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**Habitat use, seasonality and ecology
of carabid beetles
(Coleoptera: Carabidae)
in native forest remnants,
North Island, New Zealand**

**A thesis presented in partial fulfilment of the requirements for the degree of
Master of Science
in Ecology
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Abstract

The Carabidae (Insecta: Coleoptera) is one of the largest insect families in New Zealand with an estimated 600 species, 90% of which are endemic. Carabids have received a considerable amount of attention in the Northern Hemisphere, but next to nothing is known about the biology of carabids in New Zealand. The aim of my research was to increase our knowledge about the ecology, population dynamics, and life history of carabids in New Zealand native forests.

The morphology and biology of two species of endemic carabids, *Mecodema oconnori* Broun and *Megadromus capito* (White) was studied in detail. *Mecodema oconnori* was strongly sexually dimorphic, whereas *M. capito* males and females were very similar in size and weight. During the course of the study, I discovered several very small *M. oconnori* males with red legs, and these may belong to a separate species. The habitat use and movement of *M. oconnori* and *M. capito* in a native forest remnant was investigated using several different sampling techniques, including manual searches, live capture pitfall trapping, and harmonic radar tracking. Manual searches of carabid resting sites proved to be the most effective method for locating these beetles, as both species displayed a high degree of site fidelity, and were repeatedly found under the same sites. Harmonic radar tracking was not very successful, largely because I was unable to identify beetles when they were in underground burrows.

The population dynamics and seasonality of several species of carabids were investigated in order to understand more about their life cycles. Manual searches of resting sites were used to estimate the seasonal abundance of *M. oconnori* and *M. capito* throughout the year, and removal pitfall trapping was also carried out for six months. The searches revealed that both *M. oconnori* and *M. capito* were present in all months of the year, in contrast to the results from previous pitfall trapping studies. Females of five species of carabids were dissected to investigate their reproductive phenology. *Mecodema oconnori* had extremely low fecundity, with a mean egg number of only 1.6 eggs per female. In contrast, *M. capito* had the highest fecundity, with up to 28 eggs per female. Both *M. oconnori* and *M. capito* females contained eggs in their ovaries from October to March, suggesting that these species have a long period of reproductive activity. *Megadromus*

capito larvae were caught in all months of sampling (from October to March) and the three instars overlapped temporally, which implies a long period of larval emergence and development. *Megadromus capito* larvae were most abundant in January-February and teneral adults were found in February and March, suggesting that this species is a spring breeder. *Mecodema oconnori* also appears to be a spring breeder, although its peak in reproductive activity was slightly later than *M. capito*, in late spring-summer.

The effect of rodent control on carabid beetle assemblages was investigated at Lake Papaitonga Scenic Reserve using paired treatment (poisoned) and non-treatment (non-poisoned) areas. Controlling rodents did not have a significant effect on the carabid assemblages, or on the abundance of other invertebrate taxa, although some carabid species appeared to have benefited from the reduced rodent densities. The abundance of carabids in pitfall traps was significantly correlated with the numbers of amphipods and springtails, which suggests that carabids may aggregate in areas of high prey density. There was also a correlation between carabids and other beetles, but this was more likely to result from a similar response to the environmental characteristics at each trap.

There are many questions still to be answered about the habitat use and ecology of carabids in New Zealand, as well as the effects of introduced predators and environmental factors on carabid population dynamics. Longer-term studies are needed to gather more information on the pre-adult stages and reproductive activity of adults, as this is essential to fully understand the life history of New Zealand carabids.

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This thesis has been an epic journey of challenges and obstacles for me, and is not quite everything I hoped it would be, but I have learnt so much during this study that I don't regret any of it, and it has been an extremely valuable life experience.

Finally, I would like to thank all of the amazing carabid beetles that allowed me to intrude into their daily lives and come away with a bit more understanding of how they live. I would also like to offer a sincere apology to the countless thousands of invertebrates that died in the name of science during my study. I only hope that we can use this information wisely for their future conservation.

"When the last individual of a race of living things breathes no more,
another heaven and another earth must pass before such a one can be again"

William Beebe

Table of Contents

ABSTRACT	i
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS	v
LIST OF FIGURES	x
LIST OF TABLES	xiii
LIST OF COVER PLATES	xiv
CHAPTER ONE: Introduction	1
1.1 The importance of invertebrates.....	1
1.2 The family Carabidae.....	2
1.3 Carabids as biological indicators.....	3
1.4 Carabids as biological control agents.....	5
1.5 New Zealand Carabidae.....	6
1.6 Conservation of carabids in New Zealand.....	8
1.7 Conclusions.....	10
1.8 Aims of this project.....	11
CHAPTER TWO: Morphology and biology of two endemic carabid beetles: <i>Mecodema oconnori</i> Broun and <i>Megadromus capito</i> (White)	13
2.1 Introduction.....	13
2.2 Methods.....	14
2.2.1 Study site	14
2.2.2 Carabid species in this study	17
2.2.3 Determining the gender of each species	17
2.2.4 Manual searches of habitat resting sites	19
2.2.5 Live capture pitfall trapping	20
2.2.6 Rodent tracking tunnels	21
2.2.7 Statistical analyses	22
2.3 Results.....	23
2.3.1 Abundance of carabids at Browns Bush	23
2.3.2 Sex ratio	23
2.3.3 Morphological measurements	23
2.3.3.1 <i>Megadromus capito</i>	24
2.3.3.2 <i>Mecodema oconnori</i>	24
2.4 Discussion.....	29
2.4.1 Sex ratio	29

2.4.2	Morphological measurements	29
2.4.3	Factors affecting adult body size	30
2.4.4	Conclusions	31

CHAPTER THREE: Habitat use and movement of two endemic carabids in a native forest remnant 33

3.1	Introduction	33
3.2	Methods	37
3.2.1	Study site	37
3.2.2	Manual searches of habitat resting sites	37
3.2.3	Live capture pitfall trapping	38
3.2.4	Harmonic radar tracking	38
3.2.5	Environmental variables	40
3.2.6	Statistical analyses and mapping	41
3.3	Results	42
3.3.1	Abundance of carabids at Browns Bush	42
3.3.2	Recapture rates	43
3.3.2.1	Searches of habitat resting sites	43
3.3.2.2	Live pitfall trapping	44
3.3.3	Comparison of sampling methods	44
3.3.4	Occupancy of habitat resting sites	45
3.3.5	Spatial dispersion among the pitfall traps	46
3.3.6	Movement of carabids between resting sites	47
3.3.7	Harmonic radar tracking	51
3.3.8	Environmental variables	52
3.3.8.1	Temperature	52
3.3.8.2	Rainfall	53
3.3.8.3	Habitat characteristics of the pitfall traps	53
3.4	Discussion	54
3.4.1	Habitat use	54
3.4.2	Activity and movement	57
3.4.3	Comparison of sampling methods and their limitations	62
3.4.4	Estimates of population density	65
3.4.5	Conclusions	66

CHAPTER FOUR: Population dynamics, seasonality, and life history of New Zealand carabid beetles 67

4.1	Introduction	67
4.2	Methods	71
4.2.1	Study sites	71
4.2.2	Manual searches of habitat resting sites at Browns Bush	71

4.2.3	Live capture pitfall trapping at Browns Bush	75
4.2.4	Removal pitfall trapping at Lake Papaitonga Scenic Reserve	75
4.2.5	Climatic variables	77
4.2.6	Statistical analyses	77
4.3	Results	78
4.3.1	Seasonal abundance of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> at Browns Bush	78
4.3.2	Seasonal changes in body mass of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> at Browns Bush	80
4.3.3	Population dynamics of carabids in live pitfall traps at Browns Bush	82
4.3.4	Abundance of carabids in pitfall traps at Lake Papaitonga Scenic Reserve	84
4.3.5	Seasonality of adult carabids at Lake Papaitonga Scenic Reserve	86
4.3.6	Seasonality of carabid larvae at Lake Papaitonga Scenic Reserve	89
4.3.7	Female reproductive phenology	89
4.3.8	Climatic variables	91
4.3.8.1	Temperature	91
4.3.8.2	Rainfall	91
4.4	Discussion	93
4.4.1	Seasonal activity of carabid beetles	93
4.4.2	Carabid life history	98
4.4.3	Reproductive phenology and egg production	100
4.4.4	Seasonality of individual species	104
4.4.5	Conclusions	107
 CHAPTER FIVE: The effects of rodent control and the abundance of other invertebrates on carabid assemblages		109
5.1	Introduction	109
5.2	Methods	111
5.2.1	Study site	111
5.2.2	Rodent control and tracking tunnels	111
5.2.3	Invertebrate sampling	112
5.2.4	Environmental variables	112
5.2.5	Statistical analyses	113
5.3	Results	115
5.3.1	Rodent abundance in each sampling area	115
5.3.2	Abundance and diversity of Carabidae	116
5.3.3	The effect of rodent control on carabid abundance	117
5.3.4	Composition of the carabid assemblages in each area	120
5.3.5	Carabid body size distribution	121
5.3.6	Changes in carabid abundance over time	122
5.3.7	Spatial dispersion of carabids in each area	123

5.3.8	Abundance of other invertebrates	125
5.3.9	Composition of other invertebrates in each area	126
5.3.10	Relationship between the abundance of carabids and other invertebrates	129
5.3.11	Relationship between carabids and the environmental variables	130
5.4	Discussion	132
5.4.1	The effect of predation on carabids	132
5.4.2	The effect of other invertebrates on carabid assemblages	136
5.4.3	The effect of the environmental variables on carabid assemblages	137
5.4.4	Limitations of pitfall trapping and sampling design	139
5.4.5	Conclusions	140
CHAPTER SIX: General discussion and conclusions		141
6.1	Findings of my study	141
6.2	Future work	142
6.3	Conclusions	143
REFERENCES		145
APPENDICES		169
Appendix 1: List of vascular plant species at Browns Bush.		169
Appendix 2: Distribution and body size of carabid species in this study.		171
Appendix 3: Rodent abundance at Browns Bush - tracking tunnel rates (Aug, Sept, Nov 1999).		172
Appendix 4: Multivariate analysis of <i>Mecodema oconnori</i> morphological measurements.		172
Appendix 5: Fluctuations in weight of a male and female <i>Mecodema oconnori</i> kept in the laboratory.		173
Appendix 6: Mean monthly air temperature at Browns Bush and Levin Weather Station (January 1999 – March 2000).		174
Appendix 7: Total monthly rainfall at Levin Weather Station (January 1999 – March 2000).		174
Appendix 8: Results of a two-way analysis of variance on carabid movement distances at Browns Bush.		175
Appendix 9: Movement patterns of carabid beetles at Browns Bush.		176

Appendix 10: SAS program used for analysis of variance of carabid abundance at Lake Papaitonga Scenic Reserve.	178
Appendix 11: Tracking tunnel rates in each sampling area at Lake Papaitonga Scenic Reserve.	179
Appendix 12: Detrended correspondence analysis of the carabid assemblages in each sampling area at Lake Papaitonga Scenic Reserve.	180
Appendix 13: Detrended correspondence analysis of the other invertebrates in each sampling area at Lake Papaitonga Scenic Reserve.	181
Appendix 14: The relationship between the environmental variables and the number of carabids caught at Lake Papaitonga Scenic Reserve	182
GLOSSARY	183

LIST OF FIGURES

Figure 2.1. Map of Browns Bush study site and arrangement of pitfall traps.	15
Figure 2.2. Characteristics of <i>Mecodema oconnori</i> used to determine gender.	18
Figure 2.3. Characteristics of <i>Megadromus capito</i> used to determine gender.	18
Figure 2.4. Ponga log used as a resting site by carabids at Browns Bush.	19
Figure 2.5. Live capture pitfall trap used in the mark-recapture study of carabid beetles at Browns Bush.	21
Figure 2.6. Frequency distribution of body lengths of <i>Megadromus capito</i> males and females at Browns Bush.	25
Figure 2.7. Relationship between body mass and length of <i>Megadromus capito</i> males and females at Browns Bush.	25
Figure 2.8. Frequency distribution of body lengths of <i>Mecodema oconnori</i> males and females at Browns Bush.	26
Figure 2.9. Relationship between body mass and body length of <i>Mecodema oconnori</i> males and females at Browns Bush.	27
Figure 2.10. Multivariate analysis of <i>Mecodema oconnori</i> body measurements.	28
Figure 3.1. Transponder design used for harmonic radar tracking of carabids.	39
Figure 3.2. Harmonic radar tracking of carabids at Browns Bush.	39
Figure 3.3. Frequency distribution of the number of sightings per individual for <i>Mecodema oconnori</i> and <i>Megadromus capito</i> caught in searches of resting sites.	43
Figure 3.4. Total number of carabids (<i>Mecodema oconnori</i> and <i>Megadromus capito</i>) caught in searches of resting sites versus live pitfall traps at Browns Bush.	44
Figure 3.5. Mean number of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> found under different types of habitat sites at Browns Bush.	46
Figure 3.6. Frequency distribution of all carabids in pitfall traps at Browns Bush compared to a Poisson (random) distribution.	46
Figure 3.7. Map of the movement pattern of a <i>Megadromus capito</i> female.	49
Figure 3.8. Map of the movement pattern of a <i>Mecodema oconnori</i> male.	50
Figure 3.9. Relationship between mean daily air temperature and the number of carabids caught in live pitfall traps.	52

Figure 4.1. Map of Lake Papaitonga Scenic Reserve, Levin.	73
Figure 4.2. Pitfall trap used for sampling carabids at Lake Papaitonga Scenic Reserve.	76
Figure 4.3. Mean number of new and recaptured <i>Mecodema oconnori</i> and <i>Megadromus capito</i> males and females found per search at Browns Bush.	79
Figure 4.4. Relative abundance of male <i>Mecodema oconnori</i> and <i>Megadromus capito</i> found in searches of resting sites at Browns Bush.	80
Figure 4.5. Mean body mass of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> in searches of habitat resting sites at Browns Bush.	81
Figure 4.6. Total number of <i>Mecodema oconnori</i> , <i>Megadromus capito</i> , and <i>Holcaspis mucronata</i> caught in live pitfall traps at Browns Bush on each trapping occasion.	82
Figure 4.7. Relative abundance of male <i>Mecodema oconnori</i> and <i>Megadromus capito</i> caught in pitfall traps at Browns Bush.	83
Figure 4.8. Total abundance of Carabidae (adults and larvae) caught at Lake Papaitonga Scenic Reserve in each month of sampling.	86
Figure 4.9. Changes in the total abundance of carabids at Lake Papaitonga Scenic Reserve from October 1999 to March 2000.	87
Figure 4.10. Total abundance of nine ‘minor’ species in pitfall traps at Lake Papaitonga Scenic Reserve from October 1999 to March 2000.	88
Figure 4.11. Relative abundance of male <i>Mecodema oconnori</i> , <i>Megadromus capito</i> , and <i>Holcaspis sinuiventris</i> caught in pitfall traps at Lake Papaitonga Scenic Reserve.	88
Figure 4.12. Total abundance of <i>Megadromus capito</i> larvae in pitfall traps at Lake Papaitonga Scenic Reserve in each month of sampling.	89
Figure 4.13. Number of dissected females of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> found with and without mature eggs from October 1999 to March 2000.	91
Figure 4.14. Relationship between mean monthly air temperature and the total number of individuals caught in pitfall traps at Lake Papaitonga Scenic Reserve.	92
Figure 5.1. Mean number of tunnels with rodent tracks in each sampling area and poisoned versus non-poisoned areas at Lake Papaitonga Scenic Reserve.	115
Figure 5.2. Total number of carabids (adults and larvae) caught in each sampling area at Lake Papaitonga Scenic Reserve.	117
Figure 5.3. Total number of <i>Megadromus capito</i> , <i>Mecodema oconnori</i> , <i>Selenochilus</i> sp., <i>Holcaspis mucronata</i> , <i>Holcaspis sinuiventris</i> , and “minor species” caught in each sampling area at Lake Papaitonga Scenic Reserve.	119

Figure 5.4. Detrended correspondence analysis results for the carabid beetle assemblages in each sampling area at Lake Papaitonga Scenic Reserve.	120
Figure 5.5. Mean body length of carabids in each sampling area at Lake Papaitonga Scenic Reserve.	121
Figure 5.6. Total number of carabids caught in each sampling area at Lake Papaitonga Scenic Reserve over time.	122
Figure 5.7. Spatial dispersion of <i>Megadromus capito</i> in pitfall traps at Lake Papaitonga Scenic Reserve.	124
Figure 5.8. Mean number of other invertebrates per trap caught in each sampling area at Lake Papaitonga Scenic Reserve (October 1999).	125
Figure 5.9. Total number of Acarina and Collembola in each sampling area at Lake Papaitonga Scenic Reserve (October 1999).	126
Figure 5.10. Total number of individuals of some of the major invertebrate groups in each sampling area at Lake Papaitonga Scenic Reserve (October 1999).	127
Figure 5.11. Detrended correspondence analysis results for the other invertebrates in each sampling area at Lake Papaitonga Scenic Reserve.	128
Figure 5.12. Relationship between the total number of carabids and the total number of Amphipoda and other Coleoptera caught in pitfall traps at Lake Papaitonga Scenic Reserve.	130
Figure 5.13. Environmental characteristics of each sampling area at Lake Papaitonga Scenic Reserve.	131

LIST OF TABLES

Table 2.1. Total number of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> caught at Browns Bush using manual searches of resting sites and live pitfall traps.	23
Table 2.2. Sex ratios of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> caught at Browns Bush.	24
Table 2.3. Mean body length and mean body mass of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> at Browns Bush.	24
Table 3.1. Total number of <i>Mecodema oconnori</i> and <i>Megadromus capito</i> marked and recaptured in habitat searches and live pitfall traps at Browns Bush.	42
Table 3.2. Mean occupancy of different types of resting site by <i>Mecodema oconnori</i> and <i>Megadromus capito</i> at Browns Bush.	45
Table 3.3. Spatial dispersion of carabids in pitfall traps at Browns Bush.	47
Table 3.4. Number of recaptured <i>Mecodema oconnori</i> and <i>Megadromus capito</i> that moved between habitat resting sites at Browns Bush.	47
Table 3.5. Mean total and mean weekly distance moved between habitat resting sites by <i>Mecodema oconnori</i> and <i>Megadromus capito</i> at Browns Bush.	48
Table 3.6. Pearson correlations between the environmental variables of each pitfall trap and the numbers of carabids caught.	53
Table 4.1. Summary of a number of attempts to classify temperate carabid species according to their life history strategy.	69
Table 4.2. Total number of adult carabid beetles caught at Lake Papaitonga Scenic Reserve in pitfall traps over six months of sampling.	84
Table 4.3. Total number of males and females for six of the carabid species caught at Lake Papaitonga Scenic Reserve over six months.	85
Table 4.4. Reproductive phenology of female Carabidae.	90
Table 4.5. Pearson correlations and Bonferroni probabilities between carabid abundance at Lake Papaitonga Scenic Reserve and mean monthly air temperature and total monthly rainfall.	92
Table 5.1. Composition of the carabid assemblages in each sampling area at Lake Papaitonga Scenic Reserve.	116
Table 5.2. Results of a t-test of the number of carabids caught in treatment versus non-treatment areas at Lake Papaitonga Scenic Reserve.	117

Table 5.3. Results of a repeated measures analysis of variance of the number of carabids caught in the four sampling areas at Lake Papaitonga Scenic Reserve.	118
Table 5.4. Results of a repeated measures analysis of variance of the total number of carabids caught in each sampling area from October 1999 to March 2000.	123
Table 5.5. Spatial dispersion of carabids in pitfall traps at Lake Papaitonga Scenic Reserve.	123
Table 5.6. Results of an analysis of variance of the mean number of other invertebrates per trap in the four sampling areas at Lake Papaitonga Scenic Reserve.	126
Table 5.7. Results of an analysis of variance of the mean number of individuals per trap in each sampling area for some of the major invertebrate groups at Lake Papaitonga Scenic Reserve.	127
Table 5.8. Pearson correlations and Bonferroni probabilities between the total abundance of carabids and other invertebrates at Lake Papaitonga Scenic Reserve.	129

LIST OF COVER PLATES

Cover plate 1. *Mecodema oconnori* (Broscini) male.

Cover plate 2. Close-up of male *Mecodema oconnori* head.

Cover plate 3. Sheets of corrugated iron used as resting sites by carabid beetles at Browns Bush.

Cover plate 4. Recently hatched *Megadromus capito* (Pterostichini) eggs and first-instar larvae at Browns Bush.

Cover plate 5. Shattered remains of *Mecodema oconnori* and *Megadromus capito* resulting from predation.

Cover plate 6. *Megadromus capito* female with distended abdomen, probably gravid.

Cover plate 7. *Ctenognathus bidens* from Lake Papaitonga Scenic Reserve, Levin.

Chapter One

Introduction



Cover plate 1. *Mecodema oconnori* (Broscini) male. Photograph by Felix Collins.

“I may here state, for the information of those who have not the inclination or leisure to study entomology, that the group *Carabidae* is one of the most highly developed of the order Coleoptera, and consists almost entirely of useful insects.”

Captain T. Broun (1892)

Introduction

1.1 The importance of invertebrates

The family Carabidae (Coleoptera: Adephaga) is part of the class Insecta, which makes up a significant proportion of the world's biodiversity (Oliver and Beattie 1996). Insects have been described as “the little things that run the world” (Wilson, 1987) because they are integral parts of ecosystems, and play an important role in the facilitation and maintenance of ecosystem services (Myers 1996). Insects, and the wider group invertebrates, provide critical energy links between trophic groups through plant herbivory, decomposition, predation, and by being a food source for other animals (Jones *et al.* 1994, Lawton 1994, Yen & Butcher 1997). They provide essential services for humans such as crop pollination, soil regulation, and biological pest control (Myers 1996, Yen & Butcher 1997). Invertebrates are also physically involved in shaping ecosystems as ecosystem engineers e.g. earthworms and termites (Jones *et al.* 1994, Lawton 1994). They are closely linked to the regulation of ecosystem functions such as biogeochemical and hydrological cycles (Myers 1996). Despite the obvious importance of invertebrates in ecosystems, very little is understood about how their declining biodiversity will affect ecosystem functioning.

The 1992 International Convention on Biodiversity placed a responsibility on national governments to conserve biodiversity. Insects contribute overwhelmingly to known species diversity, with about 53% of all described species (751,000 spp.) being insects (Wilson 1992). Estimates for the Insecta have ranged as high as 30 million species (Erwin 1982), although more conservative estimates of 5-10 million are currently favoured (Stork 1988, Sutton and Collins 1991, Godfray *et al.* 1999). Only an estimated 10-15% of the world's insect fauna is currently described (May 1990, Stork 1988), and research and conservation of invertebrates is greatly hampered by this “taxonomic impediment” (New 1995). Very little is known about the basic biology, distribution, conservation and taxonomic status of a large proportion of the world's biodiversity, and inventory and description of insect species is essential in order to conserve the world's ecosystems.

Basic biological and ecological information is also required to understand, model and predict the impacts of environmental change on invertebrates and biodiversity (Ward 2000). Sound conservation management requires sound biological understanding, and for this reason, it is essential that we learn more about our invertebrate fauna, and the factors affecting their distribution and survival.

1.2 The family Carabidae

The Carabidae (or ground beetles) have a global distribution, and are one of the most speciose beetle families in the world with an estimated 40,000 species – more than 4% of all insect species (Thiele 1977). They are a dominant component of the terrestrial invertebrate fauna, and are present in a variety of habitats ranging from alpine meadows to deserts, grasslands, and tropical rainforests (Thiele 1977).

Carabids are *holometabolous* insects, i.e. they undergo a complete metamorphosis (Klimaszewski & Watt 1997). The carabid larva is described as *campodeiform*, with a prognathous head and long, well-developed legs (Klimaszewski & Watt 1997). Carabid larvae are carnivorous and actively hunt for their prey (Evans 1977a). They are also highly cannibalistic, and may eat their own siblings (Goulet 1976). The larval stage is the main growth phase, and is largely responsible for determining adult size (Evans 1977a, Ernsting *et al.* 1992). The larvae go through three instars, and when they have completed their feeding and growth they enter the pupal phase, during which the larva is transformed into an adult beetle (Evans 1977a, Klimaszewski & Watt 1997). Carabid pupae are generally inactive and remain below the soil surface in burrows in order to avoid predation (Evans 1977a). Adult beetles emerge from pupae fully developed, and are called *teneralis* or *callows* (Lövei & Sunderland 1996). Teneralis can be detected by the presence of a pale, soft exoskeleton, which may take several weeks to darken and harden (Lövei & Sunderland 1996). Many carabids are quite long-lived compared to other beetles, and may live up to seven years (Baumgartner *et al.* 1997). Some species may take more than one year to complete their life cycle from egg to adult (Kirk 1974, Lövei & Sunderland 1996).

Carabid beetles have received a considerable amount of attention in the Northern Hemisphere, particularly in Europe (Ward 2000). A vast array of detailed information is available on a range of topics, such as life history strategies (Gilbert 1956, Greenslade 1965, Paarmann 1979, den Boer & den Boer-Daanje 1990, van Dijk & den Boer 1992, Horne 1992, Kennedy 1994), dispersal power (den Boer 1970, Rijnsdorp 1980, Best *et al.* 1981, Wallin 1987, Frampton *et al.* 1995), habitat preferences (Wallin 1986, Baguette 1993, de Vries *et al.* 1996, Atienza *et al.* 1996), and ecological requirements (Thiele 1977, Davies & Margules 1998, Rushton *et al.* 1990).

Carabids have been used as study subjects for testing a wide range of ecological theories, both in the field and in the laboratory (Thiele 1977, Stork 1990). The topics covered include the factors involved in population regulation (den Boer 1981, 1985a, 1987), causes of community structure (den Boer 1980, Loreau 1986, Gerdner *et al.* 1987), metapopulation dynamics (Davies & Margules 1998, Petit & Burel 1998), and interspecific interactions such as competition (Lenski 1982, 1984, den Boer 1985b, Andersen 1988, Loreau 1990a,b, Niemelä 1993, Griffith & Poulson 1993, Currie *et al.* 1996). Carabids have been subjected to a vast number of laboratory experiments to determine the effects of abiotic factors such as temperature, humidity, and light levels on their activity, reproduction, and diet preferences (Thiele, 1977, Ernsting & van der Werf 1988, Chaabane *et al.* 1993, Jorgensen & Toft 1997).

1.3 Carabids as biological indicators

There is an increasing need to seek and adopt methods for rapid detection and assessment of biota, and to rank the species or faunas in some logical way for conservation priority (New 1995). Indicator species provide a tool for conservation managers to assess ecosystem condition without having to identify and quantify all aspects of biodiversity (Pearson 1994). Indicator species can be divided into three main categories: (1) Environmental indicators, (2) Ecological indicators, and (3) Biodiversity indicators (McGeoch 1998). The first two types of indicator may be used in monitoring studies that evaluate changes in habitats or ecosystems over time such as successional stage or habitat degradation (Rodriguez *et al.* 1998). In this case, the most suitable indicator will be one that is sensitive to environmental change. On the other hand, *biodiversity indicators* are

involved in inventory studies that record distribution patterns of taxa or ecological units in space, often with the purpose of identifying areas for establishing nature reserves (Rodriguez *et al.* 1998). Here, the best indicator will be one whose distribution or abundance correlates with those of other taxa. For example, Oliver and Beattie (1996) showed that the species richness of only three beetle families – Carabidae, Scarabaeidae and Pselaphidae – was positively correlated with the richness of all other beetle families, and suggested that they had potential as biological indicators.

Some authors have suggested criteria for the selection of indicator taxa (Pearson 1994, McGeoch 1998). The usual requirements are:

1. Taxonomically well known and stable
2. Biology and natural history well understood (e.g. limiting resources, enemies, physical tolerances, complete life cycle)
3. Easily sampled
4. Broad geographic and ecological range (so that results will be broadly applicable)
5. Sensitive to ecological change
6. Representative of other taxa
7. Potential economic importance

Numerous authors have recognised the potential of using terrestrial invertebrates as indicators in monitoring programs (Hutcheson 1990, 1999, Sutton & Collins 1991, Lawton *et al.* 1998, Godfray *et al.* 1999), although very little research has been carried out to determine whether they are useful in practice (McGeoch 1998). Carabid beetles have been promoted as ecological indicators because they fit many of the proposed selection criteria (Thiele 1977, Casale 1990, Dufrêne *et al.* 1990, Maelfait & Desender 1990, Maelfait *et al.* 1990, Luff 1996, Dufrêne & Legendre 1997, Rykken *et al.* 1997). They are easy to sample, relatively abundant, and individual species usually occupy specific habitats and respond to changes in environmental conditions.

Carabid communities are often used to classify sites or habitat types (Refseth 1980, Eyre & Rushton 1989, Eyre 1990, Eyre & Luff 1990, Luff *et al.* 1992). For example, Eyre and Luff (1990) found that analysis of carabid assemblages alone provided a relatively rapid

assessment of grassland habitats in England, and suggested that carabids could be of considerable use in terrestrial environmental monitoring.

Particular species or assemblages may be useful indicators of habitat quality or environmental change (Rushton *et al.* 1990, Stork, 1990, Michaels and McQuillan 1995). For example, Pearson and Cassola (1992) found that tiger beetles (Cicindelidae) (close relatives of carabids) were particularly sensitive to habitat modification and suggested that they may be indicators of ecological degradation. Similarly, Rodriguez *et al.* (1998) concluded that tiger beetles were suitable bioindicators for monitoring degradation and regeneration of tropical forests because of their habitat specialisation. Boscaini *et al.* (2000) used carabid beetles as a tool for assessing habitat quality of river ecotones. Carabids have also been used to demonstrate the impact of industrial air pollution (Lesniak 1971, cited in Thiele 1977), and Quinn *et al.* (1991) used carabid assemblages to investigate the effects of habitat type and perturbation from insecticides on community dynamics.

1.4 Carabids as biological control agents

Carabids are polyphagous predators, and eat a wide variety of smaller insects, as well as earthworms, snails and spiders (Thiele 1977, Lövei & Sunderland 1996). They play an important role in the nutritional chain, and in the annual production of ecosystems (Kaczmarek 1963 cited in Thiele 1977, Vennila & Rajagopal 2000). Many authors have suggested that carabids may be effective biological control agents against agricultural pests because of their predatory nature (Allen & Thompson 1970, Luff 1973, Valentine 1980, Blake *et al.* 1994, Weseloh 1985, Wratten 1987, Chiverton 1988, Baines *et al.* 1990, Hance 1990, Sivasubramaniam *et al.* 1997, Menalled *et al.* 1998, Kromp 1999). For example, Gibson *et al.* (1997) found that several species of carabid are potential biocontrol agents of the New Zealand flatworm (*Artioposthia triangulata*), which is a recognised agricultural pest in Britain because of its impact on native earthworms and soil fertility.

Carabids often respond in a density-dependent manner to the abundance of their prey, i.e. they increase their predation rate in denser populations of their prey, and tend to control their population levels (Crowson 1981). For example, one or two species of small carabids

prey extensively on the eggs of the Cabbage Root-Fly (*Hylemyia brassicae*) (Coaker & Williams 1963), and are a major factor in limiting field populations of this agricultural pest (Mitchell (1963). Some carabids are known to aggregate in areas of high aphid density within fields, and may assist in maintaining aphid numbers below economically damaging levels (Bryan & Wratten 1984, Winder 1990). In addition, phytophagous carabid species may be of use in controlling plant weed species by consuming their seeds (Blake *et al.* 1994).

1.5 New Zealand Carabidae

The New Zealand indigenous beetle fauna makes up 50% of the known New Zealand insect fauna, and has 90% endemism at the specific level (Watt 1982, Emberson 1995). Carabidae is the third largest beetle family in New Zealand, with 445 described species (Klimaszewski & Watt 1997), and an estimated 200 undescribed species (A. Laroche and M-C. Larivière, pers. comm. 2000). New Zealand Carabidae consist of six subfamilies (Carabinae, Cicindelinae, Migadopinae, Scaritinae, Trechinae, and Harpalinae), 16 tribes, and approximately 75 genera (Klimaszewski & Watt 1997), although taxonomic revision is underway and the number of genera is likely to increase (A. Laroche, pers. comm. 2001). New Zealand also contains approximately 29 species of introduced carabid beetles, although the true number is probably slightly higher (Pilgrim 1963, A. Laroche and M-C. Larivière, pers. comm. 2000).

Probably as little as 50% of New Zealand's native insect fauna has been described, and the level of knowledge is very uneven among the various taxa (Howarth & Ramsay 1991, Emberson 1995). Despite the fact that insects constitute well over half the described biodiversity in New Zealand (Emberson 1995), we are still far behind the rest of the developed world in terms of knowledge about our invertebrate fauna (Watt 1982). This is true even for taxonomically well-known families such as Carabidae. Basic information about carabid life history and ecology is completely lacking, and we are still at the inventory and taxonomic description stage for many species (New 1995, 1998, A. Laroche, pers. comm. 2000). Mooed and Meads (1985) stated that "In New Zealand, little is known of the ecology of Carabidae in native forests other than the general distribution of some species (Hudson 1934), and changes in their seasonal abundance in a

hard beech forest (McColl 1975)". Sixteen years later, the situation has not improved greatly, and our knowledge of New Zealand carabids is still about 50 years behind that of their Northern Hemisphere counterparts.

Very little has been published on the ecology and life history of endemic New Zealand carabids, and only limited and scattered information is currently available. The few published studies are mainly concerned with carabid beetles in agricultural environments, and their application as biological control agents (e.g. Sunderland *et al.* 1995). Part of the problem undoubtedly lies in the small number of people conducting research on invertebrates in New Zealand. There is a serious shortage of entomologists in New Zealand, considering the estimated number of arthropod species (around 20,000), and a lack of expertise in systematics and taxonomy (Watt 1976, Heath 1987). Watt (1976) pointed out that the number of researchers working on invertebrates in New Zealand was equivalent to assigning one botanist to work on the entire vascular flora and one-fifth of a vertebrate zoologist to cover the entire land vertebrate fauna including birds (Watt 1976).

Nevertheless, the importance of carabids is beginning to be recognised in New Zealand, and a catalogue of all New Zealand Carabidae (including Cicindelidae) is due to be published in the Fauna of New Zealand series in June 2001 (André Larochelle and Marie-Claude Larivière, pers. comm. 2000). The catalogue includes information for each species on taxonomy, distribution and habitat, as well as biological aspects such as diet, reproduction, and seasonal activity, and will be an essential tool for future research on carabids in New Zealand.

New Zealand carabids may be suitable as indicator taxa because they are often restricted to a certain type of habitat or plant community (Mooed & Meads 1992). Mooed and Meads (1992) suggested that the distribution of carabids may be affected by disturbance to their natural habitat, and that analysis of carabid communities could provide an indication of site stability. Hutcheson (1990) discovered that malaise-trapped beetles could be used to characterise habitat type and successional stage, and Mooed and Meads (1985) found that beetle species richness was representative of other terrestrial insect groups. Similarly, Yen *et al.* (1996 cited in Ward 2000) found that carabid beetles were representative of all other invertebrates in their response to large-scale habitat disturbance in Australia.

1.6 Conservation of carabids in New Zealand

Conservation of New Zealand carabids is hampered by taxonomic uncertainty over the identity and number of species in our fauna. For example, a recent revision of the tribe Harpalini in New Zealand produced 17 new endemic genera which had not been previously described (A. Larochelle, pers. comm. 2001). In addition, the lack of biological information about our native carabid beetles makes their conservation a challenge.

A number of carabid species may require conservation efforts to ensure their survival. The Department of Conservation currently lists two species of Carabidae in Category A – “Highest Priority Threatened Species” – *Mecodema costellum costellum*, and *Mecodema laeviceps* (Molloy *et al.* 1994). There are two species in Category B – “Second Priority Threatened Species” – *Megadromus* sp. (Picton), and *Oregus inaequalis*. Four species are listed in Category X – “Species which have not been sighted for a number of years, but which may still exist” – *Mecodema costellum* sp., *Mecodema punctellum*, *Megadromus antarcticus* subsp.1, and *Megadromus antarcticus* subsp.2. A further 48 species are listed in Category I – “Species about which little information exists, but which are considered threatened” – *Mecodema* (25 spp.), *Megadromus* (12 spp.), *Maoripamborus* (2 spp.), *Zeopoecilus* (5-6 spp.), *Holcaspis falcis*, *Brullea antarctica*, and carabid Kamo (undescribed genus).

There are a number of threats to carabid diversity, but the major factors causing decline of biodiversity are the impacts of invasive organisms, and the alteration of habitats and communities (Ramsay 1988, Howarth & Ramsay 1991). Human modification to ecosystems has increased the rate of species extinction above those of background rates by two or three orders of magnitude (Lawton & May 1995). In Western Europe, loss of habitats since 1950 has resulted in significant changes in the composition of the carabid beetle fauna, and loss of species (Desender & Turin 1989).

Gigantism and flightlessness is common in New Zealand insects which have evolved in the absence of mammals, making them particularly vulnerable to the impacts of introduced predators (Ramsay 1978, Emberson 1995). For example, the accidental introduction of rats to Big South Cape Island resulted in the extinction of a large flightless

weevil (Ramsay 1978). The introduction of kiore (*Rattus exulans*) into New Zealand is thought to have led to the extinction of several species of flightless insects (Ramsay 1978, King 1990). The majority of carabids in New Zealand are flightless, and many are large-bodied, hence they may be particularly vulnerable to predation by introduced predators.

New Zealand's carabid beetles are nearly always associated with native forest, a habitat that has been drastically reduced since human arrival (Klimaszewski & Watt 1997). Urban development, pollution, deforestation, and conversion of indigenous vegetation to agricultural use have all contributed to the loss of native habitat. Native forest now constitutes only 23% of the total land area (Klimaszewski & Watt 1997), and much of the remaining forest is fragmented and highly modified.

Overseas studies have shown that fragmentation of habitat leads to a reduction in population size and its potential for long-term survival, ultimately leading to species loss (Turner 1996, Davies and Margules 1998). Fragmentation may also affect ecosystem processes such as soil and hydrological cycles, which in turn affect species composition (Saunders *et al.* 1991, Margules *et al.* 1994, Turner 1996). Increasing fragmentation and insularisation of remnant habitats reduces the chance of carabid dispersal across unfavourable landscapes, and the re-founding of local populations in the event of stochastic extinction (den Boer 1990, Niemelä *et al.* 1993, Michaels & McQuillan 1995, Petit & Burel 1998). In particular, species which require old-growth forests appear to be especially vulnerable to the effects of forest harvesting and fragmentation (Niemelä *et al.* 1993, Spence *et al.* 1996, Niemelä 1997).

New Zealand species may be particularly vulnerable to fragmentation of their forest habitat because they are predominantly flightless and probably have a low dispersal ability (see den Boer 1970, Lövei & Cartellieri, in press). Lövei and Cartellieri (in press) found that carabid densities in forests in the Manawatu, New Zealand were considerably lower than those in the Northern Hemisphere, and referred to them as "collapsed".

In Australia, a number of studies have examined the effects of land-use management and disturbance on carabid beetles (Michaels & McQuillan 1995, Horne & Edward 1997, Davies and Margules 1998). Michaels & McQuillan (1995) discovered that carabid beetles were sensitive to ecological changes resulting from logging, and that old-growth species were at risk when the forest became too small and fragmented to maintain viable populations. Carabids may also be vulnerable to the effects of fertilisers and chemicals used in agricultural systems (Blake *et al.* 1994).

Some studies have revealed that the diversity of carabids often bears little resemblance to vegetation or mammal diversity (Crisp *et al.* 1998). In Australia, Michaels and Mendel (1998) found that sites that were ranked the highest in terms of carabid beetle fauna were not the same as sites ranked highest based on vegetation diversity. Similarly, in New Zealand, Lövei and Cartellieri (in press) found that carabid assemblages in the Manawatu were species-poor even in botanically-rich forest reserves. This means that an inventory of plant species alone may not adequately represent all aspects of diversity in a protected natural area, and that conservation of carabid beetles may be overlooked in the current reserve network in New Zealand.

1.7 Conclusions

Current knowledge of New Zealand carabids, like most of our insects, is insufficient to meet the requirements for their conservation, or their potential use as indicator species and biocontrol agents (Ramsay 1988). Information about their diets and feeding habits is required, and on the relationships between carabids and other invertebrate groups. Understanding the habitat preferences and spatial behaviour of carabid beetles is critical for their effective conservation and management. In addition, knowledge is needed about the impacts of introduced predators on carabid populations, and the effect of environmental factors such as weather on their seasonal activities and life cycles.

1.8 Aims of this project

The aim of my research was to increase knowledge about the ecology and life history of carabids in New Zealand native forests. The chapters begin at the level of the individual beetle and progress through to carabid population dynamics and finally the factors affecting whole carabid assemblages. Chapter Two presents information about the morphology and biology of two species of endemic carabids, *Mecodema oconnori* Broun and *Megadromus capito* (White). Chapter Three examines the habitat use and movement of these carabids within a native forest remnant using several different sampling techniques. Chapter Four explores the population dynamics, seasonality, and life cycles of several species of New Zealand carabids. Chapter Five investigates the impacts of introduced predators and other invertebrates on carabid beetle assemblages, as well as the effects of environmental and habitat factors. Chapter Six provides a general discussion and conclusions about the findings of my study, with recommendations for further research on carabids in New Zealand.

Chapter Two

Morphology and biology of two endemic carabid beetles: *Mecodema oconnori* Broun and *Megadromus capito* (White)



Cover plate 2. Close-up of male *Mecodema oconnori* head. Photograph by Felix Collins.

“One principal cause of the little attention paid to entomology has doubtless been the ridicule so often thrown upon the Science...in the minds of most men the idea of the trifling nature of his pursuit is so strongly associated with that of the diminutive size of its objects that an *Entomologist* is synonymous with everything futile and childish.”

William Kirby (1815)

Morphology and biology of two endemic carabid beetles: *Mecodema oconnori* Broun and *Megadromus capito* (White)

2.1 INTRODUCTION

Patterns of carabid body size are of great ecological interest, as body size may be related to the type of habitat, availability of prey, and local environmental factors (Blake *et al.* 1994). Adult body size in carabids is primarily determined by factors affecting the larval stage, as this is the main growth period (Lövei and Sunderland 1996). Both temperature and food supply affect larval development time, and hence the final size and weight of adult beetles (van Dijk & den Boer 1992, van Dijk 1994, Ernsting & Isaaks 1997). Adult body size, in turn, may affect the probability of survival, with smaller beetles having a higher mortality risk, and a lower degree of reproductive success (van Dijk 1994, Baumgartner *et al.* 1997).

Multivariate analysis of carabid morphology can be used to investigate differences between sexes and species, and within individuals of the same species from different habitats. For example, Baguette *et al.* (1990) employed multivariate analysis to separate several different species of *Abax* (Carabidae). Using only morphological criteria they were able to discriminate individuals of the same species and sex from different geographical locations. They concluded that “morphometry appears to be a powerful tool in the population biology of carabid beetles”. In addition, the sex ratio of a species may reveal aspects of its population dynamics and breeding behaviour (Wallin 1989).

The taxonomy of New Zealand Carabidae is reasonably well known, with over 445 described species (Klimaszewski & Watt 1997), however next to nothing is known about their biology or ecology. The aim of this chapter is to present information about the morphology and biology of two species of endemic New Zealand carabids, *Mecodema oconnori* Broun and *Megadromus capito* (White).

2.2 METHODS

2.2.1 Study site

This study was carried out at Browns Bush in the Horowhenua district, North Island, New Zealand (Figure 2.1). Browns Bush is a privately-owned lowland forest remnant of less than 1 ha situated 4 km south of Levin on McLeavey Road (Latitude 40°40'S, Longitude 175°16'E). The forest is surrounded by pasture and is relatively isolated, as the nearest forest is more than 1 km away. The study site experiences a mean annual rainfall of approximately 1100 mm, with an average of 48 frost days per year (Burgess 1988). Severe frost is uncommon. The forest canopy is dominated by tawa (*Beilschmiedia tawa*) and karaka (*Corynocarpus laevigatus*), and contains scattered podocarps such as totara (*Podocarpus totara*) and miro (*Prumnopitys ferruginea*). The canopy is fairly open and the understorey is sparse, however there is good regeneration of some species e.g. karaka and pigeonwood (*Hedycarya arborea*). The forest has been heavily disturbed in the past by grazing of cows, sheep and pigs (John Brown, pers. comm. 1999), and is littered with pieces of corrugated iron, timber, metal, and wire. There are a number of introduced plant species in Browns Bush; both weeds and deliberate plantings (for list of species see Appendix 1). The forest also contains an area of planted native trees which do not naturally occur in the forest e.g. kauri (*Agathis australis*), kowhai (*Sophora microphylla*), and whau (*Entelea arborescens*) (see Figure 2.1). Introduced birds such as starlings (*Sturnus vulgaris*), magpies (*Gymnorhina tibicen*), and thrushes (*Turdus philomelos*) frequent the forest, as well as mammals such as mice (*Mus musculus*), ship rats (*Rattus rattus*), possums (*Trichosurus vulpecula*), and hedgehogs (*Erinaceus europaeus*). Despite its history of disturbance, Browns Bush still contains significant populations of native carabid beetles, and other native species such as morepork (*Ninox novaeseelandiae*), kereru (*Hemiphaga novaezealandiae*), fantail (*Rhipidura fuliginosa*), grey warbler (*Gerygone igata*), and common skink (*Oligosoma nigriplantare*).

Four carabid species are present at Browns Bush: *Mecodema oconnori* (Cover plate 1), *Megadromus capito* (Cover plate 6), *Holcaspis mucronata* (Broun), and *Harpalus affinis* (Schrank). *Harpalus affinis* is an introduced European carabid that has colonised the Manawatu, and is spreading rapidly throughout the North Island (Townsend 1992).

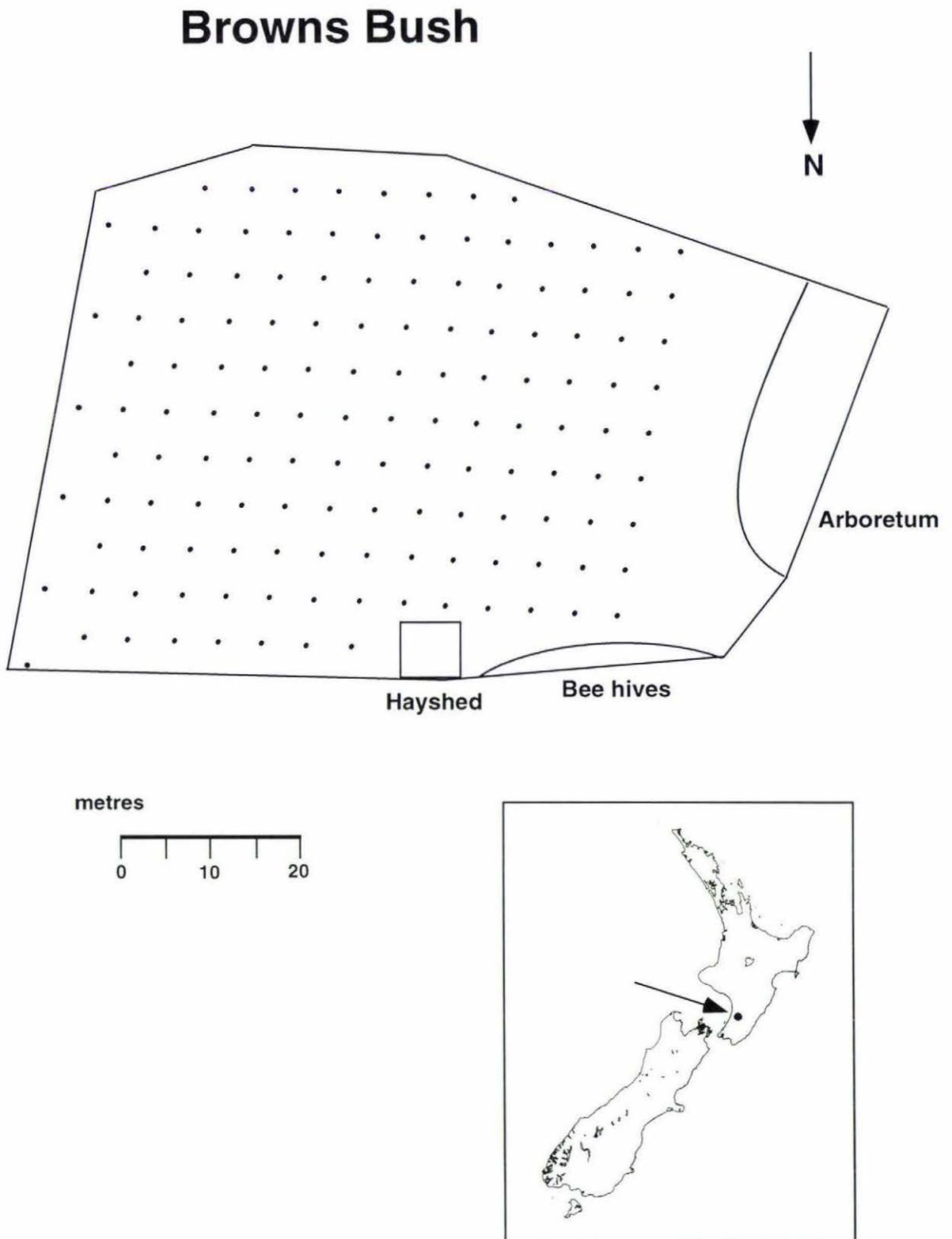


Figure 2.1. Map of Browns Bush, Levin (Latitude 40°40'S, Longitude 175°16'E) showing the arrangement of the pitfall traps in a 5 x 5 m grid. The arboretum contains a number of planted native trees that do not naturally occur in the area (see Appendix 1).

2.2.2 Carabid species in this study

This study focussed on the two largest species of carabid beetle at Browns Bush: *Mecodema oconnori* (described in Britton 1949), and *Megadromus capito* (Britton 1940) (see Appendix 2). Both species are common on the lowland plains of Horowhenua and Manawatu (Townsend 1994).

The genus *Mecodema* belongs to the primitive tribe Broscini, which has its centre of diversity in the southern hemisphere (Britton 1949). *Mecodema oconnori* is described as subapterous, fossorial, hydrophilous to mesophilous, and a slow runner (André Larochelle and Marie-Claude Larivière, pers. comm. 2000). *Mecodema oconnori* is considered ground-dwelling, although individuals have been known to climb several metres (Ian Townsend, pers. comm. 1999). Their diet consists of a variety of smaller invertebrates such as earthworms (I. Townsend, pers. comm. 1999) and small spiders (A. Larochelle and M-C. Larivière, pers. comm. 2000). *Mecodema oconnori* was described by Hudson as one of the commonest species of *Mecodema* in New Zealand (cited in Britton 1949).

Megadromus capito is a member of the tribe Pterostichini, which is one of the largest tribes in New Zealand, with 77 described species, and an estimated 25 un-described species (A. Larochelle and M-C. Larivière, pers. comm. 2000). *Megadromus capito* is described as subapterous, fossorial, mesophilous, a moderate runner, and a good burrower (*ibid*). Their diet consists of small arthropods, mites and spiders (*ibid*).

2.2.3 Determining the gender of each species

In *M. oconnori*, as in all broscines, males may be differentiated from females by several morphological features without the need for dissection. Firstly, male *Mecodema* usually have single setae at the base of the last abdominal sternite, whereas females always have two or more setae (I. Townsend, pers. comm. 1999) (Figure 2.2). It is sometimes also possible to observe the genitalia without dissection, as the beetles may evert part of their genitalia during handling. When viewed from underneath, the male genitalia are asymmetrical, while the female's are symmetrical. The male elytra are also usually proportionally wider than those of the female.

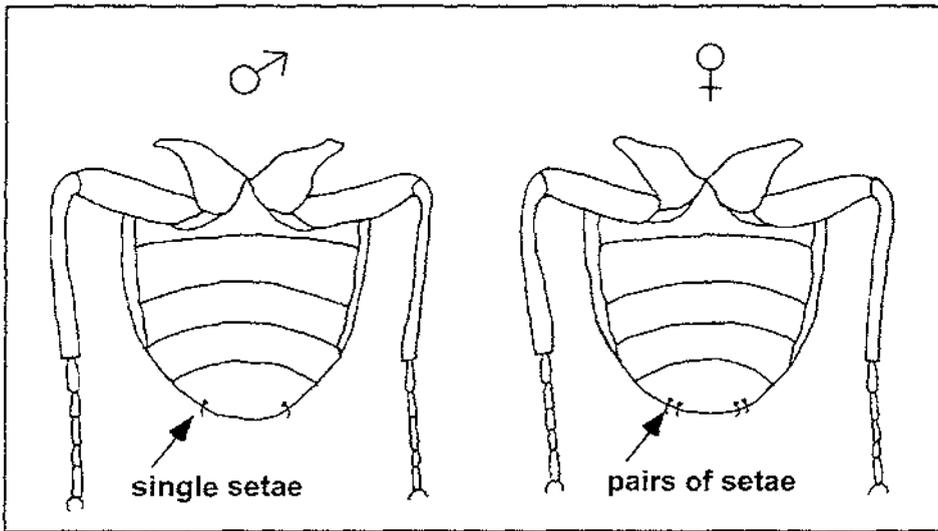


Figure 2.2. Characteristics of *Mecodema oconnori* (Broscini) used to determine gender. Males (left) have single setae at the base of the last abdominal sternite, whereas females (right) have pairs of setae.

In *Megadromus capito*, as in all pterostichines, males may be identified by the presence of expanded front tarsal segments (I. Townsend, pers. comm. 1999) (Figure 2.3).

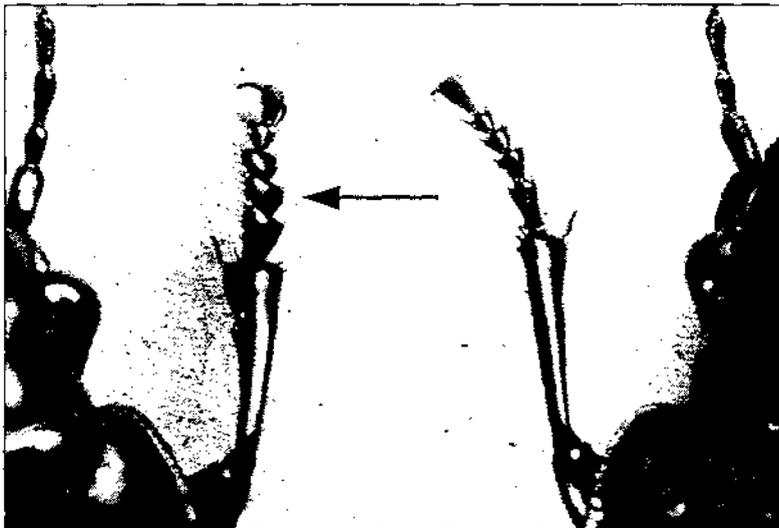


Figure 2.3. Characteristics of *Megadromus capito* (Pterostichini) used to determine gender. Front tarsal segments of male (left) and female *M. capito*. Males have expanded front tarsi (arrow). Photograph by Felix Collins.

2.2.4 Manual searches of habitat resting sites

Manual searches were carried out under habitat resting sites at Browns Bush for *Mecodema oconnori* and *Megadromus capito*. ‘Habitat resting sites’ were defined as any available resting site for carabid beetles such as fallen trees, ponga logs (Figure 2.4), pieces of timber, and corrugated iron (Cover plate 3). A total of 99 sites were classified into one of five categories: wood, ponga, timber, metal, or rubber mat. The first two types came from natural tree falls that occurred in the forest, whereas the other types were made from artificial materials that had been left in the forest. Each resting site was individually marked and its position recorded in relation to a fixed reference point using a sighting compass and measuring tape. Searches of all sites were carried out approximately weekly from April 1999 to March 2000, except in January 2000. A number of preliminary searches were also made in February and March 1999 to identify all of the potential resting sites in the forest. Occasional visits were also made at other times throughout 2000.



Figure 2.4. Ponga log used as a resting site by carabids at Browns Bush. Manual searches of these sites were carried out in order to investigate habitat occupancy by *Mecodema oconnori* and *Megadromus capito*. Photograph by Felix Collins.

All beetles (except *H. mucronata*) were individually marked using numbered Queen bee labels (Christian Graze, Weinstadt, Germany) which were attached to the beetle using Supa glue™ (Selleys). Labels were placed in the middle of the pronotum of *M. oconnori*, and in the middle of the elytra of *M. capito*. Total body length (from the tip of the mandible to the end of the abdomen) was measured for each beetle using vernier callipers. Several other morphological measurements were also taken from *M. oconnori*: maximum pronotum width, maximum pronotum length, maximum elytra width, and maximum elytra length (all in mm). All beetles were weighed to the nearest 0.01 g using portable field scales (Jadever SNUG 300™, Ansutek Commercial Suppliers). All beetles were marked and measured in the field, and then released where they were originally found within an hour of capture.

2.2.5 Live capture pitfall trapping

A total of 147 pitfall traps were used to carry out a mark-recapture experiment on *Mecodema oconnori* and *Megadromus capito* at Browns Bush. Any other carabid beetle species caught in the traps (e.g. *Holcaspis mucronata*) were recorded, but were not individually marked or sexed. The pitfall traps were arranged in a 5 x 5 metre grid containing 141 traps (Figure 2.1). However, due to the irregular shape of Browns Bush, there were not always equal numbers of traps in each row. An additional row of six traps, 10 metres apart, was also placed on the eastern edge of the forest in order to sample the forest boundary there.

Each pitfall trap consisted of a plastic food container (diameter 10.2 cm) sunk into the ground so that the top of the container was level with the soil surface (Figure 2.5). A plastic dinner plate mounted on two metal pins was placed over it, in order to prevent rain and leaf litter from entering the trap. A few centimetres of soil and leaf litter (from the study site) were placed in the bottom of each trap to provide shelter for the beetles. When the traps were not in use, they were left in place and sealed with a plastic lid.

Beetles were individually marked using numbered bee labels, and a number of morphological measurements were taken from each carabid beetle as described above (Section 2.2.4). All beetles were marked and measured in the field, then released within an hour of capture on the southern side of the pitfall trap they were caught in, within one metre of the trap.

Live pitfall traps were operated in November and December 1999, and February and March 2000, on a total of nine trapping occasions. On each occasion, the containers were left open for approximately 24 hours. To allow a comparison between the two sampling methods, searches of resting sites were carried out on the same day that the live pitfall traps were opened up.



Figure 2.5. Live capture pitfall trap used in the mark-recapture study of carabids at Browns Bush. Traps were filled with leaf litter and soil only. Photograph by Felix Collins.

2.2.6 Rodent tracking tunnels

In order to determine the densities of potential predators prior to the live pitfall trapping experiment, nine tracking tunnels were set up in a grid at 25 metre intervals throughout the forest (for design of tracking tunnels see Bennett 2001). The tracking papers were treated with ferric chloride dye, and the tunnels were baited with peanut butter. Tracking was carried out in August, September, and November 1999, and tunnels were run for three consecutive nights each time (see Appendix 3).

2.2.7 Statistical analyses

Pearson chi-square tests were used to determine whether there were significant differences between the sex ratios of each species caught by the two sampling methods (SYSTAT 6.0, SPSS Inc. 1996). T-tests were used to determine whether there were significant differences in the mean mass and length of males and females of each species (SYSTAT 6.0). Principle component analysis and canonical variate analysis were carried out on the morphological measurements of *M. oconnori* to see whether there were differences in morphology between the two sexes. The variables used in the analysis were total body length, maximum pronotum width, maximum pronotum length, maximum elytra width, maximum elytra length, and body mass. Discriminant analysis was used to see how accurately *M. oconnori* individuals might be assigned to a particular sex using a linear discriminant function. All multivariate statistical analyses were performed using SAS 6.12 (SAS Institute Inc. 1996).

2.3 RESULTS

2.3.1 Abundance of carabids at Browns Bush

A total of 698 carabid beetles were captured at Browns Bush from February 1999 to March 2000 using manual searches of habitat resting sites and live capture pitfall trapping. *Mecodema oconnori* comprised 48.1% of the carabids caught (336 individuals), *Megadromus capito* 44.6% (311 individuals), and *Holcaspis mucronata* 7.3% (51 individuals). The number of *M. oconnori* and *M. capito* males and females caught by the two different sampling methods is shown in Table 2.1. A total of 262 *M. oconnori* and 260 *M. capito* were found in habitat searches, and 74 *M. oconnori* and 51 *M. capito* were captured in live pitfall traps (Table 2.1). Fifty-one *H. mucronata* were also caught in the live pitfall traps, but the sex of these individuals was not determined.

Table 2.1. Total number of *Mecodema oconnori* and *Megadromus capito* caught in searches of habitat resting sites and live pitfall traps at Browns Bush (February 1999 - March 2000).

Sampling method	<i>Mecodema oconnori</i>		<i>Megadromus capito</i>		Total
	Males	Females	Males	Females	
Habitat searches	166	96	158	102	522
Live pitfall traps	35	39	32	19	125
TOTAL	201	135	190	121	647

2.3.2 Sex ratio

Overall, males of both species were more abundant than females, however there was a difference in the sex ratio of *M. oconnori* caught by the two sampling methods (Table 2.2). 63.4% of the *M. oconnori* individuals caught in habitat searches were male, whereas only 47.3% of the individuals in the live pitfall traps were male, and this difference was significant (χ^2 test, $df = 1$, $p = 0.013$). In contrast, the sex ratio of *M. capito* was relatively constant, with 60.8% of the beetles caught in habitat searches being male, compared to 62.7% in the live pitfalls (χ^2 test, $df = 1$, $p = 0.791$).

Table 2.2. Sex ratios of *Mecodema oconnori* and *Megadromus capito* caught in searches of habitat resting sites and live pitfall traps at Browns Bush (February 1999 - March 2000).

Sampling method	Sex ratio (males : females)	
	<i>Mecodema oconnori</i>	<i>Megadromus capito</i>
Habitat searches	1 : 0.58	1 : 0.65
Live pitfall traps	1 : 1.11	1 : 0.59

2.3.3 Morphological measurements

2.3.3.1 *Megadromus capito*

Megadromus capito was the smaller of the two carabid species (Table 2.3), with a body length ranging from 19.90 – 24.60 mm for males, and 18.94 – 24.80 mm for females. Body weight ranged from 0.17 – 0.54 g for males, and 0.19 – 0.61 g for females. The frequency distribution of *M. capito* body lengths shows a relatively normal distribution for both sexes, and a considerable amount of overlap between males and females (Figure 2.6). Consequently, there was no significant difference between the mean body mass of males and females (t-test, df = 304, p = 0.114), and a marginally significant difference in mean body length (t-test, df = 306, p = 0.047) (Table 2.3).

Table 2.3. Mean body length and mean body mass of *Mecodema oconnori* and *Megadromus capito* at Browns Bush (\pm standard error).

Measurement	<i>Mecodema oconnori</i>		<i>Megadromus capito</i>	
	Males	Females	Males	Females
Mean body length (mm)	36.79 \pm 0.12	33.75 \pm 0.12	22.47 \pm 0.07	22.05 \pm 0.10
Mean body mass (g)	1.51 \pm 0.02	1.11 \pm 0.01	0.39 \pm 0.00	0.37 \pm 0.01

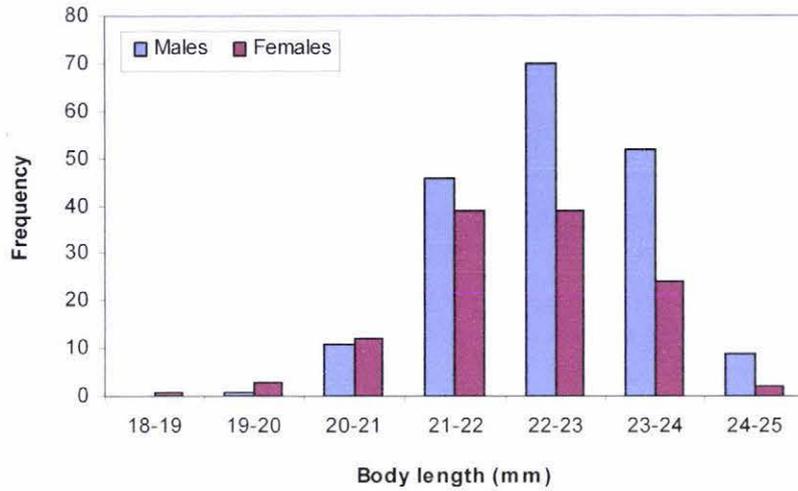


Figure 2.6. Frequency distribution of body lengths of *Megadromus capito* males and females at Browns Bush (n = 310).

Body length and mass were significantly correlated in both males (Pearson correlation = 0.777, $p < 0.001$) and females (Pearson correlation = 0.653, $p < 0.001$), although there was a considerable amount of spread around the general trend (Figure 2.7). For example, a number of females were heavier than males, and several males were lighter than expected from their body size.

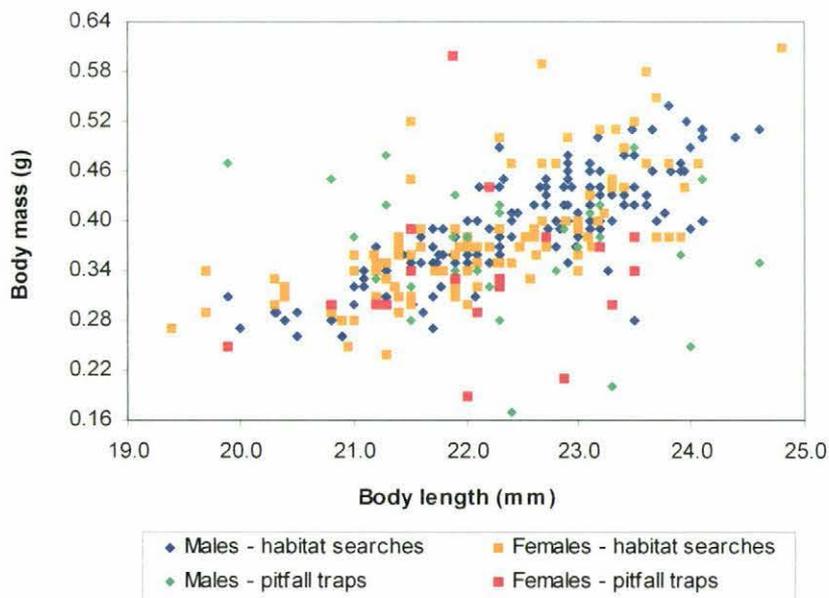


Figure 2.7. Relationship between body mass and length of *Megadromus capito* males and females at Browns Bush (n = 306).

2.3.3.2 *Mecodema oconnori*

The body length of *M. oconnori* ranged from 31.30 – 41.20 mm for males, and 30.14 – 37.10 mm for females, while mass ranged from 0.88 – 2.38 g for males, and 0.72 – 1.56 g for females. The frequency distribution of *Mecodema oconnori* body lengths shows a bimodal normal distribution, with males and females having separate maxima (Figure 2.8). There were significant differences in mean body length (t-test, $df = 331$, $p < 0.001$) and body mass (t-test, $df = 331$, $p < 0.001$) between the two sexes, with males being significantly larger and heavier than females.

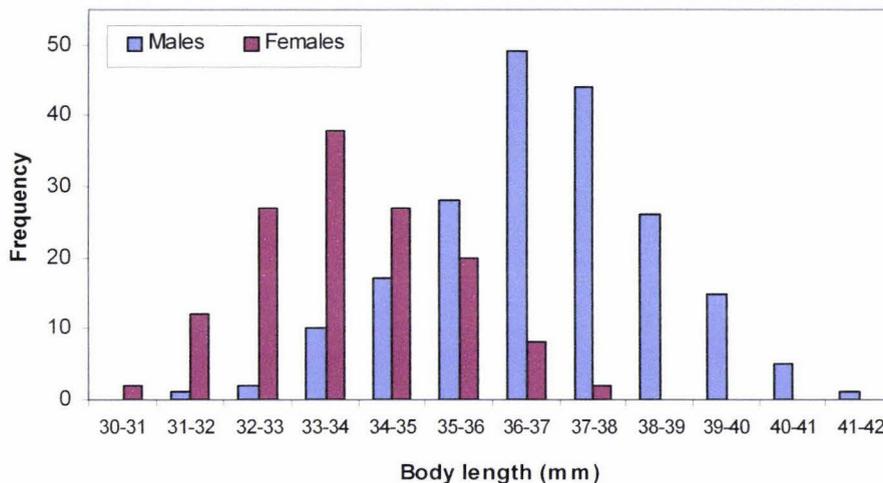


Figure 2.8. Frequency distribution of body lengths of *Mecodema oconnori* males and females at Browns Bush (n = 336).

There was a significant correlation between body length and mass of both males (Pearson correlation = 0.806, $p < 0.001$) and females (Pearson correlation = 0.748, $p < 0.001$) (Figure 2.9). Generally, the body lengths and masses of males and females were well separated, although there was some overlap. Several of the male *M. oconnori* were noticeably smaller than usual, and were well below the mean body length and mass of *M. oconnori* females. These males also appeared to have reddish legs (M. Hutchison, pers. obs.).

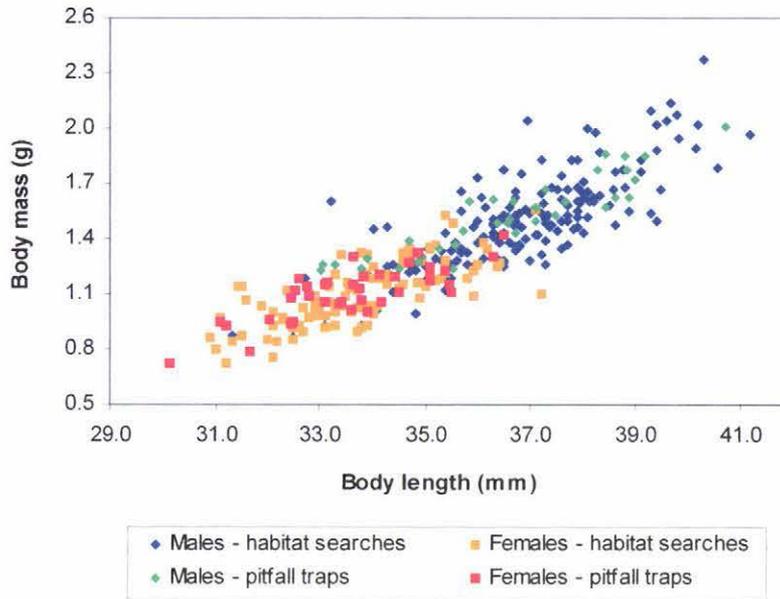
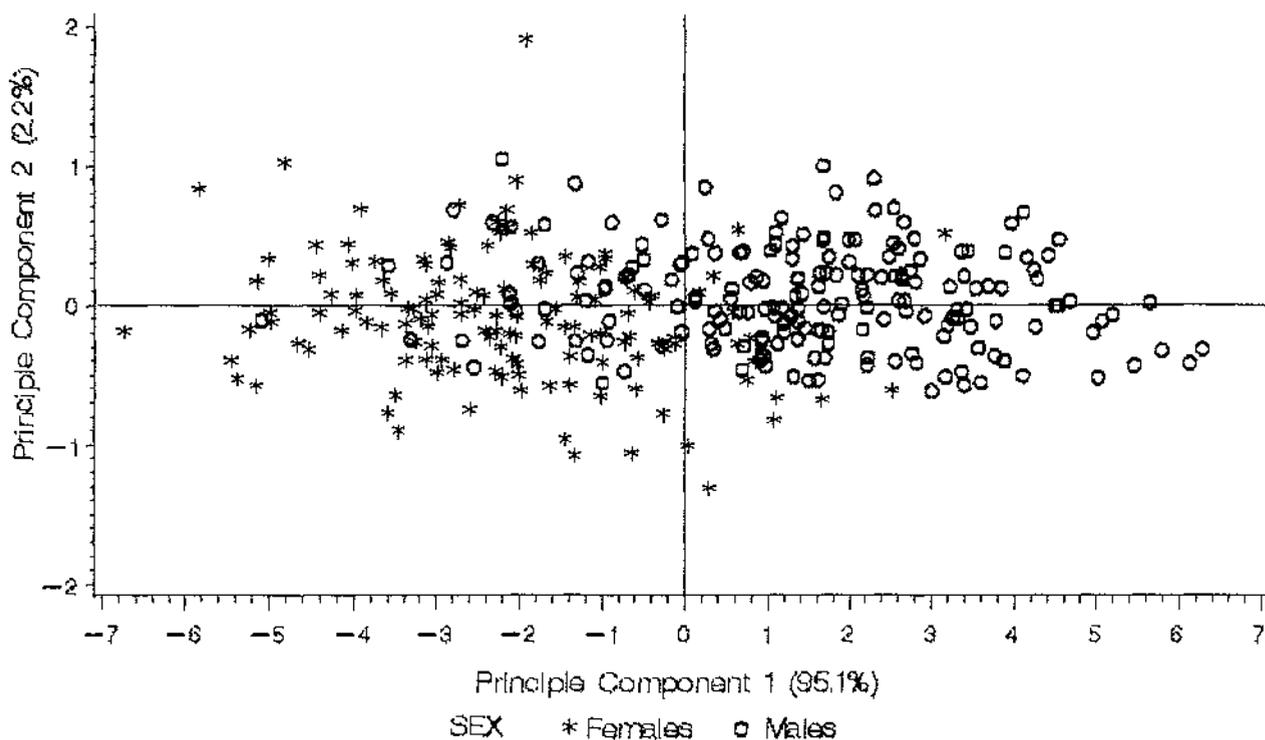


Figure 2.9. Relationship between body mass and length of *Mecodema oconnori* males and females at Browns Bush (n = 333).

Principle component analysis of the six morphological measurements of *M. oconnori* revealed that the two sexes could be adequately separated using only one of the six measurements: total body length (Figure 2.10a). The first principle component accounted for 95.1% of the variation between the two sexes, and was dominated by a strong positive score for *total body length* (see Appendix 4a). Therefore, the first axis represents an increase in length, with females at the negative end of the axis being shorter than males at the positive end. The second principle component did not separate the sexes much further (accounting for only 2.2% of the variation), but had a strong negative score for *elytra length*. Canonical variate analysis (Figure 2.10b) found that the greatest difference between males and females was in their pronotum width, as the first canonical variate had a strong positive score for *pronotum width* (see Appendix 4b). This indicates that the females at the negative end of this axis tend to have narrower pronotums than the males at the positive end.

Discriminant analysis was also used to see how accurately *Mecodema oconnori* individuals might be assigned to a particular sex using the six morphological measurements. Overall, 90.4% of the females and 84.8% of the males were correctly classified using the linear discriminant function, with an overall error rate of only 12.4%.

(a) Principle component analysis



(b) Canonical variate analysis

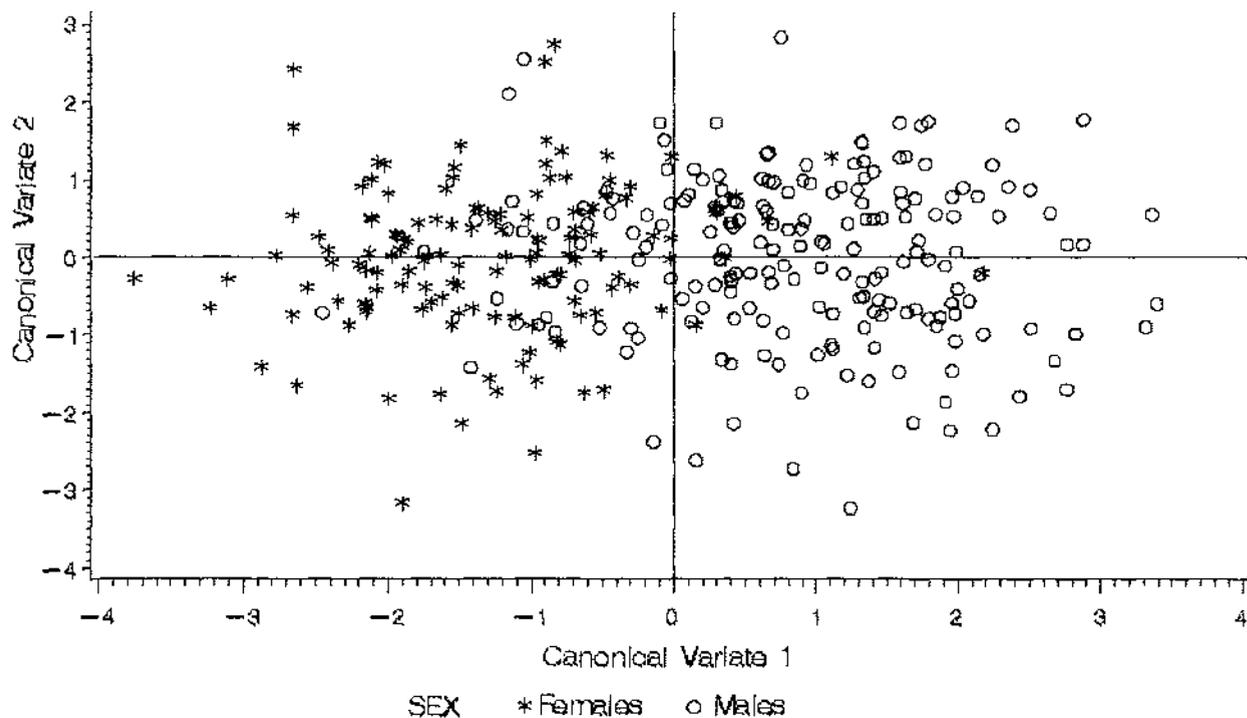


Figure 2.10. Multivariate analysis of *Mecodema oconnori* body measurements: (a) Principle component analysis, and (b) Canonical variate analysis. Only the first two axes are shown.

2.4 DISCUSSION

2.4.1 Sex ratio

Males of both *M. oconnori* and *M. capito* were generally more common than females, but the two sampling methods produced different sex ratios of *M. oconnori*. More *M. oconnori* females than expected were caught in live pitfall traps compared to manual searches of resting sites. However, care is required when interpreting sex ratios from pitfall trapping data because the catch is a combination of both activity and abundance, which are in turn affected by a number of abiotic and biotic factors (Briggs 1961, Mitchell 1963b, Southwood 1978, Adis 1979, Halsall & Wratten 1988, Holopainen 1992, Topping & Sunderland 1992) (see Chapter Three, section 3.4.3). Male and female carabids respond differently to these factors and may possess different “catchabilities” (Ericson 1979). The use of preservatives, for example, has been shown to influence the catch and sex ratio of beetles caught in pitfall traps, as males and females may be differentially attracted to these substances (Luff 1968, Ericson 1979, Holopainen 1990, Holopainen 1992). This means that the higher proportion of *M. oconnori* females caught in pitfall traps (compared to searches) may reflect a higher activity rate or easier ‘trappability’ than males, rather than greater abundance.

2.4.2 Morphological measurements

Mecodema oconnori is obviously sexually dimorphic, with males being significantly larger and heavier than females. In contrast, *M. capito* males and females are similar in size and weight, although females may be considerably heavier than males when gravid. Females of both species showed greater variation than males in the body mass to length ratio. Females with a high body mass to length ratio are likely to be gravid, because the eggs may increase body mass considerably (see Chapter Four, section 4.3.7). Several *M. capito* individuals were much lighter than expected, and these appeared to be newly hatched tenerals because they had soft, pale exoskeletons.

Multivariate techniques were used in this study to differentiate the sexes of *M. oconnori* based on a number of morphological measurements. Both principle component analysis (PCA) and canonical variate analysis (CVA) showed clear separation between males and females along the first axis. In PCA this axis represented an increase in total body length from females to males, while CVA revealed that the maximum separation between the sexes was found in their pronotum width, with males having wider pronotums than females. In a similar study, Baguette *et al.* (1990) used principle component analysis and canonical variate analysis of morphological criteria to separate several species of *Abax* (Carabidae), and to detect differences in individuals of the same species from different habitats. The results from the discriminant analysis of *M. oconnori* indicate that it is possible to accurately predict the sex of an unknown individual using only simple morphological measurements.

Several of the male *M. oconnori* found at Browns Bush were noticeably smaller than usual, and had reddish legs. These males were misclassified as females in the discriminant analysis because of their small size and weight. Ian Townsend (pers. comm. 1999) has suggested that *M. oconnori* may comprise two similar species. Several genera in New Zealand which normally have black legs may also display red-legged forms (Townsend 1965). Within the genus *Mecodema*, several species have been separated based on this characteristic (Townsend 1965). It is possible that the small males with red legs at Browns Bush may be a separate species from the more common *M. oconnori*, although it is difficult to establish this without extensive taxonomic work and genetic analysis.

2.4.3 Factors affecting adult body size

Adult body size in carabids is primarily determined by factors affecting the larval stage, as this is the main growth period (Lövei and Sunderland 1996). Both temperature and food supply affect larval development time, and hence the final size and weight of adult beetles (van Dijk & den Boer 1992, van Dijk 1994, Baumgartner *et al.* 1997, Ernsting & Isaaks 1997). Adult body size in *Notiophilus biguttatus* Fabricius was affected by temperature during the larval period, because temperature strongly influenced the feeding rate of larvae (Ernsting *et al.* 1992). Limiting the food supply resulted in a prolonged larval period, lower growth rate, and smaller adult body size. Adult body size, in turn, may affect the

probability of survival, with smaller beetles having a higher mortality risk, and a lower degree of reproductive success (van Dijk 1994, Baumgartner *et al.* 1997).

Carabid body weight can fluctuate dramatically depending on the food supply and state of satiation (van Dijk 1994). Chaabane *et al.* (1993) found that *Abax ater* Villers typically consumed 7-19% of their body weight per day in the laboratory, however carabids may consume up to 80% of their own weight in one meal (van Dijk 1994). Male *M. oconnori* at Browns Bush were often found with hugely distended abdomens, indicating that they had recently consumed a large meal. One male was unusually heavy when initially found, and was subsequently kept in captivity for several months on a diet of *Tenebrio* larvae (mealworms), as this is the most commonly used artificial diet for raising carabids (Goulet 1976). The male lost weight rapidly when it was starved for several days, but once food was supplied again it regained weight until a relatively constant level was reached (see Appendix 5).

Carabids in the field regularly experience food shortage (Lenski 1984, Ernsting *et al.* 1992, Lövei & Cartellieri 1996), and can survive long periods of starvation e.g. up to 70 days in *Pterostichus lepidus* Leske (van Dinther 1964, cited in Ernsting *et al.* 1992). Loreau (1983, cited in Chaabane *et al.* 1993) found that about half of the carabids caught in the field had empty stomachs, which implies that beetles may only feed once or twice a week. Nelemans (1988) compared adult body size in field-collected and laboratory-reared specimens of *Nebria brevicollis* Fabricius and concluded that in the field larval food supply was limited.

2.4.4 Conclusions

Mecodema oconnori and *Megadromus capito* show different degrees of sexual dimorphism, with *M. oconnori* males and females being clearly separated by their body size. Males of both species were generally more common than females, although different sampling methods produced different sex ratios. Further evidence is given that *M. oconnori* may comprise more than one species. Multivariate analysis of morphological data appears to be an important tool for both taxonomic and ecological studies.

Chapter Three

Habitat use and movement of two endemic carabid beetles in a native forest remnant



Cover plate 3. Sheets of corrugated iron used as resting sites by carabid beetles at Browns Bush. Photograph by Felix Collins.

“Judging simply from their structure, habits and economy, there are reasons why beetles ought to excel every other class of organised beings as exponents of the past geography of the globe”

Andrew Murray (1870)

Habitat use and movement of two endemic carabids in a native forest remnant

3.1 INTRODUCTION

Studying the spatial behaviour of individuals is an important part in understanding the population dynamics of carabid species (Turchin 1991, Firle *et al.* 1998). Carabidae often show aggregated or clumped distribution patterns (Greenslade 1963b, Reise and Weidemann 1975, Luff 1986, Niemelä *et al.* 1986, Grüm 1990, Gruttke & Weigmann 1990, Niemelä *et al.* 1992, Blake *et al.* 1994, Kennedy 1994), and these may be caused by habitat patchiness or uneven prey distributions (Mols 1979, Bryan & Wratten 1984, Weseloh 1987). They may also result from chemical communication between carabid beetles via an aggregation and/or sex pheromone (Luff 1986). Carabids may respond to microhabitat cues, such as soil moisture (Lindroth 1949, Niemelä *et al.* 1987, de Vries *et al.* 1996, Eyre & Luff 1990, Niemelä *et al.* 1992, Gardner *et al.* 1997, Huk & Kuhne 1999) or vegetation cover (Mitchell 1963b, Baguette 1993, Magura & Tothmeresz 1997), which they orient towards (or against), thus determining their habitat use (Evans 1983).

Interspecific competition is believed by some to be an important force affecting carabid assemblages (Lenski 1982, 1984, Loreau 1986, Müller 1987, Griffith & Poulson 1993, Currie *et al.* 1996), however others have suggested that interspecific competition is not common among carabids (den Boer 1980, 1985, 1986, Hengeveld 1985, Andersen & Skorping 1990, Loreau 1990b, Niemelä 1993). Interspecific competition can be defined as an interaction in which individuals of different species have a negative effect upon each other by affecting access to resources (Alley 1982). The interactions may take place either 'indirectly' through resource (exploitative) competition or 'directly' through interference competition (Keddy 1989). Patterns of resource use, such as habitat occupancy or temporal activity patterns, may suggest whether competitive interactions are occurring.

Many studies overseas have investigated the daily movement patterns and long range dispersal abilities of carabid beetles (Greenslade 1963a, den Boer 1970, Baars 1979b, Rijnsdorp 1980, Wallin & Ekbohm 1988, Wallin 1991, Charrier *et al.* 1997, Chapman *et al.* 1999, Murrell & Law 2000). Complex mathematical and computer models have been applied to different types of movement, and these allow predictions of an individual's range over its lifetime (Drach & Cancela da Fonseca 1990, Firlie *et al.* 1998). However, nothing is known about the dispersal abilities of New Zealand carabids, yet this may be particularly important for their conservation in fragmented habitats (Lövei & Cartellieri, in press).

A variety of abiotic and biotic factors affect carabid activity and movement. Abiotic factors include climatic variables such as temperature (Barlow 1973, Baars 1979b, Luff 1982, Brunsting 1983, Atienza *et al.* 1996, Baumgartner *et al.* 1997, Honek 1997) and rainfall (Ericson 1979), or habitat characteristics such as vegetation structure (Greenslade 1964b, Crist & Ahern 1999). Biotic factors include physiological aspects such as the hunger level (Grüm 1971, Mols 1979, Wallin 1991, Frampton *et al.* 1995) and reproductive state (Lys & Nentwig 1991) of the individual animal.

There are a variety of methods for sampling epigeal arthropods such as carabids, but these vary considerably in their effectiveness at trapping each species, and tend to sample quite different sections of the carabid assemblage (Williams 1959, Holland & Smith 1999). Comparisons between sampling techniques are rare, but such information would be useful when trying to select the most appropriate technique for the species under investigation (Holland & Smith 1999). Moeed & Meads (1987) advised using more than one sampling method to study New Zealand forest invertebrates because species may be active in several different habitats in any 24-hour period.

Pitfall traps have been used extensively in ecological field studies of carabid beetles, although they have been criticised by some authors (Greenslade 1964b, Southwood 1978, Adis 1979, Halsall & Wratten 1988, Andersen 1995). Pitfall trapping has a number of limitations for studying the population dynamics of carabids because the number of beetles caught is not solely a reflection of population size, but is a combination of both abundance and activity (Halsall & Wratten 1988, Thomas *et al.* 1998). Pitfall trap catches are affected by a number of factors such as temperature (Baars 1979a, Atienza *et al.*

1996), humidity (Ericson 1979), vegetation cover (Greenslade 1964b), trap design (Luff 1975, Adis 1979, Baars 1979a), preservative type (Luff 1968, Ericson 1979, Holopainen 1990), hunger level (Mols 1979, Chiverton 1984), reproductive state, and the “catchabilities” of individual species (Greenslade 1964b, Luff 1975, Ericson 1979, Halsall & Wratten 1988, Morrill *et al.* 1990). Despite these limitations, pitfall trapping remains the most commonly used method of sampling carabid populations, and may produce meaningful results provided the data are given careful consideration (Thiele 1977, Southwood 1978, Ericson 1979, Topping & Sunderland 1992, Spence 1994, Digweed *et al.* 1995).

Only a few studies have made direct comparisons between pitfall trapping and direct counting methods (e.g. Gilbert 1956, Briggs 1961, Mitchell 1963b, Gist & Crossley 1973, Andersen 1995, Topping & Sunderland 1992, Spence & Niemelä 1994), but this is essential for isolating the components of activity and density in pitfall trap catches (Thomas *et al.* 1998). Several different sampling methods were used in my study to determine which techniques were most suitable for studying the habitat use and movement of the species concerned. Manual searches provide an estimate of the absolute abundance of species, whereas pitfall trapping mainly reflects beetle activity. Using harmonic radar for tracking beetles has a number of advantages over other methods because it allows the movement of individuals to be followed directly. Prior to my study, harmonic radar tracking of carabid beetles had only been attempted once in New Zealand, over a very short time (Lövei *et al.* 1997).

Obtaining reliable data on the density of carabids is essential if their ecology and conservation status, as well as their importance as biological control agents, is to be accurately determined. Numbers of beetles caught in pitfall traps alone, however, do not provide reliable estimates of absolute population density (Topping & Sunderland 1992, Anderson 1995, French & Elliott 1999), and estimation of the true population density of carabids is extremely difficult (Thiele 1977). Mark-recapture techniques have been used successfully to study carabid population dynamics, and population models such as the Jolly-Seber model are commonly used to estimate carabid population size from mark-recapture data (Mitchell 1963b, Greenslade 1964a, den Boer 1979b, Ericson 1977, Luff 1982, Thomas *et al.* 1998).

The aim of this chapter was to investigate the habitat use of two endemic carabids, *Mecodema oconnori* Broun and *Megadromus capito* (White), within a native forest remnant, and to determine whether there were differences in the habitats occupied by the two species. The movement patterns of individual beetles were followed in order to learn more about their locomotory activity and spatial behaviour. A range of sampling methods was used in order to compare the results from different techniques, and further understand the factors affecting beetle activity and movement.

3.2 METHODS

3.2.1 Study site

The study was carried out at Browns Bush in the Horowhenua district, North Island, New Zealand (Figure 2.1). Browns Bush is a privately-owned lowland forest remnant of less than 1 ha situated 4 km south of Levin (see Chapter Two, section 2.2.1 for a full description).

3.2.2 Manual searches of habitat resting sites

The study focussed on the two largest species of carabid at Browns Bush: *Mecodema oconnori* (Broscini), and *Megadromus capito* (Pterostichini). Some casual observations were also made of *Holcaspis mucronata* (Broun) (Pterostichini). Manual searches for *M. oconnori* and *M. capito* were carried out under habitat resting sites at Browns Bush in order to investigate habitat occupancy and beetle movement (see Chapter Two, section 2.2.4 for a full description of this method). A total of 99 resting sites were classified into one of five categories: wood, ponga, timber, metal, or rubber mat. Each resting site was individually marked and its position recorded in relation to a fixed reference point using a sighting compass and measuring tape.

Searches of all sites were carried out approximately weekly from April 1999 to March 2000, except in January 2000. A number of preliminary searches were also made in February and March 1999 to identify all of the potential resting sites in the forest. All beetles (except *H. mucronata*) were individually marked using numbered bee labels (see Chapter Two, section 2.2.4). Beetles were marked and measured in the field, and then released where they were originally found within an hour of capture. The position of each beetle was measured in relation to a fixed reference point using a sighting compass and measuring tape.

3.2.3 Live capture pitfall trapping

A grid of 147 pitfall traps was used to carry out a mark-recapture experiment on *Mecodema oconnori* and *Megadromus capito* at Browns Bush (see Chapter Two, section 2.2.5 for a full description of this method). Live pitfall traps were operated in November and December 1999, and February and March 2000, on a total of nine trapping occasions. On each occasion, the containers were left open for approximately 24 hours. Beetles were occasionally found underneath the pitfall traps when they were being opened up for sampling, and these individuals were marked and their positions recorded in the same way as for habitat resting sites. To allow a comparison between the two sampling methods, searches of resting sites were carried out on the same day that the live pitfall traps were opened up.

3.2.4 Harmonic radar tracking

Tracking of carabids was carried out using a portable transmitter-receiver made by Recco Rescue Systems, Sweden (called “harmonic radar”) (Figure 3.2). Harmonic radar was originally developed to locate avalanche victims, but it was first used to track invertebrate movements in the mid 1980s (Mascanzoni and Wallin 1986). The radar emits 1.7 W of continuous microwave radiation at a frequency of 917 MHz which is reflected by a passive reflector (called a “transponder”) at double the frequency (1834 MHz) (Mascanzoni & Wallin 1986, Lövei *et al.* 1997). The harmonic radar detects the reflected signal and transforms it into an audible signal. The advantage over other tracking methods is that the reflectors do not depend on an attached energy source, and are inexpensive to produce (Lövei *et al.* 1997). However, the reflected signal is not specific, and animals must be individually marked so they can be identified when found. Transponders used in this study were made from an S2 diode (provided by Recco Rescue Systems) soldered onto a piece of thin copper sheet, which had been cut and moulded into the shape of a carabid elytra. A thin flexible wire was soldered onto the other end of the diode to act as an aerial. The diode and copper sheet were then covered with a thin layer of Selleys Knead-it™ copper epoxy resin, which was sanded down to form a smooth surface (Figure 3.1). Transponders were then glued to the beetle’s elytra using Supa glue™ (Selleys). Detection distances for the transponders varied depending on the length of wire used for

the aerial. The aerials needed to be long enough to allow good reception, but short enough not to hinder beetle movement. An aerial length of 10 cm was used for most transponders, giving a maximum detection distance of approximately seven metres.

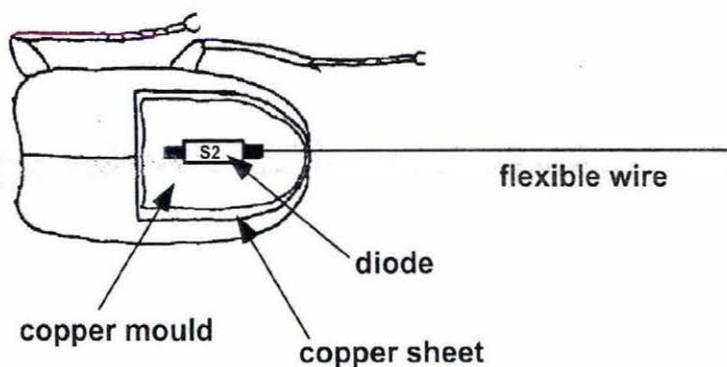


Figure 3.1. Transponder design used for harmonic radar tracking of carabids at Browns Bush. The copper sheet and diode are covered with Selleys Knead-it™ copper epoxy resin.



Figure 3.2. Harmonic radar tracking of carabids at Browns Bush. Photograph by Felix Collins.

A total of 26 *M. oconnori* and two *M. capito* at Browns Bush were fitted with transponders. Searching with harmonic radar was carried out the day after they were fitted with the transponders, and then at varying intervals. Harmonic radar tracking was also carried out at Browns Bush over night on two occasions, and beetles with transponders were located at hourly intervals for 24 hours.

3.2.5 Environmental variables

Air temperature at Browns Bush was recorded every two hours using a Hobo XT temperature data logger (Onset Computer Corporation) and a Tinytalk data logger (Gemini Data Loggers, UK) from mid-April 1999 to February 2000. The second temperature data logger stopped recording prematurely in mid-February 2000, so mean daily air temperature for February and March 2000 was taken from the Levin Weather Station (operated by NIWA), which is less than five kilometres from Browns Bush. The temperature recorded at Browns Bush was usually several degrees cooler than at the weather station, so a correction factor was used to make the Levin Weather Station data comparable with the data from Browns Bush. Mean monthly air temperature was calculated for both sites (see Appendix 6). Total daily rainfall measurements from January 1999 to March 2000 were also acquired from the Levin Weather Station (see Appendix 7).

The following environmental variables were measured at each pitfall trap location: leaf litter depth (cm), forest canopy cover (%), and vascular plant ground cover (%). A 1 x 1 metre quadrat (divided into 100 squares of 10 x 10 cm) was used to sample the environment immediately surrounding each trap. At each trap, four measurements of leaf litter depth (cm) were taken randomly, one from each quarter of the quadrat. Canopy cover was estimated for the forest canopy directly above the pitfall trap (an area of approximately 5 m²). The percentage ground cover of all vascular plant species below 30 cm was estimated, as well as the percentage ground cover of logs and tree trunks in each quadrat.

3.2.6 Statistical analyses and mapping

Pearson chi-square tests were used to determine whether there was a significant difference between the sex ratios caught by the two main sampling methods (habitat searches and live pitfall traps). Pearson chi-square tests were also used to investigate differences between the sexes in the proportions of recaptures and beetles that moved between resting sites. Analysis of variance (ANOVA) was used to determine whether there were differences between the species in their occupancy of the four types of resting sites. Two-way ANOVA (on both raw and \log_{10} transformed data) was used to determine whether there were significant differences between species and sex in the distances moved, and whether there was an interaction between species and sex. The relationship between temperature and rainfall and the number of carabids caught was analysed using Pearson correlations and Bonferroni probabilities. The data used for the correlation with rainfall were \log_{10} transformed because they were highly skewed. All statistical analyses were carried out using SYSTAT 6.0 (SPSS Inc. 1996).

For analysis of beetle movement, polar co-ordinates (distance and direction) were converted to rectangular X-Y co-ordinates using a Hewlett Packard 41C scientific calculator. The X-Y co-ordinates were used to create a map of the beetles' movement patterns using the program SIGMAPLOT 1.02 (Jandel Corporation 1994). The distance moved between sightings was calculated using basic trigonometry.

The spatial dispersion of carabids caught in the live pitfall traps was analysed by comparing the observed catches for each trap with those expected from a Poisson (random) distribution. An index of dispersion was calculated using the equation: $I = s^2 / x$, where I = index of dispersion, s^2 = variance, and x = mean (see Niemelä *et al.* 1986, Niemelä 1990). Index values close to one indicate an agreement with the Poisson series, i.e. random dispersion between the traps. Index values significantly greater than one (i.e. $s^2 > x$) indicate aggregated dispersion. The agreement of the index with the Poisson series was tested with a χ^2 test ($df = n-1$): $\chi^2 = I(n-1)$, where n is the number of sampling units. The power of the test is highly dependent on sample size, so the lower the catch per area, the more likely it is that the observed pattern will agree with a Poisson series.

3.3 RESULTS

3.3.1 Abundance of carabids at Browns Bush

A total of 698 carabid beetles were captured at Browns Bush over 14 months using manual searches of habitat resting sites and live pitfall trapping. *Mecodema oconnori* comprised 48.1% of the carabids caught (336 individuals), *Megadromus capito* 44.6% (311 individuals), and *Holcaspis mucronata* 7.3% (51 individuals). The number of *M. oconnori* and *M. capito* males and females caught by the two different sampling methods is shown in Table 3.1. Approximately equal numbers of *M. oconnori* (262) and *M. capito* (260) were found in the habitat searches, while slightly more *M. oconnori* were captured in the live pitfall traps (74 compared to 51 *M. capito*). Fifty-one *Holcaspis mucronata* were also caught in the live pitfall traps, although no comparison with searches can be made because they were not sampled using the latter method. There was a significant difference between the frequencies of male and female *M. oconnori* caught using the two sampling methods, with a higher proportion of females being caught in the live pitfall traps than in manual searches (χ^2 test, $df = 1$, $p = 0.013$) (also see Chapter Two section 2.3.2). However, there was no significant difference in the sex ratio of *M. capito* caught by the two methods (χ^2 test, $df = 1$, $p = 0.791$).

Table 3.1. Total number of *Mecodema oconnori* and *Megadromus capito* marked and recaptured in habitat searches and live pitfall traps at Browns Bush from February 1999 to March 2000.

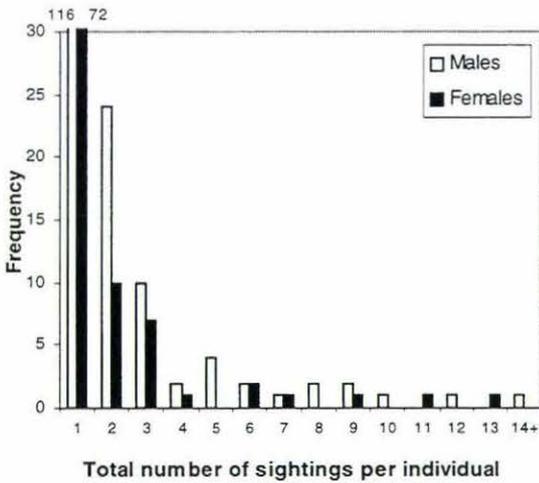
Sampling method	Number of beetles marked		Number recaptured (% of marked)		Overall recapture rate (%)
	Males	Females	Males	Females	
* Habitat searches					
<i>Mecodema oconnori</i>	166	96	50 (30.1%)	24 (25.0%)	28.2%
<i>Megadromus capito</i>	158	102	55 (34.8%)	41 (40.2%)	36.9%
* Live pitfall traps					
<i>Mecodema oconnori</i>	35	39	0 (0.0%)	1 (2.6%)	1.4%
<i>Megadromus capito</i>	32	19	2 (6.3%)	0 (0.0%)	3.9%

3.3.2 Recapture rates

3.3.2.1 Searches of habitat resting sites

The overall recapture rate was higher for *M. capito* than *M. oconnori*, although in both species less than 40% of marked beetles were recaptured (Table 3.1). There was no significant difference between the sexes in the proportion of beetles recaptured for *M. oconnori* (χ^2 test, $df = 1$, $p = 0.505$) or *M. capito* (χ^2 test, $p = 0.559$). *Mecodema oconnori* males were recaptured slightly more often than females (1.92 ± 0.19 times on average versus 1.76 ± 0.21), although there was no significant difference in the mean number of sightings per individual (t-test, $df = 260$, $p = 0.581$) (Figure 3.3a). In contrast, for *M. capito* the mean number of sightings per individual was higher for females (2.34 ± 0.35 versus 1.80 ± 0.12 for males), but again this difference was not significant (t-test, $df = 258$, $p = 0.091$) (Figure 3.3b). The maximum number of sightings of a single individual was 29 for a *M. capito* female, and 22 for a *M. oconnori* male.

(a) *Mecodema oconnori*



(b) *Megadromus capito*

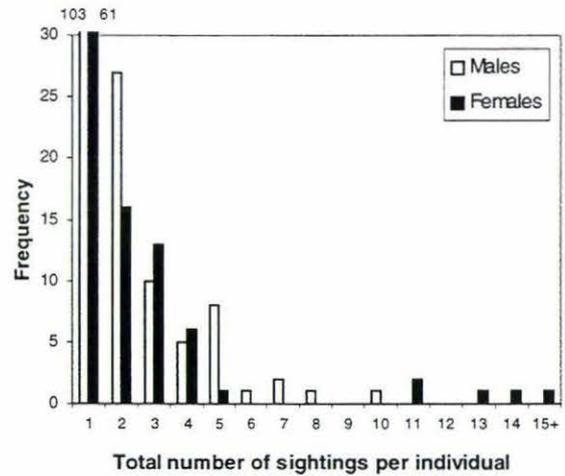


Figure 3.3. Frequency distribution of the number of sightings per individual for (a) *Mecodema oconnori* and (b) *Megadromus capito* caught in searches of resting sites at Browns Bush. NB. One *M. oconnori* male was seen 22 times, and one *M. capito* female was seen 29 times.

3.3.2.2 Live pitfall trapping

A total of 176 carabid beetles were captured in pitfall traps at Browns Bush over the nine trapping occasions: 74 *M. oconnori*, 51 *M. capito*, and 51 *H. mucronata*. However, very few *M. oconnori* and *M. capito* were recaptured in the pitfall traps, with an overall recapture rate of only 2.4% for both species combined (Table 3.1). Only two marked *M. oconnori* and four marked *M. capito* were recaptured in the live pitfall traps over the entire trapping period, and half of these were originally found in habitat searches. *Holcaspis mucronata* caught in the pitfall traps were not marked, so recapture rates could not be determined.

3.3.3 Comparison of sampling methods

In general, the two sampling methods tended to capture about the same number of *M. oconnori* and *M. capito*, and there was a strong correlation between their catches (Pearson correlation = 0.884, $n = 8$, $p = 0.004$) (Figure 3.4). However, in March, the number of beetles caught in the live pitfall traps dropped below the numbers being found in habitat searches.

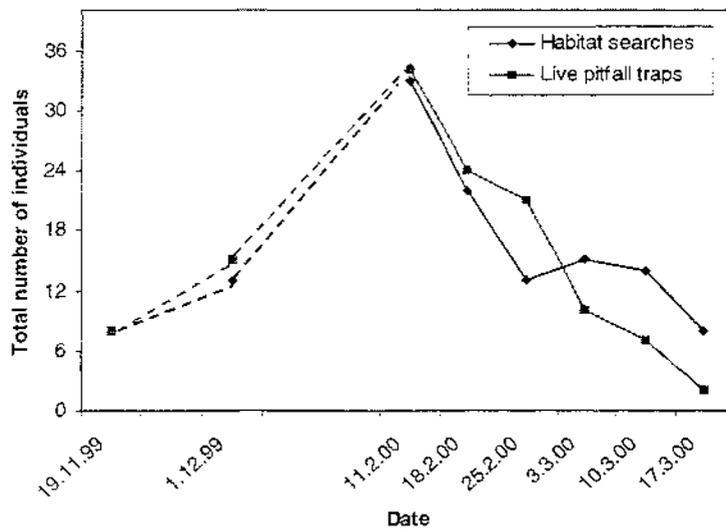


Figure 3.4. Total number of carabids (*Mecodema oconnori* and *Megadromus capito*) caught in searches of habitat resting sites versus live pitfall traps at Browns Bush. NB. Dotted line indicates sampling dates that were not at weekly intervals.

3.3.4 Occupancy of habitat resting sites

The number of beetles occupying each resting site over all the searching occasions was averaged to give a mean for each habitat type (Table 3.2). There was a significant difference in the overall mean occupancy of the different types of resting site (ANOVA, $df = 3$, $F = 10.778$, $p < 0.001$), with metal sheets being the most frequently occupied sites by both species (Table 3.2). This preference was particularly striking for *M. oconnori*, where metal sheets had a significantly higher occupancy level than all the other habitat types (Tukey post-hoc test, $p < 0.001$) (Figure 3.5). The two species showed differences in occupancy of the remaining habitat types, but the interaction between habitat type and species was not significant (Two-way ANOVA, $df = 3$, $F = 2.439$, $p = 0.066$).

The second most frequently occupied habitat type by *M. oconnori* was wood, closely followed by ponga, while very few individuals were found under timber (Figure 3.5). Four *M. oconnori* individuals were also found under a rubber mat during the study. In contrast, the second most frequently occupied habitat type by *M. capito* was timber, and this was just below the occupancy level for metal (Figure 3.5). The next most occupied habitat type for this species was ponga, while wood had the lowest level of occupancy.

Table 3.2. Mean occupancy of different types of resting site by *Mecodema oconnori* and *Megadromus capito* at Browns Bush (\pm standard error). # The number for 'Rubber mat' is not a mean because there was only one resting site of this type. * $p < 0.001$, ** $p < 0.01$ indicates a significant difference in mean occupancy between the habitat types (not including 'Rubber mat').**

Type of resting site	Number of sites	Mean occupancy by <i>Mecodema oconnori</i>	Mean occupancy by <i>Megadromus capito</i>	Overall mean occupancy
Wood	34	2.74 (± 0.91)	2.09 (± 0.41)	4.82 (± 0.96)
Ponga	30	2.60 (± 0.99)	5.03 (± 1.15)	7.63 (± 1.68)
Metal	22	9.10 (± 1.87)	6.86 (± 1.49)	15.55 (± 2.69)
Timber	12	1.33 (± 0.43)	6.42 (± 2.65)	7.75 (± 2.90)
# Rubber mat	1	4.00	0.00	4.00
p-value		< 0.001 ***	0.002 **	< 0.001 ***

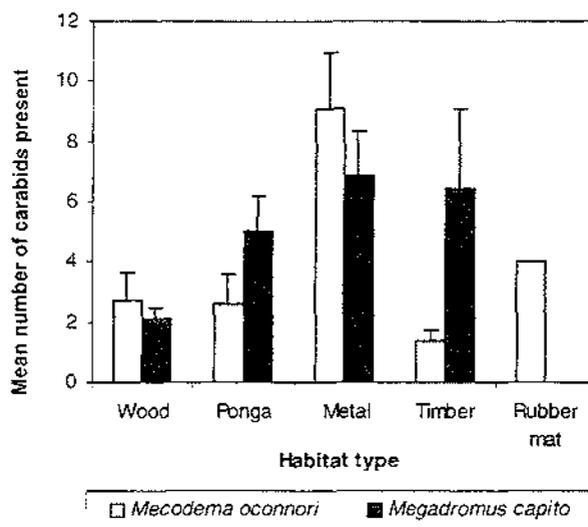


Figure 3.5. Mean number of *Mecodema oconnori* and *Megadromus capito* found under different types of habitat sites at Browns Bush (n = 99). Error bars indicate standard error. NB. The number for rubber mat is not a mean because there was only one habitat of this type.

3.3.5 Spatial dispersion among the pitfall traps

The overall distribution of carabids caught in live pitfall traps was random, because it was not significantly different from a Poisson distribution (Figure 3.6). The dispersion indices and chi-squared tests showed that there was no significant aggregation in any of the species (Table 3.3).

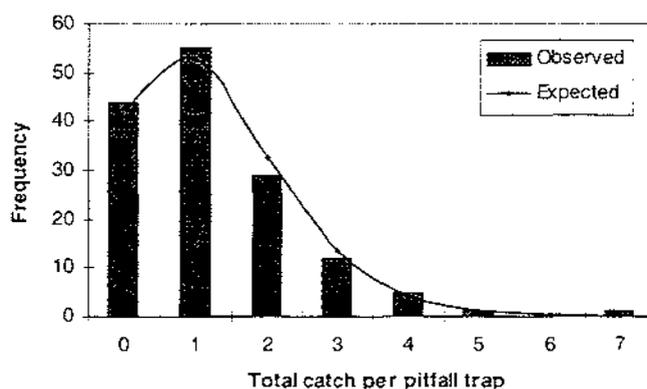


Figure 3.6. Frequency distribution of all carabids caught in pitfall traps at Browns Bush compared to a Poisson (random) distribution.

Table 3.3. Spatial dispersion of carabids in pitfall traps at Browns Bush. The dispersion index (I) = s^2 / x (where s^2 = variance, x = mean). A dispersion index of 1 or greater indicates aggregated dispersion. The agreement of the index with the Poisson series was tested using a χ^2 test. 'NS' means that the dispersion is not significantly different from random ($p > 0.05$).

	Mean number per trap	Dispersion index (I)	χ^2 statistic
<i>Mecodema oconnori</i>	0.503	1.030	27.812 NS
<i>Megadromus capito</i>	0.374	1.362	36.785 NS
<i>Holcaspis mucronata</i>	0.347	1.052	28.414 NS
TOTAL Carabidae	1.231	1.169	31.561 NS

There was no correlation between the numbers of *M. oconnori* and *M. capito* caught in each trap (Pearson correlation, $r = -0.026$, $p = 1.00$) or between *M. oconnori* and *H. mucronata* ($r = -0.016$, $p = 1.00$), or between *M. capito* and *H. mucronata* ($r = 0.030$, $p = 1.00$). This indicates that the three different species were caught in different pitfall traps and were distributed independently of each other throughout the forest.

3.3.6 Movement of carabids between resting sites

Some aspects of the movement patterns of beetles can be deduced from the searches of habitat resting sites. The proportion of beetles in which movement was detected varied between species and between the sexes (Table 3.4). *Megadromus capito* individuals showed slightly more tendency to move than *M. oconnori* individuals (51% moved compared to 42% for *M. oconnori*). Half of the *M. oconnori* females that were recaptured showed some movement between resting sites, whereas only 38% of males showed movement, however this difference was not significant (χ^2 test, $df = 1$, $p = 0.536$). The situation was reversed for *M. capito*, with 60% of males showing movement between resting sites and only 39% of females, but again this difference was not significant (χ^2 test, $df = 1$, $p = 0.241$).

Table 3.4. Number of recaptured *Mecodema oconnori* and *Megadromus capito* that showed movement between habitat resting sites at Browns Bush.

Species	Number of beetles recaptured		Number that moved (% of recaptures)		Overall % that moved
	Males	Females	Males	Females	
<i>Mecodema oconnori</i>	50	24	19 (38.0%)	12 (50.0%)	41.9%
<i>Megadromus capito</i>	55	41	33 (60.0%)	16 (39.0%)	51.0%
TOTAL	105	65	52 (49.5%)	28 (43.1%)	47.1%

The minimum distance moved by each individual was calculated using the information from searches of resting sites, but the actual distance moved was probably much higher than this because the paths of beetles between resting sites were not followed directly. *Mecodema oconnori* and *M. capito* showed some differences in the total distances moved (Table 3.5). For *M. capito* the largest individual distance moved was 92.3 metres by a male over 23 weeks. For females the largest distance moved was 35.8 metres over 30 weeks. In comparison, the largest distance covered by *M. oconnori* was only 24.53 metres by a male over 26 weeks, and 30.7 metres by a female over 6 weeks. An estimate of the minimum distance moved per week was also calculated by dividing the total distance covered by each individual by the number of weeks between the first and last sightings (Table 3.5).

Table 3.5. Mean total and mean weekly distance moved between habitat resting sites by *Mecodema oconnori* and *Megadromus capito* at Browns Bush (\pm standard error).

Carabid species	Mean total distance moved (m)		Mean weekly distance moved (m)	
	Males	Females	Males	Females
<i>Mecodema oconnori</i>	6.98 (\pm 1.56)	7.29 (\pm 2.47)	3.27 (\pm 2.05)	2.82 (\pm 1.15)
<i>Megadromus capito</i>	11.87 (\pm 3.15)	6.99 (\pm 2.17)	2.86 (\pm 0.94)	1.49 (\pm 0.47)

The mean total distance moved was higher for *M. capito* than *M. oconnori* (10.3 m versus 7.10 m respectively), although the difference was not significant (Two-way ANOVA, \log_{10} data, $df = 1$, $F = 0.457$, $p = 0.501$) (see Appendix 8). In contrast, the mean weekly distance moved was slightly higher for *M. oconnori* than *M. capito* (2.84 m/week versus 2.41 m/week), but again the difference was not significant (Two-way ANOVA, \log_{10} data, $F = 0.000$, $p = 0.998$). There was no significant difference between *M. oconnori* males and females in the mean total distance moved (t-test, \log_{10} data, $df = 29$, $p = 0.972$), or mean weekly distance moved ($p = 0.922$) (Table 3.5). Likewise, the mean total distance moved (t-test, \log_{10} data, $df = 47$, $p = 0.179$) and mean weekly distance moved ($p = 0.182$) by *M. capito* males and females were not significantly different. There was no significant interaction between species and sex in the mean total distance moved (Two-way ANOVA, \log_{10} data, $df = 1$, $F = 0.751$, $p = 0.389$) or mean weekly distance moved ($F = 0.790$, $p = 0.377$) (see Appendix 8).

The pattern of movement between habitat resting sites was mapped for carabid beetles that were recaptured a number of times (see below and Appendix 9). The majority of beetles remained in a small area (within a few metres) over the course of the study, although some beetles also showed longer range movements. For example, Figure 3.7 shows the movement pattern of a *M. capito* female at Browns Bush over 17 weeks (11 sightings). The total distance moved was 14.97 metres, and the minimum distance moved each week was 0.88 metres. The female spent periods during which little movement was detected, e.g. the sightings between 24.9.99 and 4.11.99, but also showed longer range movements, travelling several metres between some sightings (e.g. between 22.7.99 and 6.8.99).

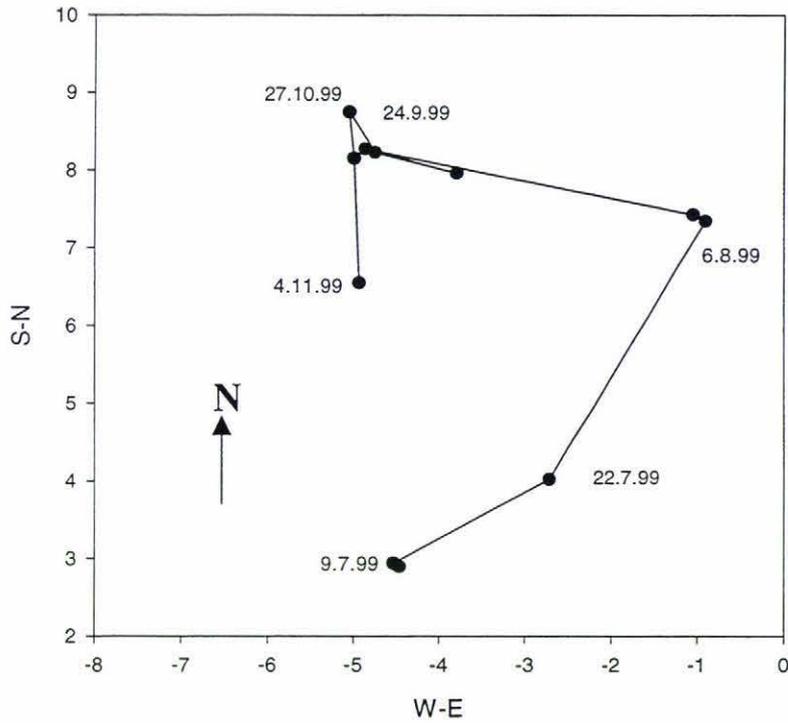


Figure 3.7. Map of the movement pattern of a *Megadromus capito* female at Browns Bush over 17 weeks from 9.7.99 to 4.11.99 (11 sightings). The units on both axes are in metres (ignore sign of units). The positions plotted were derived from polar co-ordinates. The total distance moved was 14.97 metres. The minimum distance moved was 0.88 m per week.

The most frequently sighted *M. oconnori* individual was a male that moved a total of 19.06 metres over 16 weeks (Figure 3.8). The minimum weekly distance moved by this male was 1.19 metres. The male displayed periods of relative inactivity, alternating with periods of longer range movement. For example, it moved 6.2 metres between resting sites over 10 days (between 30.4.99 and 10.5.99), but moved less than a metre between 10.5.99 and 4.6.99.

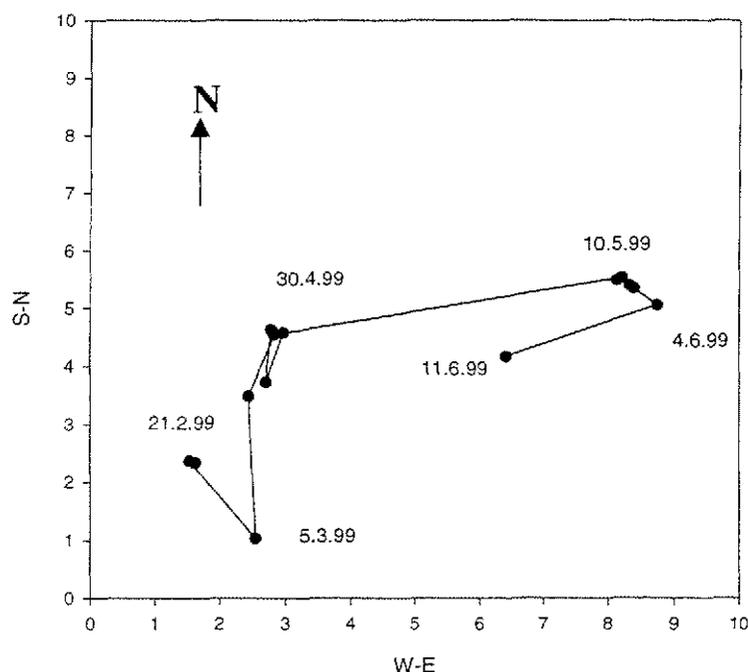


Figure 3.8. Map of the movement pattern of a *Mecodema oconnori* male at Browns Bush over 16 weeks from 21.2.99 to 11.6.99 (22 sightings). The units on both axes are in metres. The positions plotted were derived from polar co-ordinates. The total distance moved was 19.06 metres. The minimum distance moved was 1.19 metres per week.

3.3.7 Harmonic radar tracking

A total of 26 *M. oconnori* and two *M. capito* were fitted with transponders at Browns Bush. There were a number of unforeseen problems in tracking these carabids with harmonic radar, and these meant that it was not possible to locate transponded beetles on every searching occasion. One of the characteristics of harmonic radar tracking is that an individual must be physically sighted in order to identify it because the diodes do not emit a unique signal for each animal. This was often not possible because the carabids in this study were fossorial and spent a considerable amount of time underground and in logs, where they could not be seen. Hence, it was often not possible to positively identify which individual had been found, so the benefits of using the radar were lost.

Some beetles also lost the aerials from their transponders, and this reduced the detection distance markedly. Several beetles were found with their transponder aerial entangled in logs, and the aerials appeared to be a hindrance to their movement. One transponded *M. oconnori* male was found dead in the leaf litter with only the elytra remaining, and it appeared to have been eaten by a vertebrate because of the chew marks on the elytra.

Another problem experienced with radar tracking was the frequent spurious signals given off by metal objects at Browns Bush such as wire, pieces of iron, and steel poles. Water and humidity also interfered with the signal, so it was very difficult to locate beetles during rain. Most of the transponded beetles were found again by hand searching of resting sites rather than using the radar, as this latter method proved more reliable. Because of these problems, the data from the harmonic radar tracking are too incomplete for meaningful analysis of carabid movement.

3.3.8 Environmental variables

3.3.8.1 Temperature

There was no relationship between mean daily temperature and the numbers of *M. oconnori* (Pearson correlation, $r = 0.220$, $n = 36$, $p = 0.227$) or *M. capito* ($r = -0.231$, $n = 36$, $p = 0.203$) found in searches of habitat resting sites. However, there was a significant positive correlation between mean daily temperature and the number of *M. oconnori* individuals caught in the pitfall traps ($r = 0.675$, $n = 9$, $p = 0.047$) (Figure 3.9). The correlation for *M. capito* was also positive, but it was marginally non-significant ($r = 0.652$, $n = 9$, $p = 0.058$). In contrast, *H. mucronata* showed a negative relationship with temperature, although the correlation was not significant ($r = -0.149$, $n = 9$, $p = 0.702$) (Figure 3.9).

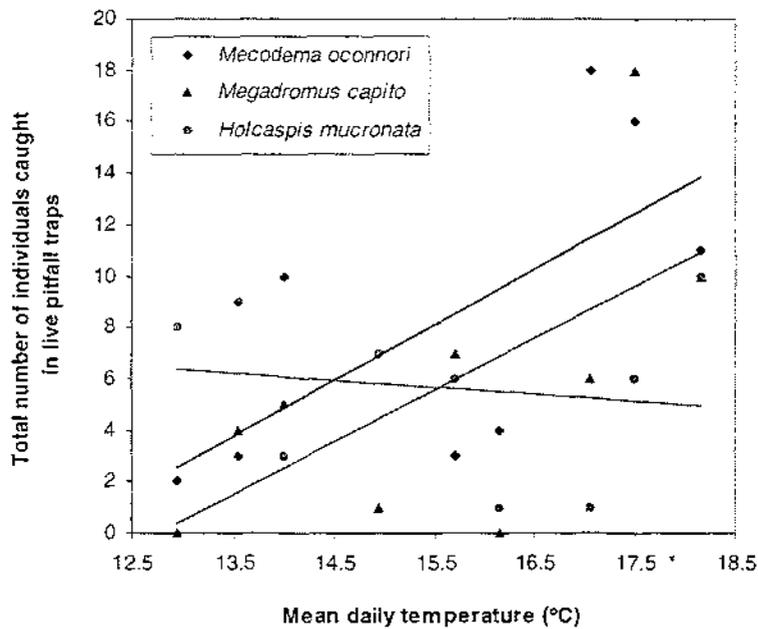


Figure 3.9. Relationship between mean daily air temperature (°C) and the number of carabids caught in pitfall traps at Browns Bush (number of samples = 9).

3.3.8.2 Rainfall

There was a significant positive correlation between total daily rainfall and the number of *M. oconnori* found in searches of habitat resting sites (Pearson correlation, $r = 0.331$, $n = 36$, $p = 0.043$). The relationship for *M. capito* was also positive, but it was not significant ($r = 0.272$, $n = 36$, $p = 0.098$). In contrast, the relationship between total daily rainfall and the number of carabids caught in pitfall traps was negative, but none of the correlations were significant for *M. oconnori* ($r = -0.192$, $n = 9$, $p = 0.621$), *M. capito* ($r = -0.493$, $n = 9$, $p = 0.179$), or *H. mucronata* ($r = -0.211$, $n = 9$, $p = 0.586$).

3.3.8.3 Habitat characteristics of the pitfall traps

There was a significant correlation between leaf litter depth around each pitfall trap and the total number of *H. mucronata* caught (Pearson correlation, $r = 0.256$, $n = 147$, $p = 0.002$), but the abundances of *M. oconnori* and *M. capito* were not related to leaf litter depth (Table 3.6). Plant cover and canopy cover were not significantly correlated with any of the carabid species (Table 3.6).

Table 3.6. Pearson correlations between the environmental variables of each pitfall trap and the total numbers of carabids caught. ** $p < 0.01$, * $p < 0.05$ indicates a significant correlation, 'NS' = non-significant ($p > 0.05$).

Carabid species	Plant cover (%)	Canopy cover (%)	Leaf litter depth (cm)
<i>Mecodema oconnori</i>	0.095 NS	0.019 NS	0.033 NS
<i>Megadromus capito</i>	-0.023 NS	0.103 NS	0.104 NS
<i>Holcaspis mucronata</i>	-0.138 NS	0.111 NS	0.256 **
TOTAL Carabidae	-0.026 NS	0.129 NS	0.211 *

3.4 DISCUSSION

3.4.1 Habitat use

Both of the native carabids in this study made extensive use of artificial resting sites at Browns Bush, with pieces of metal being the most frequently occupied sites by both species. *Megadromus capito* has been described as “one of the few native carabids to have adapted reasonably well to habitat changes” (Townsend 1994), and *Mecodema oconnori* appears to share the same characteristics. The metal may be a favoured resting site for these carabids because it provides the best shelter from the weather, and offers good protection from predators such as birds. However, the two species showed some differences in their occupancy of the other resting sites. *Megadromus capito* was regularly found under pieces of timber, but this was the least favoured habitat type for *M. oconnori*. The area covered by each resting site was not measured in this study because of the difficulty in comparing metal and timber with three-dimensional habitats such as ponga and logs, where beetles can burrow into them. In general, the metal sites had a larger area in contact with the ground than the other sites, whereas timber covered the smallest area. Thus, it seems that *M. oconnori* may have been excluding *M. capito* from the larger resting sites, forcing *M. capito* to occupy different sites in order to avoid competition or antagonism between the species. Both species were occasionally found together under larger pieces of metal, but they were much more frequently seen with conspecifics.

Interspecific competition is believed by some to be an important factor affecting carabid assemblages (Lenski 1982, 1984, Loreau 1986, Müller 1987, Griffith & Poulson 1993, Currie *et al.* 1996), however others have suggested that interspecific competition is not common among carabids (den Boer 1980, 1985, 1986, Hengeveld 1985, Andersen & Skorping 1990, Loreau 1990b, Niemelä 1993). Patterns of resource use, such as habitat occupancy, may indicate whether competitive interactions are occurring. For example, Anderson (1988) found negative pair-wise associations in microhabitat use of riparian *Bembidion* species in Norway, implying that competition occurred between the species. Spence and Hughes Spence (1988) reported a strong negative pair-wise association between the introduced *Pterostichus melanarius* (Illiger) and the native *P. adstrictus* Eschscholtz in human-modified habitats in Canada. However, in natural aspen-poplar

forest, *P. melanarius* showed no general negative effect nor any negative pairwise associations with the native species (Niemelä and Spence 1991). Thus, it appears that the influence of competition may change depending on the type of habitat occupied, and whether resources are limited for the species concerned.

There appears to be some evidence for resource partitioning between *M. oconnori* and *M. capito* at Browns Bush, as the two species showed differences in their occupancy of resting sites. However, it is not known whether resting sites were limited, and whether the two species were actually competing for these sites. Nevertheless, there were signs that aggressive interactions were occurring between the two species. When one individual of each species was placed in the same container for 10 minutes, the confrontation resulted in *M. oconnori* killing *M. capito* (M. Hutchison, pers. obs.). Shattered *M. capito* remains were found next to a *M. oconnori* individual underneath a log that *M. oconnori* was occupying, indicating possible predation by the larger species (M. Hutchison, pers. obs.).

There is further evidence for niche differentiation between the carabids at Browns Bush. *Holcaspis mucronata* was very seldom seen under the resting sites occupied by *M. oconnori* and *M. capito* (M. Hutchison, pers. obs.), despite its being caught frequently in the live pitfall traps. This indicates that *H. mucronata* was relatively common, but was not using the same habitats as the two larger species. However, more rigorous experiments are needed to establish the influence of competition on the carabid assemblage at Browns Bush, as many factors may affect resource utilisation of each species (see Loreau 1990b).

Microhabitat factors such as soil moisture (Lindroth 1949, Niemelä *et al.* 1987, de Vries *et al.* 1996, Eyre & Luff 1990, Niemelä *et al.* 1992, Baguette 1993, Gardner *et al.* 1997, Huk & Kuhne 1999), soil organic content (Szujecki 1987, Butterfield 1997), temperature (Atienza *et al.* 1996), shade (Chapman *et al.* 1999), vegetation cover (Mitchell 1963b, Baguette 1993, Magura & Tothmeresz 1997), and leaf litter type (Williams 1959, Niemelä *et al.* 1992, Guillemain *et al.* 1997, Koivula *et al.* 1999) are important in carabid habitat selection. At Browns Bush, some resting sites were continuously occupied by carabids, while others were only occupied once (M. Hutchison, pers. obs.). This suggests that some sites were more favourable than others, but it is not known what factors the beetles were responding to.

Soil moisture appears to have a particularly strong influence on habitat selection by carabid beetles. Baguette (1987) found that humidity and soil acidity were the two most important factors in determining the distribution of carabids in Belgian forests, while soil water holding capacity and soil trophic status also had a significant effect (Baguette 1993). Lindroth (1949) discovered that the distributions of some *Harpalus* species were correlated with the distribution of calcareous soils, and that beetles were responding to the increased temperatures and drier microclimates associated with these soils.

Mecodema oconnori, like most species in the Broscini, appears to be very sensitive to humidity levels (A. Larochelle, pers. comm., 2000). At Browns Bush, *M. oconnori* individuals seemed to spend considerable time in underground burrows, and were less common on the ground surface during dry weather (M. Hutchison, pers. obs.). Similarly, Luff (1978) observed that larger carabid beetles tended to burrow deep into the soil during the day (up to 25 cm) in order to obtain shelter from desiccation. When *M. oconnori* individuals were present on the soil surface, they were usually found in the wettest parts under the resting sites (M. Hutchison, pers. obs.). There was a positive relationship between the number of *M. oconnori* found in habitat searches and total daily rainfall, which suggests that *M. oconnori* may move to the surface when humidity is high enough. Similarly, Szujecki (1987) noted that the population of *Carabus nemoralis* Müller, a distinctly hygrophilous species, became denser with increasing rainfall.

Carabids often show aggregated or clumped distribution patterns, especially during their breeding season (Greenslade 1963b, Reise and Weidemann 1975, Luff 1986, Niemelä *et al.* 1986, Grüm 1990, Gruttke & Weigmann 1990, Niemelä *et al.* 1992, Blake *et al.* 1994, Kennedy 1994). Clumped distributions may be caused by habitat patchiness or uneven prey distributions (Mols 1979, Bryan & Wratten 1984, Weseloh 1987), or as a result of chemical communication between carabid beetles via an aggregation and/or sex pheromone (Luff 1986). For example, *Calosoma sycophanta* L. males aggregated when females were sexually active, because males are attracted to fertile females and actively search for them (Weseloh 1987).

There was no sign of aggregation among the pitfall trap catches of any of the carabid species at Browns Bush, which suggests that they had a random spatial distribution

throughout the forest. However, there were differences between the species in their spatial dispersion among the pitfall traps. When two or more beetles were caught in the same trap, they were nearly always from the same species (M. Hutchison, pers. obs.). This implies that either the individual species have different distributions in the forest, or they are able to avoid being caught in the same traps.

In a similar study, Niemelä (1990) found that carabid species were not randomly distributed among pitfall traps, but occurred in aggregations which were associated with certain microhabitat types. Small-scale habitat structure around the traps was correlated with the carabid distribution pattern, for example, *Pterostichus oblongopunctatus* Fabricius was associated with a thick layer of leaf litter. At Browns Bush, *Holcaspis mucronata* showed a significant correlation with leaf litter depth around each trap, whereas the other species did not. Thus, it appears that leaf litter depth may affect the spatial distribution of some carabids at Browns Bush. The type of leaf litter may also alter the microhabitat, although this was not measured in my study. Koivula *et al.* (1999) found that leaf litter type had a significant effect on carabid abundance and distribution patterns, and suggested that this was attributable to both abiotic (humidity and temperature) and biotic factors (changes in niche structure and food supply).

Baguette (1993) found that carabid abundance in Belgian forests was closely related to vegetation characteristics such as shrub cover. Similarly, herbaceous ground cover and canopy cover were significant factors explaining the abundance and species richness of carabid beetles in plantation forests (Magura 2000, Magura & Tothmeresz 2000). In my study, however, there was no correlation between ground vegetation cover and the number of carabids caught in each pitfall trap. Likewise, the amount of overhead canopy cover had no effect on the number of carabids caught in each trap.

3.4.2 Activity and movement

The dispersal abilities of carabid beetles have been studied extensively in Europe (Rijnsdorp 1980, den Boer 1981, 1985a, Wallin 1987, Frampton *et al.* 1995, de Vries *et al.* 1996). Some of the larger species may move more than 1000 metres (den Boer 1970), but most individuals cover less than 200 metres in their lifetime (Baars 1979b, den Boer 1981,

Klazenga & de Vries 1994). My study is mainly concerned with the movements of beetles within the forest remnant rather than long-range dispersal between remnants, but beetles appear to occasionally disperse out of the forest habitat, because some *M. oconnori* were found under corrugated iron 50 metres away from Browns Bush across a farm paddock (I. Townsend, pers. comm., 1999). Similarly, Rijnsdorp (1980) estimated that in *Carabus problematicus* Herbst, a forest-inhabiting species, 4-8% of the marked individuals dispersed out of the forest into 'unfavourable' environments.

Daily movement distances vary between species, but most carabids appear to move less than 20 metres in a 24-hour period. For example, Ericson (1979) estimated daily movement of about 4m/day for *Pterostichus cupreus* (L.) in cereal fields, and Greenslade (1964a) observed that *Nebria brevicollis* (Fabricus) and *Pterostichus madidus* (Fabricus) commonly travelled 10 m in a 24-hour period. Mitchell (1963b) estimated average daily movement of 1.6 and 0.4 m for *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank) respectively. Mean distances moved varied from 7.6 to 16.1 m per day for carabid species inhabiting winter wheat crops (Lys & Nentwig 1991), and about 16 m per day for *Harpalus rufipes* De Geer in cereal fields (Wallin & Ekbom 1988). The mean distance covered per day by *Abax ater* Villers males was 1.8 m, and their average home range was estimated to be 660 m² (Loreau & Nolf 1993). *Abax parallelepipedus* (Pill. & Mitt.) averaged roughly 1.8 m per day (Charrier *et al.* 1997), but some individuals showed no movement for more than half the time they were followed. Blake *et al.* (1994) reported mean movement distances of 8.5 and 12.2 m per day for two carabid species in an Iowa cornfield, but some individuals were very active and moved up to 91 m in one day. In comparison, the carabids at Browns Bush appeared to be fairly inactive, as the mean distance moved per week by *M. oconnori* and *M. capito* was less than four metres, i.e. less than 60 cm per day. Males of both species were slightly more active than females, but this difference was not significant.

Carabid beetles can move rapidly and cover large distances in a short time (Wallin 1987). For example, Mascanzoni and Wallin (1986) reported that one individual moved almost 30 metres within an hour. However, beetles may also be quite inactive for long periods, when very little movement is detected. Periods of walking alternate with periods of cleaning, resting, mating or ovipositing, usually at sheltered places under vegetation cover

or in litter (Mols 1979). Wallin (1987) referred to these periods as “discontinued dispersal activities”, during which beetles may burrow and be inactive for several days.

Baars (1979b) identified two main types of movement in carabid beetles. Beetles display periods during which they move small distances in continually changing directions, termed ‘random walk’. This alternates with periods in which long distances are covered in a more or less constant direction, called ‘directed movement’. Carabid beetles usually move randomly in a favourable habitat, and switch to a more directed course in an unfavourable habitat in order to escape those conditions (Baars 1979b, Rijnsdorp 1980, Wallin & Ekbohm 1988, Wallin 1991). Grüm (1971, 1990) found that the activity of satiated individuals was higher in sub-optimal habitats than in optimal habitats, and that carabids moved smaller distances in favourable heterogeneous habitats compared to homogenous (unfavourable) habitats. Morrill *et al.* (1990) asserted that carabid survival in favourable environments, with adequate prey, suitable moisture, and moderate temperature would require comparatively little (directed) movement.

The carabids at Browns Bush appeared to display elements of both types of movement, although the majority of beetles showed very little directed movement. Many beetles were repeatedly recaptured under the same resting site, or within a few metres of their original location. One *M. capito* female showed remarkable habitat permanence by being under the same ponga log every week for more than six months. Similarly, Thomas *et al.* (1998) found that most carabids were recaptured close to their release position, and showed a tendency to remain within a limited area. Crowson (1981) also referred to nocturnally hunting carabids being found day after day under the same stone, indicating regular return after successive hunting trips.

Some studies have reported very high recapture rates for carabids using pitfall traps. For example, Holland and Smith (1999) reported a capture efficiency of 80% or higher for large carabid species. However, typical recapture rates are much lower. For example, Blake *et al.* (1994) reported recapture rates ranging from 1.7% to 14.0% for two carabids in a cornfield, and Lys and Nentwig (1991) found recapture rates from 2.9% to 27.3% for five species of carabids in a winter wheat field. In my study, recapture rates in live pitfall traps were extremely low, despite several hundred beetles having been marked before the

start of the experiment. This implies that the beetles at Browns Bush were not very active, or were able to avoid being recaptured in the traps. In contrast, the recapture rate in habitat searches was considerably higher than in pitfall traps, although it was still less than 40%. Beetles were most likely to be recaptured under the resting site where they were originally found, and showed a tendency to remain within a small area. These results suggest that the carabids at Browns Bush display some kind of site fidelity or homing behaviour. The low numbers of recaptured beetles could also be due to emigration or mortality of marked beetles (Weseloh 1987). A possible source of error is the loss of labels from the beetles, which may have resulted in some beetles being marked twice, hence lowering recapture rates. The rate of label loss in my study is not known, but Lys and Nentwig (1991) reported up to 20% loss of bee labels after one day.

Carabid activity and movement may be affected by climatic variables such as temperature, rainfall, and humidity. Many authors found a positive correlation between temperature and carabid locomotor activity (Barlow 1973, Baars 1979b, Luff 1982, Brunsting 1983, Atienza *et al.* 1996, Baumgartner *et al.* 1997, Honek 1997), while others found no relationship (Mitchell 1963b, Ericson 1979). Brunsting (1983) observed a low level of activity in *Pterostichus oblongopunctatus* Fabricius on cold days and a high level on warm ones, and found that walking speed was positively correlated with temperature. Baars (1979b) discovered that the distance covered per day by carabid beetles appeared to depend on temperature, and Moeed & Meads (1985) reported that the abundance of six carabid species in native New Zealand forests was correlated with temperature. Likewise, the pitfall trap catches of *M. oconnori* and *M. capito* showed a positive relationship with mean daily temperature, implying that beetles were more active during warmer weather. However, very high temperatures and low humidity tend to reduce the activity of carabids at the soil surface, as carabids are very sensitive to moisture levels (Jones 1979). Similarly, McColl (1975) found that prolonged hot dry conditions during summer depressed activity in Collembola and spiders in a beech forest.

Rainfall appears to have a variable influence on carabid movement. Carabids may show increased activity immediately after rain (Thomas *et al.* 1998), but movement appears to be greatly reduced during prolonged periods of heavy rain (Baars 1979b). For example, Ericson (1979) observed that heavy rain inhibited the activity of *Pterostichus cupreus* (L.),

and lead to decreased pitfall trap catches. At Browns Bush, there was no significant correlation between rainfall and the number of carabids caught in pitfall traps, but very few beetles were caught during heavy rain. Moeed & Meads (1985) also found that the number of carabids trapped in native forest was not correlated with rainfall.

Biotic factors such as hunger level and reproductive state may also influence activity. Hungry beetles are more active than satiated ones, presumably because of increased foraging activity in search of food (Mitchell 1963a, Grüm 1971, Baars 1979b, Lenski 1984, Wallin 1991, Frampton *et al.* 1995). Grüm (1990) found that beetles with additional food moved less than those with potential food shortage. Carabids often show a high frequency of turning movements and a shorter distance per move directly after feeding (Mols 1979, Wallin & Ekbohm 1988). Many carabids show increased surface activity during their reproductive period, probably because of their search for mates (Lys & Nentwig 1991).

Several authors have found that the amount of ground vegetation has an effect on beetle movement, and hence pitfall trap catches (Greenslade 1964b, Crist & Ahern 1999). Open habitats allow greater speed of movement, resulting in higher trapping frequencies than habitats with a dense vegetative cover (Greenslade 1964b). This applies particularly to larger carabid species, which usually move faster than smaller ones, and may be impeded by dense vegetation and leaf litter (Greenslade 1964b). However, there was no correlation between the amount of ground plant cover and the number of carabids caught in each pitfall trap at Browns Bush, so carabid movement did not appear to be affected by the density of ground vegetation. Nevertheless, the catches of *H. mucronata* showed a significant correlation with leaf litter depth around each trap, which implies that the movement of this small species was not impeded by deep leaf litter.

Some studies have reported sexual differences in activity and the distances covered (Greenslade 1965, Ericson 1977, den Boer 1979b, Rijnsdorp 1980, Brunsting 1981, Atienza *et al.* 1996). In general, males appear to be more active than females (Rivard 1965, Loreau & Nolf 1993), especially during the breeding season when they are searching for mates (Greenslade 1965). For example, Baumgartner *et al.* (1997) reported that mean recapture rates in pitfall traps were higher in males, implying that males were

more active than females. Ericson (1977) also found that males had higher recapture rates, but suggested that this was because females dispersed over a wider area. In my study, searches of resting sites revealed that *M. oconnori* males were more likely to be recaptured than females, while the opposite was true for *M. capito*. In contrast, pitfall trapping produced no recaptures of *M. oconnori* males or *M. capito* females. Significantly more *M. oconnori* females were caught and recaptured in pitfall traps compared to manual searches. This suggests that females may have been more active than males during the trapping period, or that they were more likely to be caught in pitfall traps. However, there was no significant difference in the mean distance moved between the sexes of either species in this study.

The diel activity of carabids has been investigated overseas, both in the lab and in the field (Greenslade 1963a, Thiele 1977, Preiszner & Karsai 1990), and several authors have used time-sorting pitfall traps to divide the catch into different time periods (Williams 1958, 1959, Luff 1978, den Boer 1979b, Rijnsdorp 1980, Desender *et al.* 1984, Alderweireldt & Desender 1990, Kegel 1990, Chapman & Armstrong 1997). Forest species appear to be predominantly nocturnal, perhaps because of their inability to tolerate low humidity, whereas field species are usually diurnal, although some species may be 'plastic' with activity in both periods (Williams 1959, Greenslade 1963a, Desender *et al.* 1984, Chapman & Armstrong 1997). Daytime activity was observed in predominantly nocturnal species during low temperatures and high humidity (Chapman & Armstrong 1997), and diurnal species are sometimes active on warm nights (Greenslade 1963a). Diel activity was not investigated in my study, although the majority of endemic New Zealand Carabidae are thought to be nocturnal because of their forest-dwelling habits (A. Larochelle and M-C. Larivière, pers. comm., 2000).

3.4.3 Comparison of sampling methods and their limitations

Although pitfall traps have been used extensively in ecological field studies of carabid beetles (Southwood 1978), they have a number of biases and have been criticised by some authors (Greenslade 1964b, Southwood 1978, Adis 1979, Halsall & Wratten 1988, Andersen 1995). The major problem is that the number of beetles caught in a pitfall trap is determined by activity as well as density (Halsall & Wratten 1988, Thomas *et al.* 1998).

Pitfall trap catches are therefore affected by a number of abiotic and biotic factors such as temperature (Baars 1979a, Atienza *et al.* 1996), humidity (Ericson 1979), vegetation cover (Greenslade 1964b), trap design (Luff 1975, Adis 1979, Baars 1979a), preservative type (Luff 1968, Ericson 1979, Holopainen 1990), hunger level (Mols 1979, Chiverton 1984), reproductive state (Lys & Nentwig 1991), and the “catchabilities” of individual species (Greenslade 1964b, Luff 1975, Ericson 1979, Halsall & Wratten 1988, Morrill *et al.* 1990). For example, larger species are more likely to be caught in pitfall traps because they are more active and find it harder to escape from the traps (Luff 1975, Spence & Niemelä 1994, Andersen 1995). Arboreal species may be under-represented in pitfall traps because of their ability to climb out of the traps (Halsall & Wratten 1988, Michaels & McQuillan 1995). It has also been suggested that nocturnal species more easily fall into pitfall traps than diurnal ones (Greenslade 1964b).

Catch and sex ratio are affected by the type of preservative used in pitfall traps. For example, traps filled with ethylene glycol caught significantly more carabids than traps filled with water, and tended to increase the proportion of females caught (Holopainen 1990, Holopainen 1992). Similarly, the sex ratio was biased towards females when formalin was used as a preservative compared to water (Ericson 1979).

Catches in pitfall traps tend to be highest soon after the traps are placed in the soil, and this has been termed the “digging-in effect” (Greenslade 1964b, 1973, Digweed *et al.* 1995). Carabids seem to be attracted to the disturbance caused by the insertion of the traps, perhaps due to increased prey abundance (Adis 1979), increased CO₂ levels (Joose & Kapteijn 1968), or a decrease in barriers to movement by flattening of soil and leaf litter (Greenslade 1964b). However, the digging-in effect should have been minimal at Browns Bush because the pitfall traps were in the ground between one and eight weeks before the start of the live trapping experiment.

Only a few studies have made direct comparisons between pitfall trapping and absolute counting methods (e.g. Gilbert 1956, Briggs 1961, Mitchell 1963b, Gist & Crossley 1973, Andersen 1995, Topping & Sunderland 1992, Spence & Niemelä 1994), although this is essential for detecting sampling bias and isolating the components of activity-density in pitfall trap catches (Thomas *et al.* 1998). For example, Gilbert (1956) compared soil

extraction with pitfall trapping for several species of *Calathus* in Wales, and found differences in the proportions of larvae caught by the two methods. The majority of larvae caught in pitfall traps were *C. erratus* Sahlberg, but direct soil extraction revealed that *C. mollis* (Marsham) and *C. melanocephalus* (L.) were actually more abundant. Andersen (1995) compared open pitfall traps and quadrat sampling of Carabidae in microhabitats on river banks. He found no correlation between the relative abundance of carabid species in the two sampling methods, and concluded that quadrat sampling gave a more reliable estimate of the absolute abundance of different species. However, Gilbert (1956) compared the numbers of beetles under artificial refuges with those caught by pitfall trapping, and found that the two sampling methods gave similar results.

In my study, the numbers of *M. oconnori* and *M. capito* caught in live pitfall traps were very similar to the numbers found under habitat resting sites for most of the trapping period. Large numbers of beetles were found under habitat resting sites in summer, and this coincided with a peak in activity during the warm season. However, fewer beetles were caught in the pitfall traps in March, yet the numbers found under resting sites were still high. This implies that the beetles were becoming less active, probably because of lower temperatures. The positive correlation between temperature and pitfall trap catches for *M. oconnori* and *M. capito* tends to confirm the link between temperature and activity. These observations highlight the importance of comparing sampling methods in order to avoid misinterpreting the results.

Because the movement of individuals could not be followed directly, the distances moved by the carabids in my study are likely to be much lower than the actual distances moved. Most of my observations on carabid movement were made using information from searches of habitat resting sites, but there are some inherent limitations with this method. The majority of recaptures were of beetles that were frequently found under the same resting site, implying that they had not moved between sightings. However, it is likely that beetles were foraging in the leaf litter at night and returning to the resting sites during the day. When the beetles did move from the resting sites, their positions were not known as the leaf litter was not searched. Nevertheless, both species showed a definite tendency to remain within a small area and repeatedly return to the same resting sites over many weeks, suggesting some kind of site fidelity or homing instinct.

Tracking of carabid beetle movement has been carried out using a number of techniques (Riley 1989, Riecken & Raths 1996). For example, Baars (1979b) used radioactive labelling to follow carabid beetles in the Netherlands, but most of the beetles died within seven weeks from the effects of radiation. Harmonic radar was used successfully for tracking carabid movement in a number of studies (Mascanzoni & Wallin 1986, Wallin 1987, Charrier *et al.* 1997), however there were a number of problems with harmonic radar tracking in my study. One of the major problems was the difficulty in identifying beetles once they had been located because of the fossorial nature of *M. oconnori* and *M. capito*. Both species spend a large amount of time underground and in logs, where they cannot be seen. Hence, it was often not possible to positively identify which individual had been found, and the benefits of using the radar were lost. All of the overseas studies that used harmonic radar (Mascanzoni & Wallin 1986, Hockmann *et al.* 1989, Charrier *et al.* 1997) were conducted in open vegetation and the carabid species that were tracked were not fossorial. Prior to my study, harmonic radar had only been used once for tracking New Zealand carabids. Lövei *et al.* (1997) found movement distances of a few metres per night for *Plocamostethus planiusculus* (White) at Keebles Bush, but no long term directional movement was detected, as the beetles were only followed for several nights.

3.4.4 Estimates of population density

A number of studies have used population models such as the Jolly-Seber model to estimate carabid population size from mark-recapture data (Mitchell 1963, Greenslade 1964a, den Boer 1979b, Ericson 1977, Luff 1982, Thomas *et al.* 1998). However, because of the low recapture rates in my study, estimation of population density using these models would be extremely unreliable, and the standard errors would probably be higher than the actual population estimates (Mitchell 1963b, Greenslade 1964a, Ericson 1977). One of the basic assumptions of mark-recapture models is that every individual has the same chance of being caught (den Boer 1979b, Nelemans *et al.* 1989). However, at Browns Bush the number of recaptures varied widely between individuals and the frequency distribution was highly skewed, with some individuals being recaptured many times. Because of these problems, the only realistic estimates of population size for *M. oconnori* and *M. capito* are the minimum population sizes of 340 and 310 respectively, based on the total number of beetles marked over the course of the study.

3.4.5 Conclusions

Artificial resting sites were frequently used by both species in my study, but *M. oconnori*, the larger species, appeared to be excluding *M. capito* from the larger resting sites. Interspecific competition for habitat resting sites may be occurring between *M. oconnori* and *M. capito* at Browns Bush, but it remains to be proven experimentally. Both species showed a tendency to remain within a small area and repeatedly returned to the same resting sites over many weeks, suggesting some kind of homing behaviour. There were no significant differences between the species or sexes in their activity or distances moved. Manual searching of habitat sites proved to be the most effective sampling technique for *M. oconnori* and *M. capito*, as harmonic radar tracking was not suitable for these fossorial carabid species.

Chapter Four

Population dynamics, seasonality, and life history of New Zealand carabid beetles



Cover plate 4. Recently hatched *Megadromus capito* (Pterostichini) larvae and eggs at Browns Bush. Photograph by David Mudge.

“Much research is focussed on big things that are fun to kill, and things that fly and look pretty...
Organisms should be selected because they are good model systems for ecology
rather than simply pleasant hobbies”

Paul Keddy (1991)

Population dynamics, seasonality, and life history of New Zealand carabid beetles

4.1 INTRODUCTION

A wealth of information exists about the population dynamics, seasonal activity, and life history of Northern Hemisphere carabids, with detailed studies spanning many years (e.g. Gilbert 1956, Williams 1959, Mitchell 1963a, Rivard 1964, Greenslade 1965, Murdoch 1966, Brunsting 1981, Niemelä *et al.* 1989, Ernsting *et al.* 1992, van Dijk & den Boer 1992, Kennedy 1994, van Dijk 1994, Fadl & Purvis 1998). However, very little is known about the life cycles of New Zealand carabids, and basic information about their developmental stages and reproductive biology is completely lacking. Only one published study exists which explicitly deals with the seasonal dynamics and reproductive phenology of carabids in New Zealand (Cartellieri & Lövei 2000).

The seasonal pattern of activity in carabids is related to their reproductive biology, with the highest catches of beetles usually coinciding with their main breeding period (Murdoch 1966, Barlow 1973, Szujewski 1987, Lys & Nentwig 1991). This means that much can be learned about the life cycles of carabids from studying the seasonal fluctuations in their population numbers. Carabids exhibit a range of life history strategies, and these are strongly influenced by local environmental conditions (Thiele 1977, den Boer & den Boer-Daanje 1990). The regulation of annual activity rhythms in carabids is mainly determined by photoperiod and temperature (Thiele 1977).

Carabid species have traditionally been divided into two different types of life cycle: spring breeders and autumn breeders (Larsson 1939). Spring breeders carry out reproductive activities such as mating and egg laying in spring, and produce larvae that develop in late spring and summer. In contrast, autumn breeders mate and lay eggs in autumn, and produce larvae in autumn and winter. However, Lindroth (1949) recognised that many species did not fit the traditional scheme, and instead suggested divisions based on the over-wintering life-stage. Spring breeders generally over-winter as adults, whereas autumn breeders have larvae that survive over the winter.

However, Lindroth (1949) also noted that some species had a flexible reproductive period and could breed during both seasons. For example, Paarmann (1990) observed that *Poecilus lepidus* Leske adults were reproductively active in both spring and autumn, and Fadl and Purvis (1998) identified the presence of an autumn-breeding cohort in *Loricera pilicornis* (Fabricus), *Bembidion lampros* (Herbst) and *Bembidion aeneum* Germar, which were traditionally regarded as spring breeders. In addition, den Boer & den Boer-Daanje (1990) discovered that the reproductive periods of 68 species of carabids in the Netherlands were spread uninterruptedly over the entire year, so that spring and autumn breeders could not be separated. Adults of most species appeared to hibernate after reproduction and participate again in following years, so that a division into larval and adult hibernators was inadequate. They proposed that carabids might be divided into summer developers and winter developers, based on the main season in which larval growth occurs.

Many carabid species appear to live longer than one year, and also reproduce more than once (Luff 1980, Baars & van Dijk 1984a, den Boer & den Boer-Daanje 1990, Baumgartner *et al.* 1997). This makes studying their life cycles more complicated, because the activities of different generations may overlap, and larvae may be produced at several different times of year. Schjøtz-Christensen (1965) was probably the first to dissect sufficient females to distinguish between activities relating to reproduction, and other locomotory activities such as foraging. He discovered that in some *Harpalus* species old beetles reproduce again in successive years, resulting in teneral beetles appearing outside the usual reproductive period.

Thiele (1977) reviewed a large number of papers and suggested five different types of annual rhythm in carabids in the temperate zones (see Table 4.1). Paarmann (1979) extended this system even further, distinguishing two types of spring breeder and two types of multi-seasonal development based on a more mechanistic interpretation of environmental control during periods of dormancy (Table 4.1).

Table 4.1. Summary of a number of attempts to classify temperate carabid species according to their life history strategy (copied from Fadl & Purvis 1998).

Larsson (1939)	Lindroth (1949)	Thiele (1977)	Paarman (1979)
'Spring breeders'	'Adult overwinterers'	Type 1: Spring breeders with summer larvae and adult hibernation	Type 1: Spring breeders with obligate female gonad dormancy terminated by change from short to long day length Type 2: Spring breeders with facultative female gonad dormancy induced by short day length
'Autumn breeders'	'Larval overwinterers'	Type 2: Species with winter larvae and reproduction in summer and/or autumn, but without adult dormancy Type 3: Species with winter larvae and young adults in spring which undergo aestivation prior to reproduction	Type 3: Autumn breeders without summer gonad dormancy but with temperature-controlled winter larval dormancy Type 4: Autumn breeders with obligate summer gonad dormancy terminated by change from long to short day length
	'Unstable breeders'	Type 4: Species with 'flexible' reproduction in either spring or autumn and larvae which develop in summer or winter Type 5: Species which require more than one year to develop	Type 5: Development potentially free from dormancies, with facultative temperature-controlled and adult gonad and larval dormancy in winter Type 6: Species requiring more than one season and with obligate female gonad dormancy ended by a change from short to long day length Type 7: Species requiring more than one season with facultative temperature controlled larval and adult gonad dormancy

Almost all of the research into the seasonal activity of carabids has been carried out in the Northern Hemisphere, and it is not known whether New Zealand carabids show the same types of annual rhythm. Northern Hemisphere species have experienced past and present climatic severity, which has resulted in strong seasonal cycles in most insects (Roberts 1978). In contrast, New Zealand has a relatively mild island climate with a lack of distinct seasonality (Watt 1978, Roberts 1978, Howarth & Ramsay 1991). Watt (1978) remarked that many large carabids in New Zealand display "little or no seasonality", and that adults and larvae may occur throughout the whole year. From these observations, it would follow that New Zealand carabids are most likely to conform to Types four and five from Thiele (1977), however this has yet to be established.

The majority of studies overseas have used pitfall trapping alone to study carabid seasonal activity (e.g. Rivard 1964, Jones 1979, Brunsting 1981, Luff 1982, Lys & Nentwig 1991, Ernsting *et al.* 1992, Horne 1992, Niemelä *et al.* 1992). However, pitfall trapping has a number of limitations for studying the population dynamics and seasonality of carabids because the catch is not solely a reflection of population size, but is a combination of both abundance and activity (see Chapter Three, section 3.4.3). For this reason, the main method used to investigate carabid population dynamics in my study involved manual searching of habitat resting sites for live beetles, as this is relatively independent of locomotory activity. In addition, two types of pitfall trapping (live capture and removal sampling) were used for shorter periods to estimate activity and determine female reproductive phenology.

The aim of this chapter was to investigate the population dynamics and seasonality of New Zealand carabid beetles in North Island lowland forests. The ultimate aim of this research was to gain knowledge about the life history of carabids in New Zealand, and to compare the observed strategies with those of Northern Hemisphere species.

4.2 METHODS

4.2.1 Study Sites

This study was carried out at Browns Bush (Figure 2.1) and Lake Papaitonga Scenic Reserve (Figure 4.1). Both are in the Horowhenua district, North Island, New Zealand, and are approximately 4 km apart from each other. Browns Bush is a privately-owned lowland forest remnant of less than 1 ha situated 4 km south of Levin (see Chapter Two, section 2.2.1 for a full site description). All studies on live carabids were carried out at Browns Bush. Lake Papaitonga Scenic Reserve covers an area of 122 ha, and is located 4 km south-west of Levin. The reserve includes the lake itself, and a remnant of indigenous lowland forest surrounding the lake (approximately 52 ha). The forest vegetation consists of a canopy of tawa (*Beilschmiedia tawa*), pukatea (*Laurelia novae-zealandiae*), titoki (*Alectryon excelsus*) and kohekohe (*Dysoxylum spectabile*), with emergent podocarps such as kahikatea (*Dacrycarpus dacrydioides*) and rimu (*Dacrydium cupressinum*). Swampy areas (approximately 16 ha) are dominated by raupo (*Typha orientalis*), flax (*Phormium tenax*), and *Carex secta/Hebe salicifolia* shrubland (Devine 1997). Lake Papaitonga Scenic Reserve contains a population of the protected native snail, *Powelliphanta traversi traversi* (Powell), which has a very restricted distribution and is listed as a “Category B threatened species” (Molloy *et al.* 1994). Experiments at Lake Papaitonga involved removal sampling of carabid beetles using pitfall traps.

4.2.2 Manual searches of habitat resting sites at Browns Bush

Manual searches were carried out under habitat resting sites at Browns Bush for two large endemic carabids, *Mecodema oconnori* Broun and *Megadromus capito* (White) (see Chapter Two, section 2.2.4 for a full description of this method). Searches were done approximately weekly from April 1999 to March 2000, except in January 2000. A number of preliminary searches were also made in February and March 1999 to identify all of the potential resting sites in the forest. Occasional visits were also made at other times throughout 2000. All beetles found were individually marked using numbered bee labels, then weighed and measured.

Lake Papaitonga Scenic Reserve

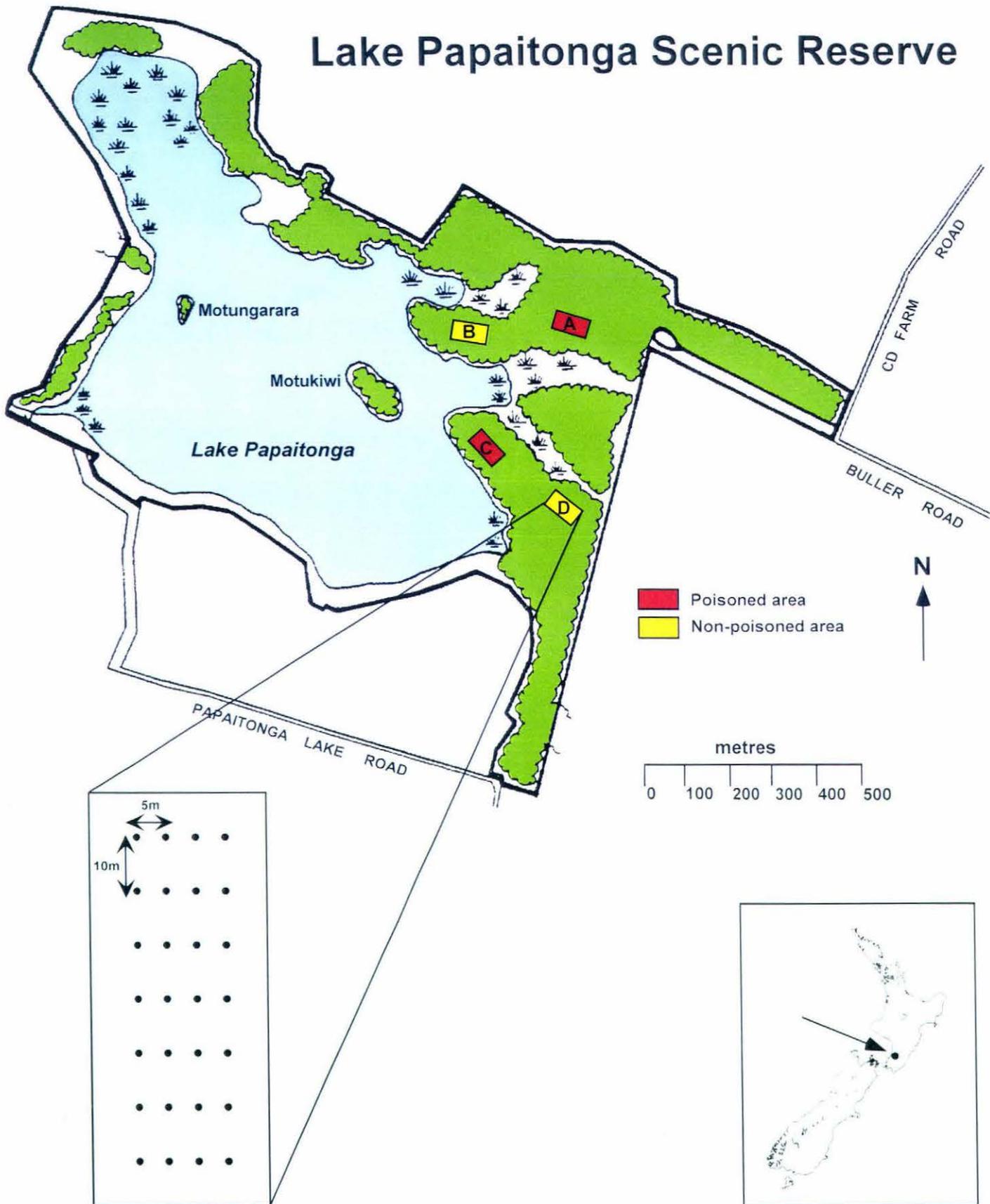


Figure 4.1. Map of Lake Papaitonga Scenic Reserve, Levin (Latitude $40^{\circ}39'$, Longitude $175^{\circ}13'E$) showing treatment (poisoned) and non-treatment (non-poisoned) areas. The enlargement shows the arrangement of pitfall traps in each sampling area.

4.2.3 Live capture pitfall trapping at Browns Bush

A grid of 147 pitfall traps was used to carry out a mark-recapture experiment on *Mecodema oconnori* and *Megadromus capito* at Browns Bush (see Chapter Two, section 2.2.5 for a full description of this method). All beetles found were individually marked using numbered bee labels, then weighed and measured. Other carabid species caught in the traps (e.g. *Holcaspis mucronata* Broun) were recorded, but were not individually marked or their sex identified. Live pitfall traps were operated in November and December 1999, and February and March 2000, on a total of nine trapping occasions. On each occasion, the containers were left open for approximately 24 hours.

4.2.4 Removal pitfall trapping at Lake Papaitonga Scenic Reserve

Invertebrate sampling was carried out using pitfall traps filled with 95% ethylene glycol (antifreeze) as a preserving agent. A total of 112 pitfall traps were operated continuously for six months from October 1999 to March 2000 inclusive. The study site was divided into four sampling areas, with 28 traps in each area (Figure 4.1). The traps were arranged in a five by ten metre grid, with seven lines of traps (10 m apart), and four traps in each line (5 m apart), covering a total area of 900 m² (Figure 4.1). Each trap consisted of a piece of plastic down pipe (77 mm diameter) sunk into the ground with a plastic cup (75 mm diameter) placed inside. Each trap was covered with a plastic dinner plate (spray painted black to make them less obvious to people) mounted on two wire pegs pushed through the plate (Figure 4.2). Half way through the six months of sampling, wire mesh barriers (mesh size 25 mm) were placed around the outside of the traps to prevent *Powelliphanta traversi traversi* from being caught and killed in the traps. The traps were emptied every two weeks for the first two months (October and November), then every four weeks subsequently. The results from the fortnightly samples were pooled to give a monthly total comparable to the rest of the samples.

Pitfall trap samples were inspected under a binocular microscope, and all carabids (including larvae) were removed and stored in 70% ethanol. Electronic callipers were used to measure the total body length from the tip of the mandible to the end of the abdomen of all specimens. Adult carabids were identified to species, but many of the larvae could not

be accurately identified to species or even to genus because of the lack of identification keys for New Zealand larvae. The only larvae identified to species were those of *Megadromus capito* (White). They were determined to genus by Peter Johns, and I was able to identify them to species based on known larvae caught at Browns Bush. *Megadromus capito* larvae were separated into first, second and third instar on the basis of head capsule width (Barlow 1973).

The sex of adult beetles was determined for species in the tribes Broscini and Pterostichini (see Chapter Two, section 2.2.3). Females from these tribes were dissected to determine their reproductive state. Two classes were identified: gravid females with (mature) eggs, and females without eggs. The elytra were removed, and the abdomen was set in wax and covered in alcohol with the dorsal side facing upwards. The abdomen was cut open under a dissecting microscope, and the total number of eggs in each female was counted. The length and width of each egg was measured to the nearest 0.01 mm using an ocular micrometer or electronic callipers, depending on the size of the eggs. The total ‘wet’ mass of eggs per female was determined to the nearest 0.01 g.



Figure 4.2. Pitfall trap used for sampling carabids at Lake Papaitonga Scenic Reserve. Note the wire mesh barrier used to prevent *Powelliphanta traversi traversi* snails from entering the traps. Photograph by Felix Collins.

4.2.5 Climatic variables

Mean daily and mean monthly air temperature from October 1999 to March 2000 were taken from the Levin Weather Station (operated by NIWA), which is less than five kilometres from both study sites (see Appendix 6). Total daily rainfall measurements from October 1999 to March 2000 were also acquired from the Levin Weather Station (see Appendix 7).

4.2.6 Statistical analyses

The relationship between carabid abundance at Lake Papaitonga Scenic Reserve and two climatic variables (mean monthly air temperature and total monthly rainfall) was analysed using Pearson correlations and Bonferroni probabilities (SYSTAT 6, SPSS Inc.1996).

4.3 RESULTS

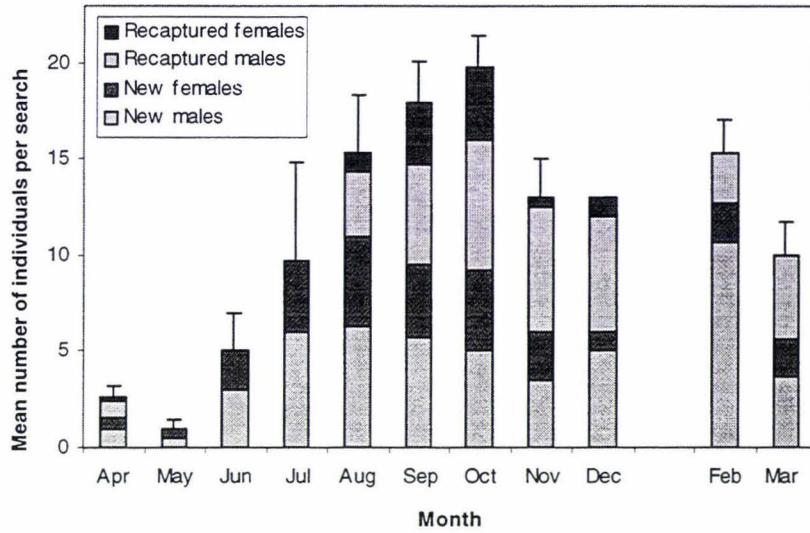
4.3.1 Seasonal abundance of *Mecodema oconnori* and *Megadromus capito* at Browns Bush

A total of 262 *M. oconnori* and 260 *M. capito* were found in searches of resting sites at Browns Bush from February 1999 to March 2000. *Mecodema oconnori* adults were present in all months that were sampled, but their abundance varied considerably throughout the year (Figure 4.3a). Very few were found in autumn (April - May), but numbers increased from June onwards to a peak in spring (September - October). No marked *M. oconnori* were recaptured from May to July, and in addition, no marked females were recaptured in February or March 2000.

In comparison, *M. capito* adults showed less seasonal variation in abundance, and were present in moderate numbers throughout the year (Figure 4.3b). *Megadromus capito* had slightly higher numbers in winter (June - July), and decreased numbers in November (spring). Few females were found in October, and only one new (unmarked) female was found during the entire month. Very few new males were found in November. The numbers of recaptured beetles was highest from June to August, but decreased in September and October when new beetles were much more abundant.

The proportions of each sex varied throughout the year for both species (Figure 4.4). Male *M. oconnori* were generally more abundant than females throughout the year, especially in summer (December to February), although the proportions of males and females were equal in May (autumn). Males of *M. capito* were generally more abundant than females, but females outnumbered males in winter (July and August), and in December.

(a) *Mecodema oconnori*



(b) *Megadromus capito*

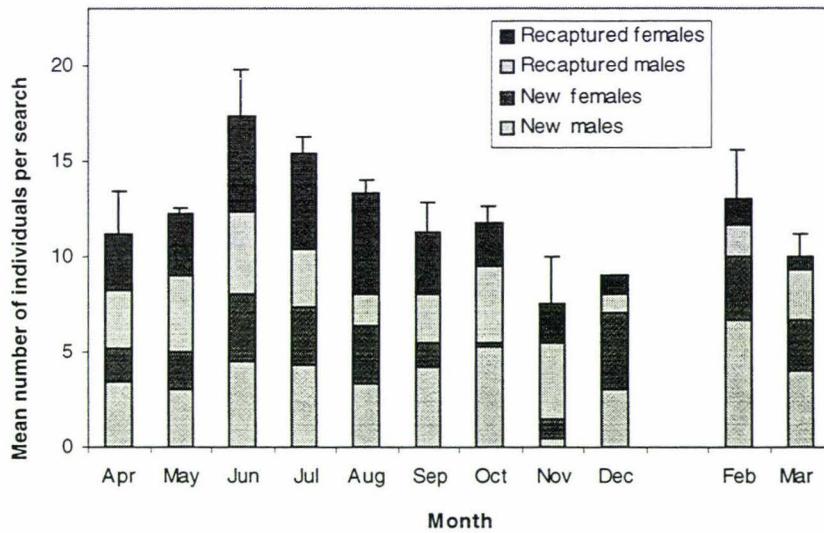


Figure 4.3. Mean number of new and recaptured (a) *Mecodema oconnori* and (b) *Megadromus capito* males and females found per search of resting sites at Browns Bush (April 1999 - March 2000). Error bars (standard error) are for the total number of individuals (males plus females) per month. NB. No searches were carried out in January 2000.

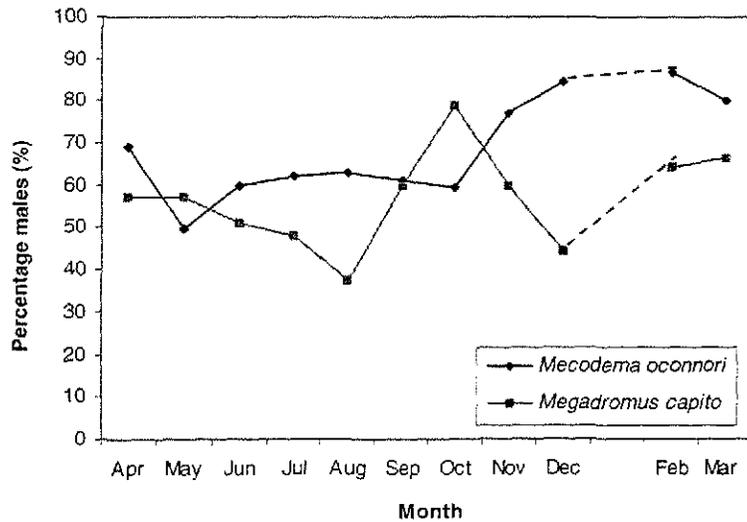


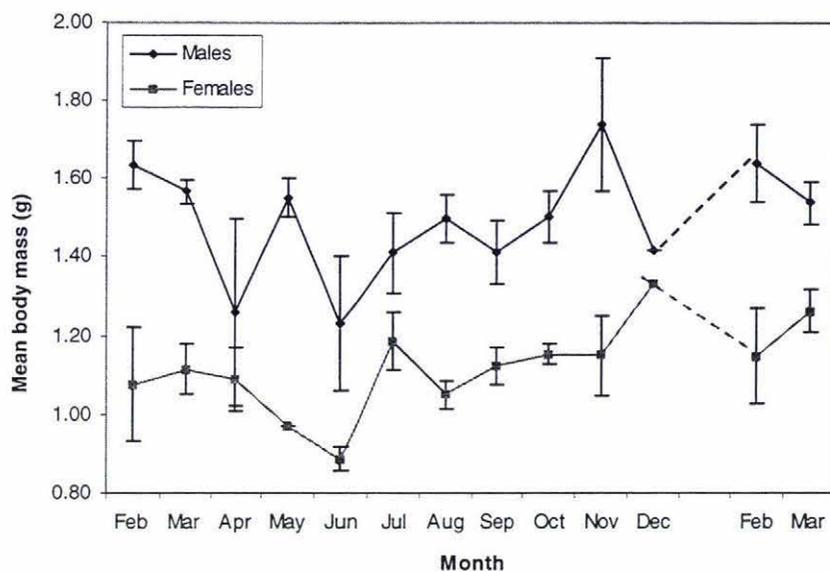
Figure 4.4. Relative abundance of male *Mecodema oconnori* and *Megadromus capito* found in searches of habitat resting sites at Browns Bush (April 1999 - March 2000).

4.3.2 Seasonal changes in body mass of *Mecodema oconnori* and *Megadromus capito* at Browns Bush

The mean body mass of males and females of both species displayed seasonal fluctuations (Figure 4.5). *Mecodema oconnori* males had a higher mean body mass than females for the entire 14 months of the study (Figure 4.5a). In contrast, the masses of male and female *M. capito* often overlapped (Figure 4.5b). *Mecodema oconnori* males and females both showed a reduction in mean mass in winter (June), and a maximum in spring-summer (November for males and December for females) (Figure 4.5a).

Megadromus capito males maintained a fairly constant mean mass throughout the year, with a slight maximum in December (summer), whereas females showed much greater seasonal fluctuations (Figure 4.5b). The mean mass of females was low in autumn and winter (May - June), and increased to a maximum in September and November (spring), when females became heavier than males. Female mean mass was extremely low in October, and this was because only one very small unmarked female was caught.

(a) *Mecodema oconnori*



(b) *Megadromus capito*

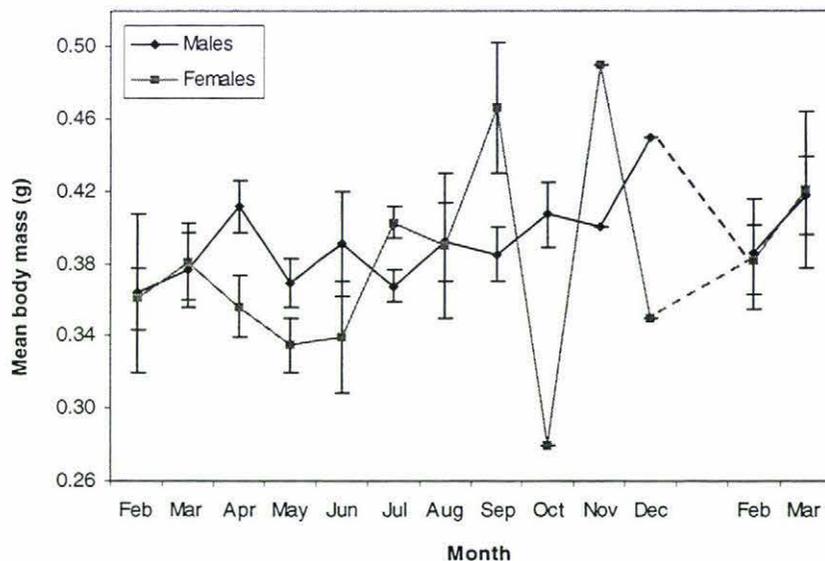


Figure 4.5. Mean body mass of (a) *Mecodema oconnori* and (b) *Megadromus capito* in searches of habitat resting sites at Browns Bush (February 1999 - March 2000). Error bars indicate standard error. NB. No searches were carried out in January 2000.

4.3.3 Population dynamics of carabids in live pitfall traps at Browns Bush

A total of 176 carabid beetles were captured live in pitfall traps at Browns Bush over nine trapping occasions. These comprised: 74 *Mecodema oconnori* (42.0% of total), 51 *Megadromus capito* (29.0%), and 51 *Holcaspis mucronata* (29.0%). *Mecodema oconnori* and *M. capito* showed similar abundances over time, with the numbers caught increasing to a peak in February (summer), and then declining again in March (early autumn) (Figure 4.6). However, *M. capito* numbers reached a peak one week sooner than *M. oconnori*, and declined before them as well. No *M. capito* individuals were caught on either the first or last trapping occasions. Three teneral adults of *M. capito* were caught during the trapping experiment: two males in February, and one female at the beginning of March.

In contrast to the two larger species, the catches of *H. mucronata* fluctuated erratically from week to week and showed no overall seasonal trend (Figure 4.6). However, there was a slight peak in numbers at the end of February, and catches remained high during March.

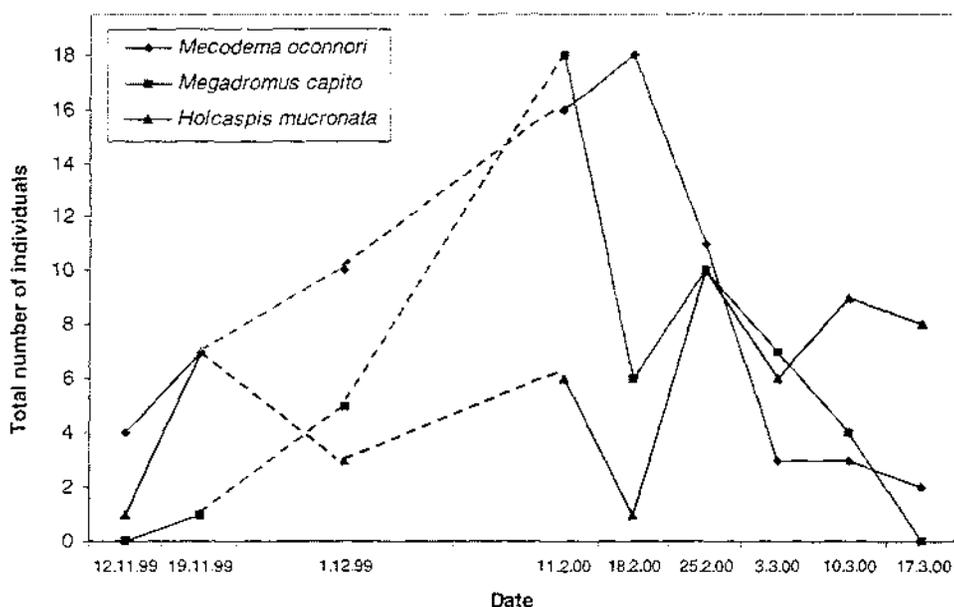


Figure 4.6. Total number of *Mecodema oconnori*, *Megadromus capito*, and *Holcaspis mucronata* caught in live pitfall traps at Browns Bush on each trapping occasion. NB. Dotted line indicates sampling dates that are at more than weekly intervals.

Mecodema oconnori and *M. capito* showed large fluctuations in their sex ratios over the course of the live trapping experiment (Figure 4.7). Males of *M. capito* were more numerous than females throughout the trapping period, although the proportion of males declined from November until the sex ratio was equal in mid-March. The sex ratio of *M. oconnori* was biased towards males on the first trapping occasion, but the proportion of males dropped dramatically the following week and remained less than half until mid-February. Females dominated the catches from late February onwards, and only one male was caught during the whole of March.

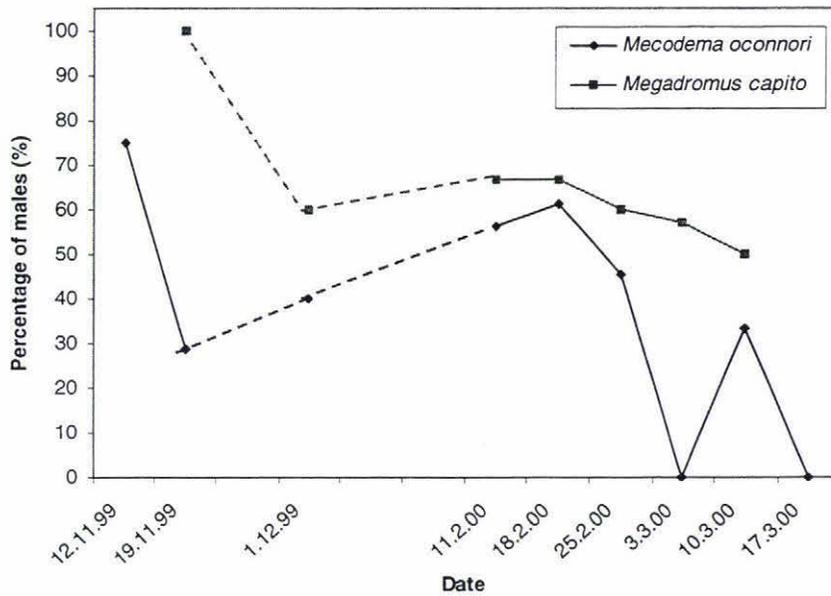


Figure 4.7. Relative abundance of male *Mecodema oconnori* and *Megadromus capito* caught in pitfall traps at Browns Bush on each trapping occasion. NB. Dotted line indicates sampling dates that are at more than weekly intervals.

4.3.4 Abundance of carabids in pitfall traps at Lake Papaitonga Scenic Reserve

A total of 501 adult carabid beetles from seven tribes and 14 species were caught during six months of pitfall trapping at Lake Papaitonga Scenic Reserve (Table 4.2). However, a specific name could not be assigned to all specimens because several of the genera are in need of taxonomic revision (A. Larochelle, pers. comm. 2000). The only introduced species caught at Lake Papaitonga Scenic Reserve was *Harpalus affinis* (Schrank). Approximately 90% of the adults comprised just three species. *Megadromus capito* was the most abundant species (71.3%), followed by *M. oconnori* (11.0%), and *Selenochilus* sp. (*ruficorne*) (7.2%). Five species were only represented by a single individual (see Table 4.2). A total of 85 carabid larvae were also caught, and 70 of these were identified as *M. capito* (82.4% of the larvae). All three larval instars of *M. capito* were present: 48 were first instar, 11 second instar, and 11 third instar.

Table 4.2. Total number of adult carabid beetles caught in pitfall traps at Lake Papaitonga Scenic Reserve over six months of sampling (October 1999 to March 2000).

Species	Tribe	Total number of individuals	Proportion (%)
<i>Ctenognathus bidens</i> Chaudoir	Platynini	1	0.2
<i>Ctenognathus</i> sp. Fairmaire	Platynini	1	0.2
<i>Harpalus affinis</i> (Schrank) *	Harpalini	2	0.4
<i>Holcaspis mucronata</i> Broun	Pterostichini	18	3.6
<i>Holcaspis sinuiventris</i> (Broun)	Pterostichini	16	3.2
<i>Mecodema oconnori</i> Broun	Broscini	55	11.0
<i>Megadromus capito</i> (White)	Pterostichini	357	71.3
<i>Megadromus vigil</i> (White)	Pterostichini	4	0.8
<i>Molopsida antarctica</i> (Laporte de Castelnau)	Tropopterini	1	0.2
<i>Molopsida strenua</i> (Broun)	Tropopterini	1	0.2
<i>Oopterus</i> sp. Guérin	Zolini	1	0.2
<i>Plocamostethus planiusculus</i> (White)	Pterostichini	3	0.6
<i>Selenochilus</i> sp. (<i>ruficorne</i>) Chaudoir	Meonini	36	7.2
<i>Zolus</i> sp. Sharp	Zolini	5	1.0
TOTAL adults		501	1.0

* indicates introduced species.

The sex of each individual was determined for the six species of carabids in the tribes Pterostichini and Broscini (Table 4.3). More males than females were caught of each species, and no *Megadromus vigil* (White) females were caught (Table 4.3). The sex ratio of the two *Holcaspis* species was also highly biased towards males. *Mecodema oconnori* had the most even sex ratio, but females still only accounted for 40% of the catch of that species.

Table 4.3. Total number of males and females for six of the carabid species caught at Lake Papaitonga Scenic Reserve over six months (October 1999 to March 2000).

Carabid species	Total number of males (%)	Total number of females (%)	Sex ratio (males : females)
<i>Holcaspis mucronata</i>	14 (77.8)	4 (22.2)	1:0.29
<i>Holcaspis sinuiventris</i>	13 (81.2)	3 (18.8)	1:0.23
<i>Mecodema oconnori</i>	33 (60.0)	22 (40.0)	1:0.67
<i>Megadromus capito</i>	225 (63.0)	132 (37.0)	1:0.59
<i>Megadromus vigil</i>	4 (100.0)	0 (0.0)	1:0.0
<i>Plocamostethus planiusculus</i>	2 (66.7)	1 (33.3)	1:0.5

4.3.5 Seasonality of adult carabids at Lake Papaitonga Scenic Reserve

The total catch of adult carabids at Lake Papaitonga Scenic Reserve was high in October (spring), but declined in November and December (Figure 4.8). Adult numbers increased again in summer (January - February), but declined again at the start of autumn (March). Fewer larvae were caught, but they followed the same pattern of abundance as the adult beetles, with numbers being highest in October, January, and February, and lowest in December (Figure 4.8).

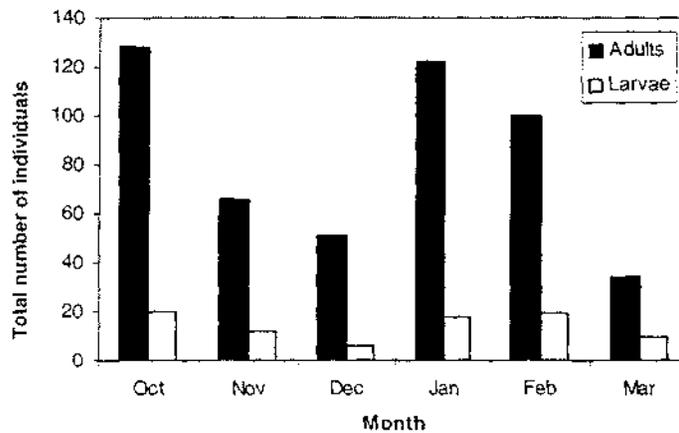
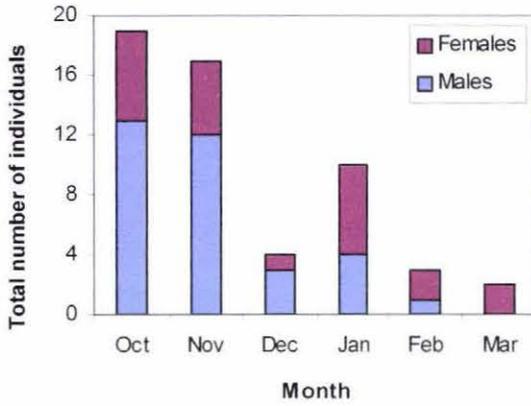


Figure 4.8. Total abundance of Carabidae (adults and larvae) caught at Lake Papaitonga Scenic Reserve in each month of sampling (October 1999 – March 2000).

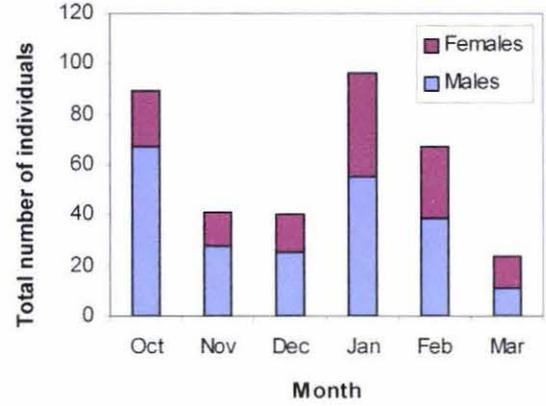
Fluctuations in the abundance of the most dominant species, *M. capito*, are responsible for most of the seasonal pattern in Figure 4.8 above (see Figure 4.9b). The catches of *M. capito* adults were highest in October and January, and lowest in March. Only two *M. capito* teneral were caught during the six months of sampling, and these were both caught in February. *Mecodema oconnori* was most abundant in spring (October and November), but numbers dropped off markedly in December, February and March (Figure 4.9a).

Holcaspis mucronata and *Holcaspis sinuiventris* (Broun) both showed a peak in February (Figure 4.9c,d), but *H. mucronata* numbers were still high in March, while *H. sinuiventris* numbers decreased. *Selenochilus* sp. was most abundant in January and February (summer), but completely disappeared from the samples in March (Figure 4.9e). The remaining nine 'minor' species were caught in very low numbers throughout the sampling period, but their catches were highest in October and February (Figure 4.10).

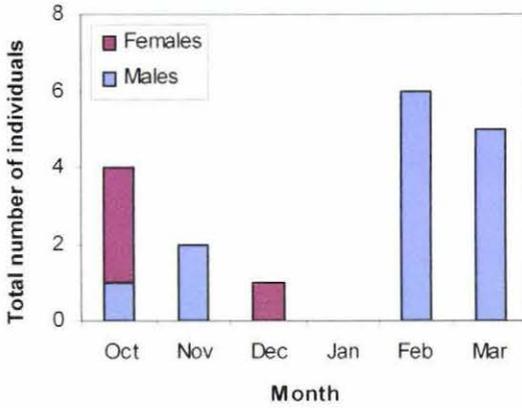
(a) *Mecodema oconnori*



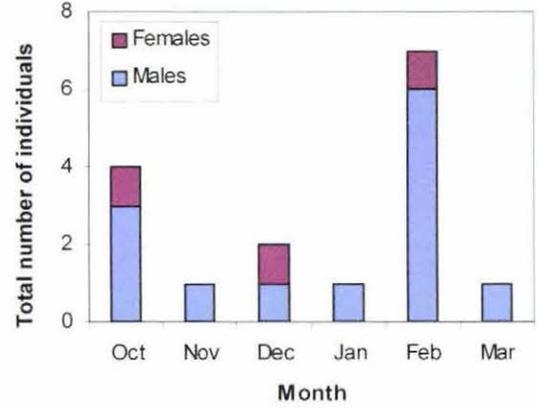
(b) *Megadromus capito*



(c) *Holcaspis mucronata*



(d) *Holcaspis sinuiventris*



(e) *Selenochilus* sp.

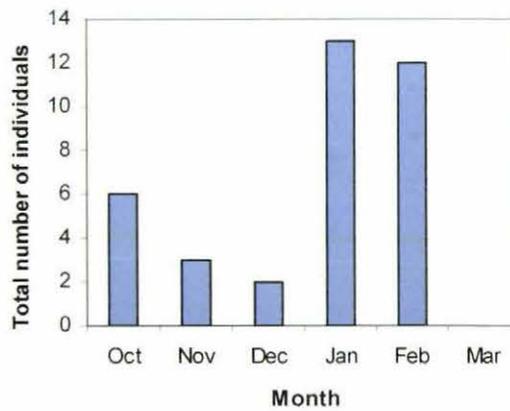


Figure 4.9. Changes in the total abundance of carabids in pitfall traps at Lake Papaitonga Scenic Reserve from October 1999 to March 2000. (a) *Mecodema oconnori*, (b) *Megadromus capito*, (c) *Holcaspis mucronata*, (d) *Holcaspis sinuiventris*, and (e) *Selenochilus* sp.

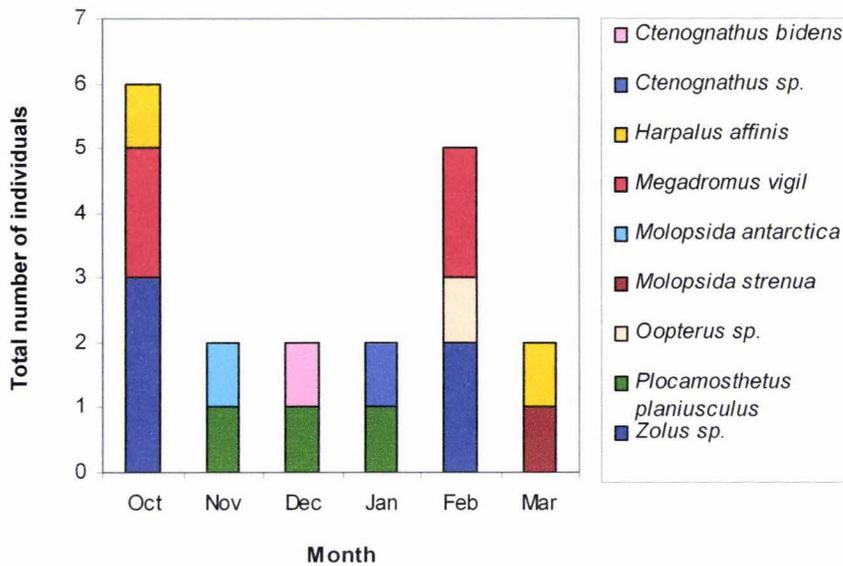


Figure 4.10. Total abundance of nine 'minor' species in pitfall traps at Lake Papaitonga Scenic Reserve from October 1999 to March 2000.

The proportion of female *M. oconnori* and *M. capito* increased from January onwards, as the overall catches were declining (Figure 4.11). This was particularly striking for *M. oconnori*, where females were much more abundant than males from January to March. *Holcaspis sinuiventris* showed large fluctuations in its sex ratio over time, but males were more numerous than females in every month except December (Figure 4.11).

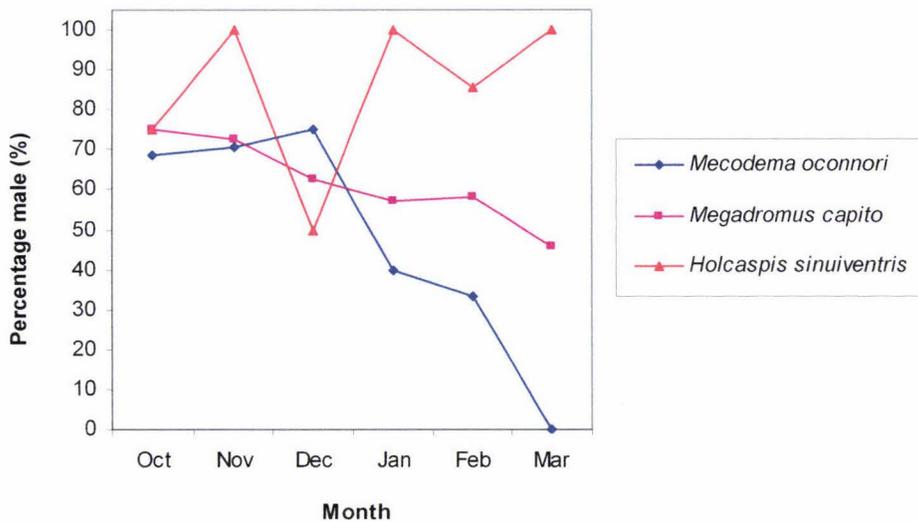


Figure 4.11. Relative abundance of male *Mecedema oconnori*, *Megadromus capito*, and *Holcaspis sinuiventris* caught in pitfall traps at Lake Papaitonga Scenic Reserve (October 1999 - March 2000).

4.3.6 Seasonality of carabid larvae at Lake Papaitonga Scenic Reserve

Seasonal changes in the abundance of *M. capito* larvae at Lake Papaitonga Scenic Reserve are shown in Figure 4.12. First instar larvae were found in all months of sampling, and had a peak in numbers in January and February (summer). In contrast, second instar larvae were only found in the latter half of the sampling period from January to March. The majority of third instar larvae were caught in October, although two were also caught in November and one in January.

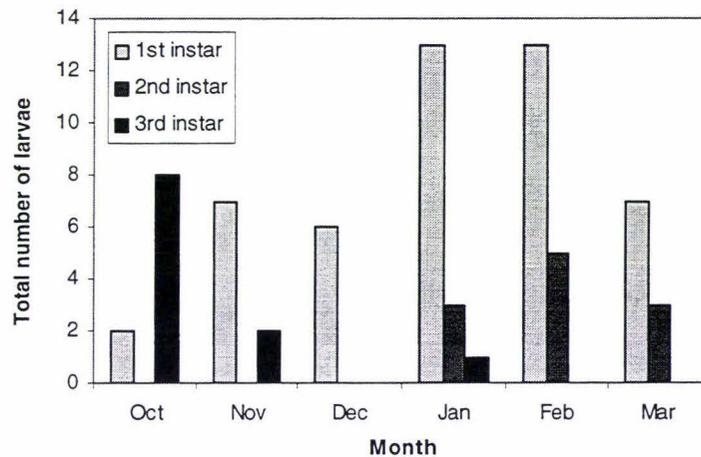


Figure 4.12. Total abundance of *Megadromus capito* larvae at Lake Papaitonga Scenic Reserve in each month of sampling (October 1999 - March 2000).

4.3.7 Female reproductive phenology

The reproductive phenology of five species of carabids at Lake Papaitonga Scenic Reserve was investigated. A total of 84 females were dissected, comprising 54 *Megadromus capito*, 22 *Mecodema oconnori*, four *Holcaspis mucronata*, three *H. sinuiventris*, and one *Plocamostethus planiusculus* (White). The proportion of females that contained eggs varied between the species, as did the size and number of eggs (see Table 4.4). *Plocamostethus planiusculus* was the only species in which no eggs were found.

Table 4.4. Reproductive phenology of female Carabidae: proportion of females with eggs, mean egg number per female (\pm standard error), maximum egg number per female, mean egg size, and mean proportion of egg mass to female body mass.

Carabid species	Number of females dissected	Proportion of females with eggs (%)	Mean no. of eggs per female	Maximum no. of eggs per female	Mean egg length x width (mm)	Mean % egg mass
<i>Megadromus capito</i>	54	64.8	10.5 \pm 0.92	28	3.71 x 1.85	23.5
<i>Mecodema oconnori</i>	22	81.8	1.6 \pm 0.15	3	5.29 x 4.00	4.0
<i>Holcaspis mucronata</i>	4	100.0	7.8 \pm 1.25	9	2.73 x 1.61	-
<i>Holcaspis sinuiventris</i>	3	66.7	2.0 \pm 0.0	2	2.85 x 1.61	-
<i>Plocamostethus planiusculus</i>	1	0.0	-	-	-	-

Mecodema oconnori appears to have very low fecundity, with a maximum number of three eggs per female (Table 4.4). However, *M. oconnori* also had the largest eggs, with a mean length of 5.3 mm, and they were proportionally wider than those of the other species (Table 4.4). *Megadromus capito* had the highest fecundity of any species, with up to 28 eggs per female. It also had the second largest egg, with a mean length of 3.7 mm. The proportion of egg mass to female body mass was markedly different for *M. oconnori* and *M. capito* (Table 4.4). *Mecodema oconnori* eggs ranged from 1-8% of the female body mass, whereas *M. capito* eggs were relatively much heavier, with eggs weighing as much as 85% of a female's body mass. *Holcaspis mucronata* had from four to nine eggs per female, whereas the two gravid *H. sinuiventris* females had two eggs each. Both species had very similar-sized eggs, although the eggs of *H. sinuiventris* were slightly longer than those of *H. mucronata*.

Females of *M. oconnori* and *M. capito* were found with eggs in every month of sampling from October to March (Figure 4.13). All of the *M. oconnori* females caught in December, February and March had eggs, although a low number of females were caught in these months (Figure 4.13a). All *M. capito* females contained mature eggs in October, however by March, the proportion of gravid females was less than half (Figure 4.13b). Both *H. mucronata* and *H. sinuiventris* females had eggs in October and December, but the one *H. sinuiventris* female dissected in February was not gravid.

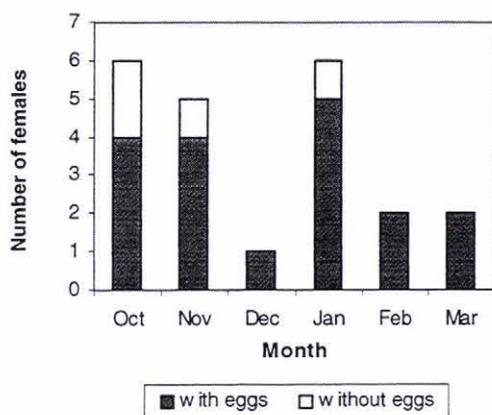
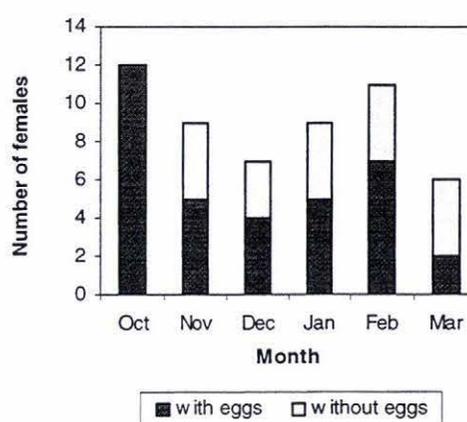
(a) *Mecodema oconnori*(b) *Megadromus capito*

Figure 4.13. Number of dissected females of (a) *Mecodema oconnori* and (b) *Megadromus capito* found with and without mature eggs from October 1999 to March 2000 at Lake Papaitonga Scenic Reserve.

4.3.8 Climatic variables

4.3.8.1 Temperature

Nearly all of the carabid species at Lake Papaitonga Scenic Reserve showed a positive relationship between mean monthly air temperature and the number of individuals caught (Table 4.5, Figure 4.14). However, only the correlation for *Selenochilus* sp. was significant (Pearson correlation, $r = 0.746$, $p = 0.034$; Figure 4.14d), as the number of samples was fairly small ($n = 8$). The relationship between larval numbers and temperature was also positive, but again the correlation was not significant ($r = 0.642$, $p = 0.086$, Figure 4.14d). In contrast, *M. oconnori* showed indications of a negative relationship with monthly temperature, although the correlation was not significant ($r = -0.366$, $p = 0.374$, Figure 4.14b).

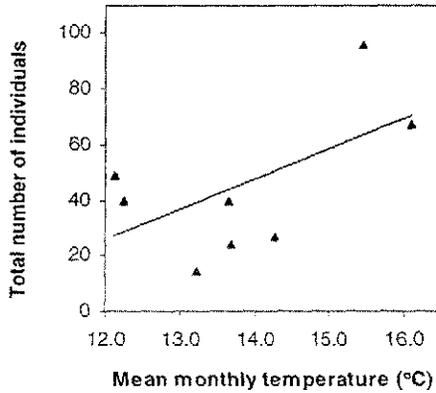
4.3.8.2 Rainfall

Most of the carabid species and carabid larvae appeared to have a positive relationship between total monthly rainfall and their catches, however none of the correlations were significant (Table 4.5). In contrast, the numbers of *H. mucronata* and *H. sinuiventris* had negative relationships with rainfall, but again these were not significant (Table 4.5).

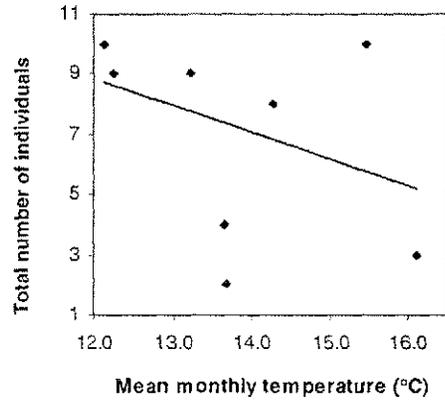
Table 4.5. Pearson correlations (r) and Bonferroni probabilities (p-values) between carabid abundance at Lake Papaitonga Scenic Reserve and mean monthly air temperature (°C), and total monthly rainfall (October 1999 – March 2000) (n = 8 in all cases). Significance level: * p < 0.05, NS = non-significant (p > 0.05).

Carabid species	Mean air temperature (°C)		Total rainfall (mm)	
	Pearson correlation coefficient (r)	P-value	Pearson correlation coefficient (r)	P-value
<i>Megadromus capito</i>	0.578	0.133 NS	0.422	0.299 NS
<i>Mecodema oconnori</i>	-0.366	0.374 NS	0.058	0.892 NS
<i>Holcaspis mucronata</i>	0.241	0.566 NS	-0.559	0.151 NS
<i>Holcaspis sinuiventris</i>	0.442	0.272 NS	-0.154	0.715 NS
<i>Selenochilus</i> sp.	0.745	0.034 *	0.279	0.505 NS
Total larvae	0.642	0.086 NS	0.103	0.808 NS

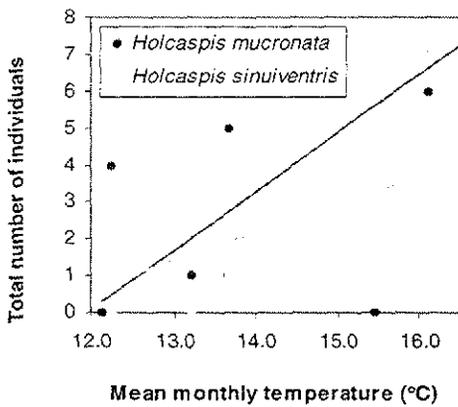
(a) *Megadromus capito*



(b) *Mecodema oconnori*



(c) *Holcaspis mucronata* & *H. sinuiventris*



(d) Larvae and *Selenochilus* sp.

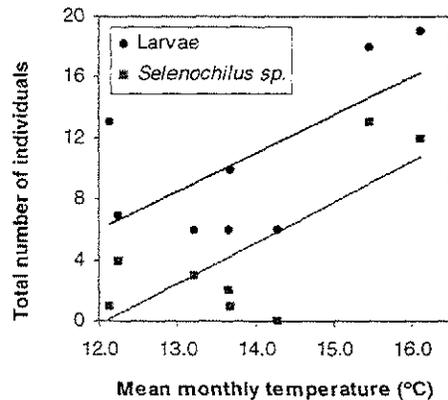


Figure 4.14. Relationship between mean monthly air temperature (°C) and the total number of individuals caught in pitfall traps at Lake Papaitonga Scenic Reserve: (a) *Megadromus capito*, (b) *Mecodema oconnori*, (c) *Holcaspis mucronata* and *Holcaspis sinuiventris*, and (d) carabid larvae and *Selenochilus* sp. NB. Mean fortnightly temperature was used for the four samples in October and November, as these traps were emptied every two weeks.

4.4 DISCUSSION

4.4.1 Seasonal activity of carabid beetles

Several studies in New Zealand have found that carabids are most abundant in pitfall traps during spring and summer (Somerfield 1974, Butcher and Emberson 1981, Moeed & Meads 1985, Moeed & Meads 1986). For example, Butcher and Emberson (1981) found that carabids on Banks peninsula were most abundant between November and March, and their increase in numbers during October and November coincided with an increase in ambient temperature. Similarly in my study, an unnamed species of *Selenochilus* was most abundant in pitfall traps at Lake Papaitonga Scenic Reserve in summer, and the number caught was significantly correlated with mean daily temperature. Catches of *M. capito*, *H. mucronata*, and *H. sinuiventris* were also highest in summer, but none of them showed a significant relationship with temperature.

In contrast to the findings of previous pitfall trapping studies, manual searches under resting sites at Browns Bush revealed that *M. capito* numbers were actually highest in winter, and that *M. oconnori* was also relatively common throughout the winter. The activity of these carabids in late autumn and winter is unknown, because pitfall trapping was only carried out in the warmer months, but it is likely to be minimal then because of the low temperatures (see Chapter Three, section 3.4.2).

The seasonal pattern of activity in carabids is closely related to their reproductive biology, and the highest catches of beetles usually coincide with their main breeding period (Barlow 1973, Szujewski 1987, Lys & Nentwig 1991). For example, Rijnsdorp (1980) found that the maximum catch of *Carabus problematicus* Herbst coincided with the highest percentage of females with eggs, and the highest numbers of eggs in their ovaries. Somerfield (1974) observed that the pitfall catches of carabids in forests around Auckland were significantly higher in spring compared with other seasons, whereas winter catches were often the lowest. He attributed the high spring numbers to increased activity of carabids at the onset of their breeding season, and to rising temperatures that promoted activity. Horne (1992) discovered that the seasonal abundance of *Notonomus gravis* (Chaudoir) in Victoria, Australia was highest in summer, and this coincided with an

increase in temperature and the emergence of new adults. Winter, on the other hand, was characterised by the lowest activity and capture rate.

Weather factors such as temperature and rainfall have a strong influence on the reproductive and seasonal activity of carabid beetles (Niemelä *et al.* 1989). For example, Weber and Klenner (1987) found that the start and duration of spring activity in *Carabus auronitens* F. was largely dependent on temperature. Paarmann (1976, cited in Crowson 1981) observed that many carabid species on the Mt Kivu massif in Zaire had seasonal breeding cycles related to the incidence of wet and dry seasons. Females in a swampy area produced ripe eggs towards the end of the rainy season, so that larval development would occur during the dry season when inundation of the habitats would be unlikely. Conversely, in North Africa the extremely low humidity in summer means that winter reproduction is compulsory for carabids (Thiele 1977). In contrast to these examples, none of the carabids at Lake Papaitonga Scenic Reserve showed any significant relationship with rainfall, and only one species showed a significant relationship with temperature. This is probably because mean temperature does not vary greatly in these lowland forest habitats in the North Island.

The initial catch of carabids at Lake Papaitonga Scenic Reserve was high in October but declined markedly in November and December. The high catch in October (spring) could have resulted from increased activity during the breeding season, coupled with rising temperatures, or may be related to the “digging-in” effect of pitfall traps (Greenslade 1964b, see Chapter Three, section 3.4.3). The subsequent decline in numbers may have been caused by depletion of the local carabid populations, as carabids were sampled without replacement (Luff 1975, Ericson 1979, Digweed *et al.* 1995). At both of my study sites, the catches of carabids increased again in February, and then showed a decline in March that coincided with a decrease in temperature. Similarly, a study in carrot fields in Canterbury, New Zealand found that the total number of carabids was highest in December and January, and declined in March and April (Sivasubramaniam *et al.* 1997). Butcher and Emberson (1981) also reported a decline in carabid numbers in late February to March, although this occurred several weeks before temperatures dropped, and they attributed it to lower humidity levels instead.

Extremes of temperature and humidity appear to have a negative effect on activity and reproductive success of carabids (Murdoch 1966). For example, Baars & van Dijk (1984a) found that heavy rainfall resulted in high mortality of adults and larvae of *Pterostichus versicolor* Sturm in the Netherlands. High temperatures and low humidity may induce diapause in some carabids (Thiele 1977), and even cause mortality under severe conditions (Murdoch 1966). During a drought in England, Greenslade (1964a) reported a ten-fold decrease in the numbers of *Nebria brevicollis* (Fabricus), as well as low fecundity and larval survival. Similarly, I found a very low number of *M. oconnori* adults at Browns Bush in April and May 1999 following a very hot, dry summer (M. Hutchison, pers. obs.). Carabid beetles, particularly species of *Mecodema*, are very sensitive to humidity levels (Thiele 1977, A. Larochelle, pers. comm. 2000), and the dry weather may have resulted in high mortality of adults and larvae, or caused adults to retreat into underground burrows where the soil is moister. Species of *Mecodema* appear to be more active at the soil surface during the rainy season (A. Larochelle pers. comm. 2000), and there was a significant correlation between daily rainfall and the numbers of *M. oconnori* found under resting sites at Browns Bush (see Chapter Three, section 3.3.8.2). Greenslade (1964a) concluded that “wet seasons are the most favourable for Carabidae, and result in successful larval generations”, and this appears to be true for *M. oconnori*.

Activity may be limited to a single season in places with a strong seasonal weather pattern, but in milder climates, activity may occur throughout the year (Paarmann 1990). In most parts of the world, there is at least one season of the year in which conditions are unfavourable for feeding or growth of adults and larvae (Crowson, 1981). At such times, many species cease all activities, and enter diapause (Crowson, 1981). For example, Murdoch (1966) observed the behaviour of carabids in cool-climate marshes and found indications of obligatory adult dry-season diapause in drier habitats.

The majority of Northern Hemisphere carabids have experienced past and present climatic severity that has led to strong seasonal cycles (Roberts 1978). In contrast, New Zealand is characterised by a mild island climate with a distinct lack of seasonality (Hurnard 1978, Howarth & Ramsay 1991), and winter diapause appears to be rare among New Zealand insects (Watt 1978). Interestingly, cave-dwelling carabids in the tribe Trechini also show

no signs of diapause or a seasonal reproductive cycle, presumably because of the constant climatic conditions (Deleurance & Deleurance 1964, cited in Thiele 1977).

Seasonal changes in the sex ratio have been reported for many species, and are mainly caused by differences in the activity of males and females (Thiele 1977). Greenslade (1965) discovered that there were differences in the seasonal activity of males and females of *Pterostichus madidus* (Fabricus) in England, with females showing a much higher proportion of over-winterers. Brunsting (1981) observed that the catches of *Philonthus decorus* Gravenhorst females were higher in summer during their reproductive period, and suggested that this resulted from increased activity connected with food gathering and oviposition. I found that the proportion of *M. oconnori* females in both types of pitfall traps increased dramatically from late summer to autumn, and only one male was caught during the whole of March. However, searches of resting sites revealed that the sex ratio was still biased towards males in March, implying that the lack of males caught in pitfall traps was because they were less active. The cause of this differential activity is unknown, although it is probably related to the behaviour of females during the reproductive season. In Australia, Horne (1992) found that a lower than average proportion of *Notonomus gravis* (Chaudoir) females were trapped in February-March, and suggested that the change in sex ratio was the result of decreased activity of females during the breeding season. *Notonomus gravis* females displayed parental care over their eggs, and were inactive during egg incubation. Similarly, the very low proportion of *M. capito* females that I found in October at Browns Bush may also be related to their egg guarding behaviour (see section 4.4.3 below).

Very little can be said about the seasonal activity of the remaining carabid species at Lake Papaitonga Scenic Reserve because very few individuals of each species were caught, and there is taxonomic uncertainty over the identity of some of the species. There are currently six described species of *Selenochilus* in New Zealand (A. Larochelle and M-C. Larivière, pers. comm. 2000), and the species in my study is most likely to be *Selenochilus ruficorne* (Broun), although this genus is in need of revision (A. Larochelle, pers. comm. 2000). Adults of *S. ruficorne* have been found elsewhere in all months of the year except July and August (A. Larochelle and M-C. Larivière, pers. comm. 2000). At Lake Papaitonga Scenic Reserve, *Selenochilus* sp. was present from October to February, and showed a maximum

in numbers in January and February that was significantly correlated with mean daily temperature.

Seven species of *Zolus* have been described in New Zealand, but the tribe Zolini needs revision because of probable synonymy (A. Larochelle, pers. comm. 2000). In my study, individuals of *Zolus* sp. were caught in pitfall traps in October, November and February, indicating activity in both spring and summer. A similar species, *Zolus femoralis* Broun, was found in spring, summer, and autumn in the Orongorongo Valley (Moeed & Meads 1985). *Oopterus* is another genus in the Zolini, with 25 named species in New Zealand, although the true number is probably twice this (A. Larochelle and M-C. Larivière, pers. comm. 2000). Moeed and Meads (1986) caught low numbers of *Oopterus laevicollis* during spring and summer, and the one individual of *Oopterus* that I caught occurred in February. *Molopsida antarctica* (Laporte de Castelnau) adults have been found from September to December, and in July (Townsend 1997), but I only caught one individual in my study, in December. *Megadromus vigil* (White) adults have been found at most times of the year (McCull 1975), with teneral occurring in March (A. Larochelle and M-C. Larivière, pers. comm. 2000), but I only caught two adults in November and two in February.

There are 19 species of *Ctenognathus* described in New Zealand, but the true number is probably only half this because of synonymy (A. Larochelle and M-C. Larivière, pers. comm. 2000). Only one of the two *Ctenognathus* specimens in my study could be assigned to a definite species: *Ctenognathus bidens* Chaudoir (Cover plate 7). This species was previously caught throughout the year, with a peak in October (Somerfield 1974), and teneral adults were reported in December (A. Larochelle and M-C. Larivière, pers. comm. 2000). However, I only caught one *C. bidens* adult at Lake Papaitonga Scenic Reserve in December. The other *Ctenognathus* species at Lake Papaitonga is most likely to be *C. adamsi* (Broun), although this name is thought to represent a “species complex” comprising more than one species (A. Larochelle, pers. comm. 2000).

4.4.2 Carabid life history

Carabids have a wide range of life history strategies, and there have been a number of attempts to classify species based on the season in which reproduction occurs (see Table 4.1). Many species do not fit the usual division into spring or autumn breeders, and display activity in more than one season (Fadl & Purvis 1998). Some authors have reported a bimodal pattern of activity in carabids, with adults being active in two seasons (Barlow 1973, Allen *et al.* 1977, Weber & Klenner 1987, Niemelä *et al.* 1989, Cartellieri & Lövei 2000). For example, Barlow (1973) discovered that adults of *Carabus nemoralis* Müller, a spring breeder in eastern Canada, exhibited a bimodal peak in seasonal activity, in spring and autumn. The increase in numbers in spring corresponded with the emergence of adults from hibernation after the winter, and increased activity of adults during the reproductive period. The subsequent decline during late spring-summer was due to progressive inactivity and death of spent individuals. The second peak in autumn was caused by the emergence of teneral adults from the previous spring (Baumgartner *et al.* 1997).

Many species have flexible reproductive periods which largely depend on the climatic conditions they experience (Thiele 1977). For example, *Calathus micropterus* Duftschmid over-winters mainly as an adult in Scandinavia (cold winter), but as a larva in central Europe (mild winter) (Lindroth 1949). Reproduction may be limited to a single season in places with a strong seasonal weather pattern, but in milder climates, reproduction may occur throughout the year (Paarmann 1990). For example, *Notiophilus biguttatus* Fabricius reaches maximum egg production in spring, and stops in summer, but has a relatively low and constant level of egg production during autumn and winter (Ernsting and Isaaks 1991). Mitchell (1963a) found that *Trechus quadristriatus* (Schrank) reproduced during most of the year in England, and over-wintered as both adults and larvae. Fadl & Purvis (1998) discovered that adults of *Loricera pilicornis* (Fabricius), originally classified as a spring breeder, often survive more than a year and reproduce again in late summer/autumn in Ireland. This results in two separate cohorts of beetles within the same population, as tenerals emerge from pupation at different times of year. Lövei and Cartellieri (2000) investigated the reproductive activity of two endemic carabids in the Manawatu, New Zealand. They observed that *Plocamostethus planiusculus* (White) and *Megadromus turgidiceps* (Broun) had two distinct activity periods, with adults present in spring

(August-September) and autumn (January-April). *Plocamostethus planiusculus* was active in both seasons, whereas *M. turgidiceps* occurred only in the autumn.

Many carabids appear to live for more than one year (den Boer 1979b, van Dijk 1979a,b, Luff 1980, Rijnsdorp 1980, Brunsting 1981, Ernsting *et al.* 1992, Assmann & Janssen 1999), and adults older than six years have been reported (Baumgartner *et al.* 1997). Several authors used the presence of a *corpora luteum* in female carabids to identify “old” females that have already produced and oviposited eggs (Gilbert 1956, Greenslade 1965, Barlow 1973, Baars and van Dijk 1984a, Fadl & Purvis 1998). For example, Brunsting (1981) was able to distinguish *Pterostichus oblongopunctatus* Fabricius females that were in their fourth breeding season. However, it was not possible to identify corpora lutea in the female carabids in my study, because of soft tissue degeneration in ethylene glycol while in the pitfall traps.

Different generations of beetles in the same population may not breed at the same time of year. For example, den Boer (1979c) found that the reproductive season of old beetles was completely different from young beetles. When the young beetles start reproduction, the few old beetles that are still active are already spent. This makes it difficult to study carabid life cycles using patterns of seasonal activity because reproductive activity is not restricted to a single season and it may overlap. Rijnsdorp (1980) studied the life cycle of *Carabus problematicus* Herbst in a Dutch forest and discovered that at least three age classes of females could be present in any one season. Ernsting *et al.* (1992) reported that *Notiophilus biguttatus* sometimes lived up to three years and were reproductively active for more than two years, resulting in multiple overlapping generations.

The majority of carabids develop from egg to adult in less than one year (Barlow 1973, Baars & van Dijk 1984a), although development can last up to four years under harsh climates or adverse food conditions (Kirk 1974, Lövei & Sunderland 1996). For example, in northern England, *Carabus problematicus* Herbst has an annual life cycle at altitudes below 800m, and a biannual one above this (Butterfield 1986).

The development time from egg to adult is unknown for New Zealand carabids, but several lines of evidence suggest that it is probably more than a year for some species. For

example, a study by Lövei and Cartellieri (2000) indicated that *P. planiusculus* appears to have a life span of more than one year, and probably also reproduces more than once. During my study, I reared a *M. capito* larva for five weeks before it died of unknown causes, but the larva showed no signs of moulting to the next instar (M. Hutchison, pers. obs.). The length of the first stadium, at greater than five weeks, suggests that the larval stage of *M. capito* may persist for several months. The duration of my study was too short to determine the maximum life span of *M. oconnori* or *M. capito* adults at Browns Bush, but both species appear to live for more than one year. The longest period that a *M. oconnori* adult was followed was almost eight months, and a *M. capito* female was observed for approximately six months. The life span of *M. oconnori* is likely to be at least two years, as other broscines may take three or four years to complete their life cycle (A. Larochelle, pers. comm. 2000). Several *M. oconnori* and *M. capito* adults were found to survive over the winter at Browns Bush, and Ian Townsend (pers. comm. 1999) also observed *M. oconnori* individuals that lived for more than one year.

In my study, larvae of *M. capito* were caught from October to March at Lake Papaitonga Scenic Reserve, and the seasonal activity of the three instars overlapped. The majority of first instar larvae were found in January and February (summer), suggesting that egg-laying had taken place the previous spring. However, third instar larvae were most numerous in October, whereas second instar larvae were only found from January to March. The most likely explanation for the overlapping instars of *M. capito* is that oviposition occurs throughout the year, and development from egg to adult takes more than one year.

4.4.3 Reproductive phenology and egg production

The female carabids dissected in my study were found to contain relatively few eggs compared to overseas species, which may have up to a hundred eggs per female (Ernsting *et al.* 1992). Similarly, Lövei and Cartellieri (2000) noted that females of *Megadromus turgidiceps* and *Plocamostethus planiusculus* contained few eggs. The extremely low fecundity of *M. oconnori* in my study appears to be quite unusual, and is one of the lowest reported egg numbers globally. Rivard (1964) dissected females from 30 species of carabids in Canada, and concluded that species with “a maximum of less than 10 eggs

seem to have an abnormally low reproductive potential". However, Barlow (1973) suggested that the low number of eggs in *Carabus nemoralis* (the median number was 9) was a reflection of the oviposition rate rather than total fecundity, because eggs are laid singly over a period of weeks.

The number of eggs in the ovaries may be a good indication of the total number of eggs laid (van Dijk 1986), although this is not always the case (van Dijk 1979b). For example, van Dijk & Boer (1992) found that neither the number of eggs in the ovaries, nor the number of eggs laid per female per week, gave a reliable estimate of actual egg production. The number of eggs laid over the entire reproductive season varies widely between species, with some species producing several hundred eggs in one season (Ernsting *et al.* 1992, van Dijk 1994). For example, *Calathus melanocephalus* L. laid almost 700 eggs in 14 weeks in the laboratory (van Dijk & den Boer 1992), and *Nebria brevicollis* females laid 334 eggs each on average in one reproductive season (Nelemans *et al.* 1989).

Egg laying behaviour differs widely between carabid species, with some species laying a single batch of eggs per season, while others lay continuously throughout the reproductive period (Murdoch 1966, Baars & van Dijk 1984b). Many species appear to have a complex seasonal phenology and an extended oviposition period in which reproduction may occur at any time of year (Ernsting *et al.* 1992). For example, Fadl & Purvis (1998) found that several species of *Bembidion* had nearly continuous oviposition periods, interrupted only by adverse mid-winter conditions, which resulted in newly emerged adults being found in most months of the year.

New Zealand carabids appear to have a long period of reproductive activity, with females at Lake Papaitonga Scenic Reserve being found with mature eggs for at least six months of the year. Unfortunately, removal sampling was not carried out over winter, but it is possible that the carabids there lay eggs throughout the year. The long reproductive period shown by these species is probably a result of New Zealand's mild oceanic climate and lack of seasonality (Watt 1978). In comparison, Rivard (1964) found that most carabid species in Eastern Ontario had a breeding period of about three months, with only one generation per year. Rijnsdorp (1980) observed that *Carabus problematicus* females had

eggs in their ovaries for three months of the year, but he also found that females could survive to reproduce again in subsequent years, resulting in up to three age classes in any one season. Fecundity appears to vary depending on the age of females (Petersen 1998). For example, Rijnsdorp (1980) reported that old females of *C. problematicus* produced fewer eggs than young females, however, van Dijk (1979b) found that older beetles had a longer egg-laying period and produced more eggs than young females.

Egg production and oviposition are strongly affected by food supply, and females with a shortage of food produce very few eggs (Murdoch 1966, van Dijk 1979b, Baars & van Dijk 1984b, Ernsting *et al.* 1992, van Dijk 1994). Temperature is also an important factor affecting reproduction in carabids, with females requiring a specific temperature range for egg laying (van Dijk & den Boer 1992, Baumgartner *et al.* 1997, Ernsting & Isaaks 1997). For example, van Dijk (1979b) observed that the start of egg laying in *Pterostichus coerulescens* (L.) was strongly influenced by temperature, and found a high correlation between temperature and the length of the reproductive period. Similarly, larval development and survival are highly affected by abiotic conditions such as temperature and soil moisture (Petersen 1998), and biotic factors such as food supply, predation and parasitism (Nelemans *et al.* 1989). When larval food supply is limited, life span may be prolonged because growth and development take longer (Ernsting *et al.* 1992).

Ernsting *et al.* (1992) found that nearly all food consumed by *Notiophilus biguttatus* females in spring was converted directly into egg production, and that female weight increased substantially while male weight remained relatively constant. Similarly, the mean body mass of *M. capito* females at Browns Bush was highest in spring, while male body mass did not increase dramatically. My dissections of *M. capito* females from Lake Papaitonga Scenic Reserve confirmed that females in October contained the highest numbers of mature eggs, and that eggs comprised up to 80% of female body mass. Thus, the observed weight increase of females at Browns Bush in spring is probably caused by egg development in these months. In contrast, female mean mass decreased markedly in December, and by March, less than half the dissected females contained eggs. The results suggest that the majority of females had started laying eggs by October, and had finished by late summer. In contrast, *M. oconnori* females did not show the same large increase in mass as *M. capito*. My dissections revealed that egg mass made up a small proportion of

female body mass in *M. oconnori* (4% on average), as only one or two eggs were present per female. *Mecodema oconnori* females reached their greatest mass in December (summer), and the proportion of females with eggs was very high from December onwards. This suggests that *M. oconnori* may begin egg production and oviposition slightly later than *M. capito* in late spring to summer.

Egg number does not appear to depend on the size of the species, as small species may produce many more eggs than larger species (Thiele 1977). In fact, Grüm (1984) found that egg number tended to decrease as body mass increased. Similarly, the largest carabid at Lake Papaitonga Scenic Reserve, *M. oconnori*, had the lowest number of eggs. Several studies have also reported a negative relationship between egg size and number (Wallin *et al.* 1992, Ernsting & Isaaks 1997, Petersen 1998). Likewise, there appears to be trade-off between egg size and number in *M. oconnori*, as most females produced only one or two very large eggs, compared to *M. capito* which produced a higher number of smaller eggs. Interestingly, *M. capito* was also the most abundant species caught in pitfall traps at Lake Papaitonga Scenic Reserve, which suggests that there may be a relationship between egg production and the density of adults.

Eggs and larvae experience very high mortality in the field, often as a result of parasitism and predation (van Dijk & den Boer 1992). For this reason, production of a large number of eggs would be necessary to ensure successful recruitment of larvae (van Dijk & den Boer 1992). However, species which exhibit parental care over their offspring generally produce few eggs, as individual mortality would be lower (Thiele 1977). Many species of carabid, principally in the tribe Pterostichini, display parental brooding behaviour over their eggs and larvae (Thiele, 1977, Brandmayr & Brandmayr 1979). Some species construct mud cells or subterranean burrows to protect the eggs from fungal attack and desiccation, while others guard them from predators (Brandmayr & Brandmayr 1979). *Megadromus capito* displays parental care over its eggs and first instar larvae, but also had the highest fecundity of any species in my study. In contrast, *M. oconnori* females contained a very low number of eggs, and this suggests that it might also exhibit parental care over its one or two offspring. Other members of the Broscini in Europe exhibit parental care over their eggs by digging a specially constructed soil chamber, e.g. *Broscus cephalotes* (Thiele 1977). Thus, it seems that the egg-laying strategy of *M. oconnori* might

be directed towards finding the best oviposition sites, rather than production of a high number of eggs (see van Dijk & den Boer 1992). Previous observations confirm that *M. oconnori* lays its eggs in underground burrows, and the larvae and pupae are not active on the soil surface (A. Laroche, pers. comm. 2000). Thus, the entire development of the pre-adult stages occurs underground, which would reduce the chances of its offspring being preyed upon.

4.4.4 Seasonality of individual species

Mecodema oconnori Broun

Previously, *M. oconnori* adults were found from October to April, but had not been caught in pitfall traps during winter (A. Laroche and M-C. Larivière, pers. comm. 2000). However in my study, manual searching of resting sites revealed that *M. oconnori* adults were present throughout the year, and were most abundant in late winter-spring. The absence of *M. oconnori* from pitfall traps in winter is probably because the beetles are inactive during this period, and spend most of their time in burrows and under logs. In my study, the proportion of *M. oconnori* females that contained eggs was very high from January onwards, suggesting that the peak in reproductive activity may occur in late spring to summer. No marked beetles were found under resting sites at Browns Bush in June and July, despite nearly 40 individuals having been marked prior to this. A possible explanation for this could be that many individuals die after they have reproduced.

Studying the life cycle and reproductive behaviour of *M. oconnori* has proven very difficult because of the fact that most of its life cycle takes place beneath the soil. Like other members of the Broscini, *M. oconnori* females lay their eggs deep in underground burrows, and all of the pre-adult stages are spent underground (A. Laroche, pers. comm. 2000). Larvae of *Mecodema* have never been caught in pitfall traps, as they are not surface-active (A. Laroche and M-C. Larivière, pers. comm. 2000), and no teneral adults have been found either (I. Townsend, pers. comm. 2000). Despite the lack of information on most stages of its life cycle, *M. oconnori* was thought to be a spring-summer breeder (A. Laroche and M-C. Larivière, pers. comm. 2000), and the results of my study tend to agree with this.

***Megadromus capito* (White)**

Other authors have observed *M. capito* females on eggs in November (A. Larochelle and M-C. Larivière, pers. comm. 2000), and in my study, a female was found guarding eggs at Browns Bush in mid-October. The larvae hatched in late October (Cover plate 4), and one individual was collected and kept in captivity for five weeks before it died. Teneral have previously been found from January to March (A. Larochelle and M-C. Larivière, pers. comm. 2000), and the five teneral in my study occurred in February and March. Females were found with eggs from October to March at Lake Papaitonga Scenic Reserve, but the proportion with eggs declined from October onwards. Higher numbers of *M. capito* have been caught in late summer-autumn (A. Larochelle and M-C. Larivière, pers. comm. 2000), and this is probably the result of newly emerged adults entering the population. These observations all suggest that *M. capito* is a spring breeder, with the main period of reproductive activity in spring and early summer. Adults were found to over-winter at Browns Bush, and probably live for more than one year.

***Holcaspis mucronata* Broun**

Holcaspis mucronata has been found in all months of the year, but appears to be a spring breeder with teneral emerging in January and February (A. Larochelle and M-C. Larivière, pers. comm. 2000; Lövei, in press). I caught *H. mucronata* in low numbers from October to December at Lake Papaitonga Scenic Reserve, and it was most abundant from February to March. Gravid females were found in October and December in my study, which provides further evidence that this species is a spring-summer breeder. Similarly, three other species of *Holcaspis* on Banks Peninsula were reproductively active in summer, and contained eggs from December to April. (Butcher and Emberson 1981).

***Holcaspis sinuiventris* (Broun)**

Adults of *Holcaspis sinuiventris* have previously been found in May, July, September, October, and December to March (A. Larochelle and M-C. Larivière, pers. comm. 2000). At Lake Papaitonga Scenic Reserve, *H. sinuiventris* was caught from October to March, with a maximum in numbers in February. Like *H. mucronata*, teneral have been found in

January and February (A. Larochelle and M-C. Larivière, pers. comm. 2000), suggesting that this species may also be a spring breeder.

Plocamostethus planiusculus (White)

Plocamostethus planiusculus occurred from November to January at Lake Papaitonga Scenic Reserve, although only three individuals were caught. In contrast, Cartellieri and Lövei (2000) reported the highest catches for this species in autumn, with a short period of activity in spring. No gravid females were caught in my study, but two periods of reproductive activity have been observed in this species, with gravid females occurring in both spring and autumn (Cartellieri and Lövei 2000). There appeared to be a difference in the activity periods of 'old' (second year or older) and young females, with old females being active in both seasons, whereas young females were only found in autumn. Cartellieri and Lövei (2000) suggested that this was because older females were able to reproduce in autumn before any of the young females were in reproductive state.

Harpalus affinis (Schrank)

Harpalus affinis was the only introduced carabid species caught at Lake Papaitonga Scenic Reserve. It originates in Europe, but has extended its range throughout the world, and is rapidly spreading throughout the North Island of New Zealand (Townsend 1992). *Harpalus affinis* is an autumn breeder in the Northern Hemisphere (Greenslade 1965), but it may have a different reproductive strategy in New Zealand. Townsend (1992, 1994) reported that adults were active in October, and plentiful in the Manawatu-Horowhenua during summer and autumn. Similarly, Sunderland *et al.* (1995) found a strong seasonal bias in *H. affinis*, with the majority of individuals being trapped in summer. Gravid females were mainly found in spring and summer, whereas teneral adults were mainly caught in autumn (Sunderland *et al.* 1995). I only caught two *H. affinis* individuals at Lake Papaitonga Scenic Reserve, in October and March, and this seems to agree with the current information on this species.

4.4.5 Conclusions

Studying the life history of carabid beetles is similar to doing a jig-saw puzzle - you need all of the pieces to see the complete picture. In order to fully understand the life cycle of carabid beetles, knowledge of all of the life stages is necessary. We need to collect information about the seasonal activity of adults, and to dissect females to determine their oviposition periods. Observation of larval and pupal development and the emergence of teneral individuals is also essential. Finally, we need to follow the activities of individual animals to determine how long their life span is. Unfortunately, some of the key pieces are still missing for New Zealand carabids, and we still do not know how many years our beetles live, because no long term studies have been done.

The complexity and variability of life cycles in carabids means that it is difficult to make generalisations about life history that are applicable across many species. However, New Zealand carabids appear to be characterised by long life span, low fecundity, and an extended egg-laying period. At least in North Island lowland forests, New Zealand carabids are “species with ‘flexible’ reproduction in either spring or autumn, and larvae which develop in summer or winter”, as well as “species which require more than one year to develop” (Types four and five from Thiele 1977, Table 4.1).

Chapter Five

The effects of rodent control and the abundance of other invertebrates on carabid assemblages



Cover plate 5. Shattered remains of *Mecodema oconnori* and *Megadromus capito* resulting from predation. White square = 1cm². Photograph by Alastair Robertson.

“Whenever I hear of the capture of rare beetles,
I feel like an old warhorse at the sound of a trumpet”

Charles Darwin

The effects of rodent control and the abundance of other invertebrates on carabid assemblages

5.1 INTRODUCTION

Carabids are preyed upon by a wide variety of animals, including almost every kind of bird, and in particular by insectivorous mammals (Thiele 1977). In Europe and North America, predators of carabids include owls, badgers, skunks, shrews, moles, bats, frogs, and reptiles (Murdoch 1966, Larochele 1974, 1975a,b, Thiele 1977). In New Zealand, hedgehogs (*Erinaceus europaeus*) (Campbell 1973, Berry 1999, Hendra 1999), starlings (*Sturnus vulgaris*) (Wood 1973), kiwi (*Apteryx* spp.) (Gurr 1952, Bull 1959, Watt 1971, Reid *et al.* 1982, Colbourne & Powlesland 1988), magpies (*Gymnorhina tibicen*), thrushes (*Turdus philomelos*), stoats (*Mustela erminea*) (A. Larochele, pers. comm. 2000), and spiders (Mike Bowie pers. comm. 2000) are all known to prey upon carabids. After reviewing a large number of studies on the effects of predation on carabids, Thiele (1977) concluded that “predacious enemies are undoubtedly an important factor in the regulation of the population density of carabids”.

The introduction of rodents to New Zealand has undoubtedly had a major impact on our endemic invertebrate fauna, and several recorded extinctions have been attributed to rodent predation (Ramsay 1978, King 1990). Many New Zealand insects are large-bodied and flightless - characteristics which make them extremely vulnerable to predation by introduced mammals (Howarth & Ramsay 1991) There is evidence overseas that rodents are significant predators of carabid beetles and have a considerable effect on carabid communities (Parmenter and MacMahon 1984, Parmenter and MacMahon 1988, Churchfield *et al.* 1991). It is likely that this is also the case in New Zealand (G. Lövei, pers. comm. 1999), although very little is known about the behaviour of rodents towards our native carabids, or whether rodents have a significant impact on carabid assemblages. There are no published records of predation by rats on carabids in New Zealand, although carabids have been positively identified in rat stomachs in two unpublished studies. Carabid beetles were the most common form of adult beetle found in the stomachs of the

ship rat (*Rattus rattus rattus*), Norway rat (*Rattus norvegicus*), and kiore (*Rattus exulans*) on Stewart Island (Sturmer 1988). Rickard (1996) also found carabid remains in ship rat stomachs from Westland. None of the other diet studies on rats in New Zealand have identified the beetles consumed to family level (e.g. Best 1969, Daniel 1973, Innes 1979, Gales 1982), therefore the occurrence of carabids may have been overlooked.

The diversity and abundance of carabid assemblages may also be affected by the abundance of other invertebrate groups, and several studies have found a correlation between the numbers of carabids and other invertebrates (Lenski 1984, Lys & Nentwig 1991, van Dijk 1994). The cause of these relationships may vary, depending on the species concerned and the environmental conditions they experience. One explanation is that carabids may respond to the abundance of their prey and aggregate in areas of high prey density (Niemelä *et al.* 1986). Another explanation is simply that carabids react in the same way to environmental factors as other invertebrates (Baguette 1993).

The overall aim of this chapter was to investigate the effect of controlling rodents on the carabid beetle assemblage at Lake Papaitonga Scenic Reserve, Levin. The relationship between carabid abundance and the abundance of other invertebrates was also examined. In addition, the effects of environmental factors such as temperature, rainfall, and habitat characteristics on carabid assemblages were considered.

5.2 METHODS

5.2.1 Study site

This study was carried out at Lake Papaitonga Scenic Reserve (Latitude 40°39'S, Longitude 175°13'E) in the Horowhenua district, North Island, New Zealand (Figure 4.1). The reserve covers an area of 122 ha, and is located 4 km south-west of Levin (see Chapter Four, section 4.2.1). The reserve includes the lake itself, and a remnant of indigenous lowland forest surrounding the lake (approximately 52 ha). Rodents present at the reserve include the ship rat (*Rattus rattus*) and house mouse (*Mus musculus*), and other predators such as the stoat (*Mustela erminea*), ferret (*Mustela furo*), weasel (*Mustela nivalis*) (S. Bennett, pers. comm. 2000), hedgehog (*Erinaceus europaeus*) (Brockie 1990), and possum (*Trichosurus vulpecula*) are also present.

The study site was divided into four sampling areas. These comprised two 'treatment' areas where rodent poisoning was carried out (areas **A** and **C**), and two 'non-treatment' areas (areas **B** and **D**) (Figure 4.1). Areas A and B were on one peninsula extending into the lake, and areas C and D were on another peninsula, separated from the first by a swampy area. The treatment and non-treatment areas were at least 150 metres apart on each peninsula.

5.2.2 Rodent control and tracking tunnels

Rodent poisoning was carried out in areas A and C using Philproof bait stations filled with Talon® bait (brodifacoum poison) from October 1998 to April 2000 (see Bennett 2001 for a full description of the methods). Brodifacoum is an anticoagulant that kills small mammals such as rats and mice, but is relatively harmless to invertebrates (Shirer 1992). Baits were replaced as needed. Rodent abundance in each sampling area was monitored by Shaun Bennett using tracking tunnels from August 1998 to April 2000 (see Bennett 2001 for tunnel design). Tracking tunnels were operated over three nights in the last week of each month, and tracking rates were averaged over the three nights. The data are used here with permission from Shaun Bennett (Massey University).

5.2.3 Invertebrate sampling

Invertebrate sampling was carried out using pitfall traps filled with 95% ethylene glycol (antifreeze) as a preserving agent (see Chapter Four, section 4.2.4 for a full description). A total of 112 pitfall traps were operated continuously for six months from October 1999 to March 2000 inclusive. Within each sampling area, the pitfall traps were arranged in seven lines of four traps, giving a total of 28 traps in each area (Figure 4.1). The traps were emptied every two weeks for the first two months (October - November), then every four weeks subsequently. The results from the fortnightly samples were pooled to give a monthly total comparable to the rest of the samples.

Pitfall trap samples were inspected under a binocular microscope, and all carabids (including larvae) were removed and stored in 70% ethanol. Total body length was measured for all specimens. Adult carabids were identified to species, but many of the larvae could not be accurately identified to species or even to genus because of the lack of identification keys for New Zealand larvae. The only larvae identified to species were those of *Megadromus capito*. They were determined to genus by Peter Johns, and I was able to identify them to species, based on known larvae caught at Browns Bush.

The abundance of invertebrate taxa other than Carabidae was determined for the first month of sampling only (October). All invertebrates were identified to order, and to family if possible. Each specimen was also placed in one of four size classes: 0-2 mm ('tiny'), 3-5 mm ('small'), 6-10 mm ('medium'), and 10+ mm ('large'). Specimens were then stored in 70% ethanol.

5.2.4 Environmental variables

Environmental variables measured in each sampling area were: soil depth, leaf litter depth, forest canopy cover (%), vascular plant ground cover (%), and leaf litter species composition. These variables were measured individually for each pitfall trap, using a 1 x 1 metre quadrat (divided into 100 squares of 10 x 10 cm) to describe the environment immediately surrounding each trap. For each trap, four measurements of soil depth (cm) and leaf litter depth (cm) were taken randomly, one from each quarter of the quadrat.

Forest canopy cover was estimated directly above the pitfall trap (an area of approximately 5 m²). The percentage ground cover of all vascular plant species below 30 cm was also estimated, as was the percentage ground cover of logs and tree trunks in each quadrat. Soil moisture levels in each sampling area were measured by Shaun Bennett (see Bennett 2001 for methods).

5.2.5 Statistical analyses

Repeated measures analysis of variance (RMANOVA) was used to determine whether there were differences between the numbers of rodent tunnels tracked in each sampling area (SAS 6.12, SAS Institute 1996). Tukey's post-hoc tests were then used to identify which areas were significantly different from each other. T-tests were also utilised to see whether rodent tracking rates were significantly different between poisoned and non-poisoned areas (SYSTAT 6.0, SPSS Inc. 1996). RMANOVA was carried out to determine whether there were differences in the abundance of carabids between the four sampling areas (see Appendix 10 for SAS program). Analysis of variance (ANOVA) was used to analyse whether there was a difference in the abundance of other invertebrates in the four sampling areas (SYSTAT 6.0, SPSS Inc. 1996). The effect of the treatment (i.e. rodent poisoning) on carabid abundance and the abundance of other invertebrate taxa was analysed using T-tests.

Detrended correspondence analysis (DECORANA), an ordination technique, was carried out on the carabid beetle assemblages and other invertebrate groups using PC-ORD 4.0 (MJM Software Design 1999). The analysis was done on a per trap basis (n = 112), using the total numbers of each carabid species (or total numbers of each invertebrate order) caught in each trap. The relationship between the invertebrate assemblages and the environmental variables was also examined using DECORANA. This involves comparing the two data matrices to see whether there is any correlation between the main matrix (the invertebrate assemblages) and the secondary matrix (the environmental variables).

The spatial dispersion of the pitfall trap catches within each area was analysed by comparing the observed catches with those expected from a Poisson distribution. An index of dispersion was calculated using the equation: $I = s^2 / \bar{x}$, where I = index of dispersion, s^2

= variance, and \bar{x} = mean (see Niemelä *et al.* 1986, Niemelä 1990). Index values close to one indicate an agreement with the Poisson series, i.e. random dispersion between the traps. Index values significantly greater than one (i.e. $s^2 > \bar{x}$) indicate aggregated dispersion. The agreement of the index with the Poisson series was tested with a χ^2 test (df = n-1): $\chi^2 = I(n-1)$, where n is the number of sampling units. The power of the test is highly dependent on sample size, so the lower the catch per area, the more likely the observed pattern agrees with the Poisson series. For this reason, only species with five or more individuals in each area were analysed separately from the total number of carabids per area.

T-tests were used to analyse whether there was a significant difference in the total number of carabids caught in 'inner' versus 'outer' pitfall traps over the six months (SYSTAT 6.0). Inner traps (n = 10) were surrounded by other traps, while outer traps (n = 18) were on the outside of the trapping grid. The relationship between the abundance of carabids and other invertebrate taxa was analysed using Pearson correlations and corrected Bonferroni probabilities (SYSTAT 6.0). Some of the data were \log_{10} transformed because of the large difference in magnitude between the catches of carabids and other taxa.

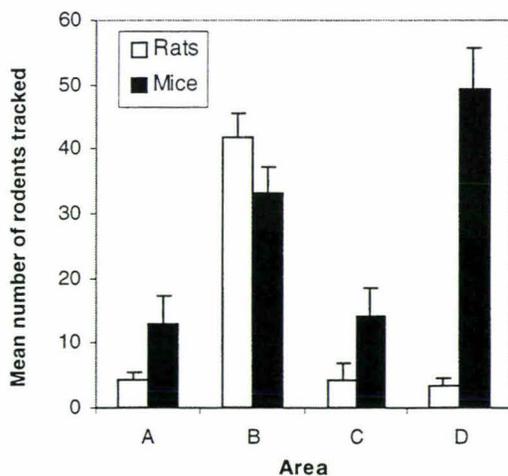
5.3 RESULTS

5.3.1 Rodent abundance in each sampling area

Tracking tunnels were used to estimate an index of rodent population levels in each of the four sampling areas from August 1998 to April 2000 (see Appendix 11). There was a significant difference in rat abundance between the four areas (RMANOVA, $df = 3$, $F = 57.43$, $p < 0.001$), and area B (a non-poisoned area) had significantly higher tracking rates than the other areas (Tukey post-hoc test, $p < 0.001$ in all cases) (Figure 5.1a). There was also a significant difference in mouse abundance between the four sampling areas (RMANOVA, $df = 3$, $F = 12.704$, $p < 0.001$) (Figure 5.1a).

The abundance of both rats (t-test, $df = 70$, $p < 0.001$) and mice (t-test, $df = 70$, $p < 0.001$) was significantly different between the treatments, with the poisoned areas having significantly lower tracking rates than the non-poisoned areas (Figure 5.1b).

(a) Rodent abundance in each sampling area



(b) Poison versus non-poisoned areas

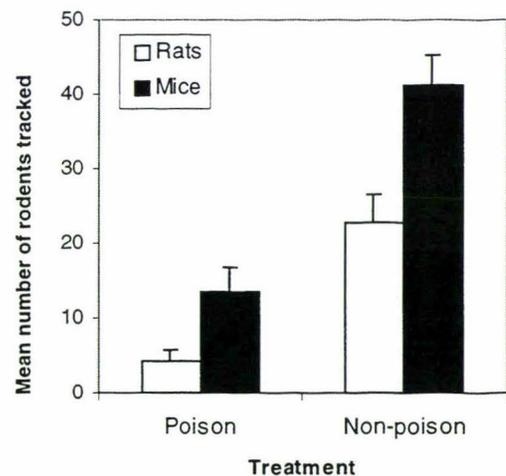


Figure 5.1. Mean number of tunnels with rodent tracks in (a) each sampling area, and (b) poisoned versus non-poisoned areas at Lake Papaitonga Scenic Reserve (August 1998 – April 2000). Treatment areas (poisoned) = A and C; non-treatment areas (non-poisoned) = B and D. (Tracking tunnel data from Bennett 2001, unpublished thesis).

5.3.2 Abundance and diversity of Carabidae

A total of 501 adult carabid beetles from seven tribes and 14 species were caught over the six-month sampling period (Table 5.1). Eighty-five carabid larvae were also caught in the traps. Approximately 90% of the adults comprised just three species. The most abundant species was *Megadromus capito* (71.3%), followed by *Mecodema oconnori* Broun (11.0%), and *Selenochilus* sp. (*ruficorne*) Chaudoir (7.2%). Area A had the most diverse carabid assemblage with 11 species, seven of which were only represented by a single individual. Areas C and D both had eight carabid species, while Area B had the lowest diversity with seven species (Table 5.1).

Table 5.1. Composition of the carabid assemblages in each sampling area at Lake Papaitonga Scenic Reserve: total number of adults and larvae caught over 6 months of sampling. Treatment areas (poisoned) = A and C, non-treatment areas (non-poisoned) = B and D.

Species	Sampling area				Total number
	A	B	C	D	
<i>Ctenognathus bidens</i>	1	0	0	0	1
<i>Ctenognathus</i> sp.	0	0	1	0	1
<i>Harpalus affinis</i> *	1	0	1	0	2
<i>Holcaspis mucronata</i>	4	12	1	1	18
<i>Holcaspis sinuiventris</i>	1	8	2	5	16
<i>Mecodema oconnori</i>	0	0	16	39	55
<i>Megadromus capito</i>	68	51	136	102	357
<i>Megadromus vigil</i>	2	1	0	1	4
<i>Molopsida antarctica</i>	1	0	0	0	1
<i>Molopsida strenua</i>	1	0	0	0	1
<i>Oopterus</i> sp.	0	1	0	0	1
<i>Plocamostethus planiusculus</i>	2	0	0	1	3
<i>Selenochilus</i> sp. (<i>ruficorne</i>)	1	4	7	24	36
<i>Zolus</i> sp.	1	1	1	2	5
TOTAL number of individuals	83	78	165	175	501
TOTAL number of species	11	7	8	8	14
Larvae	4	8	47	26	85

* denotes introduced species.

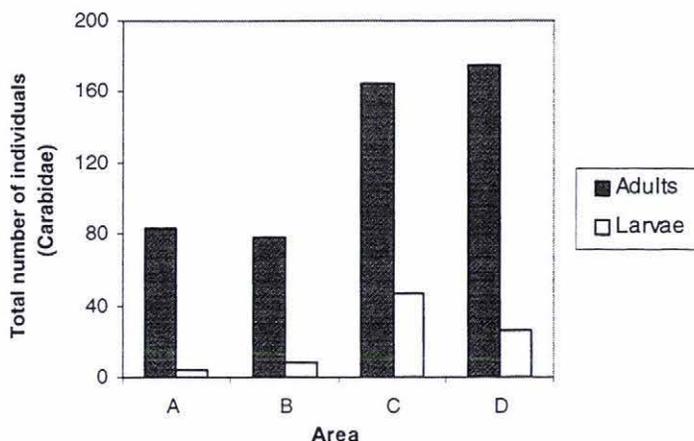


Figure 5.2. Total number of carabids (adults and larvae) caught in each sampling area at Lake Papaitonga Scenic Reserve (October 1999 – March 2000). Treatment areas (poisoned) = A and C; non-treatment areas (non-poisoned) = B and D.

5.3.3 The effect of rodent control on carabid abundance

There was no significant difference between the total number of carabids in treatment (A and C) and non-treatment areas (B and D) (t-test, $df = 22$, $p = 0.878$), so there was no overall treatment effect (Table 5.2). Likewise, when the five most common species were considered individually, none of them showed any significant differences between their abundance in poisoned and non-poisoned areas (Table 5.2).

Table 5.2. Results of a t-test of the number of carabids caught in treatment (A and C) versus non-treatment areas (B and D) at Lake Papaitonga Scenic Reserve ($df = 22$). 'NS' indicates a non-significant difference between treatments.

	Mean per treatment	p-value
Total carabids (all species)	0.878	NS
Total adults (all species)	0.955	NS
Total larvae	0.580	NS
<i>Megadromus capito</i>	0.338	NS
<i>Mecodema oconnori</i>	0.235	NS
<i>Selenochilus</i> sp.	0.143	NS
<i>Holcaspis mucronata</i>	0.161	NS
<i>Holcaspis sinuiventris</i>	0.080	NS

However, when treatment was ignored, there was a significant difference between the total numbers of carabids in the four sampling areas (RMANOVA, $df = 3$, $F = 3.98$, $p = 0.022$, Table 5.3). Areas C and D had over twice as many individuals as areas A and B (Table 5.1, Figure 5.2), and this difference was highly significant (Tukey post-hoc test, $p < 0.001$). However, there was no significant difference between the total numbers of adults ($p = 0.068$) or larvae ($p = 0.207$) in the four areas (Table 5.3).

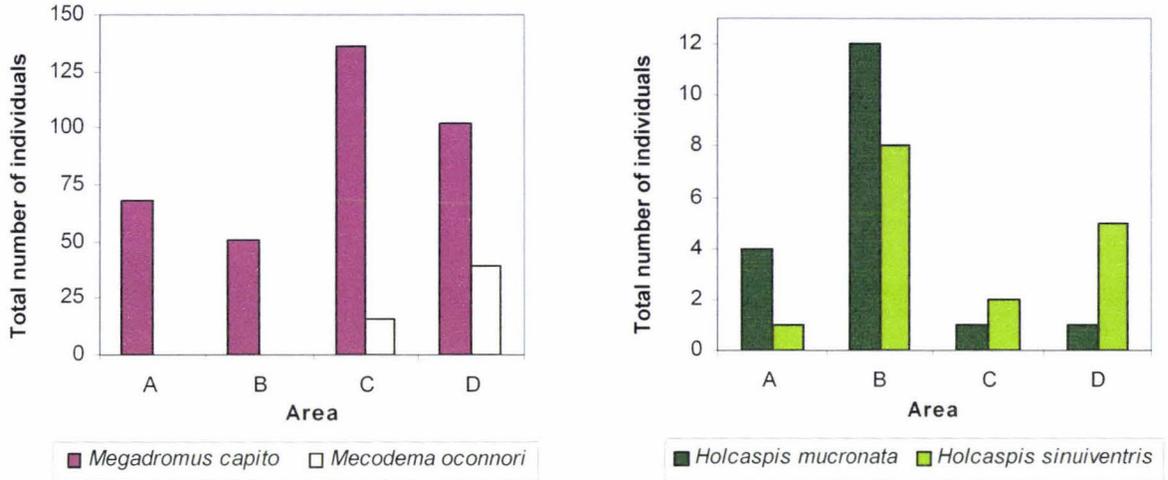
Table 5.3. Results of a repeated measures analysis of variance of the number of carabids caught in the four sampling areas at Lake Papaitonga Scenic Reserve ($df = 3$). Tukey post-hoc tests: means with the same letter are not significantly different. Significance level: ** $p < 0.01$, * $p < 0.05$, 'NS' indicates a non-significant difference.

	Sampling area				F-value	P-value	
	A	B	C	D			
Total carabids (all species)	x	x	x	x	3.98	0.022	*
Total adults (all species)	x	x	x	x	2.77	0.068	NS
Total larvae	x	x	x	x	1.66	0.207	NS
<i>Megadromus capito</i>	x	x	x	x	2.52	0.087	NS
<i>Mecodema oconnori</i>	x	x	y	y	6.41	0.003	**
<i>Selenochilus</i> sp.	x	x	x	y	3.16	0.047	*
<i>Holcaspis mucronata</i>	xy	x	y	y	5.29	0.008	**
<i>Holcaspis sinuiventris</i>	x	x	x	x	1.27	0.313	NS

Megadromus capito was caught in higher numbers in areas C and D compared with A and B (Figure 5.3a), but there was no significant difference between the four sampling areas in the mean numbers caught (RMANOVA, $F = 2.52$, $p = 0.087$, Table 5.3). *Mecodema oconnori* (Figure 5.3a) and *Selenochilus* sp. (Figure 5.3c) were caught most frequently in area D, and area D had significantly more *Selenochilus* sp. individuals than the other areas (Tukey post-hoc test, $p < 0.001$, Table 5.3). In fact, *M. oconnori* was not caught in areas A or B over the entire sampling period, and appeared to be restricted to areas C and D (Figure 5.3a).

Holcaspis mucronata and *H. sinuiventris* were caught in higher numbers in area B than the other areas (Figure 5.3b). However, the difference between the areas was only significant for *H. mucronata* ($p = 0.008$, Table 5.3), which had significantly more individuals in area B compared with C and D (Tukey post-hoc test, $p = 0.002$). The remaining carabid species ("minor species") were not caught frequently enough to detect a significant difference in abundance between the areas.

(a) *Megadromus capito* & *Mecodema oconnori* (b) *Holcaspis mucronata* & *H. sinuiventris*



(c) *Selenochilus* sp. & 'minor species'

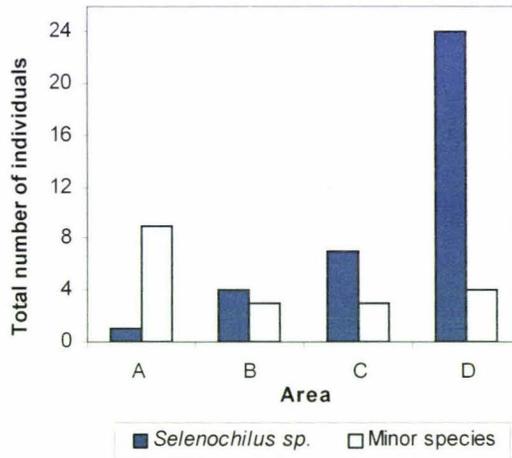


Figure 5.3. Total number of carabids caught in each sampling area at Lake Papaitonga Scenic Reserve: (a) *Megadromus capito* and *Mecodema oconnori*, (b) *Holcaspis mucronata* and *Holcaspis sinuiventris*, and (c) *Selenochilus* sp. and 'minor species'. 'Minor species' are the nine species in which five or fewer individuals were caught (see Table 5.1). Treatment areas (poisoned) = A and C; non-treatment areas (non-poisoned) = B and D.

5.3.4 Composition of the carabid assemblages in each area

The composition of carabid species was different in each sampling area at Lake Papaitonga Scenic Reserve, and detrended correspondence analysis (DECORANA) was used to illustrate these differences. The first two ordination axes explained just under half of the variation in the data (46.7%), and a plot of their scores is shown below (Figure 5.4). The plot reveals that the traps are not grouped clearly by treatment, but appear to be grouped by the peninsula they occur on. Thus, the carabid assemblages in areas A and B were quite similar to each other, as were those in areas C and D, although areas A and C had some overlap in the bottom right hand corner of the graph.

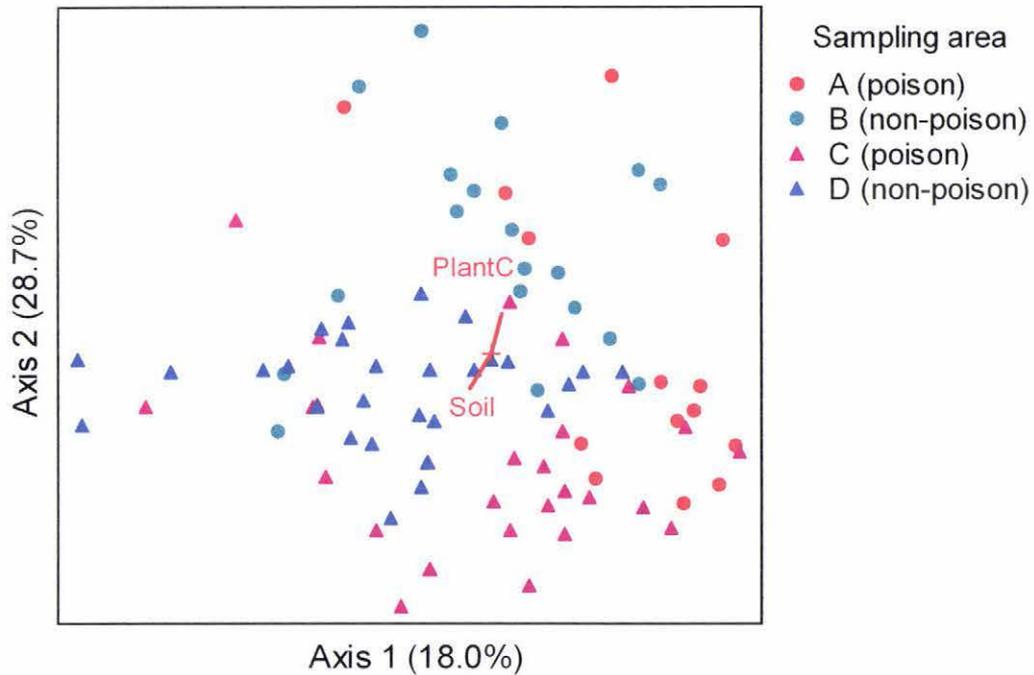


Figure 5.4. Detrended correspondence analysis results for the carabid beetle assemblage in each sampling area at Lake Papaitonga Scenic Reserve (symbols denote individual pitfall traps). The percentage of variation explained by each axis is shown in brackets. Vectors of the two most highly correlated environmental variables are shown on the graph. The direction of the vector indicates the maximum change of the variable along the axes, and the length indicates the magnitude of that change. NB. 'Soil' = soil depth and 'PlantC' = vascular plant cover.

The first ordination axis was dominated by a negative score for *M. oconnori*, and a positive score for *M. capito* (see Appendix 12a), and this means that traps at the higher end of this axis contained low numbers of *M. oconnori* and high numbers of *M. capito*. These appear to be mainly in areas A, B, and C. In contrast, the second axis was dominated by negative scores for *M. capito* and larvae, and a positive score for *H. mucronata*. Therefore, traps in the lower half of the plot, mainly in areas C and D, had high numbers of *M. capito* and larvae. Area B appears to be separated from the other areas in the upper half of the plot, largely because of its high numbers of *H. mucronata*.

The vectors of the two most highly correlated environmental variables are also shown on the graph (plant cover and soil depth), however their correlation with the carabid assemblages was very low (Appendix 12b). Areas A and B appear to be weakly associated with a higher percentage of ground plant cover, whereas areas C and D had greater soil depth (Figure 5.4).

5.3.5 Carabid body size distribution

Mean body length of carabids differed significantly between the four sampling areas (ANOVA, $df = 3$, $F = 3.727$, $p = 0.028$), and Area D had significantly larger carabids compared to Area B (Tukey post-hoc test, $p = 0.019$) (Figure 5.5). This is mainly because the largest carabid, *M. oconnori*, was most abundant in area D, but absent from A and B (see Figure 5.3a).

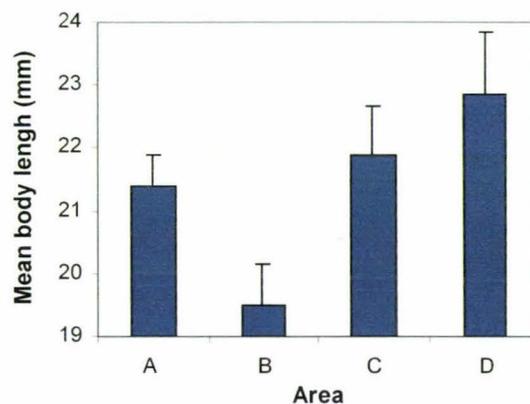


Figure 5.5. Mean body length of carabids in each sampling area at Lake Papaitonga Scenic Reserve. Treatment areas (poisoned) = A and C; non-treatment areas (non-poisoned) = B and D. Error bars indicate standard error.

5.3.6 Changes in carabid abundance over time

The number of carabids caught in each area was not constant over time (Figure 5.6). Areas C and D showed large fluctuations in numbers over six months, while areas A and B had much smaller fluctuations. Carabid numbers were high in all areas except A in October, then dropped markedly in November and December. Numbers increased in January, but declined again in February and March, although area B had a rise in February rather than in January. Carabid abundance was similar in all sampling areas in March.

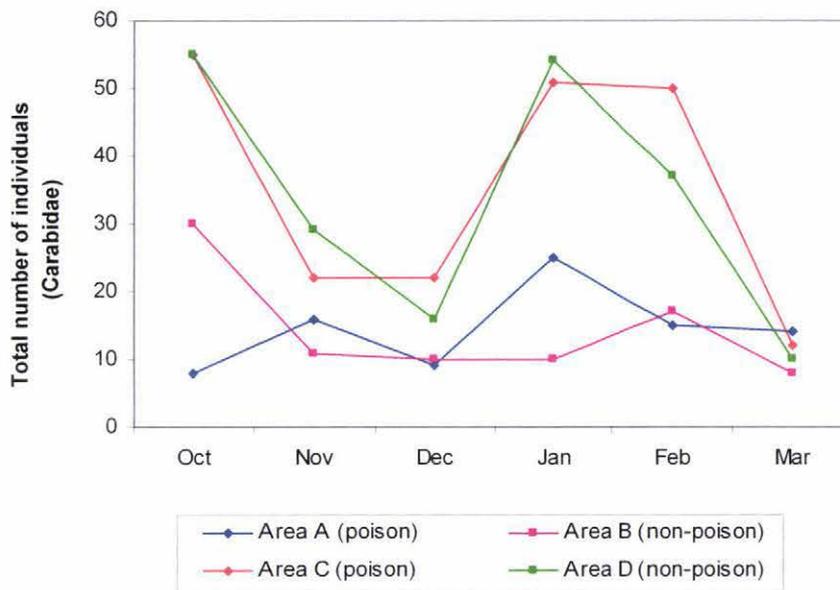


Figure 5.6. Total number of carabids caught in each sampling area at Lake Papaitonga Scenic Reserve over time (October 1999 – March 2000). Treatment areas (poisoned) = A and C; non-treatment areas (non-poisoned) = B and D.

There was a significant effect of ‘month’ on the total number of carabids caught in each area (RMANOVA, $df = 5$, $F = 17.07$, $p < 0.001$), which indicates that the difference between the areas was affected by the month of sampling. When we consider each month separately, the difference in catches between the areas was only significant for three out of the six months (Table 5.4). There was no significant difference in carabid abundance between the sampling areas in November, December or March, when the total numbers caught were lower than in the other three months (Figure 5.6).

Table 5.4. Results of a repeated measures analysis of variance of the total number of carabids caught in each sampling area from October 1999 to March 2000. Tukey post-hoc test: means with the same letter are not significantly different. Significance level: * p < 0.001, 'NS' indicates a non-significant difference between the areas in that month (p > 0.05).**

	Sampling area				P-value
	A	B	C	D	
October	x	xz	y	yz	< 0.001 ***
November	x	x	x	x	NS
December	x	x	x	x	NS
January	xz	x	yz	y	< 0.001 ***
February	x	x	y	xy	< 0.001 ***
March	x	x	x	x	NS

5.3.7 Spatial dispersion of carabids in each area

The dispersion indices indicate that the total catches of carabids were aggregated in all of the sampling areas (Table 5.5). The spatial dispersion of the five most abundant species was also analysed individually (Table 5.5). *Megadromus capito* showed significant aggregation in all four areas (see Figure 5.7). *Selenochilus* sp. was aggregated in areas C and D, but was not abundant enough in the other areas for analysis. In contrast, *M. oconnori* was not aggregated in either of the areas it was present in (C and D). *Holcaspis mucronata* and *H. sinuiventris* also showed no significant aggregation, but they were caught in low numbers in each area (*H. mucronata*, Area B: n = 12; *H. sinuiventris*, Area B: n = 8, Area D: n = 5).

Table 5.5. Spatial dispersion of carabids in pitfall traps at Lake Papaitonga Scenic Reserve (total catch over six months). Dispersion index (I) = s^2 / x (s^2 = variance, x = mean). A dispersion index of 1 or greater indicates aggregated (non-random) dispersion. Significance level for the χ^2 statistic: * P < 0.001, ** p < 0.01, * p < 0.05, 'NS' = non-significant. -- indicates that < 5 individuals were caught in that area.**

	Dispersion index (χ^2 statistic)			
	A	B	C	D
<i>Megadromus capito</i>	1.90 (51.41) **	2.31 (62.31) ***	2.52 (68.11) ***	1.93 (52.05) **
<i>Mecodema oconnori</i>	--	--	1.15 (31.15) NS	1.22 (32.85) NS
<i>Selenochilus</i> sp.	--	--	1.67 (45.00) *	2.05 (55.33) **
<i>Holcaspis mucronata</i>	--	1.28 (34.67) NS	--	--
<i>Holcaspis sinuiventris</i>	--	1.00 (27.00) NS	--	0.85 (23.00) NS
TOTAL Carabidae	2.15 (58.15) ***	2.14 (57.64) ***	2.11 (57.01) ***	2.25 (60.86) ***

The mean number of carabids caught per trap was slightly higher in outer pitfall traps compared to inner traps (5.36 ± 0.38 versus 4.98 ± 0.37), however this difference was not significant (t-test, df = 110, p = 0.623).

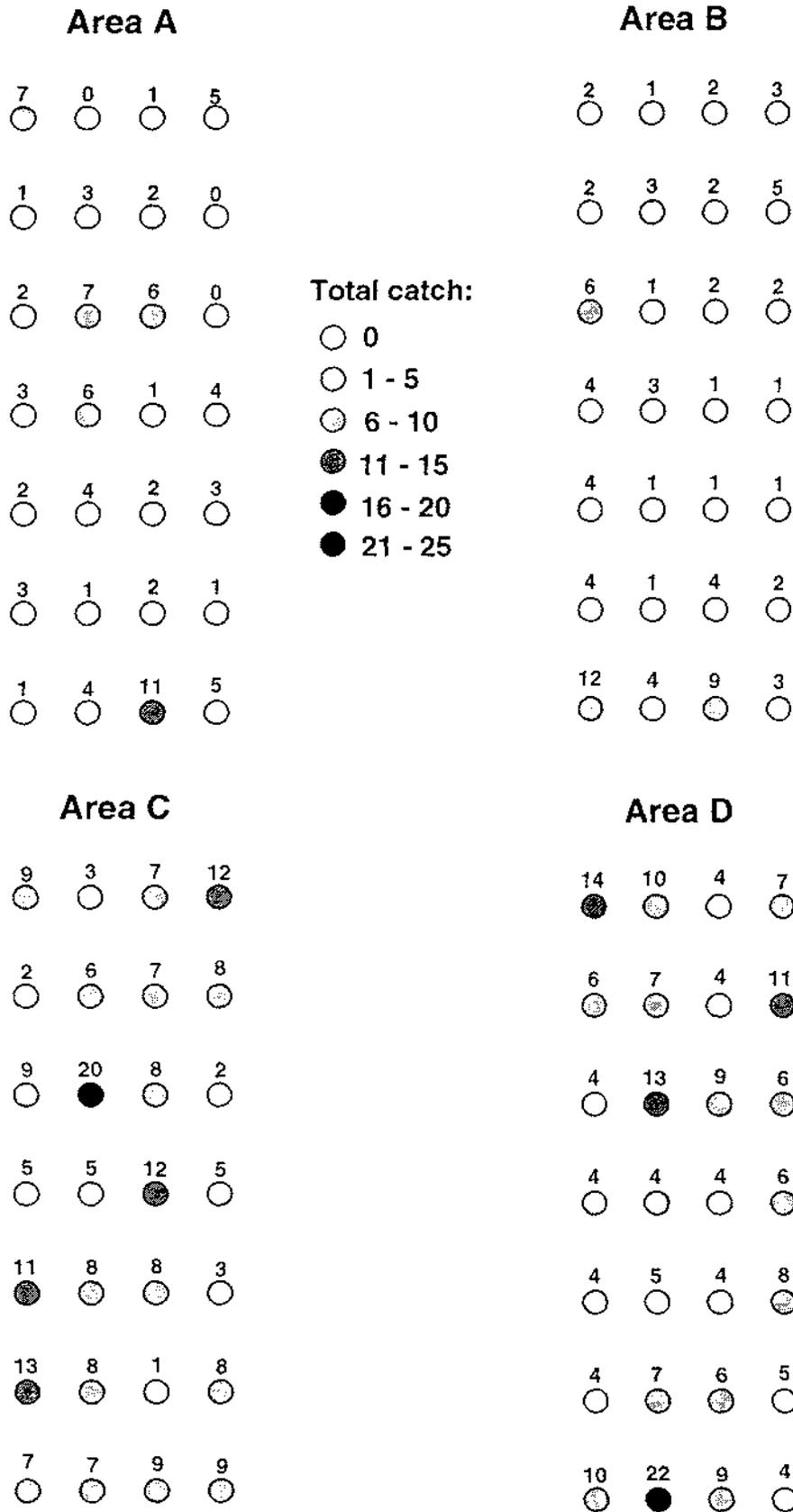


Figure 5.7. Spatial dispersion of *Megadromus capito* in pitfall traps at Lake Papaitonga Scenic Reserve. Numbers above each trap (circles) indicate the total number of individuals caught in that trap over six months.

5.3.8 Abundance of other invertebrates

A total of 31,277 individuals of taxa other than Carabidae were caught in the pitfall traps during one month of sampling (October 1999). There was a significant difference in the total number of other invertebrates between treatments, and non-poisoned areas had significantly more individuals than poisoned areas (t-test, $df = 110$, $p < 0.001$). This result is mainly due to the abundance of Collembola in each area (see overleaf in section 5.3.9).

When treatment was ignored, the total number of other invertebrates differed significantly between the four sampling areas (ANOVA, $df = 3$, $F = 10.80$, $p < 0.001$). Area A had significantly fewer individuals than the other areas (Tukey post-hoc test, $p < 0.05$, Table 5.6). There were significant differences between the numbers of individuals in each size class in the four areas (Figure 5.8, Table 5.6). Areas B and D had the highest numbers of invertebrates in the smallest size class (0-2 mm), while area A had significantly fewer individuals in the 3-5 mm size class than the other areas (Figure 5.8a). Medium-sized (6-10 mm) invertebrates were significantly more abundant in area D, and area C had significantly more large invertebrates (10+ mm) than the other areas ($p < 0.001$, Figure 5.8b).

(a) Smaller size classes (0-2 mm, 3-5 mm)

(b) Larger size classes (6-10 mm, 10+ mm)

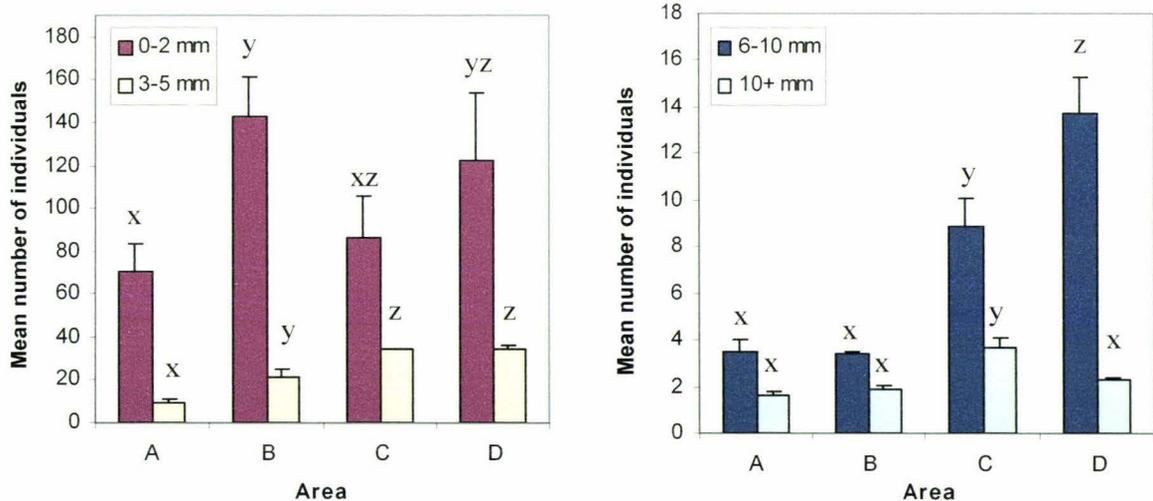


Figure 5.8. Mean number of other invertebrates per trap caught in each sampling area at Lake Papaitonga Scenic Reserve in October 1999 (a) smaller size classes, (b) larger size classes. Treatment (poisoned areas) = A and C; non-treatment (non-poisoned) areas = B and D. For each size class, means with the same letter are not significantly different (Tukey-post hoc test, ANOVA, $df = 3$, $p < 0.001$ in all cases). Error bars indicate standard error.

Table 5.6. Results of an analysis of variance of the mean number of other invertebrates per trap caught in the four sampling areas at Lake Papaitonga Scenic Reserve (df = 3). Tukey post-hoc test: means with the same letter are not significantly different. Significance level: * $p < 0.001$.**

	Sampling area				P-value
	A	B	C	D	
tiny invertebrates (0-2mm)	70.3 x	142.4 y	85.8 xz	122.3 yz	< 0.001 ***
small invertebrates (3-5mm)	8.9 x	21.0 y	33.9 z	34.6 z	< 0.001 ***
medium invertebrates (6-10mm)	3.5 x	3.4 x	8.9 y	13.8 z	< 0.001 ***
large invertebrates (10+mm)	1.7 x	1.9 x	3.7 y	2.3 x	< 0.001 ***
TOTAL invertebrates	84.6 x	168.9 y	132.5 y	173.2 y	< 0.001 ***

5.3.9 Composition of other invertebrates in each area

The composition of other invertebrates varied between the sampling areas, and there were significant differences in the abundance of some of the major groups (Table 5.7). The two most abundant groups were Collembola (springtails) and Acarina (mites) (Figure 5.9). Collembola were significantly more abundant in areas B and D (Tukey post-hoc test, $p < 0.001$), and area B had significantly more mites than the other areas (Tukey post-hoc test, $p < 0.01$, Table 5.7).

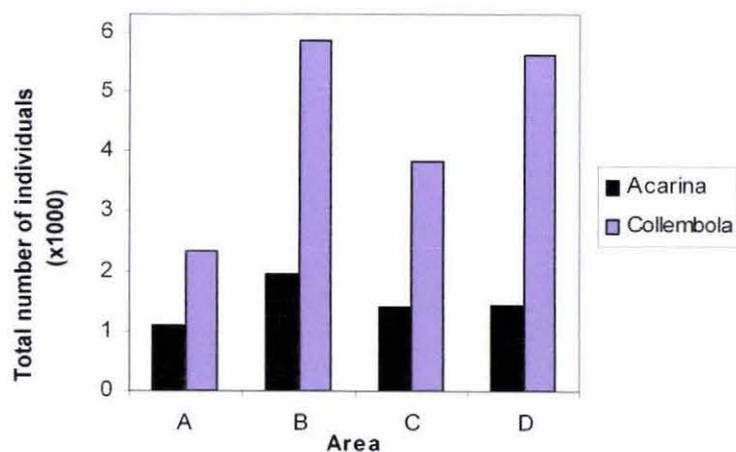


Figure 5.9. Total number of Acarina and Collembola in each sampling area at Lake Papaitonga Scenic Reserve (October 1999). Treatment (poisoned areas) = A and C; non-treatment (non-poisoned) areas = B and D.

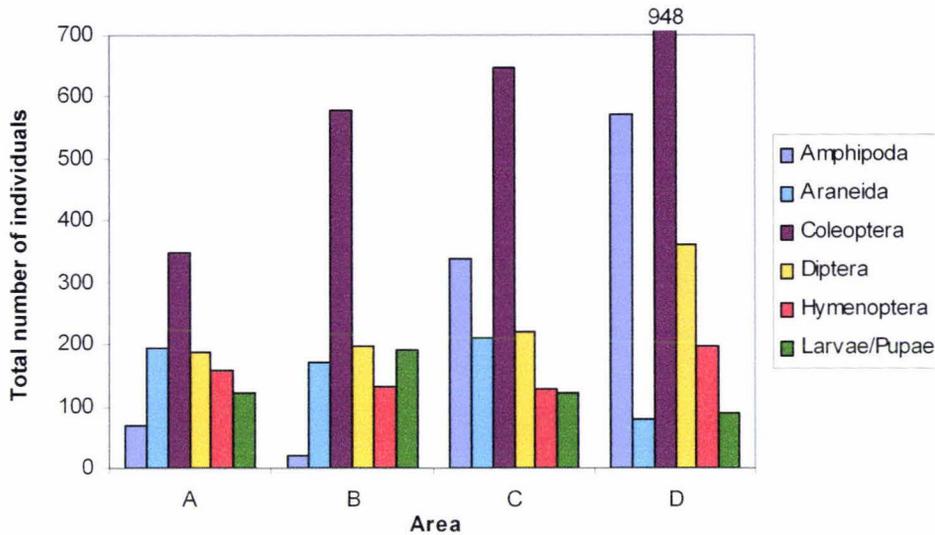


Figure 5.10. Total number of individuals of some of the major invertebrate groups in each sampling area at Lake Papaitonga Scenic Reserve (October 1999). Treatment (poisoned areas) = A and C; non-treatment (non-poisoned) areas = B and D.

Area D had significantly more beetles (Coleoptera) than the other areas (Tukey's test, $p < 0.05$ in all cases), but significantly fewer spiders (Araneida) ($p < 0.01$ in all cases) (Table 5.7, Figure 5.10). Areas C and D had significantly more amphipods than areas A and B (Tukey's test, $p < 0.05$ in both cases), and area C also had significantly more weta (Orthoptera) than A and B ($p < 0.02$). Area D had significantly more flies (Diptera) than area A (Tukey's test, $p = 0.048$), while area B had significantly more snails (Gastropoda) than area D ($p = 0.004$).

Table 5.7. Results of an analysis of variance of the mean number of individuals per trap in each sampling area for some of the major invertebrate groups at Lake Papaitonga Scenic Reserve (df = 3). Tukey post-hoc test: means with the same letter are not significantly different from each other. Significance level: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, 'NS' = a non-significant difference.

Group	Sampling area				P-value
	A	B	C	D	
Acarina	x	y	x	x	< 0.001 ***
Amphipoda	x	x	y	z	< 0.001 ***
Araneida	x	x	x	y	< 0.001 ***
Coleoptera	x	xy	y	z	< 0.001 ***
Collembola	x	y	xy	y	< 0.001 ***
Diplopoda	x	x	y	z	< 0.001 ***
Diptera	x	xy	xy	y	0.036 *
Gastropoda	x	x	x	y	0.006 **
Hymenoptera	x	x	x	x	0.091 NS
Orthoptera	x	x	y	xy	0.004 **
Larvae/Pupae	xy	x	xy	yz	0.027 *

Detrended correspondence analysis (DECORANA) was used to illustrate the differences in the composition of other invertebrates in each sampling area. The first two ordination axes explained just over a third of the variation in the data (34.3%), and a plot of their scores is shown below (Figure 5.11). Like the DECORANA of carabid assemblages, the traps appear to be separated into the two different peninsulas rather than by treatment. Areas A and B occupy the lower left of the plot, whereas areas C and D are found in the upper right of the plot. The first ordination axis had a large negative score for *Collembola* (Appendix 13a), indicating that the traps at the lower end of this axis had higher numbers of springtails - mainly those in area B. The second axis explained less than 2% of the remaining variation, but was associated with an increase in the numbers of *Amphipoda*. Thus, the traps in areas C and D had higher numbers of amphipods than areas A and B. There was no strong correlation with the environmental variables along the first axis, but axis two was correlated with increasing soil depth (see Appendix 13b).

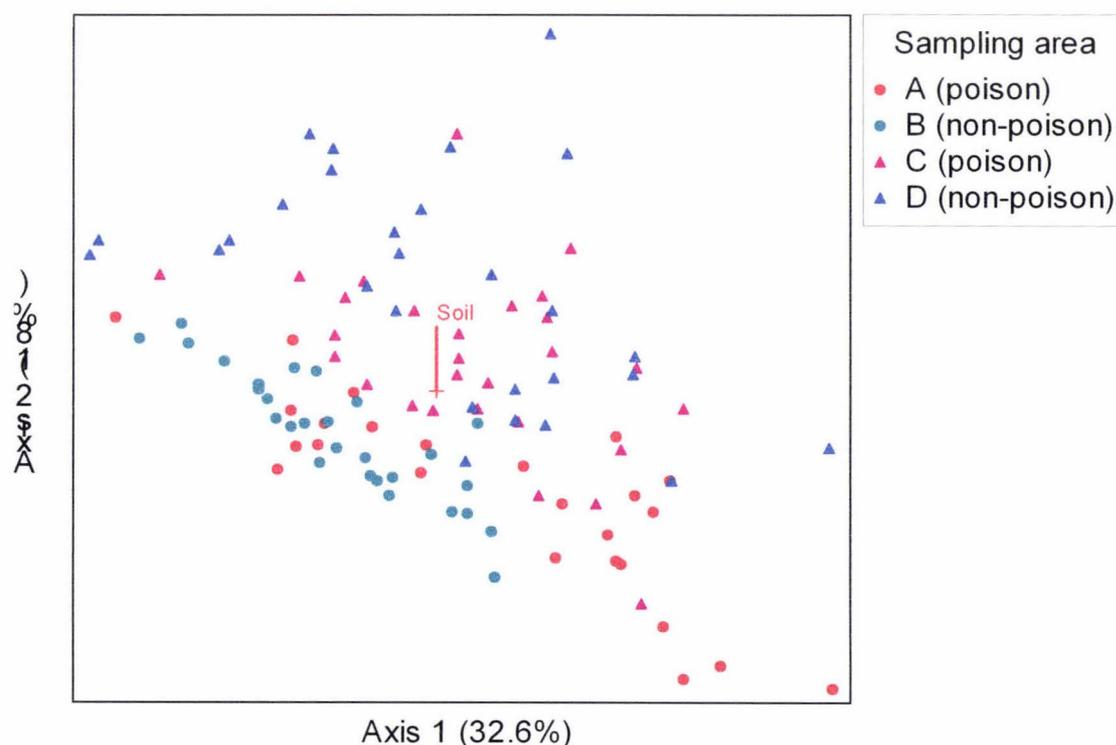


Figure 5.11. Detrended correspondence analysis results for the other invertebrates in each sampling area at Lake Papaitonga Scenic Reserve (symbols denote individual pitfall traps). The percentage of variation explained by each axis is shown in brackets. Soil depth ('Soil') was the most highly correlated environmental variable. The direction of the vector indicates the maximum change of Soil depth along the axes, and the length indicates the magnitude of that change.

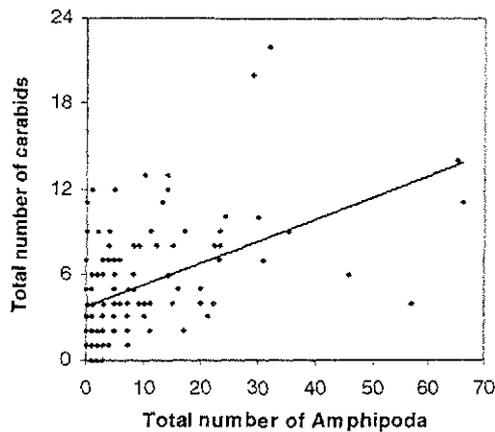
5.3.10 Relationship between the abundance of carabids and other invertebrates

There was a significant correlation between the total abundance of carabids (over six months) and the total abundance of other invertebrates (in October) in pitfall traps (Pearson correlation, $r = 0.292$, $p = 0.027$, Table 5.8). However, when the other invertebrates were separated into size classes, only the correlations between carabids and the small (3-5 mm) and medium (6-10 mm) invertebrates were significant (Table 5.8). The abundance of carabids was correlated significantly with the abundance of amphipods ($r = 0.489$, $p < 0.001$, Figure 5.12a), springtails ($r = 0.242$, $p = 0.010$), and other Coleoptera ($r = 0.207$, $p = 0.028$, Figure 5.12b). However, there was no correlation between the numbers of carabids and the numbers of Acarina, Araneida, Diptera, or Hymenoptera (Table 5.8).

Table 5.8. Pearson correlations and Bonferroni probabilities (p-values) between the total abundance of carabids and other invertebrates at Lake Papaitonga Scenic Reserve (n = 112). Data marked with # were \log_{10} transformed. Significance level: * $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, 'NS' = non-significant ($p > 0.05$).**

	Pearson correlation coefficient (r)	P-value
TOTAL invertebrates #	0.292	0.027 *
tiny invertebrates (0-2 mm) #	0.174	0.990 NS
small invertebrates (3-5 mm)	0.408	< 0.001 ***
medium invertebrates (6-10 mm)	0.372	0.001 **
large invertebrates (10+ mm)	0.269	0.062 NS
Acarina	0.090	0.343 NS
Amphipoda	0.489	< 0.001 ***
Araneida	-0.019	0.840 NS
Coleoptera	0.207	0.028 *
Collembola #	0.242	0.010 *
Diptera	0.071	0.457 NS
Hymenoptera	0.124	0.191 NS

(a) Amphipoda



(b) Other Coleoptera

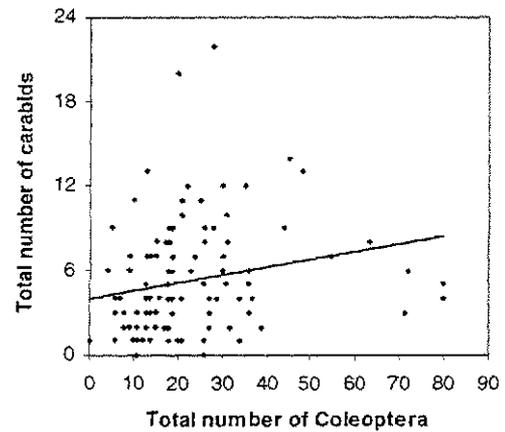


Figure 5.12. Relationship between the total number of carabids (October – March) and the total number of (a) Amphipoda and (b) other Coleoptera (October) caught in pitfall traps at Lake Papaitonga Scenic Reserve ($n = 112$).

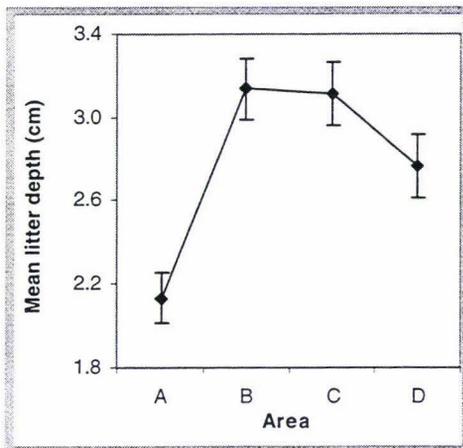
5.3.11 Relationship between carabids and the environmental variables

There was a significant difference in leaf litter depth (ANOVA, $df = 3$, $F = 12.40$, $p < 0.001$, Figure 5.13a) and soil depth ($F = 59.21$, $p < 0.001$, Figure 5.13b) between the four sampling areas. Area A had a significantly shallower layer of leaf litter (Tukey post-hoc test, $p < 0.001$ in all cases) and soil ($p < 0.01$) compared to the other areas, and area C had the greatest soil depth ($p < 0.001$). There was a significant difference in vascular plant ground cover between the four areas ($F = 7.41$, $p = 0.012$, Figure 5.13c), and area D had significantly less plant cover than the other areas (Tukey post-hoc test, $p < 0.01$). In contrast, mean canopy cover was not significantly different in each area ($F = 0.23$, $p = 0.879$), and there was no obvious difference between the soil moisture levels in the four areas (Bennett 2001, unpublished data).

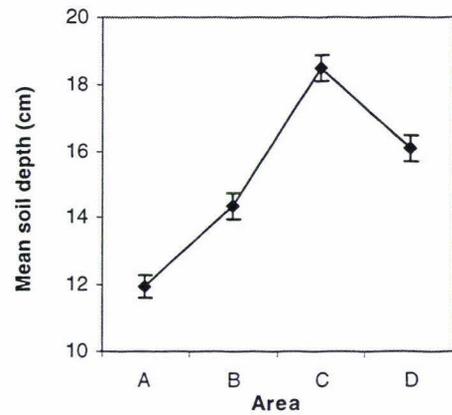
The total number of carabids caught in each trap was significantly correlated with soil depth (Pearson correlation, $r = 0.393$, $p < 0.001$). However, the relationship between carabid numbers and leaf litter depth was marginally non-significant ($r = 0.248$, $p = 0.05$), and there was no correlation with canopy cover ($r = 0.011$, $p = 0.905$). There was a negative relationship between carabid abundance and vascular plant ground cover, but the correlation was non-significant ($r = -0.189$, $p = 0.275$).

When the carabid species were considered individually, none of the species showed any correlation with the environmental characteristics measured, except *M. capito* (see Appendix 14). The abundance of *M. capito* was significantly correlated with both soil depth (Pearson correlation, $r = 0.344$, $p = 0.002$) and leaf litter depth ($r = 0.299$, $p = 0.014$). There was also a significant correlation between carabid larvae and soil depth ($r = 0.290$, $p = 0.019$).

(a) Mean leaf litter depth (cm)



(b) Mean soil depth (cm)



(c) Mean vascular plant ground cover (%)

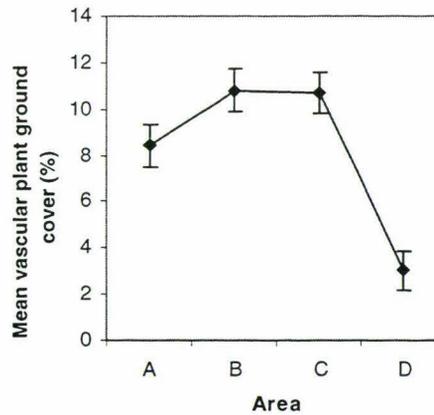


Figure 5.13. Environmental characteristics of each sampling area at Lake Papaitonga Scenic Reserve: (a) mean leaf litter depth, (b) mean soil depth, and (c) mean vascular plant ground cover. Treatment areas (poisoned) = A and C, non-treatment areas (not poisoned) = B and D.

5.4 DISCUSSION

5.4.1 The effect of predation on carabids

Several studies overseas have revealed that rodents are major predators of carabid beetles, and that rodent predation has a significant effect on carabid beetle communities (Parmenter and MacMahon 1984, Parmenter and MacMahon 1988, Churchfield *et al.* 1991). Parmenter and MacMahon (1988) compared carabid densities in enclosures with and without rodents and found that rodent predation resulted in a significant reduction in the population size of several carabid species, and may have contributed to localised extinctions of rarer species. Similarly, Churchfield *et al.* (1991) discovered that rodents had a major impact on carabids and other terrestrial invertebrates, because of their high population densities and consumption rates.

In contrast to these studies, a worldwide review of the predators of Carabidae contained no published records of rat predation on carabid beetles (Laroche 1975a). However, evidence collected in my study and several other studies suggests that rodents, particularly ship rats (*Rattus rattus*), are predators of carabids in New Zealand. For example, a study by Sturmer (1988) on Stewart Island revealed that carabids were the most common form of adult beetle eaten by three species of rodent: ship rat, Norway rat (*Rattus norvegicus*), and kiore (*Rattus exulans*). Rickard (1996) also found carabid remains in the stomachs of ship rats in Westland. During the course of my study, shattered remains of *M. capito* and *M. oconnori* exoskeletons were found at Browns Bush in what appeared to be a rat cache (Cover plate 5). Bremner *et al.* (1984) provided circumstantial evidence of rat predation on carabids in Fiordland, because carabid densities were significantly lower on islands where Norway rats were present. A pilot study on the benefits of rodent and possum control for large-bodied invertebrates revealed that carabid abundance was significantly higher in the treatment area where rat densities had been reduced by poisoning (Hunt *et al.* 1998).

A comprehensive analysis of ship rat diet by Blackwell (2000) revealed no indication of carabid remains in rat stomachs from Lake Waikaremoana, despite high numbers of carabids being caught in pitfall traps at the same site. However, Blackwell (2000)

suggested that the absence of carabids from rat guts might be related to the feeding behaviour of rats, as they may preferentially eat the softer parts of carabids, and discard the chitinous exoskeletons. Similarly, Norman (1970) observed that ship rats on Big Green Island, off the coast of Tasmania, selectively ate the soft parts of their main scarabaeid prey, leaving the hard exoskeleton. Murdoch (1966) also reported that shrews (*Sorex araneus*) spat out the elytra of *Agonum fuliginosum* Panzer (Carabidae) after eating them, and suggested that small mammals such as shrews were responsible for the heavy spring mortality in this species.

The overall finding of my study was that rodent control had no significant effect on the total abundance of carabids at Lake Papaitonga Scenic Reserve, and the composition of carabid assemblages in each area was not strongly related to the treatment. Nevertheless, the most common species, *M. capito*, appeared to have benefited from reduced rodent densities because it was more abundant in the poisoned areas (A and C) compared to the non-poisoned areas (B and D) on the same peninsula. However, most of the remaining carabid species, including *M. oconnori* and *Selenochilus* sp., were significantly more abundant in areas that were not poisoned. These potentially conflicting results might be explained by the feeding behaviour of rats. Rats are described as opportunistic feeders, and consume a wide variety of invertebrate groups, depending on their availability (Innes 1979, King 1990). Thus, we would expect rats to have a greater impact on the most numerous prey species, in this case, *M. capito*. The other carabid species were caught in much lower numbers in pitfall traps than *M. capito*, therefore rodents may not have encountered them frequently enough for them to be consumed in large numbers.

Although rodents may not present a large threat to adult carabid beetles, carabid larvae may be much more vulnerable to predation because they are soft-bodied and lack the defence mechanisms of adults (Lövei and Sunderland 1996). For example, Orbtel (1973, cited in Thiele 1977) discovered that carabid larvae comprised 13.8% of the arthropod remains in the yellow-necked field mouse (*Apodemus flavicollis*), and suggested that these mice could have a considerable impact on the survival of carabid larvae. However, I found no significant effect of rodent control on larval densities, although the highest larval numbers were found in a non-poisoned area.

Rickard (1996) demonstrated that ship rats in Westland ate large invertebrates in preference to small ones, presumably because of their greater energy reward. In my study, the carabids in area B (a non-poisoned area) were significantly smaller on average than those in the other sampling areas, and area B also had significantly higher rat tracking rates than the other areas. It is possible that rat predation on larger invertebrates may have been responsible for the absence of large carabids there. Mice tracking rates were also high in area B, but mice seem unlikely to prey on large carabids because area D, which had the highest mice tracking rates, also contained the largest carabids.

Mice and rats often respond differently to poison operations (Innes *et al.* 1995), and this was also the case at Lake Papaitonga. Rats were maintained at low densities in the poisoned areas throughout the study, but the reduction in rat numbers was followed by an increase in the population density of mice, particularly in area D (Bennett 2001). Mouse numbers often increase after poisoning, largely due to mice surviving better when interspecific competition and predation from rats is removed (Innes *et al.* 1995). This means that predation pressure on invertebrates may be maintained by an increased number of mice, thus reducing the actual benefits of the poisoning operation to invertebrates (Hunt *et al.* 1998). The interspecific interactions between rodents also make it more difficult to interpret the impact of treatment on invertebrate communities, as the effects of rats and mice may be confounded.

The poisoning itself may have had some negative effects on the carabid beetles at Lake Papaitonga Scenic Reserve. Carabid beetles (e.g. *Megadromus bullatus* (Broun)) were seen feeding on Talon® baits, and residues of brodifacoum have been found in carabid beetles (Morgan and Wright 1996). Invertebrates are unlikely to be directly killed by brodifacoum (Shirer 1992), but very little is known about the effects of brodifacoum on them, or whether secondary poisoning of insectivores is likely to occur (Spurr 1996). Spurr (1996) reported a significant change in carabid numbers between treatment (Talon® poison) and non-treatment areas in only one out of 13 months of pitfall trapping in forest reserves near Pelorus Bridge, Nelson. He concluded that poisoning rodents with Talon® had neither a detrimental nor beneficial effect on invertebrate populations. However, he also found that rodents rapidly re-invaded from surrounding (non-forest) habitat following poisoning, hence rodent densities might still have been high in the treatment area.

In addition to rodents, carabids are preyed upon by many other animals, including almost every kind of bird, and in particular by insectivorous mammals (Thiele 1977). Predators of carabids overseas include owls, badgers, skunks, shrews, moles, bats, frogs, and reptiles (Thiele 1977, Larochelle 1974, 1975a,b). One of the major predators of carabids in New Zealand seems to be the introduced European hedgehog (*Erinaceus europaeus*) (Campbell 1973, Berry 1999, Hendra 1999), although there has been little research about the effects of hedgehogs on invertebrates in native forest. Berry (1999) discovered that carabids (*Mecodema* spp. and *Holcaspis* spp.) were one of the most commonly eaten food items for hedgehogs at Boundary Stream in Hawkes Bay, and made up at least 20% of their diet. Similarly, Campbell (1973) found large numbers of *Megadromus antarcticus* (Chaudoir) in hedgehog guts in the South Island.

Other predators of carabids in New Zealand include starlings (*Sturnus vulgaris*) (Wood 1973), kiwi (*Apteryx* spp.) (Gurr 1952, Bull 1959, Watt 1971, Reid *et al.* 1982, Colbourne & Powlesland 1988), magpies (*Gymnorhina tibicen*), thrushes (*Turdus philomelos*), stoats (*Mustela erminea*) (A. Larochelle, pers. comm. 2000), and spiders (Mike Bowie pers. comm. 2000, A. Larochelle pers. comm. 2000). Tretzel (1961, cited in Thiele 1977) reported predation by ground spiders on several species of carabid, and Greene (1975) estimated that carabids constituted 40% of the prey of the black widow spider (*Latrodectus mactans*) in Washington. During my study, I found *M. capito* remains in bird droppings at Browns Bush, and these appeared to be from starlings or thrushes.

Some carabid beetles overseas have developed a defence against predators by ejecting a volatile substance which explodes on contact with the air, burning the attacker with nitrous acid (Meads 1990). However, New Zealand carabid beetles do not appear to have developed an effective defence against mammals, and may be particularly vulnerable to the impacts of introduced predators (Howarth & Ramsay 1991). New Zealand carabids attempt to defend themselves by emitting foul-smelling secretions from the anal gland, but these chemical compounds are primarily a defence against infection by bacteria and fungi (Meads 1990). The larger carabids can inflict a painful bite, and some species, such as *M. oconnori*, may feign death in the presence of an attacker (A. Larochelle, pers. comm. 2000), although neither of these strategies appear to be particularly successful either.

5.4.2 The effect of other invertebrates on carabid assemblages

Many authors have reported a correlation between carabid abundance and the abundance of other invertebrate groups (Thiele 1977, Lenski 1984, Lys & Nentwig 1991, van Dijk 1994, Butterfield 1997). The main reasons suggested for this relationship are that carabids may be affected by the densities of their potential prey, or may respond in the same way as other groups to environmental factors (Niemelä *et al.* 1986, Baguette 1993). For example, Guillemain *et al.* (1997) found that the abundance of carabids was significantly associated with the abundance of its prey, and that low prey densities resulted in low carabid abundance.

Most carabids overseas are polyphagous feeders that consume both plant and animal material (Sota 1985, Chaabane *et al.* 1993, Sunderland *et al.* 1995, Lövei and Sunderland 1996, Bommarco 1999). Though their feeding habits are little known, New Zealand carabids probably also eat a wide variety of smaller invertebrates and plant material (Moeed and Meads 1985, Lövei and Sunderland 1996). For example, Watt (1961) observed that *Ctenognathus* spp. fed on mosquitos, amphipods, and small slaters in captivity. However, many carabids, such as *M. oconnori*, use extra-oral digestion, and this makes it impossible to identify invertebrate remains in their guts because everything is liquefied (Evans 1977b, Cohen 1995). Seriological techniques such as ELISA are likely to provide results (Evans 1977b, Hance & Renier 1987, Sopp *et al.* 1992), but they are expensive and time-consuming, so they were not undertaken in this study. Nevertheless, *M. oconnori* adults were maintained for six months on a diet of earthworms (I. Townsend, pers. comm. 1999), and I kept *M. oconnori* alive for several months in captivity on a diet of *Tenebrio* larvae (mealworms) (see Appendix 5).

In my study, the abundance of carabids was significantly correlated with the numbers of amphipods, Collembola (springtails), and Coleoptera caught in pitfall traps. Collembola, and amphipods are common prey items for overseas carabid beetles (Crowson 1981, Ernsting & van der Werf 1988), and are probably also consumed by New Zealand carabids. Other authors have also found a positive correlation between carabid abundance and the density of springtails (Niemelä *et al.* 1986), and Ernsting *et al.* (1992) suggested that Collembola density might be an important determinant of habitat suitability for

carabids. Schaller (1950 cited in Ernsting *et al.* 1992) found that *Notiophilus biguttatus* Fabricus showed a numerical response to the increasing density of springtails, implying a cause-effect relationship, with springtail numbers controlling beetle density. In contrast, the correlation between the numbers of carabids and other Coleoptera at Lake Papaitonga Scenic Reserve is probably the result of a mutual response to environmental factors rather than a predator-prey relationship.

Some invertebrate groups may have a negative impact on carabid beetles through their interactions as predators or competitors. For example, ants (Hymenoptera: Formicidae) were observed attacking carabid beetles, and carabids were absent near ant nests (Kolbe 1969, cited in Thiele 1977). Similarly, Niemelä (1990) found that ants had a negative correlation with carabid abundance, and that the presence of ants had a strong influence on the probability of carabids occupying a particular habitat. However, in my study, there was no relationship between the numbers of carabids and ants caught in pitfall traps at Lake Papaitonga Scenic Reserve, possibly because ants are not a dominant component of the invertebrate fauna in New Zealand forests.

Michaels & McQuillan (1995) suggested that because carabids are generalist predators they are likely to be correlated with collective prey species within certain size classes rather than with individual species. Similarly, Loreau (1987) found that the seasonal pattern in the size of carabids was correlated with the size of prey available. In my study, there was a significant correlation between carabid numbers and the abundance of small- and medium-sized invertebrates, which are most likely to be potential prey items for carabid beetles. There was no correlation between the abundance of carabids and other large invertebrates, probably because they are more likely to be competitors or predators of carabids rather than food items.

5.4.3 The effect of environmental factors on carabid assemblages

The results of the detrended correspondence analysis revealed that the carabid assemblages on each peninsula were more similar to each other than areas with the same treatment. One possibility is that the two peninsulas were separated in the past by the channel of the Ohau River as it flowed out to sea (Devine 1997), thus leading to

divergence of the carabid communities. The absence of *M. oconnori*, the largest carabid at Lake Papaitonga Scenic Reserve, from the northern peninsula also suggests that there is a difference between the environmental characteristics of the two peninsulas. The northern peninsula appears to suffer from greater human disturbance, such as trampling and introduced weed invasion, because of its close proximity to the road end (M. Hutchison, pers. obs.). Blake *et al.* (1994) found that the most important factor determining the distribution of large carabids was the degree of disturbance, particularly of the soil. Large, short-winged taxa are usually more abundant in stable, favourable habitats (den Boer 1970, Eyre 1994), and a high frequency of disturbance can eliminate large carabid species from an assemblage (Blake *et al.* 1994).

Several studies have used ordination techniques such as DECORANA for comparing carabid assemblages with the environmental characteristics in different habitats (Comandini & Taglianti 1990, Maelfait & Desender 1990, Quinn *et al.* 1991, Baguette 1993). For example, Quinn *et al.* (1991) discovered that the spatial distribution of carabids was correlated with the percentage of clay, silt and sand in soils and the coverage of bare ground, but was not related to vegetation characteristics. Baguette (1993) also found a strong correlation between carabid assemblages from different sites and the characteristics of the soils at those sites.

In my study, the environmental variables explained very little of the differences in carabid assemblages between the sampling areas. However, only a few characteristics were measured, and carabids may have been responding to other factors that were not considered. The only species that showed a relationship with any of the variables was *M. capito*, and its abundance was significantly correlated with the depth of soil and leaf litter. Similarly, Niemelä (1990) found that *Pterostichus oblongopunctatus* Fabricus was aggregated in habitats with a thick layer of leaf litter. The percentage cover of leaf litter, ground vegetation, and forest canopy were significant factors explaining the abundance and diversity of the carabid assemblages in Aggtelek National Park, Hungary (Magura & Tothmeresz 1997, Magura *et al.* 2000), and Guillemain *et al.* (1997) found that leaf litter was strongly associated with the composition and structure of the whole carabid community.

Several of the carabid species at Lake Papaitonga Scenic Reserve had aggregated distributions among the pitfall traps in each sampling area. Clumped distributions may be caused by a number of factors including habitat patchiness, patchy prey distributions (Greenslade 1963b, Mols 1979, Grüm 1990, Luff 1986), and the distribution of interspecific competitors (Thiele 1977). *Megadromus capito* displayed aggregation in all of the sampling areas at Lake Papaitonga, and its density was significantly correlated with soil and leaf litter depth around each trap. However, none of the other species showed any correlation with the environmental characteristics measured.

5.4.4 Limitations of pitfall trapping and sampling design

Pitfall traps may not be suitable for comparing the abundance of different species between sites because the number of beetles caught in pitfall traps is not directly related to population density (Blake *et al.* 1994, French & Elliott 1999, Holland and Smith 1999, also see Chapter Three, section 3.4.3). Some species are more likely to be caught than others (Greenslade 1964b, Luff 1975), and the relative proportions of different species in pitfall traps may not be an accurate reflection of their true proportions in the community (Halsall & Wratten 1998). For example, Andersen (1995) compared open pitfall traps and quadrat sampling of carabids on riverbanks, and found that larger carabid species were highly over-represented compared to smaller ones in the pitfall traps. Therefore, the importance of the two largest carabids at Lake Papaitonga Scenic Reserve, *M. oconnori* and *M. capito*, may have been overemphasised by the pitfall traps. However, Lenski (1982) suggested that activity-density (from pitfall traps) may in fact be a more useful measure than absolute density when studying the role of a species in a community because the more active species will be more effective hunters and have a greater influence on community dynamics.

It must be acknowledged that my study has a number of limitations for assessing the effect of controlling rodents on invertebrate communities. One problem is that the carabid assemblages in each area may have been quite different before the rodent control began, but invertebrate monitoring was not carried out before the poisoning, so there is no way of knowing what the original community composition was. Hunt *et al.* (1998) and Green (2000) recommended monitoring for two years prior to poisoning, and a further three

years of post-treatment monitoring in order to demonstrate the effects of treatment on invertebrate communities. However, the duration of my masters study did not allow for long term monitoring of invertebrates at Lake Papaitonga Scenic Reserve, therefore any conclusions are only preliminary.

5.4.5 Conclusions

Native carabid beetles appear to suffer from predation by a number of introduced species, although it is not known how important this is in relation to population dynamics or community composition. Controlling rodents at Lake Papaitonga Scenic Reserve did not have a positive effect on the total abundance of carabids, although the most common species, *M. capito*, was more abundant in poisoned areas compared to non-poisoned areas, and may have benefited from reduced rodent densities. Environmental factors, such as soil type, leaf litter type, moisture level, and habitat structure, are likely to have a strong influence on the carabid assemblages in each area, however their importance was not demonstrated in my study.

Carabids have been suggested as a potential indicator group for monitoring the effects of rodent control on terrestrial invertebrates (Steve Cranwell, Department of Conservation, pers. comm. 2000). However, the results from my study and other evidence suggests that carabids are probably not a major prey item for rodents in New Zealand (A. Laroche, pers. comm. 2000). Furthermore, the abundance of carabids is not necessarily correlated with that of other invertebrate groups which may be heavily impacted by rodents. From these observations, I conclude that carabids are probably not a suitable indicator group for assessing the impacts of rodents on the rest of the invertebrate community.

Chapter Six

General discussion and conclusions



Cover plate 6. *Megadromus capito* female with distended abdomen, probably gravid.
Photograph by Len Doel.

“A beetle may or may not be inferior to man – the matter awaits demonstration;
but if he were inferior to a man by 10,000 fathoms, the fact remains that there is probably
a beetle view of things of which a man is entirely ignorant.”

G. K. Chesterton (1901)

General discussion and conclusions

6.1 Findings of my study

New Zealand carabid beetles appear to be characterised by low fecundity, an extended egg-laying period, and long life span. These features are typical of K-type species, and appear to be shared by other members of New Zealand's invertebrate fauna (Daugherty *et al.* 1993). They are likely to be related to New Zealand's long history of isolation, and lack of mammalian predators.

Artificial resting sites were frequently occupied by the two large carabids in my study, and this could be taken advantage of in habitats where there is a lack of resting sites for carabids. The usefulness of artificial resting sites for re-introductions of carabids to areas they have disappeared from is currently being tested in Canterbury (Mike Bowie, pers. comm. 2000), and could be a valuable tool for carabid conservation in New Zealand.

Making comparisons between different sampling methods proved to be very useful for understanding the biases involved in each technique, and for separating the components of activity and abundance in pitfall trapping data. Live capture pitfall trapping appears to be a potentially valuable sampling technique for carabids, as it provides a satisfying alternative to traditional pitfall trapping in New Zealand, where all invertebrates are killed.

The high density of carabids at Browns Bush is somewhat surprising, considering the small size of the remnant, and its history of disturbance and modification. However, Crisp *et al.* (1998) also found a surprising number of native beetle species in an area greatly modified by humans, and Abensperg-Traun *et al.* (1996) found that carabid beetles in Australia were more abundant in woodland remnants highly disturbed by livestock activity. Kuschel (1990) also remarked that "even the relatively small bush patches that have so far escaped destruction may contain faunas of unsuspected richness and diversity". Small lowland remnants such as Browns Bush may be incredibly valuable for conservation of carabids in New Zealand, and it is important that this is recognised by the

Department of Conservation, since many of these forest remnants occur on private land and have no ongoing management.

6.2 Future work

There is still a large amount of research to be done on carabids in New Zealand, and we have a long way to go before the knowledge of our species will be satisfactory. Further studies on habitat requirements are needed to assess which areas are of highest priority for conservation of New Zealand carabids. Information about the impacts of rodents on New Zealand carabids is also required for effective management. Laboratory trials could be carried out to observe the behaviour of rodents around carabids, and to determine once and for all whether rodents are significant predators of these beetles.

Experiments in the laboratory and the field are necessary to observe the daily activity patterns of carabids in New Zealand. Time-sorting pitfall traps would be particularly useful, but the cost of their production was prohibitive for my study. Further research on carabid movement and dispersal abilities is also required to assess their potential for dispersal between fragmented populations. This will demand the use of tracking technology, such as the harmonic radar, to enable an observer to follow the movements of individual beetles. There is also the possibility of developing new tracking techniques for carabid beetles. For example, the application of “prox tags” with individually identifiable computer chips has been suggested for mark-recapture studies (Felix Collins, pers. comm. 2000). However, development of such technology would require a reasonable investment in time and money to produce the tracking devices and develop the software.

Molecular techniques could provide answers about the genetic relationships of some species (e.g. *Mecodema oconnori*), and insight into the dynamics of carabid metapopulations (Niehues *et al.* 1996), as most of the carabid populations in lowland forests in New Zealand are highly fragmented.

One of the major problems in my study was the inability to observe *M. oconnori* and *M. capito* when they were in underground burrows. Inspection of the burrows without destroying them might be possible with the use of an endoscope, but this was only made

available in the final stages of my study, so this potentially valuable tool could not be utilised.

New Zealand carabids are generally assumed to be polyphagous predators (Klimaszewski & Watt 1997), however, very little is known about their feeding habits or dietary composition. Laboratory work should be carried out to observe carabid foraging behaviour and feeding preferences, as this may help to assess their potential as biological control agents.

Pitfall trapping during autumn and winter is required to complete our knowledge about the seasonal activity and life cycles of carabids in New Zealand. Female beetles should also be dissected during this period to determine whether they are reproductively active over the cooler months.

6.3 Conclusions

Despite the prominence of carabid beetles in ecological research overseas, interest in New Zealand has been relatively recent, and knowledge of our carabids is still decades behind that of their Northern Hemisphere counterparts. The preliminary studies that are currently being carried out in New Zealand are equivalent to studies that were done in the 1950s and 1960s in Europe and North America (e.g. Gilbert 1956, Greenslade 1964a,b, Murdoch 1966).

My study has created almost as many questions as it has answers, but it could form the starting point for more detailed, long-term studies on carabids in New Zealand. A wealth of opportunities exist for future research on New Zealand carabids. Their high species diversity and varied habits make them ideal subjects for studies on biogeography and speciation in New Zealand. Taxonomic revision of several tribes is currently underway (A. Larochelle, pers. comm. 2000), and we can look forward to having a more solid taxonomic base for ecological studies on our carabids. The publication of the Fauna of New Zealand series on Carabidae by André Larochelle and Marie-Claude Larivière in the coming months will be of huge benefit for all future carabid research in New Zealand.

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Appendices



Cover plate 7. *Ctenognathus bidens* from Lake Papaitonga Scenic Reserve, Levin. Photograph by Felix Collins.

“The beetle, panoplied in gems and gold
A mailed angel on a battle day”
Wordsworth, 'Stanzas' (1802)

Appendix 1: List of vascular plant species at Browns Bush (identified by Melissa Hutchison)

Scientific Name	Common Name	Introduced sp. *
<i>Abutilon darwinii</i>	Chinese lantern	*
<i>Agathis australis</i>	kauri	planted
<i>Alectryon excelsus</i>	titoki	
<i>Aristotelia serrata</i>	wineberry	
<i>Asparagus scandens</i>	climbing asparagus	*
<i>Asplenium oblongifolium</i>	shining spleenwort	
<i>Asplenium flaccidum</i>	hanging spleenwort	
<i>Beilschmiedia tawa</i>	tawa	
<i>Berberis darwinii</i>	barberry	*
<i>Blechnum filiforme</i>	thread fern	
<i>Brachyglottis repanda</i>	rangiora	
<i>Buddleja</i> sp.	buddleia	*
<i>Calystegia</i> sp.	convolvulus	*
<i>Coprosma areolata</i>		
<i>Coprosma grandifolia</i>	raurekau	
<i>Coprosma tenuifolia</i>		
<i>Cordyline australis</i>	cabbage tree	planted
<i>Corynocarpus laevigatus</i>	karaka	
<i>Cyathea</i> sp.	tree fern	all dead
<i>Dacrydium cupressinum</i>	rimu	
<i>Datura stramonium</i>	thornapple	*
<i>Entelea arborescens</i>	whau	planted
<i>Fuchsia excorticata</i>	tree fuchsia	planted
<i>Hedycarya arborea</i>	pigeonwood	
<i>Hoheria populnea</i>	lacebark	
<i>Knightia excelsa</i>	rewarewa	
<i>Lastreopsis</i> sp.	fern	
<i>Laurelia novae-zelandiae</i>	pukatea	
<i>Macropiper excelsum</i>	kawakawa	
<i>Melicytus ramiflorus</i>	mahoe	
<i>Microsorium pustulatum</i>	hound's tongue	
<i>Microsorium scandens</i>	fragrant fern	
<i>Muehlenbeckia complexa</i>	scrub pohuehue	
<i>Myrsine australis</i>	red mapou	
<i>Pellaea rotundifolia</i>	button fern	
<i>Parsonsia heterophylla</i>	native jasmine	
<i>Pittosporum eugenioides</i>	lemonwood	
<i>Podocarpus totara</i>	totara	
<i>Prumnopitys ferruginea</i>	miro	
<i>Pseudopanax arboreus</i>	five-finger	
<i>Pteridium esculentum</i>	bracken	
<i>Pyrrosia eleagnifolia</i>	leather leaf fern	

<i>Rhododendron</i> sp.	rhododendron	*
<i>Rhopalostylis sapida</i>	nikau palm	
<i>Ripogonum scandens</i>	supplejack	
<i>Rubus cissoides</i>	bush lawyer	
<i>Rubus fruticosus</i>	blackberry	*
<i>Solanum pseudocapsicum</i>	Jerusalem cherry	*
<i>Sophora tetraptera</i>	kowhai	planted
<i>Tradescantia fluminensis</i>	wandering willy	*
TOTAL species		50

Appendix 2: Distribution and body size of carabid species at Browns Bush and Lake Papaitonga Scenic Reserve

Species	* introduced species	Tribe	Mean body size (mm)	Distribution
<i>Ctenognathus bidens</i>	(Chaudoir)	Platynini	14.60	ND, AK, CL, WO, BP, GB, TK, WN
<i>Ctenognathus</i> sp.	Fairmaire	Platynini	13.74	WN
<i>Harpalus affinis</i>	(Schrank) *	Harpalini	11.32 (\pm 0.80)	RI, WI, WN, Europe, North America
<i>Holcaspis mucronata</i>	Broun	Pterostichini	16.21 (\pm 0.27)	throughout North Island (except TK)
<i>Holcaspis sinuiventris</i>	(Broun)	Pterostichini	15.91 (\pm 0.24)	ND, AK, WO, BP, GB, HB, RI, WI, WA, WN
<i>Mecodema oconnori</i>	Broun	Broscini	35.53 (\pm 0.34)	AK, WO, TO, TK, WA, WN
<i>Megadromus capito</i>	(White)	Pterostichini	22.81 (\pm 0.06)	RI, WI, WN
<i>Megadromus vigil</i>	(White)	Pterostichini	21.15 (\pm 0.76)	TO, HB, RI, WA, WN
<i>Molopsida antarctica</i> (Laporte de Castelnau)		Tropopterini	8.52	WN, SD, MB, NN, KA, SC
<i>Molopsida strenua</i>	(Broun)	Tropopterini	7.23	BP, WO, HB, TO, TK, RI, WI, WA, WN
<i>Oopterus</i> sp.	Guérin	Zolini	6.22	WN
<i>Plocamostethus planiusculus</i> (White)		Pterostichini	28.00 (\pm 1.12)	CL, WO, BP, TO, HB, TK, WI, WA, WN, SD, NN, MB, KA, BR
<i>Selenochilus ruficornes</i> (?)	(Broun)	Meonini	7.04 (\pm 0.19)	TO, WN
<i>Zolus</i> sp.	(Sharp)	Zolini	8.31 (\pm 0.33)	WN

Mean body length calculated from carabids caught at Lake Papaitonga Scenic Reserve. Other information taken from the unpublished Fauna of New Zealand catalogue for Carabidae (A. Laroche and M-C. Larivière, pers. comm. 2000). Regional distribution codes are: ND = Northland, AK = Auckland, CL = Coromandel, WO = Waikato, BP = Bay of Plenty, TO = Taupo, GB = Gisborne, HB = Hawkes Bay, TK = Taranaki, RI = Rangitikei, WI = Wanganui, WA = Wairarapa, WN = Wellington, SD = Marlborough Sounds, MB = Marlborough, NN = Nelson, BR = Buller, KA = Kaikoura, SC = South Canterbury (after Crosby *et al.* 1976).

Appendix 3: Rodent abundance at Browns Bush: tracking tunnel rates (Aug, Sept, Nov 1999)

All footprints on the tracking papers were identified as rat prints, and they probably belonged to the ship rat (*Rattus rattus*), as the Norway rat (*Rattus norvegicus*) is not known from the area (Shaun Bennett, pers. comm., 2000). Rat tracking rates were high in August and September, with over half the tunnels being tracked in these months. However, in November rodent densities appeared to be low enough to allow the live pitfall trapping experiment to go ahead without too much interference from rodents. Mice were also observed at Browns Bush on several occasions under some of the metal sheets.

Month	Percentage of tunnels tracked (%)			
	Night 1	Night 2	Night 3	Mean rate (3 nights)
August	33.3	44.4	88.8	55.5
September	66.6	66.6	66.6	66.6
November	22.2	0.0	11.1	11.1

Appendix 4: Multivariate analysis of *Mecodema oconnori* morphological measurements

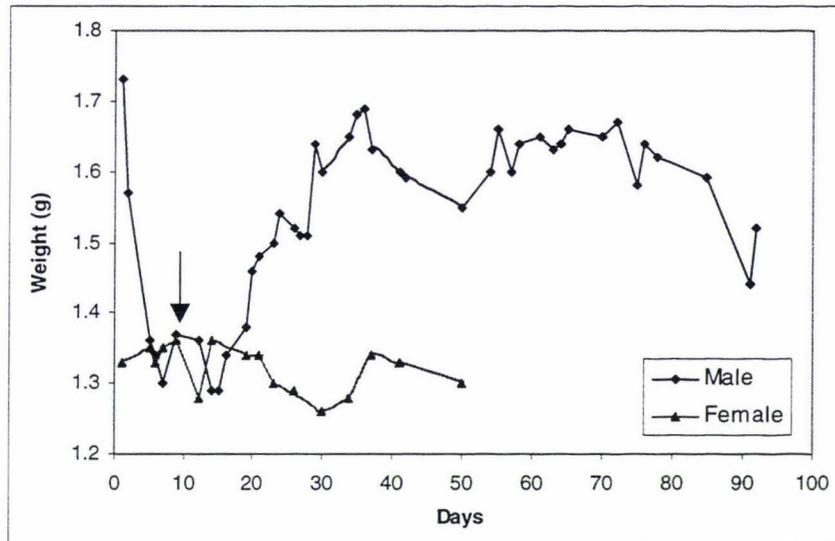
(a) Principle component analysis: eigenvectors of the first two principle components

	PRIN1	PRIN2
mass	0.09737	0.04311
total length	0.82913	0.17720
pronotum width	0.24468	0.36955
pronotum length	0.16690	0.21458
elytra width	0.23385	0.26319
elytra length	0.40083	-0.84550

(b) Canonical variate analysis: pooled within-class standardised canonical coefficients of the first canonical variate

Variable	CAN1
mass	0.29043
total length	-0.00321
pronotum width	0.75314
pronotum length	0.02445
elytra width	0.152980
elytra length	-0.178291

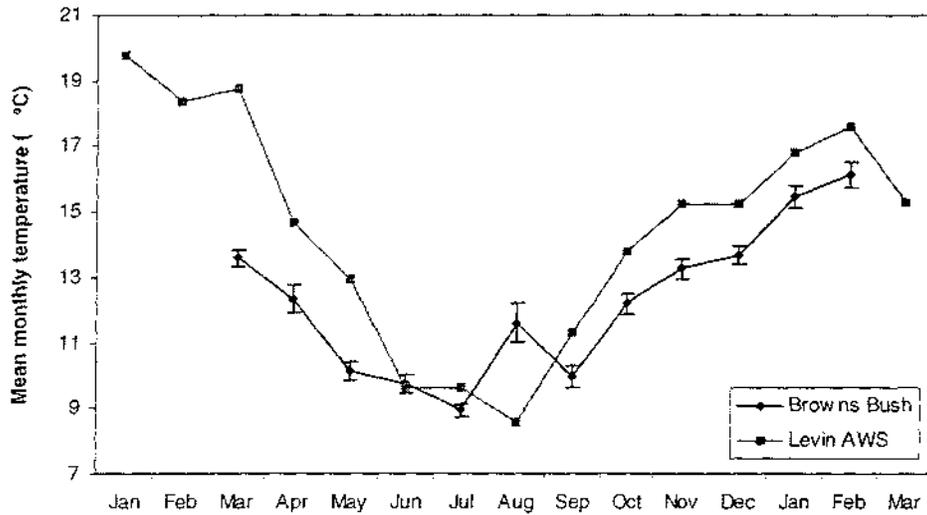
Appendix 5: Fluctuations in mass of a male and female *Mecodema oconnori* kept in the laboratory



N.B. 'Days' refers to the number of days since the beetles were first taken to the laboratory. The arrow indicates when the male started being fed.

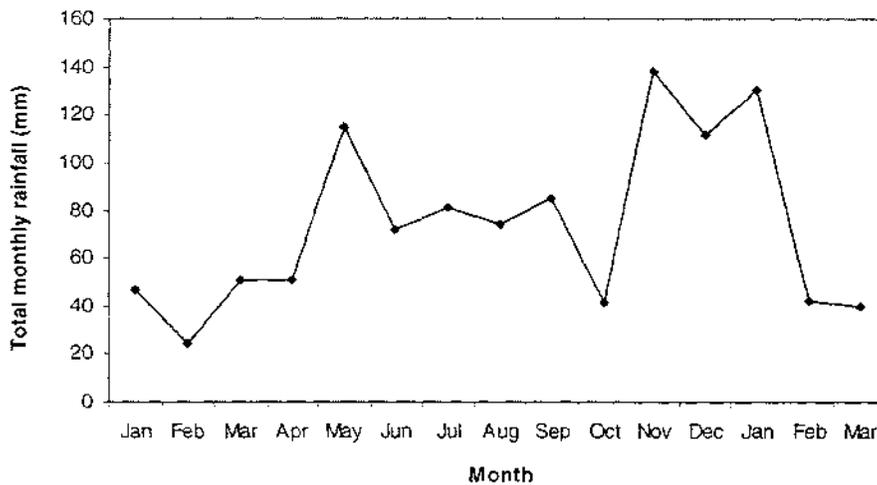
A male and female *Mecodema oconnori* were collected live from Browns Bush and kept in captivity for a number of months. Beetles were kept in separate ice cream containers filled with soil and leaf litter at room temperature. They were fed on a diet of *Tenebrio* larvae (mealworms) supplied *ad libitum*, however the male was initially starved for eight days. Beetles were weighed at least once a week, and mealworms were replaced as needed. The female died after 50 days, but the male was still alive at the end of 92 days when it was released.

Appendix 6: Mean monthly air temperature at Browns Bush and Levin Weather Station (January 1999 – March 2000)



N.B. Temperature data from Browns Bush are incomplete because the data loggers started recording later and stopped recording earlier than expected. Also, the mean temperature at Browns Bush in August is probably much higher than it should be because the first data logger stopped reading correctly when it was near the end of its capacity.

Appendix 7: Total monthly rainfall at Levin Weather Station (January 1999 – March 2000)



Appendix 8: Results of a two-way analysis of variance of carabid movement distances at Browns Bush

(a) Mean weekly distance (m)

	df	Raw data			Log-transformed data		
		F-ratio	P-value		F-ratio	P-value	
Species	1	0.158	0.692	NS	0.000	0.998	NS
Sex	1	0.804	0.373	NS	0.519	0.473	NS
Species*Sex	1	0.010	0.920	NS	0.790	0.377	NS

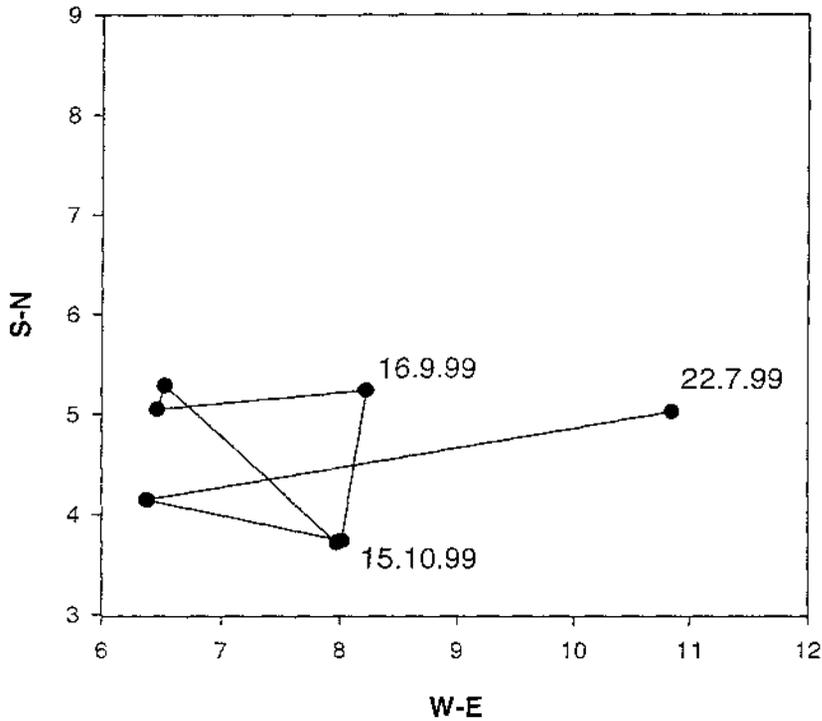
(b) Mean total distance (m)

	df	Raw data			Log-transformed data		
		F-ratio	P-value		F-ratio	P-value	
Species	1	0.600	0.441	NS	0.457	0.501	NS
Sex	1	0.594	0.443	NS	0.846	0.361	NS
Species*Sex	1	0.765	0.385	NS	0.751	0.389	NS

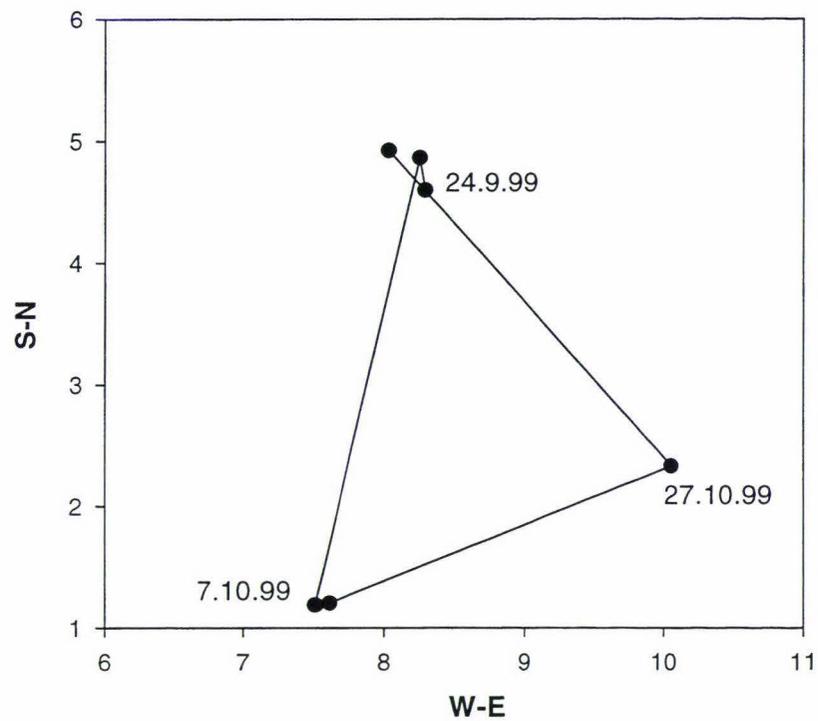
N.B. Species used in the analysis were *Mecodema oconnori* and *Megadromus capito*. 'NS' indicates a non-significant difference.

Appendix 9: Movement patterns of carabid beetles between resting sites at Browns Bush

(a) *Mecodema oconnori* (male)



Map of the movement pattern of a *Mecodema oconnori* male at Browns Bush over 12 weeks (eight sightings). The units on both axes are in metres. The positions plotted were derived from polar co-ordinates. The total distance moved was 16.02 metres, and the minimum distance moved was 2.00 m per week.

(b) *Megadromus capito* (male)

Map of the movement pattern of a *Megadromus capito* male at Browns Bush over five weeks (six sightings). The units on both axes are in metres. The positions plotted were derived from polar co-ordinates. The total distance moved was 10.10 metres, and the minimum distance moved was 1.68 m per week.

Appendix 10: SAS program used for RM-ANOVA of carabid abundance at Lake Papaitonga Scenic Reserve

Repeated measures analysis of variance to test for a difference between the total numbers of carabids caught in the four sampling areas over six months.

```

data xtrap;
input area $ Oct Nov Dec Jan Feb Mar;
cards;
A           8      16      9      25      15      14
B          30      11      10      10      17      8
C          55      22      22      51      50      12
D          55      29      16      54      37      10
;

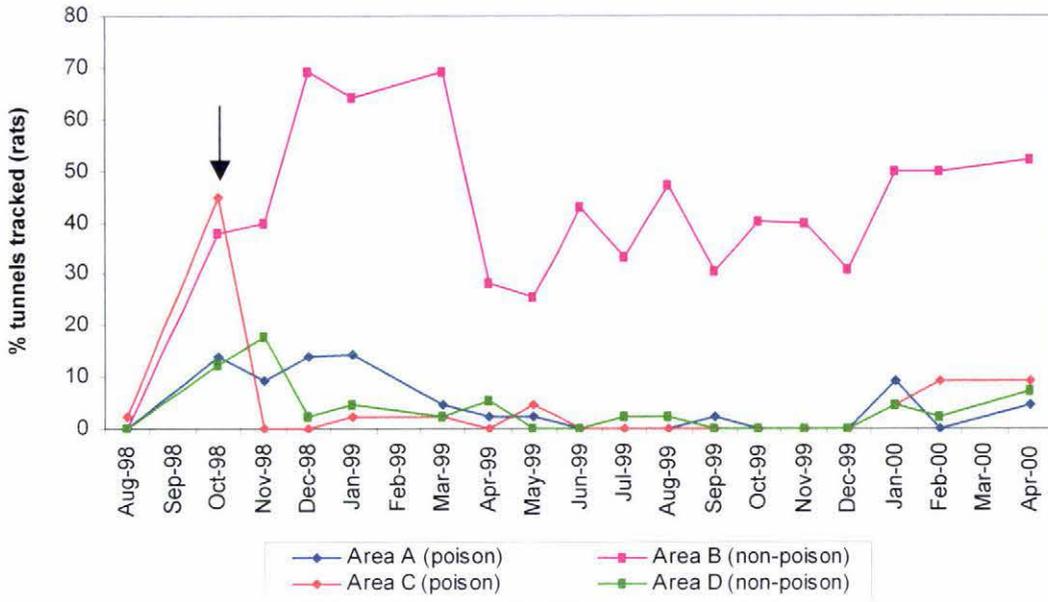
proc glm data=xtrap;
class area;
model Oct Nov Dec Jan Feb Mar = area /ssl;
LSMEANS area/PDIFF;
MEANS area/TUKEY;
repeated month 6 profile/printe summary;
output out=res predicted=p1 p2 p3 p4 p5 p6 residual=r1 r2 r3 r4 r5 r6;
run;

proc plot data=res;
plot (r1-r6):(p1-p6);
run;

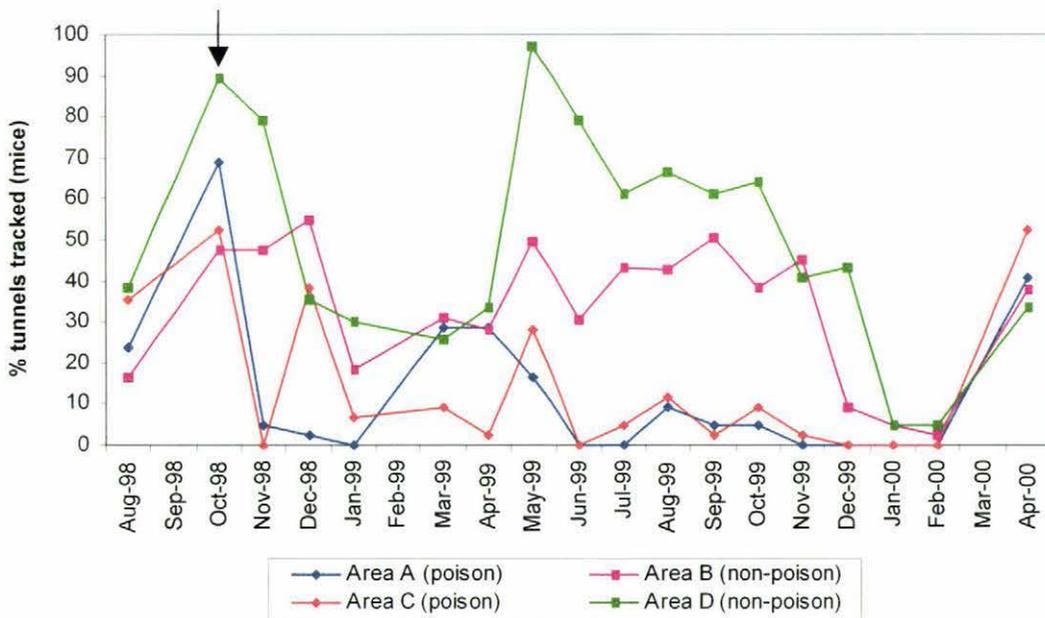
```

Appendix 11: Tracking tunnel rates in each sampling area at Lake Papaitonga Scenic Reserve (August 1998 – April 2000)

(a) Rats



(b) Mice



Monthly tracking tunnel rates in each sampling area at Lake Papaitonga Scenic Reserve (August 1998 – April 2000). Poisoned areas = A and C, non-poisoned areas = B and D. Arrow indicates when poisoning began (October 1998). (Data reproduced with permission from Bennett 2001, unpublished thesis).

Appendix 12: Detrended correspondence analysis (DECORANA) of the carabid assemblages in each sampling area at Lake Papaitonga Scenic Reserve

(a) Pearson and Kendall correlations with the first two ordination axes: carabid species (n = 109).

Carabid species	Axis 1 (18.0%)	Axis 2 (28.7%)
<i>Ctenognathus bidens</i>	0.158	-0.102
<i>Ctenognathus</i> sp.	0.126	-0.134
<i>Harpalus affinis</i>	0.078	0.025
<i>Holcaspis mucronata</i>	0.144	0.409
<i>Holcaspis sinuiventris</i>	-0.040	0.152
<i>Mecodema oconnori</i>	-0.610	-0.276
<i>Megadromus capito</i>	0.545	-0.584
<i>Megadromus vigil</i>	0.090	0.154
<i>Molopsida antarctica</i>	-0.099	0.191
<i>Molopsida strenua</i>	0.010	0.124
<i>Oopterus</i> sp.	-0.090	0.207
<i>Plocamostethus planiusculus</i>	0.025	0.103
<i>Selenochilus</i> sp.	-0.344	-0.237
<i>Zolus</i> sp.	0.207	-0.020
Larvae	-0.197	-0.682

(b) Pearson and Kendall correlations with the first two ordination axes: environmental variables (n = 109).

Environmental variable	Axis 1 (18.0%)	Axis 2 (28.7%)
Leaf litter depth	0.064	-0.146
Soil depth	-0.246	-0.332
Canopy cover (%)	0.087	-0.145
Plant ground cover (%)	0.171	0.345
Log (%)	0.094	-0.003
<i>Alectryon excelsus</i>	0.121	0.335
<i>Blechnum filiforme</i>	-0.083	0.334
<i>Dacrycarpus dacrydioides</i>	0.002	0.326
<i>Hedycarya arborea</i>	0.222	0.020

Appendix 13: Detrended correspondence analysis of the other invertebrates in each sampling area at Lake Papaitonga Scenic Reserve

(a) Pearson and Kendall correlations with the first two ordination axes:
other invertebrates (n = 112).

Order	Axis 1 (32.6%)	Axis 2 (1.8%)
Acarina *	-0.206	-0.067
Amphipoda	-0.060	0.725
Araneida *	0.007	-0.264
Archaeognatha	-0.106	0.427
Blattodea	-0.110	0.001
Chilopoda *	0.136	-0.109
Coleoptera	0.090	0.382
Collembola	-0.699	0.407
Diplura	0.154	-0.113
Diplopoda *	0.018	0.376
Diptera	0.364	-0.073
Gastropoda (snails) *	-0.038	-0.210
Hemiptera	-0.062	0.120
Hymenoptera	0.028	0.025
Isopoda	0.040	0.056
Lepidoptera	-0.164	0.129
Neuroptera	-0.039	-0.028
Oligochaeta *	0.015	-0.016
Opiliones *	-0.042	0.072
Orthoptera	0.025	0.233
Phasmatodea	0.178	-0.219
Pseudoscorpiones *	-0.021	0.085
Psocoptera	0.056	0.286
Siphonaptera	-0.091	-0.029
Thysanoptera	0.157	-0.171
LARVAE/PUPAE *	0.184	-0.455

* indicates taxonomic grouping other than Order.

(b) Pearson and Kendall correlations with the first two ordination axes:
environmental variables (n = 112).

Environmental variable	Axis 1 (32.6%)	Axis 2 (1.8%)
Leaf litter depth	-0.056	0.121
Soil depth	0.014	0.420
Canopy cover (%)	-0.012	-0.038
Plant ground cover (%)	-0.061	-0.131
Log (%)	-0.236	0.060
<i>Alectryon excelsus</i>	-0.235	-0.175
<i>Asplenium bulbiferum</i>	0.241	-0.290

Appendix 14: Correlations between the environmental variables and the number of carabids caught in pitfall traps at Lake Papaitonga Scenic Reserve

Pearson correlations between the environmental variables and the abundance of carabids (October 1999 – March 2000). Significance level: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, 'NS' = non-significant ($p > 0.05$).

	Soil depth (cm)		Leaf litter depth (cm)		Vascular plant ground cover (%)		Canopy cover (%)	
TOTAL Carabidae	0.393	***	0.248	*	-0.189	NS	0.011	NS
<i>Megadromus capito</i>	0.344	**	0.299	*	-0.090	NS	0.031	NS
<i>Mecodema oconnori</i>	0.252	NS	-0.014	NS	-0.224	NS	0.003	NS
<i>Holcaspis mucronata</i>	-0.190	NS	0.021	NS	0.232	NS	0.019	NS
<i>Holcaspis sinuiventris</i>	0.045	NS	0.059	NS	0.009	NS	-0.202	NS
<i>Selenochilus</i> sp.	0.181	NS	-0.056	NS	-0.192	NS	-0.059	NS
Total larvae	0.290	*	0.165	NS	-0.227	NS	0.067	NS

GLOSSARY

aestivation – a period of dormancy or *diapause* in summer

brachypterous – with short wings that do not cover the abdomen, unable to fly

campodeiform – a type of larvae with a prognathus head, long, well-developed legs, and long, unisegmented or multisegmented *urogomphi*

chorion – the outer shell of an arthropod egg

corpora luteum (pl. *corpus luteum*) – the distinctive ring of debris left in a vacated ovarian follicle after an egg has been laid by a female

diapause – a period of arrested development and reduced metabolic rate, during which growth, differentiation, and metamorphosis cease; a period of dormancy not immediately referable to adverse environmental conditions

elytron (pl. *elytra*) – a thickened, leathery front wing, serving as a covering for the hind wings.

emergence – the act of the adult insect leaving the pupal case or the last nymphal skin

epigean – living on the soil surface

eurytopic – living in a wide range of habitats

fossorial – living underground

gravid – carrying eggs

holometabolous – with complete metamorphosis, in which the larva is very different from the adult and transforms dramatically by means of a pupal stage.

hygrophilous – preferring wet soils

instar – the insect between successive moults, the first instar being between hatching and the first moult

macropterous – possess fully functional wings (as opposed to *brachypterous*)

mesophilous – preferring moist soils

oviposit – to lay or deposit eggs

pronotum – the dorsal sclerite of the prothorax

pupa – (pl. *pupae*) the stage between the larva and adult in insects with complete metamorphosis, a non-feeding and usually inactive stage

sclerite – a hardened body wall plate bounded by sutures or membranous areas

sclerotized – hardened

silvicolous – forest-dwelling

stenotypic – having a narrow habitat preference

tarsus (pl. *tarsi*) – the leg segment immediately beyond the tibia, sometimes consisting of one or more “segments” or subdivisions (tarsomeres).

teneral – recently pupated individual with a pale, soft exoskeleton (also called ‘callow’)

tribe – a subdivision of a sub-family, containing a group of related genera (end in *-ini*).

seta – (pl. *setae*) a hair or bristle

urogomphi – paired processes found on the ninth abdominal segment of coleopteran larvae

NB. Definitions were taken from Borror, Triplehorn and Johnson (1989), and Klimaszewski and Watt (1997).