers?/insects?
23m	1	Castanospermum australe flowers/insects

Table 3: Home range areas (65% and 95%) harmonic mean, sex and body weight of 8 collared animals and tree species diversity index for each home range.

ID number	Core 65% HM ha	95% HM ha	Sex	Body weight (g)	Simpson's Diversity index (canopy trees)	
					65%HM	95%HM
564	0.07	0.50	FEMALE	64	8.07	6.00
616	0.06	0.21	FEMALE	87	7.09	5.74
602	0.07	0.22	FEMALE	83	0	5.69
656	0.07	0.56	MALE	93	7.00	5.20
588	0.07	0.45	MALE	95	7.06	6.06
634	0.06	0.67	MALE	101	5.08	5.50
524	0.09	0.31	MALE	102	5.60	4.44
545	0.11	0.41	MALE	115	4.88	4.19

Canopy tree species diversity

Tree diversity was negatively correlated with body weight both for the 95% (correlation coefficient = -0.750; *P*=0.032) and 65% harmonic mean areas (correlation coefficient = -0.893; *P* =0.007, Table 3). Home range size was not significantly correlated with tree diversity for either 95% (correlation coefficient = 0.077; *P*=0.857) or 65% harmonic mean (correlation coefficient = 0.064; *P*=0.879, Table 3) areas.

Resource Availability

The 95% harmonic mean home range area increased linearly with (and therefore dependent on) the number of canopy trees (slope =0.70, R^2=0.497, *P*=0.05) but for the 65% harmonic mean home range, the number of canopy trees remained the same with increasing core 65% harmonic mean area (Slope =0.002, R^2=0, *P*=0.996). This means that in core areas (65% HM), *M. cervinipes* home ranges encompass a similar number of canopy trees, irrespective of area size.

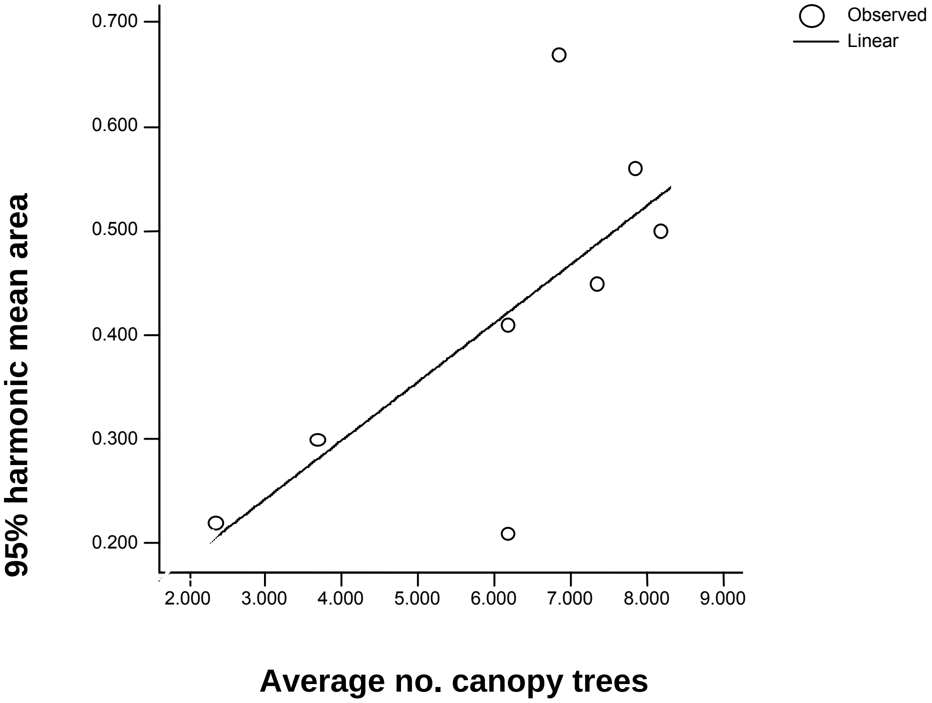

Figure 4: The relationship between home range area (95% harmonic mean) and the number of canopy trees (slope=0.70, R^2=0.497, *P*=0.05).

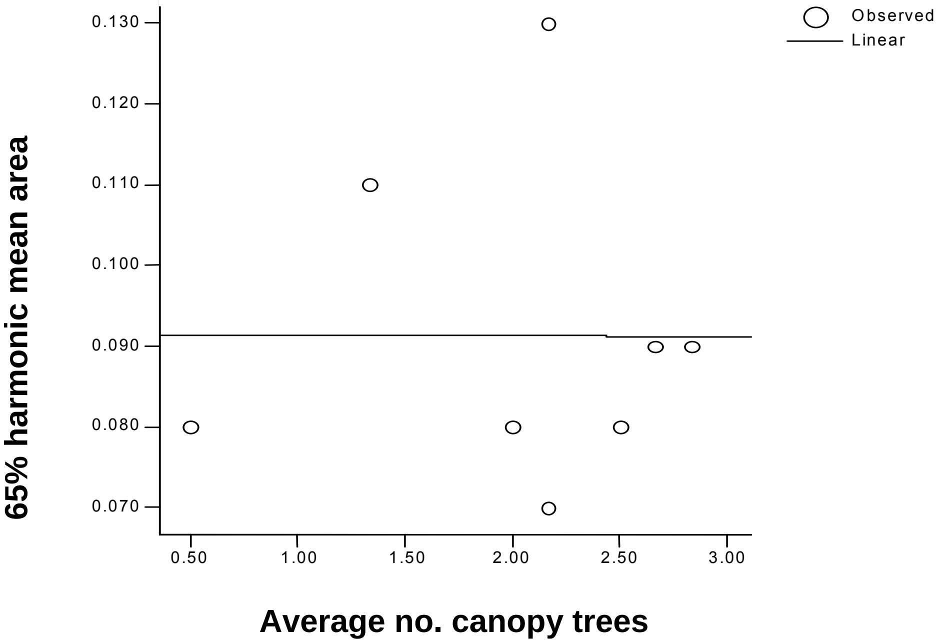

Figure 5: The relationship between home range area (65% harmonic mean area) and the average number of canopy trees (slope =0.002, R^2=0, *P*=0.996).

Discussion

Arboreal activity

Arboreal activity differed between individuals but there were no significant sex differences. In this study, possible reasons for arboreal behaviour include nesting locations and feeding preferences. The ability to access the canopy allows *M. cervinipes* to exploit resources that are either unavailable to (nesting sites) or available before (fruits/flowers/nuts), its terrestrial competitors. *M. cervinipes* individuals were observed in the canopy on many occasions (Rader pers. obs.), however specific details on feeding preferences or social activities were difficult to obtain, due to their sensitivity to disturbance, their small size and their preference for bushy tree crowns. Nest sites were diverse, ranging from burrows under root systems to canopy leaf balls, and despite the high degree of arboreal activity less than 30% were situated in the canopy.

Home Range Size

Home range size determined in this study was similar to that of Wood (1971) who found ranges were approximately 50 m across (i.e. 0.25ha). However Wood (1971) calculated ranges based on trapping records so they are not closely comparable with this study.

In utilizing an area as their home range, enough resources including food shelter and mates would need to be available for individual survival and reproduction requirements (Maitz and Dickman 2001). Canopy trees are most likely an important resource. On the study site at least one species of canopy tree is flowering or fruiting in each month of the year (Howlett pers. comm.). In this study *M. cervinipes* was observed feeding and nesting (Tables 2 and 3) in canopy trees and was more frequently trapped at times coinciding with the flowering of *Syzygium sayeri* and *Acmena graveolens*. All but one of the core home ranges overlap, as well as with other unmarked *M. cervinipes*, so the resources within core areas provide adequate resources for more than one individual *M. cervinipes*.

Territorial behaviour has previously been observed in *M. cervinipes* (Redhead 1995), however, in this study there was no indication of territorial exclusion, so it is unclear if social constraints influenced the differentiation of, and access to resources among individuals. The relationship between territory size and body size has been documented for many mammals (Calder 1984; McLoughlin and Ferguson 2000). However, body weight was not found to influence *M. cervinipes* home range size for both 95% and 65% harmonic mean areas. This suggests the larger (presumably more dominant) individuals do not necessarily occupy larger territories or exclude smaller individuals from high resource areas. Other studies in taiga (Smith and Schaefer 2002) and deciduous woodland (Soutiere 1979), established that subordinate individuals occupy larger home ranges enclosing unfavourable habitat. This may explain the lack of correlation between home range size and body weight in this study, as although rainforest resources are abundant year-round (Emmons 1995), they tend to be patchy in distribution (Julien-Laferriere 1999).

Larger total (95% harmonic mean) home ranges enclose more canopy trees within their boundaries (Figure 4) but a larger home range size and more canopy trees may not necessarily imply best quality resources or most productive areas. Resource quality influences home range size (Lindstedt *et al*. 1986; McLoughlin and Ferguson 2000) so perhaps territorial behaviour may be in response to competition for resource quality. If this is the case, one would expect the home ranges of larger (more dominant) individuals to encompass the more productive resources, which may actually be contained within smaller home ranges (Ferguson and Mcloughlan 2000).

The most productive trees or selection of trees may more effectively delineate home range (Wauters and Dhondt 1992; Wunderle 1995; Relyea *et al*. 2000). The relationship between core 65% harmonic mean area and the number of canopy trees (Figure 5) supports this, suggesting individuals may be occupying core home ranges based on the number of canopy trees as opposed to the size of ranges. If this is the case, then canopy trees may be an important resource that limits the abundance/distribution of *M. cervinipes.* Core range size seems to depend on including a minimum number of canopy trees. Core home ranges of all rats consisted of an average of 2 individual canopy trees (range 2-6) of the same or different species. Canopy trees are a resource used by *M. cervinipes*.

Flowering and fruiting of canopy trees is staggered throughout the year so there may be only a few species flowering/fruiting concurrently. To ensure a year-round supply of resources therefore, one would expect an assortment of different species to be preferable as opposed to numerous trees of the same species within a home range. Consequently, one would expect range size to be negatively related to canopy diversity. In addition, if one assumes canopy trees are an important resource to rodents, greater tree species diversity within a home range would result in less energy expended traveling to obtain year round resources. The significant negative correlation between tree species diversity and body weight suggests larger individuals are occupying areas with lower canopy tree species diversity. Resources other than canopy trees may affect this relationship. Areas with fewer canopy tree species often contain dense layers of subcanopy/ understorey/vine species, which could result in more insects and/or more cover from predators.

More detailed data with respect to rodent resource preferences, spatial and temporal distribution of resources within home ranges and territorial behaviour are needed to clarify these relationships further. Anecdotal observations suggest other understorey plants and vines were fruiting and flowering but were not recorded in detail in the present study. The core home range consisted of only a few canopy trees per animal, so other vegetation layers may prove to also be important indicators of rat home range size.

CHAPTER 6: SUMMARY AND CONCLUSIONS

Vertical distribution of arboreal/scansorial mammals

Biodiversity estimates are inaccurate if arboreal species are overlooked

Assessing biodiversity is an essential step in establishing conservation priorities in environmental management and facilitates informed decision-making. Species diversity is the most basic unit of data collection in this process. When arboreal/scansorial mammal species are present, failure to trap in the canopy may result in underestimates of diversity or the complete exclusion of some species. These inaccuracies could result in the application of inappropriate conservation status or management strategies that are neither comprehensive or adequate.

A tropical rodent assemblage is vertically stratified.

Vertical stratification has been demonstrated for many faunal assemblages including birds, bats, reptiles and mammals (Fonseca and Kierulff 1989, Stallings 1989, Woodman *et al*. 1995). It is a strategy by which many species can coexist due to the many niches created, thereby reducing interspecific competition (Schoener 1974, Cameron and Kincaid 1982, Barry *et al*. 1984).

In this study, all four height strata contained differing assemblages of between 3 and 6 small mammal species. Although previous studies suggested arboreal activity by several of these species, the extent of arboreal behaviour of *M.*

cervinipes and *U. caudimaculatus* has never been quantified. In fact results from this study suggest both species more commonly use strata above ground. In addition, this study demonstrated that the failure to trap the prehensile-tailed rat in the past is not wholly because it is rare or uncommon but because it most frequently uses canopy strata and is therefore unlikely to be captured in the usual ground-level trapping studies.

The relationship between rodents, resources and flowering canopy trees

In the attempt to relate rodent abundance and activity with canopy resources, this study compared the amount of flowers, fruits and new foliage around each trap site with trapping records. There was no significant relationship. However, the captures of two canopy using rodents (*M. cervinipes* and *P. mollipilosus*) were correlated with the number of flowering canopy tree species suggesting that arboreal space use may be driven by canopy resource availability, at least in these two species.

The influence of consumption by rodents, presence of beetle larvae and seed size on the germination success of *A. graveolens* seeds

Relationship between A. graveolens, beetles and rodents

There was an interaction between rodent removal of fruit pulp and beetle presence on the germination success of *A. graveolens* seeds.

Removal of fruit pulp may enhance germination success due to the removal of a germination inhibitor. This could function to increase the chances that the fruit has been dispersed before germination. When beetles were present in the fruit pulp, the results seemed to show the opposite effect, i.e. those fruits with the greatest pulp had the higher germination success. However, beetle damage was assessed before seeds were placed in the greenhouse and at this time, beetles were still actively eating pulp (pers. obs.). This probably resulted in beetles continuing to eat the pulp for the remainder of the study, resulting in a similar effect to rodent predation, ie, germination inhibitors are removed in fruit pulp.

Seed size and its effects on beetle presence, pulp remaining and germination

Germination success, the amount of pulp remaining on fruits and the number of fruits with beetle holes all increased with seed size. Larger seeds often have higher germination success due to greater energy stores (Foster 1986; Howe 1990). However, the interaction between the proportion of pulp remaining and seed size is most likely due to rodent preference or competency handling. Large seeds had the most pulp remaining and small seeds the least, probably because a majority of the rodents are medium sized (60-100grams) and probably have greater difficulty handling larger fruits.

Larger seeds with more pulp reflect a more abundant resource for the beetles that consume *A. graveolens* fruit pulp, leading to the positive relationship between seed size and beetle presence.

Pulp consumers under natural conditions

Rodents were the main consumers of *A. graveolens* fruit pulp. However, several other vertebrates also ate the fruits/seeds including cassowaries, pigs, bats and bandicoots.

Spatial use by *M. cervinipes*, a tropical rainforest rodent

Arboreal behaviour and resource use

M. cervinipes is a scansorial rodent utilizing the canopy for nesting and feeding. Observations and radio-tracking results suggest dominant canopy trees are an important resource for both nesting and feeding purposes, which most likely explains the frequent use of above-ground strata.

M. cervinipes home range size has been estimated by live trapping (Wood 1971) to be about 0.25ha (50 x 50 m) and in the current study was estimated to be about 0.42 ha (95% harmonic mean percentile).

Canopy trees provide important food and nesting resources for *M. cervinipes*. Core home range sizes of the eight individuals were related to the number of canopy trees within each home range area.

Conclusions: ecological implications of this study

The removal of pulp from *Acmena graveolens* fruits by rodents may enhance germination success and thus be an important ecological process affecting recruitment of seedlings. Rodent activity also increases the likelihood of seeds entering the dispersal process (if carried away or cached). The significance of dispersers of large-seeded fruits in enhancing recruitment and maintaining diversity has been previously noted (Janzen 1971, Schupp 1988, Willson and Whelan 1990, Forget 1993, Theimer 2001) however this study suggests that smaller pulp consumers may play a similar role. The spatial and temporal distribution of tropical rainforest trees is therefore better understood when in relation to the use of space and resources by its resident rodent population.

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