Copyright in relation to this thesis

Under the Copyright Act 1968 (several provisions of which are referred to below), this thesis must be used only under the normal conditions of scholarly fair dealing for the purposes of research, criticism or review. In particular no results or conclusions should be extracted from it, nor should it be copied or closely paraphrased in whole or in part without the written consent of the author. Proper written acknowledgement should be made for any assistance obtained from this thesis.

Under Section 35(2) of the Copyright Act 1968 'the author of a literary, dramatic, musical or artistic work is the owner of any copyright subsisting in the work'. By virtue of Section 32(1) copyright 'subsists in an original literary, dramatic, musical or artistic work that is unpublished' and of which the author was an Australian citizen, an Australian protected person or a person resident in Australia.

The Act, by Section 36(1) provides: 'Subject to this Act, the copyright in a literary, dramatic, musical or artistic work is infringed by a person who, not being the owner of the copyright and without the licence of the owner of the copyright, does in Australia, or authorises the doing in Australia of, any act comprised in the copyright'.

Section 31(1)(a)(i) provides that copyright includes the exclusive right to 'reproduce the work in a material form'. Thus, copyright is infringed by a person who, not being the owner of the copyright, reproduces or authorises the reproduction of a work, or of more than a reasonable part of the work, in a material form, unless the reproduction is a 'fair dealing' with the work 'for the purpose of research or study' as further defined in Sections 40 and 41 of the Act.

Section 51(2) provides that "Where a manuscript, or a copy, of a thesis or other similar literary work that has not been published is kept in a library of a university or other similar institution or in an archives, the copyright in the thesis or other work is not infringed by the making of a copy of the thesis or other work by or on behalf of the officer in charge of the library or archives if the copy is supplied to a person who satisfies an authorized officer of the library or archives that he requires the copy for the purpose of research or study'.

"Thesis' includes 'treatise', dissertation' and other similar productions.

D PATTERSON
2.2.99
FIRE, RESOURCE LIMITATION AND SMALL MAMMAL POPULATIONS IN COASTAL EUCALYPT FOREST

ELIZABETH F. SUTHERLAND

A thesis submitted for the degree of Doctor of Philosophy in the School of Biological Sciences, University of Sydney, July 1998.

fac. of Sc.
STATEMENT OF RESPONSIBILITY

This thesis is my own original work, except where specifically acknowledged.

Liz Sutherland

Liz Sutherland
31 July 1998
ABSTRACT

In this thesis I examine the effect of fire on small mammals, and investigate in particular the responses of small mammals to post-fire resource availability and fire regime. Specifically this study aims to i) identify patterns of plant, invertebrate and small mammal richness and abundance under different fire frequency regimes, ii) determine the immediate response of small mammals to fire by measuring fire-induced mortality and shifts in use of micro- and macrohabitat, and iii) quantify the responses of the small mammal community responses of the constituent species populations to food and nest site availability in dry sclerophyll forest affected by bushfire. This study was conducted in Ku-ring-gai Chase National Park, New South Wales, 48% of which was burnt by high intensity bushfire on 7 January 1994.

Fire frequency was investigated to determine if site history is a factor influencing patterns of faunal and floral response to single fire events. In this study, replicate sites representing a 20-year history of 1, 2, 3, and 4 fires, and having a consistent time since previous fire, were studied to determine if patterns in vegetation, invertebrate and small mammal abundance and richness could be determined. The investigation was first conducted in 1996 and repeated in 1997.

Sites with higher fire frequency were associated with greater herb cover and lower numbers of shrub stems. Shrub cover also decreased with increasing fire frequency although, with increasing time since fire, there was a tendency for shrub cover to even out across fire frequency treatments. Neither the average maximum height of the shrub layer, nor the rate of regrowth, differed between fire frequency treatments.

The total abundance and ordinal richness of invertebrates did not vary significantly in response to fire frequency, and neither abundance nor ordinal richness was correlated reliably to any of the measured vegetation or rock characteristics. The patterns of response of invertebrate Orders varied. Hymenopterans, specifically Formicidae, were the most abundant group, and were in similar numbers in sites with a history of 1, 3 and 4 fires, but were less abundant in 2-fire sites. Collembolans demonstrated a pattern of decreasing
abundance with increasing fire frequency from 1 to 3 fires. Orthopterans and araneans were most abundant at sites with a history of 3 fires. Discrimination of animals at a lower taxonomic level, such as family or morphospecies, may have allowed variability in the assemblages of species between treatments to be clarified.

The response of small mammal populations to fire frequency appeared to be associated with the effects that fire frequency had on the vegetation cover, however, no causal relationships were identified. The abundance of *Rattus fuscipes* in 1996, 2 years after the 1994 fire, tended to be higher in sites with a 1 or 2 fires than in sites with 3 or 4 fires, although the difference between treatments was not statistically significant. By 1997, however, there were more individuals present in 4-fire sites than in other treatments. This change in pattern was not correlated with any measured vegetation or abiotic variable. The population structure, with regards to sex ratio and proportion of juveniles in the population, did not vary significantly between treatments.

The abundance of *Antechinus stuartii* tended to increase in response to increasing fire frequency from 1 to 3 fires, but declined in the 4-fire treatment sites. These responses were not significant and were not correlated with any of the measured vegetation, rock or invertebrate abundance and richness variables. Population dynamics did not vary in response to fire frequency.

The immediate individual responses of *R. fuscipes* and *A. stuartii* to fire were investigated using radio-tracking before and after a low-intensity prescribed fire. There was no confirmed mortality of animals as a result of this fire. Weight loss of both *A. stuartii* and *R. fuscipes* individuals during the month after the fire indicate that food resources, or opportunities for foraging, may have been limiting.

Radio-tracking indicated that *A. stuartii* moved through both burnt and unburnt forest during the post-fire period, although unburnt forest was preferred. Most individuals visited the unburnt forest regularly, and capture records indicate that within the burnt forest *A. stuartii* roamed at least 13 m from the nearest patch of unburnt vegetation. The fire appeared to allow the colonisation of the introduced species *Mus domesticus* and *Rattus*
norvegicus into the forested areas, although individuals were captured only in unburnt patches, and then only infrequently.

The Ku-ring-gai Chase small mammal community appeared to respond to the 1994 bushfire in the following way. Before the fire, as indicated by trapping in unburnt sites, R. fuscipes and A. stuartii were present in high numbers. After the fire, the abundance of these two species remained several times higher than that of other small mammal species, and this dominant position in the community probably excluded the effective establishment of most other species in the early seral stages by competitive advantage. M. domesticus and Cercartetus namus colonised around 16 months after the fire, although once present, M. domesticus established quickly whereas C. namus did not become established until the end of 1995. Populations of M. domesticus did not reach the high abundances or plague conditions previously recorded. Petaurus breviceps and Rattus rattus were both recorded sporadically during the same year. Two years after the fire the first Isoodon obesulus were captured, and three years after, during the last trapping session, Perameles nasuta and Rattus lutreolus were recorded for the first time.

Populations of R. fuscipes were lower in burnt control sites than in unburnt sites, although the mechanisms producing this difference remain unclear. The body condition, reproductive activity, proportion of males to females and the trap-revealed longevity of permanent residents did not differ significantly between burnt control and unburnt sites. More transient individuals were recorded in burnt than unburnt sites.

Within the burnt resource (food, nest site) supplementation sites, there was an initial increase in R. fuscipes abundance in response to food addition, concomitant with improved body condition during May and August 1995 in food supplementation sites. The response was not sustained, however, and neither food nor nest addition had a significant effect on the abundance of R. fuscipes populations over the duration of the study. Resource supplementation led to increased population stability with more permanent residents and fewer transients in experimental than in control sites. There was a higher proportion of female R. fuscipes at sites with food and nest supplementation, and higher juvenile recruitment into experimental sites during the first year of supplementation.
Naturally occurring habitat or vegetation features were not associated consistently with *R. fuscipes* abundance. During 1995, *R. fuscipes* abundance was related positively to an absence of ground vegetation and to the presence of cover above 100 cm. This pattern was reversed the following year with a significant positive association with vegetative cover between 21 and 100 cm in height. *R. fuscipes* abundance was related negatively to the number of trees or logs at trap stations, but positively to the proportion of trees with hollows.

The abundance of *A. stuartii* was not altered greatly by fire. The average maximum abundance reached by *A. stuartii* during the study was roughly equivalent in burnt control and unburnt sites, although the average minimum abundance was lower in burnt control than in unburnt sites. Body condition, the proportion of females to males, and the relative proportion of transients, residents and permanent residents did not differ between burnt control and unburnt sites. There was no significant difference in the longevity of permanent residents in burnt and unburnt sites.

Food supplementation led to significant increases in *A. stuartii* during 1995, but seemed, paradoxically, to cause a decrease in abundance over the duration of the study. Within the burnt treatment sites, the abundance of *A. stuartii* at food only and food and nest supplementation sites increased during 1995, relative to the nest only and control sites. During the second year of supplementation, however, abundance was most similar between food only and nest only sites; sites with both food and nest supplementation were similar to control sites. The effect of resource supplementation appeared to diminish over time, with some evidence that as populations increased in response to food, nest availability became a limiting factor.

Interestingly, food supplementation appeared to affect the social structure of *A. stuartii* by reducing dispersal and increasing longevity of males within food supplementation sites. The longevity and recruitment of females did not vary in response to the experimental treatments.

The abundance of *A. stuartii* was not associated consistently with any ground cover, vegetative cover or microhabitat variables. Patterns of association appeared to reflect
patterns of post-fire regrowth. During 1995, abundance was associated negatively with the presence of a dense canopy, but related positively to the presence of cover between 100 and 200 cm in height. In 1996 and 1997, *A. stuartii* abundance was related positively to vegetative cover above 100 cm in height, and also, in contrast to 1995, to canopy cover.

Populations of *M. domesticus* did not vary significantly in response to food and nest supplementation. However, the two sites where *M. domesticus* was able to establish breeding populations were food supplementation sites. *M. domesticus* demonstrated a significant preference for areas of bare ground and a negative association with leaf litter, trees and logs. It was the combination of the availability of bare ground and supplementary food that led to the highest numbers of *M. domesticus*, and the establishment of populations.

The low capture rate of *C. nanus* made it difficult to identify trends in post-fire population response. *C. nanus* was not associated consistently with ground cover, vegetative or habitat features. Although *C. nanus* was recorded in greatest numbers at sites provided with supplementary food, the highest capture rates occurred when local food trees, with inflorescences close to the ground, were blooming. The possibility of food addition altering the trappability of this species is discussed.

Overall, this study suggests that patterns of small mammal population recovery after fire are not driven solely by resources. I propose that differences in community and population responses to fire, reported in this and other studies, are likely to be a result of interspecific competition within a species pool unique to each study site.
ACKNOWLEDGMENTS

Firstly, I would like to thank my parents, Don and Marg Sutherland, for introducing me to the Australian bush. Despite my protests, at some point I started to enjoy it. Their constant support, interest, and encouragement, throughout this project and my whole life, has been fantastic. I can’t begin to express how much I admire them. They also proved to be excellent proof readers and grammar correctors, although, mum, put, in, commas, everywhere, and dad took them all out again.

My friends have been my saviour during this project. Their ability to distract me has been a blessing (although has slowed the process down somewhat). Although some have never really understood what I do or why (“Did you say RATS?”, “What is that disgusting smell in your car?”, “What’s with all this peanut butter?”), they continue to associate with me. Specifically I would like to thank the lab. I could not have hoped for a funnier or more entertaining group of people to share a confined space with for 4 years. Gayle’s anti-co-ordination, Paul’s nudity, Bobby’s hairstyles, Al’s missing teeth, Pete shooting the car, I could go on and on. Outside the uni group, Clare and Tex have always known the answer to my problems (the answer is usually beer), and my school-days friends have always brought me back down to earth (again, usually with beer). Although I can’t mention everyone here, I hope they all know how much they mean to me.

This project was made possible by the help of many field assistants who volunteered to come out with me for periods ranging from days to weeks. In a roughly chronological order I would like to thank Simon Letchford, Clare Murphy, Ian “Tex” Beer, Robyn Staples, Jay Beh, Paul Mahon, Olivia Crowe, Alistair Glen, Bobby Tomayo, Hani Peri, Dave Jones, Sharon Roach, Marianne Ympa, Eric Backpacker, Shaan Gresser, Binghi Cameron, Jason Errey, Jayne Foster, Kirsty Milner, Claire Goldsborough, Ben Stewart, Danielle O’Connor, Peter Banks, Gayle McNaught, Ricky Spencer, Rebecca Drury, Lorena Gwyther, Trina Carney, Bethia Thomas, Nicholas Ogden, Stuart Godwin, Susan Davis, Rhys Blackmore, Angela Dunnett, Sasha Curthoys, Jennie Crosby, Adele Reid, Michelle Cox, Matt Curran, Nicholas Digges, Nerida Williams, Wendy Maitz, Ben Simpson, Kerry Mooring, Lara Hess, Kylie Robert, Samantha Davis, Bill Vickery, Jeremy Little, Adele
Haythornthwaite, Rowena Hayes, Anne Sutherland, Marg Sutherland and Don Sutherland. Special thanks to Shaan, Rowena and Simon who practically had to swim around my sites during thunderstorms.

A big, Coopers-encrusted, thanks goes to my supervisor, Chris Dickman, who has the ability to turn mountains back into molehills, and then stomp on the molehills until they disappear altogether. He has been an absolute inspiration. Shame about the Dickman-curse! I should have known that all my results would be non-significant - I could have saved a lot of time and peanut butter if I’d accepted it from the outset.

Other people who were invaluable to this project include Ross Bradstock and Peter Myerscough who provided pieces of planty, and other, advice. Alistair Glen was essential to the field work, and never complained! Bobby Tomayo helped countless times in the field and sorted through many invertebrate pitfalls. Warwick Angus gave names to invertebrate "unknowns". Anthony Ferguson kept me out of the way of the prescribed fire. Steve Cox produced the maps (again and again). Paul Mahon sorted out my mathematical shortcomings. Zootech (Ralph, Kylie and George) found and fixed equipment, as well as chasing the odd pigeon out of my office. Peter Banks, Dieter Hochuli, Gayle McNaught, Don Sutherland, Marg Sutherland and Chris Dickman made comments on earlier drafts of this thesis.

Finally, I want to thank Simon Letchford, my partner during this whole process. His patience and understanding are exceptional. His humour and love are priceless. I’m sorry it took so long!
CONTENTS

ABSTRACT i
ACKNOWLEDGMENTS vi
CONTENTS viii
FIGURES xv
TABLES xviii

CHAPTER 1: MECHANISMS OF RECOVERY AFTER FIRE OF AUSTRALIAN SMALL MAMMALS: A REVIEW AND SUGGESTIONS FOR FURTHER RESEARCH

1.1 INTRODUCTION 1

1.2 IMPACT OF FIRE ON SMALL MAMMALS 1

1.2.1 REDUCED POPULATION NUMBERS 1

1.2.2 REDUCED RESOURCE AVAILABILITY 4

1.2.2.1 Food 4

1.2.2.2 Cover 7

1.2.2.3 Nest sites 11

1.2.3 INCREASED COMPETITION 12

1.2.4 INCREASED PREDATION 14

1.2.5 REDUCED INDIVIDUAL FITNESS 16

1.2.6 SUMMARY OF THE EFFECTS OF FIRE ON SMALL MAMMALS, MECHANISMS OF RECOVERY AND RECOMMENDATIONS FOR FUTURE RESEARCH 17

1.3 RESOURCE MANIPULATION STUDIES 18

1.3.1 Food supplementation 18

1.3.2 Cover supplementation 21

1.4 AIMS OF THIS STUDY 22

CHAPTER 2: STUDY SITE DESCRIPTION

2.1 INTRODUCTION 24

2.2 GEOLOGY AND GEOGRAPHY 24

2.3 VEGETATION 25

2.4 FIRE HISTORY: PRE-EUROPEAN SETTLEMENT 27

2.5 FIRE HISTORY: POST-EUROPEAN SETTLEMENT 29

2.6 KU-RING-GAI CHASE NATIONAL PARK: RECENT FIRE HISTORY 30

2.7 CONCLUSION 31
CHAPTER 3: **Effect of Fire Frequency on Vegetative Cover, Terrestrial Invertebrate Abundance and Richness, and Small Mammal Abundance in Ku-ring-gai Chase National Park**

3.1. **Introduction**

3.1.1 **What is Fire Frequency?**

3.1.2 **The response of vegetation to frequent fire**

3.1.3 **The response of invertebrate fauna to frequent fire**

3.1.4 **The response of vertebrate fauna to frequent fire**

3.1.4.1 **Birds**

3.1.4.2 **Mammals**

3.1.4.3 **Reptiles**

3.1.4.4 **Amphibians**

3.1.5 **Aims**

3.2 **Methods**

3.2.1 **Site selection and establishment**

3.2.2 **Data collection**

3.2.2.1 **Vegetation and rock**

3.2.2.1.1 **Herb, shrub and rock cover**

3.2.2.1.2 **Tree cover**

3.2.2.1.3 **Data analysis**

3.2.2.2 **Terrestrial invertebrates**

3.2.2.2.1 **Data collection**

3.2.2.2.2 **Data analysis**

3.2.2.3 **Small mammals**

3.2.2.3.1 **Trapping and handling**

3.2.2.3.2 **Data analysis**

3.3 **Results**

3.3.1 **Vegetation patterns**

3.3.1.1 **Cover of shrubs, herbs and rock**

3.3.1.2 **Number of trees and canopy cover**

3.3.2 **Invertebrates**

3.3.2.1 **Abundance**

3.3.2.2 **Richness**

3.3.2.3 **Invertebrate abundance and richness in relation to vegetation and rock cover**

3.3.3 **Small mammals**

3.3.3.1 **Abundance and population structure of *Rattus fuscipes***

3.3.3.1.1 **Rattus fuscipes** population estimates

3.3.3.1.2 **Rattus fuscipes** response to vegetation and rock cover
3.3.3.1.3 *Rattus fuscipes* response to invertebrate abundance and richness 61

3.3.3.2 Abundance and population structure of *Antechinus stuartii* 62

3.3.3.2.1 *Antechinus stuartii* population estimates 63

3.3.3.2.2 *Antechinus stuartii* response to vegetation and rock cover 63

3.3.3.2.3 *Antechinus stuartii* response to invertebrate abundance and richness. 64

3.3.4 Summary of results 64

3.4 Discussion 66

3.4.1 Vegetation 66

3.4.2 Terrestrial invertebrates 67

3.4.3 Small mammals 69

3.4.4 Conclusions 74

CHAPTER 4: Immediate responses of small mammals to fire

4.1 Introduction 76

4.1.1 Aims 77

4.2 Methods 77

4.3 Results 80

4.3.1 Habitat 80

4.3.2 Trapping and radio-tracking 81

4.3.4 Summary of results 83

4.5 Discussion 84

4.5.1 Immediate responses of small mammals to low intensity fire 84

4.5.2 Logistical and methodological problems in studying fire 87

4.5.3 Conclusions 90

CHAPTER 5: Response of a small mammal community to resource availability after fire

5.1 Introduction 92

5.1.1 Aims 94

5.2 Methods 94

5.2.1 Site selection and establishment 95

5.2.2 Resource manipulation 95

5.2.2.1 Food availability 96

5.2.2.2 Nest availability 98

5.2.3 Data collection 99

5.2.4 Data analyses 99

5.3 Results 100
### Chapter 6: Population Responses of *Rattus fuscipes* to Resource Availability After Fire

#### 6.1 Introduction

6.1.1 Aims

#### 6.2 Methods

6.2.1 Experimental Design and Data Collection

- 6.2.3.1 Small Mammals
- 6.2.3.2 Vegetation
- 6.2.3.3 Microhabitat

6.2.2 Data Analyses

- 6.2.4.1 Small Mammals
- 6.2.4.2 Ground Cover and Vegetation
- 6.2.4.3 Microhabitat

#### 6.3 Results

6.3.1 Population Dynamics in Unburnt Sites

6.3.2 Population Dynamics in Burnt Sites

- 6.3.2.1 Abundance
- 6.3.2.2 Body Condition
- 6.3.2.3 Population Structure
- 6.3.2.4 Reproductive Responses

6.3.3 Population Response to Natural Resource Availability

- 6.3.3.1 Ground Cover
- 6.3.3.2 Vegetative Cover
- 6.3.3.3 Habitat Components

6.3.4 Summary of Results

#### 6.4 Discussion

6.4.1 Effect of Fire on *Rattus fuscipes* Populations

6.4.2 Effect of Resource Availability on *Rattus fuscipes* Populations After Fire

117
120
120
121
122
123
123
124
125
126
126
126
131
131
135
138
141
144
144
146
151
151
153
153
157
6.4.2.1 Food 157
6.4.2.2 Nests 160
6.4.2.3 Food and Nests 161
6.4.3 Conclusions 162

CHAPTER 7: Population responses of Antechinus stuartii to resource availability after fire

7.1 Introduction 164
7.1.1 Aims 167
7.2 Methods 168
7.3 Results 168
7.3.1 Population dynamics in unburnt sites 168
7.3.2 Population dynamics in burnt sites 173
7.3.2.1 Abundance 173
7.3.2.2 Body condition 175
7.3.2.3 Population structure 179
7.3.2.4 Reproductive responses 182
7.3.3 Population responses to natural resource availability 183
7.3.3.1 Ground cover 184
7.3.3.2 Vegetative cover 184
7.3.3.3 Habitat components 184
7.3.4 Summary of results 184
7.4 Discussion 186
7.4.1 Effect of fire on Antechinus stuartii populations 186
7.4.2 Effect of resource availability on Antechinus stuartii populations after fire 188
7.4.2.1 Food 188
7.4.2.2 Nests 192
7.4.2.3 Food and Nests 193
7.4.3 Conclusions 193

CHAPTER 8: Population responses of Mus domesticus to resource availability after fire

8.1 Introduction 194
8.1.1 Aims 197
8.2 Methods 197
8.2.1 Experimental design and data collection 197
8.3 Results 197
8.3.1 Population dynamics in burnt sites 197
8.3.1.1 Abundance 197
8.3.1.2 Body condition
8.3.1.3 Population structure
8.3.1.4 Reproductive responses
8.3.2 Population responses to natural resource availability
8.3.2.1 Ground cover
8.3.2.2 Vegetative cover
8.3.2.3 Habitat components
8.3.3 Competitive interactions with other small mammal species
8.3.3.1 Species associations?
8.3.4 Summary of results

8.4 Discussion
8.4.1 Effect of resource availability on Mus domesticus populations after fire
8.4.2 Effect of interspecific interactions on Mus domesticus populations after fire
8.4.2.1 Predation
8.4.2.2 Competition
8.4.3 Conclusions

Chapter 9: Population responses of Cercartetus nanus to resource availability after fire
9.1 Introduction
9.1.1 Aims
9.2 Methods
9.2.1 Experimental design and data collection
9.3 Results
9.3.1 Population dynamics in burnt sites
9.3.1.1 Abundance
9.3.1.2 Body condition
9.3.1.3 Population structure
9.3.1.4 Reproductive responses
9.3.2 Population responses to natural resource availability
9.3.2.1 Ground cover
9.3.2.2 Vegetative cover
9.3.2.3 Habitat components
9.3.3 Summary of results
9.4 Discussion
9.4.1 Effect of resource availability on Cercartetus nanus populations after fire
9.4.2 Habitats of Cercartetus nanus
9.4.3 Conclusions

Chapter 10: General Discussion

10.1 Individual, Population and Community Responses of Small Mammals to Fire
  10.1.1 Fire Regime as a Determinant of Responses of Small Mammals to Fire
  10.1.2 Responses of Individual Small Mammals to Fire
  10.1.3 Responses of Small Mammal Communities to Fire
  10.1.4 Responses of Small Mammal Populations to Fire

10.2 Why Are the Results from This Study Different from Those Expected?
10.3 Conclusions

References
FIGURES

Figure 2.1: Map of Ku-ring-gai Chase National Park showing the Lambert Peninsula (West Head) and Bobbin Head.

Figure 3.1: Site location and fire frequency history of Ku-ring-gai Chase National Park.

Figure 3.2: The average number of pre-fire shrub stems per quadrat, in sites of 1, 2, 3, and 4 fires within the last 20 years.

Figure 3.3: The average height of shrub vegetation, in sites of 1, 2, 3, and 4 fires within the last 20 years.

Figure 3.4: Average score for shrub cover, in sites of 1, 2, 3, and 4 fires within the last 20 years.

Figure 3.5: Average cover score for herb cover, in sites of 1, 2, 3, and 4 fires within the last 20 years.

Figure 3.6: Average cover score for rock cover (a = Useful rock, b = Embedded rock), in sites of 1, 2, 3, and 4 fires within the last 20 years.

Figure 3.7: Number of trees in sites of 1, 2, 3, and 4 fires within the last 20 years.

Figure 3.8: Percentage canopy cover in sites of 1, 2, 3, and 4 fires within the last 20 years.

Figure 3.9: Average capture rates of invertebrates per pitfall, across sites of 1, 2, 3, and 4 fires in the last 20 years.

Figure 3.10: Average abundance of Hymenoptera (number / pitfall) across sites of 1, 2, 3, and 4 fires in the last 20 years.

Figure 3.11: Average abundance of Collembola (number / pitfall) across sites of 1, 2, 3, and 4 fires in the last 20 years.

Figure 3.12: Average abundance of Orthoptera (number / pitfall) across sites of 1, 2, 3, and 4 fires in the last 20 years.

Figure 3.13: Average abundance of Araneae (number / pitfall) across sites of 1, 2, 3, and 4 fires in the last 20 years.

Figure 3.14: Invertebrate abundance within the four fire frequency treatments as shown by a two-dimensional plot of multidimensional scaling (MDS) analysis.

Figure 3.15: Rattus fuscipes KTBA across sites of 1, 2, 3, and 4 fires in the last 20 years.

Figure 3.16: Rattus fuscipes estimated populations (Petersen’s weighted mean) across 1, 2, 3, and 4 fire treatments.

Figure 3.17: Antechinus stuartii KTBA across sites of 1, 2, 3, and 4 fires in the last 20 years.

Figure 3.18: Antechinus stuartii estimated populations (Petersen’s weighted mean) across 1, 2, 3, and 4 fire treatments.

Figure 4.1: Percentage cover of vegetation and ground habitat variables in burnt and unburnt sites.

Figure 5.1: Location of experimental study sites within Ku-ring-gai Chase and Garigal National Parks.

Figure 5.2: Nest box design.

Figure 5.3: Number of small mammal species recorded at each site over the entire study period.

Figure 5.4: Species richness and occurrence of small mammals during each trapping period.
Figure 5.5: Changes in the relative abundance of each species over the study period.

Figure 6.1: The bush rat, *Rattus fuscipes* (a), and distribution within Australia (b).

Figure 6.2: *Rattus fuscipes* KTBA in (a) unburnt sites, and (b) burnt control sites.

Figure 6.3: Average number of juvenile *Rattus fuscipes* KTBA in unburnt sites and all burnt sites combined, across all trapping periods.

Figure 6.4: Body condition index of adult *Rattus fuscipes* between burnt control sites (c) and unburnt sites (ub).

Figure 6.5: Percentage of the *Rattus fuscipes* population that was transient, or resident, and permanent residents in burnt control (c) and unburnt (ub) treatments.

Figure 6.6: The mean number of female and male *Rattus fuscipes* KTBA in burnt control (c) and unburnt sites (ub).

Figure 6.7: Average longevity of permanent resident female and male *Rattus fuscipes* in burnt control (c) and unburnt sites (ub).

Figure 6.8: *Rattus fuscipes* KTBA in food and nest (a), nest (b), food (c), and control (d) treatment sites.

Figure 6.9: Body condition index of adult *Rattus fuscipes* between treatment sites; males and females combined.

Figure 6.10: Body condition index of adult male and female *Rattus fuscipes* between treatments.

Figure 6.11: Mean number of female and male *Rattus fuscipes* across treatments.

Figure 6.12: Percentage of individuals in *Rattus fuscipes* populations transient, resident, and permanently resident in treatment sites.

Figure 6.13: Average trap-revealed longevity of permanent resident a) female and b) male Rattus fuscipes across different treatments.

Figure 6.14: a) average number of juvenile *Rattus fuscipes* per trapping session (represented as columns), within each treatment, and b) average number of juvenile *Rattus fuscipes* within treatments during each trapping session.

Figure 6.15: Number of juvenile *Rattus fuscipes* KTBA in treatment and control sites throughout study.

Figure 6.16: Ground cover frequency for a) leaf litter, b) bare ground, c) rock, d) grass/shoots, e) live wood, f) dead wood.

Figure 6.17: Vegetation cover frequency for a) 0 - 20 cm, b) 21 - 50 cm, c) 51 - 100 cm, d) 101 - 200 cm, e) > 200 cm.

Figure 7.1: The brown antechinus, *Antechinus stuartii* (a), and distribution within Australia (b).

Figure 7.2: *Antechinus stuartii* KTBA in (a) unburnt sites and (b) burnt control sites.

Figure 7.3: Body condition index of *Antechinus stuartii* in burnt control sites (c) and unburnt sites (ub).

Figure 7.4: Proportion of female to male *Antechinus stuartii* in burnt control (c) and unburnt (ub) treatments.
Figure 7.5: Percentage of individuals in *Anthechinus stuartii* populations transient, resident, or permanently resident in burnt control (c) and unburnt (ub) treatments.

Figure 7.6: Average trap-revealed longevity of permanent resident female and male *Anthechinus stuartii* in burnt control (c) and unburnt (ub) sites.

Figure 7.7: *Anthechinus stuartii* KTBA in a) food and nest, b) nest, c) food, and d) control treatment sites.

Figure 7.8: Body condition index of female and male *Anthechinus stuartii* between treatments.

Figure 7.9: Body condition index of *Anthechinus stuartii* between treatments; males and females combined.

Figure 7.10: Proportion of female to male *Anthechinus stuartii* across treatments.

Figure 7.11: Percentage of individuals in *Anthechinus stuartii* populations transient, resident, or permanently resident in treatment sites.

Figure 7.12: Average trap-revealed longevity of permanent resident a) female and b) male Antechinus stuartii across different treatments.

Figure 7.13: Average number of juvenile female and male *Anthechinus stuartii* KTBA during the February recruitment period of 1995, 1996 and 1997.

Figure 8.1: The house mouse, *Mus domesticus* (a), and distribution within Australia (b).

Figure 8.2: *Mus domesticus* KTBA in food and nest (a), nest (b), food (c), and control (d) treatment sites.

Figure 8.3: Body condition index of adult *Mus domesticus* between treatment sites; males and females combined.

Figure 8.4: Body condition index of adult female and male *Mus domesticus* in food addition sites.

Figure 8.5: Bare ground cover frequency at each site within treatments a) food and nest, b) nest only, c) food only, d) control.

Figure 9.1: The eastern pygmy possum, *Cercartetus nanus* (a), and distribution within Australia (b).

Figure 9.2: *Cercartetus nanus* KTBA in food and nest (a), nest (b), food (c), and control (d) treatment sites.

Figure 9.3: Body condition index of adult *Cercartetus nanus* between treatment sites, males and females combined.

Figure 9.4: Body condition index of adult female and male *Cercartetus nanus* across all sites.
### TABLES

**Table 3.1**: Frequency and between fire interval of fires at each site.  
**Table 3.2**: Table of cover abundance scores in relation to percentage cover within a quadrat.  
**Table 3.3**: Two-way ANOVA on maximum shrub height between years and different fire frequency treatments.  
**Table 3.4**: Two-way ANOVA on post-fire shrub cover between years and different fire frequency treatments.  
**Table 3.5**: Correlation coefficients for vegetation and habitat features.  
**Table 3.6**: Average Sorensen’s coefficient of similarity ($S_s$; Sorensen 1948) on invertebrate Order richness between treatments.  
**Table 3.7**: One-way ANOVA of the percentage of male and female Rattus fuscipes (Arcsine transform) between fire frequency treatments.  
**Table 3.8**: One-way ANOVA of the percentage of adult males and females in populations of Rattus fuscipes (Arcsine transform) between fire frequency treatments.  
**Table 4.1**: Table of cover abundance scores in relation to percentage cover within a quadrat.  
**Table 5.1**: Effect of supplementary food and nests on mammalian species richness.  
**Table 6.1**: Differences between the average number of juvenile *Rattus fuscipes* KTBA in burnt control and unburnt sites in each trapping session.  
**Table 6.2**: One-way ANOVA testing for differences in the body condition of adult *Rattus fuscipes* KTBA between burnt control sites and unburnt sites during each trapping session.  
**Table 6.3**: Two-way ANOVA (a) and two-way repeated measures ANOVA (b) of *Rattus fuscipes* abundance (KTBA) between treatments.  
**Table 6.4**: Two-way ANOVA of adult *Rattus fuscipes* body condition between food and nest treatments a) during each trapping session, and b) all trapping sessions combined.  
**Table 6.5**: Two-way ANOVA on the body condition of adult male and female *Rattus fuscipes* between treatments.  
**Table 6.6**: Two-way ANOVA comparing the percentage of *Rattus fuscipes* transients, resident and permanent residents across treatments.  
**Table 6.7**: Two-way ANOVA on trap-revealed longevity between experimental treatments for female and male *Rattus fuscipes*.  
**Table 6.8**: Two-way ANOVA of juvenile *Rattus fuscipes* KTBA between treatments, during each trapping session.  
**Table 6.9**: Two-way ANOVA of ground cover between burnt and unburnt sites, and years (time).  
**Table 6.10**: Principal Components Analysis (PCA) of ground cover data.  
**Table 6.11**: Two-way ANOVA of vegetation height categories between burnt and unburnt sites, and years (time).  
**Table 6.12**: Principal Components Analysis of vegetation cover data.
Table 6.13: Principal Components Analysis of habitat data.

Table 7.1: One-way ANOVA testing for differences in the body condition of *Antechinus stuartii* between burnt control and unburnt sites during each trapping session.

Table 7.2: One-way ANOVAs of the relative abundance of transient, resident and permanent resident *Antechinus stuartii* between burnt control and unburnt sites.

Table 7.3: Two-way ANOVA (a) and two-way repeated measures ANOVA (b) of *Antechinus stuartii* abundance (KTBA) between treatments.

Table 7.4: Two-way ANOVA of *Antechinus stuartii* body condition between food and nest treatments a) during each trapping session, and b) all trapping sessions combined.

Table 7.5: Two-way ANOVA comparing the proportion of female to male *Antechinus stuartii* across treatments.

Table 7.6: Two-way ANOVA comparing the average percentage of transients, residents and permanent residents in *Antechinus stuartii* populations across treatments.

Table 7.7: Two-way ANOVA on trap-revealed longevity between experimental treatments for female and male *Antechinus stuartii*.

Table 8.1: Two-way ANOVA (a), and two-way repeated measures ANOVA (b), of *Mus domesticus* abundance (KTBA) between treatments.

Table 8.2: Two-way ANOVA of *Mus domesticus* adult body condition between food and nest treatments, for a) females, b) males, and c) females and males combined.

Table 8.3: One-way ANOVA of the amount of bare ground between sites in 1995, 1996 and 1997. Quadrats within sites used as replicates.

Table 9.1: Two-way ANOVA (a), and two-way repeated measures ANOVA (b), of abundance of *Cercartetus nanus* (KTBA) between treatments.
CHAPTER 1: MECHANISMS OF RECOVERY AFTER FIRE OF AUSTRALIAN SMALL MAMMALS: A REVIEW AND SUGGESTIONS FOR FURTHER RESEARCH

1.1 INTRODUCTION

The Australian landscape is affected frequently by fire. As such, a general belief has emerged that many Australian species, both animal and plant, are fire-adapted. However, as Gill (1975) discussed, there are many combinations of fire intensity, season and frequency, and it may be that species are adapted to particular fire regimes rather than to fire per se. The population responses of animals to fire have often been studied (e.g., Recher et al. 1974; Catling and Newsome 1981; Fox 1981, 1982, 1983), and the recent reviews by Catling (1991), Friend (1993), Whelan (1995) and Wilson (1996) provide comprehensive summaries of population and community responses of small mammals to fire in Australia. Generally, however, patterns of response rather than mechanisms behind population recovery have been investigated, and evidence linking population recovery with changes in the post-fire environment is often weak or circumstantial.

The responses of mammals to fire, particularly rodents and small marsupials, are better known than those of other vertebrates in Australia. The evidence that is available indicates a complex pattern of individual species responding to fire in a variety of ways. Drawing generalised conclusions from these studies is further complicated by different patterns of response that are shown within individual species in different habitats, or even within the same habitats at different locations.

1.2 IMPACT OF FIRE ON SMALL MAMMALS

1.2.1 REDUCED POPULATION NUMBERS

Fire has the immediate potential effect of reducing population size through direct mortality. Bates (1980), for example, estimated the pre-fire abundance of the common ringtail possum, Pseudocheirus peregrinus, common brushtail possum, Trichosurus vulpecula, short nosed bandicoot, Isoodon obesulus, fox, Vulpes vulpes and bush rat, Rattus fuscipes, by counting the number of scorched bodies per hectare after an intense fire.

1. Sections of this Chapter have been accepted for publication under the following citation: Sutherland E. F. and Dickman C. R. (in press) Mechanisms of Recovery after Fire by Rodents in the Australian Environment: A review. Wildlife Research
However, mortality cannot be quantified in studies that compare population density or abundance before and after a fire event, or between burnt and unburnt patches, as these measures do not distinguish between mortality and emigration (Whelan 1995). Mortality can be quantified only by following the fate of individuals present in an area through a fire event. Tagging of individual animals can also yield valuable information on changes in habitat use, home range size and diet.

Unfortunately, no studies have reliably quantified mortality of Australian small mammals during fire, although Friend (1979) recorded apparent mortality of *R. fuscipes*, during clearing and burning of land for forestry purposes. Few researchers have the resources to radio-track and monitor individuals, perhaps for several years, in the hope that a bushfire will happen to cross their site at some stage. Working with agencies that conduct prescribed burns is possible but has limitations. There is a limited ‘window of opportunity’ regarding the time of year when burns can be conducted safely, and planned burns are often cancelled at the last minute due to wind, rain, volunteer availability or high air pollution risk.

Haim and Izhaki (1994) have suggested that patterns in the abundance of small mammals after fire may be explained by their physiological abilities. Wagner’s gerbil, *Gerbillus dasyurus*, and Tristram’s jird, *Meriones tristrami*, were both found during the second and third years after fire in a Mediterranean pine forest. *G. dasyurus* is usually found in extremely arid rocky habitats of the Sinai Peninsula, Israel, whereas *M. tristrami* is a burrow dweller confined to semi-arid regions of the same country. *G. dasyurus* can withstand higher temperatures and greater water deprivation than *M. tristrami* and was found, accordingly, in more xeric habitats than *M. tristrami* after fire.

Mammal populations may recover following fire by recolonisation of an area through increased immigration or increased in situ reproduction. Following a land clearing and burning operation, in which eucalypt forest was removed and a pine plantation established, Friend (1979) noted that although resident *R. fuscipes* disappeared from cleared areas, these sites were recolonised by subadults within 1 to 2 months. Leonard (1972) also recorded many subadult *R. fuscipes* in burnt sites, although he considered them transient. This is supported by White (1992) who found that, although *R. fuscipes* re-established a
population within 18 months of a prescribed burn, most individuals were transient adult males. Post-fire population recovery by pale field rats, *Rattus tunneyi*, and eastern chestnut mice, *Pseudomys gracilicaudatus*, was also attributed to high immigration from unburnt areas, maintained by high reproductive effort (White 1992). Recher *et al.* (1974) recorded an influx of swamp rats, *Rattus lutreolus*, onto burnt plots in grassy habitat, and also, after these sites flooded, into burnt areas of adjacent forest where they had not been previously recorded. *R. lutreolus* is often the first native species to successfully recolonise heathland after fire (Catling 1986) and, once established, alters its reproductive strategy to breed at lower body weights than in preferred habitats.

Increased *in situ* reproduction of small mammals has not been confirmed to occur in fire-affected habitats in Australia, although changes in reproductive strategy appear to be common. Leonard (1972) showed reproduction in *R. fuscipes* to be reduced greatly following fire, with females not surviving into their second reproductive year. Adult females appeared to move to adjacent unburnt areas to wean their young, making the burnt areas available to colonising subadults. More dramatically, Thompson *et al.* (1989) found no recruitment of *R. fuscipes* into the population for two reproductive seasons following a prescribed burn. Cowley *et al.* (1969) and Recher *et al.* (1975), however, found that following fire *R. fuscipes* began breeding earlier in the year than usual. The results of Cowley *et al.* (1969) may actually reflect an influx of juveniles into the burnt area as reported by Friend (1979), rather than a change in the timing of reproduction. Population recovery of *R. fuscipes* is probably dependent upon the degree of habitat alteration. Humphries and Tolhurst (1992) reported that populations in sites where control burns removed less than 50% of the cover recovered after one breeding season, sites where 50 to 80% of the cover was removed recovered after three breeding seasons, and sites where all vegetation was removed had not recovered at the conclusion of the study, three years after the fire. Successful population recovery was attributed to breeding in unburnt patches (Humphries and Tolhurst 1992).

The rock-rats *Zyzomys argurus* and *Z. woodwardi* also show fewer lactating and pregnant females in the year following a fire, with lower juvenile recruitment than in pre-fire years (Begg *et al.* 1981). Thus, although reproduction was affected, it was not in a way
that would facilitate a recovery in the population. *R. lutreolus*, on the other hand, may be reproductively active at a lower body weight in previously (to the fire) unoccupied sites than in preferred habitat types (Catling 1986), thus allowing for a relatively rapid increase in numbers of individuals.

Cockburn (1981) demonstrated that the silky mouse, *Pseudomys apodemoides*, can respond rapidly to resource fluctuations caused by disturbances such as fire or drought, due to a female-biased sex ratio and promiscuous breeding strategy. Other species, however, respond to such perturbations by alterations in life history patterns. The heath rat, *Pseudomys shortridgei*, for example, shows an annual breeding strategy in the early stages of succession, with breeding in the year of birth and high juvenile but low adult survival (Cockburn *et al.* 1981). However, later in the succession *P. shortridgei* shifts to a perennial breeding system, with high adult and low juvenile survival (Cockburn *et al.* 1981). Cockburn *et al.* (1981) attributed this switch to restrictions on the rate of maturation of rats during late succession due to low productivity of mature heath systems, the advantages of enforcing dispersal in the deteriorating environment of late succession, and the advantages of spreading reproductive effort over several years when the availability of unoccupied habitat is low and unpredictable.

1.2.2 REDUCED RESOURCE AVAILABILITY

Most declines in population numbers of small mammals after a fire appear to be due to habitat alteration and reduced availability of resources, especially food, cover and nest sites. Whether the declines are as a result of mortality or emigration is, however, yet to be determined (Section 1.2.1).

1.2.2.1 FOOD

The effect of altered food levels on population recovery after fire has received little direct attention, although it has been much discussed (e.g., Bamford 1985; King 1985; Masters 1993; Reid *et al.* 1993). Several researchers have implied that a direct relationship exists between changing cover levels and food availability (e.g., Masters 1993; Reid *et al.* 1993), although this may not necessarily be the case. Additionally, the food requirements of many species are not well known. Recher and Christensen (1981) suggested that animals
that feed on soil and litter organisms may be most affected by reductions in post-fire food availability. Litter invertebrates can suffer a 50% reduction in species richness and between 50 and 90% reduction in abundance immediately after hazard-reduction burns (Leonard 1974). However, an investigation of the reduced post-fire abundance of *Antechinus flavipes*, an opportunistic insectivore, showed no correlation with invertebrate abundance, suggesting that the availability of food was not a limiting factor for this species (Hindmarsh and Majer 1977).

Even when the 'usual' diet of a species is known, it may still be important to take into account seasonal variation, or the habitat shifts that often occur after fire (see below). This is because some species undergo a dietary shift to survive the post-fire period, especially in its initial stages. *R. fuscipes*, for example, has a 50% arthropod component in its diet in some areas in summer, and 20% in winter (Hall and Lee 1982). As most bush fires occur over summer, and arthropods are largely removed by fire (Leonard 1974), it seems reasonable to expect that if the species is to persist in an area after fire a significant dietary shift will need to take place. Considering that the vegetative component of the local environment is also greatly reduced by fire, a previously small component of the diet may increase in significance. Fungus may become a dominant food for some small mammals after fire (Johnson 1995), even if generally the proportion of fungus in the diet is small (Hall and Lee 1982). Christensen (1980) recorded an increase in digging activity and consumption of fungi by *Bettongia penicillata* after fire, and suggested that either sporocarp production or accessibility had increased. Claridge (1992) disputed the suggestion that fire stimulates sporocarp production and supported Christensen's (1980) proposal that increased fungus consumption after fire is a result of improved accessibility with the removal of ground vegetation. Claridge and May (1994) further questioned the selection of fungi as a food source due to its poor nutritional quality. Recent studies indicate that between one and three years after fire there is no difference between the amount of Zygomycetous mycorrhizal fungi consumed by *R. fuscipes* in burnt and unburnt areas (P. A. McGee, G. S. Pattinson and E. F. Sutherland, unpublished data). However, Luo and Fox (1995) found evidence that *P. gracilicaudatus* and *R. lutreolus* may compete for fungi during early (1.5 years) and mid (3.5 years) post-fire regeneration stages.
In situations where the diets of target species are not studied or are incompletely known, it may still be possible to use indirect methods to assess the effects of food limitation on population size. For example, Catling et al. (1989), by conducting an experiment to measure rates of water flux in animals before and after a fire, concluded that populations of *R. fuscipes* and the insectivorous marsupial *Antechinus stuartii* were not limited by shortages of food or water after a prescribed burn. It was assumed that food shortage would be reflected in reduced water flux, loss of body weight and fat reserves, and an increase in mass-specific body water.

A number of further studies have suggested that post-fire recovery of small mammals is dependent upon the return of food resources over time. Masters (1993) and Reid et al. (1993) suggested that the long-term colonisation of burnt sites by the desert mouse, *Pseudomys desertor*, the sandy inland mouse, *P. hermannsburgensis*, and the spinifex hopping-mouse, *Notomys alexis*, was in response to gradually increasing food availability. Haim and Izhaki (1994) also suggested that the succession of small mammals after fire in an Israeli pine forest followed the pattern of food availability. Fire-stimulated production of large quantities of seeds and seedlings favoured granivorous and herbivorous species in the first instance, and later the insectivorous species responded to the recolonisation and recovery of invertebrate populations (Haim and Izhaki 1994). However, Bamford (1985) found no correlation between increasing invertebrate numbers after fire, and the percentage of invertebrates in the diets of ash-grey mice, *Pseudomys albocinereus*, and other small mammals present at his study site. Similarly, King (1985) found no correlation between invertebrate biomass and the abundance of partially insectivorous *R. fuscipes*, although this study was hindered by a lack of replication and large between-site variance.

Reduced food availability may also cause an increase in foraging activity, home-range size and/or home range overlap. Begg et al. (1981) attributed increased capture rates of *Z. argurus* after a fire to increased foraging movements, although King (1985) found that the movements of *R. fuscipes* between captures after fire did not differ from their movements prior to fire. Thompson et al. (1989) found no evidence that *R. fuscipes* increased home ranges after fire, with individuals maintaining their pre-burn ranges until
disappearing from the population in the months that followed the fire. Finally, low food availability may lead to animals emigrating from a burnt patch. Thompson et al. (1989) discussed the occurrence of emigration after fire, although it was not attributed directly to either food or habitat depletion.

Dietary generalists may persist in an area by concentrating on usually uncommon or inaccessible foods that increase in availability after fire. Luo and Fox (1996) demonstrated an association between food resource use and changes in relative abundance of *P. gracilicaudatus* and *R. lutreolus*, over successional time since fire. They suggested that the primary mechanism allowing the coexistence of these two species is food partitioning during autumn and winter and during mid-successional stages, and habitat partitioning during spring and summer and during late successional stages. Both species showed differential use of resources during early and mid-successional stages after fire. Specialist strategies may also be effective in the post-fire environment (Whelan 1995). A specialist granivore or a species that requires fresh shoots, as examples, may boom in the immediate post-fire environment due to the massive seed release and rapid growth of new vegetation that follows fire (Gill 1981). Other specialists, however, will not persist in the post fire environment until their required food source is re-established.

1.2.2.2 COVER

The relationship between the complexity of habitat structure and small mammal abundance has often been noted, especially in forest environments. More structurally complex environments usually have higher abundance and species richness of fauna (Catling 1991). If shrubs, ground cover and litter are removed, the reduction in forest complexity results in a corresponding reduction in small mammal diversity and abundance (e.g., Recher et al. 1974; Braithwaite and Gullan 1978; Friend 1979; Newsome and Catling 1979; Fox and McKay 1981; Catling 1986; Lunney et al. 1987).

In forests of southeastern Australia, Catling (1991) identified *A. flavipes, A. swainsonii, A. minimus*, *Cercartetus nanus*, *Acrobates pygmaeus*, *Pseudomys novaehollandiae*, *R. lutreolus* and *R. fuscipes* as being disadvantaged by habitat simplification after disturbance such as fire. On the other hand, *Sminthopsis murina, S.*
leucopus, P. gracilicaudatus, P. oralis, Phascogale tapoatafa, Melomys burtoni, Rattus rattus and Mus domesticus were advantaged by reduced habitat complexity. However, P. novaehollandiae has previously been noted to prefer the early post-fire successional stages (e.g., Posamentier and Recher 1974; Kemper 1977; Fox and McKay 1981), and recent experimental reduction of habitat structure in heath by Fox et al. (in review) and Monamy (unpubl. data.), has demonstrated that the abundance of P. novaehollandiae is increased by habitat simplification, whereas the abundance of P. gracilicaudatus declines proportionately to the amount of structure removed. The appearance of two introduced species, R. rattus and M. domesticus, in Catling’s (1991) ‘advantaged by habitat simplification’ category emphasises the opportunistic nature of these species, invading unoccupied or under-utilised niches (Recher et al. 1974; Newsome et al. 1975; Braithwaite and Gullan 1978; Fox 1982).

The habitat preferences of some small mammals are well known. R. lutreolus has been associated with dense, damp understorey and the availability of hollow logs and stumps (Green 1967, 1972; Fox 1983; Monamy and Fox in press), although Catling (1986) also noted an association with thickets of taller vegetation. The abundance of P. novaehollandiae is associated positively with vegetation density at 20cm and the presence of bare ground, but negatively with vegetation cover as a whole (Posamentier and Recher 1974). This would suggest that the optimum habitat for P. novaehollandiae is mid-seral regenerating heath (Posamentier and Recher 1974). R. fuscipes displays a preference for dense vegetation below 50cm (Lunney and Ashby 1987; Lunney et al. 1987), and its recovery after fire is often attributed to regeneration of ground vegetation (Catling et al. 1981) and leaf litter (Fox and McKay 1981). The uniformity of vegetation may also be important, as Thompson (1983) found a negative correlation between R. fuscipes abundance and habitat patchiness. Lunney et al. (1987) demonstrated a gradient of increasing trapping success of R. fuscipes with increasing percentage of ground cover after fire; this finding was supported also by Heislers (1980), who determined that R. fuscipes did not colonise after fire until there was greater than 40% ground cover. King (1985), however, found a negative correlation between R. fuscipes abundance and the species richness of herbs and shrubs after fire.
Animals may respond to reduced cover by exhibiting post-fire habitat shifts. Fox (1983) found that, for four years after fire, *R. lutreolus* and *R. fuscipes* were found only in dense ground cover provided by swamp forest, although trapping 5 to 6 years after the fire indicated that both species had returned to their pre-fire habitats. However, such relationships may be complicated by competition. Unlike Fox (1983), Catling (1986) demonstrated that in the absence of *Pseudomys* spp., *R. lutreolus* returned to its preferred habitats only 2 years after fire. In addition, Monamy and Fox (in press), showed a seasonal intraspecific effect with female *R. lutreolus* excluding males from preferred habitats outside the breeding season, but males expanding their range during the breeding season to move into the females’ territories, thus allowing long-tailed mice, *Pseudomys higginsi*, to shift into the habitat occupied formerly by male *R. lutreolus*. Cowley et al. (1969) found that *R. fuscipes* were displaced away from their usual places of capture after fire. Similarly, Friend (1979) suggested that adult *R. fuscipes* with established territories may die *in situ* during perturbations, whereas newly independent subadults may move out of affected areas.

Kemper (1977) reported that some tagged *P. novaehollandiae* shifted after fire from their pre-fire ranges to patches of unburnt heath and forest. Interestingly, these shifts were not immediate but occurred between two and four weeks after the fire (Kemper 1977). *Z. woodwardi* also shows post-fire habitat shifts, moving from closed forest, where most of the ground cover and leaf litter had been removed, to structurally complex, rocky scree slopes (Begg et al. 1981).

Reduction of cover could conceivably lead to animals minimising their activity in order to reduce their risk of predation. Christensen and Kimber (1975) found that the home range sizes of individual *R. fuscipes* decreased after fire, even though the population remained approximately the same size. This could be a reflection of reduced activity, due to a perceived increase in predation risk related to there being less cover. However, there have not yet been any studies to demonstrate that reduced cover resources lead to a change of predator avoidance behaviour, although increased predation risk is often assumed. This is discussed further in Section 1.2.4.
Reduction of cover could also lead to emigration from a burnt area, as noted for *R. fuscipes* by Thompson *et al.* (1989), although not attributed definitely to any particular environmental features. Christensen and Kimber (1975), however, found that *R. fuscipes* did not leave a burnt area for nearby unburnt patches, but instead that there was immigration onto the burnt plots by immature males. Alternatively, species may partition the remaining habitat in order to reduce competition for available resources (Luo and Fox 1996). Most commonly, however, the post-fire recovery of rodents, and other small mammals, is regarded as a direct response to vegetation regrowth.


Outside Australia, researchers in Argentina (Ojeda 1989), India (Rana 1985), Israel (Haim and Izhaki 1994), Mexico (Fa and Sanchez-Cordero 1993), South Africa (Willan and Bigalke 1981; van Hensbergen *et al.* 1992; Rowe-Rowe 1995) and the USA (Cook 1959; Lawrence 1966; Beck and Vogl 1972, Christian 1977; Crowner and Barrett 1979, Wirtz
1981; McGee 1982; Clark and Kaufman 1990), have also associated abundance of small mammals with the level of vegetative cover after fire.

Until recently, however, there has been little experimental evidence to demonstrate that these correlations reflect causal mechanisms of recovery. Recent habitat manipulation studies involving the removal of vegetation to reduce heath complexity have shown that *P. novaehollandiae* increases in abundance, *R. lutreolus* decreases in abundance, and *P. gracilicaudatus* declines in proportion to the percentage of vegetation removed (Fox *et al.* in review; Monamy unpubl. data). Nevertheless, in the majority of cases it is not known if the animals are responding to the shelter, food, structure, nest availability, microclimate or other associated factors that regrowth is providing.

1.2.2.3 NEST SITES

The effect of fire on the availability of nest sites and nesting material for small mammals has also been largely overlooked in Australia. Inions *et al.* (1989), in a study of the availability of nesting hollows in trees for *T. vulpecula* and the western ringtail possum, *Pseudocheirus occidentalis*, found that high-intensity fire reduced the availability of trees with hollows by 38%, although in the long term it increased the rate of hollow formation by direct excavation or by providing sites for fungal or termite attack. There are no published studies that gauge the effect of nest site destruction on small mammals.

Small mammals nest in a variety of places, including leaf litter, underground burrows, rock crevices, fallen logs and tree hollows both at ground level and above ground, depending on the species (Dickman 1991). Dickman (1991) recommended that prescribed burning and post-logging burning be minimised to reduce destruction of nest-sites used by small ground-dwelling mammals. The removal of nest sites could conceivably lead to habitat shifts, increased home range size and/or overlap, increased nest sharing, or emigration. Mortality during fire can also be affected by position of nest sites. Burrowers are conceivably safer from flames, heat and perhaps smoke than surface or arboreal nesters. Lawrence (1966) identified the 'minimum survival qualities' of a burrow as being greater than 12 cm in depth, with several surface openings and insulated by dry mineral soil. Deep rock crevices and nests under logs or in tree trunks insulated by living bark were also
protected from fire and heat (Lawrence 1966). Differential survival of small mammals through fire in the Sonoran Desert, USA, has been attributed to nest location, with *Neotoma albicula*, living in stick nests, suffering higher mortality than syntopic burrow dwellers (Simons 1991). Similarly, topography has an effect, with animals living along ridges more likely to be affected than those along creeks (Whelan 1995).

1.2.3 INCREASED COMPETITION

Intra- and interspecific competition within a small mammal community can also determine the success of recolonisation after fire. If necessary resources such as food, cover and nests are depleted by fire, competition should be expected for what remains. Although Adler (1985), in a study of a small mammal community in the USA, suggested that intraspecific competition was more important in determining patterns of habitat use than interspecific interactions, it is the latter that has received most attention in Australia. Fox (1983), for example, demonstrated a post-fire habitat shift of *S. murina* away from forest areas whereas *A. stuartii* shifted towards that habitat, and suggested that a competitive displacement of *S. murina* from forested areas by *A. stuartii* was the mechanism responsible.

Catling (1986) found that in the absence of *Pseudomys* spp., *R. lutreolus* was able to switch from its usual ‘late regeneration niche’ to become an early coloniser of burnt heathland, thus indicating that *Pseudomys* spp. may be competitively superior to *R. lutreolus* in early successional stages. However, Higgs and Fox (1993) found evidence of both intra- and interspecific competition among *R. lutreolus* and *P. gracilicaudatus* during a removal experiment to determine their relationships. Initially when *R. lutreolus* was removed from experimental plots, animals were replaced by individuals of the same species, thus indicating intraspecific competition. However, when all *R. lutreolus* were finally removed the abundance of *P. gracilicaudatus* increased and it expanded its range into microhabitats occupied formerly by *R. lutreolus*, while reducing its range in its former microhabitat. Higgs and Fox (1993) interpreted these results as evidence that the larger *R. lutreolus* had been excluding *P. gracilicaudatus* from preferred microhabitats through greater competitive ability. The competitive effects reported by Higgs and Fox (1993) were shown to depend on body size (Thompson and Fox 1993). Reduction of *P. gracilicaudatus*
abundance allowed more juvenile and sub-adult *R. lutreolus* to colonise the removal sites than the control sites (Thompson and Fox 1993). In addition, Higgs and Fox (1993) suggested that the increased abundance of *R. lutreolus* late in succession indicates increasing competitive ability with time after fire or other disturbance. This was supported further by Luo and Fox (1995) who, by analysing dietary information from the same removal experiment, found that the presence of *R. lutreolus* induced a dietary shift by *P. gracilicaudatus* between the early and mid post-fire regeneration stages.

Body size is unlikely to be the only determinant of dominance in interspecific competition, however, as a competitive interaction between *R. lutreolus* and *R. fuscipes* has also been suggested by Newsome *et al.* (1975) based on an inverse relationship between their population curves. In support of this, Maitz (1995), in a removal experiment, found that *R. lutreolus* excluded *R. fuscipes* from wet sedge habitat.

Monamy and Fox (in press) reported that in wet sclerophyll forest during winter, female *R. lutreolus* are competitively superior to male *R. lutreolus*, excluding males from the preferred dense vegetation, whereas during the summer reproductive season males shift into the habitat occupied by females. The movement by males, however, leads to a shift of *P. higginsi* into the habitat occupied formerly by the male *R. lutreolus*. Monamy and Fox (in press) suggested that although *R. lutreolus* and *P. higginsi* both appear to prefer similar microhabitats, *P. higginsi* is unable to compete with individuals twice their body weight. Monamy (1997) supported these findings with a parallel study of *R. lutreolus* and *P. gracilicaudatus* in heathland. Female *R. lutreolus* again occupied areas of densest vegetation, relegating male *R. lutreolus* and both sexes of *P. gracilicaudatus* to surrounding areas with less dense vegetation. These studies suggest that intersexual competition within dominant species can drive patterns in community structure (Monamy 1997; Monamy and Fox in press).

Pople (1983) and Fox and Pople (1984) showed that a pulsed removal of *P. novaehollandiae* resulted in increased abundance and broader habitat use by *M. domesticus*. However, Fox and Gullick (1989), in a reciprocal field experiment, demonstrated that at high densities *M. domesticus* competitively excludes *P. novaehollandiae*. *M. domesticus* is
able to overcome *P. novaehollandiae*’s competitive superiority only by sheer numbers. However, these high density or plague conditions are often reported during post-flre succession, particularly after high rainfall (Leonard 1972; Christensen and Kimber 1975; Recher *et al.* 1974, 1975; Newsome *et al.* 1975; Friend 1979; Catling *et al.* 1981; Fox and McKay 1981; Fox 1982, 1983; Lunney and Ashby 1987; Lunney *et al.* 1987; Kemper 1990; Wilson *et al.* 1990), and as such could have a detrimental effect on the recovery of *P. novaehollandiae* and other native species after fire.

Although certain species may shift habitat due to competition, it is not clear for what resources they are competing; whether it be shelter, food, nest sites or other resources, or if there is also an associated dietary shift. Importantly, however, competition is both a population and community level interaction, and its effects need to be interpreted at both scales if the processes at work are to be clarified.

1.2.4 INCREASED PREDATION

Many natural bushland areas have been isolated into functional ‘islands’ by clearing for agriculture, silviculture and urban development. Fire further restricts native mammals to smaller patches within these areas, greatly increasing the risk of predation upon the survivors of fire (Catling 1991). Risk is increased due to the severe reduction of cover in which to seek refuge, and reduction of food leading to an increase in foraging activity. Begg *et al.* (1981), for example, found that the capture rate for *Z. argurus* increased after fire despite a decrease in animals known to be alive. This they ascribed to increased activity in response to limited food. Christensen (1980) demonstrated that after fire, almost half the individuals of a *B. penicillata* population were killed by predators. Such rates of predation could lead to the local extinction of rarer species (Kinnear *et al.* 1988; Burbidge and McKenzie 1989). Very few data of this type exist with respect to small mammals, although Christensen and Kimber (1975) attributed high post-flre mortality of *R. fuscipes* to increased predation. Newsome *et al.* (1983) proposed that the post-flre predation on small (rodents and dasyurids), medium (possums and rabbits) and large-sized prey (macropods) by dingoes, *Canis lupus dingo*, was disproportionately high in relation to the low prey abundance. Newsome *et al.* (1975), on the other hand, believed that predation was not
important in the collapse of rodent populations due to the abruptness and unpredictability of fire events.

Fire increases accessibility of land to predators. The introduced predators, foxes, *Vulpes vulpes*, and cats, *Felis catus*, forage commonly along roadways and paths rather than through undergrowth (May and Norton 1996; Mahon *et al.* 1998). Fire simplifies the vegetation structure, reducing much of the undergrowth, allowing a higher proportion of the habitat to become available to predators (Newsome *et al.* 1983). Not only can predators then forage across a broader range of habitats, but their high mobility allows them to travel quickly into fire-affected areas. Other highly mobile predator species such as birds are also able to take advantage of the reduced cover (Baker 1940; Beck and Vogl 1972; Loyn *et al.* 1986). Loyn *et al.* (1986), in a study of sooty owl, *Tyto tenebricosa*, predation of mammals from rainforest in East Gippsland, Victoria, determined that whereas before fire the owls preyed on a range of arboreal and terrestrial mammals, after fire their diet was exclusively *R. fuscipes*, despite arboreal mammals still being available in the area. This they attributed to lack of terrestrial cover for *R. fuscipes*, whereas arboreal mammals were able to shelter in hollows despite the lack of canopy cover. Thus predation pressure on small mammals that have survived the fire is likely to be increased; exacerbated further by their loss of cover. However, even with a relative increase in prey due to increased availability, the post-fire decline in small prey species may still cause a decline in predator numbers through falling food reserves (Whelan 1995).

The impact of predation in post-fire communities is often assumed but rarely quantified. *V. vulpes* and *F. catus*, in particular, have been implicated in the decline of many native species (Dickman 1996a, 1996b). Predator numbers can be estimated by spotlighting, track counts and scat collection, and the analysis of scat contents can provide an accurate representation of diet (Bider 1968; Caughley 1977; Wilson *et al.* 1996). Newsome *et al.* (1983), in a study of the predator-prey dynamics between *C. l. dingo* and different prey classes after fire in south-eastern NSW, found increased rates of post-fire predation upon reduced prey populations, relative to pre-fire predation rates. There was some evidence that high predation upon macropods suppressed post-fire population recovery for two years following fire, although this was not apparent for either small or medium-sized
mammals (Newsome et al. 1983). The true impact of predators on a post-fire environment can be gauged only by conducting replicated, long term removal experiments; such experiments are essential in determining not only the impact of predators on recovering populations, but also for understanding the community processes that are at work.

1.2.5 REDUCED INDIVIDUAL FITNESS

Reduced resource availability, increased stress, predation risk and perhaps injuries from fire can all lead to a reduction of individual fitness. This has further consequences at the population level, with reduced reproductive potential and survival rate. However, changes to individual fitness have only rarely been considered in post-fire studies. Catling (1986), for example, found that female R. lutreolus were reproductively active at lower body weights in marginal habitats than in preferred habitats. However, although some rodents have the capability to reproduce when very young if conditions are favourable, it would be expected that R. lutreolus in preferred habitat would be more likely to reproduce at low body weights. Alternatively, if individuals in marginal habitat were slower growing due to inferior resources, it would be expected that their reproductive success would be lower. It would be useful to distinguish whether weight reduction after fire is a reflection of changes in age structure or access to inferior resources.

Catling et al. (1989) measured rates of water flux before and after a prescribed fire to determine if shortages of food and/or water affected the fitness of animals after fire. Neither A. stuartii or R. fuscipes appeared to decline in condition after the fire, and as such, individual and population fitness were considered not to be affected. This may, however, be a reflection of the patchiness and low intensity of prescribed fires, lack of replicate sites, or the short-term nature of the study. A similar study after wildfire, with increased replication and a longer duration, could yield more conclusive results.

Non-intrusive field-work practices also allow for an index of condition or health of an animal to be made easily by measuring the ratio of body weight to a standard skeletal measurement, such as head length. Unfortunately this is rarely done. Additional notes, such as external parasite load and injuries could also be taken into account during analyses of individual fitness.
1.2.6 SUMMARY OF THE EFFECTS OF FIRE ON SMALL MAMMALS, MECHANISMS OF RECOVERY AND RECOMMENDATIONS FOR FUTURE RESEARCH

It is apparent that there remains much to understand regarding the impact of fire on small mammals in Australia, and the mechanisms that allow survival at individual and population levels. Further, there has been little treatment of the problem at the community level. Although some research has addressed competition between two species, there is none that considers a suite of species that is affected simultaneously by a fire event. In addition, it is essential that we quantify the effect of predation if community processes are to be clarified. It is unrealistic to view individual organisms or species as if they are isolated from the environment as a whole (Whelan 1995). Characteristics of the surrounding vegetation, for example, will influence the heat and smoke experienced by an animal during a fire, and the availability of resources afterwards. Although individual and population studies are clearly valid, they are of most use if considered as part of the larger community.

Studying the impact of fire on individuals is essential if we are to establish mortality rates, where animals seek refuge, and to understand behavioural responses to fire. However, the intrinsic problems of trying to predict when, where, and if, a bushfire will occur often leaves the researcher with little option but to work with lower intensity, often patchy, prescribed fires. Although these have their value, the questions of intensity, scale and seasonal effects on mammals are often left unanswered.

Obviously, experimental procedures that do more than monitor population fluctuations in the post-fire environment are most urgently needed. This is especially true given the lack of replication and control in many previous studies on fire responses of vertebrates (Whelan 1995). Experimental manipulations of resource availability, competitive interactions and predation rates are required to clarify the processes that determine demographic fluctuations.

Patterns of population response to fire have been described many times, are highly variable and often site and species-specific (Whelan 1995). Most studies are conducted at the population level, however, and as Whelan (1995) has discussed, there are difficulties in generalising across studies with so much intrinsic variability in order to provide clear
management goals. Given these problems, establishing the mechanisms of response of species to fire may provide clearer guidelines for managers of natural systems. Experimental manipulation of habitat variables in post-fire conditions is particularly critical to distinguish which features of the habitat are essential for species recovery. How individuals respond to, or utilise those features, is equally important. If preferred habitat can be quantified, and prerequisites for post-fire population growth identified, it should be possible to make predictions regarding a species survival and recovery after a fire of known intensity, frequency and season, and also to provide effective management recommendations. Resource manipulation, particularly of food, has been used extensively to determine if resource availability is limiting to small mammal populations in many situations (see below). However, resource manipulation has been applied rarely to post-fire communities, although it potentially provides an effective means to experimentally determine the mechanisms driving small mammal responses to fire.

1.3 RESOURCE MANIPULATION STUDIES

1.3.1 FOOD SUPPLEMENTATION

Food availability has often been postulated as the primary factor limiting population growth in mammals; however difficulties in quantifying food availability in the field have meant that other approaches need to be taken (Boutin 1990). The removal or addition of food in replicated sites allows resident populations of study animals to be monitored in response to the manipulations, and in comparison to control groups. Behavioural, reproductive, demographic and community responses have been investigated (see Boutin 1990 for full review). The majority of food supplementation studies has been conducted in northern hemisphere temperate and boreal regions, with only a handful of Australian studies (Boutin 1990). Within Australia, the effect of supplementary food has been investigated for *A. leo* (Leung 1994), *A. agilis* (Dickman 1989), *A. stuartii* (Banks 1991), *Isodon obesulus* (Broughton and Dickman 1991), *Melomys capensis* (Leung 1994), *M. domesticus* (Newsome 1970; Newsome and Catling 1983; Bomford 1987a; Bomford and Redhead 1987), *N. alexis* (Predavec 1994), *P. hermannsburgensis* (Predavec 1994), *R. fuscipes* (Press 1982; Banks 1991), *Rattus leucopus* (Leung 1994) and *R. lutreolus* (Banks 1991).
In general, food addition leads to a decrease in individual home range size, although this is often a function of increased immigration and therefore a higher density of animals. Mares et al. (1982) demonstrated that, in the absence of immigration, home range size of chipmunks, *Tamias striatus*, increased with food supplementation. Ostfeld (1986) also showed that, although animals usually defended exclusive areas, the home range overlap of female voles, *Microtus californicus*, increased with additional food. However, food addition can also lead to dominant individuals monopolising food sources and driving competitors away, thereby reducing population density and increasing home range size (Monaghan and Metcalfe 1985; Broughton and Dickman 1991).

Boutin (1990) concluded that, for the majority of species studied, food supplementation leads to an increased proportion of the population breeding, from an earlier age, and in a breeding season that begins earlier and extends longer than in control groups. Clutch or litter size is often greater, as is the body weight and growth rate of individuals. It follows that in a significant proportion of studies, food supplementation has resulted in increased population density or rate of population growth. However, whereas food addition tends to increase the magnitude of seasonal or annual fluctuations as compared to control groups, it does not change the general pattern of population fluctuations (Boutin 1990; Krebs et al. 1995). The timing and rate of population changes are usually similar in experimental and control treatments (Boutin 1990).

Predavec (1994) found that the Australian desert rodents *N. alexis* and *P. hermannsburgensis* both responded to supplementary food, although the type of response varied. *N. alexis* males increased in body mass, and the distribution of males and females across different reproductive classes differed in the supplemented sites. This pattern resulted in an increase of abundance in *N. alexis* at supplemented sites, but only during summer. Food supplementation of *P. hermannsburgensis* did not affect body mass or distribution of reproductive classes, although captures did reflect the amount of food supplied to different sites.

There are few studies that have investigated food limitation at the community level. Species richness can increase in response to extra food (Abramsky 1978), although more
commonly competitive effects are accentuated. Brown and Munger (1985) and Bowers et al. (1987) demonstrated, in a desert rodent community, that the addition of food caused the dominant competitor to increase in density and the less competitive species to decline. Dickman (1988), in a study of the competitive effects of *A. swainsonii* on the smaller *A. agilis*, found that both food supplementation and the removal of *A. swainsonii* caused a switch in the secondary sex ratio of *A. agilis* from being female dominated, to being male dominated. The extra food and reduced competition allowed the females to invest more energy into the production of more costly sons.

Banks (1991) conducted a winter supplementary feeding experiment on sympatric *R. fuscipes*, *R. lutreolus* and *A. stuartii*, in sub-alpine habitat of the Blue Mountains of New South Wales. Both rodents showed a significant increase in population size, immigration, body weight, body condition and reproductive activity in supplementation sites. Interestingly, there was also more tail scarring of male rats at supplementation sites, indicating a likely increase of agonistic behaviour. Unfortunately, too few recaptures meant that the possible connection between this behaviour and home range size could not be assessed. The population characteristics of *A. stuartii* were not affected by supplementary feeding, although body condition did improve in supplemented sites. Interspecific interactions were also affected; although there was no association between the species before feeding began, at the end of the experiment there was a negative association between *R. fuscipes* and *A. stuartii*, with *A. stuartii* actively avoiding traps that had held rats previously.

Dickman (1989) studied the effect of supplementary feeding on a population of the closely related *A. agilis*, and found, in contrast to Banks (1991), that supplemented populations increased in numbers, mean body weight and survival. Animals also showed decreased movements between traps and smaller overlaps in home ranges where additional food was provided. Discontinuation of feeding caused a return to pre-manipulation population patterns.

In tropical rainforest, Leung (1994) determined that availability of food seasonally limited the population size of *M. capensis*, but not of the sympatric *A. leo* or *R. leucopus*.
M. capensis responded to additional food when production of fruit (a usually dominant food source) was low in the forest. Populations of R. leucopus, an omnivore, and A. leo, an insectivore, were not affected by such seasonal fluctuations. That these tropical Antechinus and Rattus species did not respond to supplementary food, whereas their temperate counterparts do (see above), he attributed to differences in food availability between the two climatic regions.

Newsome and Catling (1983) derived demographic models from M. domesticus in situations of acute food shortage, food shortage due to immigration, food abundant + cover shortage, food shortage + cover shortage, increased predation, and steady state. These models were then compared with data gathered after bushfire (Newsome et al. 1975). It was found that the immediate post-fire demography of R. fuscipes reflected the model derived from food shortage + cover shortage, with food shortage and increased predation acting in the longer term. R. lutreolus responded to food shortage and food shortage due to immigration. A. stuartii (= A. agilis) and A. swainsonii best fitted the steady state model in the short term, although some evidence indicated that food shortage due to immigration and increased predation may be important.

Thus, the availability of food is likely to become a limiting factor for many small mammals in fire-affected habitat because of the widespread removal of the herb and shrub layer, leaf-litter, bark and invertebrate fauna (Leonard 1972, 1974). However, no studies have previously attempted to experimentally manipulate food levels to test whether the availability of food is a limiting factor in the post-fire environment.

1.3.2 Cover supplementation

Habitat features, such as vegetative cover or nest site availability, have been associated commonly with small mammal abundance but rarely manipulated to demonstrate causal relationships. The response of mammals to the removal and subsequent regrowth of vegetation by fire, logging or mining has been considered by several authors (see section 1.2.2.2), and correlations made between certain species and particular habitat parameters. No authors have previously tested the validity of these correlations by the experimental manipulation of those features. This is quite easily understood. To add or remove
vegetative cover between 0 and 50 cm, for example, over an area that would cover the
home ranges of several study animals, would be difficult without causing other habitat
alterations. To remove cover in this range would cause significant ground disturbance,
perhaps affecting survival of invertebrates and thus depleting a food source.

Fox et al. (in review) and Monamy (unpubl.data) have recently had some success in
overcoming this problem by tying branches of heath vegetation closer to the stem of the
plant, thus reducing the projected cover of the plant without the removal of biomass. Wolff
et al. (1997) reduced cover availability to Microtus canicaudus populations by mowing, and
found that regardless of the pattern of habitat fragmentation, vole population size,
reproductive rates, juvenile recruitment and juvenile emigration did not differ between sites
with only 30% retention of cover and control sites with 100% cover. In fact, abundance on
all sites continued to increase (Wolff et al. 1997). However, mowing is not practical in
most natural habitats, and results in an overall loss of biomass. The alternative strategy of
adding natural cover is also impractical, as this could not be accomplished without adding
extra seed, fertiliser or an artificial cover source. Further, establishing control treatments
for these manipulations would be very difficult.

Nest site availability is somewhat easier to manipulate. Artificial nestboxes are
easily constructed and are used readily by small mammals (Wardell-Johnson 1986; Bladon
1995). Wardell-Johnson (1986) found differential use of nestboxes by A. flavipes in karri
forest of different logging history, but concluded that nest site availability was not a limiting
factor in any logging treatment. Leung (1994) provided nest-hollows for A. leo, M.
capensis and R. leucopus in rainforest on Cape York Peninsula, and concluded similarly that
nest availability was not a limiting factor in that environment. The manipulation of nest site
availability in burnt sites has not been attempted previously.

1.4 AIMS OF THIS STUDY

The general aim of this study is to clarify many of the issues raised by previous
authors regarding the response of small mammals to resource availability in post-fire forest
habitat. Further, although fire has occurred historically at frequent but irregular intervals
across the Australian landscape (Chapter 2), the effect of fire frequency has been rarely
investigated or considered in relation to research into single fire events. As such, the research presented in this thesis aims to investigate the mechanisms of response of small mammals to fire, in relation to resource availability and fire regime.

Specifically this study aims to:

- identify trends in richness and abundance of plants, invertebrates and small mammals under different fire frequency regimes (Chapter 3);
- determine the immediate response of small mammals to fire, and identify fire-induced mortality and shifts in micro- and macrohabitat use (Chapter 4); and
- quantify, by experimental manipulation, the effects of food and nest site availability on the recovery of small mammal populations living in dry sclerophyll forests affected by bushfire (Chapters 5 to 9).

The thesis is structured by presenting primary data relating to these specific aims in Chapters 3 to 9. Chapter 2 introduces the study site, while Chapter 10 discusses the overall implications of the results and draws general conclusions.
CHAPTER 2: STUDY SITE DESCRIPTION

2.1 INTRODUCTION

In January 1994 bushfires, spreading from in excess of 800 ignition points, swept across approximately 800 000 hectares of coastal New South Wales, Australia (Koperberg 1994). Fire intruded into the Sydney metropolitan region on an unprecedented scale, destroying over 300 buildings and killing 4 people (Anon. 1994). Fires in National Parks surrounding Sydney, including Ku-ring-gai Chase, Garigal, Royal, Lane Cove, Marramurra, Blue Mountains and Brisbane Waters were controlled along their urban interfaces, but largely left to burn within their boundaries. Consequently, large areas of bushland were burnt.

Ku-ring-gai Chase National Park was chosen as the principal study site for this work. It is located on the northern outskirts of Sydney, and is 14 700 hectares of bushland with a history of frequent and extensive wildfires (Conroy 1996). It is considered to be one of the most fire-prone areas in Australia due to its steep slopes, narrow valleys, highly flammable fuel types and regular extreme fire danger weather conditions (Conroy 1996). The Park has been a designated reserve since December 1894, and, as such, has been protected from the grazing and development that has altered most other remaining areas of Sydney bushland.

2.2 GEOLOGY AND GEOGRAPHY

The geology of the Sydney region is dominated by Triassic sedimentary shale and sandstone. The Sydney region occupies the central portion of the Sydney Basin, a larger geological area characterised by mid-Triassic Narrabeen shales and sandstones (Baker et al. 1986). These are overlain in the Sydney region by the younger Hawkesbury sandstone, which in lower areas is covered by Wianamatta shale. About 10 million years ago these deposits uplifted to form the sandstone plateaux that now dominate the region; the Hornsby, Blue Mountain and Woronora plateaux (Baker et al. 1986). Wianamatta shale still overlies the sandstone on some ridges and high points although most has weathered away (Fairley 1972). During the uplifting process rivers carved deep valleys into the soft sandstone; these
valleys flooded when sea levels rose at the end of the last ice age, approximately 12,000 years ago (Fairley 1972).

Ku-ring-gai Chase National Park (Figure 2.1) is located on the Hornsby Plateau, bordered to the north by the drowned river valleys of the Hawkesbury River and to the south by a shale-topped plateau now developed as Sydney’s northern suburbs. The Park is characterised by a Hawkesbury sandstone plateau that drops steeply to the west, north and east into the surrounding river valleys. The plateau is generally 150 - 215 m in elevation, with slopes of 10 - 15°. Large sandstone outcrops dominate the landscape (Conroy 1996).

The sandstone soils of the Park are shallow, infertile and have low water holding capacity (Chapman and Murphy 1989; Conroy 1996). Uniform sands and podsols are common, although patches of yellow podsols occur on hillsides where shale-derived clay is covered by sand. More fertile soils such as igneous clays or Wianamatta shale-derived red podsols are scarce (Baker et al. 1986).

2.3 VEGETATION

The dominant vegetation types of Ku-ring-gai Chase National Park are woodlands, dry sclerophyll or open forest and, in more exposed areas, heath. The woodlands and dry sclerophyll forests are mixed eucalypt communities growing on ridge tops and slopes. The openness of the canopy and low height of the trees (generally between 5 and 30 m) reflect the nitrogen and phosphorus-poor soils, high water stress, exposure to high temperatures and winds, and the frequent fire history of the area (Baker et al. 1986). The canopy cover varies from 10 - 30% in ridgetop woodlands, to 30 - 70% in sheltered open forests (Baker et al. 1986). Dominant species include scribbly gum, *Eucalyptus haemastoma*, smooth-barked apple, *Angophora costata*, yellow bloodwood, *Eucalyptus eximia*, red bloodwood, *Eucalyptus gummifera*, and old man banksia, *Banksia serrata*. The incomplete canopy cover also allows the development of structurally complex and diverse shrub and herbaceous layers (Baker et al. 1986).
“Long-track” fire trail

\[\begin{align*}
\text{N} \\
\uparrow
\end{align*}\]

Figure 2.1 Map of Ku-ring-gai Chase National Park showing the Lambert Peninsula (West Head) and Bobbin Head. Also shown is Garigal National Park.

(AMG 340 000mE, 6280 000mN: Broken Bay 9130-1-N, 1:25 000)
Chapter 2: Study site description


Mechanisms of response by Australian plants to fire have been well documented (see Keith 1996 for review). Plant species from fire-prone environments use a number of strategies to regenerate after a fire. Obligate seeders are species in which fire kills most or all of the standing plants and regeneration is dependent upon seed (Gill 1975). Many of these species store their seed in the canopy; the heat of the fire opens the seed cones, allowing the seed to fall out after the fire has past. Dormant seeds may similarly remain part of the soil seed bank until heat and/or a chemical reaction to smoke cause their germination (Keith 1996). Other species, resprouters, have the capacity to survive fire by harbouring buds under their bark (epicormic) or under the ground (rhizomes) that produce leaves soon after the fire, allowing the plant to begin photosynthesis and re-establish the energy store required to grow a new canopy (Gill 1975). Morrison (1995) further identified passive fire tolerators; species whose growth form allows their canopy to be held high above usual scorch height, and whose thick bark protects the vascular tissues.

2.4 Fire History: Pre-European Settlement

The use of fire by Aboriginal Australians to promote growth of food plants for themselves and prey animals, to clear land for hunting and travelling, and for spiritual reasons, was once widespread and is still practised in some regions of northern Australia today. Large tracts of land were burnt regularly; in some regions annually. Burning was not indiscriminate. Fire-sensitive habitats were protected, and fires not ignited unless in optimal conditions (Clark and McLoughlin 1986).
In the Sydney region, Aboriginals commonly used fire to clear areas and promote regrowth. Early settlers in the region often noted the extent of the fires. Hunter (p. 43, 1793) wrote that Aboriginals “set the country on fire for several miles extent...fires, which we very frequently saw particularly in the summer-time”. He added further that the Aboriginals “generally took the advantage of windy weather for making such fires, which would of course occasion their spreading over greater extent of ground.” (p. 55, 1793). An analysis of historical and biological records from the Sydney region indicates that sandstone country was burnt every 7 to 15 years, whereas shale ridges were burnt every 1 to 5 years (Clark and McLoughlin 1986).

The effect of this burning on the Sydney bushland was notable. Hunter (p. 53, 1793) described land near the opening of Sydney harbour, approximately 20 km from Ku-ring-gai Chase, as “the trees stand very wide of each other, and have no underwood: in short the spot I am speaking of resemble a der (sic) park”. He went on to describe extensive tracts of this open “deer park” landscape. Europeans acted to suppress the fires and “thick forests of young trees...(grew)...where, formerly, a man might gallop without impediment, and see whole miles before him.” (Mitchell p 413, 1848).

Ku-ring-gai is named after a local tribe of Aboriginals, the Guringai. They were among several groups living on the Hornsby plateau before European invasion in 1788. Their use of the land now comprising Ku-ring-gai Chase National Park is well documented by over 180 galleries of rock engravings, 15 groups of cave paintings and other sites such as middens within the Park boundaries. They are thought to have persisted in the area until about 1850 (Fairley 1972).

Martin (1971) recorded pollen of the fire-sensitive, and now regionally extinct, genera *Ackama*, *Nothofagus* and *Rhodomyrtus* in 4000 year old sediment from a lagoon near Ku-ring-gai Chase. Kodela (1984) identified charcoal sediments in deposits from within the Park starting approximately 4200 years ago and peaking 2300 years ago, with major influxes caused by high frequency or high intensity fires occurring 1700, 1300, 400, and 300 years ago. This would indicate an increase in fire activity, presumably associated with Aboriginal activities, about 4000 years ago that led to the local extinction of fire-
sensitive species, and presumably the establishment of the landscape noted by early Europeans. Sydney region Aboriginals were removed from their land by European settlement and disease. Thus the regular burning of the land ceased shortly after the arrival of Europeans, undergrowth increased and the vegetation changed toward the more familiar Australian bush as we understand it today. The effect of this upon the fauna is unknown, although Burbidge (1985) found that the disappearance of medium-sized mammals in some areas of Western Australia coincided with the movement of Aboriginals into settlements. Further, in those areas where traditional burning practices were maintained, the mammals remained (Burbidge 1985). The Sydney landscape, even after the departure of the Aboriginals, has continued to be modified by frequent wildfires.

2.5 Fire history: post-European settlement

Ku-ring-gai Chase Trust records (prior to 1967) and National Parks and Wildlife Service records (post 1967) indicate extensive wildfires (> 500 ha) in the Park in 1943, 1946, 1951, 1958, 1965, 1968, 1977, 1979, 1980, 1983, 1990 and 1994 (Conroy 1996). The largest of these was the January 1994 fire which covered an area of 7110 ha (Figure 2.1). In 1986 Conroy (1987) estimated that 25% of the vegetation of the Park was older than 21 years; after the 1994 fires he reduced this estimation to roughly 1% (Conroy 1996). Conroy (1996) also reported an increase in “shrubiness” in the nature of the vegetation since the early 1970’s and attributed this to the reduction in frequency of bushfires, and increased effectiveness of fire suppression and fire prevention.

Natural sources of ignition, such as lightning, account for < 5% of ignitions and only 1.3% of the total area of Ku-ring-gai Chase burnt by bushfires since the early 1940’s. Arson has been established as the cause of 40.8% of ignitions, and if combined with the number of fires of “unknown” cause, 57% of fires in the park can be regarded as a result of intentional or careless behaviour (Conroy 1996). Unattended campfires and powerlines also contribute significantly to the number and extent of fires in the Park (Conroy 1996).

Prescribed burns, also called fuel reduction or control burns, are conducted during the cooler months, generally from April to September in the Sydney region. They are usually low intensity, slow moving, patchy and have low scorch height. Their purpose is to
remove accumulated ground fuel, and not to affect canopy cover. Since 1974, prescribed burning for management purposes has concentrated largely along the Park’s urban interface. There are no records of prescribed burns in Ku-ring-gai Chase prior to this. The average size of these burns is 86 ha (Conroy 1996).

Of 30 prescribed burns in Ku-ring-gai Chase National Park in the 5 years prior to the 1994 bushfires, 76% were located along the urban interface. Of the total Park area of 14700 ha, 19.6% had been prescribed-burned and an additional 9.4% affected by bushfire during that period. Therefore, when the January 1994 bushfires occurred, almost 30% of the Park contained a fuel load that was less than 5 years old (Conroy 1996). Even so, many of the same areas were burnt.

2.6 Ku-ring-gai Chase National Park: Recent Fire History

Between 27 December 1993 and 16 January 1994, extreme fire weather was experienced in the coastal plains and ranges from Batemans Bay in southern New South Wales, north to the New South Wales/Queensland border. Many small fires started early in this period but were largely contained or considered too distant from development to warrant full suppression. By 2 January 1994, however, many large fires were out of control along the coast and the Sydney metropolitan district was experiencing conditions of very high fire danger (Anon. 1994).

The fire danger index (FDI) is expressed as a rating between 0 and 100, and is based on a combination of drought, recent precipitation, time since rain, current temperature, wind speed and humidity factors (Gill and Moore 1996). A FDI of 0 means a fire will not burn, whereas a FDI of 100 is the worst combination of these factors. Extreme fire weather is defined as when conditions combine to give a FDI ≥50. Depending on fuel load, under conditions of FDI 50 or greater, flame height is expected to exceed 15m, crown fires will develop and broadscale fire suppression is impossible (Anon. 1994).

Between 6 and 8 January, 231 new ignitions were reported in NSW, of which an "unprecedented proportion" appeared to be deliberately lit (Anon. 1994). The maximum FDI in the Sydney region during this period was 96, reached on 8 January at 1800 hrs
(summertime), with westerly winds of 50 km/hr, temperature of 35°C and relative humidity of 9% (Anon. 1994). Intense fire conditions continued until 9 January when conditions began to ease. All fires in NSW were contained by 16 January.

On 7 January 1994 48% of Ku-ring-gai Chase National Park was burnt. The fire was concentrated on Lambert peninsula (Figure 2.1) and predominantly affected open forest, woodlands and heath of the plateau and eastern slopes. Some hanging swamps, rainforest gullies and recently prescribed-burned woodland and open forest on the western side of the peninsula were not affected. Fire was prevented from spreading west towards Bobbin Head by fire suppression along the "Long Track" fire trail (Figure 2.1).

2.7 CONCLUSION

The 1994 fire in Ku-ring-gai Chase National Park provided an ideal opportunity to study the effects of intense fire on mammals. The well documented fire-history of the area, in addition to the large areas of sclerophyll forest and woodland both burnt and unburnt by the fire, allowed the aims of this research to be addressed with adequate replication and the establishment of control sites. Details are provided in the following chapters of experimental site locations and their specific fire history (refer to Sections 3.2.1 and 5.2.1). Field work began in August 1994, 7 months after the fire.
CHAPTER 3: EFFECT OF FIRE FREQUENCY ON VEGETATIVE COVER, TERRESTRIAL INVERTEBRATE ABUNDANCE AND RICHNESS, AND SMALL MAMMAL ABUNDANCE IN KU-RING-GAI CHASE NATIONAL PARK

3.1. INTRODUCTION

Historically, fire has occurred at frequent intervals across the Australian landscape (Chapter 2), yet most bushfire studies in Australia have concentrated upon biotic responses to the most recent single fire events (Whelan 1995; Woinarski and Recher 1997). The effects of the total fire regime, including frequency, intensity, extent, and season of fire, have received little attention. However, certain aspects of fire regime have been studied independently. Questions concerning the effect of fire intensity and season upon plants and animals have been addressed using comparisons between control or prescribed burns (low intensity fires during autumn and winter) and summer bushfires (e.g., Catling 1991; Brooker and Brooker 1994; Tolhurst 1996). The effect of fire frequency, however, has received less attention, and although information exists on the effect of fire frequency upon some plant, invertebrate and avian communities, very little is known about the response of Australian mammals or other vertebrates to a frequent fire regime. The aim of the research presented in this chapter is to identify patterns of response of vegetation, invertebrates and small mammals to different numbers of fires in eucalypt forest over a 20 year period.

3.1.1 WHAT IS FIRE FREQUENCY?

Fire frequency is the average number of fires occurring over a given time period, and is one of the factors constituting the fire regime of an area (Gill 1975, 1981). Other features of fire regime include fire intensity, season, extent (or patchiness) and the type of fire (i.e., entirely above ground, or also consuming the soil organic layer) (Gill 1975, 1981; Whelan 1995). Fire frequency has been further divided into fire interval (time between fires) and fire period [fire interval averaged over a series of fires, or “average fire interval” (Johnson 1992)] (Fox and Fox 1987).

The potential fire frequency of a site will depend primarily upon the time required to build up a fuel load able to sustain a fire, frequency of ignition, and climatic conditions
(Whelan 1995). Fuel management and fire suppression policies, therefore, can alter the frequency and thus fire regime of an area. This, in turn, may influence the biota of an area. Frequent low intensity control burning to keep fuel loads at a minimum, for example, may prevent the regeneration of plant species that require high temperatures for seed germination (Christensen and Kimber 1975; Recher and Christensen 1981; Benson 1985). Likewise, the same plant species may be prevented from regeneration by a policy of fire suppression. A balance between these two extremes of fire management is required to sustain viable local populations of many plant and animal species.

3.1.2 The response of vegetation to frequent fire

Gill et al. (1981) identified two basic strategies of vegetative response to fire. Fire-sensitive species are those that are killed by 100% leaf scorch during fire, and rely upon germination of new seedlings from a seed bank held either in the soil or the canopy, or on the dispersal of propagules from unburnt areas, to re-establish populations in the post-fire environment (Gill et al. 1981). Fire-tolerant species, on the other hand, may also suffer total canopy removal, but survive fire via a range of regenerative mechanisms including epicormic shoots, protected apical meristems, lignotubers, rhizomes and bulbs (Gill et al. 1981).

A high fire frequency may prevent the successful recruitment or regeneration of plants by disrupting life-cycle processes. As all fire-sensitive plants are killed by fire, the between-fire interval must be long enough to allow the new generation of seedlings to mature and produce seed. Particularly for plants with a canopy seed bank, which release all of their seeds after a fire, more than 2 fires within the period that it takes for the plant to mature can cause local extinctions unless at least one of the fires has a patchy distribution (Benson 1985; Cowling et al. 1990; Auld 1994). Similarly, species with a soil seed bank, of which 20 - 100% germinate after a fire, may undergo population reduction and perhaps extinction during periods of high fire frequency. Within the Hawkesbury Sandstone vegetation, as found at the field sites used in this study, research indicates that shrub species are able to replenish their seed banks over periods ranging from 1 to 9 years (Benson 1985; Auld and Myerscough 1986). However, there is considerable variation in rates of maturation within communities, populations and after different fire events. In addition,
Bradstock et al. (1995) suggested that variation in fire frequency and occasional fires after a short between-fire interval, may be tolerated and even promote species diversity within a community.

Similar to the maturation and subsequent seed-set of fire-intolerant species, the development of resprouting mechanisms, such as epicormic buds, protected apical meristems, lignotubers, rhizomes and bulbs may take several years in fire-tolerant species. Frequent fires, however, may not allow for these characteristics to develop to a size that would allow for the regeneration of these plants after successive fires. For Hawkesbury Sandstone flora, Auld (1990) and Bradstock (1990) suggested that the development of lignotubers may take between 5 and 15 years, depending on the species. Generally, however, the time required for the development of regenerative structures is largely unknown, and probably tied to a range of species-specific, environmental and historical conditions.

Morrison et al. (1995) studied the effects of fire frequency, inter-fire interval and time since fire in the dry sclerophyll forests of Ku-ring-gai Chase, Brisbane Water and Royal National Parks in the Sydney region. Fire frequency was determined as the major source of within-community variability in the relative abundances of the dominant herb, shrub and tree species. Both the time since the most recent fire, and the interval between fires over recent (< 30 years) history, were shown to influence the floristic composition of the community. With increasing time since fire there was a decline in relative abundance of fire-tolerant species in the community. Declining between-fire interval (increasing fire frequency) led to decreases in the relative abundance of fire-sensitive species, however, the effects were found to be more complicated than previously demonstrated, with increasing variability in between-fire interval associated with increased species richness of both fire-tolerant and fire-sensitive species (Morrison et al. 1995).

As a consequence of frequent fires, overall floral species loss may lead to a loss of biodiversity and the simplification of community structure. In addition, Catling (1991) suggested that high fire frequency causes a simplification of forest structure. As such,
frequent fires may have an associated effect upon the biodiversity and species assemblages of fauna.

3.1.3 The response of invertebrate fauna to frequent fire

Although Friend (1996) suggested that invertebrates have an overall resilience to fire over a wide range of habitat and climatic gradients, there is little information concerning the effects of fire frequency upon invertebrate fauna. Those studies that have been conducted lead to the prediction that high fire frequency reduces both abundance and species richness through the removal of the leaf litter, foliage and soil organic layer. Springett (1976), in a study of soil fauna in *Eucalyptus* spp. forest in south-western Australia, found reduced invertebrate densities and species richness in a frequently burnt site when compared to a long unburnt site. She attributed the difference to the reduced fuel load and soil organic matter in the regularly burnt patch. Unfortunately, interpretation of this study is hindered by a lack of site and temporal replication.

Similarly, York (1996) found, in an experiment comparing sites with a 20 year history of frequent control burning with a long unburnt site, that frequent fire led to a reduction in the abundance of springtails (Collembola), ticks and mites (Acarina), slaters (Isopoda), beetles (Coleoptera), flies (Diptera), and insect larvae. However some groups, such as spiders (Araneae), bugs (Hemiptera) and ants (Hymenoptera: Formicidae) increased significantly in abundance after frequent fires. The largest increase in abundance was of ants, where there were approximately 250% more individuals on frequently burnt sites than on unburnt sites. Although species richness was not altered by frequent burning, species assemblages did differ between treatments. Ant communities in frequently burnt areas were dominated by species with broad, omnivorous diets and generalist habitat requirements, whereas the community in long unburnt forest included seed eating species, and species with a specialist requirement for deep leaf litter and/or moist soil (York 1996).

A number of studies have indicated that the recovery of invertebrate populations after fire is rapid, with abundance sometimes surpassing pre-fire levels within the first one or two years (Christensen and Kimber 1975; Catling and Newsome 1981; Recher and Christensen 1981). Bock and Bock (1991), after measuring an initial 60% decline in
Acrididae abundance after fire in native grassland, noted that abundance returned to control levels by the second year after fire. This rapid response is attributable to the fire-induced release of nutrients and rapid vegetation regrowth (Smith 1989). However, rate of population recovery appears to decrease with increasing fire intensity (Smith 1989).

3.1.4 The Response of Vertebrate Fauna to Frequent Fire

3.1.4.1 Birds

Most of the evidence concerning the effects of fire frequency on vertebrates comes from studies of avian communities. Regularly burnt habitats may not provide the food, cover or nesting resources required by some birds. Meredith et al. (1984) suggested that the seed-eating ground parrot, Pezoporus wallicus, did not colonise heath until plants were mature enough to provide substantial food resources. Similarly, the rufous-crowned emu-wren, Stipiturus ruficeps, and the striated grass-wren, Amytornis striatus, are restricted to long unburnt hummock grasslands by a requirement for large clumps of hummock grass for nesting, and an insectivorous diet (Woinarski and Recher 1997). Reilly (1991) noted a parallel increase of invertebrate and avian abundance after fire, but did not demonstrate any causal relationship. Smith (1989), on the other hand, suggested that the recovery of a forest bird community after fire did not appear to be related to invertebrate availability.

One of the few long term studies in Australia to consider the effect of fire regime, including fire frequency, season, intensity and extent, on fauna, is that of Rowley and Brooker (1987), Brooker and Rowley (1991), Russell and Rowley (1993) and Brooker and Brooker (1994), who studied the heath-dwelling splendid fairy-wren, Malurus splendens for 18 years. Using demographic information collected over the duration of the study, Brooker and Brooker (1994) were able to model the fire effects upon this species. They showed that fire frequency and extent can drive local populations to extinction, and that timing of fire in relation to the breeding season may be more influential on population numbers than fire intensity.

Too-frequent fires appear to cause substantial reductions of avian populations (for review see Woinarski and Recher 1997). *P. wallicus*, and possibly the eastern bristlebird, *Dasyornis brachypterus*, are no longer resident in the regularly burnt heathland of Royal
National Park, N.S.W., due to a combination of reduced habitat suitability and diminished immigration due to geographic isolation (Baker 1997; Woinarski and Recher 1997). Similarly, Adam and Robinson (1996) found fewer grey-crowned babblers, *Pomatostomus temporalis*, on regularly burnt road verges than on unburnt verges, and attributed this to a fire-induced reduction of shrub cover.

### 3.1.4.2 Mammals

Considering the substantial literature on the effects of fire upon mammals, particularly small mammals, in Australia, relatively little attention has been paid to the effects of fire regime. Although seasonality and intensity of burning have been considered to some extent (e.g., Christensen and Kimber 1975; Thompson *et al.* 1989; Catling 1991; White 1992), the effect of repeated fires has rarely been investigated (Wilson 1996).

Newsome *et al.* (1975) and Catling (1986), presented data from two consecutive fires at the one location. The initial fire caused dramatic reductions in small mammal abundances, after which the previously unrecorded *Mus domesticus* reached peak densities 2 - 3 years after the fire, *Rattus fuscipes*, *R. lutreolus* and *Antechinus stuartii (= A. agilis)* peaked after 5 years, and *A. swainsonii* re-appeared only in year 6 after the fire (Newsome *et al.* 1975). All species remained present after the second fire, 8 years after the first (Catling 1986), although the structural habitat complexity was greatly reduced across much of the area and animals were found mainly in those patches with greatest complexity. These studies, however, did not consider previous fire history of the sites and Catling (1986) did not attempt to draw comparisons between areas burnt in 1972 and 1980, with those burnt only in 1980.

Catling (1991), in a review of prescribed burning practices in southeastern Australian forests, identified 25 species of mammals (excluding Chiropterans) that he considered would be disadvantaged by the habitat changes caused by high frequency fire. A regime of frequent, low intensity fires, would reduce forest complexity by reducing the height and cover of ground and shrub cover. Species reliant upon dense shrub or ground cover, or a high percentage cover of leaf litter, would therefore be unsuited to forests with a high fire frequency regime (Catling 1991). Kerle (1985) suggested additionally that high
fire frequency has led to low population densities of the northern brushtail possum, *Trichosurus arnhemensis (= T. vulpecula)* in northern Australia, due to a reduction in the number of suitable nesting hollows.

### 3.1.4.3 REPTILES

The response of Australian reptiles to fire has generally been measured only in terms of the effect of single fire events on particular species (e.g., Newsome *et al.* 1975; Fyfe 1980; Caughley 1985; Braithwaite 1987; Lunney *et al.* 1991). Humphries (1992) reported the effects of single spring and autumn control burns on eight species of skink. Species that showed the greatest population fluctuations were those with a reliance upon leaf litter for food and shelter, and those that use fallen logs. Both these habitat features are likely to be reduced by a frequent fire regime, and thus to detrimentally affect the abundance of dependent species (Tolhurst 1996).

### 3.1.4.4 AMPHIBIANS

The effect of repeated fires upon amphibians in Australia has never been studied directly, although some inferences from another study undertaken after a single fire may be made. Bamford (1992) noted that *Limnodynastes dorsalis* and *Myobatrachus gouldii* were uncommon on recently burnt sites and reached maximum abundances in long unburnt areas. Both are burrowing species and can therefore escape immediate mortality during the fire by sheltering underground (Main 1981; Bamford 1992; Friend 1993). After fire their distribution, activity patterns and breeding are linked closely to moisture availability rather than vegetation structure or pyric succession (Bamford 1992). Friend (1993), however, suggested that a well-developed ground and shrub layer may ameliorate aridity and exposure, preventing moisture loss and thus encouraging amphibians in late successional stages.

### 3.1.5 AIMS

Woinarski and Recher (1997; p.192) stated that "Consistent and frequent burning is likely to lead to sustained and possibly irreversible, changes in understory floristics and structure, including decline in litter and increase in weeds (Cowley 1971; Recher and Serventy 1991), loss of logs and hollow trees and ultimately to changes in recruitment."
patterns for canopy trees’. This, in turn, will lead to associated changes in faunal populations and communities. Inter- and intraspecific interactions may lead to similarly irreversible changes in faunal species through processes of local and regional extinction. The increased fire frequency associated with control burning regimes and proximity to urban development (Conroy 1996) is therefore a significant management issue for bushland areas, particularly those areas around human settlements.

The aims of this chapter are to investigate the effects of varying fire frequency in open *Eucalyptus* forest upon:

- herb, shrub and tree cover;
- invertebrate abundance and richness;
- small mammal abundance; and
- the association between small mammals and cover (vegetation) and food (invertebrate) variables.

### 3.2 Methods

The effect of fire frequency upon the biota of Ku-ring-gai Chase National Park (refer to Chapter 2 for site description) was investigated by surveying the vegetation, terrestrial invertebrates and small mammals in twelve sites burnt during the January 1994 bushfires, and which had a history of either 0, 1, 2 or 3 other fires during the preceding 20 years. Thus, replicate sites were established representing a fire frequency of 1, 2, 3, and 4 fires over a 20 year period. Vegetation and mammal data were collected at each site from 29 January to 2 February 1996 and from 20 to 24 January 1997, whereas invertebrate data were collected over the seven days immediately after each of these periods.

#### 3.2.1 Site selection and establishment

Twelve sites were selected in the Sydney Sandstone Complex, Open-forest and Woodland (Benson and Howell 1994) vegetation communities of Ku-ring-gai Chase National Park, using vegetation (Thomas and Benson 1985; Benson and Howell 1994), fire coverage (NPWS 1994) and topographical (Anon. 1985) maps, and ground truthing, to maximise site similarity (Figure 3.1). To ensure independence, no two sites were located within the same continuous patch of vegetation and/or fire history. The time since the most
recent fire was consistent among all sites, although the time between the other fires during the 20 year period was variable between sites (Table 3.1). Within each site a 240 m transect was established, with 25 trapping stations for mammals marked at 10 m intervals along its length.

Table 3.1: Frequency and between-fire interval of fires at each site in Ku-ring-gai Chase National Park. Note that the Years refer to the new year of that summer fire period, so that 1978, for example, refers to the fire period ranging from approximately November 1977 to March 1978.

<table>
<thead>
<tr>
<th>Site</th>
<th>No. fires</th>
<th>Year: 19--</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>78</td>
<td>79</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>x</td>
</tr>
<tr>
<td>7</td>
<td>1</td>
<td>x</td>
</tr>
<tr>
<td>12</td>
<td>1</td>
<td>x</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>x</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>x</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>x</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>x</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>x</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>x</td>
</tr>
<tr>
<td>8</td>
<td>3</td>
<td>x</td>
</tr>
<tr>
<td>9</td>
<td>4</td>
<td>x</td>
</tr>
<tr>
<td>11</td>
<td>4</td>
<td>x</td>
</tr>
</tbody>
</table>

3.2.2 DATA COLLECTION

3.2.2.1 VEGETATION AND ROCK

3.2.2.1.1 HERB, SHRUB AND ROCK COVER

Along the transect at each site, ten 2 m x 2 m quadrats were established at 20 m intervals and on alternate sides along the transect. To ensure independence of data between years, the first quadrat was located at Station 1 in 1996, and at Station 2 in 1997. Within each quadrat pre-fire shrub cover, post-fire shrub cover, post-fire herb cover and the cover of both “useful” and “embedded” rock (see below) was noted.

“Shrubs” were defined as plants with woody stems, less than 4 m in height, whereas “herbs” included all plants without a woody stem, including “true” herbs, grasses and seedlings. Pre-fire shrub cover was estimated very approximately by recording the number of burnt stems (dead and alive) within the quadrat. The maximum height of the burnt stems within the quadrat was also noted. Post-fire shrub cover and herb cover were scored using a cover abundance score relating to the percentage cover of all species combined within the
quadrat (Table 3.2). Although coarse, cover abundance scores were considered appropriate as different personnel were involved in vegetation assessment.

Table 3.2: Table of cover abundance scores in relation to percentage cover of habitat variables within a quadrat.

<table>
<thead>
<tr>
<th>Percentage cover (%)</th>
<th>Cover abundance score</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 5</td>
<td>1</td>
</tr>
<tr>
<td>5 - 20</td>
<td>2</td>
</tr>
<tr>
<td>21 - 50</td>
<td>3</td>
</tr>
<tr>
<td>51 - 75</td>
<td>4</td>
</tr>
<tr>
<td>76 - 100</td>
<td>5</td>
</tr>
</tbody>
</table>
Figure 3.1: Site location and fire frequency history of Ku-ring-gai Chase National Park.
(AMG 340 000mE, 6280 000mN; Broken Bay 9130-1-N, 1:25 000)
Chapter 3: The effect of fire frequency on flora and fauna

Rock cover was divided subjectively into two categories based on the perceived "usefulness" of the rock from a small mammal's perspective. Rock with crevices or overhangs that could provide refuge, runways, nesting or burrowing sites was considered "useful". Embedded rock, without any of the above structural features, was considered "useless" to small mammals. Indirect relationships between, for example, the percentage cover of rock and the abundance of a food type that may influence small mammal abundance, were not considered. Thus rock cover was considered as either providing structural shelter or not, and is therefore comparable to vegetative cover measurements. Useful and embedded rock cover were recorded for each quadrat using the cover abundance scores listed in Table 3.2 with the addition of a 6th category for absent.

3.2.2.1.2 TREE COVER

Trees were defined as plants 4 m or over in height, either dead or alive. One 20 m x 30 m quadrat was established between Stations 10 and 13 along each transect. Within the quadrat we noted the number of trees, the species, if they had basal, stem or no regeneration shoots, and if they were dead or alive. Percent canopy cover was also estimated at five regular positions in each quadrat.

3.2.2.1.3 DATA ANALYSIS

Within each year, average scores were calculated for all ranked variables among quadrats within each site. These average scores were then used in one-way analyses of variance (ANOVA) to determine the differences between the covers of herb, shrub, canopy and rock between fire frequency treatments. Post-hoc testing using Student-Newman-Keuls (SNK) tests determined which treatments contributed to significant ANOVA results. Average values within sites for unranked data, such as the number of trees, shrub stems and maximum shrub height were also used in analyses. Two-way ANOVA was used to detect any interaction between time and treatment when comparing increases in height and vegetation cover variables between years, between treatments. Data were tested for normality and equality of variance, and transformed where necessary using SigmaStat (Version 1.0, Jandel Corporation 1992). Transformations, where used, are noted in the text. ANOVAs were conducted using JMP (Version 3.1, SAS Institute Inc. 1995). Post-
hoc SNK tests were undertaken where significant ANOVA results had been gained, using SigmaStat.

Pair-wise Pearson product-moment correlations were also calculated between site-averaged vegetation and structural habitat variables using JMP (Version 3.1, SAS Institute Inc. 1995). Sequential Bonferroni corrections were applied to reduce the probability of Type I error in multiple comparisons (Rice 1989).

3.2.2.2 TERRESTRIAL INVERTEBRATES

3.2.2.2.1 TRAPPING AND SORTING

A cylindrical plastic pitfall tube (4 cm diameter, 10cm depth) was placed 5 metres either side of each trapping station; therefore a total of 50 pitfall traps was set at each site. Each pitfall, half filled with a 2% formalin solution, was buried with its lip flush to the ground surface, and left in place with the lid closed for 4 days to reduce the digging-in effect (Greenslade 1973). The pitfalls were then opened for 7 days, after which they were collected and labelled, then removed to the laboratory for sorting.

All samples were transferred to distilled water for sorting, and a reference collection for all Orders was preserved in 70% ethanol. All animals visible under 4x magnification of a dissecting microscope (Olympus) were recorded. Adult individuals were identified to Order, and the Coleoptera, Hymenoptera and Orthoptera were sorted further to Family. Larval specimens (0.53% of total captures) were not identified.

3.2.2.2 DATA ANALYSIS

Due to the disturbance of some traps by mammals and birds, data for each site were calculated on the basis of the number of individuals per undisturbed pitfall. An average total of 44.3 ± 1.4 (SE) pitfalls was sorted from each site in 1996. Heavy rainfall during the 1997 sampling period caused the loss of most samples so the 1997 data are not considered further.

One-way ANOVA was used to determine if there were differences in the total abundance of invertebrates, abundance of individuals in common Orders (see definition in
Section 3.3.2), Families within Orders (Section 3.2.2.2.1), and the ordinal richness between fire frequency treatments. Post-hoc determination of the fire treatments contributing to any significant ANOVA results were conducted using SNK tests. Pair-wise Pearson product-moment correlations were also calculated between invertebrate abundance and ordinal richness, and vegetation and habitat variables. Probability levels were adjusted using sequential Bonferroni corrections (Rice 1989). Data were tested for normality and equality of variance, and transformed where necessary using SigmaStat (Version 1.0, Jandel Corporation 1992). Transformations, where used, are noted in the text. ANOVAs were conducted using JMP (Version 3.1, SAS Institute Inc. 1995), whereas post-hoc SNK tests were carried out in SigmaStat.

Non-parametric multidimensional scaling (MDS) was conducted using PRIMER to determine if invertebrate community structure differed overall at the ordinal level, between treatments. The total data set, including rare Orders (see definition in Section 3.3.2), was used. One-way analysis of similarities (ANOSIM/PRIMER) was then used to test the significance of the dissimilarities between the four fire frequency treatments (Clarke 1993).

As a further test of possible differences in ordinal richness between treatments, Sorensen's coefficient of similarity ($S_r$; Sorensen 1948; Krebs 1989) was calculated for each pairwise combination of the 12 sites. An average $S_r$ was then calculated for each fire frequency treatment interaction. It was expected that sites with a similar fire frequency history (e.g., those with 1 and 2 fires over the preceding 20 years), would have higher average $S_r$ than those with a very different fire frequency history (e.g., those with 1 and 4 fires over the preceding 20 years) (Krebs 1989).

3.2.2.3 SMALL MAMMALS
3.2.2.3.1 TRAPPING AND HANDLING

Each site was trapped with one Elliott live capture trap (10 x 8 x 30 cm) positioned at each of the 25 trapping stations spaced at 10 m intervals along the transect. Traps were baited with a mixture of peanut butter, rolled oats and honey, provided with a handful of non-absorbent cotton wool for bedding, and wrapped in a plastic bag for insulation. The
twelve sites were trapped simultaneously over four consecutive nights in January 1996 and 1997; a total of 1200 trap nights each year.

Two cage live-capture traps (Mascot: 20 x 20 x 60 cm) were also set at each site, at trap stations 10 and 20, over the same periods. Cage traps were baited with half an apple and a slice of bread coated with peanut butter and honey. However, the data from cage traps were very sparse and so are not considered further here.

All animals captured in Elliott traps were identified to species, and their sex, weight and reproductive condition noted. *R. fuscipes* was classified as juvenile or adult on the basis of body mass; females weighing < 50 g and males weighing < 60 g were considered juvenile (Heislers 1980; Woodside 1983). *A. stuartii* males, due to their semelparous breeding cycle (Woolley 1966; Moore 1974; Dickman 1982; Section 7.1), would have all been the same age during the study. Female *A. stuartii* in January populations, on the other hand, may have either been new recruits or breeding females from the previous year. New recruits were considered juvenile as they were recently weaned, and were differentiated from adult females from the lack of pouch development (Woolley 1966; Dickman 1985). Adult female *A. stuartii* had long and discoloured fur around the pouch area and were generally larger than juveniles (Woolley 1966; Dickman 1985).

Animals were given semi-permanent tags, specific to the day of capture, using non-toxic black marker pens (Pentel Co. Ltd.). Thus, although animals were not marked individually, an animal could be identified as a recapture, and the days of previous recapture known. This allowed the number of individuals of each species known to be alive (KTBA; Krebs 1966) within each site to be determined, in addition to population estimates being made (see Section 3.2.2.3.2).

### 3.2.2.3.2 DATA ANALYSIS

Within each year, the numbers of individuals of each small mammal species known to be alive at each site were compared using a one-way AVOVA (JMP Version 3.1, SAS Institute Inc. 1995) to determine if differences existed between fire frequency treatments. Unlike in the analyses of vegetation cover, two-way ANOVAs investigating time (year) as
the second factor could not be computed due to lack of independence of the fixed transects between years. Data were tested for normality of distribution and equality of variance using Sigma Stat (Version 1.0, Jandel Corporation 1992), and transformed if necessary using the same software. All transformations are noted in the text. Post-hoc determination of the treatments contributing to any significant ANOVA results were conducted in SigmaStat.

Data were further analysed to examine firstly, differences in population structure, by comparing the percentage of males and females within sites between treatments, and secondly, differences in age structure by comparing percentages of juveniles and adults within sites between treatments. Data were arcsine-transformed and one-way ANOVA used to compare treatments (JMP Version 3.1, SAS Institute Inc. 1995).

Capture and recapture data were further used to provide population estimates for each site using Petersen's weighted mean technique (Begon 1979). This estimator has a number of assumptions, but it was considered that, given the short period (4 days) over which the data were collected, that these assumptions were likely to have been met. The assumptions are that firstly, there are no births or immigration, secondly, marked animals leave the population at the same rate as unmarked individuals, thirdly no marks are removed, and fourthly, the probability of capturing an individual is the same for all individuals in the population (Caughley 1977). The stochastic Jolly-Seber model (Jolly 1965; Seber 1965; Caughley 1977), was also tested, however with a limited capture period, and relatively few recaptures in some sites, the population estimates were unreliable. The estimated population for each site was used in a one-way ANOVA to compare the four fire frequency treatments (JMP Version 3.1, SAS Institute Inc. 1995). As before, data were tested for normality of distribution and equality of variance using SigmaStat (Version 1.0, Jandel Corporation 1992), and transformed if necessary using the same software. All transformations are noted in the text. Post-hoc testing to establish which fire treatments contributed to significant ANOVA results were also conducted using SigmaStat.

The abundance of small mammals (KTBA) was further correlated (using Pearson product-moment correlations) with measures of vegetation and rock cover, and invertebrate abundance and richness to determine if there were any relationships between the variables.
Correlations were conducted using JMP (Version 3.1, SAS Institute Inc. 1995). Sequential Bonferroni corrections were applied to probability values to take into account the increased likelihood of Type I error resulting from multiple comparisons (Rice 1989).

3.3 Results

3.3.1 Vegetation patterns

Measurements of vegetation were of two kinds; the number of shrub and tree stems over a given area of a site, and the available cover these vegetation types, and herbs provided. Cover measurements included those of pre- and post-fire shrubs, post-fire herbs and forest canopy. For completeness, the other major cover variable at the sites, rock, is included in this section.

3.3.1.1 Cover of shrubs, herbs and rock

The number of pre-fire shrubs (woody stems < 4 m in height, showing signs of fire scars) in 1996 showed a tendency to decrease with increasing numbers of fires over time (Figure 3.2). There was, however, no significant difference in the number of stems between fire treatments in 1996 ($F = 2.064$, df $3,8$, $p = 0.184$; Figure 3.4). By 1997 there appeared to have been a reduction in the number of shrubs recorded in sites of only one fire, although numbers remained consistent with 1996 results in the other fire treatments (Figure 3.2). This reduction in number of stems over time was examined by a two-way ANOVA between year and treatment, however the interaction result was not significant ($F = 1.281$, df $3,16$, $p = 0.315$). Similarly, in 1997 there was also no significant difference in the number of pre-fire shrub stems recorded between treatments ($F = 1.239$, df $3,8$, $p = 0.358$).
Figure 3.2: The average number of pre-fire shrub stems per quadrat, in sites of 1, 2, 3, and 4 fires within the last 20 years. Time since last fire is consistent between all sites. Means are shown + standard error.

The maximum height of the shrub layer was not significantly different between treatments in 1996 ($F = 0.581$, df $3, 8$, $p = 0.644$), or 1997 ($F = 2.700$, df $3, 8$, $p = 0.116$; Figure 3.3), despite apparently rapid growth in sites of lower fire frequency. A two-way ANOVA conducted on the entire data set, using year and treatment as fixed variables, showed that neither of the main effects was significant (Table 3.3). By considering the interaction term, it is further apparent that the rate of growth in the shrub layer was not significantly different between treatments of different fire frequency (Table 3.3).

Figure 3.3: The average height of shrub vegetation, in sites of 1, 2, 3, and 4 fires within the last 20 years. Time since last fire is consistent between all sites. Means are shown + standard error.

Table 3.3: Two-way ANOVA on maximum shrub height between years and different fire frequency treatments.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>treatment</td>
<td>3</td>
<td>2.788</td>
<td>0.074</td>
</tr>
<tr>
<td>year</td>
<td>1</td>
<td>1.816</td>
<td>0.197</td>
</tr>
<tr>
<td>treatment*year</td>
<td>3</td>
<td>0.351</td>
<td>0.789</td>
</tr>
<tr>
<td>error</td>
<td>16</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
In 1996, the percentage cover of shrubs appeared higher in sites with a history of one and two fires over 20 years, than in sites with a history of three or four fires over the same period, however this difference was not significant ($F = 0.643$, df$_{3,8}$, $p = 0.609$; Figure 3.4). By 1997, the average percentage shrub cover had become more consistent between treatments ($F = 2.195$, df$_{3,8}$, $p = 0.166$; Figure 3.4). There was no significant interaction between treatment and year, although cover was greater in sites with 1 and 2 fires than in those with 3 and 4 fires when years were combined (Table 3.4).

![Figure 3.4: Average score for shrub cover, in sites of 1, 2, 3, and 4 fires within the last 20 years. Abundance score of 1 = < 5% cover, 2 = 5 - 20%, 3 = 21 - 50%, 4 = 51-75% and 5 = 76 - 100%. Time since last fire is consistent between all sites. Means are shown + standard error.](image)

**Table 3.4:** Two-way ANOVA on post-fire shrub cover between years and different fire frequency treatments.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>treatment</td>
<td>3</td>
<td>5.300</td>
<td>0.002</td>
</tr>
<tr>
<td>year</td>
<td>1</td>
<td>2.425</td>
<td>0.121</td>
</tr>
<tr>
<td>treatment*year</td>
<td>3</td>
<td>0.346</td>
<td>0.792</td>
</tr>
<tr>
<td>error</td>
<td>16</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The percentage cover of herbs appeared to increase with fire frequency (Figure 3.5). Despite this trend, however, during both 1996 and 1997 there were no significant differences in the amount of herb cover between treatments ($1996$ $F = 1.128$, df$_{3,8}$, $p = 0.394$; $1997$ $F = 1.459$, df$_{3,8}$, $p = 0.297$). Nor was a significant interaction effect between treatment and time detected by two-way ANOVA ($F = 1.943$, df$_{3,16}$, $p = 0.124$). Although this trend appears opposite to that for shrub cover, the percentage cover of herbs and shrubs was not correlated in both 1996 and 1997 ($r = 0.046$, $p = 0.832$).
Figure 3.5: Average score for herb cover, in sites of 1, 2, 3, and 4 fires within the last 20 years. Abundance score of 1 = <5% cover, 2 = 5 - 20%, 3 = 21 - 50%, 4 = 51-75% and 5 = 56 - 100%. Time since last fire is consistent between all sites. Means are shown + standard error.

The percentage of rock cover for 1996 and 1997 was pooled for analyses as it was considered unlikely to have changed either over time, or in response to fire frequency. Rock cover may, however, have had significant interactions with the biota of the area. Figure 3.6a shows that the overall percentage cover of useful rock (refer to Section 3.2.2.1.1 for definition) varied insignificantly across treatments ($F = 1.282$, df $3,20$, $p = 0.308$), and generally provided less than 5% cover across the site. Similarly, the percentage cover of embedded rock did not vary significantly between treatments, and overall covered only a small proportion of the ground area ($F = 0.985$, df $3,20$, $p = 0.420$; Figure 3.6b).

Figure 3.6: Average cover score for rock cover (a = Useful rock, b = Embedded rock), in sites of 1, 2, 3, and 4 fires within the last 20 years. Abundance score of 1 = <5% cover, 2 = 5 - 20%, 3 = 21 - 50%, 4 = 51-75% and 5 = 76 - 100%. Time since last fire is consistent between all sites. Means are shown + standard error.

There were no significant correlations between either useful or embedded rock cover and any of the vegetation variables measured (Table 3.5). As expected, however, an increase in the number of shrub stems was associated with a corresponding increase in
percentage shrub cover, and the percentage covers of useful and embedded rock were correlated positively with each other (Table 3.5).

Table 3.5: Correlation coefficients for vegetation and habitat features. * = p< 0.05, ** = p<0.01 (after Bonferonni correction).

<table>
<thead>
<tr>
<th></th>
<th>no. stems</th>
<th>herb cover</th>
<th>shrub cover</th>
<th>useful rock</th>
<th>embedded rock</th>
</tr>
</thead>
<tbody>
<tr>
<td>no. stems</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>herb cover</td>
<td>-0.220</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>shrub cover</td>
<td>0.427*</td>
<td>0.046</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>useful rock</td>
<td>-0.309</td>
<td>-0.029</td>
<td>0.074</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>embedded rock</td>
<td>-0.100</td>
<td>-0.041</td>
<td>-0.153</td>
<td>0.579**</td>
<td>1.000</td>
</tr>
</tbody>
</table>

3.3.1.2 NUMBER OF TREES AND CANOPY COVER

The common tree species across all sites were Angophora costata, Eucalyptus haemastoma, E. eximia, E. gummifera and Banksia serrata. The number of trees recorded at each site did not differ significantly between treatments in either year (1996 F = 3.271, df 3,8 , p = 0.080; 1997 F = 2.203, df 3,8 , p = 0.165). Figure 3.7 clearly shows, however, that there were considerably more trees in sites that had been burnt only once during the preceding 20 years. The interaction term from two-way ANOVA further demonstrated that the number of trees did not change between fire frequencies over time (F = 0.247, df 3,16 , p = 0.863).

![Figure 3.7: Number of trees in sites of 1, 2, 3, and 4 fires within the last 20 years. Time since last fire is consistent between all sites. Means are shown + standard error.](image)

The percentage canopy cover did not vary significantly between fire frequency treatments in either year (1996 F = 0.244, df 3,8 , p = 0.864; 1997 F = 2.187, df 3,8 , p = 0.167). Between 1996 and 1997 there was considerable growth in the canopy layer (Figure
3.8). However, growth of the canopy between years did not vary with respect to fire frequency history ($F = 0.640$, df$_{3,16}$, p = 0.601), presumably due to high variance in cover between sites.

![Graph]: Percentage canopy cover in sites of 1, 2, 3, and 4 fires within the last 20 years. Time since last fire is consistent between all sites. Means are shown ± standard error.

**3.3.2 Invertebrates**

Over 8000 invertebrates were collected in the week of sampling during 1996. The most common Orders were Acarina (mites and ticks), Araneae (spiders), Coleoptera (beetles), Collembola (springtails), Dermaptera (earwigs), Hymenoptera (ants, bees and wasps) and Orthoptera (crickets and grasshoppers). Orders represented by less than five individuals per site (e.g., archaeognatha, blattodea, chilopoda, isopoda, pseudoscorpionidae) were designated as rare.

**3.3.2.1 Abundance**

The total abundance of invertebrates did not vary between treatments ($F = 2.482$, df$_{3,8}$, p = 0.135). Figure 3.9 suggests that the lowest invertebrate abundances were in sites with a history of 2 fires in the preceding 20 years, although generally variability within treatments was high.
Figure 3.9: Average capture rates of invertebrates per pitfall, across sites of 1, 2, 3, and 4 fires in the last 20 years. Time since last fire is consistent between all sites. Means are shown ± standard error.

Over half (51.4%) of all captures were hymenopterans, and of this group over 99.5% were from the family Formicidae (ants). The abundance of hymenopterans did not differ significantly between treatments (\( F = 1.528, \text{df} \, 3, 8, \, p = 0.280 \)), although this result is due largely to the high variability of data from different sites. Figure 3.10 suggests that the abundance of ants tended to be lower at sites with 2 fires over the preceding 20 years than in any of the other treatments.

Figure 3.10: Average abundance of Hymenoptera (number / pitfall) across sites of 1, 2, 3, and 4 fires in the last 20 years. Time since last fire is consistent between all sites. Means are shown ± standard error.

Given that Hymenoptera were such a large proportion of the captured invertebrates, this group was removed and the data re-examined for overall abundance differences between sites of different fire frequencies. No significant difference in the number of invertebrates, not including hymenopterans, was found between sites of different fire frequency histories (\( F = 0.601, \text{df} \, 3, 8, \, p = 0.633 \)).
The second most common group was Collembola, representing 17.9% of total captures. Although abundance did not vary significantly between treatments ($F = 0.445, \text{df } 3,8, p = 0.728$), Figure 3.11 shows a steady decline in abundance with increasing numbers of fires, until abundance again increases in the 4-fire frequency sites. This result may be an artefact of there being only 2 replicate sites within the 4-fire treatment, although the high variability across other treatments indicates that this group may be responding to other environmental conditions in addition to, or instead of, fire history.

![Figure 3.11: Average abundance of Collembola (number / pitfall) across sites of 1, 2, 3, and 4 fires in the last 20 years. Time since last fire is consistent between all sites. Means are shown + standard error.](image)

The third most abundant group was Orthoptera, making up 8.5% of the total invertebrate capture. The family Gryllidae accounted for 77% of the total captures within this group, although specimens of Gryllacrididae (21%), Acrididae and Tettigonidae were also recorded. There were significant differences in the abundance of orthopterans between treatments ($F = 4.188, \text{df } 3,8, p = 0.047$), with SNK analysis determining that there were more individuals recorded in sites of 3 fires than in other treatments (Figure 3.12). Both Gryllidae and Gryllacrididae showed very similar patterns of distribution to the overall orthopteran distribution (Figure 3.12).
Figure 3.12: Average abundance of Orthoptera (number / pitfall) across sites of 1, 2, 3, and 4 fires in the last 20 years. Time since last fire is consistent between all sites. Means are shown + standard error.

The only other group to vary significantly in abundance between treatments was the Araneae (F = 9.251, df 3,8, p = 0.006). Spiders were most common in 3-fire sites, although there is not a linear relationship with spiders either becoming more or less abundant with increasing numbers of fires over time (Figure 3.13). SNK tests determined that although spiders were higher in abundance at 3-fire treatment than 2-fire treatment sites, the differences between other treatments were less obvious. Given the low variance between replicates within the 1 and 2 fire treatments, however, it may be that fire alters the habitat in such a way that favours different assemblages of species in areas of different fire history. Unfortunately, analysis at species level was not possible during this study to confirm or refute this.

Figure 3.13: Average abundance of Araneae (number / pitfall) across sites of 1, 2, 3, and 4 fires in the last 20 years. Time since last fire is consistent between all sites. Means are shown + standard error.
3.3.2.2 RICHNESS

Thirty Orders of invertebrates were identified during this study. However, there was no significant difference in the number of Orders represented in sites of different fire frequency ($F = 0.216$, df$_{3,8}$, $p = 0.883$). Removing all records of rare Orders (Orders with less than 5 individuals at that site) on the basis that they may represent chance captures or transient animals rather than residents, also resulted in no significant difference in ordinal richness between treatments ($F = 2.030$, df$_{3,8}$, $p = 0.188$).

Non-parametric multidimensional scaling (MDS) upon the entire data set (including rare Orders) was used to determine if the community assemblages differed between treatments. Figure 3.14, a 2-dimensional plot of the sites within treatments, shows a lack of obvious grouping of sites, and thus a lack of similarity of the ordinal assemblages between treatments. The relatively high stress value of 0.20 is associated usually with plots that are difficult to interpret (Clark 1993), and ANOSIM confirmed further that there were no significant relationships in composition of Orders between treatments ($R = 0.173$, $p = 0.14$, 5000 permutations).

![Figure 3.14: Invertebrate abundance within the four fire frequency treatments as shown by a two-dimensional plot of multidimensional scaling (MDS) analysis. Series 1 to 4 indicate fire frequencies 1 to 4 respectively.](image)

This non-significant result is supported further by the pairwise calculation of Sorenesen's coefficient of similarity ($S_o$) between all sites. Table 3.6 presents a matrix of the average $S_o$ for all treatment interactions. Visual interpretation of Table 3.6 indicates that similar treatments (e.g., 1-fire and 2-fire, 2-fire and 3-fire etc.) are no more or less similar
than widely different treatments (e.g., 1-fire and 4-fire). Thus there are no more Orders in common between sites in treatments of similar fire frequency history than between treatments of vastly differing fire frequency history; as such, it may be concluded that fire frequency has no effect upon the ordinal richness of invertebrates in this habitat type.

Table 3.6: Average Sorensen’s coefficient of similarity (S; Sorensen 1948) on invertebrate Order richness between treatments.

<table>
<thead>
<tr>
<th></th>
<th>1-fire</th>
<th>2-fire</th>
<th>3-fire</th>
<th>4-fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-fire</td>
<td>1.000</td>
<td>0.740</td>
<td>0.726</td>
<td>0.727</td>
</tr>
<tr>
<td>2-fire</td>
<td></td>
<td>1.000</td>
<td>0.735</td>
<td>0.733</td>
</tr>
<tr>
<td>3-fire</td>
<td></td>
<td></td>
<td>1.000</td>
<td>0.757</td>
</tr>
<tr>
<td>4-fire</td>
<td></td>
<td></td>
<td></td>
<td>1.000</td>
</tr>
</tbody>
</table>

3.3.2.3 INVERTEBRATE ABUNDANCE AND RICHNESS IN RELATION TO VEGETATION AND ROCK COVER

The total abundance of invertebrates was not correlated significantly with any of the vegetation or habitat features recorded. At the ordinal level, the abundance of dermapterans tended to increase with increasing shrub height \((r = 0.598, p = 0.040)\), and the abundance of coleopterans tended to increase with increasing canopy cover \((r = 0.586, p = 0.045)\), although neither of these associations was significant after Bonferroni correction.

Similarly, the number of Orders (richness) recorded in each site was not correlated with any of the vegetation or habitat measurements, although if those Orders with only one individual at a site were discarded from the analysis, ordinal richness was correlated positively with percent canopy cover \((r = 0.605, p = 0.037)\). However, as this trend was not maintained if other rare groups were excluded (i.e., those Orders with less than 5 individuals at a site), it is possible that this result may be attributable to Type I error.

3.3.3 SMALL MAMMALS

Four species of small mammals were captured during this study; the bush rat, *Rattus fuscipes*, the brown antechinus, *Antechinus stuartii*, the eastern pygmy possum, *Cercartetus nanus*, and the house mouse, *Mus domesticus*. *R. fuscipes* and *A. stuartii* were both captured in sufficient numbers to be considered in the following sections; as only 3 *C. nanus* and 1 *M. domesticus* were captured during both 1996 and 1997, these data are not considered further.
3.3.3.1 Abundance and Population Structure of *Rattus fuscipes*

The abundance of *R. fuscipes* did not vary significantly between treatments in 1996 (F = 0.512, df = 3,8, p = 0.686). In 1997, however, SNK tests demonstrated that there were significantly more animals in sites of four fires, and less in sites of 3 fires, than in other treatments (F = 17.3, df = 3,8, p = 0.001), although these findings should be treated with some caution as the assumption of normal distribution was not met. Trends in Figure 3.15 suggest that while 2 years after fire (1996) more *R. fuscipes* tended to be found in sites with a history of fewer fires, 3 years after fire populations had increased rapidly in the sites with the maximum of 4 burns. Numbers increased generally between years at all except the 3-fire treatment sites (Figure 3.15).

![Figure 3.15: Rattus fuscipes known to be alive (KTBA) across sites of 1, 2, 3, and 4 fires in the last 20 years. Time since last fire is consistent between all sites. Means per transect are shown + standard error.](image)

The population structure of the *R. fuscipes* populations was investigated by comparing the percentage of males and females in the total populations, between treatments. Data were arcsine transformed. In both years, the percentage of males and females did not vary significantly between treatments (Table 3.7).

The age structure of the populations was also investigated by comparing the percentage of the population, within each sex, that was adult. Data were arcsine transformed. Neither males nor females, in 1996 or 1997, showed any difference in age structure between treatments (Table 3.8).
Table 3.7: One-way ANOVA of the percentage of males and females in populations of *Rattus fuscipes* (Arcsine transform) between fire frequency treatments.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>female</td>
<td>3, 8</td>
<td>1.45</td>
<td>0.299</td>
</tr>
<tr>
<td>male</td>
<td>3, 8</td>
<td>3.01</td>
<td>0.095</td>
</tr>
<tr>
<td>1997</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>female</td>
<td>3, 8</td>
<td>0.344</td>
<td>0.795</td>
</tr>
<tr>
<td>male</td>
<td>3, 8</td>
<td>0.248</td>
<td>0.860</td>
</tr>
</tbody>
</table>

Table 3.8: One-way ANOVA of the percentage of adult males and females in populations of *Rattus fuscipes* (Arcsine transform) between fire frequency treatments.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>female % adult</td>
<td>3, 8</td>
<td>1.08</td>
<td>0.412</td>
</tr>
<tr>
<td>male % adult</td>
<td>3, 8</td>
<td>0.07</td>
<td>0.973</td>
</tr>
<tr>
<td>1997</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>female % adult</td>
<td>3, 8</td>
<td>2.15</td>
<td>0.172</td>
</tr>
<tr>
<td>male % adult</td>
<td>3, 8</td>
<td>1.31</td>
<td>0.336</td>
</tr>
</tbody>
</table>

3.3.3.1.1 *RATTUS FUSCIPES* POPULATION ESTIMATES

Due to the limited time frame over which trapping information was collected, Petersen's weighted mean estimate (Begon 1979) was used to predict population size within sites. The population estimate for each site was then used in a one-way ANOVA to determine if differences existed between treatments. The estimated population of *R. fuscipes* did not vary significantly during 1996 ($F = 0.608$, df $3,8$, $p = 0.629$; data not normally distributed and not rectifiable by standard transformation methods). The high variance contributing to this non-significant result (Figure 3.16), is a result of one site within the 1-fire treatment that recorded 12 individuals but no recaptures over the 4 day trapping session, and a concomitantly high but unreliable population estimate. In 1997, however, the estimated population size of *R. fuscipes* was significantly different between treatments ($F = 8.22$, df $3,8$, $p = 0.008$; In transform), with 1-fire and 4-fire treatments identified as having significantly higher populations than 2-fire and 3-fire treatments. Post-hoc analysis using SNK tests indicated that the differences in population estimates between
1-fire and 3-fire treatments, between 3-fire and 4-fire treatments, and between 2-fire and 3-fire treatments contributed to the significance of this ANOVA result.

![Graph showing population estimate across 1, 2, 3, and 4 fires](image)

Figure 3.16: *Rattus fuscipes* estimated populations (Petersen's weighted mean) across 1, 2, 3, and 4-fire treatments. Time since last fire is consistent between all sites. Means are shown + standard error.

### 3.3.3.1.2 *Rattus fuscipes* Response to Vegetation and Rock Cover

The stability of *R. fuscipes* population numbers at the 3-fire sites between 1996 and 1997 may indicate that a required habitat feature of this species was also stable over this period. Section 3.3.1.1 showed that the percentage of shrub cover, number of shrub stems and maximum shrub height did not vary between 1996 and 1997 at the 3-fire sites, although there was an increase in herb cover. If *R. fuscipes* was responding to vegetation, and specifically shrub regrowth after fire, this may explain the lack of change in abundance between years. However, correlations of both 1996 and 1997 data did not indicate any significant relationship between *R. fuscipes* abundance and any of the measured vegetation or rock characteristics.

### 3.3.3.1.3 *Rattus fuscipes* Response to Invertebrate Abundance and Richness

Invertebrates have been demonstrated to comprise a significant proportion of *R. fuscipes* diet, particularly in summer (Cheal 1987). As such, the abundance of *R. fuscipes* in 1996 was correlated with the abundance of each invertebrate Order recorded, as well as to total invertebrate abundance, from the same year. After Bonferroni corrections no significant correlations were found between the abundance of *R. fuscipes* and any particular invertebrate order. *R. fuscipes* abundance was correlated negatively with total abundance of invertebrates \((r = -0.600, p = 0.039)\), although this result is likely to be an artefact of the negative correlation *R. fuscipes* also had with the most abundant invertebrate group, the
hymenopterans \((r = -0.619, p = 0.032, \text{ Section 3.3.2.1})\). No significant associations were found between \textit{R. fuscipes} abundance and invertebrate Order richness.

### 3.3.3.2 Abundance and Population Structure of \textit{Antechinus stuartii}

\textit{Antechinus stuartii} showed a similar pattern of response to fire frequency in both 1996 and 1997. In both years, abundance was greater with increasing fire frequency until the 3-fire treatment, but dropped dramatically in the 4-fire treatment (Figure 3.17). However, one-way ANOVA indicated that the differences between treatments were not significant \((1996 F = 2.60, df_{3,8}, p = 0.124; 1997 F = 1.38, df_{3,8}, p = 0.318)\).

![Figure 3.17: \textit{Antechinus stuartii} known to be alive (KTBA) across sites of 1, 2, 3, and 4 fires in the last 20 years. Time since last fire is consistent between all sites. Means per transect are shown + standard error.](image)

The larger number of individuals in the 3-fire treatment during 1996 is explained partially by the significantly higher percentage of females in this treatment \((F = 4.45, df_{3,8}, p = 0.041; \text{ arcsine transform})\), whereas males were evenly distributed across sites \((F = 1.34, df_{3,8}, p = 0.328; \text{ arcsine transform})\). In 1997 there was no difference in the percentage of the population that was male or female, between treatments \((\text{male } F = 2.16, df_{3,8}, p = 0.171; \text{ female } F = 0.421, df_{3,8}, p = 0.743; \text{ arcsine transform})\).

An analysis of the age structure of the female populations was conducted to see if differences existed between treatments. Males were not considered as, due to the annual male die-off every August and September, all males caught during this study were new recruits. In 1996, 2 years after the fire, a significantly higher percentage of females was parous in 1-fire treatments than in other treatments \((F = 5.43, df_{3,8}, p = 0.025; \text{ arcsine})\).
transform), with 80% of captured females having bred the previous year. The 2-fire and 3-fire treatments had 33% and 50% of the female population parous, respectively, whereas sites in the 4-fire treatment had no female captures. By 1997, however, there was no difference in the age structure of female *A. stuartii* between treatments (F = 1.96, df\textsubscript{3,8}, p = 0.199; arcsine transform).

### 3.3.3.2.1 ANTECHINUS STUARTII POPULATION ESTIMATES

Petersen's weighted mean population estimate was used to predict population numbers at sites within each fire-frequency treatment. One-way ANOVA was then used to compare the estimated populations between treatments. During 1996, there was no significant difference between treatments (F = 3.71, df\textsubscript{3,8}, p = 0.061; square root transform), although estimated *A. stuartii* populations were considerably higher in 3-fire treatments than others (Figure 3.18). Similarly there was no significant difference between estimated population sizes of *A. stuartii* between fire frequency treatments during 1997 (F = 2.51, df\textsubscript{3,8}, p = 0.133).

![Figure 3.18: Antechinus stuartii estimated populations (Petersen's weighted mean) across 1, 2, 3, and 4-fire treatments. Time since last fire is consistent between all sites. Means are shown + standard error.](image)

### 3.3.3.2.2 ANTECHINUS STUARTII RESPONSE TO VEGETATION AND ROCK COVER

There were no significant correlations between *A. stuartii* abundance and any of the measured vegetation or rock variables, in either 1996 or 1997.
3.3.3.2.3 *ANTECHINUS STUARTII* RESPONSE TO INVERTEBRATE ABUNDANCE AND RICHNESS

There was no significant association between the abundance of *A. stuartii* and the total abundance of invertebrates \((r = -0.278, p = 0.383)\). Similarly, there were no significant correlations between *A. stuartii* abundance and the abundance of any of the more common invertebrate Orders. Although a significant correlation between Archaeognatha and *A. stuartii* \((r = 0.605, p = 0.037)\) was indicated, this result is not significant after Bonferroni correction and is, further, of doubtful reliability due to the extremely low capture rate of archaeognathans (indicating a possibility of Type 1 error). No significant associations were found between *A. stuartii* abundance and the ordinal richness of invertebrates.

3.3.4 SUMMARY OF RESULTS

The differences in vegetation measures between fire frequency treatments were more apparent in 1996, two years after the preceding fire, than in 1997 although few patterns were statistically significant. In 1996, there were patterns of decreasing numbers of shrub stems, and less shrub cover, with increasing fire frequency. By 1997, however, there was a tendency towards decreased numbers of shrub stems at sites that had had only 1 fire in 20 years, and overall shrub cover had evened out across treatments. The average maximum height of the shrub layer did not differ significantly between treatments, and nor was there a difference in growth rates between years, in sites of varying fire frequency history. Herb cover, on the other hand, tended to increase with increasing fire frequency, although, again, the difference between treatments was not statistically significant.

The total abundance and ordinal richness of invertebrates did not vary significantly between treatments, and neither variable was correlated reliably to any of the measured vegetation or rock characteristics. The most abundant group was the Hymenoptera: Formicidae, that represented over 50% of total captures. The abundance of this group, however, did not vary significantly in response to fire frequency, although substantially fewer individuals were captured at sites with a 2-fire history. The litter and soil-dwelling Collembola were the next most abundant Order and, although this taxon showed no significant difference in abundance between treatments, it demonstrated a pattern of decreasing abundance with increasing fire frequency from 1 to 3 fires. Although abundance
increased again in the 4-fire treatment, this may be attributable to the limited site replication. Both orthopterans and araneans were most abundant at sites with a history of 3 fires. Within the orthopterans, both Gryllidae (77% of captures) and Gryllacrididae (21% of captures) were most abundant at 3-fire sites, although present in lower numbers in other treatments. The pattern amongst the Araneae was less definitive, although the low variability in spider abundance between replicates within the four 2-fire treatments and three 3-fire treatments indicates that the discrimination of animals at a higher taxonomic level, such as family or morphospecies, may have allowed detection of differences in the assemblages of species between treatments.

The abundance of *R. fuscipes* in 1996, 2 years after the previous fire, tended to be higher in sites with a history of low fire frequency than in sites with 3 or 4 fires over the preceding 20 years, although the difference between treatments was not statistically significant. By 3 years after fire, however, populations known to be alive in 4-fire sites were greater than in other treatments. This change in pattern was not correlated to any measured vegetation of rock variable, although in 1996 the abundance of *R. fuscipes* was found to be correlated negatively to the total abundance of invertebrates, and specifically to the abundance of hymenopterans. The population structure, with regards to sex ratio and the proportion of juveniles in the population, did not vary significantly between treatments.

The abundance of *A. stuartii*, during both years, tended to increase in response to increasing fire frequency from 1 to 3 fires, but declined in the 4-fire treatment sites. There was, however, no significant difference in abundance of this species between the four treatments in either year. Further, these patterns of abundance were not correlated to any of the measured vegetation, rock or invertebrate abundance and richness variables. In 1996, two years after fire, the population structure varied between treatments with a higher percentage of females occurring in the 3-fire populations than in other treatments, although males were distributed evenly across all sites. In the same year, there were also significantly more parous females in the 1-fire sites than in other treatments. Neither population sex ratio or age structure varied between fire frequency treatments in 1997.
3.4 DISCUSSION

3.4.1 VEGETATION

Catling (1991) stated that frequent fire reduces forest structure and complexity by reducing the shrub layer, and by promoting the dominance of either a grassy or herbaceous understorey (Bradfield 1981; Hodgkinson and Harrington 1985), or an understory of fern and monocotyledons (Gill 1975). On the other hand, forest burnt less regularly supports a more complex shrub understorey (Gill 1975; Bradfield 1981; Gill 1983; Catling 1991).

The 1996 results of this study provide tentative support for these conclusions, with a trend of decreasing numbers of shrub stems per unit area with increasing fire frequency. The average height of the shrub layer was also generally higher in sites with a low fire frequency than in sites with 3 or 4 fires over the last 20 years, although this difference was not significant in either year. Interestingly, there was an apparent change in average shrub height between 1996 and 1997 indicated in Figure 3.5, where height appeared to increase more in 1 and 2-fire sites than in 4-fire sites, while the 3-fire sites showed no change between the successive years. A non-significant interaction between fire frequency and time, however, indicated that the rate of growth did not differ between treatments. Similarly, the average percentage shrub cover did not vary significantly between treatments, except when years were combined.

The general lack of significant results for cover of shrubs and herbs between treatments may reflect high levels of variation within treatment sites, but may also be a reflection of the sampling design. Both the percentage of herb cover and the percentage of shrub cover were measured using coarse sampling ranks designed to encompass a range of percentage cover units, and therefore to account for discrepancies caused by having different personnel collecting data. Although the data are reliable for broad-scale survey, the methodology does not allow for fine detail to be scored. In this study, most readings fell into the 2 (5 - 20%) or 3 (21 - 50%) ranks, therefore limiting the data set to only two categories covering a 45% range. A finer scale, balanced by the degree to which a range of people are able to accurately estimate percentage cover, would have led to a more precise data set and perhaps have distinguished true differences between treatments.
The number of trees also tended to decline with increasing fire frequency, although this pattern was not reflected in the percentage canopy cover. Particularly in 1996, two years after fire, there were considerably more trees in 1-fire sites even though the percentage canopy cover was quite similar across all treatments, generally varying from 10 to 20%. There was considerable growth in the canopy cover between 1996 and 1997, with 1-fire sites showing a larger increase in percentage canopy cover than other treatments. By 1997, 1-fire sites had an average percentage canopy cover of 38%, whereas the other treatment averages ranged from 15 to 25%. This would indicate that the recovery of the canopy after wildfire is higher in sites with a low fire frequency history.

3.4.2 TERRESTRIAL INVERTEBRATES

Neither the total abundance of terrestrial invertebrates nor the richness at Order level varied between fire frequency treatments during this study. Over half of all captures were ants (Hymenoptera: Formicidae), and although their abundance did not differ significantly between treatments, there were considerably fewer individuals in 2-fire sites than in other treatments. This pattern was not explained by any of the vegetative or rock variables measured during the study. York (1996), on the other hand, found after a long term study that ant abundance was much higher in frequently burnt forest compared to long unburnt forest. Species richness within the Formicidae was found not to differ between treatments, although species assemblages were different (York 1996). York’s (1996) study is not really comparable to the results of this study, however, as he had not controlled for the factor of time since fire. Sorting to morphospecies during the present study may have differentiated between the fire frequency treatments more effectively.

Springtails (Collembola) were the next most common group represented in trapping data. Their abundance decreased with increasing fire frequency between 1 and 3 fires, but increased again in the 4-fire treatment. The fall in abundance with increasing fire frequency was expected as Tolhurst (1996) has demonstrated that springtails and other leaf-litter dwellers are in low abundance soon after fire due to low litter loads. As leaf litter load has been shown to increase exponentially with time since fire (Fox et al. 1979), it would be expected that a high fire frequency would not allow sufficient accumulation of litter. Thus a pattern of increasing springtail abundance with decreasing fire frequency would be
expected. Similarly, York (1996) found approximately 15% fewer springtails on frequently burnt sites than on unburnt sites and attributed this to a reduced litter layer. However, this response is incongruous with the relatively high abundance of springtails at 4-fire sites. The two sites representing four fires, however, had extremely variable numbers of springtails with Site 9 recording over five times the number of springtails than Site 11. Higher replication within this treatment would have been desirable to determine more precisely the response of this group to high fire frequency. Unfortunately this was not possible given the fire history of Ku-ring-gai Chase National Park (Figure 3.1). It is probable that springtails were responding to environmental factors outside those resultant of fire, as Tolhurst (1996) noted that very dry soil conditions were associated with lowered springtail abundance, irrespective of burning history.

Orthopterans were another common group in this study; represented largely by members of the Gryllidae and Gryllacrididae. Their abundance was relatively consistent across areas of 1, 2 and 4 fires, but significantly higher in 3-fire sites. This did not correlate with any of the vegetation or rock cover variables measured. The effect of frequent fire is largely unknown for the orthopterans, although Whelan and Main (1979) found that grasshoppers (Acrididae) were removed by fire in eucalypt woodland, and that the extent or patchiness of the fire influenced the rate of population recovery. Timing of fire with respect to the grasshopper's lifecycle may also affect survivorship and post-fire populations. Gillon (1972) noted several species of African Acrididae that appear to time their breeding cycle so that the young are old enough to fly by the beginning of the peak burning season.

Spiders (Araneae) were also most abundant in 3-fire sites, although there were no trends in abundance related to increasing fire frequency. York (1996) found more spiders in frequently control-burnt sites than in unburnt sites, but his study did not account for differences of time since fire or varying numbers of fires over time. In the present study, the variability in the number of spiders between sites within treatments was very low. This could indicate that the species assemblages within the treatments were quite different from one another, but very similar between replicates within treatments. This supports Friend's (1995, 1996) suggestion that spiders may be good environmental indicators due to the specific requirements, longevity and low dispersal ability of some members of this group.
Furthermore, overall abundance did not correlate to any of the measured habitat characteristics so spiders do not appear to be simply responding to differences in the availability of cover. This does not rule out, however, that their abundance may be related to other environmental features such as moisture or biotic interactions (e.g., Main 1976; Wise 1984; Spiller and Schoener 1994). Analysis to family or species level is required to confirm the patterns.

Friend (1996) raised doubts that studies of invertebrate fire ecology in Australia, to date, can be summarised effectively to provide any consensus of opinion about impacts of fire. The temporal and spatial variability of invertebrate populations is so driven by environmental factors that the impacts of fire may be largely overridden (Friend 1996). Friend (1996) stressed, further, that this is particularly the case where only a broad level of taxonomic resolution is utilised. In addition, sampling techniques are often biased towards particular groups of invertebrates at the expense of others. Hindmarsh and Majer (1977) demonstrated that using two different sampling methods, pitfall traps and leaf litter samples, within the same sites gave quite different results. Whelan (1995) suggested that the Hindmarsh and Majer (1977) data confirm that pitfall traps estimate invertebrate activity rather than abundance. Actively foraging groups, such as beetles, may be over-represented in pitfall trap samples, whereas sit-and-wait predators, such as some spiders, may be underestimated. As such, a more extensive sampling program combining different collection techniques, as well as a finer level of specimen classification, should be conducted to determine the true effects of fire frequency upon invertebrate fauna.

3.4.3 SMALL MAMMALS

The two small mammal species common to the study area showed differences in their responses to fire frequency. However, although trends in their responses were clearly evident, the differences in abundance between treatments were not significant. Rattus fuscipes was distributed relatively evenly across all sites with varying fire frequency history in 1996, two years after the most recent fire. One year later, however, there had been an apparent boom in the populations in the highest fire frequency treatment. The possibility that this increase was a chance effect or an artefact of sampling design may be discounted by the very low variance between the two replicate sites within the 4-fire treatment.
Whereas *R. fuscipes* populations at 1, 2 and 4-fire sites increased between years, the number of animals known to be alive at 3-fire sites did not change over the same period. Again, there was no variance between the three replicates within the 3-fire treatment in 1997, and the lack of population increase between years is thus unlikely to be a result of chance or inadequate sampling, but rather, a response to the constant availability of resources or some other environmental variable.

However, I found no significant correlations between *R. fuscipes* abundance and the vegetation and rock cover parameters measured. As discussed above (Section 3.4.1), this may have been because the ranking system used was too coarse to distinguish differences between treatments. Thus the relationship between *R. fuscipes* abundance and the various vegetation categories may have been significant if a finer scale of data collection had been employed. Nonetheless, it appears that the patterns of re-establishment of *R. fuscipes* after the 1994 fires, and the impacts that fire history had on population growth, were related to the regeneration of vegetation.

During 1996, when *R. fuscipes* populations were similar across the fire frequency treatments, the average maximum shrub height was also similar between treatments. The increases in the average maximum shrub height at 1, 2 and 4-fire sites by 1997 were matched by increases in *R. fuscipes* abundance within these treatments. However, at 3-fire sites where there was no increase in maximum shrub height between years, the *R. fuscipes* populations did not increase. Although at 3-fire sites other factors, such as the number of shrub stems, did not vary between the two years either, there were also no increases in 2-fire or 4-fire treatments where *R. fuscipes* populations did increase. As such, these other factors are unlikely to determine *R. fuscipes* abundance. Similarly, the changes in abundance seem unrelated to either shrub or herb cover, although as mentioned above this may be due to the level of sampling being unable to distinguish fine scale differences. Interestingly, the only treatment with significant increases in herb cover between 1996 and 1997 was the 3-fire treatment. This may be due to the lack of change in the height of the shrub vegetation, but as the percentage shrub cover and the number of stems did not vary it is not clear by what mechanism this would have occurred. Nevertheless, if *R. fuscipes*
populations respond to the cover provided by vegetation, only the patterns of change in maximum shrub height appear associated with *R. fuscipes* abundance.

On the other hand, if new growth on shrubs, leading to increases in average maximum height, provided a food source for *R. fuscipes* that was not provided by either herbs or the new establishment of shrub seedlings, it could follow that *R. fuscipes* populations recovering after fire were responding primarily to food availability. Similarly, the abundance of *R. fuscipes* may have been expected to vary in response to terrestrial invertebrate abundance, as invertebrates are another possible food source (Cheal 1987). However, a negative correlation was found between the abundances of these two groups. Given that this is the opposite response that would be expected if *R. fuscipes* were being attracted to an area or encouraged to breed by a highly abundant and available food resource, it seems unlikely that there is a causal relationship between invertebrates and *R. fuscipes* abundance. The significant result is probably attributable to Type I error. To determine the effect of food and cover resources upon *R. fuscipes* populations after fire an experimental approach must be taken. Manipulation of resource availability in a post-fire situation, in conjunction with the monitoring of appropriate control treatments, could establish the mechanisms that determine *R. fuscipes* abundance (Section 1.3).

*Antechinus stuartii* displayed a quite different response to increasing fire frequency to *R. fuscipes*, with abundance increasing steadily in parallel with increasing fire frequency until dropping at sites representing 4 fires. The highest abundances of *A. stuartii* were found consistently at sites with a 3-fire history, despite one of the 3-fire sites having a different temporal distribution of fires over the 20 year period than the other two replicates from this treatment (Table 3.1). The fall in abundance between 3-fire and 4-fire sites may be due either to the fire frequency, or to the low inter-fire interval between the last 3 fires at the 4-fire sites (Table 3.1). The most recent fires at 4-fire sites occurred during the 1989/90, 1991/92 and 1993/94 fire seasons, and are likely to have influenced the floristic composition of the area (Woinarski and Recher 1997) as well as reducing the number of shrubs and trees (Section 3.3.1).
Although there tended to be fewer shrubs and less shrub cover at 4-fire sites than in other treatments, the difference was not significant. Thus, unless there is a threshold of low shrub number or shrub cover that *A. stuartii* cannot tolerate, it is unlikely that these features determine *A. stuartii* abundance at sites of varying fire frequency history. In fact, as the maximum height of the shrub layer and the percentage of shrub cover did not vary much between 3-fire sites and 4-fire sites, it is unlikely that any feature of the shrub layer was involved in determining *A. stuartii* abundance. Similar conclusions may be drawn from the herb cover data.

Tree cover conceivably could be important for *A. stuartii* as this species is semi-arboreal; nesting in trees but often foraging terrestrially (Wood 1970; Braithwaite 1983; Dickman 1991; Lazenby-Cohen 1991). However, neither the number of trees nor the percentage canopy cover varied significantly between the sites with the highest and lowest *A. stuartii* abundances (3-fire and 4-fire sites respectively). Similarly, invertebrate abundance could be a factor determining this species abundance as *A. stuartii* is largely insectivorous (Fletcher 1977; Hall 1980; Dickman 1982; Dickman *et al.* 1983; Green 1988). Again, however, in this study there were no relationships between *A. stuartii* abundance and the total terrestrial invertebrate abundance, the abundance of any particular Orders, or ordinal richness. As such, the parameters measured during this study gave no indication of what environmental, cover, nesting or feeding requirements may be driving the observed trends in *A. stuartii* abundance over areas of different fire frequency. Similarly inconsistent results relating the abundance of *A. stuartii* to environmental variables have also been obtained by Barnett *et al.* (1978), Statham (1982), and Steeves (1990).

Although the patterns of population abundances of *R. fuscipes* and *A. stuartii* have been discussed above in relation to various vegetation characteristics, correlation analysis did not find any significant relationships between the abundance of these two small mammal species and any of the cover (vegetation and rock) or food (vegetation and invertebrates) variables measured during this study. This suggests problems with some aspects of the sampling methodology; either the coarseness of the percentage ranks used for cover estimation (Section 3.4.1), small sample size, or assessment of variables that were inappropriate to the study species. The sampling was designed as a snapshot survey; to
simultaneously sample 12 sites representing four different fire frequency treatments, for vegetation, terrestrial invertebrates and small mammals. Snapshot surveys remove the problems associated with temporal variability in environmental conditions that may influence animal activity and behavioural patterns, and thus capture rates. However, they also provide a smaller sample size than does repeated sampling of the same sites. Thus, especially for small mammals that have a relatively low capture rate per unit of sampling effort, trends in abundance may be hard to distinguish.

In this study Petersen's weighted mean estimate was used in conjunction with the actual known to be alive data. There are four critical assumptions of population estimation based on mark-recapture data. Firstly, marked and unmarked animals have an equal chance of being captured. Secondly, there is no birth or immigration into the population, thirdly, marked and unmarked animals are subject to the same rates of mortality and emigration, and fourthly, marks cannot be lost or removed (Begon 1979; Krebs 1989).

Marked and unmarked animals will have the same chance of being captured only if individuals become neither trap-happy nor trap-shy (Elton 1942; Crowcroft 1966; Southern 1973; Caughley 1977; Krebs 1989). This may be a response to either the trapping or handling of the animals, but in either case it must be assumed that the capture of an animal will not make it either more or less likely to be captured again. Further, the short duration of this study allows for the assumption of no birth or immigration into the population.

The third of these assumptions can only be met if the marking technique will not interfere with the survival chances or health of the animal. If a tag makes an animal more conspicuous to predators or competitors, or if it physically impedes movement or causes behavioural changes, then it is unlikely that marked and unmarked animals will have the same risk of mortality. In the present study, semi-permanent non-toxic black felt pens were used so this assumption was almost certainly met. It is doubtful if the usual tagging techniques used for small mammals, ear tags and particularly toe-clipping, could be employed without breaking these assumptions. Conspicuous or injured animals are at higher risk of predation, and injured animals have higher risk of infection (Fairly 1982; Korn 1987).
Finally, marks may not be lost or overlooked. Semi-permanent pen may work for a period of four days, but in trapping programs running over longer periods, a permanent tagging system needs to be established. Eartags are often used for small mammals and are largely effective except that they may be ripped out during fights. If purely recapture data are required, the scarred ear tissue often provides enough information, as the type of scar is quite distinguishable from those caused by fighting animals (pers. obs.). Occasionally, however, a whole ear may be removed and it is unknown if the animal was previously tagged. Some researchers provide insurance against such occurrences by double tagging (e.g., Bray 1994). Many researchers use toe-clipping, especially if working with animals with very small ears, as they believe that this technique is less likely to result in the loss of tags, even though animals may lose toes during agonistic encounters. This technique may also leave tissue prone to infection and cause behavioural changes that could alter the chance of trappability (Fairly 1982; Korn 1987).

This last point emphasises the problems with many of the survey techniques employed by both private and public organisations during the preparation of Environmental or Faunal/Species Impact Studies associated with development proposals. Brief surveys, or those with low sampling effort, may fail to identify rarer species, particularly if there are seasonal fluctuations in either abundance or behaviour. Hibernating species, for example, are unlikely to be captured during winter trapping surveys, nor aestivating species over summer. Low sample sizes often encourage planners to attempt to extrapolate further information from the data. Methods of population estimation are then used for this purpose; often without any acknowledgement of the assumptions inherent in their use.

3.4.4 CONCLUSIONS

Although the trends of small mammal abundance in response to the history of fire frequency appear to be associated with the effects that fire history have on the vegetation cover, no consistent causal relationships were indicated by this study. To determine the mechanisms by which fire history affects patterns of small mammal abundance, an experimental approach needs to be undertaken whereby putatively important resources are manipulated in the environment. Before the issue of resource use and availability can be assessed in relation to fire history, however, the initial question is how resource availability
affects patterns of small mammal population recovery after a single fire event. Chapters 5 to 9 attempt to address this question by assessing the response of a small mammal community, and population responses of the common species within the community, to manipulated levels of food and nest site availability.

An important first step, however, is to establish the immediate effects of fire upon individual animals, and this is undertaken in Chapter 4.
CHAPTER 4: IMMEDIATE RESPONSES OF SMALL MAMMALS TO FIRE

4.1 INTRODUCTION

Little is known about the immediate responses of small mammals to fire. Although some authors have measured a decline in the abundance of some species after fire and attributed this decline to mortality (e.g., Newsome et al. 1975; Fox 1982), none have been able to directly quantify the effect of fire upon survivorship. To reliably estimate mortality, death must be distinguished from emigration (Whelan 1995).

Fox (1982) noted that of 74 animals tagged during three months preceding a fire, only 4 were captured one month after. He attributed this population decline to mortality but admitted that no carcasses were found; however, the time elapsed since the fire could have allowed scavengers to remove any remains. Chew et al. (1958) and Newsome et al. (1975) recorded large numbers of small mammal carcasses immediately after a fire, and noted a corresponding decline in small mammal abundance. However, it is also possible that post-fire shifts in behaviour occur. Animals may become more trap-shy in the open habitat created by fire, for example, resulting in lower abundance being recorded than in densely covered unburnt sites.

Post-fire population declines may not be entirely attributable to mortality, as some species exhibit post-fire habitat shifts leading to emigration away from burnt areas (Kemper 1977; Friend 1979; Begg et al. 1981; Fox 1983). Friend (1979) demonstrated that whereas adult *R. fuscipes* with established home-ranges may die in situ during fires, newly independent sub-adults move out of affected areas. Christensen and Kimber (1975), on the other hand, found that *R. fuscipes* did not move from burnt to nearby unburnt patches, and that immature males immigrated onto the burnt plots. Cowley et al. (1969) noted no immediate mortality of *R. fuscipes*, as measured by capture rate, after a spring fuel-reduction fire, although a displacement away from pre-fire home ranges was evident. Particularly in studies where the post-fire population has not been measured immediately after a fire, but in the weeks and months following, population declines are likely to be a combination of mortality, emigration and changes in habitat use leading to altered
trappability. Mortality may also be either an immediate result of heat or smoke, or a delayed response to reduced resource availability or increased predation risk with the removal of cover.

4.1.1 AIMS

This chapter aims to determine the immediate effects of a prescribed hazard reduction fire on the survival and habitat use of small mammals in eucalypt forest. The design of this study was aimed towards gathering baseline data concerning the survival of small mammals during fire and in the immediate post-fire environment, and at developing techniques that could be used on a larger scale in studies with more personnel and financial resources.

4.2 METHODS

This study took place in an area of dry sclerophyll eucalypt forest associated with Heathcote National Park, south of Sydney, NSW, Australia. The (6 sq. km) area was burnt on 25 August 1996 for the purpose of reducing fuel loads close to residential areas, and minimising the risk of bush fires during summer. As with the sites used for other aspects of this study, in Ku-ring-gai Chase and Garigal National Parks, the habitat was open Eucalyptus forest growing on Hawkesbury Sandstone ridge tops and slopes. Dominant tree species included E. haemastoma, E. exima, E. gummifera, Angophora costata and Banksia serrata.

Prior to the fire, three 0.25 ha sites were established within the proposed burn area. Each site consisted of a grid of 25 trapping stations, arranged in 5 parallel lines 10 m apart, with 5 trapping stations at 10 m intervals along each line. Thus, a 40 m x 40 m (0.16 ha.) grid was centred within each site, allowing for a 5 m buffer strip along each side. Sites were separated by a minimum distance of 400 m. As this study was designed as a preliminary descriptive study, no control sites outside the proposed burn area were established and analytical procedures are therefore limited. Parallel to one side of each site, and a minimum of 20 m from the first trap line, an unpaved single lane road gave access to the site and allowed permanent radio-tracking points to be established. The roads were not open to public vehicles and were rarely used. Each of the three sites was trapped for three nights
prior to the prescribed fire. After the first night, trap numbers at Site 2 were doubled (10 trapping stations along each line with 5 m spacing) to ensure an adequate sample size for radio-tracking. Each site was trapped using one 10 x 8 x 30 cm Elliott live capture trap per station, baited with a mixture of peanut butter, rolled oats and honey. Traps were insulated with plastic bags and supplied with a bedding of non-absorbent cotton wool.

All captured small mammals were identified and tagged individually, using either ear-clips (*Antechinus stuartii*, *Mus domesticus*), or metal fingerling ear tags (*Rattus fuscipes*, *R. lutreolus*, *R. norvegicus*). The sex and weight of each individual was recorded.

*Antechinus stuartii* weighing more than 20 g and *R. fuscipes* weighing over 100 g were fitted with radio-collars (Biotrack; SS-1), consisting of a battery-operated transmitter with a 10 cm whip-antenna attached to a zip-tie plastic collar. Collars weighed less than 5% of the animal’s adult body weight (Brander and Cockran 1971), and had an approximate life of 20 days for *A. stuartii* and 40 days for *R. fuscipes*. A total of 11 *A. stuartii* (3 female, 8 male), and 7 *R. fuscipes* (4 female, 3 male) were fitted with collars in the week preceding the fire. At each site radio-collared animals were tracked for up to three nights before the fire. Animals were located using a Titley receiver, Sirtrack H-frame hand-held antenna and a hand-held prismatic compass. Three bearings were taken of each animal from fixed points along a road adjacent to the sites, and triangulation used to plot the location of the animals on a map. The error involved in accurately estimating the bearing from the antenna direction was determined by calculating the difference between bearing estimates on a collar placed by a second person with the actual bearing. This was repeated three times and the error determined as $5.2 \pm 1.2^\circ$. An attempt to locate each animal was made hourly between 1800 and 2300 hours, for one to three nights prior to the fire (depending on when the animal was captured), and for six nights over the three week period after the fire. Several daytime fixes were also taken to establish the location of nest hollows and burrows.

Volunteer Bush-fire Brigades, the NSW Fire Brigade and National Parks and Wildlife Service fire crews joined forces to burn the study area on 25 August 1996. The burn was generally patchy and low in intensity. Light rain during the week preceding the fire had dampened the litter layer and, particularly on the southern slopes that do not receive
much sunlight, the fire did not carry as well as had been expected. Although follow-up
burning of the unburnt patches was planned, resources and time did not allow the burn to be
completed. As a result of this, only Site 1 was burnt completely during this fire. Neither
Sites 2 and 3 were burnt, although both were affected by heavy smoke for several hours
during the day (pers. obs.).

Site 1 contained 2 female *A. stuartii*, 4 male *A. stuartii* and 1 female *R. fuscipes.*
Animals at this site were radio-tracked for the week following the fire, starting the night
afterwards, and also for one night 10 days after the fire, and one night 17 days after the fire.
Animals at the two unburnt sites were also tracked for four nights during the week
following the fire, and again for one night 10 days after the fire. Locations were hand
plotted to distinguish if individual movement patterns varied in response to the fire at Site 1,
or if there was any initial response to smoke at Sites 2 and 3. Home ranges were not
calculated due to insufficient data on individuals (Kenward 1987), and insufficient
replication. In addition, the limited number of location co-ordinates of animals before the
fire would not have allowed accurate before- and after-fire comparisons to be made (see
Section 4.4).

Trapping was also conducted in the two unburnt sites for three weeks after the fire,
and in the burnt site from the second week after the fire. Care was taken not to have traps
open in sites where radio-tracking was being conducted.

In addition, on the day after the fire another grid (Site 4) was established in an area
of patchily burnt bush approximately 50 m from the unburnt Site 2. Site 4 had 10 of the 25
traps on burnt ground, and 15 of the traps in unburnt patches; arranged on a 5 x 5 grid with
10 m spacing. Trapping on Site 4 and Site 1 concentrated on determining if animals were
using burnt ground when unburnt patches were available nearby, and on how far animals
cought in burnt patches were from the nearest patch of unburnt cover. Spool-and-line
tracking (Miles *et al.* 1981, Broughton and Dickman 1991) was also planned at this site.
Unfortunately, when traps were checked before leaving the site between 2300 and 2400 on
five nights after the fire, no individuals had entered the traps, so this aspect of the study
could not proceed.
Habitat information was also collected from Site 2 prior to the fire, and from Site 1 after the fire. A percentage cover index was established (Table 4.1), and the percentage cover of herbs, shrubs, canopy, leaf-litter and bare-ground or rock, was recorded from 16 randomly distributed 2 x 2 m quadrats within the sites. Measurements of these variables were carried out as described in Section 3.3.2.1. Cover categories between the burnt and unburnt sites were compared using a Mann Whitney U-test (SigmaStat; Version 1.0, Jandel Corporation 1992). The application of a test here is not to test a specific hypothesis, but rather to descriptively explore the effects of fire upon cover. Otherwise, two problems are acknowledged: Firstly, Sites 1 and 2 may have had very different vegetation before the fire, and secondly quadrat-level replication may be considered pseudoreplication (Hurlbert 1984) as between-site variability is not accounted for.

Table 4.1: Table of cover abundance scores in relation to percentage cover of habitat variables within a quadrat.

<table>
<thead>
<tr>
<th>Percentage cover (%)</th>
<th>Cover abundance score</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;1</td>
<td>1</td>
</tr>
<tr>
<td>2 - 5</td>
<td>2</td>
</tr>
<tr>
<td>6 - 20</td>
<td>3</td>
</tr>
<tr>
<td>21 - 50</td>
<td>4</td>
</tr>
<tr>
<td>51 - 75</td>
<td>5</td>
</tr>
<tr>
<td>76 - 100</td>
<td>6</td>
</tr>
</tbody>
</table>

4.3 RESULTS

4.3.1 HABITAT

After the prescribed fire, the percentage cover of herbs and leaf litter was greatly reduced (herbs \( U = 330.0, p = 0.013 \); litter \( U = 154.5, p < 0.001 \); Figure 4.1), whereas the percentage cover of bare-ground and rock increased significantly \( U = 136.0, p < 0.001 \); Figure 4.1). Neither the shrub nor canopy layer were significantly affected by the fire (shrub \( U = 300.0, p = 0.180 \); canopy \( U = 278.0, p = 0.611 \)).
4.3.2 TRAPPING AND RADIO-TRACKING

Within Site 1, the only site to be burnt, two female A. stuartii, four male A. stuartii and one female R. fuscipes were captured and fitted with radio-collars before the fire. Each individual had only three or four fixes before the fire and, with the exception of one male A. stuartii that disappeared from the site after the fire, between 8 and 24 fixes after the fire (mean = 19).

Pre-fire records of A. stuartii indicate that individuals moved over a wider area than covered by the trapping grid. Most moved either side of the maintenance track from which their location bearings were taken. Their movements across the track were probably facilitated by a small bridge at the northern end of Site 1 which allowed animals to travel in dense undergrowth under the road, without crossing in the open. The fire burnt large areas of the eastern side of the road, including the trapping grid, but did not burn the southern side of the road. One of the male A. stuartii was not captured or located by radio-telemetry after the fire, although it had consistently been tracked on the grid prior to the fire. As neither the corpse nor the collar was found it is assumed that the tag failed, or that after the fire this animal moved into adjacent unburnt bushland, out of range of the radio-telemetry equipment. All other A. stuartii continued to move through the same area after the fire, although movements were more restricted to the unburnt site of the track. There was no evidence of mortality.

Before the fire, female #1 A. stuartii nested in the area to be burnt during the day, but moved across the road during the night. After the fire less than 10% of fixes of this
individual were in burnt forest (n = 2). Similarly, after the fire female #2 *A. stuartii* was located on 29% of occasions in burnt forest (n = 5) and 71% of occasions in unburnt forest (n = 17), although being recorded only on the eastern side of the road prior to the fire. This individual continued to visit both burnt and unburnt forest on each night of tracking, although nesting in the unburnt forest. Multiple captures of female #1 *A. stuartii* indicated that mean daily body mass fell from 25.75 g (SD ± 1.06) pre-fire to 23.5 g (SD ± 0.82) after the fire. Captures of this individual were always in traps on burnt ground that ranged from 6 to 12 m from the nearest patch of unburnt forest. Given that this animal normally moved through unburnt forest, it may be that the traps were providing a food and/or shelter resource that attracted this individual to the trapping grid.

Male *A. stuartii* tended to use both eastern and southern sides of the road, before and after the fire. One male continued to use each area equally, moving through unburnt forest early in the evening, but moving to burnt forest soon after complete darkness. It is unclear if this animal remained in the burnt forest for the rest of the night or returned to the unburnt forest. However, two other males were most often found in unburnt forest after the fire (95% n = 19, and 100% n = 19, of location co-ordinates). There were no captures of males after the fire so changes in body weight could not be assessed.

The only female *R. fuscipes* recorded at Site 1 was not captured or tracked to the eastern side of the road again during the study. After the initial capture, all subsequent radio-tracking co-ordinates, both before and after the fire, were on the unburnt southern side of the road. A male *R. fuscipes* was caught on the burnt grid 2 weeks after the fire, and again 17 days later. On both occasions it was captured in traps on burnt ground; on the first occasion 2 m from the nearest unburnt patch, and on the second occasion 11 m from unburnt vegetation. Between captures its body mass fell by 46 g, from 141 g to 95 g.

After the fire a fourth grid (Site 4) was established in a patchily burnt area close to Site 2. Ten of the trap stations were located on burnt ground, and 15 of the stations on unburnt ground. Only five captures, of three individuals, were recorded in 225 subsequent trap nights, including one male *A. stuartii*, one female *Mus domesticus* and one male *R. norvegicus*. All captures were in unburnt patches. The introduced species *M. domesticus*
and *R. norvegicus* were not recorded at any other sites during the study. Their appearance at Site 4, two weeks after the fire may have been facilitated by the proximity of this site to residences less than 200 m away. The same *R. norvegicus* was recorded the following day at the unburnt Site 2, where it had forced its way into an Elliott trap already occupied by a *R. fuscipes*, and eaten it.

All animals from the unburnt Sites 2 and 3 occupied the same ranges throughout the study. All, except one male *A. stuartii*, were not recorded in nearby burnt forest. However, four days after the fire a male *A. stuartii* was noted to be moving through burnt forest near Site 3. Three male *A. stuartii* from Site 3 were recorded only sporadically after the fire, although all remained within the area. It is unclear if this was a reception problem caused by decreasing battery power, damage to the antennae, environmental signal obstruction, or if the animals were moving out of the range of the telemetry equipment. Of six *R. fuscipes* tracked in the unburnt Sites 2 and 3, one male and one female were not recorded after the fire. All other individuals continued to move through the same area as before the fire, and were not recorded to visit nearby burnt forest.

4.3.4 SUMMARY OF RESULTS

There was no confirmed mortality of animals as a result of this prescribed fire. Although two animals disappeared from tracking records in unburnt sites, this is most likely attributable to equipment failure. The loss of a male *A. stuartii* from the burnt site after the fire may be related similarly to equipment failure, or the animal’s dispersal into a nearby area out of the range of the radio-telemetry equipment.

Although survival of small mammals was apparently not affected by the prescribed fire in the immediate term, weight loss of both *A. stuartii* and *R. fuscipes* individuals during the month after the fire indicate that food resources, or opportunities for foraging, may have been limiting. A female *A. stuartii* tagged prior to the fire and still present at the conclusion of the study, was approximately 9% lighter during the post-fire period than before the fire. Similarly, the body mass of a male *R. fuscipes* living in the burnt site declined by 33% between days 15 and 32 after the fire.
Radio-tracking indicated that *A. stuartii* moved through both burnt and unburnt forest during the post-fire period, although unburnt forest was preferred. Usually over 70% of location fixes after fire were in unburnt forest. Most individuals visited the unburnt forest regularly, and capture records indicate that within the burnt forest *A. stuartii* roamed at least 13 m from the nearest patch of unburnt vegetation. Where unburnt patches were more common, however, as at Site 4, results indicate that animals preferred to remain within unburnt vegetation. A male *A. stuartii* resident in an unburnt site was noted to move into burnt forest one night, but had returned to its usual location in unburnt forest by the following day.

In addition, the fire appeared to allow the colonisation of the introduced species *M. domesticus* and *R. norvegicus* into the forested areas, although individuals were captured only in unburnt patches, and then only infrequently.

### 4.4 Discussion

#### 4.4.1 Immediate Responses of Small Mammals to Low Intensity Fire

Although the results of this study are hampered by the lack of replication and small sample size, some baseline data were gathered that demonstrate the immediate response of small mammals to fire. Most importantly was the lack of evidence of direct mortality. After patchy fire, *A. stuartii* concentrated movements in unburnt areas of the forest, although still visiting burnt areas occupied prior to the fire. This study shows that individual *A. stuartii* may undergo habitat shifts or concentrate movements into a subsection of their former range after fire. This is likely to be a result of altered resource availability, or increased levels of competition and predation risk associated with the removal of leaf litter and herbaceous vegetation.

The availability of resources, including food, cover, nest sites and water, may be limiting to small mammal populations after fire (Chapter 1). However, after a low intensity prescribed fire, the movement of animals into nearby unburnt patches would presumably be a response to the removal of food and cover, as nest sites in logs and trees are not removed, and moisture is available due to frequent patches of unburnt vegetation. Reduced food availability is indicated by the loss of body mass of the male *R. fuscipes* resident in the burnt
site during the weeks following the fire. *R. fuscipes* eat arthropods and various plant materials (Cheal 1987), and as both herb and leaf litter cover were reduced significantly by the fire it is likely that the availability of both these food types was limited. Similarly, Ward (1994) demonstrated that the body condition of male and lactating female *A. stuartii* was lower in burnt than unburnt heath. In contrast, however, Catling *et al.* (1989) concluded that neither food nor water were limiting to *R. fuscipes* and *A. stuartii* after a prescribed fire, although they admitted that this may have been a result of the highly patchy nature of the burn.

The emigration of animals from burnt sites into nearby unburnt areas in search of resources could also result in increased competition for resources between residents and new immigrants. The drop in body weight of a female *A. stuartii* after the fire could indicate reduced access to resources despite her being tracked on 90% of occasions to unburnt forest. As such, original residents of the burnt area may still make forays into their former range to take advantage of reduced competition for the few resources that are left. A larger sample size is required to determine if these patterns are real or artefactual.

The patterns of habitat shift demonstrated in the present study may also be in response to breeding pressures rather than altered resource distribution. Examination of the pouch of captured female *A. stuartii* confirmed breeding during this study. Movements of males during the breeding season are usually centred on communal nests in the area (Lazenby-Cohen 1991), and could have been expected to focus on unburnt sites in the present study if these sites contained communal nest sites. Lazenby-Cohen (1991) demonstrated that the amount of time spent by both sexes in communal nests during the breeding season was high compared to the non-breeding months, and suggested that *A. stuartii* takes time for reproductive effort from time usually spent feeding. Thus movements during this time of year may reflect reproductive, as well as foraging effort.

Predation risk may also be assumed to increase with increased movements, whether those movements are a response to reduced resource availability or reproductive behaviour. In this study, cover in the form of shrubs remained, as would burrows and rock crevices for nest sites. However, traversal of increased bare ground between resource patches and nest
sites may have led to increased vulnerability to predation. Increased activity in response to reduced food availability after fire has been shown for *Zyzomys argurus* (Begg et al. 1981). Further, increased predation pressure after fire has been demonstrated by Newsome et al. (1983), who proposed that post-fire predation on small (rodents and dasyurids), medium (possums and rabbits) and large-sized prey (macropods) by dingoes, *Canis lupus dingo*, was disproportionately high in relation to their low abundances.

The introduced *M. domesticus* and *R. norvegicus* were recorded in a patchily burnt area two weeks after fire. Although *M. domesticus* is often recorded in post-fire studies (Leonard 1972; Christensen and Kimber 1975; Recher et al. 1974, 1975; Newsome et al. 1975; Friend 1979; Catling et al. 1981; Fox and McKay 1981; Fox 1982, 1983; Lunney and Ashby 1987; Lunney et al. 1987; Wilson et al. 1990), mice generally appear months or years, rather than weeks, after fire. In this case, however, colonisation would have been facilitated by the proximity of the site to residential areas. That the captured *M. domesticus* remained in the area for at least 18 days indicates that individuals are quite capable of surviving in the early post-fire period. Further, success in burnt patches may be encouraged by the movement of native species into nearby areas of unburnt forest and, therefore, reduced competition. The highly patchy nature of this fire could have benefited *M. domesticus* further by simultaneously reducing cover that may impede movement, and by providing food and shelter in unburnt patches. All captures of *M. domesticus* were in traps within unburnt patches of vegetation at a burnt site, although no *M. domesticus* was recorded in either of the two unburnt sites.

The capture of *R. norvegicus* was unexpected due to its usual association with human development (Watts 1995). Again, its presence may have been due to nearby housing, although it remained in the forest for at least three days. Its predation upon a captured *R. fuscipes* in an Elliott trap at a nearby unburnt site emphasises that *R. norvegicus* is firstly, highly mobile and not impeded by unburnt vegetation, and secondly, a possible predator of native species. Although the situation in which the *R. fuscipes* was eaten was somewhat contrived in that there was no means of escape from the trap, the ability of the *R. norvegicus* to force open the door of the trap indicates a deliberate predation strategy. *R. norvegicus* could equally corner a native species in a burrow or nest.
4.4.2 LOGISTICAL AND METHODOLOGICAL PROBLEMS IN STUDYING FIRE

There were several logistical and methodological problems identified during this study that need to be rectified before further research of this kind can be effectively undertaken. Unfortunately, a large proportion of the problems are not under the control or jurisdiction of the researcher in these types of studies. To gather before and after data on the immediate effects of fire upon biota, a researcher needs to know when and where a fire will occur. The unpredictability of bushfires restricts the researcher to either planning and controlling their own fire, or working with organisations already burning for fuel reduction or land clearing purposes. In New South Wales prescribed fires are usually conducted by organisations such as the Volunteer Bush Fire Brigade, the National Parks and Wildlife Service, the NSW Fire Brigade, and State Forests.

Prescribed fires are often cancelled within days or hours of the proposed ignition time due to climatic, pollution or personnel problems. Many fire control agencies rely heavily on volunteer staff and numbers are not always reliable. In addition, in NSW the Environmental Protection Authority is able to cancel proposed burns near residential areas if pollution levels are considered too high. Most importantly, rain in the days and weeks preceding the fire may leave the fuel damp and unable to carry a fire. Rain, wind or high temperatures on the day of the fire may also cause cancellation as the control, and therefore safety, of the fire may be jeopardised.

In this study, notification that the fire was to proceed as planned was not available until four days before the fire. This study had previously been planned and cancelled on a number of occasions due to the postponement or cancellation of burns. In situations where considerable financial resources (in the form of radio-collars) are being invested into a study, a degree of certainty is required before field work can begin. However, even though the burn was confirmed to go ahead, rain the week before the fire had dampened the leaf litter layer and the southerly aspect of the site had meant that the fuel did not dry sufficiently before the fire. The fire moved slowly and was distributed patchily. The difficulty that the fire crews had in igniting the fire was reflected in the large areas that remained unburnt following the fire. Follow-up burning was not conducted due to lack of financial and personnel resources.
Given the late confirmation that a fire will go ahead, it is often difficult to gather sufficient pre-fire data. Although trapping can be conducted over several days or weeks prior to a planned fire on the chance that the fire does go ahead, the implementation of radio-collars could be a costly mistake. This is compounded by the limited battery life of radio-collars designed for small mammals.

The patchiness of a burn can also cause problems in adequately determining resource use. Although in this study the forest was effectively divided into two portions, one burnt and one unburnt, and animals could be accurately determined as being in either the burnt or unburnt area, within the burnt area some patches of unburnt vegetation remained. Location of individuals by triangulation methods is not accurate enough to determine microhabitat or macrohabitat use if both are patchily distributed at a relatively fine scale. Using the radio-signal to "walk in" on an active animal generally causes the animal to move in response to the researcher, although this can be useful for determining the location of more sedentary species, or nest hollows and burrows during inactivity periods.

The use of food resources could be more accurately assessed by scat analysis. Examining the faecal remains of animals captured before and at regular intervals after a fire could determine if there was a change in resource use. Simultaneous sampling of food sources, such as seeds, fungal hyphae, invertebrates and vegetative regrowth could determine if certain resources were being selected during this period. Although a number of studies have previously identified selective or opportunistic feeding patterns in a range of species and environmental systems (e.g., Green and Osborne 1981, Corbett and Newsome 1987, Banks 1997), this has rarely been attempted in fire-affected habitat in Australia (King 1985).

It had been intended to use radio-tracking to determine macrohabitat use and nest sites of individual A. stuartii and R. fuscipes, and to investigate how habitat use changed after fire. However, after the fire it was considered for a number of reasons that the home range and movements of individuals could not be accurately mapped. The comparison of habitat use, movement patterns and home range area before and after fire could not be
assessed due to the limited number of location points gained for each of the animals in the burnt site before the fire. As mentioned above, this was a result of the limited number of days between when the burn was confirmed and when it occurred, and the patchiness of the fire in leaving two of the three sites unburnt. The data that were gathered, however, indicated clearly which area of forest the animals were nesting and moving around in after the fire, and whether this area was burnt or unburnt.

Movement patterns, however, were more difficult to determine. Although at Site 1 animals could be located to either the burnt or unburnt side of the road with accuracy, there is evidence that the signals and absolute locations of the animals as mapped by triangulation methods, were inaccurate. Triangulation to determine the location of animals in nest sites, for example, sometimes estimated the location up to 20 m away from the actual location as determined by walking in on the signal. However, all three sites were near an electricity sub-station, and high-voltage power-lines passed over the area. Although the effect of electromagnetic interference upon radio-signals has not been studied directly, Parker et al. (1996) found that receivers within 300 m of high-voltage power lines contributed significantly to the bias and/or size of bearing errors during their study, and rendered their results uninterpretable. Further, Ward et al. (1986; cited in Parker et al. 1996) noted that electric fences sometimes distorted radio-fixes. During the present study, the large errors recorded in addition to the interference of signals and occasional prevention of reception of some frequencies, support the notion of electromagnetic interference. In addition, the radio-telemetry equipment also picked up powerful transmissions from a nearby Australian Army base (Holsworthy), diminishing the ability to accurately determine the radio-collar signal above other noise.

Home range calculations based on data from radio-tracking estimate only the minimum range of an animal. Times when an animal is not found, although subsequently recorded again, presumably indicate that it is out of range for the equipment being used, and therefore outside the home range predicted by standard estimation procedures. Home range calculations are likely to represent only the most sedentary individuals in the population, and will be dependent upon seasonal changes in resource availability and behaviour. As discussed above (Section 4.4.1), for example, this experiment was conducted during the A.
*stuartii* breeding period, and it is uncertain whether the behaviour recorded during this study reflected fire-induced changes in the habitat, or increasing intensity of breeding behaviour. Further, Arthur *et al.* (1989) noted that home range estimations assume that all areas within the range boundaries are used, and do not take into account differential microhabitat utilisation.

Using radio-fixes to determine habitat use may also be misleading. Palomares and Delibes (1992), in a review of radio-tracking studies, found that many researchers were unable to identify rest periods from activity periods; multiple radio-fixes of resting individuals thus underestimated the foraging habitats of the animals, with potentially important management consequences.

Microhabitat use, as well as movements at a macrohabitat scale, can be accurately determined by spool-and-line tracking (Miles *et al.* 1981, Broughton and Dickman 1991). Spools of lightweight cotton thread are attached to the nape of animals, and when released a line of thread is left along the path the animal takes through the habitat. Multiple replicate trails from the same animal can also indicate the home range of the animals, although this may be confounded if the animal uses up the length of thread (usually 100 - 200 m) before reaching the perimeters of its range. This length of thread, however, is particularly appropriate for small mammals that do not travel great distances. A benefit of this technique over triangulation of radio-signals is that the movements and range of an animal may be determined in 3-dimensional, rather than 2-dimensional space, and there is little error involved. It would be recommended for future studies of the immediate effects of fire on small mammals.

4.4.3 **Conclusions**

*Antechinus stuartii* responded to a prescribed fuel reduction burn by concentrating movements in nearby unburnt sections of the forest while continuing to make occasional forays into burnt forest. Changes in home range were unable to be determined due to low sample sizes, the timing of the fire in relation to the breeding season, and logistical and methodological problems leading to low replication and reduced accuracy of radio-telemetry signals. Post-fire weight loss measured in a female *A. stuartii* and a male *R.*
*fusipes* may have been related to reduced access to food resources, through both diminished food availability and increased competition. There was no evidence of fire-induced mortality.

It is suggested that cheaper alternatives to radio-tracking, such as spool-and-line tracking, could better indicate changes in micro- and macro-habitat use of small mammals before and after fire, due to increased accuracy and less initial expenditure if planned fires do not go ahead. The pre-fire study period could also be extended by tagging animals and gathering data early in the fuel reduction season in several areas, on the assumption that a proportion of the fires will go ahead at some stage during the season. Obviously the design of such experiments would also incorporate seasonal variability in resource availability and behaviour. In addition, a direct method of measuring resource availability and usage before and after fire needs to be incorporated into any study such as this to determine the mechanisms behind habitat selection in the immediate post-fire environment.
CHAPTER 5: RESPONSE OF A SMALL MAMMAL COMMUNITY TO RESOURCE
AVAILABILITY AFTER FIRE

5.1 INTRODUCTION

Responses of small mammal communities to fire have received considerable
attention in Australia (e.g., Leonard 1972; Newsome et al. 1975; Recher et al. 1975; Fox
Bamford 1985; Catling 1986; Lunney and Ashby 1987; Lunney et al. 1987; Wilson et al.
1990; Driessen et al. 1991; Masters 1993).

relationship in small mammals returning to heathland and eucalypt forest with time after fire.
The succession was related directly to changes in habitat, in particular the structure of the
vegetation. Fox (1982) identified four stages of recolonisation after fire. The first is the
presence of transient individuals on burnt patches as a result of dispersal from outside the
area. Second, if dispersers are able to establish residence, they become colonisers. The
third is the reproduction of colonists and the final stage is the recruitment of resident
juveniles with an associated increase in population size.

Connell and Slatyer (1977) and Fox (1982) further described succession in terms of
a habitat facilitation model where species are able to enter the succession when the changing
local and physical conditions first meet their specific requirements. As these conditions
change further, and away from the optimal conditions for each species, the animals leave the
succession. Alternatively, some species may tolerate the changes and remain in the habitat
but at reduced population levels. This has been termed the habitat tolerance model (Connell
and Slatyer 1977, Fox 1982), and is expressed as a sustained or continuing population with
reduced competitive ability. In this context, a community may be defined as a set of
organisms that occur together and that may affect each other’s abundance and distribution
through competition and habitat modification (Connell and Slatyer 1977).
Fox (1981, 1982, 1983) described a successional heathland community dominated by the rodents *Mus domesticus*, *Pseudomys novaehollandiae* and *P. gracilicaudatus* in the first instance, followed by a decline in these species and an increase in the dasyurids *Antechinus stuartii* and *Sminthopsis murina*, followed by decline in dasyurids and an increase in *Rattus* spp. in late seral stages. The habitat requirements of each species appeared to be best met at a particular stage of regeneration after disturbance. This resulted in a sequence of ecologically dominant species replacing those that were no longer within their preferred habitat, and was expressed as orderly shifts in relative abundance within the community (Fox 1983). The animals thus responded to a habitat succession, manifested by a succession of both floristic and structural vegetation types (Fox 1990).

Resource availability can also affect species richness. Abramsky (1978) found an increase in mammalian species richness associated with supplemental food, and Fox (1981) determined that species richness and diversity are functions of regeneration time and therefore, theoretically, increases in resources over time. Whether community responses to resource availability after fire in Australia are determined by individual or combinations of habitat variables are yet to be clarified. The question of adaptiveness also remains unclear. Have Australian small mammals evolved traits that are advantageous in the post-fire environment, and are maintained in the population by natural selection? For example, Australian rodents can be divided into two groups; the "old" and the "new" endemics. Old endemics (subfamily Hydromyinae) entered Australia roughly 4 to 6 million years ago and underwent an expansive evolutionary radiation resulting in approximately 60 extant species (Strahan 1995). New endemics (subfamily Murinae) entered Australia within the last million years and now number a comparatively small 8 species (Strahan 1995). Given that fire has occurred regularly across much of the Australian continent since the Pleistocene (Pyne, 1991), the radiation of old endemic species must have occurred, at least in part, concurrently and perhaps in response to fire and fire-altered habitats. On the other hand, the new endemics may not have had the evolutionary time or expansive radiation necessary to specialise in post-fire habitats. Thus, for the example above (Fox, 1981, 1982, 1983), the apparent specialisation of the old endemic *Pseudomys* spp. to early fire regeneration niches could indicate a co-evolution with fire that is not evident in the new endemic *Rattus* spp. which prefer late regeneration habitats. This concept is supported further by Friend (1993)
who, in a summary of known seral responses of Australian small mammals, categorised the five *Pseudomys* spp. listed as early successional specialists, whereas the two *Rattus* spp. listed were both late seral species.

Some researchers, however, especially in environments outside Australia, have found no evidence of a post-fire succession. Bendell (1974), in a review of 12 studies, concluded that 80% of small mammal populations demonstrated no change in abundance after fire. However, most studies reviewed by Bendell were flawed by the short period of time after fire for which the populations were monitored.

### 5.1.1 AIMS

The aim of this study is to determine the patterns and mechanisms of response of a small mammal community to increased food and nest-site availability in a post-fire forest environment. Although the models described above correlate mammalian abundance with changing habitat or resource characteristics they do not, however, determine the causal relationships involved in succession. This requires an experimental approach, with manipulation of particular habitat or resource variables and a direct quantification of response.

### 5.2 METHODS

The effect of resource availability after fire on small mammals was examined by experimentally manipulating food and cover (in the form of nest-site availability) in twelve sites in burnt sclerophyll forest and woodland near Sydney, Australia (refer to Chapter 2 for site description). Four sites in unburnt forest of the same vegetation type were also monitored to distinguish natural population fluctuations due to seasonal or other environmental factors occurring over the same period. This chapter presents the small mammal community responses to supplemented resource abundance after fire, and the following chapters (Chapters 6 to 9) detail the population responses of the four most abundant species in the community; *Rattus fuscipes, Antechinus stuartii, Mus domesticus* and *Cercartetus nanus*. 
5.2.1 SITE SELECTION AND ESTABLISHMENT

Twelve 1 - hectare sites, burnt 7 January 1994, were selected in the Sydney Sandstone Complex, Open-forest and Woodland (Benson and Howell 1994) vegetation communities of Ku-ring-gai Chase and Garigal National Parks, using vegetation (Thomas and Benson 1985; Benson and Howell 1994), fire coverage and fire frequency (NPWS 1994) and topographical (Anon. 1985) maps to maximise site similarity (Figure 5.1). To ensure independence, no two sites were located in the same continuous patch of vegetation. All sites were separated by natural barriers to animal movements such as creeks, expanses of open rock or ground, different vegetation types, or roads (Oxley et al. 1974; Barnett et al. 1978). Due to difficulties in locating sufficient independent and accessible sites within the boundaries of Ku-ring-gai Chase National Park, one site was located within the adjacent Garigal National Park. This is a piece of bushland that was once contiguous with Ku-ring-gai chase, but is now separated by an arterial road and narrow strip of urban development (Figure 5.1). Vegetation type, geology, topography and fire history are very similar in the two parks (Thomas and Benson 1985; Benson and Howell 1994; NPWS 1994). The minimum direct distance between any two sites was approximately 1.2 km, although these two sites (Sites 4 and 9) were separated by discontinuous vegetation types and a steep ridge. There were no movements of any marked animals between sites.

Four 1 - hectare sites were also established in the region of the park not affected by the 1994 fires (Figure 5.1). These were located in similar vegetation types and were again separated by barriers to animal movement, with no movements between sites recorded. Trapping commenced in August 1994.

5.2.2 RESOURCE MANIPULATION

In January 1995, the twelve burnt sites were allocated randomly to be either food supplementation only (f), nest addition only (n), food and nest supplementation (fn), or control treatments (c) for the rest of the study (three replicate sites per treatment). The distribution of treatments is shown in Figure 5.1. The fire history of sites within each treatment was similar, with sites averaging 2.17 (± 0.72 SD) fires over the previous 20 years (range 1 to 3 fires), and treatments averaging 2.16 (± 0.19 SD) fires over the same period (range 2 to 2.33 fires). Time since the most recent fire was the same at all sites (i.e., 7
January 1994). Supplementation of food and nest sites began at all sites between January 2 and 6 1995, one year after the bushfire.

5.2.2.1 Food availability

Although it would be desirable to provide natural food supplements (Dickman 1989; Boutin 1990), the difficulties in catering for dietary specialists, such as the largely insectivorous *A. stuartii* (Fletcher 1977; Hall 1980; Dickman 1982), meant that an artificial supplement had to be created. The food provided was a mixture of peanut butter, honey and rolled oats (approximate ratio of 4:1:10 by volume); the same mix as was provided and readily taken as bait by all target species. This mix is high in proteins and carbohydrates (Banks 1991), and similar mixes have previously been used successfully in supplementary feeding experiments on *Rattus* spp. (Banks 1991; Leung 1994) and *Antechinus* spp. (Dickman 1989; Banks 1991; Leung 1994).

Based on previous studies (Dickman 1989; Banks 1991; Leung 1994) food was provided initially in 15 one-litre waterproof cartons per treatment site, every two weeks. At the end of the first year, however, it was noted that all the supplementary food was being taken within a week of distribution, so the quantity was doubled to 30 containers per site, per fortnight, to ensure that the small mammals present had ready access to the additional food for most of the two week period. Food cartons were distributed evenly across each site. Half the cartons were placed at ground level to cater for terrestrial species, and half were attached between 1.5 and 2 m above the ground. It was thought that this would allow the partially arboreal *A. stuartii* and *C. nanus* access to food in the event of the larger species such as *R. fuscipes* monopolising ground food stations. Cartons were attached to trees using adhesive packaging tape, and replaced every two weeks. Care was taken to attach cartons under cover, where possible, as many small mammals will not traverse or forage on open ground (Kotler et al. 1993; Brown et al. 1994).
Figure 5.1: Location of experimental study sites within Ku-ring-gai Chase and Garigal National Parks. (AMG 340 000mE, 6280 000mN; Broken Bay 9130-1-N, 1:25 000)
Use of the supplementary food by the target species was confirmed by hair samples collected on double sided tape around the mouth of the cartons, faecal remains in and around cartons, and footprints, bite marks and scratch marks on the cartons. Some food was taken by non-target species, especially birds, although observations indicated that this was sporadic and distributed randomly across all sites in both time and space. Food supplies were usually exhausted before the next distribution. It was considered important to prevent a reliance on the supplementary food, which could prove detrimental to the small mammal populations following the end of the study. The artificial food was thus considered as additional to what was available naturally, not as a total replacement.

5.2.2.2 NEST AVAILABILITY

Artificial nests were designed to mimic both hollow logs and tree hollows. Nest boxes were constructed using 30 cm lengths of 15 cm diameter PVC pipe (Figure 5.2). Both ends were enclosed using 15 cm diameter steel lids with a 2.5 cm hole punched near the rim at each end. Ten nest boxes were distributed evenly across the “nest” and “food and nest” sites, five at ground level, five roughly 2 m above ground. Each was fixed onto a tree using fencing wire, and checked at 6 month intervals to ensure that it was still in place and that the wire was not damaging the tree. As with the food cartons, nest boxes were positioned under cover, where possible, to allow animals to move to and from the nest boxes under shelter.

![Figure 5.2: Nest box design. Nest boxes were constructed from 30 cm lengths of 15 cm diameter PVC pipe. Ends were fitted with steel lids with 2.5 cm diameter entrance holes.](image-url)
5.2.3 DATA COLLECTION

Within each site a 5 x 5 grid of trapping stations with 20 metre spacing was permanently established. Thus an 80 m x 80 m (0.64 hectare) trapping grid was centred at each 1 ha site, allowing for a 10 m buffer strip along each side. Each site was trapped using one 10 x 8 x 30 cm Elliott live capture trap per station, baited with a mixture of peanut butter, rolled oats and honey. Traps were covered with plastic bags and supplied with non-absorbent cotton wool for insulation.

Elliott traps were placed at each trapping station for 3 nights every 3 months between August 1994 and February 1997. August 1994 and November 1994 trapping was conducted to census pre-experimental populations, while all subsequent trapping sessions collected data over the period of experimental provisioning of resources. Sites were not trapped in August 1996 due to other fieldwork commitments (Chapter 4).

All 16 sites could not be trapped simultaneously for logistical reasons. Trapping was therefore conducted over approximately four weeks with a random selection of three or four sites being trapped at any one time.

All captured mammals were identified, and tagged individually using either ear-clipping (A. stuartii, C. namus, M. domesticus) or metal fingerling ear tags (R. fuscipes, R. rattus, R. lutreolus, Isoodon obesulus, Perameles nasuta, Petaurus breviceps). Animals were processed and released at the point of capture. Occupied traps were cleaned and re-set with fresh bait and bedding.

5.2.4 DATA ANALYSES

The assumptions of normality and equality of variance, underlying the use of parametric statistical analyses such as Analysis of Variance (ANOVA), were tested and transformations made, where necessary, using SigmaStat (Version 1.0, Jandel Corporation 1992). Transformed data are identified in the text. All further statistical tests were conducted with JMP (Version 3.1, SAS Institute Inc. 1995).
Responses of the small mammal community were expressed simply in terms of the numbers of species captured per site (species richness). The number of individuals known to be alive (KTBA) was used as the measure of abundance for each small mammal species (Krebs 1966). KTBA was obtained by adding the number of tagged animals captured in a particular trapping period, to the number of animals not caught but known to have been present due to their recapture (Krebs 1966; Fletcher 1977).

Community responses (numbers of species recorded) were compared between the burnt and unburnt sites using one-way analysis of variance (ANOVA), and between resource manipulation treatments in the 12 burnt sites using two-way ANOVA. To incorporate seasonal and other temporal variability into the analysis a two-way repeated measures ANOVA, with time as the repeated measure, was used to take into account the non-independence of data between different trapping sessions at each site (Sokal and Rohlf 1981; Underwood 1997).

The abundance of the four most common species, *Rattus fuscipes*, *Antechinus stuartii*, *Cercartetus nanus* and *Mus domesticus*, during each post-experimental trapping session, was compared using pairwise Pearson product-moment correlations to determine if any relationships between species were evident. Probabilities were corrected for the increased likelihood of Type-I error due to multiple comparisons, using a sequential Bonferroni correction procedure (Rice 1989). An index of relative abundance was used to illustrate further the patterns of community structure during the study. Relative abundance was calculated as the annual population maximum, divided by the maximum abundance of that species during the entire study period (Fox 1983).

### 5.3 Results

discussed in this chapter, and the population responses of the more common species *R. fuscipes*, *A. stuartii*, *M. domesticus* and *C. nanus* are analysed and discussed in more detail in Chapters 6, 7, 8 and 9 respectively.

### 5.3.1 COMMUNITY RESPONSES TO FIRE AND RESOURCE SUPPLEMENTATION

There were significantly more species in burnt sites compared to unburnt sites (df 1,14, \( F = 7.955, p = 0.014 \); Figure 5.3). In addition, two-way ANOVA indicated a significant overall effect of both food and nest availability on community, or species, richness with no treatment interaction. However, a repeated measures model accounting for multiple capture occasions from the same sites throughout the study, indicated that over the length of the study neither food nor nest supplementation had a consistently significant effect on species richness (Table 5.1).

![Figure 5.3: Number of small mammal species recorded in total at each site over the entire study period. Each column represents one site within the treatment indicated on the x-axis. fn = food and nest supplementation, f = food only, n = nest only, c = control and ub = unburnt sites.](image)

**Table 5.1: Effect of supplementary food and nests on mammalian species richness. Two-way repeated measures ANOVA.**

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>( F )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>1</td>
<td>36.628</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nest</td>
<td>1</td>
<td>5.727</td>
<td>0.048</td>
</tr>
<tr>
<td>Food*Nest</td>
<td>1</td>
<td>1.636</td>
<td>0.422</td>
</tr>
<tr>
<td>food*time</td>
<td>7</td>
<td>0.402</td>
<td>0.874</td>
</tr>
<tr>
<td>nest*time</td>
<td>7</td>
<td>0.103</td>
<td>0.996</td>
</tr>
<tr>
<td>food<em>nest</em>time</td>
<td>7</td>
<td>1.422</td>
<td>0.212</td>
</tr>
<tr>
<td>error</td>
<td>64</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Rattus fuscipes and A. stuartii were present throughout the study whereas other species were recorded only during some periods. Figure 5.4 shows the period of occupation of all species during the study. Species richness increased steadily throughout the study from two species in August and November 1994, to a maximum of seven species in February 1997.

Much of the species richness apparent in Figures 5.3 and 5.4 may be attributed to incidental captures of some species. Petaurus breviceps, for example, was caught during two trapping sessions. Similarly, the bandicoots I. obesulus and P. nasuta were captured rarely, and only during February and May. The first I. obesulus and P. nasuta were recorded 2 and 3 years after the fire, respectively, possibly indicating a differential response to the post-fire environment. Unfortunately the sample size was too low to judge the effect of resource supplementation on the bandicoot populations. The additional food was available to both species, and hair samples taken from food cartons confirmed some use. The nest boxes were unsuitable for these rarely captured species.

![Graph showing species richness and occurrence of small mammals during each trapping period.](image)

**Figure 5.4:** Species richness and occurrence of small mammals during each trapping period. Trapping session is indicated on the x axis: a94 = August 1994, n94 = November 1994, f95 = February 1995, m95 = May 1995, etc.

### 5.3.2 Relationships Between Small Mammal Species.

The population sizes of small mammals over time were correlated to identify any possible associations between species. There were significant positive correlations between R. fuscipes and A. stuartii ($r = 0.214, p = 0.036$; $ns$ after Bonferroni correction) and
between *C. nanus* and *M. domesticus* \( r = 0.325, p = 0.001 \). However, low sample sizes precluded the analysis of species associations for the other species recorded.

### 5.3.3 Evidence of succession?

The species present at the beginning of the study in the burnt areas were the same as those present in unburnt sites, indicating that no species were removed from this habitat by fire. Over the study period, however, many more species became trappable in the burnt sites (Figure 5.4), but not in the unburnt ones (Figure 5.3). *C. nanus* was first recorded 13 months after the fire, but did not become established (defined by recaptures of individuals and evidence of reproduction) until November 1995. *M. domesticus* appeared after 16 months and remained present until the end of the study. Both these species remained in low abundance throughout the study period (refer to Chapters 8 and 9). Cautious interpretation of other data indicate that *R. rattus* was first caught in August 1995 and continued to occur sporadically until the end of 1996, while *R. lutreolus* was not caught until the last trapping session in February 1997, and was then found at only one site. The patterns of recolonisation for the latter two species require confirmation based upon larger data sets.

Figures 5.4 and 5.5 demonstrate that *R. fuscipes* and *A. stuartii* populations survived the fire and that recolonisation followed with *M. domesticus, C. nanus, P. breviceps, R. rattus, I. obesus*, *P. nasuta* and *R. lutreolus* appearing, successively, over the four years after the fire. It should be stressed, however, that the data on *P. breviceps* and the bandicoots should be treated with caution due to low sample sizes and lower probability of capture (Section 5.4.1.2), as should the data on *R. rattus* and *R. lutreolus* due to low sample sizes.

An index of relative abundance was used to show when populations of each species reached their maximum size after fire (Figure 5.5). This was calculated as the annual population maximum, divided by the maximum abundance recorded per species over the duration of the study (Fox 1983). All treatments were included to incorporate all species recorded. Note that relative abundance is calculated within species and is not a measure of the abundance of one species compared to another.
The relative abundance of *R. fuscipes* did not decline with the introduction of new species. Relative abundance of this species increased steadily over time to reach maximum numbers in the unburnt sites (Figure 5.5a). In contrast, the relative abundance of *A. stuartii* declined steadily during the 3rd and 4th years after fire, but increased after this period to reach maximum abundance in unburnt sites (Figure 5.5b). The start of the decline coincided with peaks in relative abundance of *M. domesticus*, *R. rattus*, and *P. breviceps*, and continued throughout years 3 and 4 as *C. nanus* and *I. obesulus* numbers increased. The lowest relative abundance of *A. stuartii* was recorded during the 4th year after fire when 6 other species were present in the community. The highest relative abundance, on the other hand, was recorded in both the early and late post-fire stages when only one other species was present.

Within the rodents (Figure 5.5a), the introduced *M. domesticus* and *R. rattus* reached their maximum abundances during the second and third years after fire. Only upon the decline of these species was the native *R. lutreolus* captured. The rate of increase in relative abundance of *R. fuscipes* was not altered by the presence of the introduced species or *R. lutreolus*. Again, however, the difficulty in interpreting such low capture rates of *R. rattus* and *R. lutreolus* must be stressed.

Of the marsupials (Figures 5.5b and 5.5c) the mostly arboreal *P. breviceps* was captured only during the second year after fire, with another largely arboreal species, *C. nanus* peaking in abundance the following year. *I. obesulus* also reached maximum abundances during the third and fourth years after fire, whereas *P. nasuta* was recorded only during the last trapping session, in the fourth year after fire.

Overall, sample sizes of all but four species; *R. fuscipes*, *A. stuartii*, *M. domesticus* and *C. nanus*, were too small to determine if a replacement series, or succession, of small mammal species was occurring. The trajectory of increasing abundance for *R. fuscipes* indicates no obvious response to the presence of particular species or to increasing species richness. By contrast, *A. stuartii* declined in relative abundance with increasing species richness, demonstrating highest tolerances for early and late regeneration niches where only one other species was present. *M. domesticus* and *C. nanus* increased to reach their highest
relative abundances during the second and third years after fire, although the rapid declines after this could be an artefact of only one trapping session during 1997. Even so, neither species was recorded in unburnt sites at any time, thus indicating some preference for early post-fire seral stages.

![Graphs showing relative abundance over years after fire for different species](image)

Figure 5.5: Changes in the relative abundance of each species over the study period, calculated as the annual population maximum (across all treatments) divided by the maximum abundance recorded for that species (across all treatments) during the study (following the method of Fox 1983). Note that the x-axis represents the time since fire so that Year 1 is 0 - 12 months after fire, Year 2 is 13 - 24 months after fire, etc. Unburnt sites are plotted at > 8 years after fire; the minimum estimated time since the previous fire at the sites. The species are shown in groups of: a) rodents, b) scansorial and arboreal marsupials and, c) terrestrial marsupials. Note that data for the first year after fire (1994) are based on only 2 trapping sessions, year 2 (1995) on 4 trapping sessions, year 3 (1996) on 3 trapping sessions, and year 4 (1997) on 1 trapping session (refer to section 5.2.3.1). Curves are drawn by eye. Individual data points are omitted for clarity; detailed abundance data are presented elsewhere for the common species (chapters 6 to 9).
5.4 DISCUSSION

5.4.1 PATTERNS OF POST-FIRE RECOLONISATION IN A SMALL MAMMAL COMMUNITY

This study indicates that late seral forest habitat at Ku-ring-gai Chase supports only two small mammal species, *R. fuscipes* and *A. stuartii*. Fire alters the habitat in such a way that it does not make it unsuitable for either species, but may reduce their relative abundance and perhaps competitive superiority. This, and a change towards more favourable conditions for other species, allow colonisation by other small mammals in the early seral stages. *M. domesticus* and *C. nanus* colonised around 16 months after the fire, although once present, *M. domesticus* established quickly whereas *C. nanus* did not become established until the end of 1995. *P. breviceps* and *R. rattus* were both recorded sporadically during the same year. Two years after the fire the first *I. obesulus* were captured, and three years after, during the last trapping session, *P. nasuta* and *R. lutreolus* were recorded for the first time.

5.4.1.1 COMMON SPECIES

Interestingly, the two dominant species recorded in all trapping sessions and at all sites throughout this study, were *R. fuscipes* and *A. stuartii*. Both these species have been regarded previously as late successional species (Fox and McKay 1981), with a requirement for dense cover (Leonard 1972; Christensen and Kimber 1975; Barnett et al. 1978; Braithwaite et al. 1978; Dickman 1980; Heislers 1980; Catling et al. 1981; Fox 1982; Statham and Harden 1982; Newsome and Catling 1983; King 1985; Lunney and Ashby 1987; Lunney et al. 1987; Wilson et al. 1990), leaf litter (Catling et al. 1981; Fox and McKay 1981; Fox 1982; King 1985) and, in the case of *A. stuartii*, temporal and spatial predictability of resources (Friend 1993). These conditions could be expected to occur only after several years of regrowth post-fire.

Whereas the population responses of *R. fuscipes* and *A. stuartii* are presented in detail in Chapters 6 and 7, I note here that both *R. fuscipes* and *A. stuartii* appeared to survive the fire and maintain populations over subsequent years by successful reproduction and dispersal throughout the burnt sites. However, the maximum abundance of both species was recorded in the unburnt sites. *R. fuscipes* abundance increased steadily over time since fire to reach this maximum abundance, whereas *A. stuartii* demonstrated a small
decline in relative abundance between 2 and 4 years after fire, presumably to be followed by rapid increases during the late seral stages to reach maximum abundance in more mature forest.

Succession refers to the replacement sequence of species colonising a disturbed area as their habitat requirements are met, for a time, by the vegetation regrowth. Animals are responding, in fact, to the primary vegetation succession and are thus, more correctly, exhibiting secondary succession (Fox 1983, 1990). Fox (1982) described small mammal succession in terms of a "habitat facilitation model". Species enter the succession when the changing local and physical conditions first meet their specific requirements. Abundances peak when optimal habitat requirements are met and, as conditions change away from the preferred conditions, the animals leave the succession. The suitability of the habitat is expressed by changes of relative abundance within the population over time. Thus the changes in habitat, expressed as changes in vegetative cover and composition, facilitate the colonisation of small mammal species into the post-fire environment. Alternatively, small mammal species may tolerate the changing habitat at sustained but reduced population levels, with decreased competitive ability. This is termed the habitat tolerance model (Connell and Slatyer 1977; Fox 1982).

After fire in open eucalypt forest, Fox and McKay (1981) defined *R. fuscipes* and *A. stuartii* as late successional species. *R. fuscipes* occurred sporadically during the first 3 years after fire, established resident populations 5 years post-fire, and stabilised at maximum abundance after 8 years (Fox and McKay 1981). Similarly, *A. stuartii* reappeared on burnt sites after 2 years and remained in low, but steadily increasing abundance until 4 years after the fire (Fox and McKay 1981). In the absence of these species during the early post-fire years, *M. domesticus* and native *Pseudomys* spp. dominated the community. These were replaced by a mid-successional community dominated by *Sminthopsis murina* (Fox and McKay 1981).

Fox and McKay (1981) proposed that *R. fuscipes* was restricted to late successional stages by a requirement for dense ground vegetation and an accumulation of leaf litter, their colonisation thus facilitated by the changing habitat conditions. By contrast, in this study,
R. fuscipes maintained body condition and reproductive activity (refer to Chapter 6) throughout the early seral stages, despite significantly reduced leaf litter and an absence of ground vegetation (Section 6.3.3). This could suggest habitat tolerance, although there is no evidence of reduced competitive ability; R. fuscipes was the dominant species at all sites for the duration of the study. The abundances of other species, including A. stuartii, did not approach those of R. fuscipes. In addition, R. fuscipes possibly competitively excluded R. rattus from the habitat, as it appears to do elsewhere (Cox 1997). Although R. rattus did appear at some sites, it did not establish populations. It is possible that habitat conditions never became suitable for this species, although R. rattus is generally regarded as opportunistic, with few specific habitat requirements (Braithwaite and Gullan 1978).

In this study, the first new species to successfully colonise after the fire were the feral M. domesticus and R. rattus. Unlike in previous studies, however, these species did not arrive within 4 to 5 months of the fire (e.g., Christensen and Kimber 1975; Newsome et al. 1975; Catling 1986; Fox 1982, 1983, 1990), but in the second year after fire. Both species peaked in abundance between 2 and 3 years after fire, although only one sampling session in 1997 makes it difficult to determine if the decline in year 4 (Figure 5.5a) is real or an artefact of sampling effort. Neither species reached the high, or plague densities recorded elsewhere (e.g., Christensen and Kimber 1975; Newsome et al. 1975; Catling 1986; Fox 1982, 1983, 1990).

The low abundance of these introduced species and, in the case of R. rattus, the failure to successfully establish a population, could be due to the relatively high abundances of A. stuartii and R. fuscipes. The habitat and dietary preferences of R. rattus and R. fuscipes are similar (Braithwaite and Gullan 1978; Watts and Braithwaite 1978), leading to the suggestion that R. rattus may substitute for R. fuscipes where the latter is absent (Braithwaite et al. 1978). Similarly, it has been suggested that M. domesticus occupies the scansorial insectivore niche in the absence of A. stuartii (Braithwaite and Gullan 1978). High abundances of R. fuscipes and A. stuartii may have prevented the effective colonisation of introduced species into the early post-fire environment. This possibility is investigated further in Chapter 8.
The absence of Pseudomys spp. from the Ku-ring-gai community might have been expected to allow high abundances of the ecologically similar but opportunistic M. domesticus during the early post-fire seral stages. However, high abundances were not recorded, with only 47 M. domesticus being captured across all sites. Previous studies of M. domesticus after fire demonstrate coexistence with Pseudomys spp., but not with A. stuartii or R. fuscipes when the latter were in high abundance (Fox 1981, 1982, 1983, 1990). This suggests further that M. domesticus may have been excluded by A. stuartii and/or R. fuscipes.

5.4.1.2 Other species

The probability of capture of some species, given their habits, may have contributed to the observed patterns of post-fire colonisation. Whereas Rattus spp. and M. domesticus are terrestrial, and A. stuartii is scansorial but forages and moves extensively on the ground (Braithwaite 1983; Carthew 1994), the likelihood of capturing C. nanus and P. breviceps could have been reduced due to their largely arboreal nature. It is possible that both species were present in the unburnt sites but were captured only in burnt sites as reduced resource availability led to a habitat or dietary shift requiring increased terrestrial activity. Epicormic regrowth along the trunks and around the base of many trees could have provided cover to allow them to descend to the ground. Post-fire habitat (Begg et al. 1981; Fox 1983) and dietary (Luo and Fox 1996) shifts have been noted previously in terrestrial small mammal species, although these have not been investigated in relation to arboreal species. In addition, both these species were most commonly, although not always, caught in food supplementation sites. As the bait and food supplement were the same, it may be that the animals were more attracted to traps in sites where they had prior experience with the bait type.

Carthew (1994) tracked the foraging movements of arboreal marsupials between flowering Banksia spinulosa trees. P. breviceps usually glided directly onto the flowering plant or glided between trees and saplings, then descended to nearby flowering shrubs. Some terrestrial movements were also reported for this species, with animals observed to use logs as runways between B. spinulosa trees, however foraging activity was generally confined to the branches of the flowering plants (S. Carthew pers. comm). C. nanus
generally moved through the vegetation at about one metre above the ground and approached inflorescences by climbing up the stem (Carthew 1994). Radio-collared C. nanus, however, have been shown to spend more time in the canopy (84% of records) than lower in the vegetation, with only 11% of records being animals located between 1 and 5 metres above the ground (Bladon 1995). Bladon (1995) also found that C. nanus moved occasionally across the ground (5% of records). For both species, the limited terrestrial activity would decrease the probability of being caught by Elliott traps placed on the ground, as they were in this study. Nevertheless, both species were caught, C. nanus regularly (Chapter 9), and it must be assumed that the same proportion of the population at any site would be trappable and thus that the data from each site are comparable. The possibility of familiarity with the food type attracting P. breviceps into the traps should also be considered, as this species was caught only in food supplementation sites. This effect would, however, be expected to continue throughout the supplementation period and as P. breviceps was captured only during the first year of supplementation it seems unlikely that this explains the captures of this species on the ground. Similarly, as C. nanus was recorded in control sites, food sites and food and nest sites, and recapture rate did not vary between these treatments (Chapter 9), it is unlikely that prior experience with the food type differentially affected capture rate of this species.

Very little is known about the response of small arboreal marsupials to bushfire. Lunney and Barker (1986), in a survey of mammals in coastal forests of southern New South Wales, determined that C. nanus prefers altered habitats, being recorded only in logged and burnt areas of the forest and on cleared farmland. In contrast, a survey of Royal National Park, south of Sydney, New South Wales, after the 1994 bushfires revealed that C. nanus was found predominantly in unburnt areas two years after the fire, although by three years after the fire it was becoming established in burnt areas (D. Andrew unpubl. data). Similarly, in Western Australian mallee-heath, the highest abundances of the closely related C. concinnus were found in mature stands (Bamford 1986). P. breviceps, on the other hand, seems to show no preferences and has been found in both burnt and unburnt treatments of logged and unlogged forest areas, as well as farmland (Lunney and Barker 1986). Spotlighting surveys similarly revealed no difference in the abundance of this species between burnt and unburnt patches of woodland and open forest in Royal National Park.
two years after fire (D. Andrew unpubl. data). In this study both species were found only in burnt sites, although, as discussed above this may be an artefact of changed habitat use rather than of actual occurrence. Captures of *P. breviceps* in food supplementation sites, and only during the second year after fire (the first year of supplementation), indicates that the availability of food is possibly a factor which limits the occurrence of this species in the early post-fire seral stages, and that increased terrestrial movements are a result of increased foraging activity. Due to the low capture rate, however, further study is required to confirm this possibility.

Bandicoots, *I. obesulus* and *P. nasuta*, were largely excluded from capture by their size, as adults of each species grow to 850 g and 1100 g respectively (Braithwaite 1983; Stodart 1983). All captures of these species were during February and May, and involved juveniles or sub-adults (weight range of *I. obesulus* = 186 - 248 g, and *P. nasuta* = 300 - 420 g). Although both species can reproduce whenever conditions are appropriate, most reproductive activity is concentrated in the latter part of winter, spring and summer (Braithwaite 1995; Stodart 1995). *I. obesulus* was first recorded during February and May 1996, then again in February 1997, but was not caught in the trapping session between these periods. Bandicoot diggings, although not systematically recorded during this study, were noted regularly in some sites during the latter part of 1996. This would indicate a continued use of the sites from at least 2 years after the fire onward. Although *in situ* reproduction of *I. obesulus* could not be distinguished from immigration, the juvenile captured in February 1996 weighed 186 g and is likely, therefore, to be too young to have dispersed from outside the area (Stoddart and Braithwaite 1979). As such, it seems that adults were established in the site prior to the first capture and the individuals captured were a result of successful reproduction towards the end of 1995.

Newsome *et al.* (1975) attributed an immediate post-fire decline of *I. obesulus* and *P. nasuta* to the destruction of nesting material such as logs and dense ground vegetation. However, soon after the fire extensive bandicoot diggings were observed and both species became trappable. Diggings had been rare before the fire, although they were common afterward, even as the ground vegetation became quite dense. Similarly, Thompson *et al.* (1989) reported an apparent increase in the number of diggings after a prescribed burn,
although they could not distinguish if this reflected an increase in bandicoot abundance or a result of either improved visibility with the removal of the undergrowth, or of increased foraging activity. Increased numbers of diggings and track counts also indicated increased foraging activity and/or the increased abundance of bandicoots within a year of the fire to Newsome et al. (1975). Unfortunately, in the latter study, diggings and tracks were not distinguished at species level, and trapping results were not reported, so any differential response between *I. obesulus* and *P. nasuta* could not be identified.

Stoddart and Braithwaite (1979) and Fox (1980) found that *I. obesulus* and *I. macrourus*, respectively, reach their maximum abundances in fire-disturbed habitats. Conversely, however, Wilson et al. (1990) reported that *I. obesulus* stayed in low abundance until 5 to 6 years after fire. Despite this, the captures of juvenile *I. obesulus* during this study, several kilometres from the nearest large patch of unburnt habitat, indicate that this species is capable of successful reproduction and survival during early post-fire seral stages. *I. obesulus* employs a dynamic breeding strategy enabling rapid recolonisation (Friend 1993). Changes to the length of the breeding season, and the number and size of litters, are influenced by changes in adult and juvenile mortality (Stoddart and Braithwaite 1979). *P. nasuta* was not recorded until three years after the fire, indicating a delayed response in comparison to *I. obesulus*.

### 5.4.1.3 Patterns of species richness

Species richness was significantly higher in burnt forest than unburnt forest, although the provision of food and nest resources had no effect on richness over time. These findings could provide evidence of fire creating a wider diversity of habitats not available in mature forest, or indicate the specialisation or adaptiveness of Australian small mammals to fire-altered habitat.

Increasing small mammal species richness has been associated with increasing plant species diversity and the assumed parallel increase in food resources (Braithwaite et al. 1985; Wilson et al. 1990). Assuming that small mammal post-fire succession is a function of vegetation succession, Fox (1982) suggested some mechanisms that may alter the structure of mammalian communities and influence species richness. Firstly, fire may create
new habitats to which individuals in the local species pool may immigrate. Secondly, fire creates a sequence of microhabitats that are a function of time since fire, and these are selected preferentially by different mammalian species. Thirdly, frequent fire may also lead to under-utilised habitats that can be exploited by fugitive (often introduced) species. Fourth, frequent fires can lead to the evolution of early seral stage post-fire specialists. Species enter the post-fire habitat, by competitive displacement of earlier species, when the conditions suit them (succession), and finally, early successional species are able to alter the plant succession (e.g., by grazing), delaying favourable conditions arising for later successional species, and thus prolonging the mammalian succession (Fox 1982).

These patterns follow for the Ku-ring-gai small mammal community during the early to mid-seral stages, but not necessarily later in the succession. Species richness increased over the first three years after fire, but low species richness was recorded in late seral (unburnt) sites. As plant species diversity was not measured in this study, it is difficult to determine if the observed patterns of small mammal species richness are related to plant diversity or richness. Plant species diversity is often thought to decrease with increasing time since fire (e.g., Specht et al. 1958), although Keith (1996) considered this to be too broad a generalisation. Plant species diversity has previously been found to peak in late seral stages, in habitat similar to that in this study (Fox and Fox 1987; Fox 1988). Such diversity should support the greatest small mammal richness in late seral stages if the association between plant and mammalian species richness is robust.

5.4.2 ARE AUSTRALIAN SMALL MAMMALS ADAPTED TO FIRE?

Fox and McKay (1981) suggested that the preferences shown by Pseudomys spp. for early post-fire seral stages, S. murina for mid seral stages and A. stuartii and R. fuscipes for late seral stages are indicative of adaptation to specific post-fire conditions and perhaps fire-prone habitats overall. Fox (1982) further demonstrated that a mosaic of patches with different fire histories in Myall Lakes National Park, New South Wales, led to early, mid and late successional small mammal communities being maintained within the local area, increasing local species richness and diversity.
The patterns of adaptation are particularly evident among the rodents. Fire has been an integral part of the Australian landscape for millions of years (Pyne 1991). It was argued in Section 5.1 that the evolutionary radiation of the old endemic rodents must have occurred, at least in part, concurrently, and perhaps in response to fire and fire-altered habitats. New endemics, on the other hand, may not have had the evolutionary opportunity to undergo the expansive radiation necessary to specialise in post-fire habitats. This is supported by the findings of Fox and McKay (1981) and Fox (1982, 1983, 1990) who categorised the old endemic *Pseudomys* spp. as early seral specialists, and the new endemic *Rattus* spp. as late successional species, requiring dense, mature vegetation for successful reproduction.

As no *Pseudomys* spp. were present in the Ku-ring-gai Chase community, the maintenance of a population of *R. fuscipes*, with steady population growth throughout the early and mid seral stages, indicates that this species is not restricted to late seral stages, and is, rather, a habitat generalist. Given the location of many of the sites used during this study on a peninsula, and very few unburnt patches remaining in the area after the fire, it could be assumed that the *R. fuscipes* populations present at the sites were fundamentally a result of survival through the fire and subsequent reproduction. Dispersal onto the burnt sites from the nearest unburnt patches would, in some cases, have required the animals to traverse several kilometres of burnt habitat. As such, if *R. fuscipes* remain relatively abundant in the early post-fire stages they may competitively exclude *Pseudomys* spp. Alternatively, *Pseudomys* spp. may be able to utilise early post-fire seral stages more efficiently than *Rattus* spp. when both are present in the local species pool, thus effectively excluding *Rattus* spp. through superior competitive ability. However, in the absence of *Pseudomys* spp. the resource availability in early seral stages is adequate to support a growing population of *Rattus* spp. This suggests that post-fire succession is not predominantly resource or vegetation driven, but primarily a result of competition. Adaptiveness may improve competitive advantage for some species in some communities, but the patterns of recolonisation after fire in any location may thus be seen, fundamentally, as a result of the regional or local species pool.
5.4.3 CONCLUSIONS

An important outcome of this study is the suggestion that the composition of small mammal communities may govern the response patterns of individual species to fire-altered habitat. Within habitat types, the same species may occupy different regeneration niches dependent primarily upon interspecific interactions, rather than habitat requirements as described by Fox (1982). Whilst changes in small mammal communities after fire have often been correlated to changing vegetation and perhaps associated food supply (refer to Chapter 1), and species undoubtedly have certain habitat requirements that must be met in order to survive and successfully reproduce, I propose that as long as basic resource requirements are met, generalist species, in particular, are able to utilise a range of post-fire niches. Thus post-fire succession is largely dependent upon the mammal community composition.

The Ku-ring-gai Chase small mammal community appeared to respond to the fire in the following way. Prior to the fire, as suggested by trapping in the unburnt sites, *R. fuscipes* and *A. stuartii* were present in high abundance. Other small mammal species were either absent, in low abundance, restricted to small, isolated patches of vegetation with specific fire histories, or utilising the mature habitat differently than they did after the fire. When the fire occurred, some less abundant species were further isolated or removed temporarily from the community, but remained regionally active. *R. fuscipes* and *A. stuartii* numbers were reduced, by either mortality, predation or reduced resource availability, but populations remained in sufficiently high abundance to successfully reproduce and, in the case of *R. fuscipes*, increase. The abundance of these two species remained several times higher than that of other small mammal species after the fire, and this dominant position in the community probably excluded the effective establishment of most other species in the early seral stages, if not by optimal resource utilisation, then by the competitive advantage of sheer numbers. Some species, such as the opportunistic *M. domesticus* and the largely arboreal and specialised *C. namus*, were possibly able to establish populations by occupying niches not overlapping with those of *R. fuscipes* and *A. stuartii*. Even so, populations of *M. domesticus* did not reach the high abundances or plague conditions previously recorded, and neither species approached the abundances reached by *R. fuscipes* and *A. stuartii*. 
Further insight into the mechanisms underlying the community response is possible only by investigating in detail the responses of the component species. These investigations are described in the following four chapters.
CHAPTER 6: POPULATION RESPONSES OF RATTUS FUSCIPES TO RESOURCE
AVAILABILITY AFTER FIRE

6.1 INTRODUCTION

The bush rat, Rattus fuscipes, is a small (< 200 g) murid rodent native to the east,
south-east and south-west coastal regions of Australia (Figure 6.1a). R. f. assimilis is the
subspecies occurring in eastern Australia from Victoria, through NSW, to Queensland
(Figure 6.1b), and is the focus of this study. The major breeding season for R. f. assimilis is
between September and May although reproduction can occur year round (Taylor and
Horner 1973). Wild individuals of both sexes can reproduce from 12 weeks of age (Taylor
1961), and as early as 7 weeks under laboratory conditions (Taylor and Horner 1971).
Mean litter size estimates range from 3.8 (Taylor 1961) to 4.98 (Warneke 1971). Although
females may produce up to three litters in a single breeding season (Taylor and Horner
1973), few adults of either sex survive to reproduce the following year (Press 1987). The
winter breeding hiatus of R. fuscipes was considered by Banks (1991) to be due to food
limitation. Food supplementation for seven weeks during June and July led to population
increases of up to 1.8 times pre-manipulation abundances, and up to 2.7 times the control
population abundance, as well as to increases in winter reproductive activity (Banks 1991).

Rattus fuscipes is a selective omnivore. Its winter diet consists primarily of
endogenous fungi, with a small proportion of arthropod and fibrous plant material, whereas
in summer arthropods, fleshy fruit, and seed are the dominant foodstuffs (Cheal 1987). Diet
may be habitat-specific, however, as Stewart (1979) found that R. fuscipes in tall open
forest of the Australian Capital Territory was herbivoruous year round. The broad dietary
preferences of R. fuscipes have been suggested to promote the ability of individuals to
survive bushfire by dietary shifts (Lunney 1983). This suggestion was refuted by Cheal
(1987), who noted that endogenous fungi and many invertebrates are dependent largely
upon leaf litter, and may not therefore re-establish for several years after a fire. Ahlgren and
Ahlgren (1965) and Jorgensen and Hodges (1970), however, found no difference in fungal
abundance between burnt and unburnt sites in the USA. This observation is further
supported by samples of soil fungi taken during this study from Ku-ring-gai Chase National Park (P. A. McGee, G. S. Pattinson and E. F. Sutherland, unpublished data).

Laurance (1994) described *R. fuscipes* as a habitat generalist, although habitat preferences are well documented for this species. Previous studies have associated *R. fuscipes* with structurally complex vegetation (Braithwaite et al. 1978), leaf litter (Catling et al. 1981; Fox and McKay 1981; King 1985), logs (Catling et al. 1981), patchiness of the understorey (Fox and McKay 1981) and particular floristic groups (Hall and Lee 1982). In addition, an association between the abundance of *R. fuscipes* and dense ground vegetation often has been noted (Stewart 1979; Heislers 1980; Catling et al. 1981; Lunney and Ashby 1987; Lunney et al. 1987), and increases in *R. fuscipes* abundance have been correlated to the regeneration of vegetative cover (Leonard 1972; Christensen and Kimber 1975; Heislers 1980; Catling et al. 1981; Fox 1982; Newsome and Catling 1983; King 1985; Lunney and Ashby 1987; Lunney et al. 1987; Wilson et al. 1990). *R. fuscipes* nests in logs, leaf litter and in burrows underground or under rocks (Dickman 1991).

After fire, Leonard (1972) found that although there was no decline in abundance, reproduction of *R. fuscipes* was much reduced and breeding that did occur may have been delayed relative to that in populations at nearby unburnt sites. Similarly, Thompson et al. (1989) found no recruitment of juveniles into a population of *R. fuscipes* for two years post-fire, and Fox (1982) demonstrated that *R. fuscipes* has limited recolonisation potential after fire due to an inability to reproduce until later seral stages of vegetation have been achieved. In contrast to the above studies, however, Recher et al. (1975) found that although population abundance was much reduced by fire, *R. fuscipes* began breeding earlier than usual in the year following fire. Further, Friend (1979), noted rapid colonisation of cleared land by sub-adult *R. fuscipes* and considered this indicative of good post-disturbance recovery potential.
The response of *R. fuscipes* to fire may be population-specific and based on particular local environmental attributes such as resource availability. Many researchers have suggested that the successful recolonisation of *R. fuscipes* after fire is dependent upon vegetation type (Leonard 1972; Catling 1981). Further questions are being asked about the influence of the environment on the structure and stability of the four most common species were investigated by comparing the establishment of bush burnt sites with the three burnt control sites. This enabled an overall picture of small mammal demography to be established and as a basis to which the treatment effects of food supplementation could be contrasted. The investigation of natural resource availability and regeneration after fire were investigated to determine factors external to the design of this experiment that would have influenced the observed dynamics of these species. The investigations into the population responses of *R. fuscipes*, *M. stuartii*, *M. domestica* and *C. novaezelandiae* are presented in the previous section on population dynamics.

The site locations and arrangement of trapping grids are presented in the previous section.
The response of *R. fuscipes* to fire may be population-specific and based on particular local environmental attributes such as resource availability. Many researchers have suggested that the successful recolonisation of *R. fuscipes* after fire is dependent upon vegetative regrowth, and the associated increases in food and/or cover availability (Leonard 1972; Christensen and Kimber 1975; Catling et al. 1981; Fox 1982; Newsome and Catling 1983; Lunney and Ashby 1987; Lunney et al. 1987; Wilson et al. 1990). These suggestions are based on correlative evidence and mechanistic processes have yet to be quantified.

### 6.1.1 AIMS

The investigation described in this chapter aimed at determining the responses of the bush rat, *Rattus fuscipes*, to resource availability after fire. Food and nest site availability were manipulated to establish whether either or both of these factors significantly influenced *R. fuscipes* population dynamics and structure in the post-fire environment. Quantification of population responses to resource availability should help to determine the mechanisms behind the recovery of *R. fuscipes* after fire.

### 6.2 METHODS

#### 6.2.1 EXPERIMENTAL DESIGN AND DATA COLLECTION

The effect of fire on the population dynamics, reproductive behaviour, population structure and stability of the four most common species were investigated by comparing the four unburnt sites with the three burnt control sites. This enabled an overall picture of small mammal demography to be established as a baseline to which the treatment effects of food and nest supplementation could be contrasted. In addition, natural resource availability and regeneration after fire were investigated to determine factors external to the design of this experiment that could have influenced the observed dynamics of these species. The investigations into the population responses of *R. fuscipes*, *A. stuartii*, *M. domesticus* and *C. nanus* are presented in Chapters 6 to 9 respectively.

The site locations and arrangement of trapping grids are presented in the previous chapter, Section 5.2. Details of the experimental design and data analyses for Chapters 6 to 9 are provided below.
6.2.1.1 SMALL MAMMALS

All captured mammals were identified, and tagged individually using either ear-clipping (*A. stuartii*, *C. nanus*, *M. domesticus*) or metal fingerling ear tags (*R. fuscipes*). The sex, weight, reproductive condition, head length (from the tip of the nose to the occipital condyle) and any distinguishing features were recorded. Animals were processed and released at the point of capture. Occupied traps were cleaned and re-set with fresh bait and bedding.

Weight alone is often used to determine the reproductive status of *R. fuscipes* (Woodside 1983), but in this study it was considered a poor choice as the availability of food may influence body mass independently of reproduction. Taylor and Horner (1973) used head length to categorise juvenile and adult *R. fuscipes* (Taylor and Horner 1973). Their criterion of a head length of ≤ 36.9 mm to indicate a juvenile was determined from measurements of museum specimens. However, in this study it was felt that, allowing for the lesser accuracy of measurements of live animals under field conditions, this criterion alone was not entirely satisfactory. As such, during this study juveniles were categorised primarily by head length (juvenile head length ≤ 36.9 mm) although some additional animals with head lengths up to 40.0 mm and weighing < 50 g for females and < 60 g for males were classified as juvenile (Heislers 1980). The reproductive condition of adult *R. fuscipes* was recorded as scrotal or non-scrotal for males, and parous, non-parous, lactating or pregnant for females. Late pregnancy was detected by gently palpating the abdominal region of the animal to detect developing embryos. Data from other *Rattus* species were collected in the same way but are not considered further due to low sample size.

Marsupials (*A. stuartii* and *C. nanus*) were classified as juvenile or adult by the state of their pouches or testes (refer to Woolley 1966; Dickman 1985). *Mus domesticus* adults were identified by enlarged nipples in females, and descended testes or pigmented, wrinkled scrotal sacs in males; whereas juveniles were identified by the absence of conspicuous nipples and by inguinal testes.
6.2.1.2 Vegetation

Regrowth of vegetation throughout the study was monitored to identify changes in the availability of natural cover for the animals. As all sites were located within the same vegetation type (see Section 5.2.1), the sites were floristically similar. However, the structure of the regrowth could conceivably vary across sites due to unmeasured factors such as fire intensity, fire history, soil nutrients, soil moisture and level of herbivory. These differences in forest structure between sites could favour some small mammal species over others. Arboreal and terrestrial small mammals, for example, would be expected to have quite different structural habitat requirements. Vegetative cover may act as a refuge or a nest site and may also be a source of food and nesting material. Conversely, it may harbour predators or competitors.

Similarly, changes in ground cover were also measured throughout the study. The ground substrate is important for small mammals in terms of cover (trees, grass/shoots, logs, rock crevices and overhangs), burrowing opportunities (bare ground, leaf litter), nest sites (logs, rock crevices and overhangs, trees) and food (invertebrates, leaf litter, grass/shoots, trees, bark).

Vegetative cover was measured in February 1995, 1996 and 1997. In 1995, sixteen 2 x 2 m quadrats were located by randomly selecting 16 of the 25 trap stations within each site. To ensure independence between years, the first side of the quadrat was located 3 m due East (in 1995), due South (in 1996) and due North (in 1997) of the trap station. Within each quadrat, pins were placed vertically onto the ground at 40 cm intervals in a 5 x 5 grid, and the presence or absence of vegetation contacting the pin was scored from 0-20 cm, 21-50 cm, 51-100 cm, 101-200 cm and > 200 cm (P. J. Myerscough pers. comm.). Cover, from the animal’s perspective, was considered to be equally valid whether dead or alive. The ground contact of the pin was also recorded in one of ten categories; bare ground, leaf litter, bark, charcoal, rock, tree trunk, grass/leaves, log (> 15 cm diameter), sticks (< 15 cm diameter) or roots. Each quadrat recorded a maximum of 25 points for each variable, and this was averaged across all quadrats to produce a total score for each variable within a site.
In order to improve field efficiency and cost-effectiveness, the appropriate sample size required for this analyses was adjusted after the first data were collected in 1995. An analysis of the variance on the 1995 data allowed for a reduction of sample size from 16 to 8 quadrats per site in 1996. After subsequent analysis this was increased to 10 quadrats in 1997. In 1995 and 1997 all sites were sampled, however, in 1996 only half the burnt sites (sites 1, 2, 3, 4, 5 and 9) in addition to the four unburnt sites were recorded.

Vegetation data are presented in relation to the population responses of the four most abundant small mammal species (Chapters 6 to 9).

6.2.2.3 Microhabitat

At the conclusion of the study, the microhabitat around each trapping station at each site was assessed to determine, further, the availability of cover and nest sites within each site. As traps were placed in the same position throughout the study, and the microhabitat variables measured consisted of features that vary little on a temporal or spatial scale, it was considered that the microhabitat qualities measured would have remained unchanged throughout the course of the study. Within a 3 m radius of each trapping station, the presence or absence of "useful" rocks (defined as rock with crevices or overhangs that could be used by animals as shelter or runways), trees (> 4 m high, dead or alive) and logs (> 15 cm diameter) were noted. Trees were scored further for the presence or absence of visible hollows. The presence/absence data were added to give a maximum score of 25 for each factor at each site.

Microhabitat data are presented in relation to the population responses of the four dominant small mammal species (Chapters 6 to 9).

6.2.2 Data analyses

The assumptions of normality and equality of variance, underlying the use of parametric statistical analyses such as Analysis of Variance (ANOVA), were tested and transformations made, where necessary, using SigmaStat (Version 1.0, Jandel Corporation 1992). Transformed data are identified in the text. All further statistical tests were conducted with JMP (Version 3.1, SAS Institute Inc. 1995).
6.2.2.1 SMALL MAMMALS

The number of individuals known to be alive (KTBA) was used as the measure of abundance for each small mammal species (Krebs 1966). KTBA was obtained by adding the number of tagged animals captured in a particular trapping period, to the number of animals not caught but known to have been present due to their recapture (Krebs 1966; Fletcher 1977).

An index of body condition was calculated by dividing an animal's weight by its head length (Krebs and Singleton 1993). Recapture data were excluded from analyses as were juveniles (except for *A. stuartii*), obviously pregnant females and females with pouch young. *Antechinus stuartii* juveniles were not excluded as their rigid reproductive cycle ensures that all males in the population are the same age, and investigation of the data showed that there was a similar proportion of 2nd year to 1st year females across all treatments (Chapter 7).

Population stability was measured in terms of the proportion of transient and resident animals present at each site. Individuals were classed as transient if they had been caught only once, as resident if they had been caught more than once, and as permanent residents if they had been caught in more than one trapping session. As such, the transients plus the residents equalled 100% of the population, and permanent residents were a subset of the residents. Arcsine transformation of the data was not considered necessary in further analyses as the original percentages were within the range of 30 and 70% (Sokal and Rohlf 1981).

The longevity, i.e., trap-revealed longevity (Kikkawa 1964), of individuals within a site was measured as the number of trapping periods over which permanent residents were captured. Survival of individuals may be enhanced by resource availability, so it may be expected that animals in food and nest supplementation sites would remain in the area longer.

Comparisons of all population features (i.e., abundance, body condition, population stability and trap-revealed longevity) between four unburnt sites and three burnt control
sites were made using one-way ANOVA. A two-way ANOVA was used initially to test the experimental effects of food and nest supplementation over the duration of the study. The mean population response values for each species at each site, averaged over the post-manipulation trapping sessions, were used. Therefore only one value (the mean) per treatment site was used to avoid pseudoreplication (Hurlbert 1984; Spiller and Schoener 1998). To incorporate seasonal and other temporal variability into the analysis a two-way repeated measures ANOVA, with time as the repeated measure, was used to take into account the non-independence of data between different trapping sessions at each site (Sokal and Rohlf 1981; Underwood 1997). Power analysis of non-significant results was used to determine the probability of a Type II error, and to identify the increase in sample size that would be required to detect a significant effect given the variance inherent in the sample. Comparisons within trapping periods, or of averaged population measures within sites, were made using two-way ANOVA.

6.2.2.2 GROUND COVER AND VEGETATION

Ground contact variables were recorded originally in ten categories; bare ground, leaf litter, bark, charcoal, rock, tree trunk, grass/leaves, log, sticks or roots. Pairwise (Pearson product-moment) correlations between these factors and small mammal abundance (KTBA) were initially conducted, and corrected for increased probability of Type-I error resulting from multiple comparisons using a sequential Bonferroni correction procedure (Rice 1989). However, correlations provided no consistent associations for any of the mammal species recorded, so the ten ground cover variables were reduced to six categories incorporating the rarer variables; litter (leaf litter + bark + sticks), live-wood (tree + roots), dead-wood (log + charcoal), bare-ground, rock and grass/leaves. The six ground contact groups were then subjected to principal components analysis (PCA), and the components explaining most of the variation used as dependent variables in multiple linear regressions against small mammal abundance (KTBA) for the trapping period corresponding to when ground cover and vegetation measurements were made (February 1995, 1996, 1997), and the following (May) trapping period for 1995 and 1996. Components were retained in regressions when $\alpha = 0.05$ or less.
The same procedure was undertaken with the five variables representing vegetation cover at different heights. Pearson product-moment correlations failed to identify any consistent patterns of association, so principal components encompassing the variation within the five vegetative height cover variables were identified and regressed (multiple linear regression, \( \alpha = 0.05 \)) against small mammal abundance (KTBA) as described above.

### 6.2.2.3 Microhabitat

The presence of useful rock, trees, trees with hollows and logs were first correlated (Pearson product-moment) with small mammal abundance. Probabilities were adjusted to account for multiple comparisons using sequential Bonferroni corrections (Rice 1989). As no consistent patterns were found, PCA was used to group the factors into components explaining the variation. A linear regression between small mammal KTBA and the microhabitat principal components was conducted to determine any relationships, using data collected in February 1995, 1996, 1997 and May 1995 and 1996.

### 6.3 Results

#### 6.3.1 Population Dynamics in Unburnt Sites

The average number of *R. fuscipes* known to be alive (KTBA) in unburnt sites fluctuated between 6.25 and 14.8 per hectare through the study period. By comparison, burnt control (sites without food and/or nest supplementation) populations ranged between 2.5 and 8.3 animals per hectare throughout the study. Populations in the unburnt sites showed a decline from previous trapping periods every November, after which there was generally an increase over summer (Figure 6.2).
Juveniles were recruited into the population throughout the year. Figure 6.3 compares the number of juveniles in unburnt sites to the number of juveniles recorded across all burnt sites combined, during each trapping session, and indicates no consistent trend of recruitment towards any particular season in either burnt or unburnt areas. Graphical comparison between unburnt and burnt control sites is not presented as low sample size from the burnt control sites made it difficult to discern any seasonal patterns. However, statistical analysis between the average number of juveniles in burnt control and unburnt sites found no significant difference in the number of juveniles recruited into the populations during any trapping period (Table 6.1). Thus, fire did not alter the time of reproduction or recruitment success of this species in any obvious way.

The body condition, calculated as the ratio of body mass to head length (Section 5.2.4.1), of adult *R. fuscipes* was assessed to determine if differences existed between animals living in burnt control sites and unburnt sites. There was no significant difference in the body condition of animals in burnt control and unburnt sites over the entire study period.
(df 1.5, F = 1.444, p = 0.283), and analysis of individual trapping sessions indicated that there were no significant seasonal effects either (Figure 6.4; Table 6.2).

Figure 6.3: Average number of juvenile *Rattus fuscipes* KTBA in unburnt sites and all burnt sites combined, across all trapping periods. Note that this figure and Table 6.1 are not directly comparable as data from all burnt sites combined are shown here. Data from only burnt control sites are not shown due to low numbers of juvenile captures in these sites. Means are shown ± standard error. Dotted lines indicate assumed trajectory as no data are available for August 1996. Trapping period is indicated on the x axis: a94 = August 1994, n94 = November 1994, f95 = February 1995, m95 = May 1995, etc.

Table 6.1: One-way ANOVA testing for differences between the average number of juvenile *Rattus fuscipes* KTBA in burnt control and unburnt sites in each trapping session. No data are available for August 1996. Note that these data are not the same as presented in Figure 6.3.

<table>
<thead>
<tr>
<th>Trapping session</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>August 1994</td>
<td>1.5</td>
<td>0.303</td>
<td>0.606</td>
</tr>
<tr>
<td>November 1994</td>
<td>1.5</td>
<td>0.042</td>
<td>0.846</td>
</tr>
<tr>
<td>February 1995</td>
<td>1.5</td>
<td>0.714</td>
<td>0.437</td>
</tr>
<tr>
<td>May 1995</td>
<td>1.5</td>
<td>0.000</td>
<td>1.000</td>
</tr>
<tr>
<td>August 1995</td>
<td>1.5</td>
<td>0.436</td>
<td>0.539</td>
</tr>
<tr>
<td>November 1995</td>
<td>1.5</td>
<td>1.429</td>
<td>0.286</td>
</tr>
<tr>
<td>February 1996</td>
<td>1.5</td>
<td>2.820</td>
<td>0.154</td>
</tr>
<tr>
<td>May 1996</td>
<td>1.5</td>
<td>0.645</td>
<td>0.458</td>
</tr>
<tr>
<td>November 1996</td>
<td>1.5</td>
<td>0.042</td>
<td>0.846</td>
</tr>
<tr>
<td>February 1997</td>
<td>1.5</td>
<td>2.108</td>
<td>0.206</td>
</tr>
</tbody>
</table>
Figure 6.4: Body condition index of adult *Rattus fuscipes* between burnt control sites (c) and unburnt sites (ub). Data are unavailable for August 1996. Means are shown ± standard error.
Table 6.2: One-way ANOVA testing for differences in the body condition of adult *Rattus fuscipes* KTBA between burnt control sites and unburnt sites during each trapping session. No data are available for August 1996. Note that the Degrees of Freedom differ between time periods because not all sites recorded captures during each trapping session.

<table>
<thead>
<tr>
<th>Trapping session</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>February 1995</td>
<td>1.4</td>
<td>0.453</td>
<td>0.538</td>
</tr>
<tr>
<td>May 1995</td>
<td>1.4</td>
<td>4.740</td>
<td>0.095</td>
</tr>
<tr>
<td>August 1995</td>
<td>1.5</td>
<td>0.397</td>
<td>0.556</td>
</tr>
<tr>
<td>November 1995</td>
<td>1.2</td>
<td>1.208</td>
<td>0.386</td>
</tr>
<tr>
<td>February 1996</td>
<td>1.5</td>
<td>0.001</td>
<td>0.978</td>
</tr>
<tr>
<td>May 1996</td>
<td>1.3</td>
<td>2.032</td>
<td>0.249</td>
</tr>
<tr>
<td>November 1996</td>
<td>1.4</td>
<td>0.014</td>
<td>0.911</td>
</tr>
<tr>
<td>February 1997</td>
<td>1.5</td>
<td>0.006</td>
<td>0.940</td>
</tr>
</tbody>
</table>

Population structure is defined here in terms of population stability, sex ratio and individual longevity. Population stability was measured in the unburnt and the burnt control sites by the proportional representation of transient (captured once only) animals in the population over the period of the study. There was a significantly higher percentage of transient *R. fuscipes* in burnt control sites than in unburnt sites ($F = 15.050$, df $1,5$, $p = 0.012$; Figure 6.5). There was also a trend towards more residents (greater than one capture, in one or more trapping sessions) in unburnt sites, although this difference was not significant ($F = 2.461$, df $1,5$, $p = 0.176$).

![Figure 6.5: Percentage of the *Rattus fuscipes* population that was transient (captured once), resident (greater than 1 capture, in one or more trapping sessions), and permanent resident (captured in greater than 1 trapping session) in burnt control (c) and unburnt (ub) treatments. Note that: (transients) + (individuals > 1 capture) = 100% of the population within each site, and that permanent residents are a subset of the residents. Means are shown + standard error.](image)
The proportion of female to male _R. fuscipes_ did not differ between burnt control and unburnt sites over the period of the study (\( F = 0.013, \text{df} = 1,3, p = 0.913; \) Figure 6.6). Similarly, the average longevity in the trap record of female and male permanent residents between burnt control and unburnt sites was not statistically different (\( \text{df} = 1,5, \) female \( F = 2.915, p = 0.092; \) male \( F = 0.614, p = 0.439; \) Figure 6.7).

![Figure 6.6: The mean number of female and male _Rattus fuscipes_ KTBA in burnt control (c) and unburnt sites (ub). Means are shown ± standard error.](image)

![Figure 6.7: Average longevity of permanent resident female and male _Rattus fuscipes_ in burnt control (c) and unburnt sites (ub). Means are shown ± standard error.](image)

### 6.3.2 Population Dynamics in Burnt Sites

#### 6.3.2.1 Abundance

The average number of _R. fuscipes_ per hectare ranged from 2.5 to 8.3 in individual control treatment sites, 4.7 to 14.1 in nest treatment sites, 4.1 to 15.6 in food treatment sites, and 3.1 to 15.6 in food and nest treatment sites, demonstrating an overall increase in _R. fuscipes_ density in supplementation sites relative to the controls.

Figure 6.8 indicates the number of _R. fuscipes_ KTBA in the different treatment sites for the duration of the study. Over the four months immediately following the beginning of
food supplementation in January 1995, the abundance of *R. fuscipes* increased at all supplementation sites relative to control sites, which demonstrated a slight decrease in abundance over the same period. However, the rate of increase at the treatment sites was similar to that in the unburnt sites (Figure 6.2a) indicating that populations were responding, additionally, to other unmeasured environmental cues. Considering that the control populations did not increase during this initial period, it seems likely that supplementation mimicked naturally occurring changes in the unburnt environment.

![Figure 6.8: *Rattus fuscipes* KTBA in food and nest (a), nest (b), food (c), and control (d) treatment sites. Arrow indicates beginning of food and nest supplementation. Means are shown ± standard error. Dotted lines indicate assumed trajectory as no data are available for August 1996. Trapping period is indicated on the x axis: a94 = August 1994, f95 = February 1995, etc.](image)

Following initial increases there was an unexpected drop in *R. fuscipes* numbers in the six sites with food supplementation until the February 1996 trapping period. As the added food was the same as that used to bait the traps, animals may have become satiated by the added food and not attracted to traps. Other possibilities were that food was being monopolised by a few individuals, or that food was detrimental to the health and/or survival of individuals. The first of these ideas was tested by comparing the recapture rate of individuals between food supplemented and non-food supplemented sites. I hypothesised that there would be a lower recapture rate in food supplementation sites if animals there
were not attracted to the traps. However, there was no significant difference between the proportion of animals recaptured on more than one night (df $1,10$, $F = 0.430$, $p = 0.527$), or those captured during more than one trapping session (df $1,10$, $F = 0.028$, $p = 0.870$) between sites receiving and not receiving additional food. The latter of these results also indicates that the survival of animals did not differ between food and no-food treatments; a finding further supported by the survival and population growth of other species at the sites during the same period. The monopolisation of a food resource would presumably lead to fewer, larger animals being present at the site. An investigation of the body condition of *R. fuscipes* across all treatments in February 1996 found no significant effect of food supplementation (df $1,7$, $F = 0.245$, $p = 0.636$). These data are presented further in Section 6.3.2.2. As this decline in *R. fuscipes* abundance could not be adequately explained, and as food cartons were usually empty at the time of replenishment, the amount of food supplied to each site was doubled from mid February 1996 until the end of the experiment to ensure that supplements did effectively increase food availability to the animals.

Using the mean number of individuals KTBA in each site during the experimental period, two-way ANOVA indicated that neither supplementation treatment had a significant effect on *R. fuscipes* abundance (Table 6.3a). However, an interesting trend was apparent in the data (Figure 6.8) as the abundance of *R. fuscipes* increased in food only and nest only sites during the months following the start of the supplementation program, but remained relatively stable in sites where both resources were supplemented. During the second year of supplementation this effect changed, with populations increasing in food only and food and nest treatment sites, but falling in nest only sites. This interaction was not statistically significant. Two-way ANOVAs within consecutive trapping sessions were conducted to clarify some of the seasonal trends evident in Figure 6.8. There was a significant food and nest treatment interaction during May 1995, when *R. fuscipes* abundance did not increase as much in sites with food and nests provided, as in those sites with either food or nest supplementation ($F = 8.842$, df $1,8$, $p = 0.018$). Interestingly, in February 1996 there were significantly less individuals in food supplementation sites than in control or nest supplementation sites ($F = 16.333$, df $1,8$, $p = 0.004$), whereas by November 1996 this trend had reversed and there were significantly more *R. fuscipes* in food supplementation sites than control or nest supplementation sites ($F = 9.333$, df $1,8$, $p = 0.016$). Figure 6.8
demonstrates that the decline in *R. fuscipes* abundance between May and November 1996 was much greater in nest supplementation and control sites than in food supplementation sites. This resulted in more individuals present in food supplementation sites during the third summer after the fire, continuing until the final population survey in February 1997 (F = 6.250, df = 1,8, p = 0.037).

However, as the above session by session comparisons do not take into account the non-independence of data from one trapping period to another, a two-way repeated measures model was employed to further analyse temporal variation. Table 6.3b shows that there were no significant effects of resource manipulation on the abundance of *R. fuscipes* over the study period. Although the addition of food appeared to increase the magnitude of population fluctuation over time, this effect was not quite significant. The power (probability of Type II error) of this analysis (time*food) was \( \beta = 0.623 \) at \( \alpha = 0.05 \), lower than the desirable \( \beta = 0.8 \) at \( \alpha = 0.05 \). However, even a small increase in sample size, from 3 to 4 replicates per treatment, would have increased the power sufficiently to detect a significant difference. The power of other interactions (time*nest and time*food*nest) was much lower (\( \beta = 0.070 \) and 0.453 respectively) indicating that this experiment could not have detected any changes in abundance over the inherent temporal, site and seasonal variability without large increases in sample size.

Table 6.3: Two-way ANOVA (a) and two-way repeated measures ANOVA (b) of *Rattus fuscipes* abundance (KTBA) between treatments.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>a)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>food</td>
<td>1</td>
<td>2.623</td>
<td>0.144</td>
</tr>
<tr>
<td>nest</td>
<td>1</td>
<td>0.775</td>
<td>0.404</td>
</tr>
<tr>
<td>food*nest</td>
<td>1</td>
<td>0.168</td>
<td>0.693</td>
</tr>
<tr>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>time</td>
<td>7</td>
<td>1.594</td>
<td>0.356</td>
</tr>
<tr>
<td>time*food</td>
<td>7</td>
<td>3.364</td>
<td>0.066</td>
</tr>
<tr>
<td>time*nest</td>
<td>7</td>
<td>0.154</td>
<td>0.958</td>
</tr>
<tr>
<td>time<em>food</em>nest</td>
<td>7</td>
<td>1.143</td>
<td>0.348</td>
</tr>
<tr>
<td>error</td>
<td>64</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
6.3.2.2 **BODY CONDITION**

Overall, there was no significant effect of experimental treatment on the body condition of adult *R. fuscipes* (Table 6.4b). Breaking the data down into individual trapping sessions to investigate seasonal and annual differences, however, indicates that individuals in food-supplemented sites were in significantly better condition than those without extra food during May 1995 and August 1995, whereas those in nest supplementation sites tended to be in better condition in November 1996 (Figure 6.9; Table 6.4a).
Figure 6.9: Body condition index of adult *Rattus fuscipes* between treatment sites; males and females combined. Data are unavailable for August 1996. Means are shown ± standard error. fn = food and nest, f = food, n = nest, c = control sites.
Table 6.4: Two-way ANOVA of adult *Rattus fuscipes* body condition between food and nest treatments a) during each trapping session, and b) all trapping sessions combined. Degrees of Freedom differ between time periods because not all sites recorded captures during each trapping session.

<table>
<thead>
<tr>
<th>Trapping Session</th>
<th>Source of Variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1995</td>
<td>food</td>
<td>1</td>
<td>0.512</td>
<td>0.514</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.481</td>
<td>0.526</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.030</td>
<td>0.871</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 1995</td>
<td>food</td>
<td>1</td>
<td>19.219</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>1.921</td>
<td>0.208</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.213</td>
<td>0.658</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August 1995</td>
<td>food</td>
<td>1</td>
<td>13.769</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>1.441</td>
<td>0.284</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>7.192</td>
<td>0.040</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>November 1995</td>
<td>food</td>
<td>1</td>
<td>1.106</td>
<td>0.328</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>3.753</td>
<td>0.094</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.071</td>
<td>0.798</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1996</td>
<td>food</td>
<td>1</td>
<td>0.245</td>
<td>0.636</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.003</td>
<td>0.956</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.224</td>
<td>0.651</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 1996</td>
<td>food</td>
<td>1</td>
<td>0.227</td>
<td>0.647</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>3.520</td>
<td>0.098</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>1.949</td>
<td>0.358</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>November 1996</td>
<td>food</td>
<td>1</td>
<td>0.137</td>
<td>0.722</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>4.024</td>
<td>0.085</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>2.229</td>
<td>0.179</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1997</td>
<td>food</td>
<td>1</td>
<td>0.010</td>
<td>0.923</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>1.129</td>
<td>0.319</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.171</td>
<td>0.690</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whole model</td>
<td>food</td>
<td>1</td>
<td>3.130</td>
<td>0.115</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>3.536</td>
<td>0.097</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.108</td>
<td>0.751</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Adult male *R. fuscipes* were in significantly better condition than females (df = 1,22, F = 25.555, p < 0.001; Figure 6.10) across all treatments. There were no clear treatment effects on either sex, although there was a significant interaction effect for males (Table 6.5), with food and nest availability separately leading to better body condition in single treatment sites than in combined treatment or control sites.

![Graph showing body condition index of adult male and female Rattus fuscipes between treatments. Means are shown ± standard error. fn = food and nest, f = food, n = nest, c = control sites.](image)

**Figure 6.10:** Body condition index of adult male and female *Rattus fuscipes* between treatments. Means are shown ± standard error. fn = food and nest, f = food, n = nest, c = control sites.

**Table 6.5:** Two-way ANOVA on the body condition of adult male and female *Rattus fuscipes* between treatments.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>food</td>
<td>1</td>
<td>3.672</td>
<td>0.092</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>1.915</td>
<td>0.204</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>13.336</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>food</td>
<td>1</td>
<td>2.815</td>
<td>0.132</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>2.049</td>
<td>0.190</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>1.171</td>
<td>0.311</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**6.3.2.3 Population structure**

Throughout the experimental period, the ratio of female to male *R. fuscipes* significantly differed between the experimental and the control sites (Figure 6.11). Food only and nest only treatment sites had proportionally more females than males although the combined treatment sites had an approximately even sex ratio. Nevertheless, two-way ANOVA indicated that although neither food or nest supplementation alone had a significant treatment effect on the ratio of females to males (df = 1,8; food F = 2.342, p = 0.165; nest F = 2.884, p = 0.128), there was a significant interaction effect of food and nest
supplementation (df $1,8$, food*nest $F = 15.291, p = 0.005$). Figure 6.11 indicates that the number of females increased in all treatment sites when compared to the control sites. However, whereas food only and nest only supplementation sites led to higher numbers of females than males, the combined effect of these treatments led to fewer females than males in the population. Conversely, males did not increase in response to food or nest supplementation unless both resources were provided together.

![Image]

**Figure 6.11:** Mean number of female and male *Rattus fuscipes* across treatments. Means are shown + standard error. fn = food and nest, f = food, n = nest, c = control sites.

Population stability was measured as the representation of transient versus resident individuals in a population, and was compared between treatments. There was a significant interaction between the two treatments, with less transients in single factor experimental sites than control sites, but relatively more transients in the combined food and nest treatment sites than in single treatment sites (Figure 6.12; Table 6.6). Additionally, there were more permanent residents in experimental treatment sites than in controls, although there were no independent effects of either treatment alone (Table 6.6).
Figure 6.12: Percentage of individuals in Rattus fuscipes populations transient (captured once only), resident (greater than 1 capture, in one or more trapping sessions), and permanently resident (captured in more than 1 trapping session) in treatment sites. Note that: (transients) + (individuals > 1 capture) = 100% of the population within each site, and that permanent residents are a subset of the residents. Means across sites within treatments are shown + standard error. fn = food and nest, f = food, n = nest, c = control sites.

Table 6.6: Two-way ANOVA comparing the percentage of Rattus fuscipes transients, resident and permanent residents across treatments.

<table>
<thead>
<tr>
<th>Recapture rate</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transient (≥ 1 capture)</td>
<td>food</td>
<td>1</td>
<td>0.035</td>
<td>0.856</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>1.464</td>
<td>0.261</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>7.529</td>
<td>0.025</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resident (&gt; 1 capture)</td>
<td>food</td>
<td>1</td>
<td>1.603</td>
<td>0.241</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.907</td>
<td>0.369</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>28.34</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Permanent resident (&gt; 1 trapping session)</td>
<td>food</td>
<td>1</td>
<td>0.078</td>
<td>0.788</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.994</td>
<td>0.348</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>18.39</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Of 108 R. fuscipes permanent residents caught across all burnt sites after resource supplementation began, 71 were female and 37 were male. Table 5.7 and Figure 6.13 show that average longevity of male and female permanent residents did not vary between treatments. A significant interaction effect for the population as a whole was evident as, although average longevity was higher in food only and nest only treatment sites compared to control sites, animals in sites with the two treatments combined displayed no higher longevity than those in control sites.
Table 6.7: Two-way ANOVA on trap-revealed longevity between experimental treatments for female and male *Rattus fuscipes*. Degrees of freedom vary as male permanent residents were not recorded in all sites.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Source of Variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>food</td>
<td>1</td>
<td>0.072</td>
<td>0.795</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.250</td>
<td>0.631</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>2.991</td>
<td>0.122</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td></td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>food</td>
<td>1</td>
<td>0.029</td>
<td>0.871</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.029</td>
<td>0.871</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>2.020</td>
<td>0.215</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td></td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Both</td>
<td>food</td>
<td>1</td>
<td>0.011</td>
<td>0.918</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.417</td>
<td>0.527</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>5.712</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td></td>
<td>17</td>
<td></td>
</tr>
</tbody>
</table>

Figure 6.13: Average trap-revealed longevity of permanent resident a) female and b) male *Rattus fuscipes* across different treatments. Means are shown + standard error. fn = food and nest, f = food, n = nest, c = control sites.

6.3.2.4 REPRODUCTIVE RESPONSES

*Rattus fuscipes* showed no clear seasonality of breeding during this study. Juveniles were caught in every trapping session. There was no significant difference between
trapping sessions (square transform, df \(7.88\), \(F = 2.06, p = 0.057\); Figure 6.14) although more juveniles were recorded in May 1995 and February 1996 than during other periods. There was no significant difference in breeding patterns between the treatment sites over the whole study (Figure 6.15; Table 6.8b), or within individual trapping sessions, except during February 1996 when a significant treatment interaction indicated more juveniles being recruited into single-factor experimental sites than into the combined food and nest sites or controls (Table 6.8a).

![Figure 6.14: a) average number of juvenile Rattus fuscipes KTBA per trapping session (represented as columns), within each treatment, and b) average number of juvenile Rattus fuscipes within treatments during each trapping session. August 1996 data are not available. Means are shown + standard error. fn = food and nest, f = food, n = nest, c = control sites.](image)

![Figure 6.15: Number of juvenile Rattus fuscipes KTBA in treatment and control sites throughout study. Means are shown + standard error. fn = food and nest, f = food, n = nest, c = control sites.](image)
Table 6.8: Two-way ANOVA of juvenile *Rattus fuscipes* KTBA between treatments, during each trapping session.

<table>
<thead>
<tr>
<th>Trapping Session</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1995</td>
<td>food</td>
<td>1</td>
<td>0.200</td>
<td>0.666</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.200</td>
<td>0.666</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>1.800</td>
<td>0.217</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 1995</td>
<td>food</td>
<td>1</td>
<td>1.333</td>
<td>0.282</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>2.370</td>
<td>0.162</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>3.704</td>
<td>0.091</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August 1995</td>
<td>food</td>
<td>1</td>
<td>1.500</td>
<td>0.256</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.167</td>
<td>0.694</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.167</td>
<td>0.694</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>November 1995</td>
<td>food</td>
<td>1</td>
<td>0</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>2.000</td>
<td>0.195</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1996</td>
<td>food</td>
<td>1</td>
<td>2.579</td>
<td>0.147</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>2.579</td>
<td>0.147</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>8.895</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 1996</td>
<td>food</td>
<td>1</td>
<td>0.100</td>
<td>0.760</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.100</td>
<td>0.760</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>2.500</td>
<td>0.153</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>November 1996</td>
<td>food</td>
<td>1</td>
<td>1.000</td>
<td>0.347</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.250</td>
<td>0.631</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>1.000</td>
<td>0.347</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1997</td>
<td>food</td>
<td>1</td>
<td>1.800</td>
<td>0.217</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.200</td>
<td>0.667</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>1.800</td>
<td>0.217</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>b)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whole model</td>
<td>food</td>
<td>1</td>
<td>0.984</td>
<td>0.350</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.073</td>
<td>0.794</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>4.301</td>
<td>0.072</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
6.3.3 Population response to natural resource availability

6.3.3.1 Ground cover

Total scores for the ground cover categories; leaf litter, bare ground, live-wood, dead-wood, rock and grass/shoots (refer to Section 5.2.3.2), were averaged across burnt and unburnt sites to produce Figure 6.16. Significantly more leaf litter was recorded in unburnt sites than in burnt sites throughout the study (Figure 6.16a; Table 6.9). Although there was an increase in litter cover in burnt sites during the third year after the fire, to bring levels close to those at unburnt sites, this differential change over time was not significant (Table 6.9). Given this trend, there was predictably more bare ground in burnt areas than unburnt areas, although this declined throughout the study (Figure 6.16b; Table 6.9).

![Graphs showing ground cover frequency](image)

Figure 6.16: Ground cover frequency for a) leaf litter, b) bare ground, c) rock, d) grass/shoots, e) live wood, f) dead wood. ◆ burnt sites, ▲ unburnt sites. Means are shown ± standard error.
Table 6.9: Two-way ANOVA of ground cover between burnt and unburnt sites, and years (time).

<table>
<thead>
<tr>
<th>Ground cover category</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>leaf litter</td>
<td>burnt</td>
<td>1</td>
<td>15.301</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>2.772</td>
<td>0.076</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>1.237</td>
<td>0.302</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>live-wood</td>
<td>burnt</td>
<td>1</td>
<td>6.289</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>0.070</td>
<td>0.974</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>0.388</td>
<td>0.681</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dead-wood</td>
<td>burnt</td>
<td>1</td>
<td>7.279</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>0.070</td>
<td>0.933</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>1.874</td>
<td>0.168</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>bare ground</td>
<td>burnt</td>
<td>1</td>
<td>24.746</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>2.580</td>
<td>0.090</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>1.384</td>
<td>0.264</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>rock</td>
<td>burnt</td>
<td>1</td>
<td>0.367</td>
<td>0.548</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>1.927</td>
<td>0.160</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>0.061</td>
<td>0.941</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>grass/shoots</td>
<td>burnt</td>
<td>1</td>
<td>27.265</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>5.639</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>0.110</td>
<td>0.896</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

There was no significant difference in the amount of rock substrate between burnt and unburnt areas, although there was considerable variability between sites as demonstrated by the relatively large standard errors (Figure 6.16c; Table 6.9). The peak in the amount of rock recorded, and the large associated variance between sites during 1996, is likely to be an artefact of the reduced number of quadrats and less burnt sites recorded in this year in comparison to 1995. In light of this, all sites were sampled in 1997, and sample size within sites was increased (refer to section 5.2.3.2); results for 1995 and 1997 were then extremely similar (Figure 6.16c).

Although the amount of ground covered by grass and shoots was consistently lower in burnt than in unburnt areas (Figure 6.16d; Table 6.9), there was a parallel increase in this cover type throughout the study period, regardless of whether sites were burnt or unburnt.
This indicates that there had been changes in environmental conditions favourable to new growth, unrelated to the influence of fire.

Measures of live wood and dead wood were considerably smaller than other cover types as they occurred in generally large-sized but widely spaced units. Live wood included trees and roots, but was recorded as a ground cover category only if the sampling pin position happened to fall down the centre, or on the buttress, of a tree trunk or on a (rare) surface root. Dead wood included logs, tree stumps and the associated charcoal present if these features had been in the same position during the fire. By 1995, a year after the fire, fine-grained charcoal had been largely washed away or leached down through the sandy soil, leaving only some large pieces on the surface (pers. obs.). There was significantly more live wood recorded in burnt sites (Figure 6.16e; Table 6.9), attributable mainly to more surface roots being exposed in the bare, and sometimes eroding sand. In addition, although the amount of dead wood was similar in burnt and unburnt sites at the beginning of the study, there was an increase in the number of logs and stumps in burnt sites during 1995 when storms and strong winds caused many standing trees previously killed by the fire to fall (pers. obs.). The reduction of dead wood in unburnt sites during the same period is harder to explain, but may be due to small sample size.

A significant positive correlation was identified between *R. fuscipes* abundance and ground cover rock in May 1995 and February 1997 (1995 $r = 0.645$, $p = 0.023$; 1997 $r = 0.641$, $p = 0.024$); however, no other correlations with ground cover variables were found. Principal components analysis was used to condense the ground cover variables into three components explaining most of the variability for each year (Table 6.10). *R. fuscipes* abundance was not significantly related to any ground cover principal component in any year.

### 6.3.3.2 VEGETATIVE COVER

Throughout the study, in all height categories above 20 cm, unburnt sites had significantly more vegetative cover than burnt sites. The trend was also apparent below 20 cm although it was not statistically significant (Figure 6.17, Table 6.11). There were, however, no significant effects of time, with no significant increases or decreases in cover
availability over the years. Although Figures 6.17b and 6.17c indicate a steady increase in cover between 20 and 100 cm throughout the study period, the parallel increase in both burnt and unburnt sites indicates growth unrelated to recent fire effects.

Table 6.10: Principal Components Analysis (PCA) of ground cover data. The two dominant ground cover contributors (factor loadings) for each principal component are highlighted.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1995</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>eigenvalue</td>
<td>2.684</td>
<td>1.210</td>
<td>0.933</td>
</tr>
<tr>
<td>percent variation explained</td>
<td>44.731</td>
<td>20.165</td>
<td>15.545</td>
</tr>
<tr>
<td>cumulative percent</td>
<td>44.731</td>
<td>64.896</td>
<td>80.441</td>
</tr>
<tr>
<td>factor loadings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>litter</td>
<td>0.578</td>
<td>0.066</td>
<td>0.192</td>
</tr>
<tr>
<td>live wood</td>
<td>-0.119</td>
<td>0.546</td>
<td>0.720</td>
</tr>
<tr>
<td>dead wood</td>
<td>0.409</td>
<td>0.338</td>
<td>-0.107</td>
</tr>
<tr>
<td>bare ground</td>
<td>-0.573</td>
<td>-0.211</td>
<td>0.054</td>
</tr>
<tr>
<td>rock</td>
<td>-0.130</td>
<td>0.610</td>
<td>-0.649</td>
</tr>
<tr>
<td>shoots</td>
<td>0.373</td>
<td>-0.409</td>
<td>-0.093</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1996</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>eigenvalue</td>
<td>3.057</td>
<td>1.589</td>
<td>0.872</td>
</tr>
<tr>
<td>percent variation explained</td>
<td>50.955</td>
<td>26.489</td>
<td>14.525</td>
</tr>
<tr>
<td>cumulative percent</td>
<td>50.955</td>
<td>77.444</td>
<td>91.971</td>
</tr>
<tr>
<td>factor loadings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>litter</td>
<td>-0.438</td>
<td>0.360</td>
<td>-0.433</td>
</tr>
<tr>
<td>live wood</td>
<td>0.478</td>
<td>0.190</td>
<td>-0.473</td>
</tr>
<tr>
<td>dead wood</td>
<td>0.441</td>
<td>0.149</td>
<td>0.348</td>
</tr>
<tr>
<td>bare ground</td>
<td>0.544</td>
<td>-0.175</td>
<td>0.067</td>
</tr>
<tr>
<td>rock</td>
<td>-0.265</td>
<td>-0.668</td>
<td>0.244</td>
</tr>
<tr>
<td>shoots</td>
<td>-0.139</td>
<td>0.579</td>
<td>0.636</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1997</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>eigenvalue</td>
<td>2.153</td>
<td>1.605</td>
<td>1.194</td>
</tr>
<tr>
<td>percent variation explained</td>
<td>35.875</td>
<td>26.751</td>
<td>19.895</td>
</tr>
<tr>
<td>cumulative percent</td>
<td>35.875</td>
<td>62.626</td>
<td>82.521</td>
</tr>
<tr>
<td>factor loadings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>litter</td>
<td>-0.543</td>
<td>0.468</td>
<td>0.002</td>
</tr>
<tr>
<td>live wood</td>
<td>0.345</td>
<td>0.456</td>
<td>-0.023</td>
</tr>
<tr>
<td>dead wood</td>
<td>0.145</td>
<td>0.276</td>
<td>0.733</td>
</tr>
<tr>
<td>bare ground</td>
<td>0.545</td>
<td>-0.378</td>
<td>0.254</td>
</tr>
<tr>
<td>rock</td>
<td>0.370</td>
<td>0.149</td>
<td>-0.631</td>
</tr>
<tr>
<td>shoots</td>
<td>-0.361</td>
<td>-0.576</td>
<td>0.006</td>
</tr>
</tbody>
</table>
Figure 6.17: Vegetation cover frequency for a) 0 - 20 cm, b) 21 - 50 cm, c) 51 - 100 cm, d) 101 - 200 cm, e) > 200 cm cover strata. ♦ burnt sites, ▲ unburnt sites. Means are shown ± standard error.
Table 6.11: Two-way ANOVA of vegetation height categories between burnt and unburnt sites, and years (time).

<table>
<thead>
<tr>
<th>Vegetation height category</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 20 cm</td>
<td>burnt</td>
<td>1</td>
<td>3.523</td>
<td>0.069</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>0.283</td>
<td>0.756</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>0.182</td>
<td>0.835</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21 - 50 cm</td>
<td>burnt</td>
<td>1</td>
<td>6.239</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>1.966</td>
<td>0.155</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>0.353</td>
<td>0.705</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>51 - 100 cm</td>
<td>burnt</td>
<td>1</td>
<td>12.773</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>1.854</td>
<td>0.171</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>0.031</td>
<td>0.969</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>101 - 200 cm</td>
<td>burnt</td>
<td>1</td>
<td>8.515</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>0.733</td>
<td>0.488</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>0.087</td>
<td>0.917</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt; 200 cm</td>
<td>burnt</td>
<td>1</td>
<td>4.927</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td>time</td>
<td>2</td>
<td>0.021</td>
<td>0.819</td>
</tr>
<tr>
<td></td>
<td>burnt*time</td>
<td>2</td>
<td>0.314</td>
<td>0.732</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>36</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Personal observations indicated that there was a difference in the forest structures of burnt and unburnt sites. Although the presence/absence data indicated some overall differences, they did not account adequately for observed differences of density and distribution of cover in the environment. In unburnt areas there was stratification of a grassy and herbaceous ground cover, with a shrub understorey of Banksia, Hakea and Acacia spp. and a canopy of Eucalyptus and Angophora dominated. In burnt areas, grasses and herbs were in low density and much of the lower cover was provided by seedlings of shrub and canopy species. In contrast to the unburnt sites, Eucalyptus and Angophora in the burnt sites had dramatically reduced canopy cover, but fire-induced basal and epicormic shoots provided dense cover from ground level up the height of the tree trunk, in a relatively narrow radius around the tree. As the canopy re-established some of the basal and epicormic shoots died or broke off the trees, although many were still present at the end of the study.
In February and May 1995 the abundance of *R. fuscipes* was related significantly to PC2, a component defined primarily by presence of vegetation above 100 cm and the absence of cover beneath this (February $y = 3.75 (\pm 0.497 \text{ SE}) + 1.211\text{PC2 (}\pm 0.442 \text{ SE})x$, $R^2 = 0.349$, df$_{1,14}$, $F = 7.492$, $p = 0.016$; May $y = 5.938 (\pm 0.837 \text{ SE}) + 1.781\text{PC2 (}\pm 0.745 \text{ SE})x$, $R^2 = 0.290$, df$_{1,14}$, $F = 5.718$, $p = 0.031$; Table 6.12). In May 1996, by contrast, *R. fuscipes* abundance was related significantly to PC1, a factor dominated by the presence of vegetation from 21 - 100 cm but also with a considerable proportion of cover above 100 cm ($y = 7.00 (\pm 1.150 \text{ SE}) + 1.872\text{PC1 (}\pm 0.649 \text{ SE})x$, $R^2 = 0.510$, df$_{1,8}$, $F = 8.320$, $p = 0.020$). *R. fuscipes* was not significantly related to any of the 1997 vegetation principal components.

### Table 6.12: Principal Components Analysis of vegetation cover data. The two dominant vegetation height class contributors (factor loadings) for each principal component are highlighted.

<table>
<thead>
<tr>
<th></th>
<th>Principal Components</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
</tr>
<tr>
<td>1995</td>
<td></td>
</tr>
<tr>
<td>eigenvalue</td>
<td>3.017</td>
</tr>
<tr>
<td>percent variation explained</td>
<td>60.346</td>
</tr>
<tr>
<td>cumulative percent</td>
<td>60.346</td>
</tr>
<tr>
<td>factor loadings</td>
<td></td>
</tr>
<tr>
<td>0 - 20 cm</td>
<td>0.454</td>
</tr>
<tr>
<td>21 - 50 cm</td>
<td>0.521</td>
</tr>
<tr>
<td>51 - 100 cm</td>
<td>0.551</td>
</tr>
<tr>
<td>101 - 200 cm</td>
<td>0.425</td>
</tr>
<tr>
<td>&gt; 200 cm</td>
<td>0.196</td>
</tr>
<tr>
<td>1996</td>
<td></td>
</tr>
<tr>
<td>eigenvalue</td>
<td>3.492</td>
</tr>
<tr>
<td>percent variation explained</td>
<td>69.841</td>
</tr>
<tr>
<td>cumulative percent</td>
<td>69.841</td>
</tr>
<tr>
<td>factor loadings</td>
<td></td>
</tr>
<tr>
<td>0 - 20 cm</td>
<td>0.340</td>
</tr>
<tr>
<td>21 - 50 cm</td>
<td>0.476</td>
</tr>
<tr>
<td>51 - 100 cm</td>
<td>0.528</td>
</tr>
<tr>
<td>101 - 200 cm</td>
<td>0.443</td>
</tr>
<tr>
<td>&gt; 200 cm</td>
<td>0.428</td>
</tr>
<tr>
<td>1997</td>
<td></td>
</tr>
<tr>
<td>eigenvalue</td>
<td>2.737</td>
</tr>
<tr>
<td>percent variation explained</td>
<td>54.738</td>
</tr>
<tr>
<td>cumulative percent</td>
<td>54.738</td>
</tr>
<tr>
<td>factor loadings</td>
<td></td>
</tr>
<tr>
<td>0 - 20 cm</td>
<td>0.502</td>
</tr>
<tr>
<td>21 - 50 cm</td>
<td>0.523</td>
</tr>
<tr>
<td>51 - 100 cm</td>
<td>0.553</td>
</tr>
<tr>
<td>101 - 200 cm</td>
<td>0.394</td>
</tr>
<tr>
<td>&gt; 200 cm</td>
<td>0.119</td>
</tr>
</tbody>
</table>
6.3.3 Microhabitat Components

The habitat components rock, trees, tree hollows and logs were measured at the end of the study around trap stations and assumed not to have changed throughout the study period. Although some trees invariably would have become logs during the period, principal components analysis grouped these two factors together under PC1 and as such the two components were considered together when comparing habitat features to mammal abundance (Table 6.13). *R. fuscipes* was associated negatively with PC1 \( (y = 5.284 \pm 0.295 \text{ SE}) - 0.786 \text{PC}1 (\pm 0.276 \text{ SE})x, R^2 = 0.079, \text{df} _{1,94}, F = 8.091, p = 0.006 \) and positively with PC2 \( (y = 4.759 (\pm 0.323 \text{ SE}) + 1.210 \text{PC}2 (\pm 0.378 \text{ SE})x, R^2 = 0.098, \text{df} _{1,94}, F = 10.241, p = 0.002 \), indicating smaller population numbers in areas with many trees and logs but greater abundance with increased availability of tree-hollows. However, there were no differences between the availability of these habitat features between sites, treatments or burnt and unburnt areas. Given the variability in abundance of *R. fuscipes* across sites and treatments (Sections 6.3.1 and 6.3.2.1), and the low \( R^2 \) values associated with the above equations, it is therefore unlikely that these habitat features alone significantly influenced the demography of *R. fuscipes*.

Table 6.13: Principal Components Analysis of microhabitat data. The dominant habitat contributors (factor loadings) for each principal component are highlighted

<table>
<thead>
<tr>
<th></th>
<th>Principal Components</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2</td>
<td>PC3</td>
</tr>
<tr>
<td>eigenvalue</td>
<td>1.340</td>
<td>1.224</td>
<td>0.993</td>
</tr>
<tr>
<td>percent variation explained</td>
<td>33.499</td>
<td>30.606</td>
<td>24.819</td>
</tr>
<tr>
<td>cumulative percent</td>
<td>33.499</td>
<td>64.104</td>
<td>88.923</td>
</tr>
<tr>
<td>factor loadings</td>
<td>rock</td>
<td>tree</td>
<td>tree-hollow</td>
</tr>
<tr>
<td></td>
<td>-0.024</td>
<td>0.693</td>
<td>-0.037</td>
</tr>
<tr>
<td></td>
<td>0.197</td>
<td>0.393</td>
<td>0.836</td>
</tr>
<tr>
<td></td>
<td>0.978</td>
<td>-0.999</td>
<td>-0.137</td>
</tr>
<tr>
<td></td>
<td>log</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.719</td>
<td>-0.329</td>
<td>0.121</td>
</tr>
</tbody>
</table>

6.3.4 Summary of Results

Although overall abundance of *R. fuscipes* was lower in burnt control sites than in unburnt sites, the mechanisms producing this difference remain unclear. The body condition, reproductive activity, proportion of males to females and the trap-revealed longevity of permanent residents did not differ significantly between burnt control and
unburnt sites. There were, however, more transients in burnt areas, and a tendency towards more residents in unburnt areas, although the latter relationship was not significant.

Within the burnt treatment sites, there was an initial increase in *R. fuscipes* abundance in response to food supplementation, supported by improved body condition during May and August 1995 in food supplementation sites. The response was not sustained, however, and neither food nor nest addition had a significant effect on the abundance of *R. fuscipes* populations for the duration of the study.

Male *R. fuscipes* were in better condition than females in all burnt treatment sites, and had a significantly higher body condition index in the food only and nest only treatment sites than in the control sites, although this was less evident in the combined treatment sites. As mentioned above, body condition was highest in food supplementation sites during the first winter (1995), and in nest supplementation sites the following August (1996). Although males were in generally better condition than females, a higher proportion of the population was female in sites where food and nest boxes were supplied. Resource supplementation led to increased population stability with more permanent residents and less transients in experimental than in control sites. In addition, although there were almost twice as many female than male permanent residents, trap-revealed longevity did not vary between sexes or between different treatment sites.

Reproductive activity did not vary in response to experimental treatment. There were no consistent differences in the number of juveniles recruited into the population in response to either treatment or season. There were, however, more juveniles recruited into experimental than control sites during February 1996, which could reflect increased breeding activity in the first year of resource supplementation.

No naturally occurring habitat or vegetation features were associated consistently with *R. fuscipes* abundance. During 1995 *R. fuscipes* abundance was related positively to an absence of ground vegetation and to the presence of cover above 100 cm. This pattern was reversed the following year with a significant positive association with vegetative cover between 21 and 100 cm in height. *R. fuscipes* abundance was also related negatively to the
number of trees or logs at trap stations, but positively to the proportion of trees with hollows, although the variation in numbers accounted for by each microhabitat variable was less than 10%.

6.4 DISCUSSION

6.4.1 EFFECT OF FIRE ON RATTUS FUSCIPES POPULATIONS

Fire reduced the abundance of *R. fuscipes* living in open forest and woodland habitats of Ku-ring-gai Chase National Park. Numbers in burnt sites remained consistently lower than those in unburnt sites for three years after fire, although they did increase steadily over time after the fire. The mechanisms constraining the populations in burnt sites to lower abundances than in unburnt sites are not clear. The body condition, reproductive activity and longevity of permanent residents did not vary between burnt and unburnt sites, suggesting that the availability of resources is not limiting the health or survival of individuals in burnt sites. This is similar to the findings of Press (1982, 1986, 1987) who, in a comparison of *R. fuscipes* populations in unlogged cool temperate rainforest and logged and burnt dry sclerophyll forest, found that although rainforest supported denser populations, individual body condition, reproductive activity and demography did not vary between forest types.

Resource availability may still, however, have acted to reduce the number of animals supported by the burnt forest. If, for example, individuals require \( x \) amount of resource \( a \) to survive and reproduce, burnt sites with 6\( xa \) per hectare would be expected to support 6 individuals over that area, and unburnt sites with 10\( xa \) would support 10 individuals. All animals would be equally fit (assuming no density dependence), as apparently found in this study and those of Press (1982, 1986, 1987), as opposed to the scenario where both burnt and unburnt sites have 10 animals per hectare, but individuals in burnt sites receive only 60% of what they require. As such, the number of individuals in any site should be in direct ratio to the available resource base. Absolute resource abundance may have been different in burnt and unburnt sites as indicated by different *R. fuscipes* densities (Fretwell and Lucas 1969; Krebs 1985), although per-capita resource availability was presumably similar, as indicated by similarities in most measures of individual body condition and population dynamics.
The higher proportion of transient individuals in burnt than unburnt sites further supports this argument, and suggests that within a particular habitat, populations reach a saturation abundance dependent upon the resource availability. Rather than remain in a saturated area and experience reduced health and fitness due to more competition, animals may utilise inferior habitats or simply increase movements (Chapter 1). Resource availability is temporally and spatially variable, therefore increased movements could be attributable to animals responding to a perceived local saturation of conspecifics, and moving on in search of an under-utilised habitat. Conversely, animals may opportunistically track resource availability rather than maintain a foraging or home range. Wiens (1977) suggested that, in order to maintain their fitness, individuals may alter their territory or home range size in response to changes in the abundance and dispersion of resources. The increased transience measured during this experiment has previously been noted for *R. fuscipes* after fire and clearing (Leonard 1972; Friend 1979; Lunney et al. 1987; White 1992). Transiency could be an artefact of individuals moving over a wider area, thus becoming less trappable, although this seems unlikely as neither the numbers of residents and permanent residents, nor the trap-revealed longevity of permanent residents, differed between burnt and unburnt treatments in this study.

Juvenile *R. fuscipes* were caught during every trapping session, indicating not only that conditions were favourable to support the high energy requirements of reproduction, but also that reduced resource availability in burnt sites did not alter the usual reproductive patterns as exhibited by *R. fuscipes* in unburnt sites. Given the distance of burnt sites from the nearest unburnt vegetation, and therefore the improbability of immigration of animals into the experimental populations, juveniles captured in burnt sites in August 1994 indicate that successful winter breeding and recruitment occurred less than six months after the fire. This is in contrast to the findings of Fox (1982) who reported that *R. fuscipes* was unable to successfully reproduce until four years after fire in coastal heathland, and did not establish stable populations in open eucalypt forest for 3 to 5 years after fire (Fox and McKay 1981). Likewise, Thompson *et al.* (1989) found that *R. fuscipes* did not reproduce for two summers following a low intensity winter fuel reduction burn, and Leonard (1972) suggested that female *R. fuscipes* require a dense, continuous habitat in order to successfully wean their young.
During logging operations, clearing and burning of forest resulted in a dramatic reduction of *R. fuscipes* abundance (Friend 1979). None of the animals were caught subsequently on grids in adjacent uncleared forest, indicating high mortality. Interestingly, however, within 1 to 2 months of clearing, sub-adult *R. fuscipes* began recolonising the affected areas (Friend 1979). This emphasises the rapid colonising ability of *R. fuscipes* after disturbance. However, the effectiveness of colonisation is reliant upon successful reproduction. Catling (1986) demonstrated that *Rattus lutreolus* reproduced at lower body weights in marginal habitats than in preferred habitats after fire. This suggested that younger individuals were dispersing from the preferred habitat, where reproduction was suppressed by the presence of mature animals, to the nearby marginal habitat in order to utilise the available resources (Catling 1986).

The flexibility of breeding season for *R. fuscipes* in Ku-ring-gai would enhance the success of post-fire colonisation. In south-western Australia, where *R. fuscipes* has a seasonal breeding strategy leading to a summer recruitment of juveniles, a fire during January had little effect on adults but prevented successful juvenile recruitment into the population (Christensen and Kimber 1975). As *R. fuscipes* has a largely annual life-history, this triggered a precipitous drop in *R. fuscipes* abundance over the following two months, after which recolonisation of forest areas did not occur until almost two years after the fire (Christensen and Kimber 1975).

The success of *R. fuscipes* in Ku-ring gai may be attributed to several factors. Sub-adult *R. fuscipes* are good dispersers, and in favourable environments may reproduce at younger ages and in non-preferred habitats. In addition, *R. fuscipes* in some locations, such as Ku-ring-gai Chase, may further enhance their recolonising ability by breeding throughout the year. When Fox (1982) stated that *R. fuscipes* was limited in its post-fire recolonisation potential by its failure to reproduce until later seral stages, he related this failure to the lack of natural resources in the post-fire environment.

Catling *et al.* (1981) demonstrated a positive association between *R. fuscipes* abundance and leaf litter, logs and dense vegetation cover. These authors inferred from this that *R. fuscipes* would prefer mature stands of open forest with a well developed shrub
layer, and would therefore reach maximum densities in late successional stages. This inference is supported by several researchers (Fox and McKay 1981; Fox 1982, 1983, 1990; Newsome and Catling 1983; Lunney et al. 1987; Wilson et al. 1990), who have also found *R. fuscipes* to be a late successional species, preferring a well developed leaf litter layer and dense vegetative cover. However, a different response was found in the present study (see below). Further, Steeves (1990) trapped in sites representing a chronosequence of time since fire, also in Ku-ring-gai Chase National Park, and determined that *R. fuscipes* was present one year after fire, and increased steadily to reach maximum abundance 6 years after fire, after which abundance dropped.

Fox and McKay (1981) suggested that leaf litter provides an important source of the arthropods on which *R. fuscipes* feeds, although Dickman (1991) found that 25% of this species' nests were under leaf litter, and thus leaf litter could serve a dual purpose. Regardless of this, leaf litter in burnt sites throughout this study was sparse and shallow, suggesting that the presence of a well developed litter layer is not essential to the maintenance of *R. fuscipes* populations. This is supported by an absence of correlation or association of *R. fuscipes* abundance with litter components in either burnt or unburnt sites. Similarly, *R. fuscipes* populations increased in abundance in all burnt sites throughout the study regardless of the absence of dense cover. During 1995, one year after the fire, the abundance of *R. fuscipes* was associated positively with the presence of cover above 100 cm and an absence of ground cover. By contrast, the following year *R. fuscipes* were associated with vegetation cover mainly between 20 and 100 cm, with some cover above this. These vegetation characteristics reflect the changes in regrowth across the sites at these times, and I contend that the relationships between these cover variables and *R. fuscipes* abundance are not causal, but simply indicate that both the vegetation community and *R. fuscipes* population are changing independently, but in the same direction, with time since fire.

Newsome et al. (1975) recorded similar results to those in this study after fire in sclerophyll forest in southern New South Wales. They reported that fire had little or no effect on the abundance of *R. fuscipes* on their large trapping grids, and after a slow decline in abundance during the following year, numbers surged to higher than pre-fire population
levels. Interestingly, on smaller trapping grids, with a closer trap placement, *R. fuscipes* abundance was reduced dramatically after the fire. They attributed this decline to the variability of microhabitats covered by the larger grids. Large grids encompassed small water courses, swamps and changes in topography, suggesting habitat shifts and a patchy distribution of individuals as a result of the fire. Such changes in habitat use could not be determined by trapping on smaller, more uniform, grids (Newsome *et al.* 1975). Grid size in this study (0.64 ha) was between the large (2.88 ha) and small (0.09 ha) grid sizes used by Newsome *et al.* (1975) and can therefore be expected to provide some variation in microhabitat, but not to encompass larger landscape features.

Wilson *et al.* (1990) suggested that the remains of patchily distributed resources encouraged the recovery of small mammals after fire. In their study, small mammal abundances increased steadily on partially burnt sites after fire, but were slow to recover on completely burnt sites (Wilson *et al.* 1990). Catling (1986) found that *R. lutreolus* recognised poorer sections of their preferred habitat and accordingly used them less. Thus the differential use of habitat after fire may enable small mammals to increase their survival and hence the likelihood of population recovery.

6.4.2 EFFECT OF RESOURCE AVAILABILITY ON *RATTUS FUSCIPES* AFTER FIRE

6.4.2.1 FOOD

Supplementation of food began one year after the fire and resulted in both an increase in the abundance and improvement in body condition of individuals during the first winter. The effect was not sustained, however, and food supplementation had no significant effect on the abundance or demography of *R. fuscipes* for the remainder of the study. These findings indicate that the availability of food is most limiting soon after fire and that the effect diminishes swiftly with time. It follows that if food supplementation had occurred in the immediate post-fire environment a more dramatic response may have resulted. However, evidence of food limitation in rodent populations has been demonstrated in a range of undisturbed habitats (see Boutin 1990 for review; Predavec 1994), and supplementation of a fire-disturbed area, with a demonstrated reduction of resource availability, would have been expected to result in demographic responses for the duration of the study. Post-fire food shortage has previously been investigated for *R. fuscipes* by
monitoring changes in water flux and body fat after a prescribed fire (Catling et al. 1989). No population-level effect was found, although low intensity fire is usually distributed patchily, and food availability would not be expected to be as dramatically reduced as during a high intensity bushfire. Banks (1991) further investigated food limitation for this species in undisturbed sub-alpine habitat, and found a seasonal response with increases in abundance, body weight and reproductive activity in sites with food supplementation during winter. The response was not as pronounced during warmer months (Banks 1991).

Newsome et al. (1975) found that the winter body weights of female *R. fuscipes* declined after fire whereas those of males did not. As Friend (1979) reported that adult *R. fuscipes* were removed by clearing and replaced within a few months by colonising sub-adults, the pattern reported by Newsome et al. (1975) may be attributable to captures of sub-adult females in the winter after the fire. It is unclear, however, if sub-adults would colonise if adults from the population (i.e., the males in the Newsome et al. (1975) study) were still present. Similarly, age and sex biases in trappability may have distorted the Newsome et al. (1975) findings. Alternatively, after fire, males may be able to command a greater share of the available resources due to their larger size and the associated competitive advantage that size usually brings (Dickman 1991; Higgs and Fox 1993; Thompson and Fox 1993).

Boutin (1990), in a review of food supplementation studies, concluded that for a majority of rodent species studied, food supplementation leads to an increased proportion of the population breeding, from an earlier age, and in a season that begins earlier and extends longer than in control groups. Litter size is often greater, as is the body weight and growth rate of individuals. Moreover, in most studies, food supplementation has resulted in increased population density or rate of population growth. However, whereas food supplementation tends to increase the magnitude of seasonal or annual fluctuations as compared to those of control groups, it does not change the general pattern of population fluctuations. The timing and rate of population changes are usually similar between experimental and control treatments (Boutin 1990). Population declines in cyclic species such as snow-shoe hares, *Lepus americanus*, and voles, *Microtus* spp. are unable to be

There are also, however, studies where food supplementation has not resulted in increases in abundance or changes in reproductive or social behaviour. Ribble (1997) reported that *Peromyscus* spp. density did not differ between food supplementation and control sites, although female home range size and overlap appeared to increase. Further, Krebs and DeLong (1965) found that *Microtus californicus* populations declined during a year of food supplementation; this was suggested by Cole and Batzli (1978) to be due to the low nutritional quality of the supplementary food, and by Boutin (1990) to have resulted from the competitive effects of the *Mus musculus* population also present on the sites.

In the current study, recruitment of juvenile *R. fuscipes* was not affected by food supplementation, although determination of any further reproductive effects is hampered by the seemingly opportunistic breeding system. The lack of a definitive breeding season and the inability to associate juveniles with adults based on captures in the field prevents any further associations being drawn between food availability and reproductive activity or litter size. Similarly, it is difficult to demonstrate if additional food affected the proportion of the population breeding or the age distribution of reproductive individuals.

Banks (1991), however, in a supplementation experiment on *R. fuscipes* in a sub-alpine habitat, found that breeding activity increased in response to additional food. The differences between the Ku-ring-gai temperate populations and Banks’ (1991) sub-alpine populations could be attributed to differences in food availability between climatic regions, as suggested by Leung (1994). Leung (1994) found no population responses of *Rattus leucopus* to food addition in tropical rainforest, and considered this to be the result of the high productivity and lack of seasonal fluctuations characteristic of tropical systems. Interestingly, Press (1982) found that food supplementation had no effect on *R. fuscipes* populations in cool-temperate rainforest, but caused an immediate increase in abundance, and an early onset of breeding, of populations in adjacent sclerophyll forest. This would suggest that the seasonal stability of food resources does not influence population characteristics, as cool-temperate rainforest is at high altitude and presumably subject to
marked seasonal variation of conditions. Instead it seems likely that food does not become limiting in highly productive rainforest systems, whereas in sclerophyll forest food resources are not as abundant.

As with the present study, an immediate initial response to food supplementation was also recorded in *R. fuscipes* populations in open sclerophyll forest studied by Press (1982). However, the effect was not sustained, and interpretation of the results is hampered by only 10 months of food supplementation, and two post-supplementation trapping sessions. In addition, one of Press’s two control sites demonstrated a similar increase in *R. fuscipes* abundance over the same period. Nevertheless, Press (1982) concluded, tentatively, that populations of *R. fuscipes* in sclerophyll forest were limited by the availability of food.

6.4.2.2 NESTS

Nest addition alone had no effect on *R. fuscipes* abundance over the duration of the study, although during the summer of 1996, 20 months after supplementation began and 32 months after the fire, the body condition of animals tended to be highest in nest-addition sites. Nests were most probably used as temporary refuge as, although the presence of leaf litter inside the nest boxes indicated some use, no permanent nests were found. Increased body condition, without parallel increases in reproductive activity or changes in demography, could indicate that foraging activity increased in response to the regularly spaced and consistently available refuge provided from nest boxes. Alternatively, the artificial nest boxes may have been avoided during the early parts of the study when population abundance did not exceed the natural resource availability, but then became important as the population reached a critical level when the availability of such refuge became limiting. The “switch” to incorporate the artificial cover may have led to a boost in the average health of the population at that time. Increases in body weight have been observed in other species of small mammals where dense cover has reduced the risk of predation and made prolonged foraging possible (Hik 1995).

The use of nest boxes to determine if nest sites are limiting has been attempted rarely in Australia. Wardell-Johnson (1986) introduced nest boxes to areas of Western
Australian karri forest under different logging treatments and concluded that nest site availability was not limiting to small mammal populations in any treatment sites. Similarly, Leung (1994) determined that nest site availability was not limiting to small mammal populations in tropical rainforest.

The manipulation of nest availability has not been previously attempted in fire-disturbed habitats. Fire could act to create nest sites by encouraging the formation of tree hollows suitable for arboreal species, and cause tree fall and hollow fallen logs suitable for terrestrial species. However, fire could also enlarge hollows and make them unsuitable for continued occupancy by the same species. This may be of particular importance to smaller animals that prefer narrow entrances and confined spaces (Wardell-Johnson 1986, Dickman 1991).

In Ku-ring-gai there was no difference in the availability of logs or tree hollows between burnt and unburnt sites; probably a reflection of the fire history of the area (Chapters 2 and 3). Given this, it is reasonable to assume that nest box supplementation significantly increased the nest site availability within those treatment sites. *R. fuscipes* populations, however, showed no overall response to nest supplementation and were associated negatively with the abundance of logs on all sites, even though Dickman (1991) showed that over a third of individuals tracked using fluorescent pigment dust occupied nests in logs. It must be concluded that *R. fuscipes* populations were not limited by nest availability after this fire.

6.4.2.3 Food and Nests

Overall, resource supplementation appeared to have some effect during the first year, but less effect during the second year. The most significant responses were during winter of each year. During 1995 there was an increase in the magnitude of temporal population fluctuations in experimental sites, relative to control sites. This suggests a variable requirement for food and nests throughout the year. In species with an annual breeding strategy this could be linked directly to reproductive activity, but as *R. fuscipes* at Ku-ring-gai distributed breeding activity throughout the year, it seems the two are unrelated in this case. As the population fluctuations were most exaggerated over the winter of 1995,
compared to control sites, it seems that resource availability for this species may be seasonally variable.

The initial rate of increase in abundance of *R. fuscipes* in all treatment sites mirrored that in unburnt sites, although populations in burnt control sites did not increase over the same period. This suggests that the introduction of food and nest resources into the burnt sites mimicked changes in the natural abundance of resources in unburnt sites at that time. Further evidence is supplied by the increased number of permanent residents and reduced transiency of individuals in experimental sites compared to control sites; a similar pattern to that found between unburnt and burnt sites.

Naturally occurring resources differed significantly between burnt and unburnt sites in Ku-ring-gai, with predictably less leaf litter, less grass cover, more bare ground and more fallen wood in burnt than in unburnt sites. Similarly there was more vegetative cover in all height classes in unburnt sites. The addition of food to burnt sites could have replaced some of that provided in unburnt sites by leaf litter invertebrates, fungi, and dense vegetation. Similarly the additional cover supplied, plus the increased tree fall in burnt sites, may account for a similar amount of structural cover as dense vegetation in the unburnt sites. Cockburn (1978, 1979) found that stands of early and mid successional heath were more productive than mature stands. Given this, the combination of productive early successional vegetation and resource supplementation in burnt sites, may have provided similar levels of resource availability in burnt sites as was available to *R. fuscipes* populations in unburnt sites.

6.4.3 CONCLUSIONS

*Rattus fuscipes* populations in this study were reduced by fire, but increased steadily over subsequent years due to reproduction and recruitment of juveniles into the population over all seasons. Although *R. fuscipes* has previously been regarded as a late successional species, with a requirement for a dense understory and a well-developed leaf litter layer, the results of this study indicate clearly that these habitat features are not necessary to maintain a growing population of this species after fire.
Initial population increases of *R. fuscipes* in response to food supplementation indicated that the availability of food was a limiting factor during the second year after fire, although not during the third year. Overall, neither food nor nest supplementation had a consistently significant effect on *R. fuscipes* abundance. It was predicted that resource abundance generally would be most limiting immediately after fire, but would become less limiting over time. Increased population stability and body weights in treatment sites, when compared to controls, demonstrate that the resource supplementation had some effect; however, the effect was not reflected in changes of abundance. Reproduction, as indicated by the success of recruits, did not vary significantly in response to either supplementation treatment.
CHAPTER 7: POPULATION RESPONSES OF ANTECHINUS STUARTII TO RESOURCE AVAILABILITY AFTER FIRE

7.1 INTRODUCTION

The brown antechinus, *Antechinus stuartii*, is a small (< 50 g) dasyurid marsupial common to forested regions of the east coast of Australia (Figure 7.1). The taxonomy of the species within this range is currently under review (Dickman *et al.* 1998) although the subspecies occurring in Ku-ring-gai Chase National Park has been identified formally as *A. s. stuartii* (Dickman *et al.* 1988). Individuals of *A. stuartii* in any locality have a highly synchronised annual mating period of two to three weeks; this is followed by the death of all males (Woolley 1966; Moore 1974; Dickman 1982) due to stress-induced suppression of the immune system (McDonald *et al.* 1986). *A. stuartii* is semelparous and most females also die after their litters have become independent, although some females may survive to breed the following year (Cockburn *et al.* 1985). The primary stimulus to begin breeding is the rate of change of photoperiod (McAllan and Dickman 1986; McAllan *et al.* 1991), leading to a latitudinal gradation in the start of breeding (Dickman 1982); but this is complicated further by altitude as, for any given latitude, the onset of breeding is delayed with increasing height above sea level (Dickman 1982).

Breeding occurs usually during August with young born in mid to late September. Young stay attached to the mother’s teats for about five weeks, after which she leaves them in a nest while she forages (Braithwaite 1983). Juveniles leave the natal nest and become trappable in early January (pers. obs.). Females have 6 to 10 nipples, depending on the population (Cockburn *et al.* 1983), in a rudimentary pouch. The pouch is less developed than in other marsupials and consists of a fleshy circular fold of skin that envelopes the young, but does not enclose them. It is present only during the breeding season and recedes once the young are weaned. Generally enough young are born to occupy all nipples, although brood reduction by infanticide is common (Cockburn 1994). Mothers almost always wean some females, although the probability of a female being weaned declines with increasing numbers of females in the brood. Cockburn (1994) suggested this may be because females are philopatric, thus brood reduction may reduce competition and increase
the survival chances of daughters and therefore the mother's genetic line. Investing in females also increases the chance that a daughter will inherit the mother's home range, thus ensuring access to resources and reduced competition. Co-operative breeding may be an added bonus, as Cockburn (1994) noted that a female who was unsuccessful in raising her own daughters then helped her own mother suckle her young, resulting in all of the older mother's daughters being successfully weaned. On the other hand, either all or no male offspring are reared. Sons are more energetically costly; they are weaned sooner and weigh more at weaning than daughters (Cockburn 1992). As such, first year mothers with male-biased litters often die during late lactation, and second year mothers rarely invest in sons (Cockburn 1994). As males disperse widely from the area in which they were born, and must compete for space, resources and perhaps access to females, there is little benefit in investing in a low quality male. Experimental enhancement of female condition, by provision of supplementary food or reduction of competition, allows females to skew sex allocation in favour of males (Dickman 1988).

In forested sites *A. stuartii* spend most of their time in trees, usually in communal nests with up to 20 individuals (Lazenby-Cohen 1991). Only during lactation and weaning do females nest alone with their offspring. Dickman (1991) found that over 70% of nests are located in tree hollows, although logs, and rock crevices (Ward 1994, Whelan et al. 1996) are also used.

*Antechinus stuartii* is largely insectivorous although other invertebrates (Fletcher 1977; Hall 1980; Dickman 1982; Dickman et al. 1983; Green 1988), and occasional vertebrates (Green 1988) are sometimes consumed. Dickman (1982) and Dickman et al. (1983) also recorded small amounts of leaf material, whereas Ward (1994) found large quantities of pollen in the scats of animals living in heathland after fire. Carthew (1994) found that *A. stuartii* were regular visitors to *Banksia* spp. inflorescences, although whether the animals were feeding on the pollen, nectar or invertebrates attracted to the flowers was not clarified. Although *A. stuartii* often forages in trees (Wood 1970; Dickman 1991), individuals spend a substantial proportion of time on the ground foraging for leaf litter invertebrates (Braithwaite 1983), or travelling between flowering plants (Carthew 1994).
Antechinus stuartii has been associated with a variety of vegetation types ranging from tropical rainforest to heath. Previous studies, however, have identified few consistent patterns of association between A. stuartii abundance and either floristic or structural components of the plant community. McNiven et al. (1987) and Lunney et al. (1991) both stated that A. stuartii populations increased within 6 months of fire and that abundance increased steadily to 57% of pre-fire levels after 3 years, and 70% of pre-fire levels after 5 years. Recruitment of young into the population was successful only after 3 years (Fox 1982). Wilson et al. (1990) found that the abundance of A. stuartii did not increase until years 3 to 6 after fire. Friend (1993) believed that A. stuartii is restricted to this and to low post-fire successional stage by a requirement for predictable resource availability; by implication to possibly also nest sites. The rigid breeding pattern provides no assurance of successful reproduction (Lee et al. 1982), in an environment where resources are temporarily and possibly also nest sites.

Figure 7.1: The brown antechinus, Antechinus stuartii (a), and distribution within Australia (b) (from Strahan 1995). Photo: G. Little/Nature focus.
Antechinus stuartii has been associated with a variety of vegetation types ranging from tropical rainforest to heath. Previous studies, however, have identified few consistent patterns of association between A. stuartii abundance and either floristic or structural features of the environment. The abundance of A. stuartii has been correlated positively with logs (Barnett et al. 1978; Statham and Harden 1982), rock outcrops (Ward 1994), trees (Dickman 1991), plant species diversity (Fox 1982) and dense cover (Leonard 1972; Barnett et al. 1978; Dickman 1980; Fox 1982; Statham and Harden 1982), although Braithwaite (1983) and Dickman (1983) found more A. stuartii in areas with sparse ground cover. Hall and Lee (1982) and Lunney et al. (1987) found no selection for particular floristic groups, vegetation density at any height, or other habitat features. Some of the inconsistencies may be due to confusion of A. stuartii and A. agilis between studies, although both species appear to use diverse forest and woodland environments.

Although populations are reduced severely by fire, A. stuartii remains present in the environment and often breeds successfully in the first post-fire season only to experience a population crash the following year (Newsome et al. 1975; Catling et al. 1981). Population recovery is slow (Recher et al. 1975; Lunney et al. 1987; Catling et al. 1981; King 1985), impeded by a monoestrous breeding cycle (Lee et al. 1982; Friend 1993) and frequently also by environmental factors such as drought (Lunney and Barker 1986; Lunney and Ashby 1987; Lunney et al. 1987). Fox (1982) demonstrated that A. stuartii was present at a site within 6 months of fire and that abundance increased steadily to 57% of pre-fire levels after 3 years, and 70% of pre-fire levels after 5 years. Recruitment of young into the population was successful only after 3 years (Fox 1982). Similarly, Wilson et al. (1990) found that the abundance of A. stuartii did not increase until years 3 to 5 after fire. Friend (1993) believed that A. stuartii is restricted to this mid to late post-fire successional stage by a requirement for predictable resource availability; by implication food, but possibly also nest sites. The rigid breeding pattern provides no insurance against failed reproduction (Lee et al. 1982), in an environment where resources are temporally or spatially unreliable.

7.1.1 AIMS

It is the aim of the study described in this chapter to determine the population responses of the brown antechinus, Antechinus stuartii, to resource availability after fire.
Food and nest site availability were manipulated to establish if either, or both, of these factors influence the population dynamics, stability, and reproductive behaviour of *A. stuartii* after fire. The quantification of *A. stuartii* population responses to resource availability after fire could therefore determine the mechanisms behind the recovery of this species in fire-prone habitats.

### 7.2 Methods

The effect of fire on *A. stuartii* population dynamics, reproductive behaviour, population structure and stability was investigated by comparing the four unburnt sites with the three burnt control sites at Ku-ring-gai Chase National Park. This enabled an overall picture of *A. stuartii* demography to be established as a baseline to which the treatment effects of resource supplementation could be contrasted. Finally, natural resource availability was assessed to determine its potential influence on the population dynamics of this species.

The experimental design, data collection and analytical methods used for this aspect of the study are presented in Section 5.2.

### 7.3 Results

#### 7.3.1 Population Dynamics in Unburnt Sites

The average number of *Antechinus stuartii* known to be alive (KTBA) in unburnt sites ranged between 3.5 and 12.5 per hectare throughout the study period. In comparison, burnt control populations averaged from 1.1 to 11.9 individuals per hectare. Unburnt sites recorded population lows in November 1994, after the death of males, followed by steep increases in abundance due to the recruitment of juveniles into the population during summer (Figure 7.2a). Abundance fell dramatically between February and May 1995, followed by 18 months of stable but low population numbers that showed no increase until recruitment in 1997. Burnt control sites, by contrast (Figure 7.2b), showed similar patterns of population change during the first year after the fire, although abundance did not increase substantially with recruitment in February 1995. Population levels remained low throughout the second year after the fire, but increased during February and May 1996 to abundances higher than those in unburnt sites.
Figure 7.2: *Antechinus stuartii* KTBA in (a) unburnt sites and (b) burnt control sites. Means are shown ± standard error. Dotted lines indicate assumed trajectory as no data are available for August 1996. Trapping period is indicated on the x axis: a94 = August 1994, n94 = November 1994, f95 = February 1995, m95 = May 1995, etc.

The body condition, calculated as the ratio of body mass to head length (Section 6.2.2.1), of *A. stuartii* was compared between unburnt and burnt control sites to determine if there were differences between these treatments. There was no significant difference in the body condition of *A. stuartii* living in burnt control and unburnt sites throughout the study as a whole ($F = 0.122$, $df_{1,5}$, $p = 0.742$), or during any particular trapping session (Figure 7.3, Table 7.1). Further, there were no differences overall in the response of either sex ($df_{1,5}$, male $F = 0.582$, $p = 0.480$; female $F = 0.0004$, $p = 0.984$).
Figure 7.3: Body condition index of *Antechinus stuartii* in burnt control sites (c) and unburnt sites (ub). Means are shown ± standard error. Data are unavailable for August 1996.
Table 7.1: One-way ANOVA testing for differences in the body condition of *Antechinus stuartii* between burnt control and unburnt sites during each trapping session. Data are unavailable for August 1996. Note the Degrees of Freedom differ between time periods because not all sites recorded captures during each trapping session.

<table>
<thead>
<tr>
<th>Trapping session</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>February 1995</td>
<td>1.5</td>
<td>0.154</td>
<td>0.711</td>
</tr>
<tr>
<td>May 1995</td>
<td>1.2</td>
<td>0.034</td>
<td>0.871</td>
</tr>
<tr>
<td>August 1995</td>
<td>1.2</td>
<td>0.062</td>
<td>0.826</td>
</tr>
<tr>
<td>November 1995</td>
<td>1.1</td>
<td>0.001</td>
<td>0.983</td>
</tr>
<tr>
<td>February 1996</td>
<td>1.3</td>
<td>0.309</td>
<td>0.617</td>
</tr>
<tr>
<td>May 1996</td>
<td>1.4</td>
<td>0.328</td>
<td>0.598</td>
</tr>
<tr>
<td>November 1996</td>
<td>1.4</td>
<td>0.001</td>
<td>0.981</td>
</tr>
<tr>
<td>February 1997</td>
<td>1.5</td>
<td>1.806</td>
<td>0.237</td>
</tr>
</tbody>
</table>

Population structure did not vary between burnt and unburnt sites. Neither the proportion of females to males ($F = 0.222$, df $1.5$, $p = 0.658$; Figure 7.4), nor the relative abundances of transients, residents or permanent residents (Figure 7.5, Table 7.2) differed significantly overall between the two treatments.

![Figure 7.4: Proportion of female to male *Antechinus stuartii* in burnt control (c) and unburnt (ub) treatments. Means are shown ± standard error.](image)

Table 7.2: One-way ANOVAs of the relative abundance of transient, resident and permanent resident between burnt control and unburnt sites.

<table>
<thead>
<tr>
<th>Population component</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transient</td>
<td>1.5</td>
<td>0.516</td>
<td>0.505</td>
</tr>
<tr>
<td>Resident</td>
<td>1.5</td>
<td>0.499</td>
<td>0.511</td>
</tr>
<tr>
<td>Permanent resident</td>
<td>1.5</td>
<td>0.346</td>
<td>0.582</td>
</tr>
</tbody>
</table>
Figure 7.5: Percentage of individuals in Antechinus stuartii populations that were transient (captured once), resident (greater than 1 capture, in one or more trapping sessions) or permanently resident (captured in more than one trapping session). Note that: transients + > 1 capture = 100% of the population within a site, and permanent residents are a subset of residents. Means are shown + standard error. c = burnt control treatment, ub = unburnt treatment.

Trap-revealed longevity indicated that permanent residents in unburnt sites tended to remain in the same area for longer than those in burnt control sites (Figure 7.6), although this difference was not significant (F = 2.344, df 1,5, p = 0.164). There was no difference between longevity of males and females in unburnt sites (F = 4.675, df 1,2, p = 0.163) although this trend is to be regarded with caution as only 2 of 24 permanent residents recorded in unburnt sites were male, and given the strictly annual lifestyle and high dispersal probability of male A. stuartii (see Section 7.1), it would be expected that females would be recorded in the same site over a longer period than males. Considering the sexes independently, there were no significant differences in either the longevity of females (F = 1.590, df 1,4 , p = 0.276) or males (F= 0.000, p = 1.000) between burnt control and unburnt sites. All male permanent residents (burnt control n = 6, unburnt n = 2) were caught over 2 trapping sessions, whereas females were caught during 2 to 8 sessions in unburnt sites and between 2 and 5 sessions in burnt control sites.
Figure 7.6: Average trap-revealed longevity of permanent resident female and male Antechinus stuartii in burnt control (c) and unburnt (ub) sites. Means are shown ± standard error, periods represent trapping periods.

7.3.2 POPULATION DYNAMICS IN BURNT SITES

7.3.2.1 ABUNDANCE

The abundance of A. stuartii in burnt sites ranged between 0 and 15.6 individuals KTBA per hectare. Figure 7.7 indicates the average number of A. stuartii KTBA across all burnt treatments for the duration of the study. After supplementation began in January 1995, populations in both food only, and food and nest supplementation sites increased substantially compared to the control sites, whereas populations with nest only supplementation did not vary from control site abundances. This pattern changed in 1996, however, with A. stuartii abundance in food only and nest only sites becoming similar while the food and nest treatment was most similar to the control sites. The effect of resource supplementation appeared to diminish over time for this species. The highest abundance was maintained throughout the study in food and nest supplementation sites. In particular during 1995, when nest supplementation alone had no effect and food supplementation had some effect, the two resources together appeared to have an additive effect. This could indicate that initially, the availability of nest sites was not a limiting factor in the population recovery of A. stuartii, but as abundance increased in response to food supplementation, nest sites became harder to find.
Figure 7.7: *Antechinus stuartii* KTBA in a) food and nest, b) nest, c) food, and d) control treatment sites. Arrow indicates the beginning of food and nest supplementation. Means are shown ± standard error. Dotted lines indicate assumed trajectory as no data are available for August 1996. Trapping period is indicated on the x axis: a94 = August 1994, f95 = February 1995, etc.

Using data from the total number of individuals recorded at each site over the entire supplementation period, averaged over the number of post-supplementation trapping sessions (Spiller and Schoener 1998), there was a significant effect of food supplementation, and a significant food*nest interaction (Table 7.3a). Two-way ANOVAs within consecutive post-supplementation trapping sessions were used in an attempt to clarify these patterns. During August 1995, the first winter after supplementation began, there were significantly more *A. stuartii* in sites with food supplementation than in nest supplementation or control sites \( F = 16.173, \text{df} \_1,8, \text{p} = 0.004 \). This trend continued into November with numbers of *A. stuartii* in food supplementation sites remaining higher than in other sites, despite reproduction and associated male die-off in the intervening period \( F = 7.000, \text{df} \_1,8, \text{p} = 0.029 \). A significant interaction between food and nest supplementation was also recorded during November 1995, with the combined effect of these factors leading to higher abundances than where either was provided independently \( F = 7.000, \text{df} \_1,8, \text{p} = 0.029 \).

There was also a significant interaction between food and nest supplementation during May 1996 \( F = 7.049, \text{df} \_1,8, \text{p} = 0.029 \). However, this resulted from the individual effects of
food and nest supplementation leading to lower abundances of *A. stuartii* that in either control sites or combined food and nest supplementation sites.

The significant effect of food supplementation was confirmed by a repeated measures design to utilise temporal results and account for non-independence of data between trapping periods (Table 7.3b). However, there was no significant interaction between food and nest supplementation as indicated by the two-way ANOVA (above; Table 7.3.a). There was no effect of nest supplementation, although the power (probability of a Type II error) of this interaction (time*nest), was extremely low at $\beta = 0.08$ ($\alpha = 0.05$), indicating that sample size would have to increase almost 10 fold if a significant result was to be detected over the inherent temporal, site and seasonal variations.

Table 7.3: Two-way ANOVA (a) and two-way repeated measures ANOVA (b) of *Antechinus stuartii* abundance (KTBA) between treatments.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>food</td>
<td>1</td>
<td>5.619</td>
<td>0.045</td>
</tr>
<tr>
<td>nest</td>
<td>1</td>
<td>1.032</td>
<td>0.339</td>
</tr>
<tr>
<td>food*nest</td>
<td>1</td>
<td>6.977</td>
<td>0.030</td>
</tr>
<tr>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>time</td>
<td>7</td>
<td>0.952</td>
<td>0.541</td>
</tr>
<tr>
<td>time*food</td>
<td>7</td>
<td>5.668</td>
<td>0.018</td>
</tr>
<tr>
<td>time*nest</td>
<td>7</td>
<td>0.212</td>
<td>0.971</td>
</tr>
<tr>
<td>time<em>food</em>nest</td>
<td>7</td>
<td>0.582</td>
<td>0.768</td>
</tr>
<tr>
<td>error</td>
<td>64</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### 7.3.2.2 BODY CONDITION

Across treatments, male *A. stuartii* were in consistently better condition than females throughout the study ($F = 12.725$, df $1,22$, $p = 0.002$; Figure 7.8). There were no consistent seasonal effects of resource supplementation on body condition, with only one significant finding. In August 1995, despite relatively high body condition of animals in food only and nest only supplementation sites, the combined effect of these two resources led to lower body condition ($p = 0.024$; Table 7.4a). Combining the sexes within treatments showed that neither food nor nest supplementation had a significant effect on condition over the duration of the study (Table 7.4b).
Figure 7.8: Body condition index of female and male *Antechinus stuartii* between treatments. Means are shown ± standard error. fn = food and nest supplementation, f = food supplementation, n = nest supplementation and c = control.
Figure 7.9: Body condition index of Antechinus stuartii between treatments; males and females combined. Means are shown + standard error. Data are unavailable for August 1996. fn = food and nest supplementation, f = food supplementation, n = nest supplementation and c = control.
Table 7.4: Two-way ANOVA of *Antechinus stuartii* body condition between food and nest treatments a) during each trapping session, and b) all trapping sessions combined. No data are available for August 1996. Degrees of Freedom differ between time periods because not all sites recorded captures during each trapping session.

<table>
<thead>
<tr>
<th>Trapping session</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1995</td>
<td>food</td>
<td>1</td>
<td>0.047</td>
<td>0.835</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.016</td>
<td>0.902</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.000</td>
<td>0.996</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 1995</td>
<td>food</td>
<td>1</td>
<td>0.025</td>
<td>0.880</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.336</td>
<td>0.583</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>1.525</td>
<td>0.263</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August 1995</td>
<td>food</td>
<td>1</td>
<td>5.503</td>
<td>0.079</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.585</td>
<td>0.087</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>12.395</td>
<td>0.024</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>November 1995</td>
<td>food</td>
<td>1</td>
<td>0.133</td>
<td>0.739</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1996</td>
<td>food</td>
<td>1</td>
<td>1.786</td>
<td>0.223</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>1.185</td>
<td>0.312</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.077</td>
<td>0.789</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 1996</td>
<td>food</td>
<td>1</td>
<td>0.256</td>
<td>0.631</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.639</td>
<td>0.455</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.000</td>
<td>0.987</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>November 1996</td>
<td>food</td>
<td>1</td>
<td>0.003</td>
<td>0.957</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.070</td>
<td>0.805</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.009</td>
<td>0.929</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>February 1997</td>
<td>food</td>
<td>1</td>
<td>2.222</td>
<td>0.174</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.531</td>
<td>0.450</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.659</td>
<td>0.440</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td>Whole model</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>food</td>
<td>1</td>
<td>1.972</td>
<td>0.198</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>1.323</td>
<td>0.283</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.201</td>
<td>0.666</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
7.3.2.3 Population structure

There were generally more males than females recorded from each site, although there was no significant difference in the proportion of females to males between treatments (Figure 7.10; Table 7.5).

![Graph showing average no. KTBA across treatments]

Figure 7.10: Proportion of female to male *Antechinus stuartii* across treatments throughout the period of study. Means ± standard error are shown. fn = food and nest supplementation, f = food supplementation, n = nest supplementation and c = control.

Table 7.5: Two-way ANOVA comparing the proportion of female to male *Antechinus stuartii* across treatments throughout the period of the study.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>food</td>
<td>1</td>
<td>0.186</td>
<td>0.677</td>
</tr>
<tr>
<td>nest</td>
<td>1</td>
<td>0.042</td>
<td>0.843</td>
</tr>
<tr>
<td>food*nest</td>
<td>1</td>
<td>0.746</td>
<td>0.413</td>
</tr>
<tr>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Population stability was measured in terms of the proportion of transient and resident individuals between sites within treatments. The number of transient, resident and permanent resident *A. stuartii* did not differ between treatments (Figure 7.11, Table 7.6).
Figure 7.11: Percentage of individuals in *Antechinus stuartii* populations transient (captured once), resident (greater than 1 capture, in one or more trapping sessions) or permanently resident (captured in more than one trapping session) throughout the period of the study. Note that: transients + > 1 capture = 100% of the population within a site, and permanent residents are a subset of the residents. Means across sites within treatments are shown + standard error.

Table 7.6: Two-way ANOVA comparing the average percentage of transients, residents and permanent residents in *Antechinus stuartii* populations across treatments throughout the period of the study.

<table>
<thead>
<tr>
<th>Recapture rate</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transient (= 1 capture)</td>
<td>food</td>
<td>1</td>
<td>1.999</td>
<td>0.195</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>3.122</td>
<td>0.115</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.510</td>
<td>0.495</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resident (&gt; 1 capture)</td>
<td>food</td>
<td>1</td>
<td>1.999</td>
<td>0.195</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>3.122</td>
<td>0.115</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.510</td>
<td>0.495</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Permanent resident (&gt; 1 trapping session)</td>
<td>food</td>
<td>1</td>
<td>0.037</td>
<td>0.853</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.403</td>
<td>0.543</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.131</td>
<td>0.727</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The trap-revealed longevity of *A. stuartii* permanent residents (male and female combined) did not vary in response to resource supplementation (Table 7.7). However, although female permanent residents did not remain for longer periods in any particular treatment, males remained for significantly longer in food supplementation sites than in other treatment sites (Figure 7.12; Table 7.7).
Figure 7.12: Average trap-revealed longevity of permanent resident a) female and b) male Antechinus stuartii across different treatments. Means are shown + standard error. fn = food and nest, f = food, n = nest, c = control treatments.

Table 7.7: Two-way ANOVA on trap-revealed longevity between experimental treatments for female and male Antechinus stuartii. Degrees of Freedom vary as permanent residents of both sexes were not recorded in all sites.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>food</td>
<td>1</td>
<td>1.707</td>
<td>0.239</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.062</td>
<td>0.811</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>3.697</td>
<td>0.103</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>food</td>
<td>1</td>
<td>8.030</td>
<td>0.025</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.608</td>
<td>0.461</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.608</td>
<td>0.461</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female and Male</td>
<td>food</td>
<td>1</td>
<td>1.230</td>
<td>0.283</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.052</td>
<td>0.823</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>1.206</td>
<td>0.287</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
7.3.2.4 Reproductive Responses

As with the total population, the proportion of female to male juvenile *A. stuartii* during the recruitment period did not differ in response to individual treatment effects in any year (Figure 7.13). There was a significant interaction term in 1997, however, indicating that whereas combined food and nest supplementation sites had a similar ratio of females to males, food only, nest only and especially control sites had proportionately more males in their recruitment population ($F = 9.218$, $df_{1,8}$, $p = 0.016$).

In 1995 significantly more juvenile males were recruited into the food-supplemented populations than nest supplementation or control sites ($1995 \ F = 10.125$, $df_{1,8}$, $p = 0.013$; Figure 7.13a). However in 1996 there was an opposite effect with significantly less male juveniles recruited in to the food supplemented populations ($1996 \ F = 9.800$, $df_{1,8}$, $p = 0.014$; Figure 7.13b). There were no significant differences in the recruitment of males into any particular treatment or control sites during 1997. None of the treatments had a significant effect upon the number of female recruits in any year.

The total number of recruits into the population did not differ between treatment or control sites within years or between years. Similarly the ratio of juvenile to adult females in the population during the recruitment period did not differ between treatments or control sites in any year.
Figure 7.13: Average number of juvenile female and male Antechinus stuartii KTBA during the February recruitment period of 1995, 1996 and 1997. Means are shown + standard error. fn = food and nest supplementation, f = food supplementation, n = nest supplementation and c = control.

7.3.3 POPULATION RESPONSES TO NATURAL RESOURCE AVAILABILITY

The availability of natural resources was measured in terms of ground cover, vegetative cover and other habitat components, and Principal Components Analysis used to identify those factors which explained most of the variation within sites. Full descriptions of the principal components (PC) identified are presented in Section 6.6.3. *A. stuartii* abundance (KTBA) in February and May of each year was regressed against the PCs obtained from resource measurements from the same year to identify any relationships.
7.3.3.1 Ground cover

There were no significant relationships between *A. stuartii* abundance and any ground cover PC in 1995, 1996 or 1997, indicating that this species was not responding consistently to any of the ground cover variables measured in this study. Similarly, after Bonferroni corrections, there were no significant pairwise correlations between *A. stuartii* abundance and individual ground cover variables at any time.

7.3.3.2 Vegetative cover

During May 1995, the abundance of *A. stuartii* was associated negatively with PC3 \( (y = 3.063 \pm 0.535 \text{ SE}) - 2.213 \text{ PC3 (} \pm 0.780 \text{ SE)} \times; R^2 = 0.365, \text{ df } 1_{,14}, F = 8.051, p = 0.013 \), a component explained largely by an absence of vegetation from 100 - 200 cm but a well established canopy (Table 6.12). There were no significant relationships between abundance and vegetative cover in 1996, but in 1997 *A. stuartii* abundance demonstrated a weak positive association with PC2 \( (y = 4.563 \pm 0.684 \text{ SE}) + 1.272 \text{ PC2 (} \pm 0.587 \text{ SE)} \times; R^2 = 0.251, \text{ df } 1_{,14}, F = 4.694, p = 0.048 \), a principal component dominated by the presence of cover above 100 cm (Table 6.12).

*Antechinus stuartii* abundance was correlated negatively to vegetation between 20 and 50 cm during 1995 \( (r = -0.632, p = 0.028) \) and 20 to 100 cm during 1997 \( (20 - 50 \text{ cm: } r = -0.671, p = 0.017; 50 - 100 \text{ cm: } r = -0.642, p = 0.024) \), although none of these results were significant after Bonferroni corrections were applied. On the other hand, in February 1996 a positive correlation with vegetation over 200 cm \( (r = 0.697, p = 0.025; \text{ ns after Bonferroni correction}) \) was demonstrated.

7.3.3.3 Habitat components

There were no significant relationships between the abundance of *A. stuartii* and any of the habitat principal components identified in this study. Similarly, abundance was not correlated to any component consistently throughout the study.

7.3.4 Summary of results

Fire did not dramatically alter the abundance of *A. stuartii* in Ku-ring-gai Chase National Park. The average maximum abundance reached by *A. stuartii* during the study
was roughly equivalent in burnt control and unburnt sites, although the average minimum abundance was lower in burnt control than in unburnt sites. Body condition, the proportion of females to males, and the relative proportion of transients, residents and permanent residents did not differ between burnt control and unburnt sites. Permanent residents in unburnt sites tended to remain in the same site for longer than permanent residents in burnt control sites, but this difference was not significant.

Food supplementation led to significant increases in *A. stuartii* over 1995, although paradoxically seemed to cause a decrease in abundance over the duration of the study. Within the burnt treatment sites, the abundance of *A. stuartii* at food only and food and nest supplementation sites increased during 1995, relative to the nest only and control sites. During the second year of supplementation, however, abundance was most similar in food only and nest only sites with little change in population numbers. On the other hand, sites with both food and nest supplementation were similar to the controls; population growth was evident in both these treatments. The effect of resource supplementation appeared to diminish over time, with some evidence that as populations increased in response to food, nest availability became the limiting factor.

There were more males, and they were in significantly better body condition, than females in all treatments. More males were recruited into food supplementation sites than into other treatment sites in 1995, although this was balanced the following year with significantly less males recruited into food supplementation sites. Female recruitment did not vary between treatments and control sites, and overall the total number of recruits into the populations did not differ between years, regardless of treatments. Despite variable recruitment, the overall proportion of females to males did not differ between treatments either for adults or juveniles. The body condition indices of *A. stuartii* in food supplementation sites tended to be higher than those in nest or control sites, although this difference was not significant.

There was no difference in the proportion of transients, residents or permanent residents in *A. stuartii* populations under different treatments. The longevity of permanent residents was affected, however, with males tending to remain for longer periods in food
treatment sites than in nest treatment or control sites. The longevity of females, or of individuals in the population as a whole, did not vary in response to the experimental treatments.

The abundance of *A. stuartii* was not associated consistently with any ground cover, vegetative cover or microhabitat variables. During 1995, abundance was associated negatively with the presence of a dense canopy, but related positively to the presence of cover between 100 and 200 cm in height. In 1996 and 1997, *A. stuartii* abundance was related positively to vegetative cover above 100 cm in height, and also, in contrast to 1995, to canopy cover. These associations reflect the habitat changes occurring across all sites during the study period, so it is probable that these responses do not suggest causal relationships, and merely recognise the generalised habits of this species.

7.4 **Discussion**

7.4.1 **Effect of fire on Antechinus stuartii populations**

The abundance of *A. stuartii* was not reduced dramatically following fire in Ku-ring gai Chase National Park. The maximum abundance reached by populations in burnt and unburnt sites was roughly equivalent, although the average minimum abundance did fall lower in burnt sites than in unburnt sites. The body condition, proportion of females to males, and the relative proportion of transients, residents and permanent residents in the populations did not differ between burnt and unburnt sites, although permanent residents in unburnt sites tended towards increased longevity. The survival of this species after fire, with relatively little disturbance to abundance and population processes, was unexpected given previous studies (see below), but bears striking similarity to the response of a heathland population of *A. stuartii* in Royal National Park, south of Sydney, after the same fire episode in 1994 (Ward 1994; Whelan et al. 1996).

Whelan *et al.* (1996) attributed the survival of the Royal National Park population to use of extensive rock outcrops in the area by the usually arboreal *A. stuartii*, and the fire-stimulated flowering of large numbers of *Xanthorrhoea media* (grass tree) providing a rich food source in the form of pollen and nectar. Ku-ring-gai Chase National Park is very similar to Royal National Park both geologically and floristically. Both national parks have
large outcrops of Hawkesbury sandstone, commonly weathered to form overhangs, fissures and hollows. Similarly, *X. media* flowered following the fire for approximately 6 to 8 months in Ku-ring-gai; no doubt this provided an important food source for *A. stuartii* over the winter.

*Antechinus stuartii* populations have previously been noted to suffer dramatic declines, if not local extinction after fire (Newsome *et al.* 1975; Catling *et al.* 1981; Lunney *et al.* 1987) and population recovery is often slow (Recher *et al.* 1975; Catling *et al.* 1981; King 1985; Lunney *et al.* 1987). *A. stuartii* is generally regarded as a mid to late-successional species (Catling *et al.* 1981; Fox 1982; Wilson *et al.* 1990), due to a requirement for predictable resource availability (Friend 1993). Further, *A. stuartii*'s rigid breeding pattern provides no insurance against failed reproduction (Lee *et al.* 1982) in habitats where resources are temporally or spatially variable. Correlations with habitat variables have generally been inconclusive, however, suggesting that *A. stuartii* has few specific habitat requirements beyond food and provision of nest sites.

Some studies have shown that *A. stuartii* populations survive fire and reproduce successfully in the following breeding season, but fall dramatically in abundance during the second year after fire (Newsome *et al.* 1975; Catling *et al.* 1981). The populations in this study, and in Whelan *et al.* (1996), both recruited young into the population a year after fire. Although the Royal National Park study did not continue after this time, populations were maintained in Ku-ring-gai throughout the following year with successful recruitment in both 1996 and 1997.

Fire affects natural resource availability by removing or reducing the amount of organic and vegetative cover. During this study, *A. stuartii* abundance was not associated consistently with any ground cover, vegetative cover or microhabitat variables. During 1995, abundance was associated negatively with grass cover and a dense canopy. This is to be expected as there was little grass or canopy cover throughout all burnt sites, although *A. stuartii* was present in reasonably high numbers. Animals were associated positively with rocks and cover between 100 and 200 cm during this same year. Again this reflects the dominance of these habitat features in the early seral stages. Ward (1994) and Whelan *et al.*
(1996) found a similar association between *A. stuartii* and rocks in Royal National Park after the 1994 fires and, using spool and line tracking, confirmed that *A. stuartii* nest in rock crevices. Rock fissures, overhangs and crevices can also be used by small mammals as runways and temporary shelter, and may be of particular importance in disturbed habitat where much of the other cover has been removed. In 1996 and 1997, *A. stuartii* was associated positively with vegetative cover above 100 cm, and particularly to canopy cover. Again, these associations reflect the habitat changes occurring across all sites during the study period and are probably not suggestive of causal relationships, but merely recognise the generalised habits of *A. stuartii* and the flexibility of individuals in using whatever habitat components may be available.

The second summer after the fire there was a dramatic decline in *A. stuartii* abundance with low recruitment across all burnt sites. Unburnt sites neither crashed nor increased with the input of new recruits, indicating that the effect may have been environmental. This coincided with a period of low rainfall (Bureau of Meteorology 1988; Bureau of Meteorology unpubl. data), and supports the findings of Lunney et al. (1987) that drought may retard the post-fire recovery of *A. stuartii* and other small mammals.

### 7.4.2 Effect of Resource Availability on Antechinus stuartii Populations After Fire

#### 7.4.2.1 Food

There is some evidence in the literature to suggest that *A. stuartii* is not food-limited after fire. Recher et al. (1975) found that *A. stuartii* did not lose weight after fire, whereas sympatric *A. swainsonii* did. This they attributed to the scansional habits of *A. stuartii* which allowed increased foraging opportunity compared to the fully terrestrial *A. swainsonii*. Lunney et al. (1987) recorded an increase in body weight of male *A. stuartii* in 2 successive years after fire, over pre-fire body weights. Catling et al. (1989) similarly demonstrated, by measuring water influx rates, that there was no shortage of food or water after a prescribed (low intensity) fire.

There is, however, contrary evidence to suggest that the availability of food limits population recovery after fire. King (1985) recorded increased overnight movements after
fire which he interpreted as increased foraging activity due to decreased food availability, and Leonard (1972) found increased numbers of males on burnt plots after a fire, presumably as a result of increased activity or immigration. Newsome et al. (1975) demonstrated a decrease in body weight from pre-fire levels. Similarly, Ward (1994), using an improved experimental procedure from other studies, regressed pes length against body weight to determine body condition and found that males and females with young were affected detrimentally by fire. Unfortunately Ward’s results are somewhat unreliable due to small sample size.

In unburnt forest, Dickman (1989), by supplementing food, determined that *A. stuartii* (=*A. agilis*) populations were limited by food availability. Abundance increased, as did body weight and survival, and animals decreased movements between traps. Given this, it would be expected that, after fire, natural resource availability would be even lower and thus the effect of food supplementation greater.

Food supplementation, in this study, led to initial increases but then to overall decreases in abundance of *A. stuartii* over time. During the first year of supplementation, the abundance of *A. stuartii* increased in food supplementation sites relative to the populations in nest only or control treatments. However, after a drop in *A. stuartii* abundance across all sites over the 1995/1996 summer a different pattern emerged. During 1996, abundance in food supplementation only and nest supplementation only treatment sites remained low, whereas *A. stuartii* in combined food and nest treatment sites showed similar increases to the control populations. The change in pattern between years may be explained partially by patterns of recruitment. Whereas female recruitment did not differ between treatments, or between years, the number of males recruited into the populations varied.

In 1995, significantly more males were recruited into food supplementation sites than into other treatment sites. *A. stuartii* practices selective infanticide to favour either male or female-biased litters (Cockburn 1994). As sons are more energetically costly to wean (Cockburn 1992) it is tempting to assume that increased food availability may have encouraged mothers to favour male offspring (Dickman 1988). However, as food
supplementation did not begin until the beginning of January 1995, it was too late to influence the sex ratio of the new generation. Even so, as males are weaned earlier and weigh more at weaning than females (Cockburn 1992), males were in a good position to take full advantage of the supplemented food source as soon as they became independent. Their survival chances would have improved and they could have perhaps competitively excluded the smaller females as they came into the population, thus favouring a male-biased population. This seems to be the likely explanation of these recruitment patterns as, if external environmental factors or resource abundance was influencing the sex bias of the litters, it would have been expected to occur across all burnt sites and perhaps unburnt sites as well. However, a domination of food resources by one sex over the other would have been expected to result in differences in body condition. There was no difference in the body condition between treatments in February 1995, and although overall body condition of *A. stuartii* tended to be better in food supplementation sites than in other treatment sites, this difference was not significant over the entire study period.

In 1996, significantly fewer males were recruited into food supplementation sites than into other treatments. This may be a result of three factors. Firstly, a perceived over-abundance of males may have influenced the females to produce more female offspring. This would represent a frequency-dependent advantage to the rarer sex, which Fisher (1930) argued was a mechanism that should stabilise population sex ratios over the long term at parity. Secondly, the increasing population may have put local resource availability under strain, encouraging females to produce less energetically costly litters. Finally, drought conditions may have similarly favoured the production of less costly female-biased litters.

Dickman (1989) attributed an increase in abundance of food supplemented populations of the closely related *A. agilis* to increased juvenile survival although, unlike the present study, he found no differences between the responses of males and females. This is in contrast to several previous food supplementation studies where increases in abundance have been commonly the result of increased reproductive effort or immigration (see Boutin 1990 for review). As with the present study, Dickman (1989) recorded no increases in either reproduction or immigration as a result of food supplementation. In Ku-ring-gai
there were no differences between the numbers of transients, residents and permanent residents between food supplemented sites and other treatment sites. This would indicate no increased immigration into the food addition sites. Male permanent residents, however, remained longer in food supplemented sites than elsewhere. Food supplementation appeared to discourage dispersal of males from their mother’s home range. As males generally disperse widely from their birth place (Cockburn et al. 1985), food supplementation may have had the unexpected, and possibly deleterious effect, of altering the social system and local gene flow within this species. Ribble (1997) similarly recorded a decrease in dispersal of Peromyscus spp. from food supplemented sites, although the number of animals known to be alive did not vary between treatments. Overall, the increased abundance of A. stuartii in food supplementation sites during the first year may be attributed to increased survival of male recruits, at the expense of females, and increased longevity of those individuals within the sites. However, by the third year after fire, high abundances were recorded in sites only with both food and nest supplementation, whereas food supplementation, alone, apparently caused a decline in A. stuartii populations.

There is also the possibility that the increased abundance of A. stuartii in response to food supplementation during the first year of the study attracted more predators to food supplementation sites. In the food-only supplementation sites, the increased predation pressure coupled with low cover and perhaps limited refuges, could have led to a decline in abundance. In sites with both food and nest supplementation, however, the nest-boxes may have provided refuge from predators. Introduced terrestrial predators, foxes and cats, were noted only rarely at the sites and are unlikely to have exerted tremendous predation pressure due to their low abundances. It is also difficult to estimate the influence that highly mobile and/or cryptic avian and reptilian predators may have on small mammal fauna. Loyn et al. (1986), however, noted an increased proportion of R. fuscipes in the post-fire diets of Sooty Owls and attributed this to the lack of ground cover available to terrestrial small mammals after fire. The post-fire survival of some Australian mammals has been demonstrated to be reduced greatly by predation (Christensen 1980), and Kinnear et al. (1988, 1998) have suggested that such rates of predation could lead to the local extinction of rarer species.
7.4.2.2 Nest

Nest supplementation appeared to contribute to population dynamics only when population sizes were high. During 1995, nest supplementation alone had no effect, but food supplementation caused an increase in *A. stuartii* abundance. The highest population levels were reached in sites with both food and nest addition. It is probable that although nest availability was not restrictive to population growth initially, as abundance increased in response to food supplementation the availability of nest sites became limiting. The two resources apparently had an additive effect on *A. stuartii* abundance. After the dramatic fall in population numbers across all sites, over the summer of 1995/1996, sites with both food and nest supplementation recovered, whereas sites with either of the two resources alone did not. Interestingly, populations in control sites also increased in abundance in autumn 1996, suggesting external influences on local abundance beyond those measured or controlled for by the experimental design. Overall however, nest availability appears to limit *A. stuartii* abundance, although the effects are secondary to those of food availability.

As *A. stuartii* is communal, nest sites provide more than refuge for this species. Lazenby-Cohen and Cockburn (1988) used radio-tracking data to suggest that *A. stuartii* displays lek promiscuity, using communal nests as lekking arenas. They believe *A. stuartii* fulfils the requirements of lekking defined by Bradbury (1981) as: i) there is no male parental care, ii) there is an arena in which several males aggregate and to which females come, iii) the display sites contain no resources required by the females except the males themselves, and iv) the female has an opportunity to select a mate when she visits the arena. With respect to the first three points *A. stuartii*: i) display no paternal care as all males die before the birth of the young, ii) have communal nest trees in which male aggregations occur during the mating season, and iii) females have other nest sites available in their home-ranges (Lazenby-Cohen and Cockburn 1988). There is, however, little strong evidence to support the last requirement, that females have the opportunity to select males from the lekking arena, although Dickman (1993) believes that mate selection almost certainly takes place via sperm competition. Lazenby-Cohen and Cockburn (1988) reported that one female in the study did briefly (45 minutes) visit a nest where males were aggregated. This time period is probably not long enough for mating to have taken place as
Marlow (1961) found that copulation usually lasted from 9-12 hours. In addition, although communal nesting was indicated by radio-tracking data in the study of Lazenby-Cohen and Cockburn (1988), there is no evidence that these were indeed lekking arenas. Direct observations would be required to substantiate this.

Communal nesting has social advantages (Lazenby-Cohen 1991) but is rare among insectivores (Sealander 1952; Cantoni and Vogel 1989). Lazenby-Cohen (1991) suggested that *A. stuartii* nest together to conserve heat; however, whereas this has been demonstrated for taiga voles, *Microtus xanthognathus*, for example, which leave communal nests to forage one at a time while leaving the other individuals to maintain nest temperature (Canford 1984), Green (1988) noted that all *A. stuartii* left the nest during the same period, resulting in a drop in ambient temperature within the nest.

### 7.4.2.3 Food and Nests

Overall, resource supplementation had some effect on abundance, as discussed above, but little overall effect on demography. There was no difference in the proportion of transients, residents or permanent residents, nor the longevity of permanent residents between treatment sites. The combined effect of food and nest supplementation appeared to enhance the population recovery of *A. stuartii* by providing additional nesting and/or refuge opportunities at times when high local abundances due to increased food availability had saturated natural cover availability.

### 7.4.3 Conclusions

The effect of resource supplementation after fire was most obvious in the first year of the study, but then appeared to diminish gradually. Food and nest resources both appeared limiting to *A. stuartii*, although population dynamics were most strongly influenced by food availability, with nest availability becoming limiting apparently only at higher population levels. Interestingly, food supplementation also appeared to affect *A. stuartii* social structure by reducing dispersal and increasing longevity of males within food supplementation sites.
CHAPTER 8: POPULATION RESPONSES OF *Mus domesticus* TO RESOURCE
AVAILABILITY AFTER FIRE

8.1 INTRODUCTION

The house mouse, *Mus domesticus*, was probably introduced into Australia by European immigrants approximately 200 years ago. Since that time it has dispersed across the continent, and to many of Australia’s offshore islands (Figure 8.1), where it has established populations in a range of different natural habitats as well as on pastoral and urban lands. The success of *M. domesticus* is due largely to its opportunistic nature and generalist habitat and resource requirements (Braithwaite et al. 1978; Fox 1983). *M. domesticus* may remain in very low abundances, and even become locally extinct, for many months or years. However, when conditions are favourable rapid reproduction and dispersal can lead to plagues (Newsome 1983). Feral *M. domesticus* populations may be maintained from less than 1 mouse per ha, up to 700 mice per ha (Pearson 1963), and may even double this density when commensal with humans (Stickel 1979). It is worth noting that the literature on this species in Australia often refers to this animal as *Mus musculus*, however in this study I will follow the current terminology of *M. domesticus* (Berry 1981; Singleton 1995).

*Mus domesticus* are weaned at 3 to 4 weeks of age and reach sexual maturity around 3 weeks later, weighing 8 to 20 g (Mikesic and Drickamer 1992; Singleton 1995). Breeding usually occurs over summer but can extend throughout the year in mild climatic regions, especially if there is sufficient rainfall (Newsome 1983). The gestation period is about 19 days and between 4 and 8 young are born (Singleton 1995). A post-partum oestrus, rapid maturation and large litter size allow for rapid increases in population size (Singleton 1995).

Fox (1983, p.479) defined *M. domesticus* as the “supreme opportunist”, referring to the ability of this species to invade under-utilised niches. In Australia, *M. domesticus* reaches its highest densities in farm land, a habitat occupied by few native small mammals (Singleton 1995). Plague numbers have also been recorded in early post-fire seral stages,
both in Australia (see below) and elsewhere in the world (Cook 1959; Crowner and Barrett 1979). *M. domesticus* is often the first species to appear after fire, when native species have been removed or abundances dramatically reduced, and typically reaches peak abundance within 12 to 18 months after fire (Leonard 1970; Christensen and Kimber 1975; Recher et al. 1975; Newsome et al. 1975; Friend 1979; Fox and McKay 1981; Fox 1982, 1983, 1990; Catling 1986; Fox et al. 1986; Lunney and Barker 1986; Lunney and Ashby 1987; Lunney et al. 1987; Wilson et al. 1990). However, some researchers have noted a later (Catling et al. 1981), or second peak in abundance at 3 to 4 years after fire (Fox 1982, 1983, 1990; Fox et al. 1986). Likewise, *M. domesticus* may fail to reach high abundance (Bamford 1985), or not invade at all (Thompson et al. 1989), after fire.

The success of *M. domesticus* in the post-fire environment is attributed usually to the ability of this species to exploit unfilled niches and under-utilised resources (Braithwaite et al. 1978; Fox 1983). Even so, not all habitats are equally accessible to this species, as Masters (1993) found that *M. domesticus* was unable to survive in arid spinifex grassland except in years of high rainfall, and even then was more abundant on old successional sites than recently burnt areas. In addition to general habitat requirements, it appears that the patterns of response recorded for this species after fire are dependent upon the composition of the small mammal community, as native species are often able to out-compete *M. domesticus*, unless the latter is at very high densities (Fox and Gullick 1989).

*Mus domesticus* is regarded usually as an omnivore or generalist granivore (Fox 1983; Bomford 1987a), although in Australia it may occupy an insectivorous food niche, particularly in the absence of *Antechinus* spp. (Braithwaite et al. 1978). Its cover requirements are very general, with burrows formed in loose soil or leaf litter (Newsome 1983). Food appears to be a limiting resource for *M. domesticus* populations, with food supplementation resulting in increased abundances, lengthened breeding seasons and increased reproductive activity (DeLong 1967; Newsome 1970; Bomford 1987b; Bomford and Redhead 1987). However Newsome (1969a,b, 1970) determined that the availability of burrowing sites was the major resource limiting population growth, and food availability was secondary to this.
Resource limitation after fire has not been investigated directly for this species, although Newsome and Catling (1983) developed demographic models using manipulation of resources and predation on captive *M. domesticus* populations, to explain previously reported increases in abundance. This pattern has been confirmed at a national level, where *M. domesticus* abundance with natural resources available is presented in Section 5.2, and data collection and data analysis, Section 6.2.

### 8.3 Results

#### 8.3.1 Population Dynamics

#### 8.3.1.1 Abundance

A total of 47 individual *M. domesticus* was caught at all sites during this study. Of these, 20 were from Site 1, and 18 from Site 2, with food supplementation sites at Exmouth. The food supplementation site, Site 2, recorded only one individual, and the three combined food and nest supplementation sites, recorded only one individual between

Figure 8.1: The house mouse, *Mus domesticus* (a), and distribution within Australia (b) (from Strahan 1995). Photo: Dick Whitford/Nature focus.
Resource limitation after fire has not been investigated directly for this species, although Newsome and Catling (1983) developed demographic models using manipulation of resources and predation on captive *M. domesticus* populations, to explain previously observed patterns of mammal succession after fire, and to determine the mechanisms behind the observed population fluctuations.

### 8.1.1 AIMS

The study presented in this chapter aims to determine the population responses of the house mouse, *Mus domesticus*, to resource availability after fire. Food and nest site availability were manipulated to establish if either or both of these factors affected the population dynamics of *M. domesticus* in a post-fire environment. In addition, the relationship between this introduced species and native small mammals is investigated.

### 8.2 METHODS

#### 8.2.1 EXPERIMENTAL DESIGN AND DATA COLLECTION

The effect of post-fire resource availability on *M. domesticus* population dynamics, reproductive behaviour, population structure and stability was investigated. As no individuals were captured in unburnt sites, comparisons could not be drawn between populations in burnt and unburnt forest. The effect of resource availability, however, could be determined by the manipulation of food and nest site availability, and by associating *M. domesticus* abundance with natural resource availability.

The experimental design of this aspect of the study is presented in Section 5.2, and data collection and data analysis techniques are outlined in Section 6.2.

### 8.3 RESULTS

#### 8.3.1 POPULATION DYNAMICS IN BURNT SITES

##### 8.3.1.1 ABUNDANCE

A total of 47 individual *M. domesticus* was caught across all sites during this study. Of these, 22 were from Site 3, and 18 from Site 9; both food supplementation sites. However, the third food supplementation site, Site 2, recorded only one individual, and the three combined food and nest supplementation sites, recorded only one individual between
them, during the entire study. Similarly, captures in the nest only and control treatments were sporadic and rare.

Figure 8.2 shows that the first *M. domesticus* were recorded in May 1995; 16 months after the fire and 4 to 5 months after food supplementation began. Although one individual was recorded at a nest supplementation site at this time, all others were recorded in the three food supplementation sites. Within the food supplementation sites, 7 individuals at Site 9, and 4 individuals at Site 3, indicated successful colonisation by *M. domesticus*. The one animal at the third food supplementation site, Site 2, during May 1995 was the only *M. domesticus* recorded there throughout the study, indicating that, unlike the two other food supplementation sites, *M. domesticus* was unable to establish a permanent population at this site. No individuals were recorded in the combined food and nest treatments, or control sites, until later in the study.

Figure 8.2: *Mus domesticus* KTBA in food and nest (a), nest (b), food (c), and control (d) treatment sites. Arrow indicates beginning of food and nest supplementation. Means are shown ± standard error. Dotted lines indicate assumed trajectory as no data are available for August 1996. Trapping period is indicated on the x axis: a94 = August 1994, f95 = February 1995, etc.
The treatment effects were first analysed with two-way ANOVA, using data from the total number of individuals recorded at each site over the entire supplementation period, averaged over the number of post-supplementation trapping sessions (Spiller and Schoener 1998). This analysis indicated that overall, neither food or nest supplementation, nor these factors combined, had a significant effect on *M. domesticus* abundance (Table 8.1a). A repeated measures design was then used to incorporate temporal variability into the analyses, and again, neither food nor nest supplementation had a significant effect on the abundance of *M. domesticus* over the study period (Table 8.1b). These results should be treated with some caution as, although the assumption of equal variances was met, the data were not distributed normally and transformation did not rectify this problem. In addition, the power of these analyses was considerably less than desirable (food*time $\beta = 0.212$, nest*time $\beta = 0.146$, food*nest*time $\beta = 0.462$; at $\alpha = 0.05$), indicating that without more than double the sample size, this experiment could not have detected any treatment effects over the very marked temporal and site variability.

Table 8.1: Two-way ANOVA (a), and two-way repeated measures ANOVA (b), of *Mus domesticus* abundance (KTBA) between treatments.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>a)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>food</td>
<td>1</td>
<td>4.035</td>
<td>0.080</td>
</tr>
<tr>
<td>nest</td>
<td>1</td>
<td>3.631</td>
<td>0.093</td>
</tr>
<tr>
<td>food*nest</td>
<td>1</td>
<td>4.035</td>
<td>0.080</td>
</tr>
<tr>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>time</td>
<td>7</td>
<td>2.052</td>
<td>0.441</td>
</tr>
<tr>
<td>food*time</td>
<td>7</td>
<td>1.028</td>
<td>0.486</td>
</tr>
<tr>
<td>nest*time</td>
<td>7</td>
<td>0.657</td>
<td>0.703</td>
</tr>
<tr>
<td>food<em>nest</em>time</td>
<td>7</td>
<td>1.166</td>
<td>0.335</td>
</tr>
<tr>
<td>error</td>
<td>64</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

8.3.1.2 BODY CONDITION

There was no significant effect of experimental treatment on the body condition of *M. domesticus* (Figure 8.3, Table 8.2), although the effects were probably confounded by the small numbers of animals caught in treatments other than food addition. Resource supplementation had no significant effect on either female or male body condition (Table 8.2a, b), although for males, in particular, sample size was once again a problem.
Figure 8.3: Body condition index of adult *Mus domesticus* between treatment sites; males and females combined. Means are shown ± standard error. fn = food and nest, f = food, n = nest, and c = control sites.

Table 8.2: Two-way ANOVA of *Mus domesticus* adult body condition between food and nest treatments, for a) females, b) males, and c) females and males combined. Degrees of Freedom differ between categories because not all sites recorded captures of *M. domesticus*.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) females</td>
<td>food</td>
<td>1</td>
<td>0.364</td>
<td>0.589</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.295</td>
<td>0.625</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.113</td>
<td>0.759</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) males</td>
<td>food</td>
<td>1</td>
<td>1.760</td>
<td>0.411</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c) Females and males</td>
<td>food</td>
<td>1</td>
<td>1.233</td>
<td>0.329</td>
</tr>
<tr>
<td></td>
<td>nest</td>
<td>1</td>
<td>0.708</td>
<td>0.448</td>
</tr>
<tr>
<td></td>
<td>food*nest</td>
<td>1</td>
<td>0.012</td>
<td>0.919</td>
</tr>
<tr>
<td></td>
<td>error</td>
<td>4</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Similarly, there was no difference in the body condition of males and females within food supplementation sites (df 1,4, F = 0.325, p = 0.599; Figure 8.4), indicating that individuals of neither sex had preferential access to food resources.

![Figure 8.4: Body condition index of adult female and male Mus domesticus in food addition sites. Means are shown ± standard error.](image)

8.3.1.3 POPULATION STRUCTURE

Sample size was too low to determine if population structure varied between treatments. Within the two populations at food supplementation sites, however, the proportion of males to females remained approximately 1:1 throughout the study. The only exception to this was at Site 9 during May 1995, the first period for which *M. domesticus* was recorded. Then, the proportion of males to females was 5:2, with all males being adult, and one adult female and one juvenile female.

The populations at all sites were highly transient. Only one individual was captured in more than one period; an adult male that was caught in May and November 1995 in Site 9, and was therefore present in the area over 3 trapping sessions. Ten animals, across all treatments, were caught on two consecutive nights, and 2 animals were captured on three consecutive nights. Of these 12 residents, 10 were in food addition sites, 1 was in a food and nest addition site and 1 was in a control site.

8.3.1.4 REPRODUCTIVE RESPONSES

Juveniles were generally defined as individuals less than 10 g, as all females under this weight were non-parous. There were 7 juveniles recorded during the study, including one non-parous female weighing 10.25g that was considered sufficiently small to have been
born on site. Interestingly, there were juveniles caught at both Sites 3 and 9 in May 1995, indicating successful reproduction very soon after colonisation. No juveniles were captured at any sites other than 3 and 9, although a possibly pregnant female was captured in May 1996 at a food and nest site. Juveniles were captured in May and August 1995, and in February and May 1996.

8.3.2 POPULATION RESPONSES TO NATURAL RESOURCE AVAILABILITY

The availability of natural resources was measured in terms of ground cover, vegetative cover and other habitat components, and Principal Components Analysis used to identify those resource factors explaining most of the variation within sites. *M. domesticus* abundance (KTBA) in February and May 1995 and 1996, and February 1997, was regressed against the PCs obtained from resource measurements from the same year to identify any relationships. Full descriptions of the principal components (PC) are presented in Section 6.3.3.

8.3.2.1 GROUND COVER

There was a significant negative association of *M. domesticus* abundance in May 1995 with PC1 for that year (\(y = 0.813 (\pm 0.426 \text{ SE}) - 0.626 \text{ PC1} (\pm 0.269 \text{ SE})x\); \(R^2 = 0.279, \text{ df } 1,14, F = 5.427, p = 0.035\)), indicating a preference for areas with bare ground rather than litter. Similarly in 1996, *M domesticus* abundance in both February and May was associated with PC1 for 1996 (February \(y = 0.9 (\pm 0.208 \text{ SE}) + 0.796 \text{ PC1} (\pm 0.126 \text{ SE})x\); \(R^2 = 0.834, \text{ df } 1,8, F = 40.183, p < 0.001\); May \(y = 1.0 (\pm 0.698 \text{ SE}) + 1.095 \text{ PC1} (\pm 0.421 \text{ SE})x\); \(R^2 = 0.458, \text{ df } 1,8, F = 6.764, p = 0.032\)), representing a positive relationship with the presence of bare ground. There were no demonstratable relationships of *M. domesticus* abundance with any ground cover PCs in 1997 as sample size was very small (3 individuals).

The relationship between *M. domesticus* abundance and the presence of bare ground was reinforced by the positive pairwise correlation during February 1996 (February \(r = 0.928, p < 0.001\)). This correlation was not significant in 1995 however, and as mentioned above, sample size in 1997 precluded sensible analysis.
The amount of bare ground varied significantly between sites in every year (Table 8.3). Figure 8.5 demonstrates the changes in the amount of bare ground at sites within treatments over the study period. As expected, the amount of bare ground decreased over time in response to an increase in leaf litter (Section 6.3.3.1). The highest abundances of *M. domesticus* were measured at sites with a high bare ground score in addition to food supplementation (Sites 3 and 9). *M. domesticus* did not colonise food supplementation sites with low scores for bare ground (Sites 1, 2, 4, and 12), or sites with large scores for bare ground but no food supplementation (Sites 5 and 10).

Table 8.3: One-way ANOVA of the amount of bare ground between sites in 1995, 1996 and 1997. Quadrats within sites are used as replicates. Degrees of Freedom differ between years because of the different numbers of quadrats recorded (refer to 5.2.3.2).

<table>
<thead>
<tr>
<th>Year</th>
<th>df</th>
<th>F</th>
<th>p</th>
<th>transform</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>11, 180</td>
<td>18.317</td>
<td>p &lt; 0.001</td>
<td>-</td>
</tr>
<tr>
<td>1996</td>
<td>5, 42</td>
<td>11.320</td>
<td>p &lt; 0.001</td>
<td>-</td>
</tr>
<tr>
<td>1997</td>
<td>11, 108</td>
<td>8.530</td>
<td>p &lt; 0.001</td>
<td>square root</td>
</tr>
</tbody>
</table>

Figure 8.5: Bare ground cover frequency scores (means; variances not shown) at each site within treatments a) food and nest, b) nest only, c) food only, d) control.
8.3.2.2 Vegetative Cover

There were no linear or correlative relationships between *M. domesticus* abundance and vegetation cover in any year; r-values ranged from -0.720 to 0.566 (P<sub>ns</sub>).

8.3.2.3 Habitat Components

The habitat components rock, trees, tree hollows and logs were measured at the end of the study and assumed not to have changed throughout the study period. Although some trees invariably would have become logs during this period, principal components analysis grouped these two factors together under PC1 and as such the two components were considered together when comparing habitat features with mammal captures. The total abundance of *M. domesticus* from throughout the study period was associated negatively with PC1; primarily representing an association with the absence of trees and logs (y = 0.543 (± 0.140 SE) - 0.343 PC1 (± 0.131 SE)x; R<sup>2</sup> = 0.068, df<sub>1.94</sub>, F = 6.860, p = 0.010).

8.3.3 Competitive Interactions with Other Small Mammal Species

8.3.3.1 Species Associations?

The patterns of colonisation demonstrated during this study suggest that something other than resource availability may have affected the population dynamics of *M. domesticus*. Two other species were in sufficient numbers to possibly affect the colonisation success of *M. domesticus, Rattus fuscipes* and *Antechinus stuartii*. However, *M. domesticus* abundance was not correlated significantly to the abundance of either of these species (*R. fuscipes* r = 0.151, p = 0.143; *A. stuartii* r = -0.071, p = 0.493). *M. domesticus* was correlated positively to *C. rutilus* abundance (r = 0.325, p = 0.001); possibly a reflection of the significant linear relationship that both these species had with the presence of bare ground (Sections 8.3.2.1 and 9.3.2.1).

The spatial association of *M. domesticus* in relation to *A. stuartii* was further assessed by determining the number of traps occupied by either, both or neither of these species during each trapping session. Due to the limited data set, analyses were conducted on Site 3 and Site 9 data only, and pooled across all trapping sessions subsequent to the first *M. domesticus* being captured. Chi-squared analysis determined that the captures of *M. domesticus* and *A. stuartii* were not significantly associated (Site 3 df<sub>1</sub>, $\chi^2 = 0.004$, p >
0.05; Site 9 dfi, $\chi^2 = 0.390$, $p > 0.05$). Similar analyses of *M. domesticus* spatial associations with *R. fuscipes* were also non-significant (Site 3 dfi, $\chi^2 = 0.216$, $p > 0.05$; Site 9 dfi, $\chi^2 = 0.119$, $p > 0.05$).

### 8.3.4 Summary of results

Overall, food and nest supplementation had no significant effect of *M. domesticus* abundance. However, the two sites where *M. domesticus* was able to establish breeding populations were food supplementation sites. These sites were colonised between 13 and 16 months after the fire, primarily by males, and reproduction commenced quickly. Reproduction continued throughout the winter of the first year while populations were being established, but was confined to the summer months of 1996.

The populations were highly transient with most animals being captured only once. Of 47 individuals, 1 adult male remained at a site over 3 trapping periods, and a further 12 individuals were recaptured within single trapping periods. Almost all residents were from food supplementation sites.

The most significant relationship noted was the preference of *M. domesticus* for areas of bare ground. Further, the abundance of *M. domesticus* was associated negatively with the presence of leaf litter, trees and logs. It was the combination of the availability of bare ground and supplementary food that led to the highest numbers of *M. domesticus*, and the establishment of populations. *M. domesticus* did not colonise sites with high scores for bare ground and no supplementary food, nor areas with supplementary food and low scores for bare ground.

There was no evidence of competition or spatial association between *M. domesticus* and either *R. fuscipes* or *A. stuartii*. 
8.4 DISCUSSION

8.4.1 EFFECT OF RESOURCE AVAILABILITY ON *Mus domesticus* POPULATIONS AFTER FIRE

In a review of the effect of fire on small mammals, Newsome and Catling (1983) concluded that no general patterns of faunal response were evident from previous studies. In response, they developed demographic models from experiments on *Mus domesticus* populations, where resources and predators were either measured or provided in excess. The levels of these resources and predation were related to changes in demography, and six models derived to explain the population responses (Newsome and Catling 1983).

Model 1 described an acute shortage of food, with burrows being plentiful. When the mice exhausted their food supply, reproduction dropped, older mice left the population, and only juveniles remained in residence (Newsome and Catling 1983). The second model described a food shortage as a result of immigration. Immigrants were primarily adults, and both abundance and mean age initially increased before the food was exhausted, reproduction ceased and abundance dropped (Newsome and Catling 1983). Model 3 related a situation where food was abundant but shelter, in the form of burrows, was rare. Abundance fell due to dispersal of juveniles from the site, although adults remained and continued to reproduce (Newsome and Catling 1983). The fourth scenario was one where both food and shelter were rare. Older mice left the site leaving younger animals in residence, however reproduction faltered and the population went to extinction (Newsome and Catling 1983). Model 5 described a situation where increased availability of food and shelter led to a population boom, followed by an invasion of predators. The population declined despite high reproduction and a balanced age structure (Newsome and Catling 1983). Finally, the sixth model was a theoretical one of steady state (Newsome and Catling 1983).

The results of the present study do not seem to relate to any of the above models, except, in part, Model 5. With respect to most small mammal species, it would be expected that fire would reduce both food and shelter availability, at least initially. However, as *M. domesticus* burrows in sandy soil to nest (Newsome 1983), fire may actually create an overabundance of shelter by removing leaf litter and exposing bare ground suitable for
burrowing. In addition, the opportunistic feeding requirements of *M. domesticus* may mean that fire increases the availability of food, as more specialised species may not survive in the early post-fire seral stages if their specific requirements are not met (Whelan 1995).

Food-supplemented *Mus domesticus* populations have traditionally responded to increased food availability with increased abundance, lengthened breeding seasons and increased female breeding intensity (DeLong 1970; Newsome 1970; Bomford 1987b; Bomford and Redhead 1987; Boutin 1990). The findings of Newsome (1970), however, must be treated with caution as he had only one control site with which to compare his treatment sites, and the low *M. domesticus* abundance in the control plot could therefore have been location-specific (Bomford 1987b). Bomford and Redhead (1987) further considered litter size, but found no change in response to increased food availability, although supplementary casein (milk protein) in the diet did increase mean litter size from 3.4 to 4.9 (Bomford 1987c). Behavioural responses to food addition, such as changes in home range size and overlap, social structure and territoriality, have not been considered for this species (Boutin 1990).

Prior to these studies, however, Newsome (1969a, b) had determined that population size was limited primarily by the availability of suitable soil for burrowing, and only secondarily by food supply. Further study showed that populations peaked in density on sites where burrowing conditions were good and food was supplemented, but fell when the soil became too water-logged or dry to burrow in, despite additional food being available (Newsome 1970). In high density populations limited by burrowing conditions, Newsome (1970) measured a decrease in the proportion of young adults breeding, and an increase in agonistic behaviour (evidenced by tail scarring and wounds), and suggested that a dominance hierarchy existed within the populations that acted to slow breeding and promote dispersal by fighting.

The sites where *M. domesticus* were most abundant during this study were characterised by the presence of patches of bare sandy soil. As abundance was not related to the presence of the artificial nest-boxes, it may be that bare ground provided suitable burrowing conditions. This would suggest that, in accordance with Newsome (1969a, b,
1970), nest site availability limited the *M. domesticus* populations. Similarly, Chapman (1981) found evidence that shelter limited *M. domesticus* abundance more than food availability at high population densities. The fact that these populations occurred only in the presence of supplementary food in conjunction with bare ground, suggests further that both resources are potentially limiting, although the failure of *M. domesticus* populations to establish in food supplementation sites without expanses of bare ground, indicates that, in agreement with Newsome (1969a, b, 1970), availability of appropriate burrowing conditions is the primary limiting factor of *M. domesticus*; food is only limiting secondarily.

### 8.4.2 Effect of Interspecific Interactions on *Mus domesticus* Populations After Fire

#### 8.4.2.1 Predation

Differential predation pressure could have potentially excluded *M. domesticus* from some sites. Although it may be expected that predation by large terrestrial or aerial predators would have an equally detrimental effect on all small mammal species present in an area, similar resource requirements between species do not mean that habitat use is also similar. Behavioural traits may increase predation-risk of one species over another in the same environment. Predation-risk has been shown to affect micro-habitat and habitat selection (see Quennette 1990 for review; Kotler *et al.* 1993; Brown *et al.* 1994), timing of activity periods (e.g., Werner *et al.* 1983, Main 1987), length of residency in a patch (Brown *et al.* 1988), and reproductive behaviour (see Ylonen 1994 for review). Different species may respond differently to a perceived, or real, predation-risk, thus making one species more susceptible to predation than another (Brown *et al.* 1994). Particularly in a habitat recently altered by a disturbance such as fire, the ability of a species to alter its behaviour in response to changed predation-risk may lead to differential predation pressure between prey species. *M. domesticus* is able to distinguish the odours of different predators and to shift its use of habitat to reduce risk of predation accordingly (Dickman 1992).

Incidental observations of foot prints and scats indicated that the terrestrial predators, cats, *Felis catus*, and foxes, *Vulpes vulpes*, were present at some sites during some periods. However, continued presence was not noted at any site. Avian and reptilian predators, however, are highly mobile and/or cryptic, and often nocturnal, and their effect
upon small mammal abundance is difficult to gauge. Boutin et al. (1986) stressed that the small spatial scale of mammalian food supplementation studies makes it easy for predators to swamp a site, resulting in artificially high predation rates, but this is rarely factored into studies of resource limitation. It was recommended that future supplementation studies should incorporate both food and predation in a two-factor design, so that the interaction effects could be examined (Boutin 1990). Although desirable, incorporation of the effects of predators was not possible in the present study.

Predation has often been considered to increase after fire, resulting in a decline or a delayed recovery of small mammal populations. Newsome et al. (1983) demonstrated that predation upon small mammals by dingoes, *Canis lupus dingo*, after fire was disproportionately high in relation to prey availability. This they attributed to “fire-opened” habitats increasing the availability and vulnerability of prey, potentially leading to predation retarding the post-fire recovery of some small mammal populations.

The predators of *M. domesticus* may not be limited to large mammalian or avian species and reptiles, but potentially include carnivorous small mammals such as the dasyurid, *A. stuartii*. Although predominantly insectivorous (Fletcher 1977; Hall 1980; Dickman 1982; Dickman et al. 1983; Green 1988), *A. stuartii* does consume some vertebrates in the wild (Green 1988), and has been recorded to kill and eat *M. domesticus* in captivity (C. R. Dickman pers. comm). As *A. stuartii* was present at all sites (Chapters 5 and 7), there is a possibility that some predation did occur, although it was unlikely to have been at a rate that could alter population abundance. Correlations and analysis of spatial interactions did not demonstrate a negative relationship between the two species, although sample size of *M. domesticus* was very small in comparison to *A. stuartii*, so relationships are hard to distinguish.

### 8.4.2.2 Competition

It is more likely that, if any interspecific interaction suppresses *M. domesticus* abundance and population establishment, it is competition. *R. fuscipes* is a much larger animal than *M. domesticus*, with broad dietary and habitat preferences (refer to Section 6.1). Similarly to *M. domesticus*, *R. fuscipes* is terrestrial and nests in burrows under
ground and in leaf litter (Newsome 1983; Dickman 1991). There is the potential for *R. fuscipes* to be dominant over *M. domesticus* if competing for the same resources, although *M. domesticus* is renowned for occupying unfilled niches rather than competing with native species (Fox 1983). Further, the abundance of these two species was not correlated or associated spatially during this study.

*Antechinus stuartii* is scansorial, foraging extensively on the ground as well as in trees. In the absence of *Antechinus* spp., Braithwaite *et al.* (1978) suggested that *M. domesticus* may occupy an insectivorous food niche, although it is usually regarded as an omnivore or generalist granivore (Fox 1983). Thus the presence of *A. stuartii* in a habitat may exclude colonising *M. domesticus* if there are no other available niches for it to occupy. This could occur in Ku-ring-gai as *R. fuscipes* is already occupying the generalist herbivore niche, and seeds could potentially be in short supply due to an abundance of ants (Chapter 3; Braithwaite *et al.* 1978) and granivorous birds (Braithwaite *et al.* 1978). As with predation, confirmation of any competitive interactions would be obtained best from manipulative experiments.

### 8.4.3 Conclusions

The colonisation and establishment of *M. domesticus* populations after fire appears to be dependent primarily upon suitable burrowing conditions being available. At Ku-ring-gai Chase National Park this was provided in some sites by expanses of bare sandy soil. In addition to burrowing sites, however, a source of food was also required for populations to be maintained over time. It is possible that competition from *R. fuscipes*, a generalist herbivore, *A. stuartii*, an insectivore, and large numbers of potentially granivorous Formicidae (Chapter 3), did not allow *M. domesticus* populations access to natural food sources. However, food supplementation provided an additional food source that was available to this species, and when this resource was available in conjunction with suitable nest sites, populations were able to establish.
CHAPTER 9: POPULATION RESPONSES OF *Cercartetus nanus* TO RESOURCE AVAILABILITY AFTER FIRE

9.1 INTRODUCTION

The eastern pygmy possum, *Cercartetus nanus*, is a small (< 45 g), arboreal marsupial, distributed in Tasmania and along the south-eastern coast of Australia (Figure 9.1). It is found in a range of habitats including coastal heath, woodland, open and closed forest, temperate rainforest and sub-alpine forest (Bladon 1995; Turner and Ward 1995). *C. nanus* feeds on nectar, pollen, soft fruit and invertebrates (Turner 1984; Huang *et al.* 1987; Dickman and Happold 1988; Carthew 1994), and nests in small tree hollows, abandoned bird-nests and occasionally spherical nests constructed from shredded bark, or fresh leaves (Turner 1984; Ward 1990; Bladon 1995). Turner (1984) and Ward (1990) regarded *C. nanus* as predominantly solitary, however Bladon (1995) reported that 42% of all nests were shared, and although roughly half of these represented mother-young associations, the other groupings consisted of all combinations of sex and age groups. In particular, about a quarter of all communal nesting groups consisted entirely of males, and coincided with the summer breeding season. Bladon (1995) suggested that this may indicate a lek breeding system, as proposed for *Antechinus stuartii* by Lazenby-Cohen and Cockburn (1988; refer to Chapter 7).

In temperate climatic regions, reproduction may occur at any time of the year if conditions are favourable, although most births occur between late spring and early autumn (Ward 1990). Breeding is restricted to late winter and spring in colder regions such as Tasmania (Green 1973). Usually four young are born, and they are suckled in the pouch for about 30 days. After this they remain in a nest until weaning at 65 days of age (Ward 1990). Adult females usually produce two or three litters per season and, as juveniles reach maturity at approximately 5 months, this species has a high reproductive potential (Ward 1990; Turner and Ward 1995).
Figure 9.1: The eastern pygmy possum, *Cercartetus nanus* (a), and distribution within Australia (b) (from Strahan 1995). Photo: Kathy Atkinson/Nature focus.
Until quite recently, little was known of the ecology of *C. nanus*. This may be attributable to its low trappability, or its low abundance and disjunct distribution throughout its range (Dickman and Happold 1988). Although, largely arboreal, *C. nanus* does exhibit some terrestrial movements as shown by captures in Elliott and pitfall traps on the ground (Recher *et al.* 1975; Dickman and Happold 1988; Wilson *et al.* 1990; D. Andrew pers. comm.; pers. obs.), spool and line tracking (Carthew 1994) and radio-tracking (Bladon 1995).

The response of *C. nanus* to fire is largely unknown, although some researchers have encountered *C. nanus* in post-fire habitat. Although not recorded in unburnt forest, Recher *et al.* (1975) recorded *C. nanus* soon after a forest fire in southern NSW, and trapping success declined as vegetation regrew. This they attributed to *C. nanus* changing its habitat use from being predominantly arboreal, to being terrestrial during the period when most of the above ground vegetation had been removed. Similarly, Lunney and Barker (1986) recorded *C. nanus* only in sites that had been logged and burnt, and on cleared farmland. However, Bladon (1995) demonstrated that clearing had severe deleterious effects on a *C. nanus* population; Wilson *et al.* (1990) found *C. nanus* to be present both before and after a fire, although trends in abundance could not be distinguished due to an extremely low sample size. Little is known about the habitat requirements of this species, but Catling (1991) considered *C. nanus* to be disadvantaged by the simplification of forest structure caused by frequent, low intensity fires, and advantaged by the enhanced forest complexity caused by occasional, high intensity bushfires. Bladon (1995) further considered a continuous tree canopy to be an important habitat component for *C. nanus*, as it provides shelter during movements, nesting material and food.

### 9.1.1 AIMS

The study presented in this chapter aims to determine the population responses of the eastern pygmy possum, *Cercartetus nanus*, to resource availability after fire. Food and nest site availability were manipulated to establish if either or both of these factors affected the population dynamics of *C. nanus* in a post-fire environment.
9.2 METHODS

9.2.1 EXPERIMENTAL DESIGN AND DATA COLLECTION

The effect of post-fire resource availability on *C. namus* population dynamics, structure, stability and reproductive behaviour was investigated. As no individuals were captured in unburnt sites, comparisons could not be drawn between populations in burnt and unburnt forest. The effect of resource availability on post-fire populations of *C. namus*, however, could be determined by manipulation of food and nest site availability, and by associating *C. namus* abundance with the availability of natural resources.

The experimental design of this aspect of the study is presented in Section 5.2, and data collection and data analysis techniques are outlined in Section 6.2.

9.3 RESULTS

9.3.1 POPULATION DYNAMICS IN BURNT SITES

9.3.1.1 ABUNDANCE

Nineteen *C. namus* were captured during this study. The first were captured in February 1995, 13 months after the fire, and a month after resource supplementation began. No individuals were recorded during the following two trapping periods, although from November 1995, populations persisted in the burnt areas until the end of the study.

Most captures were restricted to food supplementation sites (Figure 9.2a, c) although, as indicated by the large standard errors, captures between sites within treatments were highly variable. The combined food and nest treatment had the highest number of individuals, with abundance increasing steadily until the last trapping session of the study (Figure 9.2a). The high variance evident in Figure 9.2a is a reflection of only two of the three replicates within this treatment having more than one capture. Whereas Site 1 recorded one male in November 1995, sites 4 and 12 recorded 4 and 6 individuals respectively, not including pouch young (refer to section 9.3.1.4). The only other site with comparable numbers of *C. namus* was Site 3, a food supplementation site. Site 3 recorded 5 individuals, although the 2 other sites within the treatment recorded only 1 other capture between them. The highest number of *C. namus* recorded from a single site within a trapping period was 2 adult males, 2 adult females and a juvenile female caught at Site 12.
(food and nest supplementation), during November 1996. This trapping period coincided with a localised blooming of *Angophora hispida*.

![Figure 9.2: *Cercartetus nanus* KTBA in food and nest (a), nest (b), food (c), and control (d) treatment sites. Arrow indicates beginning of food and nest supplementation. Means are shown ± standard error. Dotted lines indicate assumed trajectory as no data are available for August 1996. Trapping period is indicated on the x axis: a94 = August 1994, f95 = February 1995, etc.](image)

Although a two-way ANOVA on the total number of individuals recorded at each site over the entire supplementation period, averaged over the number of post-supplementation trapping sessions (Spiller and Schoener 1998), indicated that food had a significant effect on *C. nanus* abundance (Table 9.1a), the small sample sizes suggest that this result should be accepted with some caution. The patterns of distribution and abundance shown above (Figure 9.2) indicate that factors other than food and nest availability influenced *C. nanus* populations after fire. This is supported by a two-way repeated measures ANOVA (Table 9.1b), demonstrating that over the duration of the study, neither the food, nest nor the combined food and nest treatments had a significant effect on *C. nanus* abundance. These results must again be treated with caution, however, as although the data met the assumption of equality of variances, the sparse data were not normally distributed and transformation did not rectify this problem. In addition, the power
of these analyses was low (food*time $\beta = 0.140$, nest*time $\beta = 0.118$, food*nest*time $\beta = 0.363$, $\alpha = 0.05$), indicating that without a considerable increase in sample size, this experiment would not have been able to detect any treatment effects over the large inherent temporal and site variability.

Table 9.1: Two-way ANOVA (a), and two-way repeated measures ANOVA (b), of abundance of *Cercartetus nanus* (KTBA) between treatments.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>a)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>food</td>
<td>1</td>
<td>5.488</td>
<td>0.047</td>
</tr>
<tr>
<td>nest</td>
<td>1</td>
<td>0.220</td>
<td>0.652</td>
</tr>
<tr>
<td>food*nest</td>
<td>1</td>
<td>1.195</td>
<td>0.306</td>
</tr>
<tr>
<td>error</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>time</td>
<td>7</td>
<td>9.774</td>
<td>0.875</td>
</tr>
<tr>
<td>food*time</td>
<td>7</td>
<td>0.620</td>
<td>0.728</td>
</tr>
<tr>
<td>nest*time</td>
<td>7</td>
<td>0.485</td>
<td>0.820</td>
</tr>
<tr>
<td>food<em>nest</em>time</td>
<td>7</td>
<td>0.916</td>
<td>0.500</td>
</tr>
<tr>
<td>error</td>
<td>64</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

9.3.1.2 BODY CONDITION

Individuals in sites with food and nest addition were in significantly better body condition than those in control or food only sites ($F = 28.340$, df$_{1.5}$, $p = 0.003$; Figure 9.3). However, this finding is confounded as all *C. nanus* associated with nest supplementation were in combined food and nest supplementation sites, and a two-way ANOVA to test for treatment interaction effects was not possible due to no captures in sites with nest only supplementation. There was no significant difference in the body condition of *C. nanus* between sites receiving and not receiving food ($F = 2.069$, df$_{1.5}$, $p = 0.210$; Figure 9.3), although this result must also be treated with caution as only 2 individuals were captured outside the food supplementation sites.
Figure 9.3: Body condition index of adult *Cercartetus nanus* between treatment sites; males and females combined. Means are shown + standard error. fn = food and nest, f = food, and c = control sites. No individuals were captured in nest supplemented sites.

Female *C. nanus* were in significantly better condition than males across all sites (F = 4.702, df1,14, p = 0.048; Figure 9.4).

Figure 9.4: Body condition index of adult female and male *Cercartetus nanus* across all sites. Means are shown + standard error.

### 9.3.1.3 POPULATION STRUCTURE

There were 9 adult males, 9 adult females and 1 juvenile female *C. nanus* caught during this study. One female had four pouch young of unknown sex. The sample size was not great enough to determine if any differences in population structure occurred between sites or treatments.

Individuals were highly transient, with no permanent residents and only one resident (adult female) recorded throughout the study.
9.3.1.4 REPRODUCTIVE RESPONSES

A female with four pouch young was recorded in mid November (late spring) 1995, and a recently independent juvenile female (5 g) captured in mid November 1996. Both animals were caught in food and nest supplementation sites. No other reproductive activity was noted during the study.

9.3.2 POPULATION RESPONSES TO NATURAL RESOURCE AVAILABILITY

The availability of natural resources was measured in terms of ground cover, vegetative cover and other habitat components. The principal components (PC) identified are explained in Section 6.3.3. Multiple linear regressions of *C. nanus* abundance against the PCs obtained from resource measurements from the year of capture were used to identify any relationships.

9.3.2.1 GROUND COVER

In May 1996, there was a significant positive association between *C. nanus* abundance and PC1 \( y = 0.3 (\pm 0.244 \text{ SE}) + 0.348 \text{ PC1 (}\pm 0.147 \text{ SE})x; R^2 = 0.510, \text{ df}_{1,8}, F = 8.320, p = 0.020 \), a principal component explained largely by the presence of bare ground and live wood. However, there were no relationships between *C. nanus* and any other ground cover component at other times during the study, as indicated by either linear regression or pairwise correlations.

9.3.2.2 VEGETATIVE COVER

There were no linear or correlative relationships between *C. nanus* abundance and vegetative cover in any year.

9.3.2.3 HABITAT COMPONENTS

The microhabitat components of rock, trees, tree hollows and logs were measured at the end of the study and assumed not to have changed throughout the study period. Although some trees would have invariably become logs during this period, principal components analysis grouped these two factors together under PC1, thus grouping them together for the purpose of further analysis. *C. nanus* was not significantly related to any microhabitat principal component.
9.3.3 Summary of Results

The low capture rate of *C. nanus* made it difficult to identify any consistent trends in post-fire abundance or demography of this species. The first *C. nanus* were captured in February 1995, 13 months after the fire and one month after resource supplementation began. Although most animals were captured in food, or food and nest supplementation sites, and there was a significant food effect when trapping session were averaged, the high within-treatment variability meant that neither treatment had a significant effect overall on *C. nanus* abundance when considered over the total duration of the study.

The first post-fire reproduction appeared to occur in spring 1995, followed by a second reproductive season at the same time in 1996. There was no evidence of reproductive activity during any other period. Populations were also highly transient, and even in sites where *C. nanus* was captured consistently in most trapping periods, no recaptures between periods were noted. One female was recaptured on a subsequent night within a trapping period, but was not recorded again.

No consistent patterns of association with ground cover, vegetative or habitat features were noted, although in May 1996 *C. nanus* abundance was associated positively with bare ground. During this trapping period, 4 animals were caught across all sites, 3 of which occurred at Site 3; a site with relatively high scores for bare ground (Section 8.3.2.1). As the relationship does not hold for other trapping periods and the sample size was very low, the association may simply be a chance one. It is probable that other environmental factors, such as flowering of food species, influence the local abundance and/or trappability of this species.

9.4 Discussion

9.4.1 Effect of Resource Availability on *Cercartetus nanus* Populations After Fire

The response of *Cercartetus nanus* to fire is poorly understood, and patterns of post-fire recolonisation have been derived largely from incidental captures in post-fire habitats. After fire, *C. nanus* has usually been recorded in the early post-fire seral stages. Recher *et al.* (1975) recorded *C. nanus* "soon after" fire, whereas Wilson *et al.* (1990)
reported *C. namus* one year after fire in a swamp/heathland complex, and Dickman and Happold (1988) first captured *C. namus* 2 years after fire in open forest. In addition, Bamford (1985, 1986) recorded the closely related *Cercartetus concinnus* as disappearing from *Banksia* woodland immediately after a fire, but reappearing 3 years later. In the present study, *C. namus* became established, and was reproducing in the second and third years after fire. These findings support Catling's (1991) belief that *C. namus* would be advantaged by the increased forest complexity caused by occasional high intensity fires.

Recher *et al.* (1975) reported that *C. namus* was captured for the first time in their forest plots "soon after" a fire. They considered that, although *C. namus* must have been present prior to the fire, its largely arboreal habits meant that it was not captured in the traps that they were using on the ground. With fire removing most of the foliage from above ground strata, however, *C. namus* was forced to forage and move along the ground where the traps were located. Progressively less captures were recorded as the vegetation re-established, indicating further that *C. namus* increased its arboreal activity as vegetation regrew (Recher *et al.* 1975). However, in the present study, *C. namus* was captured for the first time 13 months after the fire, but became regularly trappable only after almost 2 years after the fire. If the habitat shift, proposed by Recher *et al.* (1975), had occurred, it would be expected that the highest numbers would have been recorded earlier, rather than later in the study; terrestrial activity would have been highest when the least vegetative cover was available.

Captures of *C. namus* in this study appeared to be associated closely with the flowering of food trees. *C. namus* is primarily a pollen and seed eater, although at times has a large proportion of insects in its diet (Huang *et al.* 1987). Many plant species in Ku-ring-gai Chase National Park had irregular and localised blooming episodes throughout the study period and, although no quantitative measurements of flowering plants were made during trapping sessions, field notes show a qualitative correlation between captures and the presence of flowers. Although *C. namus* was also caught at times when there was no apparent flowering of the common *Eucalyptus* spp., *Angophora* spp. or *Banksia* spp., the occasions when several individuals were captured within a site during one trapping session
corresponded to local blooming episodes. For example, five *C. nanus* were captured when *Angophora hispida* was flowering at Site 12 during November 1996.

*Angophora hispida* is a small tree with large leaves providing dense cover from ground level to a maximum height of 2-3 m (Baker *et al.* 1986). Inflorescences occur in clumps at all heights over the tree, and as such, foraging *C. nanus* may be attracted down to flowers near ground level, making them susceptible to capture by the traps placed nearby. Although *C. nanus* is reported as being partially terrestrial (Recher *et al.* 1975; Dickman and Happold 1988; Wilson *et al.* 1990; Cartew 1994; Bladon 1995), the dense cover provided by the ground level foliage of *A. hispida*, along with the prolific food source provided by the flowers, may increase terrestrial activity. This could lead to an increase in the probability of capture around flowering *A. hispida* and, therefore, a distortion of abundance estimates within the site. Dickman and Happold (1988) also found that the majority of captures of *C. nanus* after fire were in traps placed at the bases of trees with prolific epicormic shoots. Thus it is difficult to reliably compare the abundance, or patterns, of post-fire colonisation between treatments, as trapping records may not be representative of the population present at the site.

Familiarity with the supplementary food may also have increased the trappability of *C. nanus* at some food supplementation sites. At Site 12, 5 of the 6 *C. nanus* captured during the study occurred at traps near food stations. It may be that at sites where *C. nanus* was already conditioned into coming to ground level to feed on the food supplement, they were more likely to have come to ground level to feed on flowers when the opportunity arose. This could explain the high capture rate of *C. nanus* during the *A. hispida* flowering episode at Site 12. However, details of flowering episodes at other sites with multiple *C. nanus* captures were not accurate enough to determine if a similar pattern was occurring elsewhere. Further, as food supplement was also being provided at between 1.5 and 2 m on the same trees, it is unclear if food supplement at ground level would encourage *C. nanus* to alter its usual foraging patterns.
9.4.2 Habitat preferences of *Cercartetus nanus*

During this study, *C. nanus* was caught only in burnt sites. Similarly, Lunney and Barker (1986) recorded this species only in sites that had been logged and burnt, or cleared. This may indicate a preference for disturbed habitats. However, Bladon (1995) demonstrated, on the contrary, that populations were reduced severely by land clearing. As Lunney and Barker (1986) did not actively trap for *C. nanus*, but detected their presence by the occurrence of *C. nanus* hairs in predator scats and by an individual killed on a road, and Bladon (1995) used a combination of Elliott trapping and nest-box visitation to measure her populations, it is likely that the latter study is more reliable.

*Cercartetus nanus* in Ku-ring-gai Chase were probably captured only in burnt sites due to a combination of two factors. Firstly, reduced food and cover resources after fire may have led to a habitat shift, as suggested by Recher *et al.* (1975), to expand the range of resources available to *C. nanus*. Secondly, unburnt sites rarely provided inflorescences of *Angophora* spp., *Eucalyptus* spp. or *Banksia* spp. near ground level as epicormic or rhizomal regrowth was not present. If most terrestrial activity was in response to feeding opportunities there would have been little incentive to move on or near the ground in unburnt habitats.

Bladon (1995) asserted that continuous canopy cover is an important habitat component for *C. nanus* as it provides shelter, nesting material and food. However, a continuous canopy was not present in any of the sites where *C. nanus* were recorded during this study, and was unlikely to have occurred in the study sites of Dickman and Hapgood (1988), Bamford (1985, 1986), or Wilson *et al.* (1990), who all recorded *Cercartetus* spp. in the years following fire. *C. nanus* was not associated consistently with any particular level of ground or vegetative cover, or other habitat variables during this study. The only significant association was between *C. nanus* abundance and the presence of bare ground during May 1996, although the low sample size suggests that this relationship is questionable. Thus, the habitat requirements of *C. nanus* were not clarified by this study except to determine that a dense canopy is not an essential requirement for this species as implied by Bladon (1995), although highest population densities may be reached under such conditions.
9.4.3 CONCLUSIONS

Captures of *C. nanus* were sparse and probably not representative of the populations present at the sites during this study, making it difficult to draw reliable conclusions. However, highest capture rates occurred when local food trees, with inflorescences close to the ground, were blooming. Blooming episodes occurred sporadically and in localised patches across the sites, and likewise, the recorded distribution of *C. nanus* was patchy. *C. nanus* was recorded in greatest numbers at sites provided with supplementary food. It is possible that animals conditioned to utilise the supplementary food at ground level were also more likely to use natural food sources close to the ground when they were available, and were therefore more susceptible to capture during these periods.
CHAPTER 10: GENERAL DISCUSSION

10.1 INDIVIDUAL, POPULATION AND COMMUNITY RESPONSES OF SMALL MAMMALS TO FIRE

An important outcome of this study is the recognition that many of the generalisations reiterated by previous studies appear to be specific findings relevant to particular habitats, species and community assemblages. Trends of post-fire survival and population growth may differ between populations of the same species, even within comparable habitats, as a result of a variety of factors. Most importantly, post-fire resource availability, in the form of food and nest-sites, appears to have little overall effect on the recovery of small mammal populations after fire. Resource supplementation during the second and third years after fire had variable effects on the abundance and population parameters of small mammals in Ku-ring-gai Chase. Although food supplementation had a significant effect upon Antechinus stuartii abundance, for example, this was due to a strongly positive response during the first year of supplementation and a negative response during the following year. Likewise, Mus domesticus apparently responded to a combination of food and nest availability, although nesting requirements were met by the natural availability of bare ground to burrow in, not the nest boxes provided. However, given the overall differences in response to fire of the species present in Ku-ring-gai Chase National Park to populations of the same species elsewhere in eastern Australia, intrinsic variability between locations may have resulted in food and nest supplementation having different effects at Ku-ring gai Chase than may have been the case elsewhere.

10.1.1 FIRE REGIME AS A DETERMINANT OF RESPONSES OF SMALL MAMMALS TO FIRE

In the present study, fire frequency, as an aspect of fire regime, was studied in respect to its effect upon the vegetation and fauna. With increasing fire frequency, there was an increase in the number of shrubs and herbs, and a trend towards less trees. However, fire frequency, and its effect upon vegetative habitat components, did not have an overall effect upon the abundance and ordinal richness of invertebrates. Trends of abundance within Orders appeared to be dependent upon factors in addition to, or perhaps rather than, fire frequency, although analysis at a finer level of classification is required to
confirm this. Similarly, the small mammal species *Rattus fuscipes* and *A. stuartii* showed differing responses to fire frequency. *A. stuartii* increased in abundance in response to increasing fire frequency to reach a maximum abundance in 3-fire sites, although abundance declined dramatically in 4-fire sites. *R. fuscipes*, on the other hand, was present in similar numbers in sites across all fire frequencies two years after the most recent fire, although by three years after fire demonstrated highest abundances in sites with the most frequent fire regime. Small mammal abundance in this study appeared to follow the broad vegetation characteristics resulting from differing fire frequency histories, although these tendencies need to be confirmed by more detailed study (Section 3.4.3).

Despite basing a study within a particular habitat and vegetation type, it is difficult to account for possible variation in historical impacts upon that area. Landscape variability may not be apparent upon visual inspection of prospective sites. With particular regard to the effects of fire, the frequency, intensity, season, extent, patchiness and rate of spread of all fires to have passed over an area may have influenced the biota of the site (see Whelan 1995 for review). This information is usually unknown, and if records are available they are often incomplete. For example, although the date and extent of a fire may be known, the intensity, patchiness and rate of spread are usually not recorded unless specialist personnel and equipment are available. Although the accuracy of record keeping has improved over time, particularly with the introduction of computerised mapping techniques in recent years, few fire records are available prior to the 1950’s for most areas of Australia.

This creates problems with the experimental design of many ecological studies, whether or not the aim is to consider fire effects. There may be biotic effects of fire that are not evident during macrohabitat assessment during the site selection process. Although two areas of forest may appear similar in floristic composition, forest structure and topography, differences in fire history may lead to fundamental differences in resource availability between them. This creates further problems when trying to compare studies from apparently similar habitat types containing similar species assemblages. Fire regime has rarely been considered in Australian ecological, even fire ecology, studies (Whelan 1995). The time since the most recent fire is often the only effect considered (Whelan 1995).
10.1.2 RESPONSES OF INDIVIDUAL SMALL MAMMALS TO FIRE

The recovery of small mammal populations after fire is dependent upon the survival and subsequent reproduction of individuals present during the fire, and the immigration of animals from unburnt areas into the burnt habitat. Thus, determining the mortality of individuals during fire is necessary to establish the potential of a population to recuperate after a fire. It has often been considered that high rates of mortality immediately follow fire, either directly through the effects of flames, heat and smoke, or indirectly due to reduced food and increased risk of predation as a result of reduction in cover (Newsome et al. 1975; Bates 1980; Whelan 1995). The decline in abundance of some small mammal species after fire has often been attributed to mortality (e.g., Newsome et al. 1975; Fox 1982), sometimes supported by records of large numbers of animal carcasses in post-fire habitat (Chew et al. 1959; Newsome et al. 1975). However, no studies have been able to isolate mortality from emigration and behavioural changes that may lead to altered trappability, and thus determine the proportion of the population killed by fire.

Radio-tracking *R. fuscipes* and *A. stuartii* individuals through a low intensity prescribed burn during the present study determined that mortality is low in this type of fire. Further, as animals were recorded to move through burnt areas after the fire, when unburnt resources were available within their ranges, burnt areas were clearly still able to provide some resources to these animals. Although this study was of a low intensity and patchy fire, and as such more refuge would have been available to the animals than would be provided after a high intensity summer bushfire, it gives valuable insight into the response of individual animals to fire events. Further, it contradicts the common belief that small mammal populations are necessarily decimated by fire, and that small mammal population recovery must be determined largely by the recolonisation of burnt areas as vegetation regrowth provides necessary resources.

10.1.3 RESPONSES OF SMALL MAMMAL COMMUNITIES TO FIRE

Given that small mammals often survive fire, this study has determined that at least some individuals that survive are able to reproduce successfully within the first year after fire, and continue to rebuild population levels during the years subsequent to fire. This finding questions the generality of the habitat facilitation model of succession after fire
proposed by Fox (1981, 1982, 1983, 1990) and Fox and McKay (1981) from small mammals in heath and eucalypt forest in coastal NSW. Fox (1981, 1982, 1983, 1990) and Fox and McKay (1981) suggested that small mammals are able to colonise an area, after fire, when the local and physical conditions first meet each species’ specific habitat requirements. As the conditions change with vegetation regrowth, the habitat changes away from the optimal conditions for the species and it may either leave the community, or remain present at reduced population levels. This leads to a (secondary) succession of small mammals species occupying a site in response to a (primary) succession of vegetation regrowth (Fox and McKay 1981; Fox 1982).

Small mammal post-fire successional models suggest that, within the regional species pool of small mammals, different species are specialised to occupy different post-fire stages (Fox and McKay 1981). Species preferring open habitats will thrive in the early post-fire successional stages, and as the vegetation becomes denser, mid-successional species will dominate, followed by late-successional species returning to an area only after several years of post-fire vegetation regeneration (Fox and McKay 1981). In a eucalypt forest small mammal community of similar composition to that in Ku-ring-gai Chase National Park, Fox and McKay (1981) identified a successional community dominated by the rodents *M. domesticus*, *Pseudomys novaehollandiae* and *P. gracilicaudatus* in the years immediately following fire, followed by a decline in these species as the dasyurids *A. stuartii* and *Sminthopsis murina* increased, followed by a decline in dasyurids and an increase in *R. fuscipes* in the late successional period. Fox (1983) suggested that the pattern of succession resulted from ecologically dominant species replacing those that were no longer in their preferred habitat, and was expressed as the pattern of changes in the relative abundance of the species over time. He suggested that species re-entered the post-fire communities only when the vegetative regrowth provided that species’ resource requirements (Fox and McKay 1981; Fox 1982, 1983).

However, the pattern of succession described by Fox and McKay (1981) was quite different to the one found in the Ku-ring-gai Chase community (Chapter 5). The dominant species throughout the present study were *R. fuscipes* and *A. stuartii*. Although both these species were more abundant in unburnt forest than in burnt forest at all stages throughout
the study period, within burnt sites they were still more abundant than any other species in the community. The relative abundance of *R. fusipes* increased slightly over the study period, whereas that of *A. stuartii* declined between the first and last year. If either *R. fusipes* or *A. stuartii* were restricted to mid- to late-successional stages by certain habitat and resource requirements, as suggested by Fox and McKay (1981), they should not have survived, nor have maintained breeding populations, as they did in Ku-ring-gai Chase.

Similarly, *M. domesticus* has often been recorded soon after fire; often in plague densities (e.g., Christensen and Kimber 1975; Newsome *et al.* 1975; Catling 1986; Fox 1982, 1983, 1990). Unlike many previous studies, however, *M. domesticus* was not captured in Ku-ring-gai Chase until the second year after fire, and remained in low densities throughout the study. The absence of ecologically similar *Pseudomys* spp. at Ku-ring gai Chase may have been expected to open a niche for this opportunistic species. However, as previous studies have demonstrated that *M. domesticus* can co-exist with *Pseudomys* spp, although not with *A. stuartii* or *R. fusipes* (Fox 1981, 1982, 1983, 1990), *M. domesticus* may have been largely excluded from Ku-ring-gai Chase by the high abundance of species that in previous studies have been absent or in low abundance during the early-seral post-fire stages. Analyses to determine any negative association between *M. domesticus*, *A. stuartii* and *R. fusipes* were, however, not significant, although the power of the analyses was restricted by the low capture rate and limited range of *M. domesticus* in only a subset of the trapping grids.

I suggest that within habitat types, the same species may occupy different regeneration niches dependent primarily upon interspecific interactions, rather than habitat facilitation as described for mammals by Fox (1982). Whilst it has been demonstrated by correlation that small mammal species respond to the changing local and physical conditions after fire (e.g., Christensen and Kimber 1995; Fox 1981, 1982; Catling *et al.* 1981; Wilson *et al.* 1990), and species undoubtedly have certain resource requirements that must be met in order to survive and successfully reproduce, the mechanism that drives post-fire succession would appear to be competition.
Species that are largely opportunistic or generalist in their habitat requirements may compete with other species for resources, and success may be determined predominantly by abundance (biomass) or body-size effects. A large individual often has competitive dominance over smaller individuals of the same or other species (Dickman et al. 1991; Thompson and Fox 1993), although large populations of smaller individuals may out compete larger interspecific competitors by sheer numbers (Fox and Gullick 1989). Although some species may have habitat requirements met only at specific post-fire stages, these species are likely to be the exception rather than the rule. Thus, patterns of post-fire succession will be dependent largely upon the regional species pool.

10.1.4 Responses of small mammal populations to fire

This study has recognised that the composition of small mammal communities may govern the response patterns of individual species to fire-altered habitat. Interspecific competition for resources is likely to determine the success of populations in the post-fire environment. It would be expected that fire would reduce the availability of food, shelter and nesting requirements. Consequently, the post-fire recovery of small mammal populations after fire has often been suggested to be associated with the regeneration of vegetation, and corresponding increases in food and cover resources (e.g., Recher and Christensen 1981; Catling 1991; Masters 1993; see Section 1.2).

Food availability has been demonstrated to limit population abundance of several species of small mammals (see Boutin 1990 for review). Boutin (1990) concluded that for the majority of species studied, increased food availability led to increased reproduction and fecundity, and increased body weight and growth. As such, food supplementation generally leads to increased population density and rate of population growth, with populations more likely to respond to food supplementation when environmental conditions are poor, than when they are good (Boutin 1990). Food availability may be correlated to vegetation cover in the case of herbivorous, granivorous, frugivorous or nectivorous species; and also insectivorous species requiring vegetation and/or leaf litter to sustain arthropod abundance. Cover availability may also affect predation vulnerability and the availability of suitable nesting material or nesting sites. Given that resource availability has been demonstrated to be limiting to species in undisturbed habitats (e.g., Cole and Batzli 1978; Mares et al. 1976;
Taitt 1981; Taitt and Krebs 1981; Predavec 1994), it would be expected that after fire
limitation by both food and cover must be even greater. Thus the provision of food and
nesting resources would be expected to result in increases in population size, survival,
reproduction and body-condition parameters in a post-fire environment.

However, resource supplementation after fire in Ku-ring-gai Chase National Park
did not greatly alter the population parameters of any of the four most common small
mammal species (Chapters 6 - 9). The abundance of *M. domesticus* and *C. namus* was not
significantly affected by food supplementation over the duration of the study, although
captures of each species were related to either natural or supplementary food resources in
some situations. *M. domesticus* responded to food supplementation, but apparently only
when in conjunction with suitable burrowing conditions, and *C. namus* was recorded most
often in response to localised blooming events of food trees. *A. stuartii* had a significant
response to food supplementation over the duration of the study, although this result was
confounded by apparently opposite effects in different years.

Further, in most cases, body condition, population structure and stability, individual
longevity and reproduction were not affected by either food or nest supplementation over
the study period, although some seasonal effects were noted. During the first winter after
supplementation began the body condition of *R. fuscipes* was higher in food
supplementation sites than other sites. In addition, there was a higher recruitment of
juvenile *R. fuscipes* into the population during the summer following the commencement of
supplementation. Similarly, male *A. stuartii* tended to disperse less, leading to increased
longevity of males in food supplementation sites. Most effects were recorded during the
first year of supplementation and declined with time since fire.

It is unclear why there was not a striking response to food and nest supplementation
when other species, particularly northern hemisphere rodents (e.g., *Microtus* spp., Cole and
Batzli 1978; Taitt and Krebs 1981), have responded clearly to resource supplementation.
However, there are a number of possible explanations. Natural food and nest availability
may not have been reduced greatly by fire. Patches of unburnt vegetation remained along
creeks and gullies, and in areas sheltered by large rocks and other similar topographical
features. Perhaps these patches provided sufficient resources for animals to survive on after fire. Fire-stimulated rapid vegetation regrowth and flowering of many species would have also provided additional food sources. Sampling for invertebrates during the summers after food supplementation began indicated substantial populations of surface active invertebrates (Chapter 3). In addition, the rapid regrowth of vegetation and the re-establishment of the litter-layer after the fire would have provided additional sources of invertebrates to those sampled during this study.

Fire may also increase the availability of nest sites although, depending upon the historical fire regime of an area, it may also diminish availability of hollows. Fire can cause hollow formation in trees, and cause branches and trees to fall, creating nesting opportunities for ground dwelling species. However, in areas of high fire frequency, or after fires of high intensity, the enlarged hollows may be unsuitable for some smaller species (Dickman 1991). Burrowing opportunities may also be reduced if, for example, animals prefer to burrow under the cover of overhanging vegetation, although generally the medium in which the animal will burrow (i.e., the soil structure and hardness) will not be affected by fire. Similarly, the availability of nest sites provided by rock will not be affected by fire.

Alternatively, fire-affected habitat may undergo a shift in resource production, thereby providing surrogate food resources. As mentioned above, fire-stimulated flowering may provide an alternative food source for some species. Whelan et al. (1996) found that the largely insectivorous A. stuartii fed predominantly on pollen and nectar from the large and abundant inflorescences of Xanthorrhoea media in the year following fire in Royal National Park. Fire also stimulates the shedding of seed from the canopy seed banks of obligate seeders such as Banksia spp., providing a rich alternative food to terrestrial granivores (Gill 1981; Keith 1996).

To take advantage of alternative resource availability, small mammal species may have to undergo shifts in foraging behaviour and diet after fire. After fire, a previously small component of the diet may become dominant. Johnson (1995) has suggested that fungus may become a dominant food for some small mammals after fire, although generally the proportion of fungus in the diet may be small. Foraging strategy may also change in
order to take advantage of newly available food sources. During this study, the largely arboreal *C. nanus* was trapped consistently on the ground, indicating a possible increase in terrestrial movements as a result of altered foraging strategy.

10.2 **Why are the results from this study different from those expected?**

It is interesting that the individual, population and community responses of small mammals to fire at Ku-ring-gai Chase National Park differed so dramatically from those reported in other studies in similar vegetation in eastern Australia. The habitat of Ku-ring-gai Chase does, however, have a particular feature that may dramatically influence the survival and recovery of small mammals after fire. Ku-ring-gai Chase National Park is dominated by large areas of Hawkesbury sandstone. This provides deep fissures, hollows and overhangs beneficial for sheltering during fire, and for nesting and providing cover during movements after fire. Rocky outcrops are common throughout the national park, and all sites used during this study had a number of rocky outcrops within or adjacent to them. Rock hollows can provide insulation against the heat and flames of fire (Lawrence 1966), thus reducing mortality during fire. This perhaps explains the relatively high numbers of individuals remaining in Ku-ring gai Chase after the fire. In an area of similar topography but heath vegetation, Whelan *et al.* (1996) found that *A. stuartii* nested in hollows and cracks within sandstone outcrops, despite habitually nesting in tree hollows when available (Dickman 1991; Lazenby-Cohen 1991). Thus, this species is adaptable to alternative nesting conditions. The cracks and overhangs provided by rock outcrops may also provide cover for foraging small mammals when vegetative shelter has been reduced.

The suite of species present at Ku-ring gai Chase after the fire was also different to many other studies from eastern Australia. The community structure may have been affected by the absence of *Pseudomys* spp.; often regarded as early seral post-fire specialists (Fox and McKay 1981; Fox 1982, 1983, 1990). As discussed above (Section 10.1.3), within habitat types, the same species may occupy different regeneration niches as a result of interspecific competition, rather than the regeneration of habitat requirements over time since fire.
Finally, specific fire characteristics may have a differential effect upon the survival of small mammals and/or the availability of resources necessary for the maintenance of a population after fire. Although I have already discussed the effect of fire frequency (Chapter 3; Section 10.1.1), the timing of a fire with respect to the breeding season may also influence the number of individuals recruited into the population. If a fire occurs prior to mating, the reduced reproductive population due to emigration and/or mortality, in conjunction with the reduced resources available to lactating mothers, will lead to a reduction in the numbers of juveniles recruited into the population. A fire after recruitment has taken place, however, will be less detrimental to the population as a whole due to individual survival determining population success, as well as high immigration potential due to the dispersal propensity of the juveniles of most small mammal species (Anderson 1989). The large declines in small mammal abundance recorded previously after fires in December (Newsome et al. 1975; Recher et al. 1975) and August (Fox 1982), for example, may have been magnified by the timing of the fires with regard to the weaning and breeding seasons respectively. The fire in this study burnt Ku-ring-gai Chase in early January, after the recruitment of juvenile *A. stuartii* into the population. As *R. fuscipes* juveniles appeared throughout the year, fire season is unlikely to have been as influential on the population size of this species.

10.3 CONCLUSIONS

This study determined that some of the widely held beliefs concerning small mammal fire ecology in Australia are based on generalisations and misconceptions. It has exemplified patterns of small mammal population recovery after fire that are not resource driven, by experimentally demonstrating that resource supplementation did not alter greatly the population parameters of any of four common small mammal species. I have proposed that between-study differences in community and population response to fire, and resource availability after fire, are likely to be a result of interspecific competition within a species pool unique to each study site. In the present study, habitat and fire characteristics specific to Ku-ring-gai Chase National Park could be identified. It follows that previous studies into the fire ecology of small mammals, and perhaps other biota, may also be location and community specific. Given this, extreme care must be taken in extrapolating the measured fire responses of small mammal species to situations outside the immediate habitat and
species pool in which they exist. In the future, therefore, research into fire-driven responses of small mammals might profitably focus on locations with different combinations of species than have been studied hitherto, or manipulate experimentally the pool of species at well-studied sites to gain further insight into biotic processes that may drive successional patterns.
REFERENCES


Anonymous (1985). *Ku-ring-gai Chase National Park 1:40 000 Topographic Map* (Central Mapping Authority of New South Wales, Bathurst.)


Monamy, V., and Fox, B. J. (in press). Habitat selection by female swamp rats (*Rattus lutreolus*) drives asymmetric competition and coexistence with long-tailed mice (*Pseudomys higginsi*). *Journal of Mammalogy*


