THE ECOLOGY AND ECOPHYSIOLOGY OF MARION ISLAND HOUSE MICE, MUS MUSCULUS L.

by

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Submitted in fulfillment of the requirements for the degree of

Doctor of Philosophy

in the Faculty of Science

Department of Zoology and Entomology

University of the Orange Free State

Bloemfontein

1999

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ACKNOWLEDGEMENTS / BEDANKINGS

Professor V.R. Smith initiated this study and enabled me to spent 13^{+} months on Marion Island to do most of the field work for this study. I am indebted to him for this big opportunity, his trust in me, his supervision of my work and the amount and quality of time and energy spent on both me and the project.

Ek is ook baie dank verskuldig aan professor O.B. Kok vir sy vertroue, aanmoediging, tyd en besondere leiding tydens hierdie projek.

I thank Bruce Blake for his valuable logistical help and discussions on this project, as well as his support as a friend over the past five years (especially during the 13 months on Marion Island where we shared the laboratory).

Ek bedank elke lid van die Marion 49-ekspedisie. Hulle belangstelling in die projek en aanvaarding van my as persoon was 'n besondere bron van inspirasie. Elkeen het bygedra tot 'n verrykende en onvergeetlike avontuur. Spesiale dank aan veral Peter Lafite, Andrew Cunningham, C.T. van der Merwe en Tojan Winterbach wat by tye gehelp het met die uitsit van valle of nagwerk onder soms ongure toestande, en Tewis Nel, Michael Putter, Tojan Winterbach en Kevin Language vir meer tegniese hulp.

My sincere thanks to everybody who have made a contribution towards this work in the form of discussions and questions, especially Steven Chown, Marianna Smith, John Cooper and Niek Gremmen.

A special word of thanks also to Joan Walker for all the time spent on correcting my grammar, but also for her encouragement.

Opregte dank ook aan diegene wat raad en hulp verleen het met betrekking tot die tegniese deel van die projek. Hier dink ek aan o.a. dr. Jakobus Swart, dr. Martin van Zyl, mnr. Johan Hugo, mev. Groenewald, Yvonne Attwood en die personeel van Instrumentasie en Elektronika aan die Universiteit van die Oranje Vrystaat.

Finansiële en logistiese steun vir die Marioneiland Biologiese Navorsing is gemaak deur die Suid-Afrikaanse Departement van Omgewingsake en Toerisme, onder beskerming van die Suid-Afrikaanse Komitee vir Antarktiese Navorsing (SACAR), sonder wie die projek nie moontlik sou wees nie.

Dr. C.M. Engelbrecht en die Raad van die Nasionale Museum word bedank vir hul belangstelling en logistiese steun. Hiersonder sou die verwerking en opskryf van die resultate tot 'n groot mate onmoontlik gewees het. 'n Baie spesiale dank aan dr. C.D. Lynch, Johan Eksteen, Isak Sekhuni, Jacob Senoge en verskeie ander personeellede vir hul belangstelling, aanmoediging en hulp.

Laastens, dank aan my ouers en familie vir die besonderse ondersteuning gedurende hierdie studie. Spesiale dank aan Marinda vir haar liefde, geduld en vertroue.

Ek dank God vir hierdie fantastiese geleentheid en die persone en ondervindings wat my pad gekruis het gedurende die tyd dat hierdie studie aan die gang was. Alle eer aan Hom.

CHAPTER 1: INTRODUCTION

1.1 BACKGROUND AND MOTIVATION FOR THIS STUDY – THE HOUSE MOUSE CONUNDRUM ON MARION ISLAND

The highly opportunistic behaviour and reproductive adaptability of house mice *Mus musculus* enable them to colonize a wide variety of habitats, from cold stores at -20°C (Laurie 1946) to hot, semi-arid areas (Newsome & Corbett 1978) and deserts (Bronson 1979). They have colonized at least eight sub-Antarctic islands of which Marion Island (46°54'S, 37°45'E), where they have been present for the last *c.* 170 years (Watkins & Cooper 1986), is one.

Berry et al. (1978) found the *Mus musculus* population on the island to be endocyclic, suggesting that temperature-wise it exists close to its physiological limits. They pointed out that temperatures on the island rarely rise above the lower limit where reproduction stops in mice from less extreme climates. Bonner (1984) also considered house mice on sub-Antarctic islands to be living close to the limits of their ecological tolerance. Gleeson (1981) proposed that house mice have become firmly entrenched in the island's ecosystem and have successfully adapted physiologically to cope with the environmental conditions there. He was the first to show that the island's mice, previously thought to be mainly or even exclusively herbivores, feed predominantly on soil macroinvertebrates such as insects, snails and spiders.

An introduced small mammal predator can be expected to have profound effects on an ecosystem that has evolved in the absence of terrestrial predators larger than a spider. Gleeson & Van Rensburg (1982) and Crafford (1990a) proposed that on the island a state of dynamic, or even stable, ecological equilibrium exists between the mice and their invertebrate prey. Matthewson (1993) stated that, although the initial effects of a predator on an ecosystem that evolved in the virtual absence of predators might initially be large, mice now have little effect on the functioning of the island's ecosystem. He pointed out that the continued existence of plant species and invertebrates consumed by mice on Marion Island despite over 170 years granivory and predation supports the suggestion that a state of equilibrium exists between mice and their food sources. This ignores the fact that only since the early 1970s has there been a reasonably accurate inventory of extant plant and invertebrate species for the island – there is

before that. Certainly, there has been a significant change in the composition of the soil macroinvertebrate populations, and size class distributions of particular invertebrate species, since the 1970s (Chown and Smith 1993), and also there are very distinct differences in both these parameters between Marion Island and nearby Prince Edward Island where mice do not occur (Crafford and Scholtz 1987).

The first indication that mice might be seriously impacting on the ecology of Marion Island came from a study by Rowe-Rowe et al. (1989) who, from double-labelled water measurements of mouse energy metabolism, invertebrate energy contents and mean mouse densities, calculated that mice (at a mean annual density of 37 ha^{-1} for the lowland area as a whole; Gleeson 1981) consumed 39.4 kg ha^{-1} of invertebrates annually (all biomass and consumption rate values given in this chapter are on a dry mass basis). Moth (*Pringleophaga marioni*) larvae, weevil larvae and adults, and spiders made up 70% of the mouse diet and, across habitats, the combined mean annual biomass of these prey items was 13.2 kg ha^{-1} and mice removed 0.7% of this biomass per day, equivalent to 33.2 kg ha^{-1}, or 2½ times the biomass, per year. In section 2.5 it is shown that these invertebrates are cardinal agents determining ecosystem structure and functioning on the island, mainly because they feed predominantly on plant litter and the balance between litter accumulation and disappearance is an important factor driving plant community succession on the island and the rate of nutrient release from litter is a major limiting factor in primary production.

Using the same data as Rowe-Rowe et al. (1989), but considering only moth larvae and the rates at which they consume plant litter (60% of their dry mass per day), Crafford (1990) estimated that in 1989, in the absence of mice, moth larvae consumed about 2 500 kg litter ha^{-1} $year^{-1}$, but that mouse predation on larvae decreased this to 1 500 kg ha^{-1} $year^{-1}$.

Matthewson (1993) disputed this and, using the same data as did Rowe-Rowe (1989) and Crafford (1990), calculated that the decrease in litter consumption caused by mouse predation on moth larvae was about two orders of magnitude lower than Crafford's estimate. However, his calculation (37 mice ha^{-1} consume 37 x 1.75 g larvae = 65 g larvae *in one day*; these larvae would have consumed 60% of their mass in litter per day for 365 days, i.e. 14.2 kg per year) is flawed since it considers the effect of only one day's removal of larvae by mice. From it he questioned whether a lowering of litter consumption of 14.2 kg ha^{-1} per year, from a

mouse-free 14 500 kg ha^{-1} per year (Crafford's value) is of any consequence. Matthewson (1993) also used site-specific data in similar calculations to show that in two habitats mouse predation decreased litter consumption by moth larvae by less than 1% of what it would be in the absence of predation In the third habitat consumption was depressed by 31%, but he indicated that this value was too high "due to no habitat specific data on the percentage contribution of *P. marioni* larvae to the diet of the mice being available". From these results Matthewson concluded that the effect of mice on ecosystem functioning through their influence on litter processing by macroinvertebrates "may be less than previously expected".

Although Crafford (1990) did not show his calculations, he did give the values he used for the various variables (annual mean density of mice and percentage contribution of moth larvae to their diet, average daily food consumption by mice and litter consumption by larvae) and his estimate that mice decrease litter consumption by 1 000 kg ha^{-1} seems plausible, even a little conservative. A very simplistic computation using the same average values of the variables used by Rowe-Rowe et al. (1989) and Crafford (1990) is as follows: 37 mice each consumed 3.5 g food per day, 50% of this was moth larvae, so the average daily removal of moth larvae over the year was 65 g ha^{-1}, an annual removal of 23.6 kg larvae ha^{-1}. In essence, because mean removal rates are being considered, this is the biomass of larvae that mice would have caused to be absent from the site for ½ of the year (say 180 days), during which time they would have consumed plant litter at a rate of 60% of their dry mass per day, so they would have consumed 23.6 x 0.6 x 180 = *c.* 2500 kg litter ha^{-1}.

Whichever value one accepts as indicative of the impact of mice on litter consumption, both are high, especially considering that it refers to the effects of predation on moth larvae only - most of the mouse's other macroinvertebrate prey species are also detritivores. But even 1000 kg litter ha^{-1} is 7% of the average annual litter input on the island's lowland area (calculated from primary production values for the dominant lowland vegetation types given in Smith 1987b,c).

The results of all the studies carried out so far agree that the amount of macroinvertebrates consumed by mice is high when expressed as a percentage of the mean annual invertebrate biomass. Most of the estimates are between 0.5 and 1% per day and considering that some of the species have long lifecycles (the moth's larval stage exceeds two years, Crafford et al.

(1986) these are high rates of removal and imply that appreciable production:biomass ratios are needed to maintain population levels.

The only land bird on the island, the Lesser Sheathbill *Chionis minor*, feeds almost solely on terrestrial macroinvertebrates in winter. Kelp gulls also feed occasionally on them. The combined daily consumption by these two birds of moth larvae, spiders, weevil larvae and adults is 16 g dry mass ha^{-1} per day (Burger 1978), less than 20% of the daily consumption by mice (Rowe-Rowe 1989). Matthewson (1993) estimated that at three coastal habitats in 1991/92 mice consumed between 4 and 10 times more macroinvertebrates than did sheathbills or kelp gulls. Smith and Steenkamp (1990) proposed that mice pose a distinct threat to the sheathbill population and recent results (Huyser et al., in press) show that the sheathbill population has declined drastically on Marion Island since the mid 1970s. House mice are implicated as having caused this decline from the fact that, in the same period, sheathbill numbers on Prince Edward Island remained constant.

Mice are also having a marked impact on some endemic plant species through seed consumption. Distributions, and in many areas densities, of *Acaena magellanica*, *Pringlea antiscorbutica* and *Uncinia compacta* on Marion Island have declined since the 1970s (Steenkamp 1991). Compared with mouse-free Prince Edward Island, the density of *Uncinia compacta*, especially, is much lower on Marion Island. Mice remove and eat virtually all the seed produced by this plant (Chown and Smith 1993).

Skuas, *Catharacta antarctica* are potentially the only predators of mice on the island. They readily take captured mice offered to them at the meteorological station but there is no record of them chasing or capturing mice in the field. After a presence of *c.* 40 years, and an eradication program lasting 19 years, the island was finally rid of feral cats (*Felis catus*) in 1992 (Van Aarde 1996). The influence of the cat population on the island's biota is reviewed in Chapter 2 but none of the studies carried out on either the cats or the mice produced clear evidence as to whether cats had, or did not have, a significant influence on the island's mouse population.

The role of mice in ecosystem functioning under a changing climate at the island is discussed in section 2.5.

1.2 OBJECTIVES OF THE STUDY

This study was carried out on the island from April 1992 to May 1993 and was aimed at he following:

(i) A characterization of the temperature regime experienced by house mice on the island and of their microhabitat.

(ii) An assessment of the mouse's macroinvertebrate prey preference and of the seasonal variations in the availability of the various prey items and in their contribution to the mouse diet.

(iii) An evaluation of the seasonal changes in mouse morphometry and physiology, especially those aspects concerning food assimilation.

CHAPTER 2: THE MARION ISLAND BIOME

2.1 TOPOGRAPHY, GEOLOGY AND PAST HISTORY

Comprehensive accounts of the island's topography, geology and vulcanology are provided by Langenegger & Verwoerd (1971), Verwoerd (1971) and Chevalier (1986) Its glacial and palaeohistory are described by Schalke and Van Zinderen Bakker (1971), Hall (1978) and Scott (1985).

Marion Island and nearby Prince Edward Island are oceanic in every sense: *geographically* because of their remoteness from continents (Africa is 1 800 km to the north and Antarctica 2 300 km to the south), *geologically* because they arose from the sea floor by volcanic processes, and *ecologically* because of the overwhelming climatic and biological influence of the surrounding ocean and because they have never been connected to a continent so their ecosystems and biota have developed in isolation. The two islands are 22 km apart and are thought to have originated at the same time, possibly about ½ million years ago (Verwoerd 1971). Marion Island is 290 km^2 and Prince Edward Island 44 km^2 in area. The nearest other sub-Antarctic islands are the Crozet Island Group, 950 km to the east.

Both islands are quiescent but in 1980 a small eruption occurred and resulted in fresh lava being deposited on at least two small existing areas of Marion Island (Verwoerd et al. 1981).

The islands were formed during two main periods of volcanic activity resulting in distinct lava types.

(i) "Grey lavas": Fine-grained, compact basalts with a grey colour (K-Ar dates between *c.* 276 000 and 100 000 years, McDougall 1971). These lavas have been subjected to glaciation (Hall 1978).

(ii) "Black lavas": Strongly vesicular lavas deposited up to c. 15 000 years ago and have never been glaciated. Marion Island shows a conspicuous radial pattern of grey lava ridges and

plateaux, with the valleys and plains covered by black lava; the result of radial faulting which occurred between the two stages of volcanic activity.

From glacial tills, Hall (1978) concluded that the island has been subjected to three glaciations during the past 300 000 or so years. Other periglacial evidence suggests that temperature dropped by at least 3.5 °C during the glaciations (Hall 1981), supporting conclusions from palynological investigations (Van Zinderen Bakker 1973) and ocean floor sediment studies carried out near the island (Hays et al. 1976). The glaciers did not completely cover Marion Island and cold-resistant species probably survived the ice ages (Van Zinderen Bakker 1973).

Topographically, Marion Island consists of a central highland plateau about 1 000 m above sea level (highest peak is 1 230 m). The plateau contains no vascular vegetation, only a few species of cushion- and ball-forming moss species and lichens. The sides of the plateau slope down to a well-vegetated coastal plain (< 300 a.s.l.) that is 3-5 km wide on the northern and eastern sides and much narrower on the southern and western sides. Of the total 290 km^2 area about 138 km^2 is below 300 m altitude .

2.2 CLIMATE

Marion Island's climate is dominated by the very pronounced meteorological characteristics of the southern circumpolar oceanic region, namely, an unending succession of extra-tropical cyclones with attendant cloudy skies, abundant precipitation and, above all, strong (predominantly westerly) winds.

A detailed, but now dated, account of the island's climatic regime is provided by Schulze (1971), based on measurements made at the meteorological station, about 10m a.s.l. on the east coast. The only climate information for higher altitudes is that in Blake (1997), for two sites, 550 and 750 m a.s.l. on the islands eastern side. There is no climatic data for the less sheltered southern and western sides of the island.

Based on the data from the meteorological station the following are the main features of the island's climate (values are for the period 1949 to 1997, unless specified otherwise):

(i) Low average annual air temperature (*c.* 5.5°C) with small diurnal (mean <3°C in summer, <2°C in winter) and seasonal (4.3°C) variations. The diurnal temperature range is generally less than 6°C on most days. In every month absolute minimum temperatures are below zero and there are, on average, 16 days with absolute maximum temperatures above 15°C during the year. Absolute extremes measured at the weather station during the period 1949-1960 were -6.8°C and 22.3°C. Mean "grass-minimum" temperatures, measured 2.5 cm above the ground, for the period 1953 to 1963, varied from -0.7°C (September) to 3.5°C (February), with an annual mean of 1.2°C.

(ii) Very high precipitation (mean = 2 361 mm per annum), mainly in the form of rain and evenly distributed throughout the year, although the late winter months (August - October) are marginally drier. Snow may occur in any month but is most frequent in winter. On average, hail occurs on 15 days per year, and fog 45 days per year.

(iii) A high degree of cloudiness and hence low incidence of radiation. Annual hours of sunshine is only 30% of the maximum possible; yearly mean radiation receipt at surface *c.* 3.5 kW m^{-2} day^{-1}, compared with *c.* 7 kW m^{-2} day^{-1} at the top of the atmosphere.

(iv) Constantly high relative humidity (annual mean screen value 83%, range 4%, for 1949-1960).

(v) Strong, predominantly westerly wind. On average, gale force winds (>55 km/h) blow for more than an hour on 107 days per year.

At present, Marion is 2° of latitude north of the Polar Frontal Zone and is, with the Crozet island group the most "temperate" of the sub-Antarctic islands.

According to the climate classification system of Walter & Lieth (1967), Marion Island climate can be classified as type VIII-IX (oceanic), i.e. an extremely oceanic climate with colder

summers than the cold temperate climate of type VIII, and also lacking the cold winters. The island's climate is considerably warmer than type IX, the Arctic climate type. By Troll's climate classification scheme (Troll 1966), which relies on what he considered to be biologically relevant indices, the island is in Zone 14, the zone of highly oceanic, subpolar climates with moderately cold winters (coldest month - 8°C to + 2°C), poor in snow and with cool summers (warmest month + 5°C to + 12°C, annual fluctuation < 13°C). In the southern hemisphere this climate occurs in a belt between *c.*50° and 60°S and incorporates the sub-Antarctic islands, Falkland Islands, New Zealand shelf islands and some of the most northerly maritime Antarctic islands. In the northern hemisphere it is restricted mainly to a few oceanic areas such as the Aleutian Islands and southern Iceland.

Between 1949 and 1968 annual mean surface air temperature was fairly constant, or at least did not change in a consistent direction. Since then it has increased significantly, on average by $0.062^{o}C\ year^{-1}$, so that the total increase by 1997 was $1.8^{o}C$ (Figure 2.1a). This increase in mean air temperature was strongly associated with corresponding changes in sea surface temperature but only weakly, or not at all, with variations in radiation (Smith & Steenkamp 1990). It was also associated with decreases in total annual precipitation (Figure 2.1b). Smith & Steenkamp 1990) implicate changing atmospheric and oceanic circulation patterns as the causes of all of these changes. Similar warming has been shown at all other sub-Antarctic islands for which there are climatic records (Allison and Keague 1986, Adamson et al. 1988) and has also occurred at some Antarctic islands (Jacka et al. 1984, Lewis Smith 1990) and over the past ten years there has been an increasing interest in effects climate change on the biota and ecosystems of the subpolar region of the southern hemisphere (SCAR 1989, Smith 1993, Chown and Smith 1993, Frenot et al. 1993, Kennedy 1995). Some ecological implications of a changing climate at Marion Island are discussed in section 2.5.

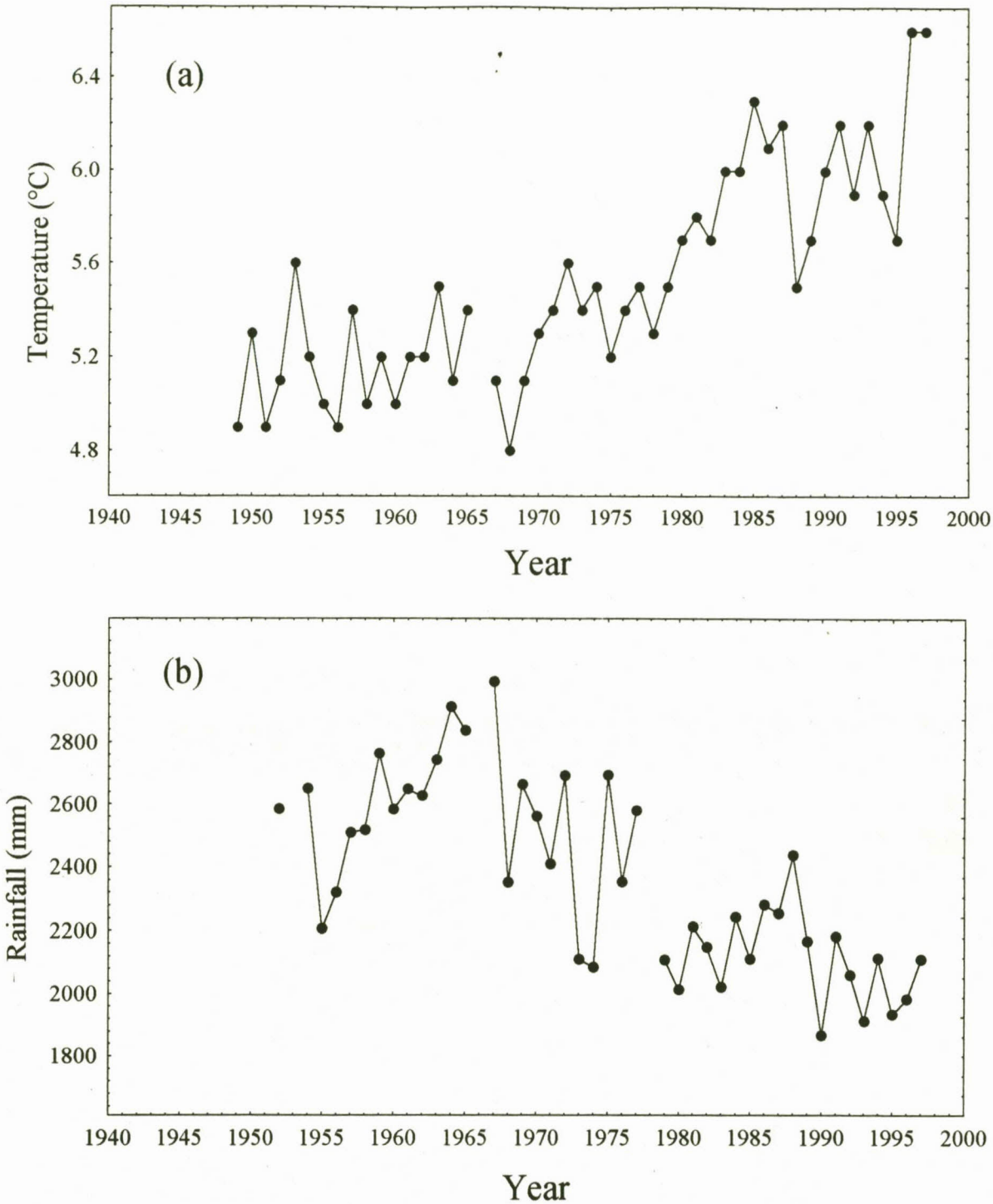

Figure 2.1. Mean annual surface air temperatures and rainfall at Marion Island (data supplied by South African Weather Bureau).

2.3 VEGETATION AND FLORA

2.3.1 Indigenous flora

Comprehensive descriptions of the plant communities and the factors that determine their distribution are provided in Huntley (1971) and Gremmen (1981). There are only 24 native vascular plant species, some of which have a wide ecological amplitude and are found in a range of habitats. Mosses (72 species are listed but about 100 species actually occur; Smith pers. comm.) and liverworts (35 species) are an important component of the vegetation. The lichen flora is poorly known; approximately 100 species have been recorded. They are mainly epilithic crustose forms and are found at all altitudes. However, there are no lichen-dominated vegetation formations similar to those occurring in sub-Arctic tundras.

2.3.2 Alien flora

Eighteen species of alien vascular plants (inadvertently introduced by man) have been recorded on Marion Island (Gremmen and Smith 1999). Eleven have become naturalized and many of these are increasing in numbers and becoming more widespread on the island. Six species often reach absolute dominance in the invaded areas. One of these, *Agrostis stolonifera* was introduced at the meteorological station in the 1960s and is now particularly widespread over about $^1/_3$ of the islands coastal plain. *A. stolonifera* severely reduces the biodiversity of areas it invades, not only of plants but also of soil fauna (Gremmen et al. 1998). Three of the alien plant species were eradicated when they were discovered. In this decade four new introductions have occurred, three involving species that had been introduced in the past but had disappeared or been eradicated.

In addition to these 18 species, live trees from South Africa, and various types of vegetable, have been planted in and around the meteorolgical station; the trees in 1950 and 1951 and vegetables at various times up to 1972. None survived for very long.

2.3.3 Vegetation

From some distance, Marion Island has a rather bleak, monotonous appearance due to the absence of any trees, shrubs, or other tall growing plants. Closer inspection, however, shows that the vegetation is neither sparse nor uniform. Despite the paucity of species, and the low-growing stature of the plants, much of the low altitude vegetation is quite dense and supports a higher phytomass than many temperate or tropical areas (Smith 1976a).

Phytosociologically, 41 plant communities have been distinguished at the association or subassociation level (Gremmen 1981). Most prominent factors affecting the distribution and occurrence of these communities are the soil water regime (especially water content and lateral subsurface water movement), the influence of salt spray, and trampling and manuring by seabirds and seals. The main patterns in the island's vegetation are represented by wet-dry and by animal influenced-noninfluenced gradients. A change from organic to mineral soil parallels the wet-dry gradient, which is also associated with a trend from sheltered to strongly exposed conditions. Together, these components account for 65% of the variation in plant species composition and cover (Smith and Steyn 1982).

Gremmen (1981) grouped the 41 plant communities into six community complexes, based mainly on their species composition, but also considering structural and ecological factors.

(i) The *Crassula moschata* (salt-spray) complex. Communities of this complex are found only at coastal sites subjected to salt-spray and inundation by waves.

(ii) The *Callitriche antarctica* - *Poa cookii* (biotic) complex. Consists of several communities, most of which occur on the coastal zone and all are influenced by trampling and manuring by animals.

(iii) The *Acaena magellanica* - *Brachythecium* (drainage line) complex. Communities of this group occur at sites having a more or less strong lateral movement through the soil or at the soil surface, such as in springs, flushes and drainage lines.

(iv) The *Juncus scheuchzerioides* - *Blepharidophyllum densifolium* (mire and bog) complex. Communities of this group form the vegetation of the island's mires and bogs and are dominated by bryophytes and graminoid plants.

(v) The *Blechnum penna-marina* (slope or fernbrake) complex. Communities of this complex dominate the vegetation of well-drained lowland slopes and consist of carpets of the fern *B. penna-marina.*

(vi) The *Andreaea* - *Racomitrium crispulum* (feldmark) complex. Cushion-forming species dominate this complex, which occurs on rocky areas exposed to strong winds, and is the dominant vegetation above 300 m altitude. Feldmark communities also occur at lower altitudes where they exhibit up to 60% aerial vegetation covers.

2.4 FAUNA

2.4.1 Indigenous fauna

No indigenous land mammals occur on Marion Island, but the island's terrestrial ecosystem is extensively influenced by the activities of marine mammals and birds during their terrestrial phases of breeding and moulting. Three seal species (the southern elephant seal *Mirounga leonina* and the fur seals *Arctocephalus tropicalis* and *A. gazella*) are found on the island.

The total breeding avifauna of Marion Island has been put at more than 2 million pairs, belonging to 29 species (Cooper & Brown 1990; Siegfried 1978, 1982). These birds, chiefly populations of four penguin and 18 Procellariiformes (albatrosses and smaller petrels) species, markedly influence the structure and functioning of the terrestrial ecosystem by transferring energy and nutrients from the surrounding ocean to the island, and/or by causing erosion through trampling and burrowing (Frost 1979). Total annual guano production by populations of 14 surface nesting bird species amounts to about 4 000 tonnes (dry mass) on the coastal plain, of which pengiuns contribute 98% (Siegfried 1978). Nutrient input in inland areas, by populations of the 12 small burrowing petrel and prion species (Procellariidae and

Pelecanoididae) has not been quantified, but may be substantial. Only the lesser sheathbill *Chionis minor*, relies entirely on terrestrial food sources, feeding on soil macroinvertebrates. Kelp gulls *Larus dominicanus* and Kerguelen terns *Sterna virgata* also forage for soil invertebrates but get most of their food in the surrounding ocean (Burger 1978).

The terrestrial macroinvertebrate fauna of Marion Island is species-poor. There are 18 indigenous insect species (nine beetles, five flies and three moths), four spiders and one land snail (Hänel and Chown 1998). There are also at least three earthworm species. The paucity of species is offset in some lowland habitats by high macroinvertebrate densities.

The status of meso-and microinvertebrates is currently largely unknown but species numbers might be appreciable – for instance there are sixty mite species (Hänel and Chown 1998).

2.4.2 Alien fauna

Descriptions of the status of alien vertebrate species on Marion Island may be found in Watkins & Cooper (1986) and of the alien macroinvertebrates in Hänel and Chown (1998).

The introduced house mouse (*Mus musculus*) is currently the only land mammal on the island. Aspects of their biology are the subject of this thesis and some results of previous house mouse studies at the island were reviewed in Chapter 1.

Domestic cats (*Felis catus*) were introduced to the island in 1949 to control the house mice at the meteorological station. They quickly turned feral, and by 1975 a population of about 2 000 cats posed a real threat to the avifauna, especially small burrowing species (Van Aarde 1979, 1980, Van Aarde & Skinner 1981, Bloomer & Bester 1990). At least one of the cats' prey species (the Common Diving Petrel *Pelecanoides urinatrix*) became locally extinct (Watkins & Cooper 1986). The Grey Petrel also was not seen at the island for several years when the cat population was high. Since burrowing birds are an important source of nutrients to the island's ecosystem, especially in areas away from the coast where other forms of nutrient input are negligible (Smith 1976b), cat predation might be expected to have had a detrimental influence

on ecosystem functioning . At the height of their population density in the 1970s (about 2100 cats on the island) they would have removed 450 000 burrowing birds to meet their minimum energy requirements (Van Aarde and Skinner 1981). This would have lowered the annual input of guano by *c.* 9 500 kg (dry mass), assuming that burrowing species spend an average of 100 days on the island (Crafford and Scholtz 1987). Cats were eradicated in 1992 (Van Aarde et al. 1996). It is not known what effect this has had, or will have, on the island's house mouse population.

Other vertebrates introduced to the island in the past include two trout species, sheep, goats, pigs, a donkey, a dog, domestic fowls, geese, and two parrots (Watkins & Cooper 1986). None of these are currently found there.

Twelve alien insect species are regarded as having become naturalized on the island and a further 15 have been found intermittently, or recorded only once, and are regarded as "transient aliens" (Hänel and Chown 1998). A slug, *Deroceras caruanae* was introduced to the island in the mid to late 1960s and has since extremely successfully invaded a variety of habitats (Smith 1991).

Smith and Steenkamp (1990) argued that an ameliorating climate will be conducive to more alien invertebrates being able establish themselves on the island, and that changing atmospheric circulation patterns associated with climate change might provide opportunities for new organisms to colonize the island. This, along with escalating human activity could greatly increase colonization by cosmopolitan herbivorous insects with a good dispersal ability (Chown and Language 1994, Chown et al. 1998). Similar concerns have been made for the Antarctic region as a whole (Kennedy 1995). Certainly, on Marion Island this seems to be becoming realized – a substantial proportion of the alien insect species on the island were first recorded in the last ten years.

2.5 ECOSYSTEM FUNCTIONING

Annual primary production on Marion Island is high since the hyperoceanic climate (no very cold or arid periods) allows for a long growing season (Smith 1987b,c). Unlike most vascular plants in northern hemisphere tundra areas, the island's plants are not particularly efficient in conserving nutrients through re-allocation from old or dying tissue, so a considerable amount of "new" nutrients is required to support the high annual production, in fact, primary production is closely coupled to soil nutrient status on the island (Smith 1988).

Although seabird and seal manuring is an important source of nutrients at some (mainly shore zone) areas, most plant communities are not affected by this, and pools of available nutrients are small, even by "tundra" standards – for instance the pools of plant-available nitrogen in the island's mires are amongst the lowest found anywhere in the world (Smith 1988). Other forms of nutrient input to these communities, such as through precipitation, biological fixation or weathering of parent rock, supply <1% of the vegetation's annual requirements (Smith 1988). Increasing atmospheric CO_2 concentrations and ameliorating temperatures might lead to an even higher primary production and greater requirement for nutrients.

Other than the introduced house mouse there are no macroherbivores and even insect herbivory seems to play a minor role on the island. For instance, Crafford et al. (1986) estimated that insects consume only 3.5% of the aboveground net primary production. Almost all of the energy and nutrients captured by the vegetation thus enters a detritus, rather than grazing, chain (Smith 1977) and nutrient mineralization during decomposition is an important factor limiting uptake of nutrients by, and hence productivity of, the vegetation. However, rates of nutrient release mediated by microorganisms alone are not sufficient to account for even a fraction of the vegetation's annual requirements since microbial decomposition processes on the island are restrained by low temperature and, especially, by excessive soil moisture contents. Soil macroinvertebrates feed on litter and, through excreting the nutrients, as well as by making the egested portion of the litter that they eat more amenable to decomposition by microorganisms, are the main mediators of nutrient mineralization on the island (Smith and Steenkamp 1992a,b)

Smith and Steenkamp (1990) proposed scenarios of changes in ecosystem functioning caused by climate change that implicated mice as cardinal agents in the changes. From photosynthetic measurements made at the island and considerations from studies made on northern hemisphere tundra plants they proposed that a doubling of atmospheric CO_2 concentrations coupled with a 2°C rise in temperature will allow between 30% and 50% higher assimilation rates than in the 1980s and potentially lead to a higher primary production and a greater requirement for nutrients. Increasing temperature *per se* will not significantly enhance rates of nutrient release mediated by microorganisms alone, since microbial decomposition processes on the island, although temperature sensitive, are overwhelmingly limited by excessive soil moisture contents (Smith et al. 1993). For instance, a decrease in precipitation sufficient to halve the moisture contents of the mire peats would cause a 5 to 11-fold increase in decomposition rate, with concomitant increases in rates of nutrient release. In any event, the effects of changing temperature and moisture levels on microbially-mediated nutrient mineralization will be small compared with the influence of increased temperature on the activities of soil macroinvertebrates. Crafford (1990b) showed that the rate of feeding on litter by the macroinvertebrates increases markedly with temperature, so nutrient release should increase under climatic warming. However, Smith and Steenkamp (1990) suggested that warming will also be associated with increasing mouse numbers and predation on detritivorous macroinvertebrates, and proposed that this will exacerbate nutrient limitation on primary production, lead to an imbalance between production and decomposition and change rates of peat accumulation and patterns of vegetation succession on the island.

The scenarios proposed by Smith and Steenkamp (1990) led to the initiation of biological studies directed at identifying and quantifying changes in ecosystem structure and function on Marion Island; one of these studies was the project reported on in this thesis.

CHAPTER 3: THE MICROENVIRONMENT OF HOUSE MICE AT MARION ISLAND

3.1 INTRODUCTION

House mice occur over much of Marion Island; they have been trapped up to about 1000 m altitude and in all of the island's plant community complexes. They are increasingly impacting on the island's ecosystem through granivory and by predating on soil macroinvertebrates (Rowe-Rowe et al. 1989, Chown and Smith 1993). The latter, especially, affects ecosystem functioning since macroinvertebrates are responsible for the bulk of energy flow and nutrient cycling on the island (Crafford 1990a, Smith and Steenkamp 1992). Despite their ecological importance, little attention has been paid to the habitat preferences of the house mice at the island, or of the microenvironment they experience – that at the ground surface, and just under it in burrows.

Two major investigations of the population biology of the island's house mouse population concluded that mouse density at a particular site is affected by the availability of food and "refuges" (Gleeson 1981, Matthewson et al. 1994). The nature of refuges was not defined but it seems that they included burrows, aboveground shelters and tunnels made when the mice forage for soil invertebrates. The numbers of refuges were determined for some of the island's vegetation types but no attempt was made to estimate the densities, extents or depths of burrows. Both studies showed that the strict seasonality of breeding, and the massive winter mortality, in the island's house mouse population are caused by changes in temperature and food availability. Other studies have also indicated that temperature is an important factor for the house mouse population on the island. Berry et al. (1978) suggested that mice on the island are living close to their physiological limit, pointing out that (air) temperature rarely rises above the lower limits for reproduction in house mice living in less extreme climates and that the mice have morphological adaptations of the types forced by temperature (haemoglobin concentration, haematocrit value, brown fat, heart weight). Webb et al. (1997) showed that the mice show physiological adaptations to cold (basal metabolic rate, minimal thermal conductance).

The biological and ecological findings of all these house mouse studies were considered against air temperatures made at the island's meteorological station. None of them attempted to quantify the thermal regime actually experienced by the island's mice. Judging from microclimate measurements made as part of entomological (Chown and Crafford 1992) and botanical (Huntley 1971, Blake 1997) studies, this will certainly be different from the macroclimatic regime suggested by air temperatures taken 1.2 m above the ground.

In this chapter I describe the morphology of mouse burrow systems on the island, including the directions faced by burrow entrances and the types of plant covers in which entrances occur. The densities, depths and dimensions of burrow systems in three habitats are presented and an estimate made of the areal extent to which the mice exploit the belowground component of these habitats. The temperature regimes at the ground surface and in burrow systems are characterized and compared with that above the vegetation canopy. Densities, biomasses and energy contents of the macroinvertebrate prey types are presented for two of the habitats.

3.2 SITES AND METHODS

Three sites were studied:

1. A coastal area near Trypot Beach, about one km south of the meteorological station. The dominant vegetation at the site is a *Cotula plumosa*–dominated herbfield (the Poa cookii – Cotuletum plumosae association of Gremmen 1981) which is typical of coastal areas influenced by manuring by seabirds and seals. Following terminology commonly used in the island's ecological literature for such animal-influenced localities (e.g. Huntley 1971, Gremmen 1981, Smith 1987d), this is referred to here as the "biotic site".

2. A wet swampy area about 700 m south of the meteorological station and adjacent to the biotic site. It contains several of the plant communities belonging to the mire complex of Gremmen (1981), the most common one being the association Lycopodio magellanici – Jamesonielletum coloratae (subassociation ranunculetosum biternati). The vascular vegetation component of this community, and all the others at the site, is dominated by three graminoid species, *Agrostis magellanica*, *Uncinia compacta* and *Juncus scheuchzerioides*. The

communities differ mainly in the bryophyte species that understorey these graminoids. All occur on wet peat but the Lycopodio magellanici – Jamesonielletum coloratae association is one of the driest of those in the mire complex. In this account this site will be termed the "mire site".

3. An undulating area adjacent to, and inland of, the mire site. A thin layer of peat mixed with fine volcanic ash covers heaps of rocky and scoriaceous lava, giving the site a hillocky or hummocky appearance. The hummock slopes are well-vegetated, mainly by continuous carpets of the fern *Blechnum penna-marina*. This fernbrake association (Isopterygio pulchelli – Blechnetum penna-marinae) is the most dominant community in the site but small patches of mire vegetation occur between the hummocks. The hummock tops are most often rocky and occupied by a fellfield vegetation dominated by cushion plants and also *B. penna-marina*. Overall, the site presents the appearance of a hummocky mosaic of fernbrake slopes interrupted by rocky fellfield on the ridges and mire vegetation in the hollows. In this account this site is thus referred to as the "hummocky mosaic site" or simply as the "hummocky site".

All the entrances to burrow systems (underground corridors and chambers constructed and used by mice) were located in 90 m x 2 m transects at the three sites. The plant species cover (or other type of cover) in which each entrance occurred was noted. The burrow systems were then carefully excavated and the following noted for each: number of entrances, number, depth and dimensions of corridors and chambers, their contents, whether the burrow system was simple (no side corridors/branches) or complex (with side corridors/branches; following Downs 1989). Four transects were examined at the biotic site, five at the hummocky mosaic site and six at the mire. There were no significant differences in any of the burrow parameters between transects examined in spring (late September to early November 1992) and autumn (May 1993) so the pooled results for the two seasons are presented here.

Temperature sensors (precision thermistors, calibrated against a South African Weather Bureau mercury-in-glass thermometer and surrounded by white plastic shields) were deployed in the following positions in the hummocky mosaic and mire sites.

T1. Just above the fern canopy of a fernbrake, 15 cm above the soil surface, in the mosaic site.

T2. One cm above the soil surface between the fronds, under T1.

T3. 20 cm from T2, one cm above the soil surface in a runway through the fern carpet.

T4. Burrow corridor, 38 cm from the burrow entrance, close to T3.

T5. One cm above the peat surface of the mire site.

T6. Burrow corridor, 33 cm from the entrance. In mire site close to T5.

T7. Same corridor as T6 but 5 cm from entrance.

Average, minimum and maximum temperatures over successive 15 minute intervals were logged with a MCS 101 (MC Systems, Cape Town) data logger. Air temperatures just above the vegetation canopy at the mire site were assumed to be the same as at position T1 in the mosaic site since the two sites are so close to each other.

Three 90 m transects were established at both the biotic and mire sites and soil cores (8 cm diameter, 10 cm deep) taken at 10 m intervals along each transect in winter (June/July), giving 10 cores per transect. Macroinvertebrates in the cores and in the attached aboveground vegetation were extracted by hand and sorted by type. The individuals from the ten cores were bulked, within type, counted, oven-dried and weighed. Numbers and dry masses were converted to densities (numbers per m^2) and biomasses (g dry mass per m^2). The sampling was repeated in summer (December/January), when cores were taken 1 m to the left of the transects. Energy content of the dried invertebrates was measured using a AH12/EF/2 Newham microcalorimeter (Newham Instruments Ltd, London).

3.3 RESULTS

3.3.1 Burrow system morphology

Burrow systems were quite diverse in size and form (Figure 3.1), ranging from small, simple systems less than 0.5m long and consisting of one unbranched corridor and one chamber (some systems in the mire site did not have a chamber) to complexly-branched systems extending over an area of up to 4 m^2 and containing up to four chambers. The roofs, walls and floors of corridors were generally of compact peat with protruding roots. Chambers were similar, except that they were frequently roofed by a rock.

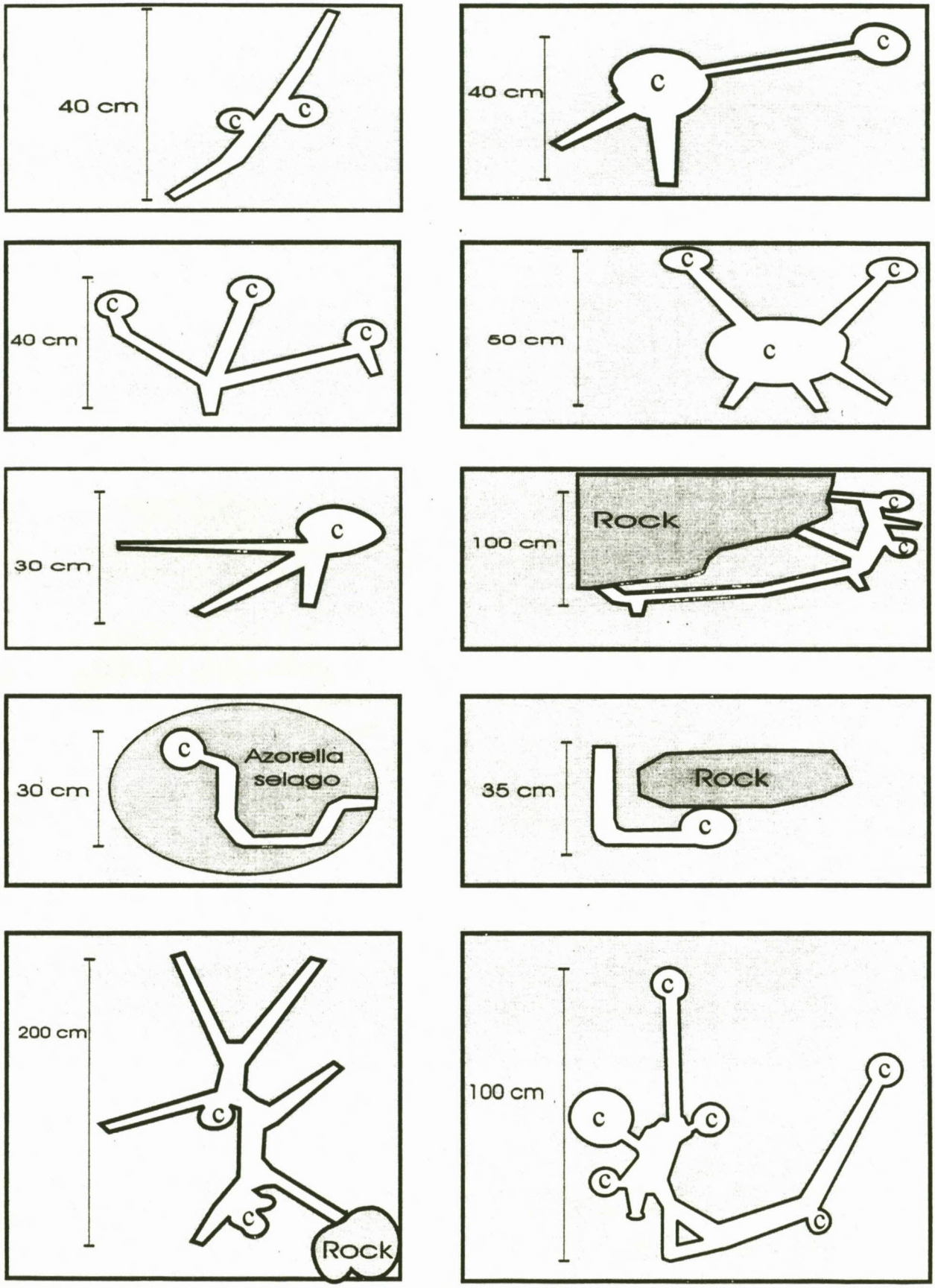

Figure 3.1: House mouse burrow systems on Marion Island (C = Nest chambers)

Mean burrow system density ranged from 300 to 403 burrow systems per hectare and was not significantly different between sites (Table 3.1). The large systems mostly occurred in the biotic site, where, on average, there were also more chambers per system than at the other two sites. The mean numbers of corridors per system was not significantly different between sites. There were up to eight entrances to a burrow system at the mire, but three or less at the hummocky mosaic and biotic sites. Total number of entrances per hectare (estimated as mean burrow density times mean number of entrances per system) at the mire (mean *c.* 1000 ha^{-1}) was greater than at the mosaic (*c.* 340 ha^{-1}) or biotic (*c.* 570 ha^{-1}) sites. Cross sectional area of the entrances varied from 4 cm^2 to 18 cm^2 with a mean of 14 cm^2 across the three sites.

In general, the frequency occurrence of entrances under a particular plant species, or in a particular substrate (e.g. in bare peat, rocky crevices), reflected the relative contributions of the plant species or substrate type/ to the overall surface cover at a site (Table 3.2). For instance, 74% of entrances at the hummocky mosaic site occurred under *Blechnum penna-marina* and *Azorella selago,* the two species that dominated the vegetation there. Bryophytes covered about half of the surface of the mire site and nearly half the entrances were found in them. The most extensive plant community at the biotic site was a *Cotula plumosa-Poa cookii* coastal herbfield and 50% of entrances occurred under these two species. However, at all three sites the observed frequencies of entrances in some cover types deviated quite markedly from that expected from their relative cover values. For instance, *A selago* cushions occupied only 15% of the hummocky site surface but contained over half of all entrances. Also, the relative occurrences of entrances in bryophytes at the site is nearly three times higher than expected from the bryophyte cover. There is an under-representation of entrances in mats of *B. penna-marina* at the hummocky site. At the mire site, entrances are greatly over-represented in albatross nests and the *Poa cookii* tussocks that surround the nests, and also, in contrast to the hummocky site, in *B. penna-marina*. There is a paucity of entrances under the grass *Agrostis magellanica*, the dominant vascular plant species at the site. In contrast, more entrances than expected occurred under *A. magellanica* in the biotic site. However, the most notable discrepancies at the biotic site were over-representations of entrances in bryophytes (which are quite rare in the site) and in bare peat and rock crevices.

Of the 149 entrances studied, 34 did not face any particular direction but opened downwards to a vertical corridor up to 6 cm long. Mostly (30 entrances), these occurred in the mire site

Table 3.1. Burrow system densities and numbers of chambers and corridors per burrow system in the three sites. P and F values are the F-ratios and their significance, from ANOVA testing of the between-site variation. Where superscripts are different, the between-site difference in mean values is significant at $P \leq 0.05$ (ANOVA and Tukey's Honest Significant Difference multiple range test).

Site	No. of transects studied	Burrow system density (mean, range; systems/ha)	Number of entrances per burrow system (mean, range)	Number of chambers per burrow system (mean, range)	Number of corridors per burrow system (mean, range)
Hummocky	5	300 (167-720) [a]	1.1 (1-2) [a]	1.1 (1-2) [a]	1.4 (1-4) [a]
Mire	6	334 (167-500) [a]	3.0 (1-8) [b]	1.2 (0-3) [a]	1.5 (1-4) [a]
Biotic	4	403 (278-500) [a]	1.4 (1-3) [a]	1.9 (1-4) [b]	1.6 (1-4) [a]
F		0.416	19.9	6.25	0.44
P		0.668	< 0.0001	0.003	0.65

Table 3.2. Percentage occurrence of burrow entrances under the various plant species (or in other types of surface) at the 3 sites. Where a value in the column "Contribution to χ^2" is given a sign it indicates that the difference between the percentage occurrence of entrances is significantly ($P<0.05$) greater (+) or less (-) than would be expected if mice had no preference for any particular type of plant cover or type of surface when establishing burrow entrances.

	Hummocky mosaic site			Mire site			Biotic site		
	Percentage relative cover	Percentage entrances	Contribution to χ^2	Percentage relative cover	Percentage entrances	Contribution to χ^2	Percentage relative cover	Percentage entrances	Contribution to χ^2
Blechnum	55	19	23.6-	1	7	36+	2	3	0.5
Azorella	15	55	106.7+	1	3	4	3	0	3
Poa cookii	2	0	2	2	10	32+	18	12	2
Agrostis magellanica	2	0	2	30	4	22.5-	2	7	12.5+
Acaena magellanica	5	0	5	-	-	-	-	-	-
Uncinia compacta	1	0	1	2	0	2	-	-	-
Agrostis stolonifera	-	-	-	4	3	0.25	2	3	0.5
Juncus scheuchzerioides	-	-	-	4	4	0.67	1	3	4
Sagina procumbens	-	-	-	3	7	5.33	4	3	0.25
Ranunculus biternatus	-	-	-	1	3	4	-	-	-
Cotula plumosa	-	-	-	-	-	-	60	38	8.07
Other vascular species	7	0	7	-	-	-	3	0	3
Bryophytes	4	11	12.3+	48	46	0.08	2	17	112.5+
Bare peat	1	0	1	1	0	1	1	7	36+
Rock crevices	8	15	6.13	2	3	0.5	2	7	12.5+
Albatross nests	-	-	-	1	10	81+	-	-	-
Total χ^2			166.7			189.3			194.8

where the surface was largely flat and horizontal, in contrast to the hummocky or even hillocky terrain of the other two sites. Figure 3.2 shows the direction faced by the remaining 115 entrances. An overwhelming proportion (average of 87% across the three sites) faced in an easterly direction, 64% toward the SE quadrant and 23% toward the NE quadrant. At the biotic site almost all (97%) of the entrances faced the SE quadrant and none opened up in a westerly direction.

Mean chamber floor area (62 to 71 cm^2 per chamber) or volume (397 – 477 cm^3) were not significantly different between the sites but chambers tended to be further below the surface at the biotic site (Table 3.3). Corridors were significantly longer, wider and higher at the biotic site, so that mean corridor floor area was about four times, and mean corridor volume about six times, greater there than at the other two sites. Corridor volume was also slightly larger at the mire site than at the hummocky site. Total chamber area and total chamber volume per burrow system (Table 3.4) at the biotic site were about 40% larger than at the other two sites but the difference was not significant at the 95% level. However, total corridor area and volume per burrow system were both very much larger at the biotic site, so that the mean area and volume of a whole burrow system for the biotic site were more than three times larger than for the other two sites.

Multiplying the mean total chamber plus corridor dimensions per burrow system in Table 3.4 by the mean burrow system densities yields the total underground areas and volumes occupied by mouse burrow systems in the three sites (Table 3.5). About $23m^2$ belowground area per hectare is exploited by mice at the biotic site, or a belowground volume of about $1300dm^3$ per hectare. Mostly, this is accounted for by corridors (c. 80% of total area or volume). In contrast, at the mosaic and mire sites, where mice exploit only about one quarter as much belowground area or volume, chambers make up more than half of the total volume. Confidences of the between site differences in Table 3.5 cannot be calculated because of the way the values were estimated but the considerable difference in belowground area or volume exploited by mice at the biotic site compared with the other two sites is almost certainly real, judging from the highly significant differences in chamber plus corridor dimensions in Table 3.4.

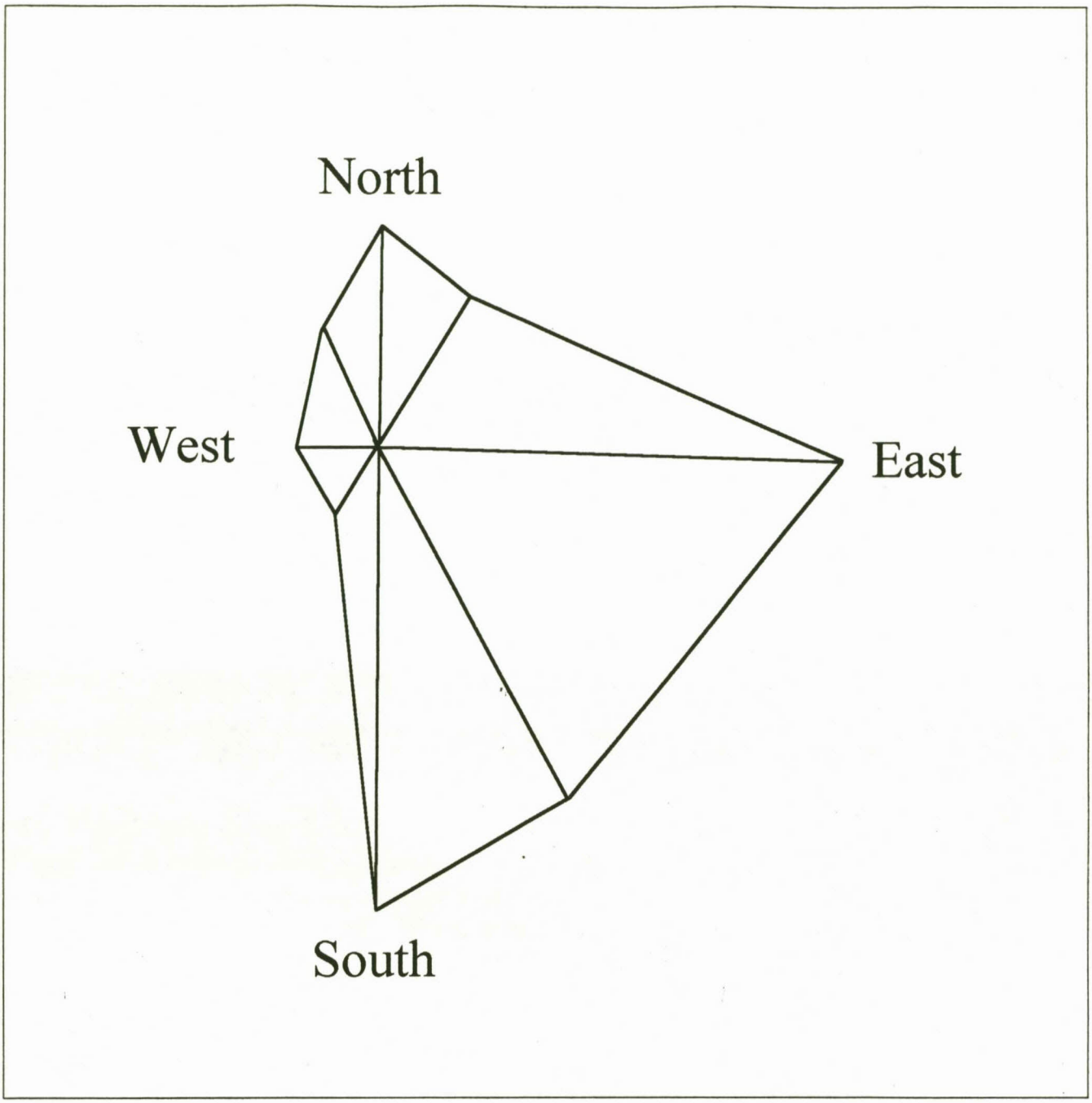

Figure 3.2. Rose diagram for the directions faced by burrow entrances. Lengths of the spokes indicate the percentage occurrence of entrances facing in the particular direction.

Table 3.3. Chamber and corridor dimensions at the three sites. Mean values (range) per chamber or per corridor are given. N, numbers of chambers or corridors measured; ND, not determined. P and F values are the F-ratios and their significance, from ANOVA testing the between-site variation. Where superscripts are different, the between-site difference in mean values is significant at $P \leq 0.05$ (ANOVA and Tukey's Honest Significant Difference multiple range test).

Site	Chambers			
	N	Area ($cm^{2)}$	Volume (cm^3)	Depth (cm)
Hummocks	19	68 (23-200)	477 (120-2000)	15^a (4-41)
Mire	25	71 (16-150)	440 (96-1200)	16^a (7-35)
Biotic	21	62 (24-150)	397 (96-1125)	24^b (9-80)
F		0.32	0.25	3.09
P		0.73	0.78	0.05

Site	Corridors						
	N	Length (cm)	Width (cm)	Height (cm)	Area (cm^2)	Volume (cm^3)	Depth (cm)
Hummocks	22	19^a (6-50)	3^a (2-6)	3^a (2-6)	60^a (12-210)	224^a (24-1050)	11 (5-20)
Mire	24	17^a (5-45)	4^b (4-6)	4^b (3-8)	70^a (20-180)	287^b (80-720)	16 (3-35)
Biotic	27	61^b (12-200)	5^c (4-8)	5^c (4-8)	291^b (60-1000)	1608^c (240-6080)	ND
F		10.7	39.4	22.9	16.4	17.5	0.5
P		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.50

Table 3.4. Total chamber and corridor sizes per burrow system at the three sites. N, number of burrow systems for which measurements were made. P and F values are the F-ratios and their significance, from ANOVA testing the between-site variation. Where superscripts are different, the between-site difference in mean values is significant at $P \leq 0.05$ (ANOVA and Tukey's Honest Significant Difference multiple range test).

	Chambers			Corridors			Chambers & Corridors		
Site	N	Total area cm^2	Total volume cm^3	N	Total area cm^2	Total volume cm^3	N	Total area cm^2	Total volume cm^3
Hummocks	17	75 (25-200)	533 (125-2000)	16	83^a (12-237)	308^a (24-1050)	16	160^a (37-410)	853^a (149-3050)
Mire	21	82 (0-320)	521 (0-2280)	20	107^a (20-340)	438^a (80-1360)	20	188^a (35-495)	956^a (123-3075)
Biotic	20	112 (36-185)	727 (144-1192)	23	464^b (60-1800)	2484^b (240-8200)	20	589^b (180-1859)	3277^b (1140-8506)
F		2.01	0.141		22.8	31.9		20.2	25.9
P		1.27	0.288		<0.0001	<0.0001		<0.0001	<0.0001

Table 3.5. Total chamber, corridor and underground burrow system area and volume at the three sites.

	Total chamber area (m^2/ha)	Total corridor area (m^2/ha)	Total underground burrow system area (m^2/ha)
Hummocks	2.26	2.48	4.74
Mire	2.74	3.57	6.31
Biotic	4.51	18.70	23.21

	Total chamber volume (m^3/ha)	Total corridor volume (m^3/ha)	Total underground burrow system volume (m^3/ha)
Hummocks	159.87	92.40	252.27
Mire	174.01	146.13	320.14
Biotic	292.82	1000.93	1293.75

3.3.2 Burrow system contents

The mice store food in the chambers, especially in autumn when 78% of chambers had a food cache. The volume stored is small (<5 cm^3 per chamber). Caches consisted of seeds (generally in the seedheads) of *Acaena magellanica*, *Azorella selago*, *Agrostis magellanica* and *Poa cookii*. Chambers sometimes contained young inflorescences of *Agrostis magellanica* or *Poa cookii*, living or dead grass leaves, dried twigs of *A. selago* or fronds of *B. penna-marina*. The quantities of these materials were too small, and they were too scattered in the chambers, to properly consider them as nesting material. Other items found in the chambers were feathers, a seabird scat, snail shells and live slugs. These were sometimes also found in the corridors.

3.3.3 Above-ground extensions of burrow systems

Burrow system entrances are often connected aboveground by 'runways', which are paths through the vegetation or tunnels through moss mats. Runways were examined at the mire and biotic sites only. They were between 3 and 5 cm wide, were more common and also longer at the mire site (mean 422 runways ha^{-1}; mean length 3.6m) than at the biotic site (95 ha^{-1}, 1.1m). The longest runway found was 12 m long. Up to three (but generally only one) runway may start from an entrance and extend in any compass direction, often leading to another entrance. They are most often straight but do change direction to avoid going over the summits of hummocks or crests of ridges. They are probably established through wear, when mice repeatedly travel a particular route through the vegetation, but plants lining runways frequently show signs of having been bitten or chewed, especially in the case of *B. penna-marina* which forms dense carpets of stiff, vertical fronds which extend up to 20cm above the runway surface. Mouse scats are common in the runways and pieces of bitten-off inflorescences and seed heads are occasionally found in them.

3.3.4 Temperature regimes inside and outside burrow systems

Table 3.6 shows monthly temperatures at various positions in the hummocky mosaic and mire sites and also air temperatures measured at the same time in a Stevenson Screen 1.2m above the ground at the nearby meteorological station.

Table 3.6. Temperatures (°C) at the various localities in the hummocky mosaic and mire sites.

Meteorological Station, 1.2 m aboveground in Stevenson Screen

	Average
January	7.7
February	9.3
March	7.8
April	7.4
May	5.4
June	4.3
July	3.6
August	3.8
September	3.6
October	4.3
November	6.0
December	6.5
Year	6.0

Month	Average	Average Daily Minimum	Average Daily Maximum	Absolute Minimum	Absolute Maximum
Hummocky mosaic site					
Above fern fronds, 15 cm above soil surface (T1)					
January	7.9	1.9	20.9	0.0	30.6
February	9.7	4.3	18.5	0.0	28.5
March	7.7	2.5	15.4	0.0	28.1
April	6.6	3.0	11.9	0.0	18.4
May	1.9	0.0	5.8	0.0	10.4
June	3.0	0.7	5.9	0.0	9.0
July	2.8	0.6	5.5	0.0	9.5
August	3.1	0.7	7.2	0.0	13.1
September	3.4	0.5	8.9	0.0	15.4
October	5.6	1.4	13.9	0.0	23.9
November	9.1	2.4	20.9	0.0	30.8
December	7.4	1.5	20.1	0.0	34.6
Year	5.7	1.7	12.8	0.0	34.6

Table 3.6 continues

Month	Average	Average Daily Minimum	Average Daily Maximum	Absolute Minimum	Absolute Maximum
1 cm above peat surface between fronds (T2)					
January	7.0	3.6	12.6	1.3	16.2
February	9.2	6.1	12.7	2.0	17.1
March	7.7	4.8	10.9	1.9	18.1
April	6.9	4.8	9.3	1.1	13.9
May	2.8	1.5	4.5	0.5	7.5
June	2.7	1.2	4.3	0.0	7.8
July	2.3	0.8	4.1	0.0	8.2
August	2.5	1.0	4.7	0.0	8.2
September	2.7	0.9	5.3	0.0	9.8
October	4.7	1.9	8.5	0.0	15.5
November	7.6	3.3	13.1	0.0	21.4
December	6.5	3.0	11.7	0.4	16.7
Year	5.2	2.8	8.4	0.0	21.4
1 cm above peat surface in a runway (T3)					
January	6.8	3.7	11.8	1.5	15.2
February	8.9	6.0	12.0	1.8	15.7
March	7.4	4.8	10.4	2.2	17.5
April	6.6	4.6	8.9	1.1	13.0
May	2.5	1.3	4.2	0.5	7.4
June	2.7	0.9	4.7	0.0	8.5
July	2.3	0.7	4.3	0.0	8.5
August	2.6	0.8	5.4	0.0	9.5
September	2.9	0.6	6.4	0.0	12.8
October	4.8	1.7	9.9	0.0	17.1
November	7.1	3.3	12.0	0.0	19.9
December	6.3	2.9	11.0	0.1	15.2
Year	5.1	2.6	8.4	0.0	19.9
In burrow corridor, 38cm from entrance (T4)					
January	7.4	6.2	8.7	4.7	11.0
February	9.5	8.3	10.6	5.8	12.6
March	8.2	7.2	9.2	5.4	13.2
April	7.5	6.7	8.2	3.8	10.5
May	4.2	3.7	4.9	3.2	5.9
June	4.5	3.9	5.0	2.8	6.2
July	3.7	3.1	4.1	0.7	5.3
August	3.7	3.2	4.8	2.3	8.2
September	3.9	3.2	4.5	0.5	6.1
October	4.6	3.6	6.1	2.6	15.4
November	7.1	5.4	8.3	3.4	12.9
December	6.9	5.6	8.1	4.0	11.0
Year	6.0	5.0	6.9	0.5	15.4

Table 3.6 continues

Month	Average	Average Daily Minimum	Average Daily Maximum	Absolute Minimum	Absolute Maximum
Mire site					
One cm above peat surface (T5)					
January	9.1	2.5	22.2	0.0	30.7
February	10.6	5.3	19.0	0.5	29.7
March	8.9	3.6	17.8	0.1	28.0
April	7.3	3.7	13.6	0.0	20.4
May	2.5	0.3	6.7	0.0	10.1
June	3.0	0.8	6.4	0.0	10.9
July	2.6	0.6	5.3	0.0	8.9
August	3.2	0.7	8.0	0.0	17.6
September	3.7	0.6	11.2	0.0	17.6
October	6.3	1.7	15.6	0.0	26.0
November	10.4	2.5	23.6	0.0	36.4
December	7.9	1.5	20.8	0.0	34.4
Year	6.3	2.1	14.1	0.0	36.4
Burrow corridor, 33cm from entrance (T6)					
January	7.8	6.0	9.9	3.8	12.3
February	9.6	8.1	11.3	3.9	15.1
March	8.2	6.8	9.7	4.1	14.0
April	7.5	6.4	8.5	2.8	11.3
May	3.7	3.0	4.6	2.2	6.4
June					
July					
August					
September					
October	7.1	3.9	11.2	1.5	15.3
November	7.2	5.1	9.3	1.9	13.7
December	7.0	5.3	8.7	2.9	11.9
Year					
Burrow corridor, 5cm from entrance (T7)					
January					
February					
March					
April					
May					
June					
July					
August					
September					
October	5.6	3.9	10.2	2.9	15.5
November	6.7	5.7	7.6	4.1	10.7
December	7.1	6.3	7.9	4.1	9.4
Year					

Monthly mean temperatures just above the plant canopy at the hummocky site (position T1) were lower than screen temperatures in late summer and winter (March to September) but higher than in the screen in spring and summer (October to February). Hence the seasonal variation in monthly mean temperatures at the top of the canopy (1.9 to 9.7°C) was slightly greater than the screen values (3.6 to 9.3°C).

Absolute minimum temperature at the top of the canopy never fell below 0°C. Absolute maximum was above 20°C from October to March and above 30°C for the midsummer months (November, December and January). Mean diurnal temperature variation (daily maximum minus daily minimum) was nearly 20°C in midsummer but less than 8°C in winter.

Annual mean temperatures 1cm above soil/litter surface in the vegetation (T2) and in a runway at the mosaic site (T3) were both about 0.5°C lower than that above the canopy. However, temperature variation at both surface positions was considerably dampened through daytime shading and nighttime prevention of heat loss by the thick vegetation cover, so that the average diurnal range over the year (5.7°C in the vegetation; 5.8°C in the runway) was about half of that at the top of the canopy (11.1°C). This was mainly due to lower daily maxima under the vegetation; absolute maximum in the vegetation was above 20°C on only one day, in November. Minimum temperatures under the vegetation were also somewhat ameliorated - only in late winter/early summer were absolute minima as low as those above the canopy.

In contrast to the two surface positions in the mosaic site, at the mire site the temperature variation 1 cm above the peat surface (T5) was not dampened compared to that of the air above the canopy. In fact the monthly average maximum temperatures at the mire surface were up to 2.7°C higher than above the canopy, while mean minimum temperatures were very similar at the two positions. Annual mean temperature at the mire surface was 0.6°C higher than at the top of the canopy, in contrast to the two surface positions in the mosaic site which were, overall, about 0.6°C colder than at the top of the canopy. This is probably a function of the much lower vegetation cover in the mire, where the graminoid canopy is very open (leaf area index, LAI, is generally under 2; V.R. Smith, unpublished data). This affords almost no shading of the surface, in contrast to most of the mosaic mire surface where direct sunlight never penetrates below the thick carpet of vertical *B. penna-marina* fronds (LAI, including dead fronds which persist for long times in the carpets, can be as high as 16; V.R. Smith,

unpublished). Even in the runway direct sunlight rarely reaches the soil surface, since sun angles are low at the island and the runway is effectively shaded by the fronds on both sides.

The most dampened diurnal and seasonal temperature variations were found 38cm deep in a burrow corridor in the mosaic site (T4, Table 3.6). There, mean diurnal temperature range was only 1.8°C, compared with 11.1°C at the top of the canopy and nearly 6°C just above he soil surface in the vegetation or in the runway. Mean monthly minimum temperatures in the burrow were, on average, about 3.5°C higher than above the canopy and about 2.5°C higher than the soil surface. Mean and absolute minima in the corridor were considerably higher than those aboveground; in fact corridor temperature dropped below 1°C only twice during the year. However, since maxima values were also highly moderated in the burrow (mean monthly maximum was above 10°C for only one month, compared with seven months above the canopy), annual mean temperature in the burrow was only marginally (0.2°C) higher than above the canopy.

Temperatures were also measured for some months at two positions in a corridor of a burrow system opening out in an *Azorella selago* cushion at the mire site. Both positions were directly under the cushion, one (T6) 5 cm deep into the corridor and the other (T7) 33 cm deep. Since measurements were not made for a whole year the seasonal temperature variations at the two positions cannot be assessed. Mean temperatures for the months when measurements were taken were close (within 0.5°C) to those for the mosaic site burrow (T4), except in October when the means for the mire burrow were over a degree higher than in the mossa.c site burrow. Monthly mean diurnal temperature ranges in the mire burrow were much more moderate than the corresponding monthly values just above the vegetation canopy (T1) or 1 cm above the mire surface (T5). For instance, the largest mean diurnal range 5 cm from the entrance in the mire burrow was 6.4°C, and 33 cm from the entrance it was 7.3°C, compared with values of 12.4°C above the canopy and 13.9°C at the mire surface in the same month (October).

The differences between the temperature regimes at the various positions in the two sites are best revealed by examining how temperatures deviated from values at the top of the vegetation canopy. The deviations are plotted in Figures 3.3 and 3.4. For convenience the austral summer months are in the center of the x axis.

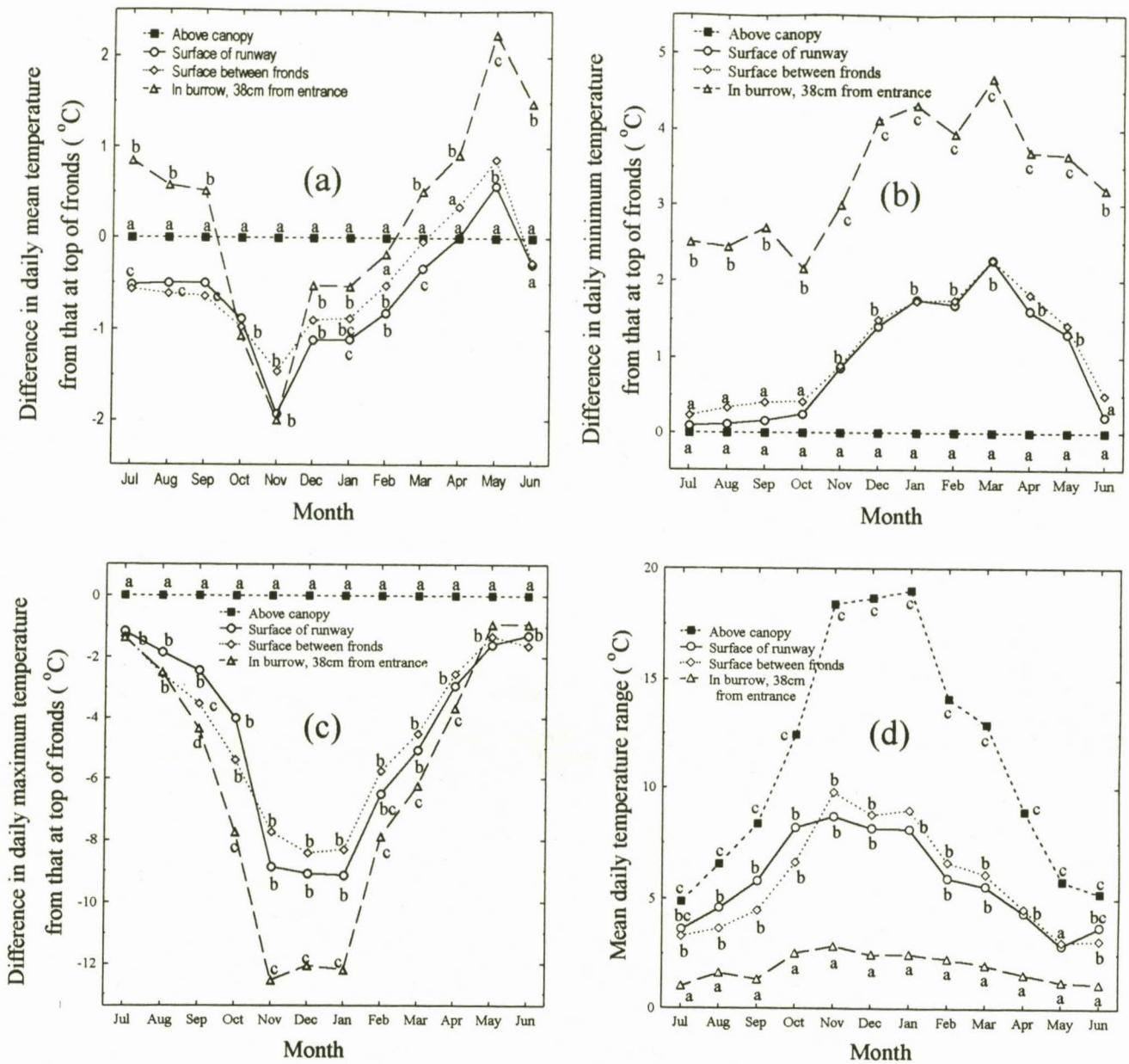

Figure 3.3. (a, b, c) Monthly mean differences in temperature from that measured just above the canopy, at different positions in the hummocky mosaic site. (d) Mean daily temperature range at these positions.

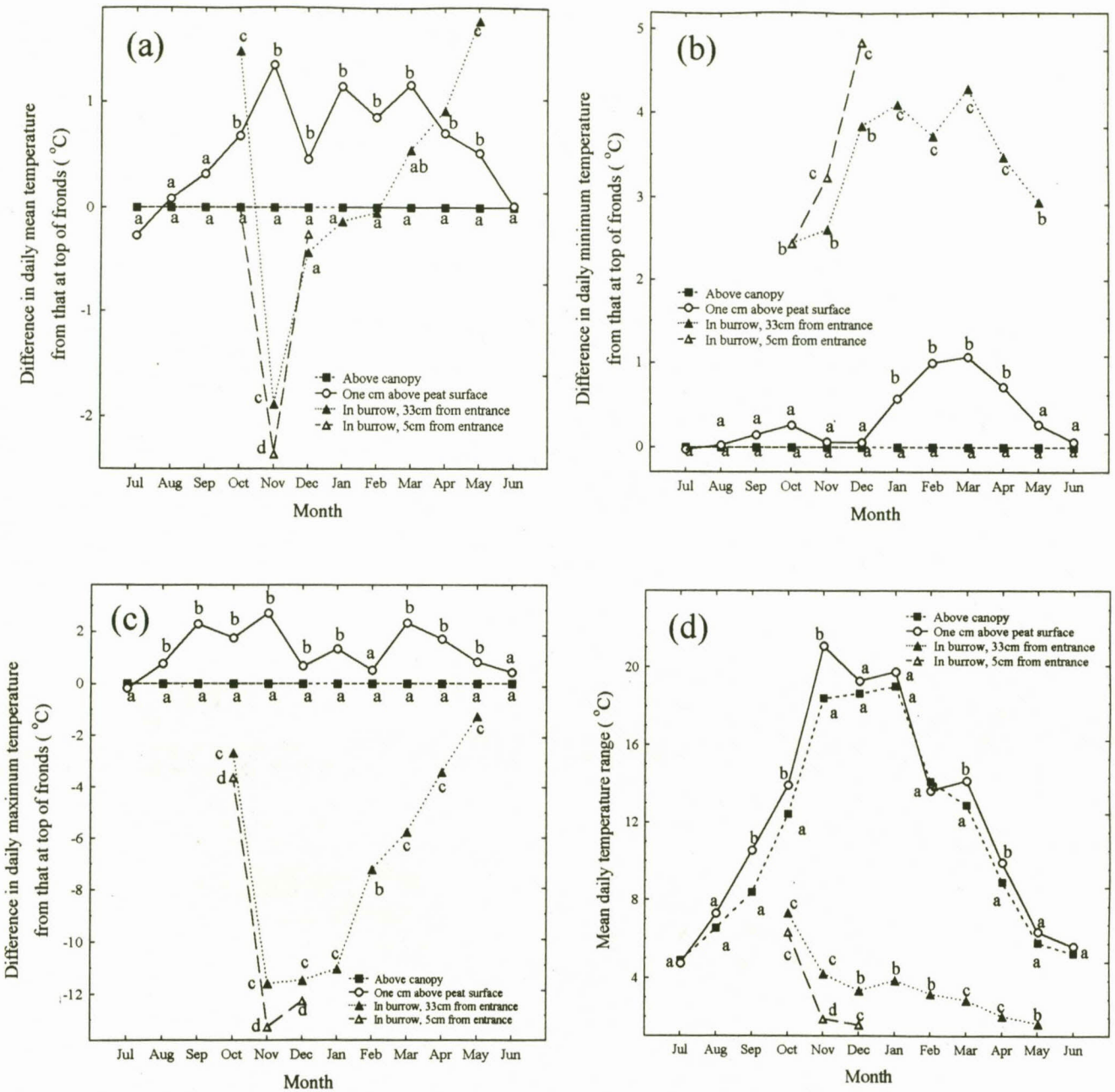

Figure 3.4. (a, b, c) Monthly mean differences in temperature from that measured just above the canopy, at different positions in the mire site. (d) Mean daily temperature range at these positions.

It is clear from Figure 3.3a that, overall, the environment just above the ground surface at the mosaic site, whether in the vegetation or in a runway, is a colder one for most of the year than that just above the canopy. Only in May are surface mean temperatures significantly higher than at the top of the canopy. The burrow environment is significantly warmer than above the canopy during Autumn and Winter (March to September but significantly colder in spring and midsummer. Burrows offer a warmer environment than the ground surface for most of the year; only in October and November are mean burrow temperatures not significantly higher than those 1 cm above the ground. Largest differences between burrow and surface or canopy temperature are from May to July, indicating a retention of summer warmth in the soil during the first half of winter. A similar situation may have existed at the mire site (Figure 3.4a), where, for the months that it was measured, mean temperature in the burrow exceeded surface and above-canopy temperatures the most in May.

The pattern of mean temperature 1 cm above the mire surface, relative to that at the top of the canopy (Figure 3.4a) contrasts strongly to that shown by surface temperature at the mosaic site (Figure 3.3a). Surface temperatures at the mire were significantly higher than at just above the canopy from October to May (i.e. the whole of summer). At the mosaic site, surface temperatures were lower than those above the canopy for most of summer. The open canopy at the mire does not appreciably shade the surface so it is able to heat up, even in spring and autumn when sun angles are low. This, with the boundary layer effect of less air movement 1 cm above the ground than at the top of the canopy, should allow considerably higher maximum temperatures to develop at the surface than higher up off the ground, which was what actually occurred for most of the year (Figure 3.4c). In contrast, although the same boundary layer consideration applies (even more so) at the mosaic site, the dense shading by the vegetation did not allow the development of high soil surface temperatures during the day, so that mean maximum values 1 cm above the ground are significantly lower than at the top of the canopy throughout the year (Figure 3.3c).

In burrows, mean maximum temperatures in summer were up to about 13°C lower than at the top of the canopy (Figures 3.3c, 3.4c). The difference between burrow and above-canopy maxima decreased in winter, down to about 1°C. Minimum temperatures, on the other hand, throughout the year were significantly higher in burrows than above the canopy or 1 cm above the ground (Figures 3.3b, 3.4b). The largest differences between burrow and canopy mean

minima (*c.* 4°C) were during late summer; thereafter the difference decreased steadily so that in late winter and spring it was only about 2.5°C.

A feature of the seasonal variation in minimum temperatures at the mosaic site (Figure 3.3b) is that from November to May, the main season for house mouse activity on the island, soil surface minima were significantly higher than at the top of the canopy. At the mire site too temperature minima just above the ground were also higher than above the canopy, although the differences were only significant from January to April (Figure 3.4b). During summer, daily minimum temperatures always occurred at night. Hence the ground surface, with its less extreme temperature minima, represents a less stressful thermal environment than that just above the canopy during the period when mice are most active.

3.3.5 Macroinvertebrate prey species

The only significant seasonal difference in macroinvertebrate prey density at the biotic site was that spiders were five times more abundant in winter than in summer (Table 3.7). Spider density was also higher in winter than in summer at the mire site. However, the most marked seasonal differences at the mire were for larvae of the flightless moth *Pringleophaga marioni* and for larvae and adults of weevils (*Ectemnorhinus* spp). All of these are important components of the mouse diet at the mire (Chapter 6) and occurred at considerably higher densities in summer than in winter.

The most conspicuous between-site difference in macro-invertebrate density was for earthworms, which were 24 times more abundant in winter and 55 times more abundant in summer, at the biotic site than in the mire. The large number of earthworms at the biotic site dominates the inter-site comparison of total macro-invertebrate numbers, which in winter were five times greater, and in summer twice as great, at the biotic site than at the mire. However, because of the marked summer increases in moth larvae and weevil larvae and adults at the mire, summer densities of these three prey types there were significantly higher than at the biotic site.

Overall, the between-site and winter-summer differences in macroinvertebrate biomass (Table 3.8) were smaller than the corresponding differences in density. This is because where a prey

Table 3.7. Mean (range in brackets) macroinvertebrate densities (numbers m^{-2}) at the biotic and mire sites in winter (W) and summer (S). Asterisks indicate the significance of the difference between adjacent means (from ANOVA and Tukey's Honest Significant Difference test), as ***P≤0.001, ** P≤0.01, *P≤0.05.

Invertebrate	Season	Biotic site		Mire
Pringlea marioni larvae	W	27 (20 – 40)		33 (20 - 40)
	S	46 (40 – 60)	***	*** 199 (159 - 239)
Weavil larvae	W	119 (99 – 139)	**	53 (40 - 60)
	S	133 (119 - 139)	***	*** 418 (398 - 438)
Weavil adults	W	20 (0 - 40)		0
	S	46 (40 - 60)	**	*** 86 (80 - 99)
Slugs	W	86 (60 - 99)		60 (40 - 80)
	S	106 (80 - 139)	**	20 (0 - 60)
Snails	W	0		13 (0 - 20)
	S	0		0
Spiders	W	265 (239 - 298)	***	93 (80 - 99)
	S	*** 53 (40 - 60)		** 40 (20 - 60)
Ticks	W	13 (0 - 40)		0
	S	0		0
Earthworms	W	1101 (1054 - 1174)	***	46 (40 - 60)
	S	1107 (975 - 1233)	***	20 (0 - 60)
Total macro-invertebrates	W	1631 (1571 - 1711)	***	298 (259 – 318)
	S	1492 (1372 - 1591)	***	*** 782 (696 - 855)
Total excluding slugs	W	1545 (1472 – 1611)	***	238 (219 –259)
	S	1386 (1273 – 1511)	***	*** 762 (696 – 796)

Table 3.8. Mean (range in brackets) macroinvertebrate biomasses (mg dry mass m^{-2}) at the biotic and mire sites in winter (W) and summer (S). Asterisks indicate the significance of the difference between adjacent means (from ANOVA and Tukey's Honest Significant Difference test), as ***P<0.001, ** P<0.01, *P<0.05.

Invertebrate	Season	Biotic		Mire
Pringlea marioni larvae	W	787 (452 - 959)		422 (351 - 538)
	S	801 (703 - 908)	**	1 789 (1 345 - 2 236)
Weevil larvae	W	495 (412 - 577)	**	114 (107 - 127)
	S	549 (466 - 662)		839 (575 - 1 067)
Weevil adults	W	48 (0 - 81)		0
	S	231 (168 - 293)		329 (267 - 372)
Slugs	W	785 (180 - 1 581)		651 (538 - 868)
	S	700 (403 - 1 063)		120 (0 - 359)
Snails	W	0		13 (0 - 19)
	S	0		0
Spiders	W	60 (52 - 66)		56 (51 - 60)
	S	29 (14 - 54)		39 (3 - 71)
Ticks	W	8 (0 - 25)		0
	S	0		0
Earthworms	W	8 641 (6 804 - 11 061)	***	487 (381 - 604)
	S	12 861 (8 660 - 15 370)	***	199 (0 - 597)
Total biomass	W	10 823 (8 478 - 14 065)	**	1 743 (1 579 - 1 864)
	S	15 172 (10 669 - 17 618)	**	3 314 (3 036 - 3 722)
Total biomass without slugs	W	10 038 (7 885 - 12 484)	**	1 092 (919 - 1 327)
	S	14 472 (10 266 - 16 984)	**	3 194 (2 825 - 3 722)

item occurred in large numbers in a particular site or season, the individuals often tended to be smaller (lighter) than where it occurred in lower numbers. For instance, *Pringleophaga marioni* and weevil larvae were twice as heavy, and weevil adults about 1/3 heavier, at the biotic site than at the mire site in summer (data not shown). Similarly, the large difference in spider numbers between winter and summer at both sites, and the greater number of spiders at the biotic site than at the mire in winter, were associated with reciprocal differences in mean body mass so that spider biomass was not significantly different between sites or seasons.

As was the case with density, earthworms dominated the macroinvertebrate biomass at the biotic site. Total invertebrate biomass was 6 times higher than at the mire site in winter and nearly five times higher in summer. If slugs are excluded (mice rarely feed on them – Chapter 6) then invertebrate biomass at the biotic site in winter was about 9 times that at the mire. Total macroinvertebrate biomass, excluding slugs, at the mire site was nearly three times larger in summer than in winter. Total biomass without slugs at the biotic site was also higher (about 44%) in summer than in winter, in contrast to density which was about 10% lower in summer.

Energy contents of the macroinvertebrates are presented in Table 3.9. *P. marioni* larvae have a significantly higher energy content (per dry mass, including ash) than any of the other regular prey items. The energy content of slugs is intermediate between that of the moth larvae and the other prey items. There were no significant differences between winter and summer or between sites in the energy contents of individual prey types; in fact, total variation within types was small (<10%). The mean calorific values in Table 3.9 were thus multiplied by mean biomass values in Table 3.8 to estimate standing stocks of energy in the macroinvertebrates at the two sites (Table 3.10). The energy contents of snails and ticks were assumed to be the same as those for slugs and spiders respectively. The errors in total energy standing stocks caused by this assumption are negligible since the overall variation in mean calorific values across invertebrate types was only about 10%), and both snails and ticks were recorded in only one season and at only one site. Because of the way in which energy standing stocks were calculated, the significances of their between-site and winter-summer differences are the same as those in Table 3.8 for the corresponding differences in biomass.

Table 3.9. Mean (range in brackets) energy content of macroinvertebrates (kJ g^{-1}, dry mass including ash). Where superscripts are different, the between-site difference in mean values is significant at $P \leq 0.05$ (ANOVA and Tukey's Honest Significant Difference multiple range test).

Invertebrate type	Energy content (kJ g^{-1})
Pringleophaga marioni larvae	^{a}23.15 (22.90 – 23.44)
Weevil larvae	^{b}20.96 (20.28 – 21.64)
Weevil adults	^{b}21.84 (21.22 – 22.29)
Slugs	^{ab}22.11 (21.57 – 22.70)
Spiders	^{b}21.84 (20.93 – 22.76)
Earthworms	^{b}21.60 (20.72 – 22.79)

Table 3.10. Energy standing stocks (kJ m^{-2}) in macroinvertebrate biomass at the mire and biotic sites.

Invertebrates	Season	Biotic site	Mire site
Moth larvae	Winter	18.2	9.8
	Summer	18.6	41.4
Weevil larvae	Winter	10.4	2.4
	Summer	11.5	17.6
Weevil adults	Winter	1.0	0
	Summer	5.0	7.2
Slugs	Winter	17.4	14.4
	Summer	15.5	2.6
Snails	Winter	0	0.3
	Summer	0	0
Spiders	Winter	1.3	1.2
	Summer	0.6	0.8
Ticks	Winter	0.2	0
	Summer	0	0
Earthworms	Winter	186.7	10.5
	Summer	277.8	4.3
Total invertebrates	Winter	235.1	38.6
	Summer	329.0	74.0
Total excluding slugs	Winter	217.7	24.2
	Summer	313.5	71.4

Total energy standing stock in the macroinvertebrate component at the biotic site was about 6 times higher in winter and about 4 times higher in summer than at the mire, due mainly to the energy contained in the large earthworm population at the biotic site.

3.4 DISCUSSION

The diagram of entrance directions (Figure 3.2) is very close to an inverted mirror image of the wind rose diagram for the island (Gremmen, 1981). The direction and force of the prevailing winds are thus probably the main determinants of the direction faced by burrow entrances. Rain-bearing winds come from the NW quadrant and blow for about 60% of the year, while SW winds bring snow and soft hail and occur for about 30% of the year. Winds with a westerly component are also fiercest; mean wind speed for southwesterlies (28km h^{-1}) and northwesterlies (30 km h^{-1}) are about double those for winds from the east (15km h^{-1}).

Azorella selago cushions appear to be the preferred localities for burrow entrances in the hummocky mosaic site, rather than the more ubiquitous carpets of *Blechnum penna-marina*, judging by the χ^2 analysis in Table 3.2. The under-representation of entrances in *Blechnum penna-marina* cover is especially notable since the fern occurs predominantly on the east facing slopes favored for entrances. The fern carpet consists of densely packed fern fronds under which occurs a tough, woody layer of interwoven rhizomes, up to 15 cm deep which is hard to penetrate.

At the hummocky mosaic and biotic sites, bryophytes are relatively uncommon, being represented by loose mats of *Brachythecium rutabulum* and *Drepanocladus uncinatus* in particularly sheltered localities on east-facing slopes. The moss mats are easily penetrated and so is the underlying peat. This combination of shelter, easy penetration and easterly aspect probably accounts for the fact that the percentage occurrence of entrances in bryophytes at the hummocky and biotic sites is considerably greater than expected from the contribution of bryophytes to the total vegetation cover of the sites. Bare peat and rocky crevices represent relatively dry (in the case of rock crevices also sheltered) habitats, which might explain why both are indicated as preferred areas in which to establish burrows at the biotic site.

Wandering Albatross nests and the stands of *Poa cookii* surrounding them are both favored localities for burrow entrances in the mire; together they comprise 60% of the χ^2 for this site (Table 3.2). Both are enriched by manuring and contain higher densities of soil macroinvertebrates, especially larvae of the moth, *Pringleophaga marioni*, a the major diet item for mice at the site (Chapter 6). The analysis in Table 3.2 is only for entrances to genuine burrow systems, i.e. those leading to an underground corridor/s habitually used by mice and that mostly contained a nest chamber. Many openings, especially in and around albatross nests, lead to short (< 15 cm) tunnels made when mice forage for macroinvertebrates and these were not regarded as burrow systems. However, it is likely that some burrow systems around albatross nests start in this way.

The main deterrent to burrow establishment at the mire site is almost certainly waterlogging. The driest parts of the mire site are those where *B. penna-marina* occurs. This, along with the fact that in the mire the fern does not form impenetrable rhizome mats in the mire, unlike at the hummocky site, but is understoried by a fairly dry carpet of *Jamesoniella colorata* or *Racomitrium lanuginosum* on stable peat, accounts for the fact that in the mire, burrow entrances are relatively over-represented in *B. penna-marina* cover, in contrast to at the mosaic site where they are underrepresented in the fern cover. *Agrostis magellanica*, on the other hand, is found at waterlogged localities in the mire site and fewer than expected entrances occur under it, unlike at the biotic site where the grass occurs mainly on sheltered, relatively dry, slopes and is associated with a greater than expected number of entrances.

Based on mean temperatures it is clear that burrows offer a warmer environment than that at the ground surface at the mosaic site, excepting in early summer. Burrow temperatures at the mire were measured only from October to May and monthly means were lower than at the surface in summer but significantly higher in October and May. At both sites burrows are warmer than the air at the top of the vegetation canopy in late summer and winter but colder during early to mid summer. To consider more closely the thermal regimes at the different positions in the sites might affect house mice, an index of warmth ("heat sum", in degree hours above 0°C) was calculated and partitioned according to those times of the year, or of the day, when temperature might be particularly important in regulating house mouse activity on the island.

October to April is the main reproductive season for house mice on the island; no pregnant, and only a few lactating mice are found outside this period (Chapter 4). The heat sum for this period in the burrow at the biotic site (36988 deg. h) was 5% less that at the top of the canopy (39084 deg. h), but 7% greater than in the runway (34589 deg. h).

Considering the two months before and after this main breeding season period, i.e. August/September, when temperature constraints on the population are lessening, and May/June, when temperature constraints are increasing, further emphasizes the importance of burrows in the thermal biology of the island's mice. For these four months the heat sum for the burrow at the mosaic site (11899 deg. h) was 42% greater than at the top of the canopy (8355 deg. h) and 52% greater than in the runway (7847 deg. h).

In contrast, the heat sum in the runway was 12% less from October to April, and 6% less during August, September, May and June, than at the top of the canopy. Hence the runway surface seems to be a colder environment than that above the canopy during the breeding period and in the two month windows before and after it.
However, it is probably the nighttime warmth that mice experience in the runway that is important, since it is during the night that mice are most active outside their burrows - they rarely venture aboveground in daylight. For the breeding season the total heat sum at night for the runway surface (13446 deg. h) was 13% greater than above the canopy. During the four months peripheral to the breeding season, total heat sums for the runway (3279 deg. h) and at the top of canopy (3364 deg. h) were very similar.

Nighttime warmth during the breeding season in the burrow (17578 deg. h) was 47% greater, and during the four peripheral months (5940 deg. h) 77% greater, than at the top of the canopy. Over the whole year, total nighttime warmth in the burrow (24883 deg. h) was 53% higher than at the top of the canopy (16317 deg. h) and 42% higher than in the runway (17528 deg. h). At night burrows are thus considerably warmer microenvironments than those found aboveground.

Total density and, especially, total biomass of the mouse's macroinvertebrate prey types were considerably higher at the biotic site than at the mire, especially in winter. This was due mainly to large numbers of earthworms at the biotic site. Summer densities and biomasses of moth larvae and weevil larvae and adults were actually lower at the biotic site, possibly

because the considerably higher (about 4-fold) summer mouse density at the biotic site (Matthewson et al. 1994) lead to greater predation pressure on these preferred prey items than at the mire.

Mouse numbers drop precipitously during winter, more so at the biotic site than at the mire (Gleeson 1981, Matthewson et al. 1994), so that miminum winter mouse densities at the mire are less than a quarter, and at the biotic site less than a tenth, of peak summer values. Predation pressure therefore decreases to a greater extent in winter, compared with summer, at the biotic site than at the mire. Areas manured by seabirds and seals (like the biotic site studied here) have large standing crops of vegetation and plant litter (Smith 1978a), a high soil and plant nutrient status (Smith 1978b), and also high rates of decomposition (Smith et al. 1993) and soil heterotrophic activity (Grobler et al. 1987). All these factors are conducive to the productivity of soil invertebrates, which means that the macroinvertebrate populations at biotically-influenced areas might benefit more from lessened predation by mice in winter than populations in the less productive, and much less fertile, mire localities. This, along with the fact that predation pressure in winter is alleviated to a greater extent at the biotic site, might explain why winter and summer total macroinvertebrate densities at that site were not significantly different, whereas winter density at the mire fell to about 40% of the summer value.

Seasonal and between-site differences in the standing stocks of energy contained by macroinvertebrate populations were the same as the corresponding differences in biomass, with earthworms contributing about 80% of the total energy in macroinvertebrates at the biotic site, but only 27% (in summer) or 6% (winter) at the mire. Due mainly to the large reserves of energy in earthworms, the total energy standing stock in mouse prey types items (all items excepting slugs in Table 3.10) at the biotic site was nine times higher than at the mire in winter, and nearly five times higher in summer.

Total density and biomass of macro-invertebrates have now been observed at its lowest ever (Tables 3.11 and 3.12). Burger (1978) found that a biotic vegetation type is the vegetation type with highest densities and biomass of macro-invertebrates. During 1992/93 this was still the case. Different methods were used to report density and biomass in this and previous studies. Also, the fact that no fiducial limits from previous studies were available made statistical comparisons impossible. The following conclusions can, nevertheless, be made:

Earthworms have declined most. Their biomass in the biotic site was 32%, and in the mire 5% of the values found in nearby similar sites in 1976/77. Mean density of earthworms in 19 habitats on the island's eastern coastal plain in 1976/77 was higher than the highest found in 1992/93. Spider and weevil larvae (and it seems also snails and *P. marioni* larvae) biomass has also decreased. Only slugs have shown a definite increase in density (mean annual density for 19 habitats in 1976/77 is lower than the lowest density in the mire during this study) and biomass (88% increase in the biotic site; more than 90% increase on the mire).

Table 3.11. Macro-invertebrate density (number/m^2) in different vegetation types during this and previous studies done at Marion Island. A, *Pringleophaga marioni* larvae; B, *Pringleophaga marioni* adults; C, weevil larvae; D, weevil adults; E, slugs; F, snails; G, spiders; H, ticks; I, earthworms; nd, not determined; *, Burger 1978 (*Clasmatocolea humilis - Agrostis magellanica* mire and *Cotula plumosa* biotic community); #, Gleeson 1981.

PREY TYPE:	A	B	C	D	E	F	G	H	I	TOTAL
Biotic vegetation type										
Winter	26.5	0.0	119.3	19.9	86.2	0.0	265.2	13.3	1 100.4	1 631
Summer	46.4	0.0	132.6	46.4	106.1	0.0	53.0	0.0	1 107.0	1 491
1976/77*	nd	nd	nd	nd	nd	nd	nd	nd	nd	5 553
Mire vegetation type										
Winter	39.8	0.0	53.0	0.0	59.7	13.3	92.8	0.0	46.4	305
Summer	205.5	0.0	417.6	86.2	19.9	0.0	39.8	0.0	19.9	789
1976/77*	nd	nd	nd	nd	nd	nd	nd	nd	nd	1 467
Sum of 4 vegetation types										
Winter#	20	nd	200	28	nd	nd	90	nd	nd	nd
Summer#	26	nd	208	35	nd	nd	34	nd	nd	nd
Mean annual density in 19 vegetation types										
1976/77*	46	1	106	25	18	33	41	nd	1 354	1 980

Table 3.12. Macro-invertebrate biomass (dry mass)(grams/m^2) in different vegetation types during this and previous studies done at Marion Island. A, *Pringleophaga marioni* larvae; B, *Pringleophaga marioni* adults; C, weevil larvae; D, weevil adults; E, slugs; F, snails; G, spiders; H, ticks; I, earthworms; nd, not determined; *, Burger 1978 (*Clasmatocolea humilis - Agrostis magellanica* mire and *Cotula plumosa* biotic community); #, Gleeson 1981; $, Crafford 1990a.

PREY TYPE:	A	B	C	D	E	F	G	H	I	TOTAL
Biotic vegetation type										
Winter 1992	0.79	0.00	0.49	0.05	0.78	0.00	0.06	0.01	8.64	10.83
Summer 1992	0.80	0.00	0.42	0.23	0.70	0.00	0.03	0.00	13.46	15.64
1976/77*	0.97	0.00	0.75	0.35	0.09	0.00	0.29	nd	43.14	45.59
Winter 1987$	c. 4.00	nd	nd	nd	nd	nd	nd	nd	nd	nd
Summer 1987$	c. 5.50	nd	nd	nd	nd	nd	nd	nd	nd	nd
Mire vegetation type										
Winter 1992	0.42	0.00	0.11	0.00	0.65	nd	0.06	0.00	0.51	1.75
Summer 1992	1.79	0.00	0.80	0.33	0.12	0.00	0.04	0.00	0.20	3.28
1976/77*	0.28	0.00	1.30	0.38	0.00	0.00	0.02	nd	9.84	11.82
Winter 1987$	c. 0.80	nd	nd	nd	nd	nd	nd	nd	nd	nd
Summer 1987$	c. 1.00	nd	nd	nd	nd	nd	nd	nd	nd	nd
Sum of 4 vegetation types										
Winter#	0.44	nd	0.58	0.09	nd	nd	0.29	nd	nd	nd
Summer#	0.51	nd	0.59	0.06	nd	nd	0.14	nd	nd	nd
Mean annual biomass in 19 vegetation types										
1976/77*	0.62	0.02	0.42	0.12	0.22	0.32	0.14	nd	14.63	16.49
1987$	0.93	nd	nd	nd	nd	nd	nd	nd	nd	nd

CHAPTER 4. SEASONAL CHANGES IN AGE CLASS STRUCTURE AND REPRODUCTIVE STATUS OF HOUSE MICE AT MARION ISLAND

4.1 INTRODUCTION

It has been suggested that increasing temperatures since the late 1960s on Marion Island might have resulted in an increase in the numbers of feral house mice on the island (Smith and Steenkamp 1990). Aspects of the population biology of the island's house mice were studied in 1979/80 (Gleeson 1981, Gleeson and Van Rensburg 1982) and again in 1991/92 (Matthewson 1993, Matthewson et al. 1994) and it was shown that at two of the three habitats examined peak densities at the end of summer were, in fact, substantially higher in 1991/92 than in 1979/80. One possible reason is that ameliorating temperatures have extended the duration of the breeding season of house mice on the island.

Breeding in feral house mouse populations is regulated by a number of physiological and environmental factors Of the latter, temperature and food availability are generally the most important (Bronson 1979). The 1979/80 study at the island concluded that temperature, as well as high end-of-season mouse densities resulting in increased competition for food, were responsible for cessation of breeding in autumn and also a high mortality of mice in autumn and early winter. However, temperatures was not measured in that study, nor was the onset or cessation of breeding related to climatic measurements made at the island's meteorological station.

Macroinvertebrates such as insects, spiders and earthworms form the major part of the house mouse diet on the island (Gleeson and Van Rensburg 1982, Chapter 6); in fact, predation on macroinvertebrates represents, overwhelmingly, the biggest impact that mice exert on ecosystem functioning on the island (Rowe-Rowe et al. 1989, Crafford 1990b, Chown and Smith 1993). Densities and biomasses of the important macroinvertebrate prey species were determined in 1979/80. They actually changed very little between early summer when reproductive activity was increasing, mid summer when mouse densities were high and almost all adult mice were reproductively active, and autumn/early winter when numbers

were still high but the proportion of reproductively active mice was rapidly decreasing. No attempt was made to relate seasonal changes in macroinvertebrate numbers, or in some sort of "availability index" for the macroinvertebrate prey (for example macroinvertebrates density as a function of mouse density) to the onset or cessation of mouse reproductive activity. Matthewson et al. (1994) concluded (erroneously, as it will be shown here) that the timing of the onset and termination of breeding in 1991/92 was not different to 1979/80, and accepted the conclusions from the 1979/80 study that cessation of breeding at the end of the season could be ascribed to declining temperature and increasing competition for food. Neither temperature nor macroinvertebrate numbers were determined in 1991/92.

In this chapter I describe the seasonal changes in age class distribution and reproductive status of mice captured at three sites on the island in 1992/93, the austral summer immediately after the one in which Matthewson (1993) carried out his study. The timing of the breeding season is related to changes in photoperiod, temperature means, minima and maxima, and to the availability of invertebrate prey. The findings are compared with those of the previous studies in order to see whether what changes in house mouse reproductive biology occurred over the twelve year period.

4.2 MATERIALS AND METHODS

A monthly trapping programme was carried out between April 1992 and May 1993 at the three sites described in Chapter 3. Two of the sites (biotic and hummocky mosaic) are the same ones studied in 1979/80 and 1991/92. The mire site used here is very similar to, and close by, the dry swamp site employed in the two previous studies.

At each site transects were established, at least 10 m apart and well away from those used to estimate burrow system characteristics and soil macroinvertebrate densities (Chapter 3). An average of eight nights per month were devoted to trapping in each site. Thirty snap-traps were deployed 10 m apart along two or more of the transects at sunset and retrieved at first light. Bait consisted of raisins soaked in peanut butter, rolled oats, vegetable oil and golden syrup. A particular transect was not used more than once in a three month period.

The mice were processed within three hours of removal from the traps. They were sexed and ascribed to seven age classes according to the degree of wear of their upper right molar teeth (Table 4.1). Gleeson (1981) defined the classes by relating tooth wear of known-age Marion Island mice to the molar surface attrition pattern described by Lidicker (1966). This age class categorization was used in the two previous house mouse studies on the island. Male reproductive activity was assessed from whether males were scrotal or non-scrotal and females classed according to whether they had imperforate or perforate vaginas, were pregnant or lactating.

4.3 RESULTS

4.3.1 Sex and age class composition of captured mice

More males than females were caught at the three sites although the difference was not significant for the biotic site (Table 4.2). Males dominated the catch most in winter and spring; the difference became smaller in summer and disappeared in autumn. Only two class 1 ($\leq$ 1 month old) mice were caught during the study, both in spring at the biotic site.

Males and females showed similar seasonal changes in age class distribution (Figure 4.1). Class 4 contained the most mice in winter (June to September), class 6 the most in spring (October and November) and class 3 the most in summer and autumn (December to May). The few exceptions to this pattern were mainly at the hummocky site where class 3 females were more frequent than class 4 in winter, class 5 females more frequent than class 6 in spring, and class 5 and 6 males occurred in equal proportions in spring. The only other exception was that more class 6 than class 3 females were caught at the mire site in summer. In fact, class 6 individuals formed an important component of the summer population of both sexes at all three sites. This cohert (11 - 13 months old) would have been born the previous summer. By autumn there were few class 6 mice at any of the sites. Only 34 class 7 mice ($\geq$ 13 months) were caught, 31 of them in spring and summer.

Table 4.1. Age-related characteristics of the right upper molar tooth row of seven age classes of Marion Island house mice. The scheme is that of Gleeson (1981), redescribed by Matthewson (1993) using standard terminology.

Age class	Months		Characteristics
1	0-1	M1:	Not fully emerged.
		M2:	Not fully emerged.
		M3:	Not erupted.
2	>1-2	M1:	Dentine of cones t1, t2 and t3 not exposed. Dentine of cones t4 to t8 slightly exposed. Dentine of cones t7 and t8 not confluent.
		M2:	Cones t3 to t8 show slight wear. Dentine of cones t5 and t6 is not confluent.
		M3:	Dentine not exposed (no wear).
3	>2-4	M1:	Slight wear of cones t1, t2 and t3. Dentine of cones t4, t5 and t6 is confluent as is that of cones t7 and t8.
		M2:	Noticeable dentine exposure of cone t3. Dentine of cones t5 and t6 becoming confluent. Noticeable wear of cones t7 and t8 which are not confluent.
		M3:	Slight exposure of dentine.
4	>4-9	M1:	Dentine of cones t1 and t2 confluent.
		M2:	Dentine of cones t5 and t6 is confluent as is that of cones t7 and t8.
		M3:	Noticeable exposure of dentine.
5	>9-11	M1:	Dentine of cones t2 and t3 confluent. Dentine of cones t6 and t3 becoming associated. Heavy wear of cones t7 and t8.
		M2:	Dentine of cones t3 and t6 becoming confluent. Dentine of cones t7 and t8 confluent.
		M3:	Heavy wear of all cones.
6	>11-13	M1:	All cones worn heavily. Dentine of cone t3 confluent with that of t6. Dentine of t4 starting to become joined to t7.
		M2:	Dentines of cones t3 and t6, t4 and t7, t6 and t8 are confluent.
		M3:	Dentine of all cones is associated.
7	>13	M1:	Dentine of all cones associated but cones sometimes still discernible.
		M2:	Minimal enamel, dentine of all cones is associated.
		M3:	No enamel, cones not discernible.

Table 4.2. Sex of mice caught at the three sites and of mice caught in different seasons.

	Male	Female	χ^2	p
All mice	540	398	21.5	<0.001
Biotic site	230	200	2.1	0.15
Hummock site	125	83	8.5	0.004
Mire site	-185	-115	16.3	<0.001
Winter	212	145	12.5	<0.001
Spring	80	41	12.5	<0.001
Summer	159	126	3.8	0.05
Autumn	89	86	0.06	0.81

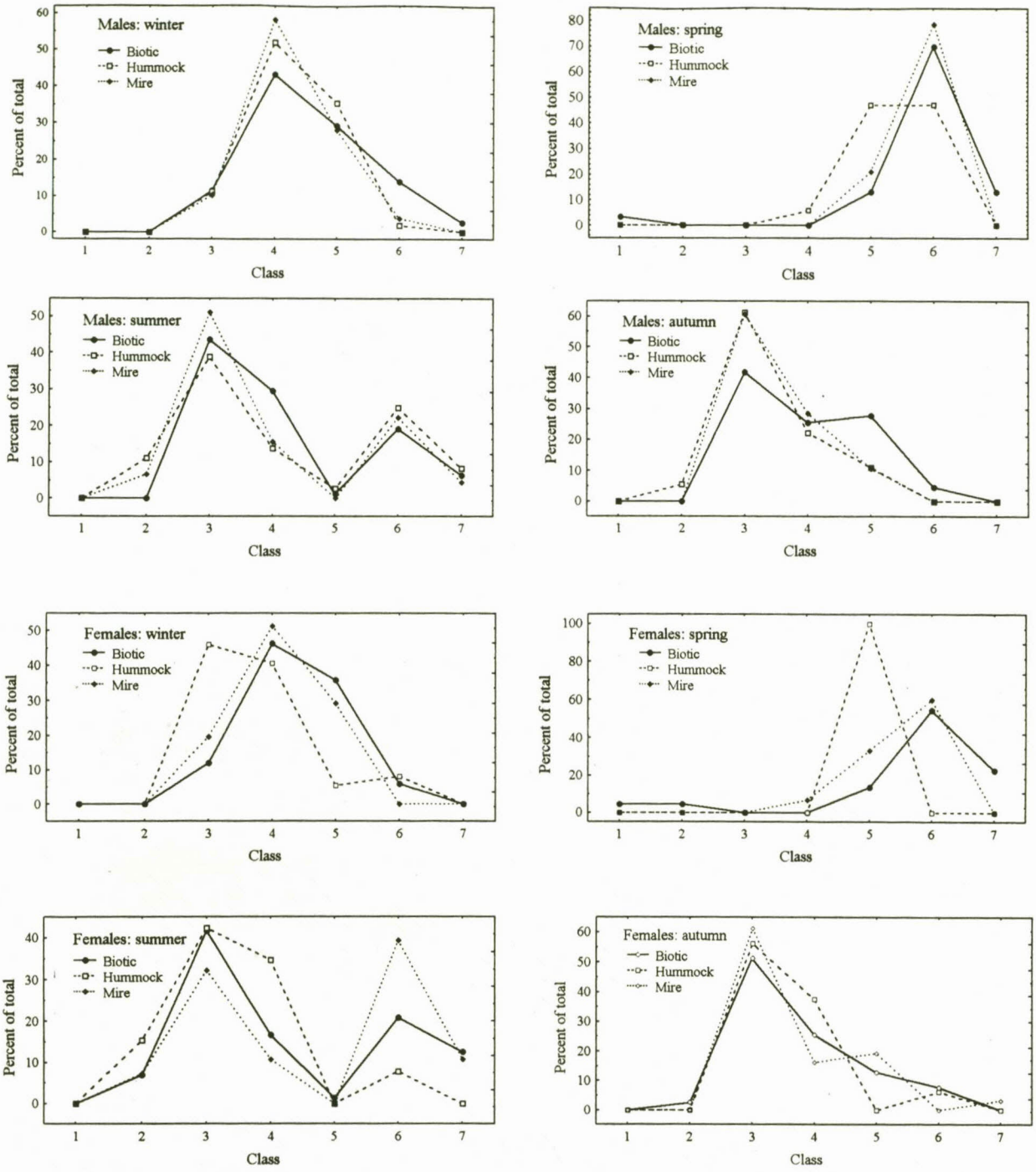

Figure 4.1. Percentage of mice in the various age classes in the four seasons at the three sites.

4.3.2 Sexual maturity and seasonality of reproductive status

The seasonal changes in reproductive status were identical at the three sites so the composite sample of mice was used in the analysis that led to the results presented in Table 4.3 and Figure 4.2. Since class 1 and 2 mice were always reproductively inactive (males non-scrotal, females with imperforate vaginas), only age class 3 to 7 individuals (here referred to as "adult" mice) were included in the analysis.

Females became reproductively active (perforate vaginas) in age class 3, or 2 to 3 months old (Table 4.3). The lightest perforate mouse weighed 13.3 g. The youngest pregnant and the youngest lactating females were also in class 3. Pregnant or lactating females were found in all age classes greater than class 2; even in class 7, 72% of the females were either pregnant or lactating. The youngest scrotal male was in age class 3 and weighed 13.1 g. Scrotal mice predominated all higher age classes; in fact, all of class 7 and 92% of class 6 males were scrotal.

In June and July none of the females were reproductively active. In August 4% of the females were perforate (Figure 4.2a) and the first pregnant females were found in October. By November all adult females were perforate or pregnant. The incidence of pregnancy peaked in December when just over 50% of adult females were pregnant. By January all adult females were reproductively active (perforate, pregnant or lactating). The last pregnant mice were found in (late) April and the last lactating and perforate mice in May. After January, but especially after March, the proportion of imperforate females increased sharply. At all three sites the youngest females were the first to become sexually inactive (Table 4.3). For instance, in January none of the adult females were imperforate. In February, March and April all imperforate adults were in age class 3. Only in May were imperforate class 4 and 5 individuals found for the first time

Scrotal males (one in class 5 and three in class 4) were caught in midwinter (June and July), but formed only a small percentage of the catch (Figure 4.2b). The proportion of scrotal males started increasing after July but rose most sharply, from 25% to over 90%, between August and September. It remained high throughout the whole of spring and summer, until March, after which it declined rapidly. As was the case with females, the first males to become non-reproductive were from the younger classes (Table 4.3). None of the adult classes contained

Table 4.3. Age classes to which pregnant and/or lactating females (P&L), females with perforated vaginae (PV), reproductively non active females (NON) and scrotal and non-scrotal (Non-S) males on Marion Island belonged over 12 months; include both adult and sub-adults.

Month	Female		Male	
	Reproductive state	Age classes	Reproductive state	Age classes
January	P&L	6 & 7	Scrotal	3,4,6 & 7
	PV	3	Non-S	2 & 3
	NON	2		
February	P&L	3 – 7	Scrotal	3 - 7
	PV	3,4 & 6	Non-S	2 & 3
	NON	2 & 3		
March	P&L	3,4,6 & 7	Scrotal	3,4,6 & 7
	PV	3 & 4	Non-S	2 - 4
	NON	2 & 3		
April	P&L	3 – 6	Scrotal	3 - 6
	PV	3 – 6	Non-S	3
	NON	2 & 3		
May	P&L	3,4,5 & 7	Scrotal	4 & 5
	PV	3 & 4	Non-S	2 - 5
	NON	3 - 5		
June	P&L	none	Scrotal	4 & 5
	PV	none	Non-S	3 - 5
	NON	3 - 6		
July	P&L	none	Scrotal	4
	PV	none	Non-S	3 - 5
	NON	3 - 5		
August	P&L	none	Scrotal	4 - 6
	PV	4	Non-S	4 & 5
	NON	3 - 6		
September	P&L	none	Scrotal	4 - 7
	PV	3 – 6	Non-S	4
	NON	4 - 6		
October	P&L	5 & 6	Scrotal	5 - 7
	PV	5 – 7	Non-S	1,5 & 6
	NON	1,2,5 & 7		
November	P&L	4 – 6	Scrotal	4 - 7
	PV	5 & 6	Non-S	5 & 6
	NON	none		
December	P&L	3,6 & 7	Scrotal	3,5,6 & 7
	PV	3 & 6	Non-S	none
	NON	2 & 3		

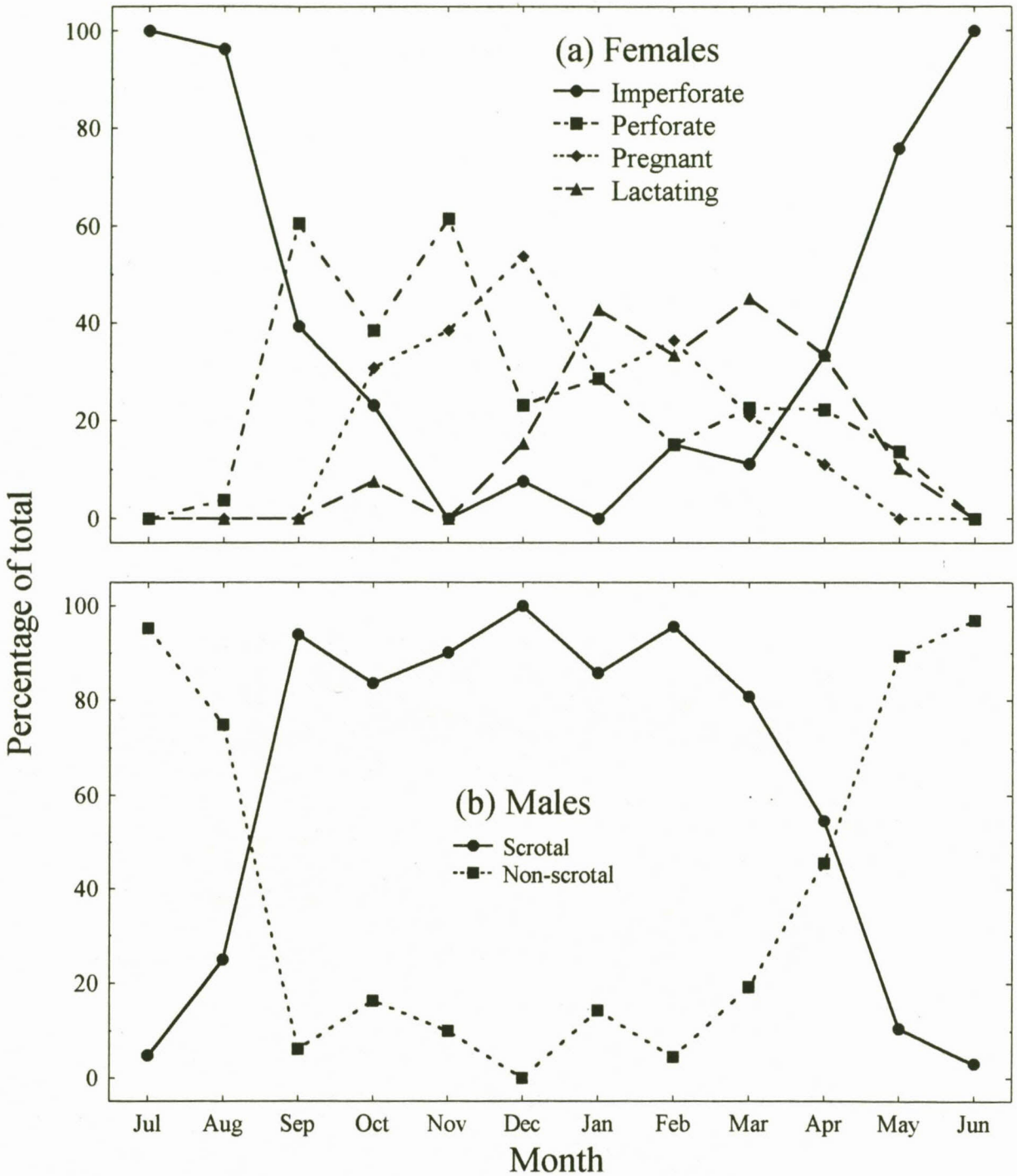

Figure 4.2. Seasonal changes in reproductive status of mice. Samples from the three sites were pooled. For convenience, the austral summer months are in the centre.

non-scrotal individuals in December. By January some class 3, by March some class 4, and by May some class 5, males had become non-scrotal.

Seasonal changes in the proportion of reproductively active adult females and males both reflected reasonably closely the changes in temperature 1 cm above the soil surface (Figures 4.3 and 4.4). Interestingly, in both sexes the incidence of reproductively active mice correlated better with average maxima than with average minima. For both sexes, the incidence of reproductive activity correlated less well with mean monthly air temperatures 1.2 m above the ground at the nearby meteorological station (for females r^2= 0.46, P=0.01, for males r^2 = 0.266, P=0.09, data not shown).

Despite the significant correlations between soil surface temperature and female reproductive activity in Figure 4.3, the increase in the proportion of reproductively active females in late winter was not synchronous with the main increase in temperature. For instance, the 4 to 60 % increase in the incidence of reproductive activity between August and September was accompanied by only a 0.3 ^{0}C increase in mean temperature, a 1 ^{0}C increase in average maximum temperature and a 0.2 ^{0}C decrease in average minimum temperature. Only after September did the values of the three temperature parameters started to increase sharply toward the summer maxima; for instance between September and October mean temperature rose by 1.9 ^{0}C, average maximum by 3.5 ^{0}C and average minimum by 1.1 ^{0}C. Similarly, in late summer all three temperature parameters started decreasing well before the main decline in the incidence of female reproductive activity. Between February and March mean, average minimimum and maximum values all fell by about 1½ ^{0}C but the proportion of reproductive females remained high at about 90%. However, the big drop in all three temperatures (mean by 4.1 ^{0}C, average maximum by 4.7 ^{0}C and average minimum by 3.3 ^{0}C) occurred two months later (between April and May) and this was associated with a large decline, from 67% to 24%, in the percentage of reproductively active females. By May the values of all three temperature parameters had declined to, or close to, their winter minima and only a few females were still reproductively active.

The late winter increase in the incidence of reproductive activity in males started before the main rise in mean and average minimum temperatures – by even more than was the case for females. By September, when mean and minimum temperatures were still close to their midwinter values, almost all males were already scrotal. Rather, the increase in the proportion

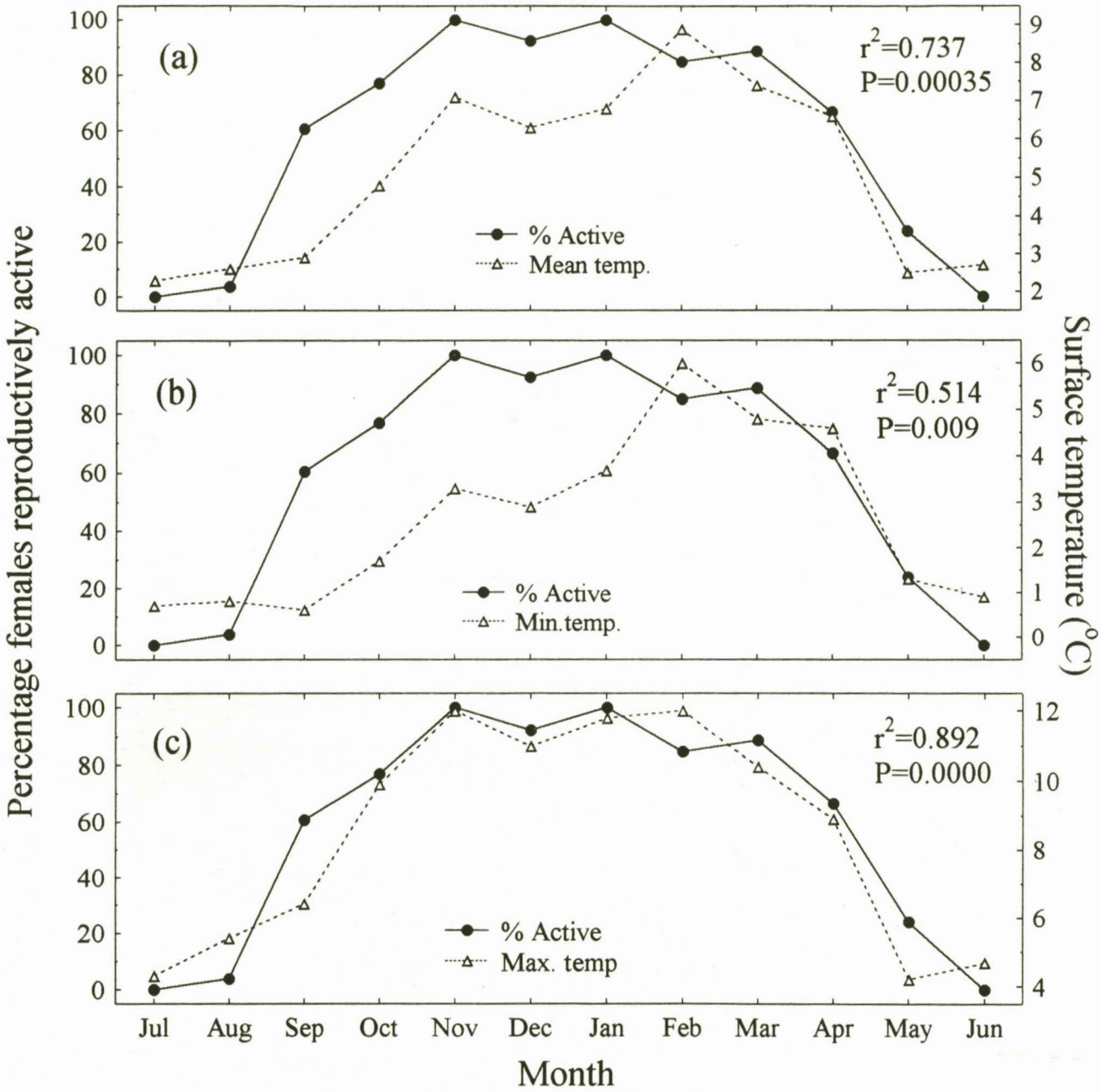

Figure 4.3. Seasonal changes in the proportion of adult females (age class >2) that were reproductively active and (a) monthly mean temperature, (b) monthly average minimum temperature and (c) monthly average maximum temperature during the study period. r^2 is the squared correlation coefficient of the correlation between proportion reproductively active females and the particular temperature parameter.

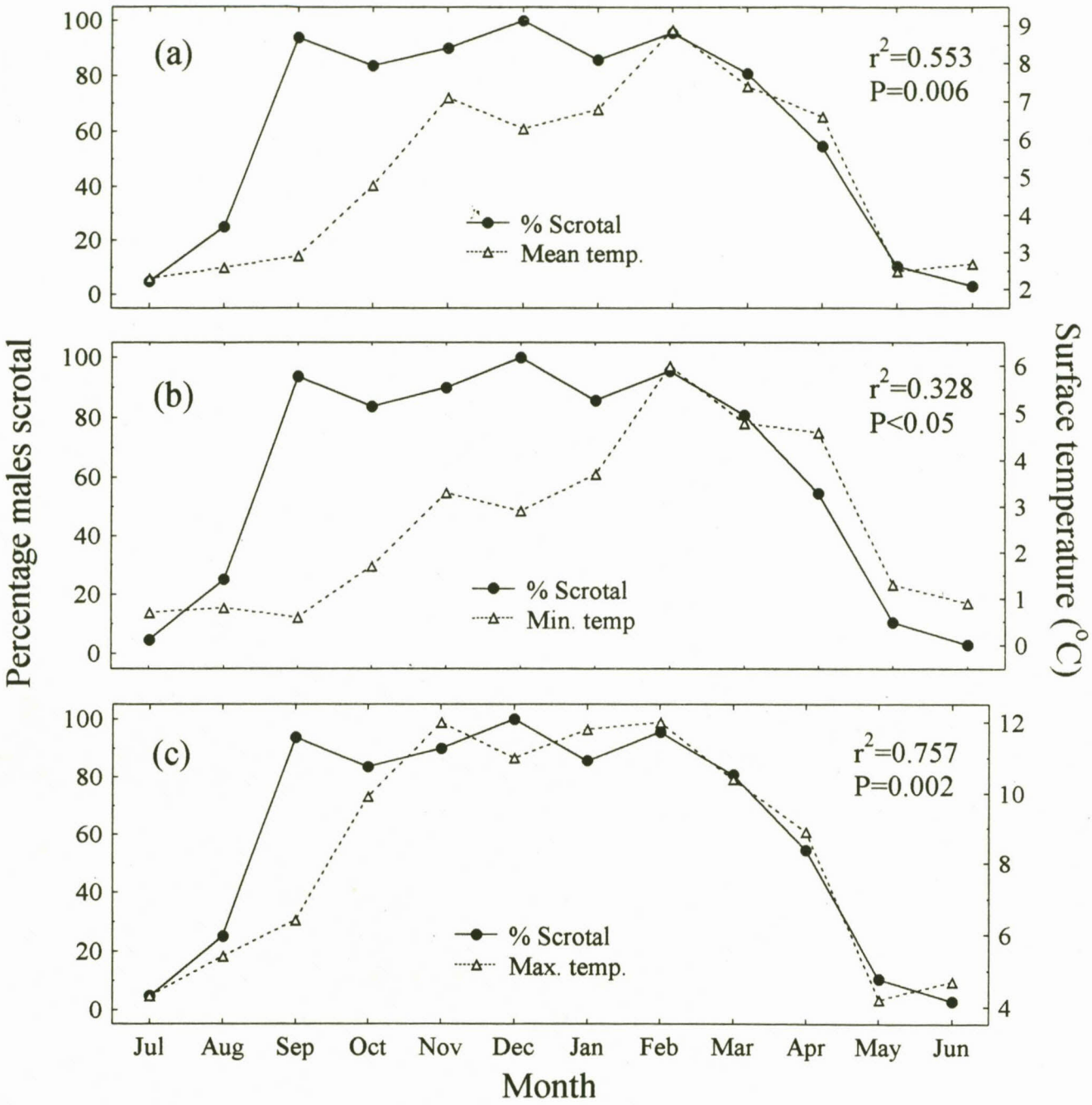

Figure 4.4. Seasonal changes in the proportion of adult males (age class >2) that were reproductively active and (a) monthly mean temperature, (b) monthly average minimum temperature and (c) monthly average maximum temperature during the study period. r2 is the squared correlation coefficient of the correlation between proportion reproductively active males and the particular temperature parameter.

of scrotal males coincided more closely with the rise in average maximum temperature (Figure 4.4c). Unlike with females, the start in the decline in the proportion of reproductively active males coincided exactly with the late summer decreases in the values of all three temperature parameters.

4.4 DISCUSSION

The death-trapped samples collected here contained a significant preponderance of males in all seasons but autumn. However, since mice were not trapped out at any of the study sites it is uncertain to what extent to which this reflects the sex ratios of the populations. A study in which 1427 mice were culled the previous year (May 1991 to March 1992) in a coastal area very close to the sites used here showed that sex ratios were significantly biased towards males in all seasons (Matthewson et al. 1994). From capture-and-release results Gleeson (1981) concluded that sex ratio was not significantly different from unity in any of six trapping sessions carried out between May 1979 and April 1980 in the biotic and hummocky sites, and a nearby mire similar to the one studied here. At the same three sites in 1991/92, Matthewson et al. (1994), using capture-and-release results, found significantly more adult (mass>13 g) males than females in all seasons excepting spring, in contrast to what was found in the study reported on here – that males outnumbered females most in winter and spring.

Age class composition of captured mice changed markedly during the year in a pattern that was essentially common to all three sites. In spring, older (especially class 6, 11 - 13 months) mice dominated the population. In summer class 6 remained important but class 3 (2 - 4 months) was predominant. Class 3 became even more predominant in autumn, when it comprised 40 - 60% of the males and 50 - 60% of the females across the three sites. In winter, class 4 was the most frequent one for both sexes, except that there were similar numbers of class 3 and 4 females at the biotic site.

Age class 6 mice made up, on average over the three sites, 32% of the total population and nearly 40% of the reproductively active group, in spring and summer. These mice would have been in class 3 or 4, and hence reproductively active, the previous summer and autumn. This shows that a substantial proportion of mice that are old enough to breed in one summer probably survives the winter to form an important component of the breeding population

throughout much of the following summer. The fact that only 3 of the mice caught in autumn and winter (about 0.5% of the catch) were older than 13 months (class 7), together with the big decrease in class 6 mice between summer and autumn (Figure 4.1) suggests that the onset of winter increases mortality of especially these older mice.

The age at which females reach sexual maturity (pregnant or lactating) was the same in this study as in 1991/92 (Matthewson et al. 1994), i.e. age class 3, or from two months old. All younger females were non-reproducrtive (imperforate). Pregnant age class 3 mice were also found in 1979/80 (Gleeson 1981). Eleven "reproductively active" females in age class 2 were also reported for 1979/80 but in that study any female that weighed ≥14 g was considered to be reproductively active. On that criterion some of the age class 2 females caught in both studies in the 1990s would also have been considered as reproductive. On the basis that the youngest pregnant mice were in age class 3, and the fact that pregnant age class 3 females were found at about the same time of the year (December) in the 1979/80 as in the two later studies, it is thought that age at sexual maturity has not changed since 1979/80.

From the data presented by Gleeson (1981) it is impossible to ascertain at what age male mice became scrotal in 1979/80. Similarly, although it was recorded whether or not the captured mice were scrotal or not in the 1991/92 study, this information was not provided on a per-age-class basis so comparison with the results presented here cannot be made. Testis mass was used as the criterion for male reproductive activity in 1991/92 and on that basis it was concluded that "males attain sexual maturity at an age of two months" , i.e. age class 3 (Matthewson et al. 1994). However, Matthewson (1993) presents testis mass data from the same study that show that 25% of males in age class 2 were considered to be reproductively active, and 31% as possibly reproductively active.

The fact that nearly three quarters of age class 7 females were either pregnant or lactating shows that female mice on the island breed until death, which may occur at more than 13 months. For males too, even the oldest individuals contribute to the sexually active population - all age class 7 males and 92% of age class 6 males caught were scrotal.

Berry et al. (1978), estimated the time of birth of 92 Marion Island housemice from their apparent ages when caught and concluded that breeding is probably continuous on Marion

Island. The strong pattern found here of a predominance of older mice in spring and summer, and of younger ones in autumn and winter, suggests that breeding is strongly seasonal, and agrees with the findings of the 1979/80 and 1991/92 studies.

In 1992/93 there was a strong seasonality in the proportion of reproductively active mice. All females captured in June and July 1992 were imperforate. Four percent of females were perforate in August and this increased to 60% in September. The proportions of reproductively active females (perforate, pregnant or lactating) fell from 88% of adult females in March to 66% in April and 24% in May. The sharpest drop, and the time when less than 50% of adult females become non-reproductive, was therefore between April and May. This suggests that the reproductive season for female mice on the island is from early September to late April. If pregnant or lactating mice are taken as indicators of breeding, these were found for the first time in October and their proportions declined from 66% in March, to 43% in April and 10% in May. Hence, the main breeding season for mice on the island in the 1992/93 summer was October to April, the same as was found the previous summer (Matthewson et al. 1994) when the "season of intense reproductive activity" (based on the period when at least 50% of mice were pregnant or lactating) was from October to April.

Although a few males remained scrotal throughout winter, the proportions of scrotal individuals rose very sharply between July and September and decreased as sharply between March and May. If estimated as the period when >50% of the mice are scrotal, then the main reproductive season for males in the 1992/93 season was early September to April, coinciding with the period when females were reproductively active. Matthewson et al. (1994) found that in the previous season the peak reproductive season for males (based on testis weight) was August to March. They did not present the testis weight data but state that "mean testis weight remained low from May to August" and "increased rapidly during September". The same study was reported in more detail by Matthewson (1993) where it is stated that the percentage of adult (body mass >13 g) males "which were scrotal or had palpable testes remained low from May to August and then increased rapidly from August to September, remaining relatively high until the last trapping session in March". The data presented in that account also clearly shows that the winter minimum in percentage of adult scrotal males occurred in August. Hence the first month of the main reproductive period for males in 1991 was September, as in 1992. The percentage scrotal adult males (81%) in March 1992 was also identical to that reported here for March 1993. Had sampling in the 1991/92 study continued

it is likely that a considerable proportion of the scrotal males would have been found in April; in 1993, 55 % of adult males were still scrotal in April. Hence, reappraisal of the results of the 1991/92 study suggests that the main season of reproductive activity for males was early September to April, the same as found in 1992/93.

The main late winter increase in the proportion of reproductively active mice, especially males, occurred well before mean and average minimum temperatures started to really rise (Figures 4.3 and 4.4). The increase in the incidence of reproductive activity was more synchronised with the average maxima, which rose more sharply, and earlier, than the other two temperature parameters. Toward the end of summer, between February and March, all three temperature parameters started to decrease, simultaneously with a decline in the proportion of scrotal males. In the same period the proportion of pregnant females fell from 36% to 21% (data not shown) but that of perforate and, especially, lactating mice increased, so that the proportion of reproductively active females remained high until March, and started to really decrease after April. For males then, the start of the decline in reproductive activity coincided with when temperature first started coming down, whereas with females it occurred at least a month afterwards.

If, then, temperature is important in influencing housemouse reproduction on the island it seems that rising daily maxima provides the cue for the initiation of reproductive activity. Declining (mean, minima and maxima) temperature signals the onset of cessation of reproduction although the number of lactating females only starts declining later.

Other factors that might regulate when mice are reproductively active at the island include photoperiod and food availability. For both sexes the seasonal variation in the percentage mice that are reproductively active was strongly correlated with changes in the monthly mean of daylength (Figure 4.5). The late winter increase in reproductive individuals was closely synchronous with lengthening days and the decline started two (males) or three (females) months after days started shortening. This is a very similar pattern to the seasonal relationship between reproductive activity and temperature and it is likely that the reproduction:daylength relationship is actually a manifestation of the close correspondence between daylength and temperature at the island. From studies that showed that feral housemouse populations do not breed seasonally when subjected to marked seasonal variations in daylength but not temperature, and also from the fact that mice kept in constant darkness breed normally,

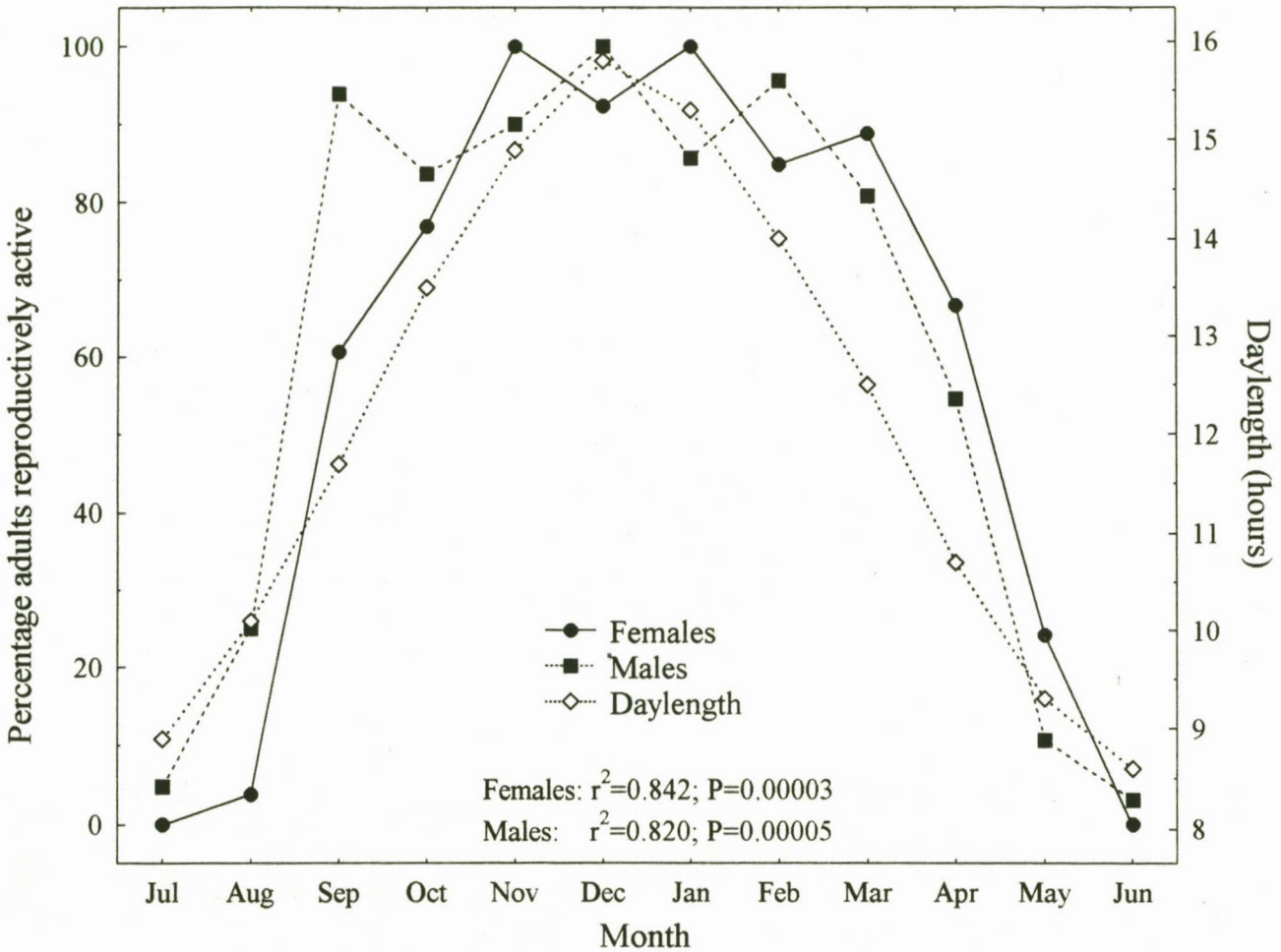

Figure 4.5. Seasonal variation in the proportion of reproductively active adult (age class >2) mice in the population and in daylength.

Bronson (1979) concluded that photoperiodic regulation of reproduction in housemice is weak or absent.

In the year before this study was carried out, Matthewson et al. (1994) found that mouse densities increased 6 to 13 fold at the three sites during spring and summer and reached peak values in May. They ascribed the subsequent winter decrease in density to temperature-mediated cessation of breeding and a decline in food supply, but did provide information on by how much food availability actually declined from summer to winter. Mice feed mainly on macroinvertebrates such as insects, snails, earthworms and spiders (Chapter 6, also Gleeson 1981). In Chapter 3 it was shown that densities of moth larvae and weevil adults and larvae (important items in the diet of the island's mice) at the mire site were significantly lower in winter than in summer of 1992/93. At the biotic site there were no significant summer-winter differences in densities of any of the macroinvertebrate components of the mouse diet; in fact spiders actually occurred in higher numbers in winter. Macroinvertebrate densities were not measured in the hummocky mosaic site.

To see to what extent food availability, on a per mouse basis, changed between early summer, when the proportion of reproductively active mice was strongly increasing, and early winter, when it was strongly decreasing, macroinvertebrate densities and biomasses at the biotic and mire sites (Chapter 3) were divided by mouse densities reported for these sites by Matthewson et al. (1994) (Table 4.4). By early winter the number of invertebrates per mouse had declined 5 fold at the biotic site and 18 fold at the mire, compared with numbers per mouse in early summer. For the biotic site the decrease in food availability was even greater when considered on the basis of the change in invertebrate biomass per mouse between summer and winter. Hence, at the end of summer the island's housemouse population is faced with decreasing temperatures and a sharp drop in the relative availability of food, and both factors are probably important in causing the decline in reproductive activity (and the sharp decline in mouse density) during early winter.

It is especially interesting to compare the seasonality of reproductive activity found in the studies carried out between 1991 and 1993 with that found in 1979/80 (Gleeson 1981). In the 1979/80 study mice were live-trapped and snap-trapped during six sessions that varied from 11 to 61 days and some sessions included parts of up to three calendar months. Hence, the resolution of the data is not as fine as those yielded by the monthly sampling used in the

Table 4.4. Mouse densities and macroinvertebrate densities and biomasses in spring/early summer, and in autumn/early winter at the biotic and mire sites. Mouse densities are those reported for November and May 1991 at the biotic site and November and June 1991 at the mire site by Matthewson *et al.* (1994). Macroinvertebrate densities and biomasses are from Table 3.7 and 3.8 and exclude slugs.

	Spring/early summer	Autumn/early winter
Biotic site		
Mouse density (mice ha^{-1})	43	242
Macro-invertebrate density (thousands $ha^{-1)}$	13 860	15 450
Macro-invertebrate biomass (kg ha^{-1})	145	100
Macro-invertebrates per mouse (thousands $mouse^{-1}$)	322	64
Macro-invertebrate biomass per mouse (kg $mouse^{-1}$)	3.4	0.4
Mire site		
Mouse density (mice ha^{-1})	9	51
Macro-invertebrate density (thousands $ha^{-1)}$	7 620	2 380
Macro-invertebrate biomass (kg ha^{-1})	32	11
Macro-invertebrates per mouse (thousands $mouse^{-1}$)	847	47
Macro-invertebrate biomass per mouse (kg $mouse^{-1}$)	3.6	0.2

1991/93 studies and comparison between the two periods is not straightforward, which probably lead Matthewson et al. (1994) to conclude that "the length of the breeding season (in 1991/92) was similar to that recorded earlier (in 1979/80)". However, careful consideration of the data shows that the period of reproductive activity has in fact changed quite markedly since 1979/80.

In a trapping session lasting from 31 August to 26 October 1979 (i.e. the whole of September and most of October), 52% of the adult males (mass >12.5g) were scrotal (average for the biotic, hummocky and mire sites), compared with 94% in September 1992 (Figure 4.2b) and 100% in September 1991 (Matthewson 1993). In the previous trapping session (27 June to 28 August) 7% of males were scrotal, compared with an average of 15% for July and August 1992 and about 27% for July and August 1991. The lower incidence of scrotal males in late winter/early spring of 1979/80 than in the corresponding periods in 1991 and 1992 suggests that male reproductive activity might have started later in 1979/80.

At the end of the 1979/80 summer, in a trapping session from 2 March to 9 April (i.e. almost all of March and about $^1/_3$ of April) an average of 64% of males were scrotal, compared with 81% in March 1992 and March 1993 and 55% in April 1992. A mean value for March/April 1993, with the March value weighted to contributes a three times more than the April one, is 75%, higher than the March/April 1980. Hence it seems that male reproductive activity may have started to decline earlier, or at least declined more quickly, in 1979 than in 1993.

With females, differences in the onset and cessation of reproductive activity between 1979/80 and 1991/93 are much more distinct. In 1979, no pregnant or lactating mice were found in the trapping session that included the whole of September and most of October. As late as 26 October there were no pregnant or lactating mice in any of the three sites, in contrast to October 1991 when about 12 % of adult females were pregnant (Matthewson et al. 1994), and October 1992 when 38% were either pregnant or lactating. In 1991 pregnant females were present as early as September. It is clear then that the breeding season started at least a month, and possibly 1½ months, earlier in 1991/93 than in 1979/80. Even in a trapping session that included most of November and half of December, only 26% of mice were pregnant or lactating in 1979, compared with 38% (November) and 69% (December) in 1992 and >90% for both months in 1991 (Matthewson 1993). Hence, even well into late spring and early

summer, the incidence of pregnant and lactating females was considerably lower in 1979/80 than in 1991 or 1992.

In 1980 no pregnant or lactating mice were found at the biotic or mire sites, and only 8% of adult females were pregnant or lactating at the hummocky site, after the first of March (Gleeson 1981). In contrast, in March 1992 about 67% of live-trapped adult females at the biotic site were still pregnant or lactating (Matthewson 1993), and about $^1/_3$ of snap-trapped females at a nearby coastal site were pregnant (Matthewson et al. 1994). In March 1993, 65% of all adult females from the three sites were pregnant or lactating; in fact, just over 10% of females were still pregnant in April and about 10% still lactating in May. Clearly, the mouse breeding season, if taken as the period when adult females are pregnant or lactating, ended between one and two months later in 1991/93 than in 1979/80. Considered with the earlier appearance of pregnant mice in spring in 1991 and 1992, this is strong evidence that the reproductive season for mice has increased considerably, by at least two months, since 1979/80.

The later cessation of breeding in 1992 and 1993 is especially remarkable considering that peak mouse densities at the end of summer were considerably higher than in 1979/80 (at least for the biotic and hummocky mosaic sites; Matthewson et al. 1994). Density and biomass of the prey invertebrates in almost all of the island's habitats have also decreased since the 1970's (Chapter 3), so the availability of food, on a per mouse basis, might be expected to have been lower in 1991/93 than in 1979/80, especially toward autumn and early winter when mouse densities are high. Gleeson (1981) presented seasonal changes in composite biomass values for *Pringleophaga marioni* larvae, spiders, weevil larvae and weevil adults which, from stomach contents, he considered these to be the main macroinvertebrate food items in the mouse diet. Table 4.5 compares the biomass of this group of invertebrates at the biotic and mire site during May and June 1979 with values in June 1992, and mouse densities in May/June 1979 with those in May/June 1991. In 1992, invertebrate biomass in autumn at the biotic site was less than a half, and at the mire site about a quarter, of the corresponding values in 1979 (significance of these differences cannot be assessed since no fiducial limits are available for the 1979 data). In autumn/early winter of 1991 mouse densities at the biotic site were about double those in 1979 ($P<0.05$; Matthewson et al. 1994) but those at the mire were slightly lower than in 1979 ($P>0.05$). Assuming mouse densities were the same in 1992 as in 1991 then the "availability" of the four invertebrate food items, on a per mouse basis,

Table 4.5. Mouse densities and invertebrate biomass at the end of the breeding season (autumn, early winter) in 1979/80 and 1991/92. The 1979 values are for a sampling period lasting from 10 May to 24 June (Gleeson 1981). The 1991/92 mouse densities are for May (biotic site) and June (mire) 1991 (Matthewson *et al.* 1994) and the invertebrate biomasses are for June 1992 (winter sample, Table 3.8). Invertebrate biomass comprises moth larvae, weevil larvae and adults and spiders.

	1979/80	1991/92
Biotic site		
Invertebrate biomass (kg ha^{-1})	29.1	13.9
Mouse densities (mice ha^{-1})	126	242
Invertebrate biomass per mouse (g $mouse^{-1}$)	231	57
Mire		
Invertebrate biomass (kg ha^{-1})	21.4	5.9
Mouse densities (mice ha^{-1})	66	51
Invertebrate biomass per mouse (g $mouse^{-1}$)	324	116

was only ¼ (biotic site) or $^1/_3$ (mire) of that in 1979. Hence, greater competition for food in 1991/93 was not associated with an earlier cessation of breeding compared with in 1979/80; rather the opposite was true.

Ameliorating temperatures were possibly responsible but no microclimate data are available for 1979/80. Certainly, annual mean air temperature at the nearby meteorological station increased during the 1980s (5.5 °C in 1979 and 5.7 °C in 1980, compared with 5.9 °C to 6.2 °C for 1991/92/93; Smith 1992). However, the comparison is not as clearcut if one considers late summer and early winter separately (Table 4.6). From February to April mean monthly temperature was higher, but from May to July it was lower, in 1991/92 than in 1979/80. In 1991 and 1992 a high proportion of females were pregnant or lactating in April and there were still lactating mice in May. The fact that no pregnant or lactating mice were found after March 1980, despite the greater availability of macroinvertebrate prey items, was possibly because late summer temperatures were so low, compared with those in the two 1990 studies.

Table 4.6. Monthly mean air temperatures in late summer and early winter: averages for 1979 and 1980 compared with those for 1991 and 1992.

	1979/80	1991/92
Late summer		
February	7.8	9.0
March	7.9	8.3
April	6.5	7.9
Early winter		
May	6.2	6.0
June	5.0	4.4
July	4.6	4.3

CHAPTER 5: ON THE MORPHOMETRICS OF MARION ISLAND HOUSE MICE

5.1 INTRODUCTION

Body mass and length are mainly genetically determined, but body growth and condition are also dependent on environmental conditions (Jakob et al. 1996; Thorpe 1981). Hence, as with reproduction, sex ratios and age structures (Chapter 4), morphological changes such as in body mass and length, length and shape of intestines, and kidney and adrenal mass, can provide information on a population's response to fluctuating environmental parameters.

In this section I relate body mass, body length, intestine shape and length and kidney and adrenal mass to environmental variables in order to better understand the relative degree of both environmental and social stress that Marion Island house mice experience throughout a year in four different vegetation types.

Length and shape of mouse intestines have also been related to environmental parameters. Apart from consuming more food, there are other digestive adaptations that could enable mammals to meet a greater need for nutrients during periods of higher energy needs (such as during reduced environmental temperatures, increased social stress, pregnancy and lactation, diabetes, intestinal resection, and periods of food shortage - Karasov & Diamond 1985). Higher extraction efficiency due to greater intestinal surface area at the macroscopic, microscopic and submicroscopic levels have been described in a number of studies (Buret et al. 1993; Diamond 1987; Karasov & Diamond 1985; Sibly 1981; Williams et al. 1995, and others). By lengthening of the gut (a proliferation of mucosal surface per unit length of intestine - Karasov & Diamond 1985), the intestine is enabled to process more food in a shorter time without any sacrifice in extraction efficiency (increased rates of uptake for all nutrients). Sibly (1981) found that the shape of the alimentary canal affects digestive efficiency and that it also varies with diet. Barry (1976, 1977) showed that, among closely related species, the large intestine is larger, the small intestine smaller and the caeca relatively larger and more complex in herbivores than in both carnivores and omnivores of similar size, as would be expected since the large intestine is important for nutrient and energy absorption

from cellulose after it has been broken down by microbial digestion in the caecum (Barry 1976; Schmidt-Nielsen 1985). Such a study has, however, never before been done on an omnivore in which the contribution of animal/plant to the diet fluctuates throughout the year.

Barnett (1965) reported heavier kidneys in colder environments and interpreted this as the kidneys having to work harder due to the higher rate of heat production. He also found that kidneys became heavier during pregnancy. Konarzewski & Diamond (1995) found a positive correlation between basic metabolic rate (BMR) and *inter alia* kidney mass of *Mus musculus*. They suggested that large masses of metabolic active organs are subject to natural selection through evolutionary trade-offs. On the one hand they make high energy budgets possible, but on the other hand they are energetically expensive to maintain. Changes in adrenal mass have been used as an indication of changes in environmental stress in mouse populations (Berry & Jakobsen 1975; Lidicker 1966). Adrenals enlarge (hypertrophy) in response to stress, especially to cold (Barnett 1965). Feist & Feist (1978) found that cold acclimated voles had an increased ability to synthesize adrenal enzymes.

5.2 MATERIALS AND METHODS

Data in this chapter were collected from the same mice caught for study of age class composition and reproductive status in Chapter 4.

The sexed, age-classes mice were weighed to the nearest 1 mg (females, with and without gravid uterus) and total and tail length measured to the nearest 1 mm. Mice which had lost part of their tails were excluded from tail-length measurements. Small intestine, large intestine and caecum lengths were measured to the nearest 1 mm (mesenteries were cut and straightened - not stretched, following Schieck & Millar 1985), left kidney and both adrenal glands were weighed to the nearest 1 mg, reproductive state was noted and foetuses weighed to the nearest 1 mg. Processing of the mice was completed within three hours of removal from the traps, during which time they were kept in a fridge at *c.* 3°C.

5.3 RESULTS

5.3.1 Age class, body mass, body and tail lengths

Body mass and length both increased with age class (Figures 5.1a & b). The sharpest increase was between class 2 and 3, approximately between age 1½ and 3 months. Tail length (Figure 5.1c) also increased with age from class 1 to class 4 but did not differ significantly between the higher age classes. If there were obvious signs of tails having been bitten off, or frostbitten, then they were not measured but some class 7 mice had quite short (<80 mm), apparently undamaged tails and this caused substantial variability in the tail length data for this class .

Total length (body plus tail length) increased with age up to class 6, but especially markedly between class 2 and 3 (Figure 5.1d).

The mass/length versus age class patterns in Figure 5.1 are overall ones for all the mice caught during the study. Almost identical patterns are obtained for individual sites (data not shown), although mean values for particular age classes sometimes differed significantly between sites. Both males and females showed very similar patterns to those in Figure 5.1 but the coefficients of the age class: mass/length regressions are significantly different between the two sexes, excepting in the case of tail length (Table 5.1). The slopes of mass, body length and total length versus age class relationships are significantly smaller, and the intercepts significantly larger, for males than for females. The actual values of the slopes and intercepts are meaningless because the different age classes represent different time intervals but their differences suggest that male mice are born bigger (heavier, with longer bodies), but grow more slowly, than female mice.

Mass, body length, tail length and total length means for males were all significantly greater than for females (Table 5.2). However, mean age class (Table 5.2) and also the shape of the age class frequency distribution (Figure 5.2) differed significantly between male and female samples. Age class 4 was the most frequent class for males and class 3 the most frequent for females. Classes 5, 6 and 7 accounted for 41% of the male sample but only 36% of the female sample. If this fact, that the females sampled in the investigation were overall younger than

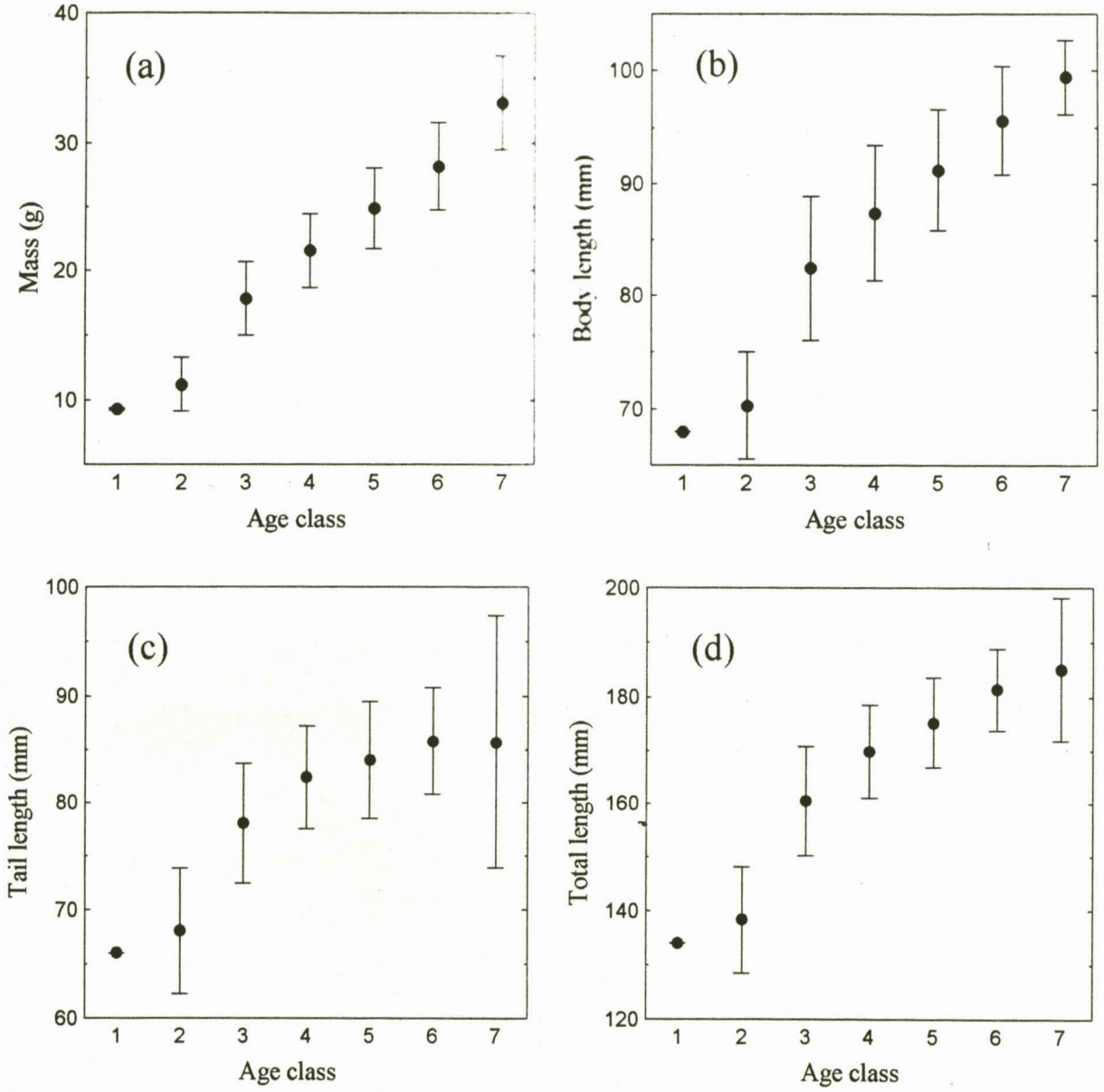

Figure 5.1. Relationship between body measurements and age class in Marion Island mice.

Table 5.1. Slope and intercept coefficients (± standard errors) of the regressions of mass, body length, tail length and total length against age class. P indicates the significance level of the between-sex difference in slope or intercept.

	Slope	Intercept
Age class versus:		
Mass		
Male	3.44 ± 0.11	7.70 ± 0.48
Female	3.91 ± 0.13	5.53 ± 0.55
P	0.01	0.01
Body length		
Male	4.15 ± 0.21	70.6 ± 0.94
Female	5.07 ± 0.24	65.8 ± 1.06
P	0.01	0.001
Tail length		
Male	2.55 ± 0.20	71.3 ± 0.89
Female	2.65 ± 0.25	69.7 ± 1.12
P	>0.1	>0.1
Total length		
Male	6.70 ± 0.32	142.0 ± 1.49
Female	7.7 ± 0.4	136.0 ± 1.79
P	0.05	0.01

Table 5.2. Mean (± standard deviation) mass, body length, tail length, total length and age class of all male and female mice trapped in the study.

Sex	N	Mass* (g)	Body length (mm)	Tail length (mm)	Total length (mm)	Age class
Male	540	22.7 ± 5.1	88.9 ± 7.5	82.5 ± 6.2	171.4 ± 12.1	4.4
Female	398	21.9 ± 5.9	87.2 ± 8.9	80.9 ± 7.2	168.0 ± 14.2	4.2
F		5.6	9.4	13.4	14.3	5.2
P		0.02	0.002	0.0003	0.0002	0.02
F_{age}		0.8	5.2	9.2	10.5	
P_{age}		0.4	0.02	0.002	0.001	

F is the variance ratio and P is its significance, from analysis of variance (ANOVA).

F_{age} and P_{age} are the ANOVA statistics if differences in age class between the samples are accounted for by including age class as a covariate in the ANOVA.

*Mass excludes fetus mass, which would add 0.2 g to the female mean but the male-female difference is still significant at $P<0.05$.

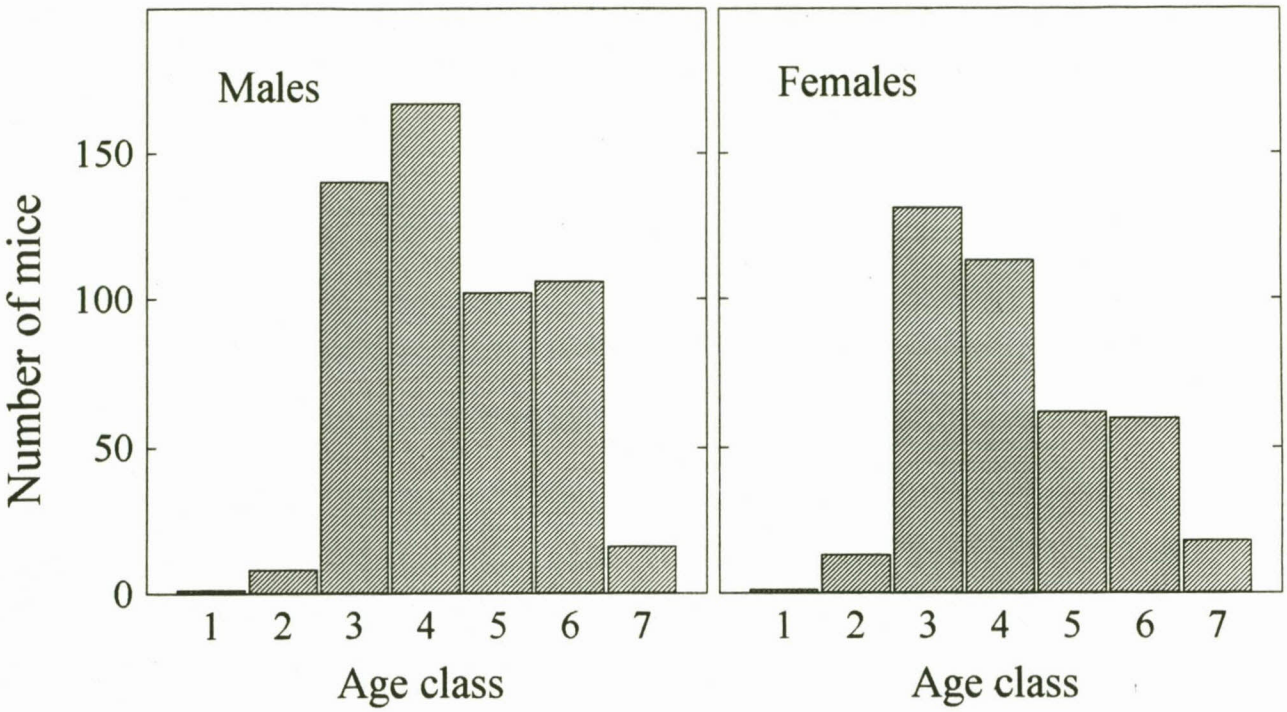

Figure 5.2. Age class distributions of all the male and female mice captured in 1992/93.

the males is accounted for (Table 5.2, F_{age} and P_{age} statistics), there was no difference in body mass between sexes but males still had longer bodies and tails than females.

The between-sex comparisons in Table 5.2 are for the total sample of mice caught in the study. Particular sites showed different permutations of this overall pattern (Table 5.3). Males from the hummocky mosaic and biotic sites were heavier and had longer bodies and tails than females. The mean age class of hummock site females (3.7) was significantly smaller than that of males (4.3) and the age class distribution of the female sample (not shown) was also significantly skewed toward the younger age classes so that 49% of females (but only 29% of males) were in age class 3 or lower. Accounting for this, none of the male-female differences in mass or length for the hummock site mice are significant at $P \leq 0.05$. For the biotic site there were no significant between-sex differences in mean age class or in the shape of the age class distribution (not shown) and including age class as covariate in the comparison in fact *increases* the significance of the male-female differences in mass and length (compare P and P_{age} for this site in Table 5.3).

The male and female samples from the mire site had the same mean age class, very similar age class frequency distributions (not shown), and did not differ in body mass, body length or tail length.

These across-site disparities in male-female size differences suggest sex specific between-site differences in mass and length and this is examined in Table 5.4. Males from the biotic site were heavier, had longer bodies and were longer overall than males from the other two sites. Biotic site males also had significantly longer tails than mire site males. Examining these differences in more detail (data not presented) showed that biotic site age class 4, 5 and 6 males were all significantly heavier and longer than males in the corresponding classes at the other two sites. Biotic site class 7 males were also heavier and longer than class 7 males from the other two sites but the differences were not significant at $P \leq 0.05$. The samples of age class 1 and 2 males were too small to do an inter-site comparison.

Hummock site females were significantly lighter and had shorter bodies than females from the other two sites (Table 5.4). However, hummock site females were, overall, significantly younger than females from the other two sites and if this is accounted for then for female mice there were no between-site differences in body mass, body length or tail length. A more

Table 5.3. Mean (± standard deviation) mass, body length, tail length, total length and age class of male and female mice at the three sites.

Site	Sex	N	Mass (g)	Body length (mm)	Tail length (mm)	Total length (mm)	Age class
Hummocky	Male	125	21.8 ± 5.1	87.2 ± 8.4	82.8 ± 6.7	170.0 ± 13.5	4.3
mosaic	Female	83	19.4 ± 4.4	83.6 ± 8.2	80.1 ± 5.4	163.7 ± 11.8	3.7
	F		12.9	8.8	8.7	11.1	15.0
	P		0.0004	0.003	0.004	0.001	0.001*
	F_{age}		0.4	0.03	0.4	0.2	
	P_{age}		0.5	0.9	0.5	0.7	
Mire	Male	185	22.1 ± 4.3	88.1 ± 6.4	81.4 ± 5.8	169.5 ± 11.0	4.3
	Female	115	22.3 ± 6.0	87.2 ± 8.6	80.6 + 6.5	167.8 ± 13.8	4.3
	F		0.2	1.0	1.1	1.3	0.05
	P		0.6	0.3	0.3	0.3	0.8
	F_{age}		0.9	1.1	1.3	1.7	
	P_{age}		0.4	0.3	0.3	0.2	
Biotic	Male	230	23.8 ± 5.5	90.5 ± 7.7	83.4 ± 6.0	173.8 ± 11.7	4.5
	Female	200	22.7 ± 6.1	88.7 ± 8.9	81.3 ± 8.3	170.0 ± 15.1	4.3
	F		3.9	4.7	8.0	8.2	1.0
	P		0.04	0.03	0.005	0.004	0.3
	F_{age}		4.8	7.9	8.4	12.3	
	P_{age}		0.03	0.005	0.004	0.0005	

F is the variance ratio and P is its significance, from analysis of variance (ANOVA).
F_{age} and P_{age} are the ANOVA statistics if difference in age class between the samples are accounted for by including age class as a covariate in the ANOVA.

*These indicate the significance of the male-female difference in mean age class. The shape of the age class distribution (not shown) differs significantly between sexes for the hummocky site (P=0.005, Kolmogorov-Smirnov test) but not for the other two sites (both, P>0.1).

Table 5.4. Mean masses and lengths of male and female mice in each of the three sites. For standard deviations see Table 5.3.

Sex	Site	N	Mass (g)	Body length (mm)	Tail length (mm)	Total length (mm)	Age class
Male	Hummock	125	$^{a}21.8^{a}$	$^{a}87.2^{a}$	$^{ab}82.8^{ab}$	$^{a}170.0^{a}$	$^{a}4.4$
	Mire	185	$^{a}22.1^{a}$	$^{a}88.1^{a}$	$^{a}81.4^{a}$	$^{a}169.5^{a}$	$^{a}4.3$
	Biotic	230	$^{b}23.8^{b}$	$^{b}90.5^{b}$	$^{b}83.4^{b}$	$^{b}173.8^{b}$	$^{a}4.4$
	F		9.3	8.7	5.6	7.7	1.2
	P		0.0001	0.0002	0.004	0.0005	0.3*
	F_{age}		13.9	12.4	5.9	10.5	
	P_{age}		<0.0001	<0.0001	0.003	<0.0001	
Female	Hummock	115	$^{a}19.4^{a}$	$^{a}83.6^{a}$	$^{a}80.1^{a}$	$^{a}163.7^{a}$	$^{a}3.7$
	Mire	83	$^{b}22.3^{a}$	$^{b}87.2^{a}$	$^{a}80.6^{a}$	$^{ab}167.8^{a}$	$^{b}4.3$
	Biotic	200	$^{b}22.7^{a}$	$^{b}88.7^{a}$	$^{a}81.3^{a}$	$^{b}170.0^{a}$	$^{b}4.4$
	F		10.4	9.5	0.9	5.6	9.0
	P		<0.0001	<0.0001	0.4	0.004	0.0001
	F_{age}		1.7	2.4	0.8	1.0	
	P_{age}		0.2	0.09	0.4	0.4	

Superscripts to left of means show homologous groupings of sites ignoring age class differences between the samples. Superscripts to the right of means indicate homologous groupings of sites if the age class differences are accounted for. Homologous groupings are by the Spjotvol and Stoline (1973) generalization of Tukey's test.

detailed analysis of inter-site differences for particular age classes (data not presented), showed that biotic site females were slightly heavier than females from the other two sites but the difference was only significant for the age class 5 group.

In Chapter 4 it was shown that the annual variation in mean age class was quite similar at the three sites, with maxima occurring in spring or early summer. Age class then declined throughout the rest of summer as newborn mice entered the population. The change in age class composition is examined here in more detail, separately for each site (Figure 5.3). Maximum mean age class was in November (biotic site) or December (hummock and mire sites). Minimum mean age class occurred in April (mire and biotic sites) or May (hummocky site), i.e. in autumn, when breeding ceased. Age class then increased steadily throughout winter as the mouse population at all three sites aged, overall, due to the absence of recruitment of young mice.

Monthly variations in body mass, body length, tail length and mean age class of males and females are shown in Figure 5.4. The strong dependence of mass and body length on age class is manifested by the annual pattern for both (Figures 5.4a,b) closely mimicking age class (Figure 5.4d). However, peak mass for both males and females occurred in December, two months later than maximum age class for males and one month later than maximum age class for females. With males, body length also peaked two months later than did age class, but for females the length and age class maxima coincided.

The monthly variation in tail length (Figure 5.4c) was approximately similar to that of age class excepting that (especially for females) tail length started increasing only at the end of winter (September or October), by which time mean age class had increased from 4 to nearly 6 (this accounted for the weak correlation of tail length with age at higher age class values - Figure 5.1c). Overall, however, monthly variation in age class accounted for a substantial proportion (males 25%, females 22%; both $P<0.0001$) of the variance in the tail length data.

If the effect of changes in population age structure is accounted for by including age class as covariate when analysing the monthly variation in body mass, body length and tail length, the annual patterns are as in Figure 5.5. Males were, relative to their age, heavier from December to May (summer and autumn) than from June to November (winter and spring) (Figure 5.5a). Females showed a similar pattern, but age-corrected mass decreased considerably more than it

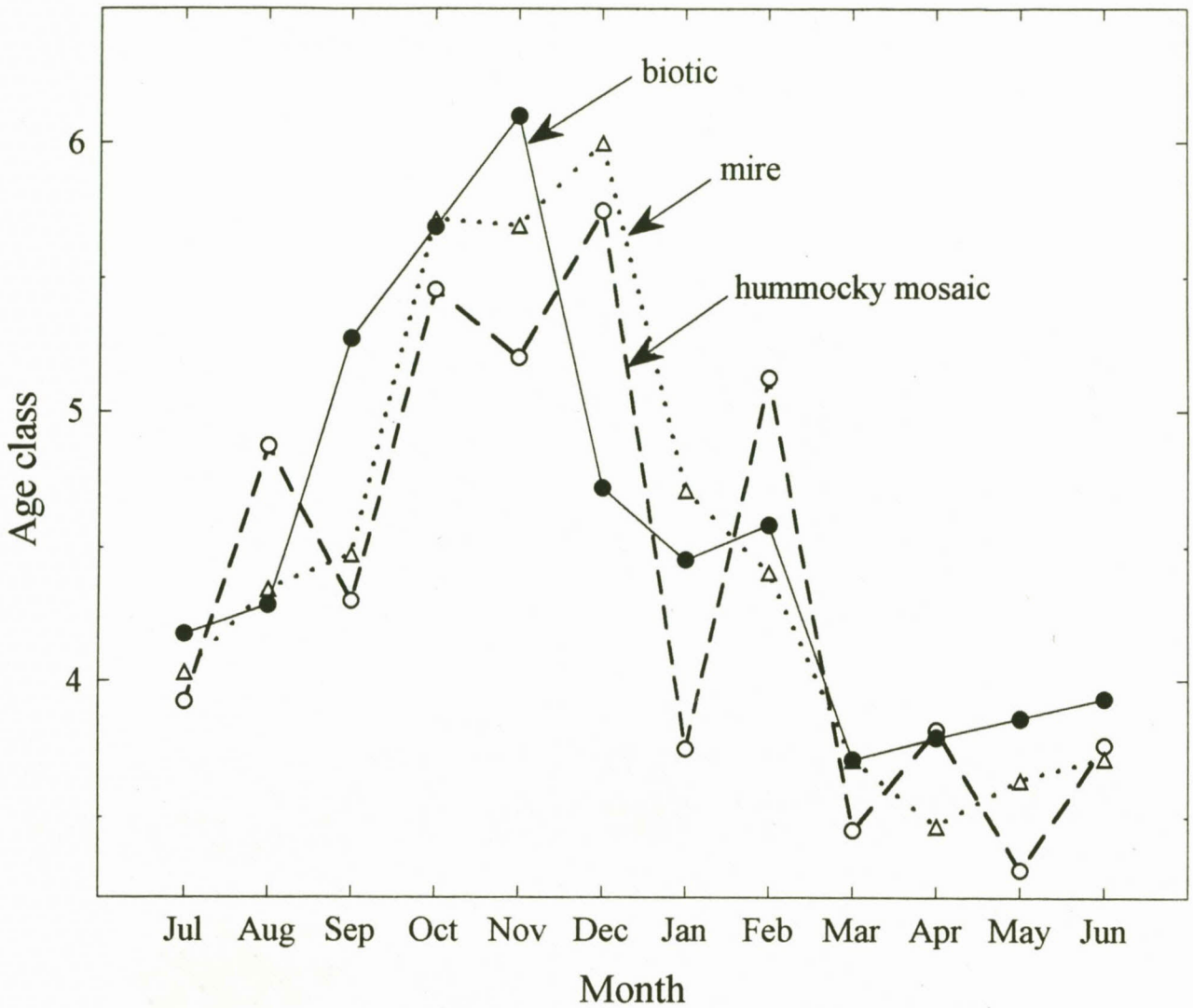

Figure 5.3. Seasonal variation in mean age class for mice (both sexes pooled) at the three sites. For convenience the austral summer months are in the centre.

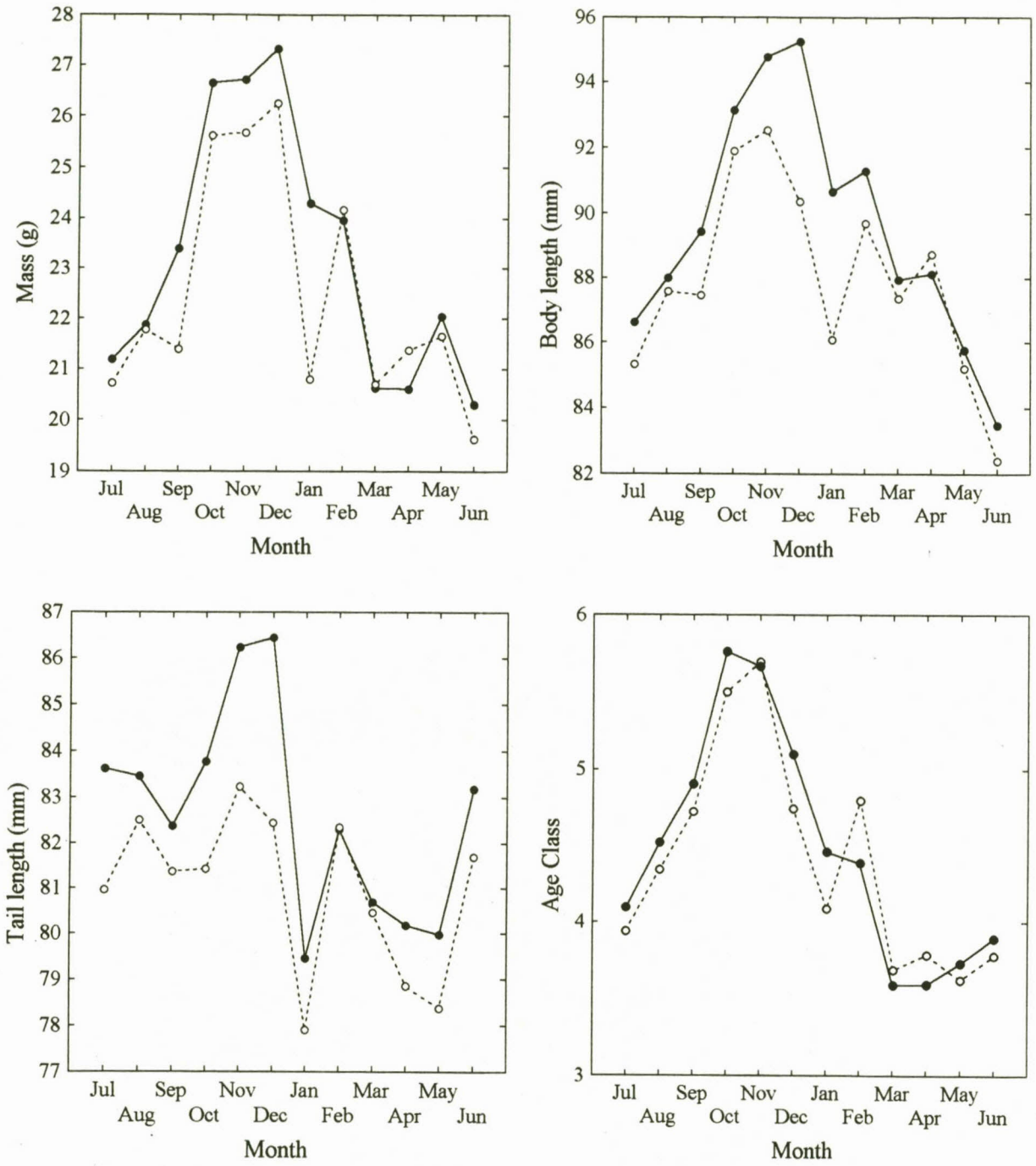

Figure 5.4. Seasonal variations in (uncorrected) body measurements for males (solid circles, line) and females (open circles, dashed line). Data from the three sites were pooled.

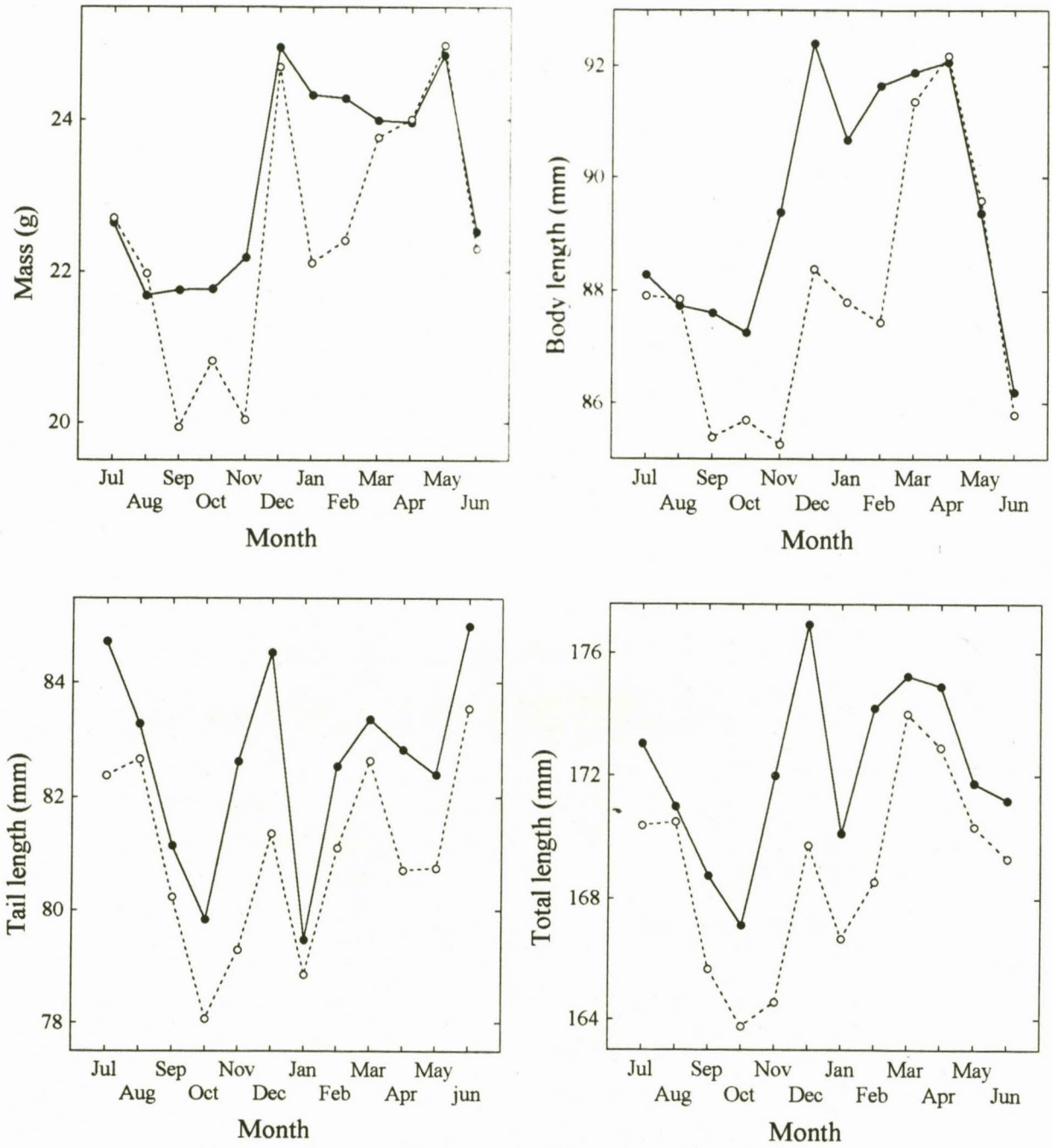

Figure 5.5. Seasonal variations in body measurements, corrcted for age class for males (solid circles, line) and females (open circles, dashed line).

did for males during winter and also dropped significantly between December and January before increasing again in the second half of summer. For both sexes, the spring-summer transition (November to December) marked the sharpest increase, and the autumn-winter transition (May to June) the sharpest decrease, in age-corrected mass.

Age-corrected mean body length (Figure 5.5b) showed a similar annual pattern to mass, except that the winter decrease started earlier (April) than was the case for mass (May). Age-corrected tail length (Figure 5.5c) showed a confusing annual pattern, with values decreasing sharply in late winter and increasing equally sharply in spring. For both sexes there was a sharp decrease in age-corrected tail length from December to January, after which values increased again throughout the rest of summer. This midsummer dip in tail length coincided with (but was much larger than) a dip in body length. Age-corrected total body length of both sexes declined throughout autumn and winter, increased sharply to peak values in December, dipped sharply between December and January and then increased again to second peaks in March (Figure 5.5d).

An interesting difference between the annual patterns of (age-corrected) body length and tail length is that body length declined after April whereas tail length only started declining after June. In fact, for both sexes corrected body length decreased by about 6mm between April and June, while in the same period tail length *increased* by 2mm. This suggests a change in body length to tail length (b:t) ratio during autumn..

B:t ratio of hummock site mice was smaller than for mice from the mire or biotic sites ($F = 8.7$; $P = 0.0001$, data not shown), but the seasonal changes in b:t were identical at the three sites. Sites were thus collapsed in the annual patterns presented in Figure 5.6a. Although b:t was quite strongly correlated with age class (Figure 5.6b, $r^2 = 0.26$; $P = 0.0001$), it varied during the year in a slightly different way. (Figure 5.4d). B:t increased markedly from June to October/November, coinciding with the main period of increase in age class. However, during the ensuing summer when age class decreased as young mice entered the population b:t remained relatively constant. It declined only in autumn, between April and June, when mean age class hardly changed at all. This autumn decrease represented 85% of the total amplitude of annual variation in b:t. In fact, on an age-corrected basis (data not shown), b:t fell from its highest to its lowest value for both sexes between April and June). Thus there was, in fact, a

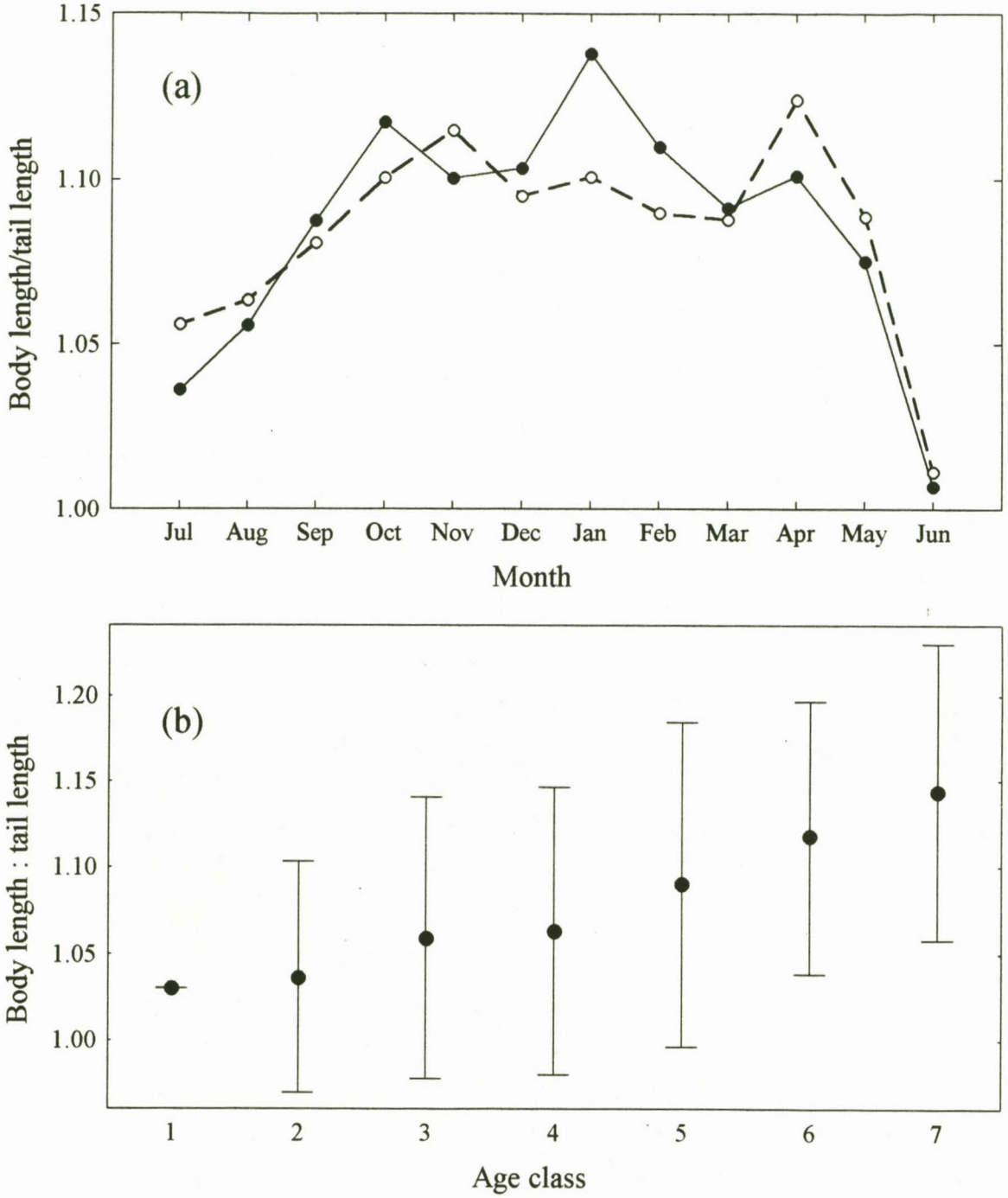

Figure 5.6. (a) Seasonal variation in body to tail length ratio for males (solid circles, line) and females (open circles, dashed line). (b) Relationship between body to tail length ratio and age class for male and female mice pooled.

very marked change in b:t ratio in autumn.

These temporal differences in b:t are explored further in Table 5.5. The months in which mice were captured were grouped seasonally (based on mean monthly temperature) according to the scheme described in the caption to the table. Winter-caught mice had a significantly smaller mean b:t than mice caught during the rest of the year, even when age class differences between seasons are accounted for. Hence, in winter mice had longer tails relative to their body length, which is opposite to what might be expected if tail length, or more specifically, tail length in relation to body length, plays a role in regulating heat loss, as implied by Allen's rule and shown in laboratory-reared mice (Harrison et al, 1959) and suggested for field populations (Thorpe 1981). However, perhaps the season when a mouse is born, or when it is young and growing most rapidly, is a more pertinent determinant of b:t than the season in which it is caught. Birth month was estimated by back-extrapolating from the capture date using the modal age of each age class. This could not be done for class 7 mice, which were excluded from the analysis.

Mice born in winter had significantly larger b:t ratios (i.e. shorter tails relative to bodies) than those born in spring or summer, whether or not age class was included as covariate in the analysis (Table 5.5). Mean b:t of spring-born mice was intermediate between these two groups.

However, it was shown in Chapter 4 that mice do not breed in winter on the island (although a few might be born in early June) and the "winter-born" group in Table 5.5 is an artefact caused by the coarse resolution of the age class classification, coupled with the use of modal months in the back-extrapolating from capture month to birth month. (The same misconstruction led to an earlier-held belief that mice breed all year round on the island; Berry et al. 1978). Mice in the winter-born group would actually have been mostly born in autumn, although there were some in class 6 that were estimated as having been born in September but might just as likely have been born in spring. Similarly, some older mice estimated as having been born in late summer might have been born in April or May, i.e. autumn. These uncertainties can be partially overcome by considering mice as belonging either to a group that developed through age classes 1 to 4 (the first *ca.*6 months of their life, during which much of their total growth takes place - Figure 5.1) in winter, or to a group that carried out its early development in summer. The "winter-grown" group includes all mice indicated as having been born in autumn or winter, except for those estimated as having been

Table 5.5. Body length:tail length ratios of mice caught or born in different seasons. Spring = October to November, Summer = December to March, Autumn = April and May, Winter = June to September.

	Body length:tail length ratio	Age class
Caught in:		
Spring	^{a} 1.13 ^{a}	5.7
Summer	^{a} 1.10 ^{a}	4.1
Autumn	^{a} 1.09 ^{a}	3.7
Winter	^{b} 1.05 ^{b}	4.3
F	19.5	83.8
P	<0.0001	<0.0001
F_{age}	16.9	
P_{age}	<0.0001	
Born in:		
Spring	^{a} 1.07 ^{a}	4.6
Summer	^{a} 1.07 ^{a}	3.8
Autumn	^{ab} 1.08 $^{a\,b}$	4.1
Winter	^{b} 1.10 ^{b}	4.6
F	6.7	37.3
P	0.0002	<0.0001
F_{age}	4.7	
P_{age}	0.0002	
First 6 months of growth in:		
Winter period	1.07	4.2
Summer period	1.10	4.4
F	9.9	
P	0.002	
F_{age}	7.8	
P_{age}	0.005	

Superscripts to left of means show homologous groupings of seasons ignoring age class differences between the samples. Superscripts to the right of means indicate homologous groupings of seasons if the age class differences are accounted for. Homologous groupings are by the Spjotvol and Stoline (1973) generalization of Tukey's test.

born in September, which, on the basis that mice do not breed in late winter so they are more likely to have been born in spring, are considered as belonging to the group that had its early life in summer. For both males and females, body length and tail length were both longer for the winter-grown group (data not shown) but the difference in body length was three times as great as the difference in tail length. This caused a significant ($P<0.0001$) difference in b:t between the two groups, whether differences in mean age class are taken into account or not (Table 5.5). It appears thus that mice that develop in winter have on average, significantly shorter tails in relation to body length than those that develop in summer. This is probably temperature-related; Harrison et al. (1959) showed that b:t ratio of laboratory reared mice is directly affected by temperature during development.

Reproductively active mice of both sexes had a significantly larger b:t ratio than non-reproductive mice, simply because b:t ratio was positively correlated with age (Figure 5.6b). Interestingly, b:t ratios of non-reproductive males and females were similar, but reproductive females had a significantly larger mean ratio (1.13) than males (1.10; $P=0.03$) and this could not be ascribed to an age class difference since the age class distribution of the two samples was identical. The difference was due to reproductive females having significantly longer (2.1 mm, on average; $P=0.003$) bodies than reproductive males; mean tail length was 0.4 mm greater for females ($P=0.6$).

5.3.2 Small intestine, large intestine and caecum lengths

Small intestine, large intestine, caecum and total intestine lengths increased with increasing age class (Figure 5.7), at least from class 2 up. Intestinal measurements were made on only two class 1 mice so the decreases in values between class 1 and 2 are probably fortuitous.

Small intestine, large intestine and caecum lengths were strongly correlated with body length (Figure 5.8). The between-sex differences in the slopes and elevations of the regression lines in the figure are not significant at $P\leq0.05$.

Biotic site mice of both sexes had significantly longer small intestines than mice from the hummock and mire sites (Table 5.6). However, if the fact that biotic site mice tended to be larger than mice at the other sites (Table 5.4) is accounted for then there were no significant

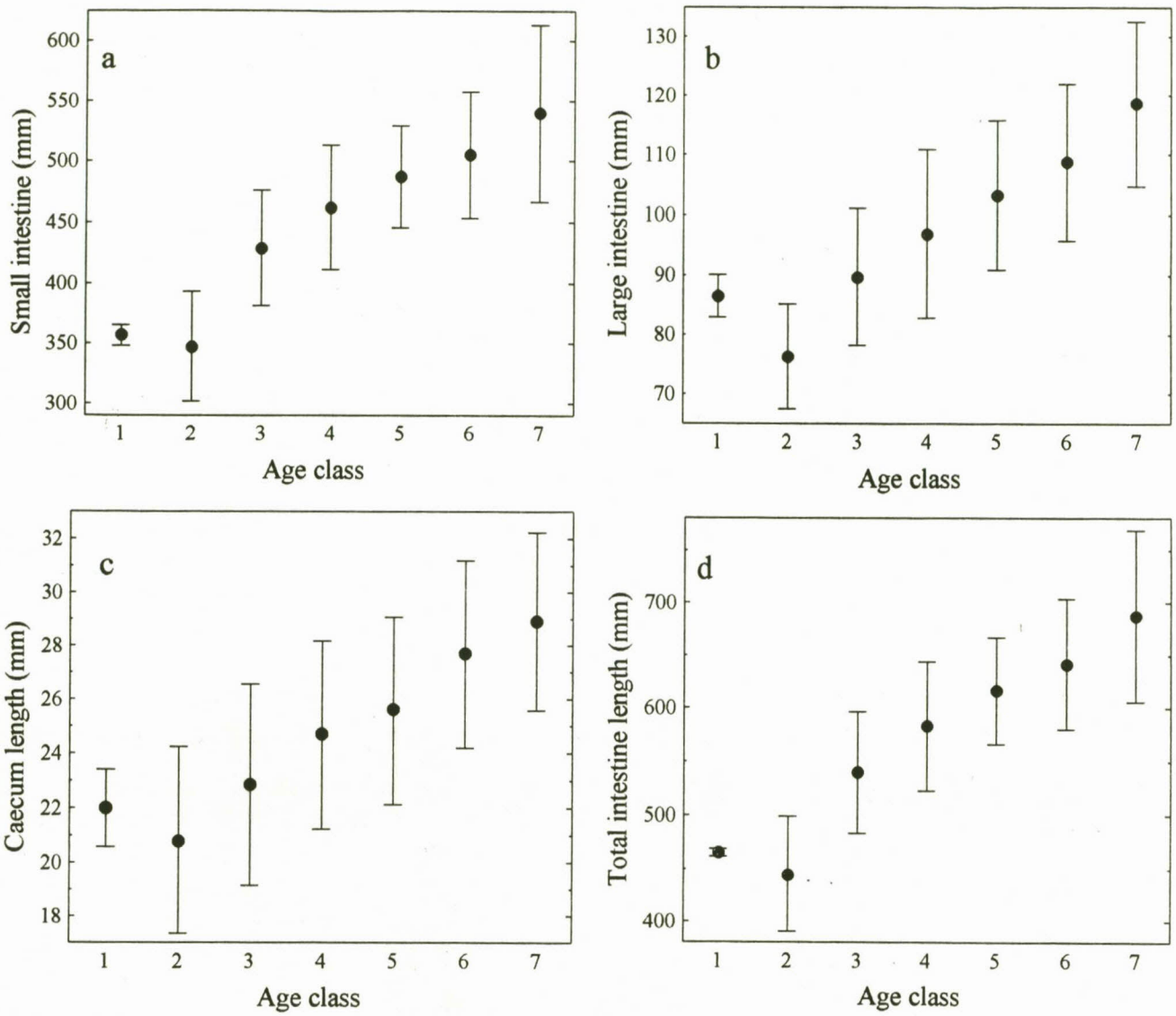

Figure 5.7. Relationship between intestine lengths and age class for male and female mice pooled.

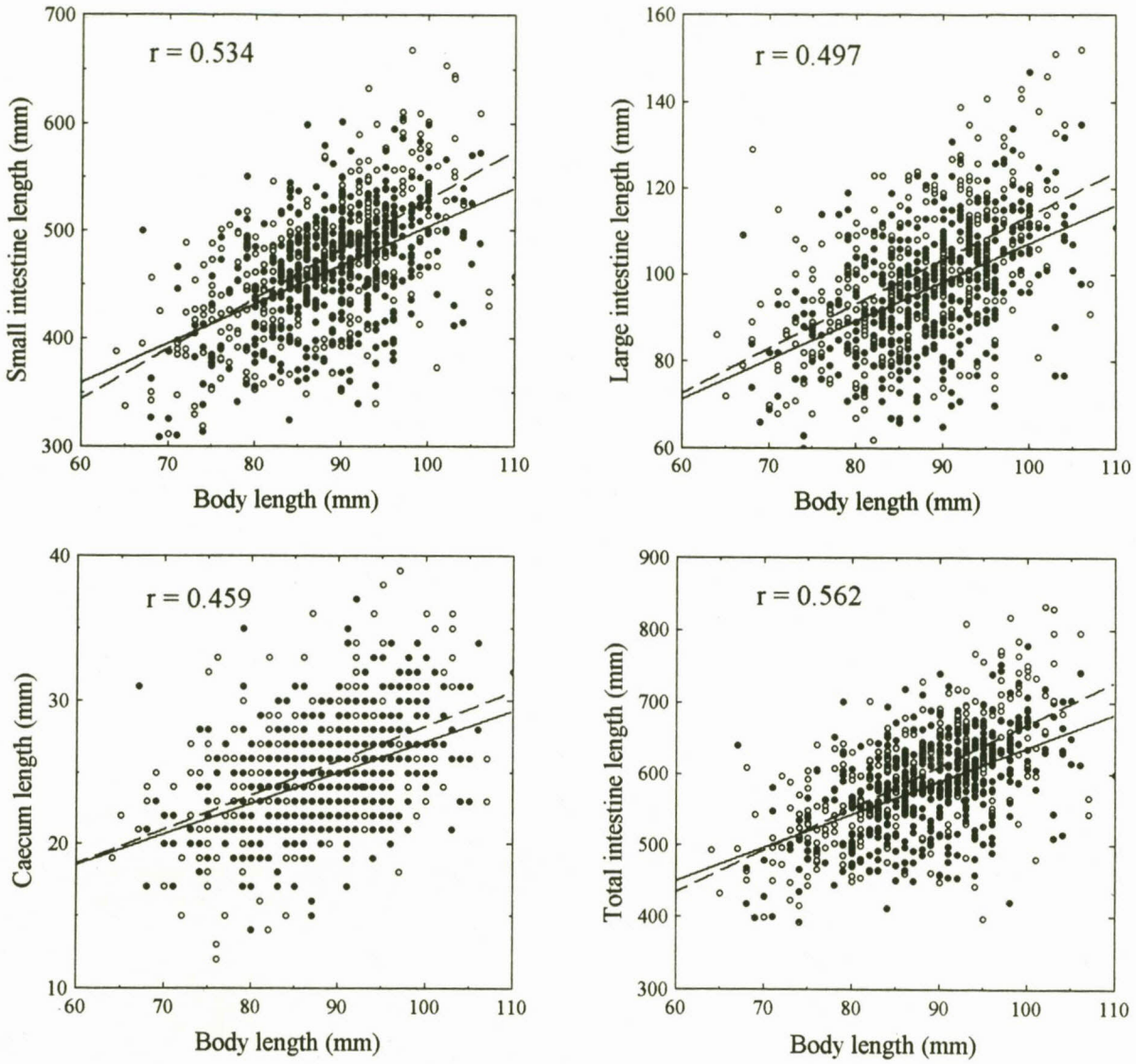

Figure 5.8. Relationship between intestine lengths and body length for male (closed circles, solid regression line) and females (open circles, dashed regression line).

Table 5.6. Mean intestinal lengths (mm) of male and female mice at the three sites. Values in parentheses are the adjusted means after accounting for differences in body length.

	Small intestine	Large intestine	Caecum	Total intestine
Males				
Hummock	^{a}456 (462^{a})	^{a}101 (102^{a})	^{a}26.4 (26.8^{a})	^{ab}586 (592^{a})
Mire	^{a}453 (456^{a})	^{b}95 (95^{b})	^{c}23.5 (23.7^{b})	^{a}572 (576^{a})
Biotic	^{b}476 (469^{a})	^{b}98 (96^{b})	^{b}25.1 (24.6^{b})	^{b}600 (589^{a})
F	7.4	6.2	21.4	6.3
P	0.0006	0.002	<0.0001	0.002
F_{length}	2.8	12.0	32.2	2.9
P_{length}	0.06	<0.0001	<0.0001	0.06
Females				
Hummock	^{a}449 (462^{a})	^{a}105 (108^{a})	^{a}26.5 (27.2^{a})	^{a}578 (597^{a})
Mire	^{ab}466 (462^{a})	^{b}100 (99^{b})	^{b}24.2 (24.1^{b})	^{a}590 (586^{a})
Biotic	^{b}479 (469^{a})	^{b}99 (96^{b})	^{b}25.5 (24.9^{b})	^{a}605 (590^{a})
F	5.1	3.1	6.7	2.5
P	0.006	0.04	0.001	0.08
F_{length}	0.7	16.3	16.2	0.6
P_{length}	0.5	<0.0001	<0.0001	0.5

F is the variance ratio and P is its significance, from analysis of variance (ANOVA).

F_{length} and P_{length} are the ANOVA statistics if difference in body length between the samples are accounted for by including body length as a covariate in the ANOVA.

Superscripts to left of means show homologous groupings of sites ignoring body length differences between the samples. Superscripts to the right of means in parentheses indicate homologous groupings of sites if the body length differences are accounted for. Homologous groupings are by the Spjotvol and Stoline (1973) generalization of Tukey's test.

inter-site differences in small intestine for either sex (F_{length} and P_{length} values in Table 5.6). Both males and females from the hummock site had longer large intestines and caeca than mice from the other two sites, especially when comparing body-length corrected values. The fact that hummock site mice had shorter small intestines, but longer large intestines and caeca, than biotic site mice suggests between-site differences in small intestine to total intestine ratio (SI:TI), large intestine to total intestine ratio (LI:TI), and caecum to total intestine ratio (C:TI) and this is supported by the analysis of these ratios in Table 5.7. For both sexes, hummocky mice had significantly smaller SI:TI, but larger LI:TI and C:TI, than mice from the mire or biotic site. The only between-sex differences in ratios within sites were at the hummock site where females had significantly smaller SI:TI and larger LI:TI than males (however, see later for an analysis of the effect of reproductive status on between-sex differences in these ratios).

Despite these between-site differences in small intestine, large intestine and caecum lengths, all three parameters showed similar patterns of annual variation at the three sites; hence mice from the three sites were considered together in the analysis that lead to the patterns shown in Figures 5.9 and 5.10. Figure 5.9 shows the annual variation in uncorrected intestine lengths and Figure 5.10 the annual variation in intestine lengths corrected for body length. Instances where particular intestine parameters did not conform to the general pattern or to the overall difference observed between sexes are discussed later.

The annual variation in the various intestine length parameters (Figure 5.9) are all quite similar to the variation in body length (Figure 5.4b). The most conspicuous difference is that small and large intestines lengths of both sexes increased markedly between April and June, whereas body length declined during the same period. Small and large intestines, and caeca, of both sexes tended to be longer in spring and early summer than at other times of the year, perhaps because in spring and early summer the population consisted mainly of older, larger mice (Figures 5.4b, d). Correcting the intestinal lengths for changes in body length should account for this but the patterns of the corrected means (Figure 5.10) are not very different to those of the uncorrected values. In relation to body length, small and large intestine and caeca lengths increased throughout autumn, winter and spring to peak values in November or December and then declined sharply during the rest of summer.

The amplitudes of the annual variation in corrected mean values of all four intestine length parameters were, on average, 30% greater for females than males, mainly because female

Table 5.7. Between-site contrasts of SI:TI, LI:TI and C:TI ratios for male and female mice. Superscripts show homologous groupings of sites by the Spjotvoll and Stoline (1973) generalization of Tukey's test.

	Site	SI:TI	LI:TI	C:TI
Males	Hummock	0.781 [a]	*0.174 [a]	0.045 [a]
	Mire	0.792 [b]	0.167 [b]	0.041 [b]
	Biotic	0.794 [b]	0.164 [b]	0.042 [b]
	F	15.0	10.7	17.7
	P	<0.0001	<0.0001	<0.0001
Females	Hummock	0.774 [a]	*0.180 [a]	0.045 [a]
	Mire	0.790 [b]	0.169 [b]	0.041 [b]
	Biotic	0.793 [b]	0.164 [b]	0.043 [b]
	F	22.6	20.1	13.4
	P	<0.0001	<0.0001	<0.0001

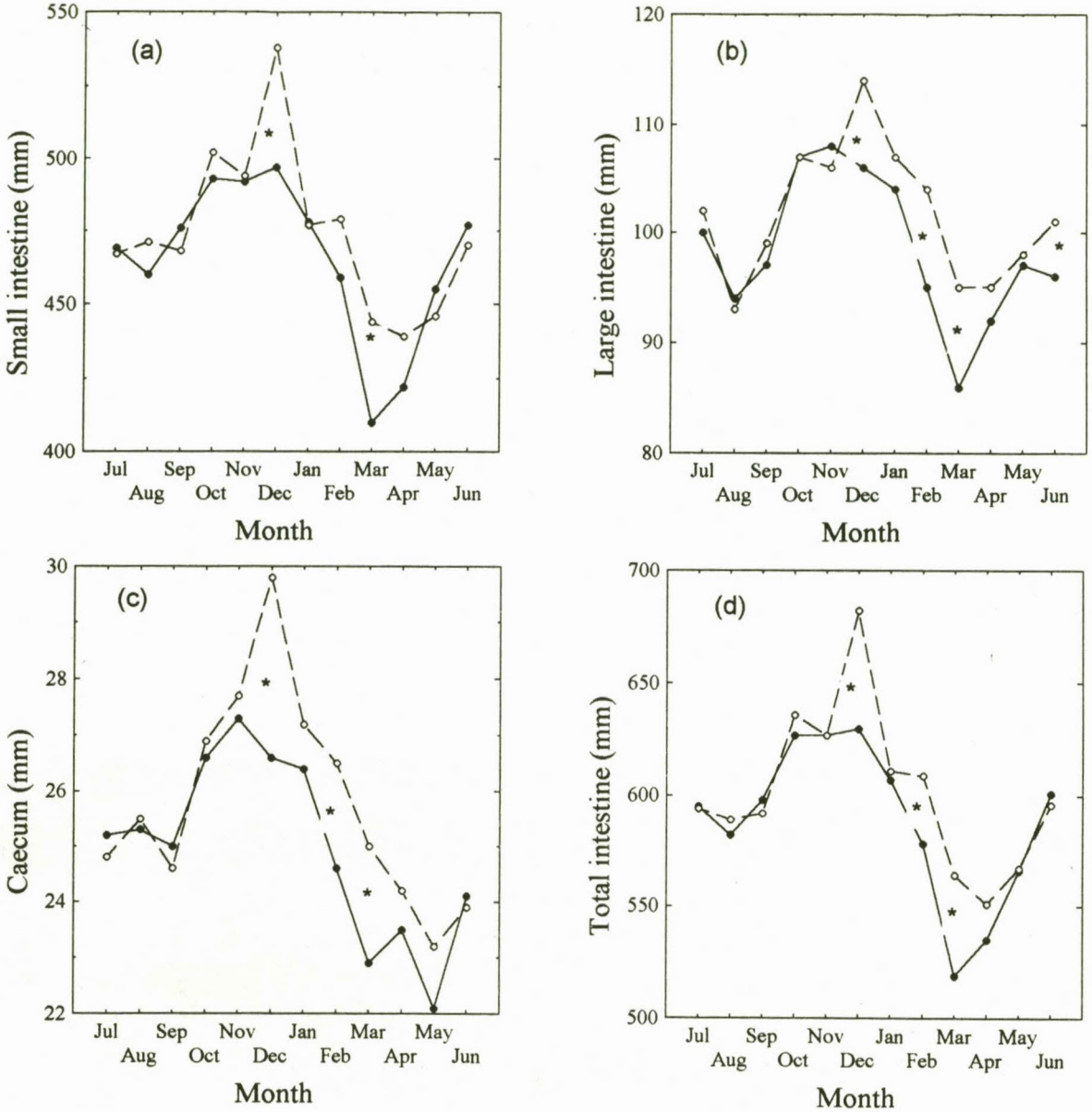

Figure 5.9. Seasonal variations in (uncorrected) intestine length measurements for males (solid circles, line) and females (open circles, dashed line). Asterisks indicate where the male-female difference in the monthly mean was significant at $P<0.05$.

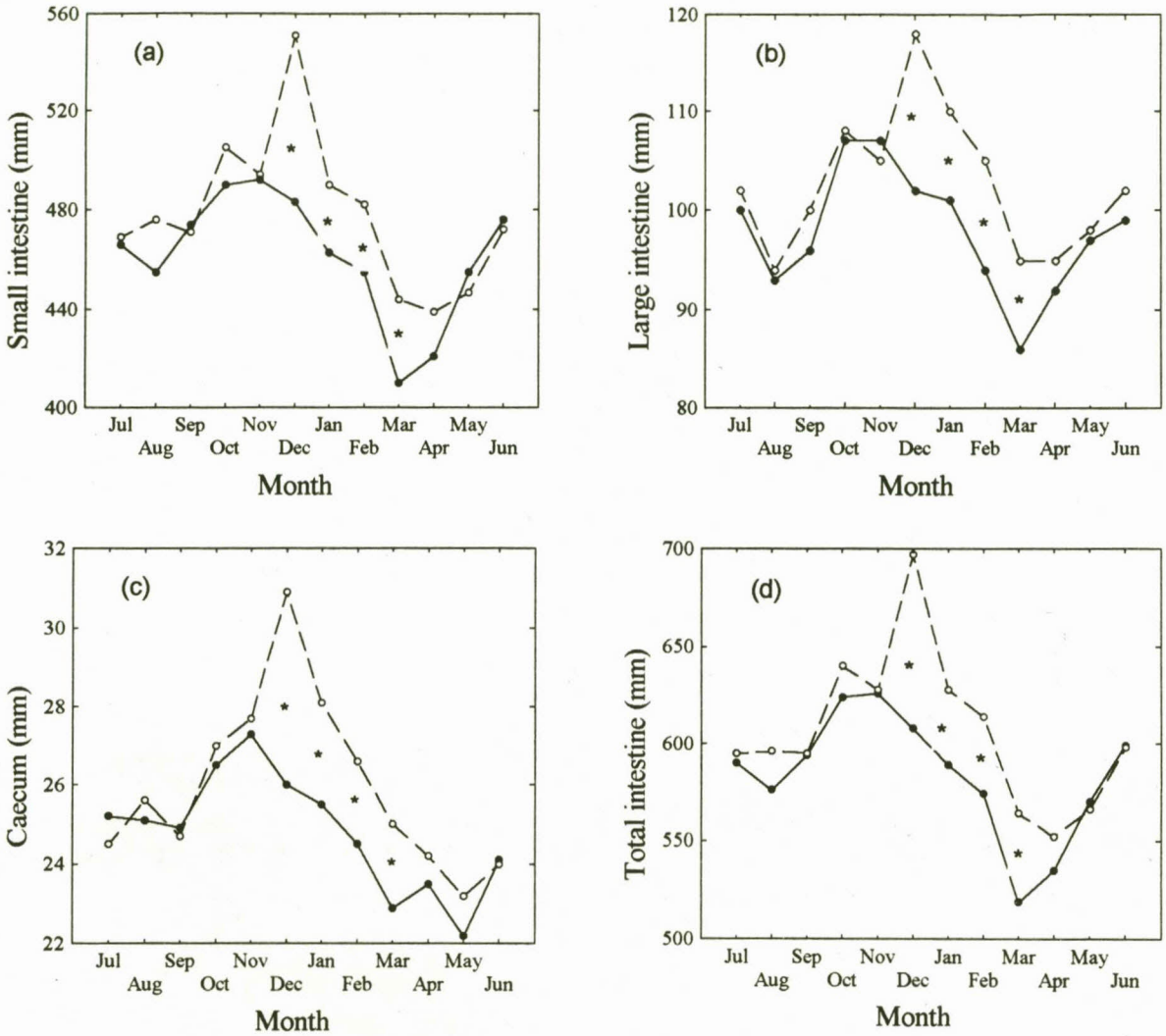

Figure 5.10. Seasonal variations in intestine length measurements corrected for body length for males (solid circles, line) and females (open circles, dashed line). Asterisks indicate where the male-female difference in the monthly mean was significant at $P<0.05$.

values reached higher midsummer peaks (Figure 5.10). In fact, female corrected means were significantly higher than male means from December to March, but not during the rest of the year. Uncorrected means were also consistently greater for females than for males from December to March but the differences were not always significant (Figure 5.9).

The possibility that reproductive activity had to do with the fact that intestine lengths differed between sexes in summer but not in winter was tested in Table 5.8. Mice that were not reproductively active did not show between-sex differences in any of the intestine length parameters whereas reproductively-active (pregnant or lactating) females had significantly longer small and large intestines and caeca than scrotal males, even accounting for the fact that, overall, the sample of reproductively active females consisted of larger bodied mice than the sample of reproductively-active males (data not shown, $P = 0.003$). Normalizing the between-sex differences in small and large intestines, and caeca, of the reproductive mice by dividing the difference by the mean value of the particular parameter shows that the male-female difference in large intestine and caecum lengths are approximately double the difference in small intestine length. Hence, reproductive females have a smaller mean SI:TI, but a larger LI:TI, than reproductively active males (Table 5.8). However, C:TI was not significantly different between the two groups. Non-reproductive males and females had almost identical intestine length ratios.

The patterns of annual variation and the male-female differences shown in Figures 5.9 and 5.10, and in Table 5.8, are representative of the patterns at the individual sites except that at the hummocky mosaic site (data not shown) small intestine and caecum length did not differ significantly between sexes. In fact, the uncorrected mean small intestine length of females was 7mm *shorter* than that of males; the only instance where the mean value of any intestine length parameter was smaller for females than for males (Table 5.6). Females were considerably smaller than males at the hummocky site (Table 5.3) and correcting for this resulted in females having *longer* small intestines relative to body length than males, but the difference was still not significant at $P \leq 0.05$. (Note that the corrected intestine lengths in Table 5.7 cannot be used to compare between males and females – they are adjusted for within-sex, between-site differences in body length and on that basis males and females at the biotic site happened to have the same corrected small intestine length. Correcting for between-sex differences in body length gives adjusted mean small intestine lengths of 455 mm for females and 450 mm for males). However, both uncorrected and body length-

Table 5.8. Mean intestine lengths of male and female mice of different reproductive states. Values in brackets are the means of intestine lengths corrected for body length. F is the variance ratio and P is its significance, from ANOVA. F_{age} and P_{age} are the ANOVA statistics if differences in body length between the samples are accounted for.

Reproductive Status		Small intestine	Large intestine	Caecum	Total intestine
Non-Reproductive	Male	454 (453)	95 (95)	23.9 (23.9)	573 (572)
	Female	455 (456)	97 (97)	24.2 (24.2)	576 (576)
	F	0.1	1.2	0.5	0.3
	P	0.8	0.3	0.5	0.6
	F_{length}	0.3	1.7	0.5	0.5
	P_{length}	0.6	0.2	0.5	0.5
Reproductive	Male	469 (474)	99 (100)	25.4 (25.6)	594 (599)
	Female	501 (497)	109 (108)	27.8 (27.6)	638 (632)
	F	18.8	34.4	34.1	24.2
	P	<0.0001	<0.0001	<0.0001	<0.0001
	F_{length}	12.0	24.8	25.0	16.4
	P_{length}	0.0006	<0.0001	<0.0001	<0.0001
		SI:TI	LI:TI	C:TI	N*
Non-Reproductive	Male	0.789	0.169	0.042	184
	Female	0.790	0.168	0.042	237
	F	0.2	0.2	0.0	
	P	0.7	0.7	0.9	
Reproductive	Male	0.790	0.166	0.043	271
	Female	0.785	0.170	0.043	105
	F	4.6	4.4	2.0	
	P	0.03	0.04	0.16	

*N is the number of mice in the particular group.

corrected small intestine lengths of reproductive females at the hummock site were considerably longer (by 27 mm and 20 mm, respectively) than they were for reproductive males.

5.3.3 Kidney and adrenal gland masses

Biotic site mice of both sexes had heavier kidneys than mice from the hummock and mire sites (Table 5.9), even accounting for the fact that biotic site mice were larger overall. Kidney index (kidney mass divided by body mass) of both males and females was, therefore, greatest at the biotic site. Hummock site males and females had heavier adrenal glands, relative to their body mass, than mice from the other two sites (body mass-corrected adrenal masses in Table 5.9).

Males had heavier kidneys and larger kidney indices than females from the same site (uncorrected means in Table 5.9 - the corrected means cannot be compared between sexes since they were adjusted for the between-site differences in body mass within each sex). In contrast, at all three sites females had heavier adrenals than males. This difference is entirely due to reproductively active mice (Table 5.10); mean adrenal mass for pregnant and lactating females was 48% greater then the mean for scrotal males, whereas there was only a 3% between-sex difference for non-reproductive mice. In the case of kidneys, comparing the mean masses and indices in Table 5.10 between sexes obscures the fact that kidney mass and kidney index were greater for males than for females only in the case of reproductive mice; non-reproductive males had slightly, but significantly, *smaller* mean kidney mass and kidney index than females (Table 5.10).

The between-sex differences in kidney and adrenal masses shown in Table 5.10 are shown by mice from each of the three sites, although in two instances particular differences were not significant at $P \leq 0.05$. Mean adrenal mass of hummock site females was 14% greater (20% if adjusted for body mass) than that of males ($P=0.08$) and uncorrected kidney mass of mire site males was 7% greater than for females ($P=0.08$).

Annual variation in kidney mass and adrenal mass were very much alike at the three sites so the overall patterns for mice from all three sites are presented here (Figure 5.11). For both

Table 5.9. Mean kidney mass, kidney index (=kidney mass/body mass) and adrenal mass of male and female mice at each of the three sites. Values in parentheses are the adjusted means after accounting for differences in body mass.

Sex	Site	Kidney mass (mg)	Kidney index ($x10^4$)	Adrenal mass (mg)
Male	Hummock	^{a} 223 (235 ^{a})	^{a} 100	9.5 (9.6 ^{a})
	Mire	^{a} 233 (242 ^{a})	^{a} 104	9.1 (9.1 ^{b})
	Biotic	^{b} 280 (259 ^{b})	^{b} 114	9.2 (9.1 ^{b})
	F	16.9	17.2	2.7
	P	<0.0001	<0.0001	0.1
	F_{mass}	9.0		4.6
	P_{mass}	0.0001		0.03
Female	Hummock	^{a} 182 (208 ^{a})	^{a} 93	10.8 (11.6 ^{a})
	Mire	^{b} 218 (207 ^{a})	^{a} 97	10.3 (10.0 ^{b})
	Biotic	^{c} 250 (234 ^{b})	^{b} 108	10.7 (10.1 ^{b})
	F	21.2	29.4	0.3
	P	<0.0001	<0.0001	0.8
	F_{mass}	21.4		4.8
	P_{mass}	<0.0001		0.03

F is the variance ratio and P is its significance, from analysis of variance (ANOVA).
F_{mass} and P_{mass} are the ANOVA statistics if difference in body mass between the samples are accounted for by including body length as a covariate in the ANOVA.
Superscripts to the left of means show homologous groupings of sites ignoring body mass differences between the samples. Superscripts to the right of means in parentheses indicate homologous groupings of sites if the body mass differences are accounted for. Homologous groupings are by the Spjotvol and Stoline (1973) generalization of Tukey's test.

Table 5.10. Between-sex differences in kidney and adrenal masses, and kidney index for mice of different reproductive states. Values in brackets are means of the masses corrected for body length.

Reproductive State	Sex	Kidney mass (g)	Kidney index (10^{-4})	Adrenal mass (mg)
Non-reproductive	Male	195 (195)	97	10.0 (10.0)
	Female	207 (207)	101	9.7 (9.7)
	F	3.6	8.5	1.5
	P	0.06	0.004	0.2
	F_{mass}	12.3		2.5
	P_{mass}	0.0001		0.1
Reproductive	Male	295 (308)	116	8.6 (8.7)
	Female	276 (263)	103	12.8 (12.7)
	F	2.7	22.2	47.0
	P	0.1	<0.0001	<0.0001
	F_{mass}	47.9		42.3
	P_{mass}	<0.0001		<0.0001

F is the variance ratio and P is its significance, from analysis of variance (ANOVA).
F_{mass} and P_{mass} are the ANOVA statistics if differences in body mass between the samples are accounted for by including body mass as a covariate in the ANOVA.

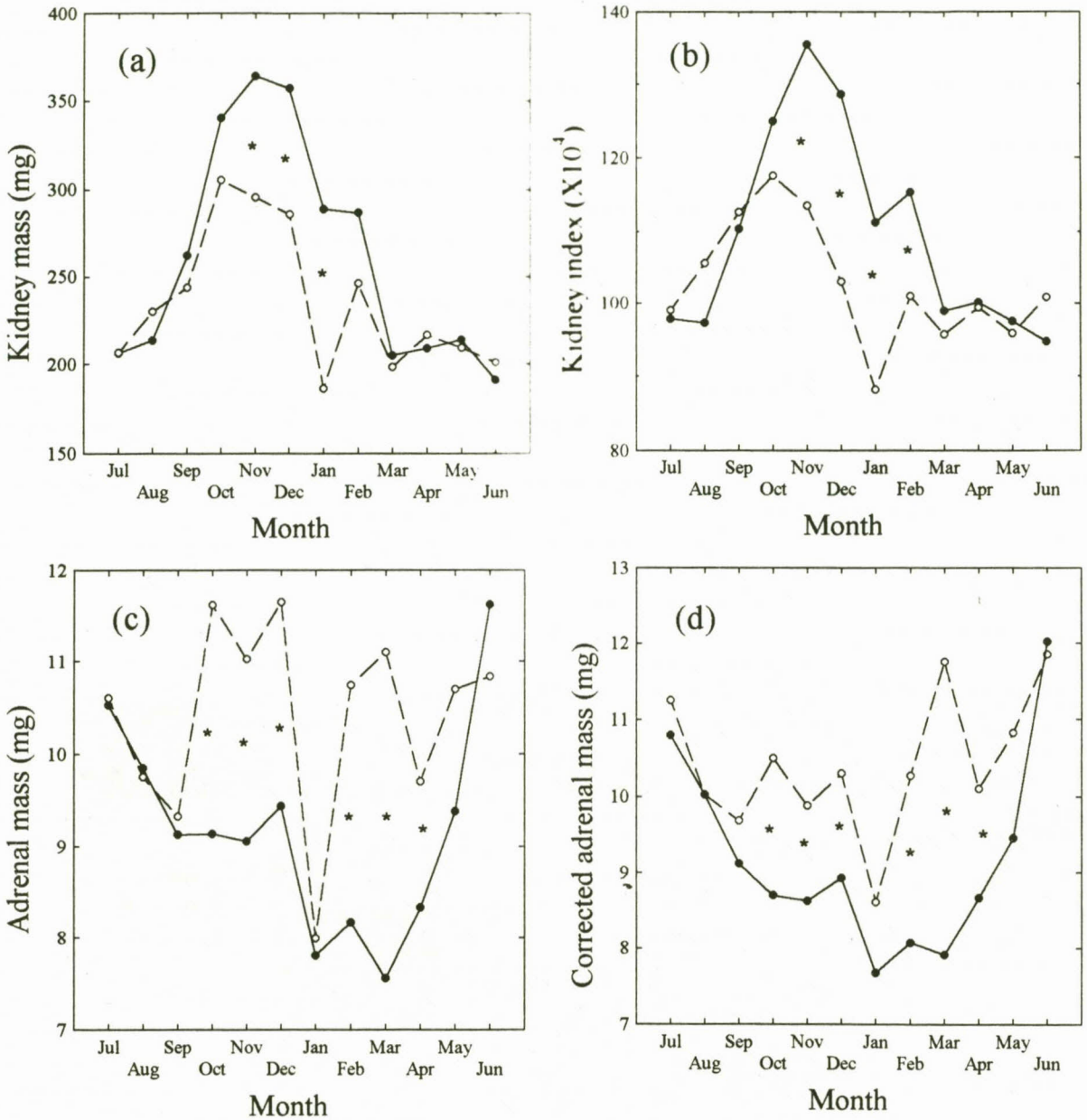

Figure 5.11. Seasonal variations in kidney and adrenal measurements for males (solid circles, line) and females (open circles, dashed line). In (d) adrenal mass was corrected for body mass. Asterisks indicate where the male-female difference in the monthly mean was significant at $P<0.05$.

sexes, annual variations in kidney mass (Figure 5.11a) were very similar to that for body mass (Figure 5.4a), with kidneys becoming heavier during the second half of winter as the population aged and mean body mass increased. Peak kidney mass was attained earlier (October or November) than peak body mass (December) and kidney mass declined throughout summer as young mice entered the population. The winter increase in kidney mass of males was sharper and carried on longer than for females, so that the peak value in spring and the subsequent monthly means throughout summer, when a large proportion of the mice were reproductively active, were higher for males than for females. This is the pattern even accounting for the fact that in summer males were larger and heavier, overall, than females (Figure 5.11b shows the variation in kidney index which is a close analogue of body-corrected kidney mass).

Female adrenal mass declined from June to September and then increased sharply in early Spring (Figure 5.11c). Values stayed high throughout summer and autumn excepting in January when there was a very sharp dip, due partly to recruitment of young, small mice (or more pertinently, *non-reproductive* mice considering the effect of reproductive state on female adrenal mass shown in Table 5.10) into the population. Males showed a somewhat different pattern; adrenal mass declined in late winter, as it did with females, but then stayed relatively constant in spring and early summer, without the sharp increase shown by females. During the second half of summer male adrenal mass declined and only started increasing in autumn. The greatest male-female difference in adrenal mass (and body mass-corrected adrenal mass, Figure 5.11d) thus occurred from October to April, when a large proportion of the population was reproductively active, with the already-mentioned exception of January, when male and female adrenal masses were not significantly different and when the proportion of non-reproductive mice was almost double that in December or February.

5.4 DISCUSSION

This study has shown the importance of taking factors such as time of the year when an individual was collected, the season when it developed to maturity, its sex and reproductive state, and also age class composition of the population as whole, into account when comparing masses and lengths of whole bodies or particular organs between populations or sub-populations of mice.

Mean body mass for all the mice trapped in this study (22.4 g) was significantly ($P<0.001$) greater than values for the samples collected in 1979/80 (19.8 g) or 1991/92 (19.9 g). A more detailed comparison that accounts for differences in sex ratios, age class composition or seasonal distribution of the samples from the different periods cannot be made, since these details are not given in the accounts of two previous investigations.

At both the hummocky mosaic and the biotic sites, but not at the mire site, male mice were significantly heavier and longer than females. At the hummocky site this was due to the male sample being, overall, older than the female sample but at the biotic site the male-female differences in mass, body length and tail length could not be ascribed to age class differences.

In the 1979/80 study, males were also found to be significantly ($P<0.001$) heavier than females and it is likely, although it cannot be shown conclusively from the data presented, that this was due to different age class distributions, as in the study reported here. For four of the six trapping periods in 1979/80 the distribution for the male sample was skewed toward the higher age classes, compared with that for females. Matthewson (1993) also reported that for the 1991/92 sample, males were significantly heavier, on average, than females. He also did not consider age class in making the comparison but it seems, from histograms he presented for the seasonal samples, that there was no difference in age class distribution between males and females. He ascribed the fact that males were heavier than females to sex-linked genetic differences or a difference in gene expression between the sexes.

Mean total lengths (body plus tail) of the mice sampled in 1979/80 and in 1992/93 were almost identical (169.2 and 170.0 mm respectively); even within sexes there were no differences. Total length was not reported for the 1991/92 study but mean body length in 1991/92 (87.3 mm) was more similar to that in 1992/93 (88.1 mm) than that in 1979/80 (85.6 mm). A sample of 92 mice caught between November 1975 and March 1976 (Berry et al. 1978.) had a mean body length of 78.1 mm, lower than in all subsequent studies.

However, what is most interesting is that between 1979/80 and 1992/93, body length of the island's mice increased significantly, from 85.6 to 88.1 mm for both sexes; for males from 86.7 to 88.9 mm and for females from 84.3 to 87.2 mm (all $P<0.001$). In contrast, tail length decreased between 1979/80 and 1992/93; for both sexes from 83.6 to 81.8 mm, for males

from 84.8 to 82.5 mm and for females from 82.3 to 80.9 mm (all $P<0.001$). This implies that body length: tail length ratio changed between 1979/80 and 1992/93, and this was very much the case. Mean b:t was 1.08±0.09 for males and for females in this study. In 1979/80 it was 1.02 for both sexes. The fiducial limits for the 1979/80 mean cannot be calculated from the data presented, at least not for the sample as a whole. However, from the data from both studies it is possible to calculate mean b:t ratios for six periods of approximately two months each (corresponding to the trapping sessions of the 1979/80 study) and to test how their mean differed between the two studies. This yields $t_{10} = 4.95$, $P<0.001$. It appears then that bodies were longer, and tails shorter, in 1992/93 than in 1979/80.

Tail lengths were not reported for the 1991/92 study but mean b:t ratio for the whole sample (1427 mice) was given as 1.1 (Matthewson 1993), similar to that a year later. However, Matthewson indicated that the b:t ratio in 1991/92 was not significantly different that in 1979/80; in fact, he explicitly states that the 1979/80 value was also 1.1. Examination of the body and tail length data given by Gleeson (1981) shows clearly that this is not the case – in one of his six trapping sessions mean b:t was 1.06 ($n = 130$) and in all the rest ($n = 57$ to 130) it was below 1.05. Mice caught in 1975/76 had a mean b:t ratio of 1.00 (Berry et al. 1978), slightly lower than the mean 1979/80 value.

There has been much criticism, and even outright disavowal, of Allen's rule (protruding parts of an animal's body will be relatively shorter in the cooler than in the warmer regions of its distribution). However, Remmert (1980) suggested that it is applicable where low temperatures prevail in both summer and winter. Marion Island, with its exceptionally isothermal cool, but warming, climate, and its introduced house mouse population, offers an exceptional opportunity to test the corollary of the rule: that a changing thermal regime should influence the relative size of an appendage, in this case the tail.

The 1979/80 investigation, and the two in 1990, all commenced around April and ended in March or April of the second year. In each instance most of the total mouse sample was caught in the first year. Also, a substantial proportion of the mice caught up to February, or even March, in the second year were born and carried out their early growth, the previous year. Even in the 1975/76 investigation, which lasted only six months, 63% of the mice were collected from November to January (Matthewson 1993). In Figure 5.12 the body to tail

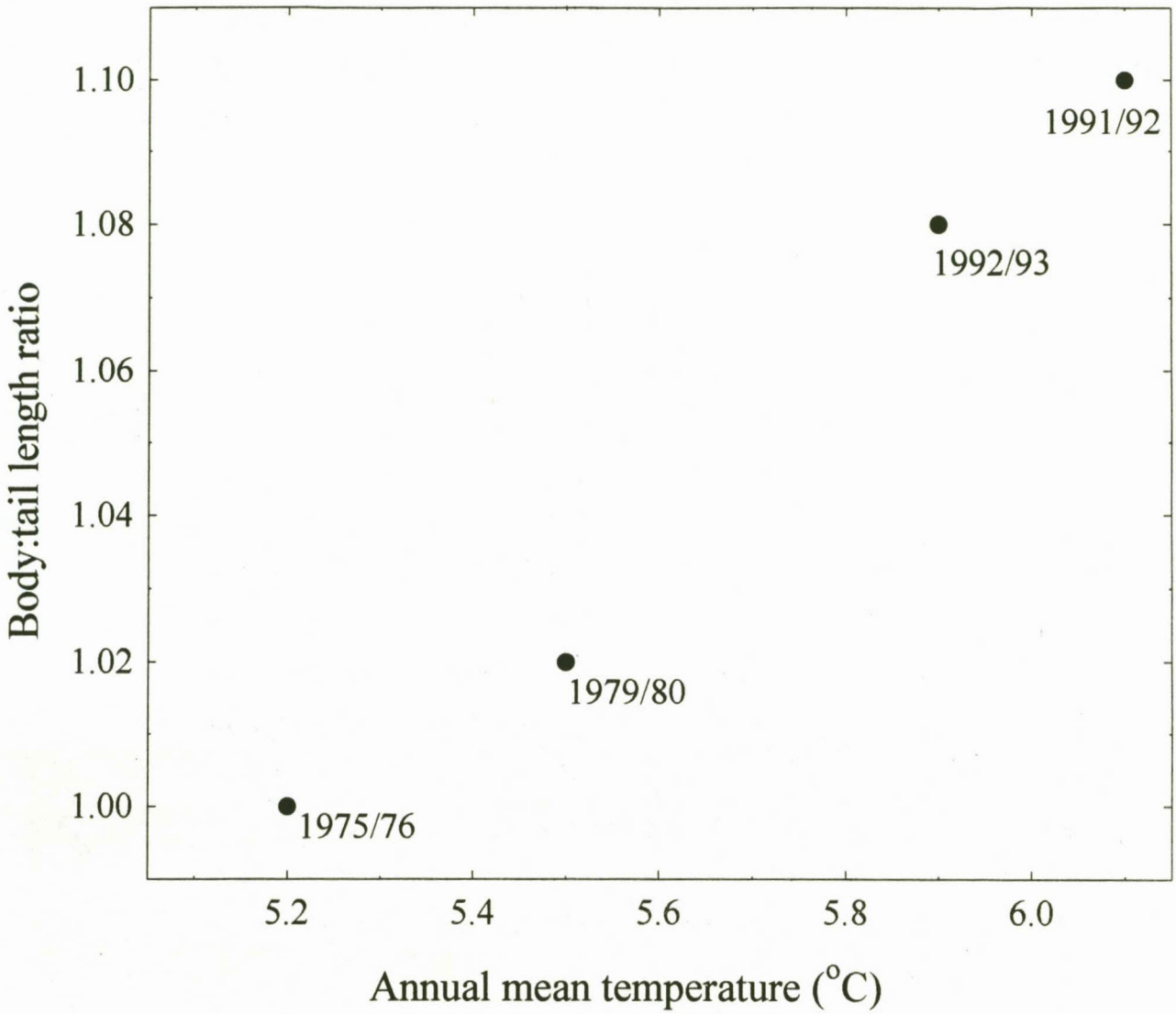

Figure 5.12. Body to tail length ratios and mean temperature for the first year of study for four investigators of mouse morphometry carried out at the island.

length ratio is plotted against annual mean air temperature for the first year of each study (e.g. 1979 for the 1979/80 investigation). Although only based on four samples, the strong positive correlation between temperature and b:t ratio is contrary to what is predicted by Allen's rule and supports conclusions from earlier studies that the rule does not seem to apply for the island's house mouse population (Gleeson 1981, Matthewson 1993). Possibly, b:t ratio depends on the mouse's overall energy needs, rather than temperature *per se*. For instance, higher mouse densities will be associated with increased competition for food and a greater need to conserve energy. One response could be a larger b:t ratio, with its thermoregulatory benefits. The significantly larger b:t ratio found here for mice that grow up in winter, compared with those that grow up in summer is in line with predictions from Allen's rule.

Comparison with mice from other sub-Antarctic and cool south temperate region islands show that temperature is a poor predictor of b:t ratio across populations, since they all have different founder populations and tail length is strongly genetically determined. For instance, mice at Gough Island (isothermal but significantly warmer climate than Marion Island) have a mean b:t ratio of 1.07 (Rowe-Rowe and Crafford 1992), similar to that of the Marion Island population. Macquarie Island (isothermal but slightly colder than Marion) and South Georgia (considerably colder than Marion) mice both have much larger b:t ratios (1.22 and 1.21 respectively; Berry and Peters 1975, Berry et al. 1979) than at Marion Island.

Generally, house mice reach their maximum size well before they reach maximum age, but all three studies carried out to date show that on Marion Island mice increase in size throughout their life; body mass and length both increase with age class right up class 7, (>13 month old). Matthewson (1993) suggested that this is because the asymptotic mass of the island's mice is high, due genetic factors rather than an adaptation to the environment, and that the long time taken to reach their asymtotic mass is due to this mass being high, rather than because of slow growth rates. The asymptotic mass of Marion Island mice cannot be determined with any confidence but mean mass of age class 7 mice was between 32 and 34.3 g, depending on season, and the heaviest mouse caught was an age class 7 female weighing 41.3 g. It is instructive to compare house mouse growth on Marion with that on Mana Island (off the SW coast of North Island, New Zealand), since there are several parallels between the two populations (isolation, lack of predators and competitors, strongly seasonal breeding, large seasonal fluctuations in population density). In addition to being warmer, Mana Island difffers from Marion in that its vegetation contains an abundance of vascular plant species, many of

which produce large seeds (Timmins et al. 1987), so it is possible that food is less limiting than at Marion Island. On Mana Island, mice reach their estimated asymptotic mass (24 g) quite early, at 6 to 8 months (Efford et al. 1988). Marion Island mice take about 12 months (age classes 5 to 6) to attain this mass, so they do grow more slowly. This could be due to genetic differences but might just as well be related to lower temperature and more limited food resources on Marion Island.

The seasonal variations in body mass and length reported here were very similar to those reported from earlier studies (Gleeson 1981, Matthewson 1993) and were associated with a strong seasonal change in age class distribution. Body mass and length were largest in spring and early summer (October to December) when the proportion of older animals in the population was highest. Mean body size then declined sharply in January as sub-adult mice entered the trappable population. It declined further in autumn and early winter due to a high mortality of older (age class >5) mice and the continued recruitment of young mice, and then increased during the second half of winter as the remaining population grew older. However, if these seasonal changes in age class are accounted for, then the male population was actually heavier in summer and autumn than in winter and spring, with a similar situation in females, except that there was a significant dip in age-corrected mean mass and length in January and February. For both sexes there was a well-defined increase in age-corrected mass and length in the transition from spring to summer and an equally well defined decrease in the transition from autumn to winter. If the earlier studies had considered the effect of seasonal variation in mean population age they would almost certainly have shown the same.

Intersite differences in mass, body length and tail length were sex-specific, with biotic site males significantly heavier and longer than males from the other two sites, and this was independent of differences in age class composition. In females, age class differences accounted for most of the inter-site variation in body mass and length. However, within age class, biotic site females also tended to be consistently larger than females from the other two sites although the difference was only significant for age class 5. This can perhaps be related to the amount of food-related stress experienced at the different sites. In mammals, nutrition when young can have an influence throughout life and individuals handicapped when young may never catch up. The biotic site had the highest invertebrate prey density and biomass (Chapter 3), but early summer mouse densities at the biotic site are not greater than at the other two sites (in fact, in 1991/92 they were, if anything, higher) so perhaps a greater food

availability during the period when the mice were developing through the early age classes allowed for a larger body size at the biotic site.

For both sexes, mice at the hummocky mosaic site had relatively shorter small intestines (smaller SI:LI ratio) and relatively longer large intestines and caeca (larger LI:TI and C:TI ratios), than mice from the other two sites, suggesting a greater proportion of plant material in the diet of hummock site mice. Stomach content analysis in fact showed that the importance value (an index integrating the percentage occurrence and volumetric contribution of a diet item) of plants in the mouse diet at the hummocky site was three times greater than that at the mire and more than double that at the biotic site (Chapter 6).

Despite the fact that, overall, all the intestinal length variables were significantly positively correlated with body mass and length, there were differences in the patterns of seasonal variation between body size and intestinal lengths. Mean body mass and length started to increase from June, but mean length of the alimentary tract organs started to increase two to three months earlier, i.e. in late summer and autumn. This period is particularly stressful since mouse densities are at their highest, invertebrate prey densities are relatively low and temperature is decreasing.

Higher energy demands during reproduction has been shown to be associated to increased intestinal lengths in mice (Barnett 1973) and the fact that reproductively active females had significantly longer small intestines, large intestines and caeca than reproductively active males, whereas there were no corresponding differences for non-reproductive mice, indicates that reproduction is especially taxing for females. The difference in small intestine length was less than that in large intestine length, so reproductive females had smaller mean SI:TI, but larger mean LI:TI ratios than reproductive males Since large intestine and caecum in small omnivorous mammals, lengthen as the contribution of plant material to the diet increases, whereas small intestine length remains unaffected (Schieck & Millar 1985), this suggests that the increased energy demand of female reproduction is met by an increased uptake of plant, rather than animal, material. This was, in fact, the case: the volumetric contribution of plant material to the stomach contents of pregnant and lactating females was, on average over the three sites, 62% greater ($F=6.7$; $P<0.01$) than for reproductively active males. For non-reproductive mice the contribution of plants to the diet was only 18% more for females than for males ($F1.3$, $P=0.25$).

The mean kidney indices found in this study (males; females) were higher than was found by Gleeson (1981) in 1979/80 (males 10.7 vs 10.3mg/g P=0.03; females 10.6 vs 9.8 mg/g, P=0.001). Mean adrenal mass was also higher than in 1979/80 (males 9.3mg vs 7.1 mg, females 10.6 vs 8.8 , Mean adrenal gland mass of males (9.30 ± 2.42 mg; 0.43 ± 0.13 mg/g) and females, both P=0.001).

Kidney index increased very sharply in the second half of winter so that for both males and females the highest values were attained in spring, after which they decreased just as sharply. Increased kidney mass in relation to cold has been noted for other house mouse populations (Barnett et al. 1975) and large kidneys are an important factor related to the over-winter survival of mice (Berry et al. 1978) so Marion Island house mice are perhaps maximizing their survival potential by having heavy kidneys (high kidney index) and increasing this index during the months when highest stress levels occur, a fact already mentioned by Gleeson (1981) who found highest kidney indices in the cold winter months. If, however, cold were the only factor influencing kidney mass, then the latter should have decreased, not increased, since 1979 because temperatures have increased. The higher temperature may indirectly be responsible for the shift in period/time when kidneys are heaviest. In 1992/93 kidney index was greatest in spring whereas in 1979/80 it was greatest in winter. This shift over a *c.* 12 year period might be interpreted as follows: The colder environment may now have, relatively, lesser influence on kidney mass while the influences of other factors, such as higher social stress and increased competition for food, shelter, etc. during summer and autumn and lower population densities during winter, or a combination of them, have increased.

Interestingly, reproductive males had heavier kidneys, but lighter adrenals, than reproductive females. Larger adrenals are particularly related to cold-induced stress in pregnant and lactating females (Barnett and Munro (1971).

The results presented in this chapter suggest that mice on Marion Island experience stress differently at different sites and times of year, that males experience stress differently to females, and that reproductive state also plays a role.

It appears that:

(i) During winter and spring mice at the mire site experienced the least stress, and in summer mice at the biotic site experienced the least.

(ii) Reproductive females experience higher stress levels than reproductive males.

(iii) Males and subadult females experience the highest levels of stress in winter, while the adult females experiences the highest stress levels in the period October – March, when a large proportion of them are reproductively active.

(iv) At the beginning of the reproductive season (late-August - October) the older males (age classes 4 - 7) experience the highest stress levels. Towards the end of the breeding season (February - April) the younger adult (age class 3) and oldest (age class 7) males experience the highest stress. From April to June the very young (age class <3) and very old (age class 7) males experience the most stress.

CHAPTER 6: FEEDING ECOLOGY OF MARION ISLAND HOUSE MICE

6.1 INTRODUCTION

Gleeson & Van Rensburg (1982) showed, from stomach content analysis, that house mice on Marion Island feed mainly on terrestrial macroinvertebrates, rather than plant material as was previously supposed. This was confirmed by Rowe-Rowe and Crafford (1989), who also used a double-labelled water technique to measure metabolic rates of the mice and, from these rates, estimated that mice were significantly impacting on the islands invertebrate populations. Crafford and Scholtz (1987) had already suggested the same thing, from a study that showed striking qualitative and quantitative differences in the insect faunas of Marion Island and nearby Prince Edward Island, where mice do not occur. Matthewson (1993) demonstrated that mouse numbers may be increasing on the island; if they are, then predation pressure on the invertebrates will also be increasing.

In this chapter, I report on an investigation into the diet of the mice in three habitats on the island and on the prey preferences of captured mice. The diet information is used, with that on macroinvertebrate biomass in Chapter 3, to estimate whether the impact of mice on their macroinvertebrate prey has changed since the previous studies were carried out.

6.2 STUDY AREA, MATERIALS AND METHODS

6.2.1 Stomach content analysis

The mice from which the stomachs were analyzed in this section were those caught in investigation of the age class distribution and reproductive status (Chapter 4). Within three hours of emptying the snaptraps the mice were weighed and then their stomachs removed, weighed, and preserved in a 25% alcohol solution. The relationship between (empty) stomach mass and whole body mass was determined on a sample of mice caught near the three study sites and this used to determine the (empty) masses of the stomachs for which the contents were

analysed. The contents of a preserved stomach were spread out in a petri dish and sorted under 12 or 25 times magnification. The percentage contribution of each item to the volume of the particular stomach's contents (PV) was estimated to the nearest 10 percent, with an additional category of 5% for a contribution estimated to be between 1 and 5% of the volume. Percentage occurrence (PC) of a particular food item in a sampling period was calculated from the number of stomachs it was found in and the number of stomachs examined. Diet variety was taken to be the number of diet items recorded in the sampling period and diet diversity was calculated, following Ebersole & Wilson (1980) as $1/\Sigma(P_i)^2$, where P (= PV/100) is the mean proportion of each of the diet items. An importance value (IV = PV*PC/100) was also calculated for each diet item (Cooper & Skinner 1978).

6.2.2 Diet item preference

Prey preferences of Marion house mice were assessed in the laboratory by giving six males each six chances to select from a variety of prey items. Five petri dishes, each containing a different live prey item were randomly placed equidistant from the entrance to a large cage. A male mouse was allowed to enter the cage and for 30 minutes the sequence in which the items were taken was recorded. Points were awarded as follows: first choice 5, second 4, third 3, fourth 2, fifth 1, not eaten 0. The prey items offered were moth larvae (*P. marioni*), weevil larvae and adults (*Ectemnorhinus similis* or *E. marioni*, possibly both were used)), earthworms (*Microscolex kerguelarum*), spiders (*Myro kerguelensis*) and slugs (*Deroceras caruanae*). The sizes of the prey items were: moth larvae between 0.14g and 0.2g wet mass; weevil adults between 0.09g and 0.11g; weevil larvae between 0.01g and 0.013g, earthworms between 0.1g and 0.2g, and slugs between 0.2g and 0.3g.

In another test, seven male and six female mice were each given the choice of different sizes (mass) of prey. The sequence in which each prey individual was taken was recorded and also the amount of time (in seconds) required to overpower and eat it. The same mice were later offered a weighed amount of seed of *Acaena magellanica, Pringlea antiscorbutica* and *Uncinia compacta*, together with water. These trials were stopped when the mouse's condition had deteriorated nearly to the point of death. The mass of seed remaining was measured.

All mice used in the laboratory tests were in age classes 3 to 5 and weighed between 18 and 27 g. They were starved for 8 hours before the test, which began about 30 minutes after sunset. Female mice used in the laboratory tests were not pregnant or lactating.

6.3 RESULTS

6.3.1 Stomach contents

The mean (wet) mass of stomach contents of the mire site was 1.01g, significantly ($P = 0.01$) greater than at the hummock (0.89g) or biotic (0.90g) sites. However, hummock site mice were smaller, and biotic site mice larger, overall, than mire site mice (Chapter 5) and larger mice might be expected to have, on average, higher stomach content masses simply because they have larger stomachs. Comparing stomach content mass: body mass ratios (sc:body ratio) should at least partially account for this and this showed that biotic site mice had, overall, significantly ($P = 0.003$) emptier stomachs (sc:body = 0.037) than mice from the mire (0.004) or hummock (0.037) sites. Considering all three sites together, stomach content mass for females was 5% greater, and the sc:body ratio 6% greater, than for males but the differences were not significant at $P \leq 0.05$. Within sites, females consistently had higher sc:body ratios than males but the difference was significant only at the biotic site.

The annual variation in stomach content mass for the three sites considered together is presented in Figure 1a, since the pattern for the individual sites were essentially similar. After high July/August values, stomach content mass declined during spring and summer so that the general pattern was one of lightest stomach contents in late summer and autumn and heaviest ones in midwinter.

Body size and mass of the mice varied markedly during the year; the means of both increased during winter and declined markedly when young mice entered the catchable population in

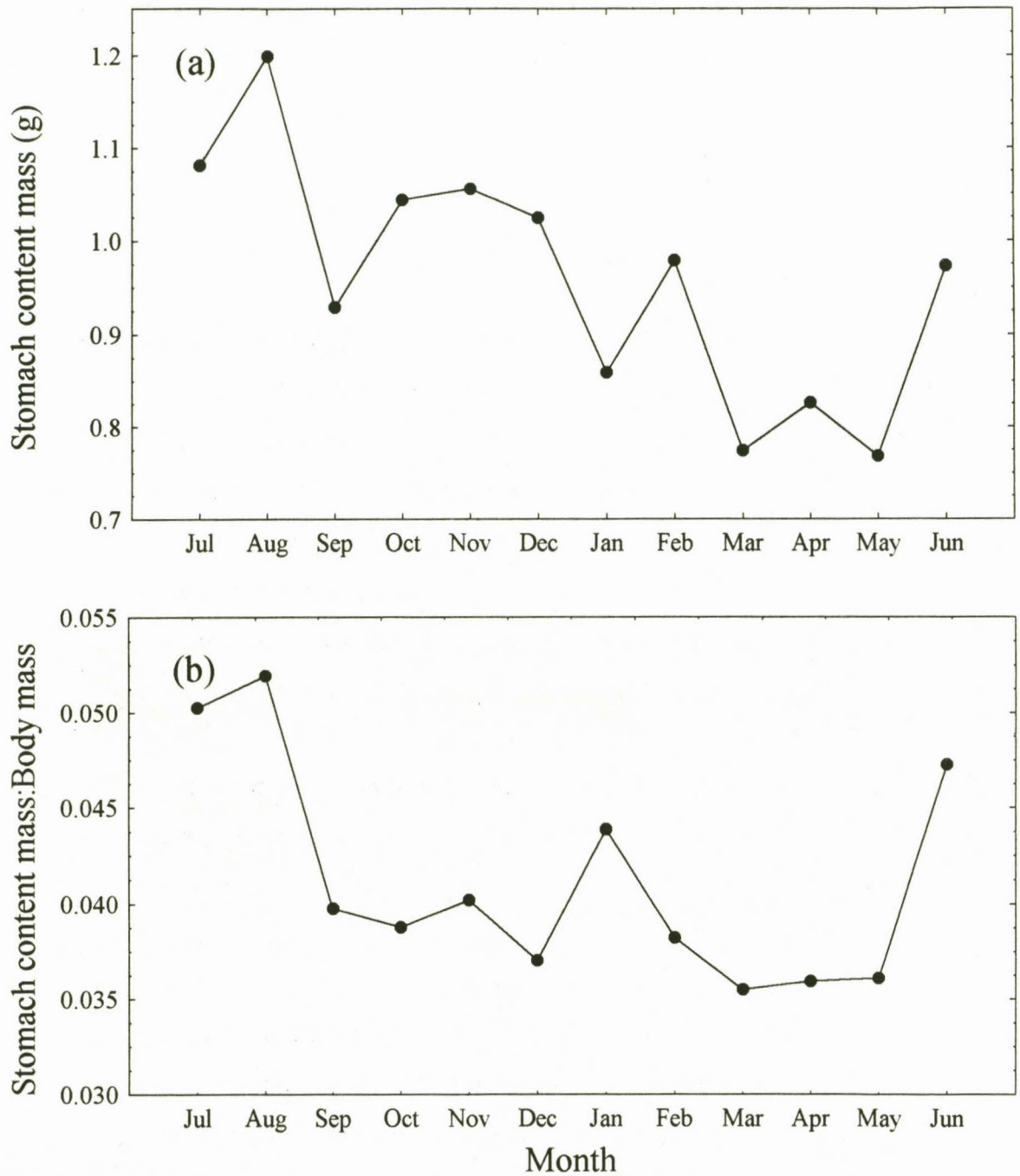

Figure 6.1. Seasonal variation in stomach content mass and stomach content mass:body mass ratio for all mice caught in the study. For convenience the austral summer months are placed in the centre.

midsummer (Chapter 4). Some of the annual variation in stomach content mass might be due to changes in body size. However, the pattern of annual variation in sc:body mass ration (Figure 1b) accentuates the difference between midwinter and the rest of the year in stomach content mass. Stomach content mass in relation to body mass is significantly higher (by 30%, $P < 0.0001$) from June to August than during the rest of the year. There is a small peak in sc:body ratio in January, mainly associated with increased amounts of plant material in the stomachs at all three sites (see later).

The biotic site showed an almost identical pattern (not shown) to the overall one in Figure 1b excepting that sc:body ratio decreased after July, rather than August. At the hummock site, the ratio declined uniformly between August and December, instead of the very sharp fall between August and September shown by the composite pattern. The mire site pattern probably deviated most from the overall one in that the July sc:body ratio was not significantly different from values in summer or autumn. All three sites showed a secondary peak in sc:body ratio in midsummer; for the hummock and mire sites this peak occurred in January, as in Figure 1b, but at the biotic site it was in December although the January value was nearly as high.

P. marioni larvae, weevil larvae and adults, and plants were the items that occurred most commonly in the stomach contents at all three sites (Table 6.1). There were very significant between-site differences in the percentage occurrence of moth larvae; 85% of the stomachs from the mice, but only 34% of those from the hummock site, contained that item. The percentage occurrence of moth larvae for the biotic site was intermediate between these two values. In contrast, the percentage occurrence of plants increased in an opposite manner; lowest at the mire and highest at the biotic site. This between-site contrast was also shown in the contributions of moth larvae and plants to the quantity (volume) of the stomach contents, where the importance of moth larvae increased, but that of plant material decreased, in the order hummock site, mire site, biotic site.

On average, weevil larvae occurred in about a quarter of the stomachs, with no significant differences in their percentage occurrence or their contribution to stomach content volume between sites. Weevil adults occurred in just over half of the stomachs at the hummock and mire

Table 6.1. Percentage occurrence in, and volume contribution to, the contents of mouse stomachs by various diet items at the three sites The values given are the annual means and where superscripts are different they indicate that the site mean differs from the others in the same row at $P \leq 0.05$, from ANOVA and Tukey's Honest Significant Difference test.

Percentage occurrence:

	Hummock	Mire	Biotic	P
Moth larvae	33.9^{a}	85.1^{c}	59.9^{b}	< 0.0001
Moth adults	10.6^{a}	30.6^{b}	11.1^{a}	0.01
Weevil larvae	27.2	31.9	20.4	0.6
Weevil adults	57.6	52.2	37.2	0.1
Earthworms	8.1	12.0	20.4	0.2
Flies	9.9	5.2	10.7	0.2
Spiders	23.8	16.2	9.9	0.1
Aphids	7.6^{a}	1.5^{a}	45.2^{b}	< 0.0001
Mites	2.4^{a}	1.3^{a}	9.6^{b}	0.001
Amphipods	0^{a}	0^{a}	3.5^{b}	0.003
Plants	77.9^{a}	48.7^{b}	56.3^{ab}	0.02
Other	13.9	12.0	20.6	0.2

Table 6.1 continues

Percentage contribution to volume:

	Hummock	Mire	Biotic	P
Moth larvae	16.1[a]	49.5[c]	36.4[b]	< 0.0001
Moth adults	3	6.4	2.7	0.13
Weevil larvae	10.5	10.3	6.9	0.7
Weevil adults	18.7[a]	9.5[b]	8.1[b]	0.003
Earthworms	3.1[a]	4.9[a]	11.6[b]	0.05
Flies	1.6[ab]	0.5[a]	2.1[b]	0.04
Spiders	4.2[a]	1.9[b]	1.6[b]	0.05
Aphids	1.5[a]	0.1[a]	5.4[b]	0.0004
Mites	0.3[a]	0.1[a]	0.7[b]	0.04
Amphipods	0[a]	0[a]	0.9[b]	0.001
Plants	35.7[a]	14.2[b]	16.4[b]	0.03
Other	5.3	2.5	7.1	0.1
Variety mean	8.2[a]	8.2[a]	11.6[b]	0.0009
Diversity mean	3.6[a]	2.8[a]	4.4[b]	0.011

sites and over a third of those at the biotic site. Their mean contribution to stomach content volume at the hummock site was about double that at the other two sites.

Earthworms were a significant diet component at the biotic site, occurring in 20% of the stomachs and making up 12% on average of the stomach content volume. Similarly, aphids and mites were significantly more often found in biotic site stomachs, which were also the only ones to contain amphipods. Aphids and mites also contributed more to stomach content volume at the biotic site than at the other two sites. Spiders were more common in, and contributed more to, the stomach contents from the hummock site.

The occurrence of flies in the stomachs of the hummocky mosaic and mire sites is surprising. The most common fly on the island is *Paractora dreuxi*, the Kelp fly, that occurs in kelp wracks on beaches. The fly remains in the stomachs from the three sites were very similar, and it was assumed that they represented *P. dreuxi*, but the hummocky and mire sites are about two hundred meters inland, well away from any kelp wracks. Kelp flies are so rarely found inland that the presence of fly remains in the stomachs of mire and hummocky site mice means either that another fly species occurs at the sites or that the mice visit the shore to forage.

Much of the plant material could not be identified to species. The identifiable component was mainly seeds of the grasses *Agostis magellanica*, Poa cookii and *P. annua*, the Kerguelen cabbage *Pringlea antiscorbutica*, the sedge *Unicinia compacta* and the rosacerus shrub *Acaena magellanica*. Leaves of all these, except the sedge, were also found in the stomachs, as were fragments of fronds of the fern *Blechnum penna-marina*. The most common mosses in the stomach contents were *Drepanocladus uncinatus*, *Racomitrium lanuginosum*, *Blepharidophyllum densifolium* and *Jamesoniella colorata*.

The "other" prey group in Table 6.1 included unidentifiable material and items that were found only very infrequently or which were suspected of having been ingested fortuitously. It included the snail *Notodisius hookeri*, the slug *Deroceros caruanae*, ticks (mainly *Ceratixodae uriae*), Enchytraeids, midges, kelp, hair and feathers. Feathers almost certainly indicate that the mice scavenge on birds and were most frequently found in the stomachs from the biotic site. Conspecific scavenging and/or cannibalism is quite common amongst the island's mice,

especially in autumn and winter and mouse hair contributed a mean of 15.9 ± 9.9% to the volume of those stomachs in which it occurred. Scats were also sometimes found in the stomachs, generally in those containing hair.

Items listed under "other" were most frequently found in, and contributed most to, the stomach contents from the biotic site but the intersite differences were not significant at $P = 0.05$. However, diet variety (the mean number of different food items found in the stomachs during the year - all plant materials form one item) and diet diversity were both significantly higher at the biotic than at the other two sites (Table 6.1).

The relative importance values ($100 \times IV/\Sigma IV$) very clearly show that four items, moth and weevil larvae, weevil adults and plant material, overwhelmingly dominate the diet of house mice on Marion Island (Figure 6.2). On average over the year they represented 92% of the diet at the hummock site, 91% at the mire and 79% at the biotic site. No other items were of much consequence, overall, in the diet of hummock site mice although the relative importance value of spiders was about five times higher than at the other two sites ($P = 0.03$). Moth adults contributed overall 5.2% to the diet of mire site mice, about five times more than at the other two sites ($P = 0.05$). Earthworms and aphids contributed materially to the diet at the biotic site and, with mites, amphipods and various items listed as "other", were the major cause of the higher diet diversity index at this site.

The importance values of both moth larvae and plant material differed significantly ($P < 0.0001$ and $P = 0.05$, respectively) across sites and clearly showed a reciprocity; moth larvae relative importance increased, and plant material relative importance decreased, in the sequence hummock, biotic, mire.

Considering the total sample of stomach contents (i.e. for all 3 sites) the average importance values and percentage contributions to stomach volume of plant material and aphids were significantly higher for females than males. For individual sites the contribution of plant material was consistently higher for females than males but the difference was only significant at $P<0.05$ at the hummock site. Stomach contents of hummock and biotic site females also contained, on average, nearly twice as much more aphids than was the case for males but the differences were

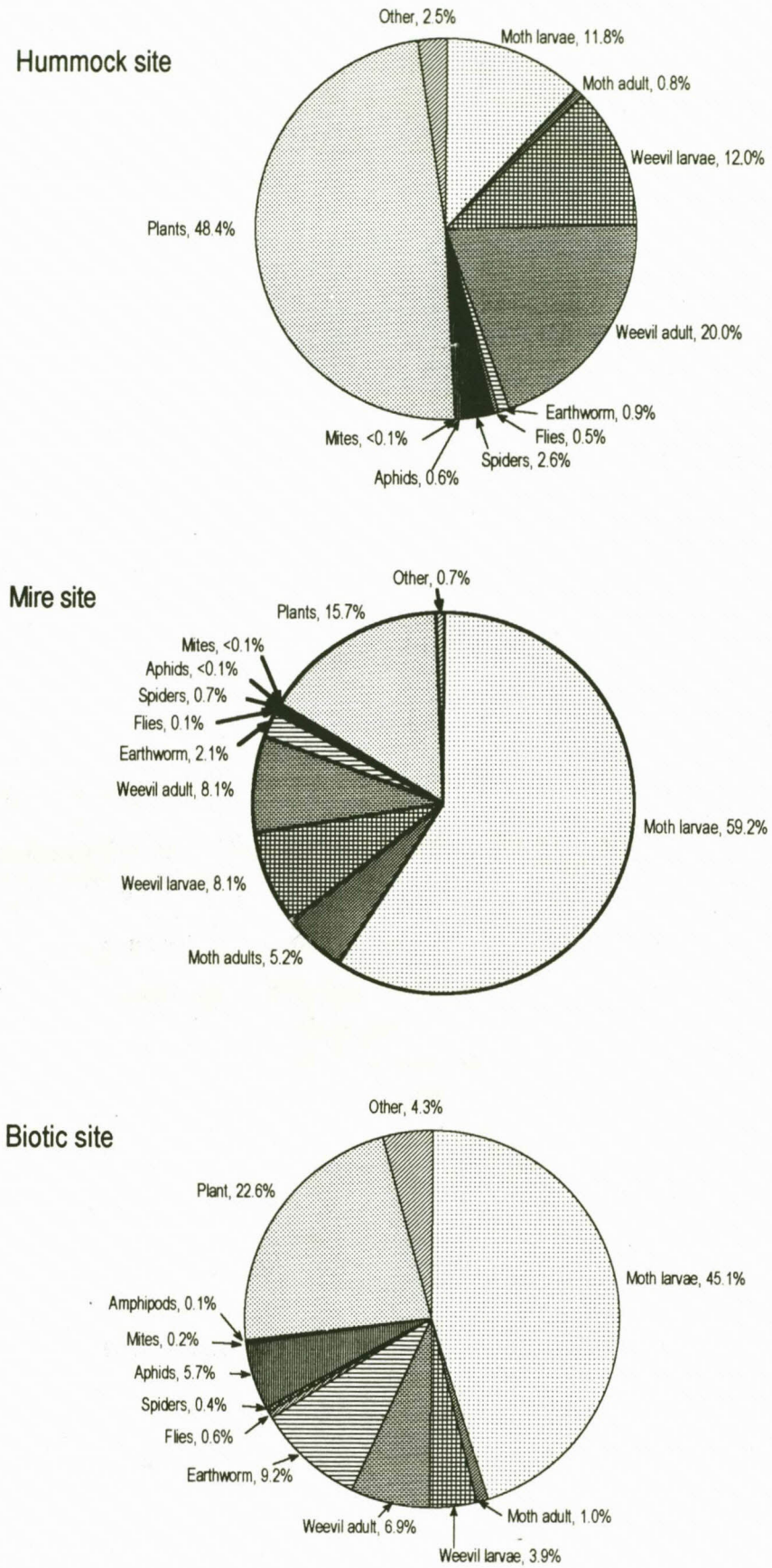

Figure 6.2. Relative importance values of diet items in the stomachs of mice from the three sites.

not significant at $P<0.05$ (at the mire site only traces - <0.2% of volume on average – of aphids were found in the stomachs of both sexes) The fact that plant material and aphids were both more important for females that males suggests that the aphids might have been ingested fortuitously along with plant material, or vice versa; however, there was a poor correlation ($r=0.07$) between the contribution of the two stomach content items and most of the stomachs that contained high percentage volume of aphids in fact had little or no plant material. The only other significant between-sex difference was for weevil larvae, which contributed about 5 times more, on average, to the diet of females than to the diet of males. At the mire site the average percentage volume contribution of weevil larvae to stomach contents was almost twice as great for males than females ($P=0.09$).

6.3.2 Seasonal variation in diet

Moth larvae importance value was relatively low (<15) for most of the year at the hummocky mosaic site (Figure 6.3a). In October it was highest. Weevils (both larvae and adults, increased in importance in the diet at the hummocky site between August and December, and disappeared from the diet in January (Figure 6.3b,d). Spiders were most important in mid winter (June to August) but even then their IV was low (Figure 6.3e). Plants (Figure 6.3c) increased in importance during the first half of summer and from January to April were the predominant diet item. Overall, there was a strong reciprocity between the relative importances of plant and animal items, with animals making up most of the diet in late winter and early summer and plants being most important in late summer and the first part of winter, although in August plants were also an important component of the diet.

At the mire site (Figure 6.4) moth larvae were the most important diet item over the whole year. Weevil larvae were important in spring and weevil adults in spring and summer. Moth adults were also a significant part of the diet in late winter at the mire. Plant material IV was less than 10 throughout the year, except in January.

At the biotic site, for most of the year macroinvertebrates, especially moth larvae, were the dominant diet items (Figure 6.5). The IV's of the invertebrates peaked in succession: weevil

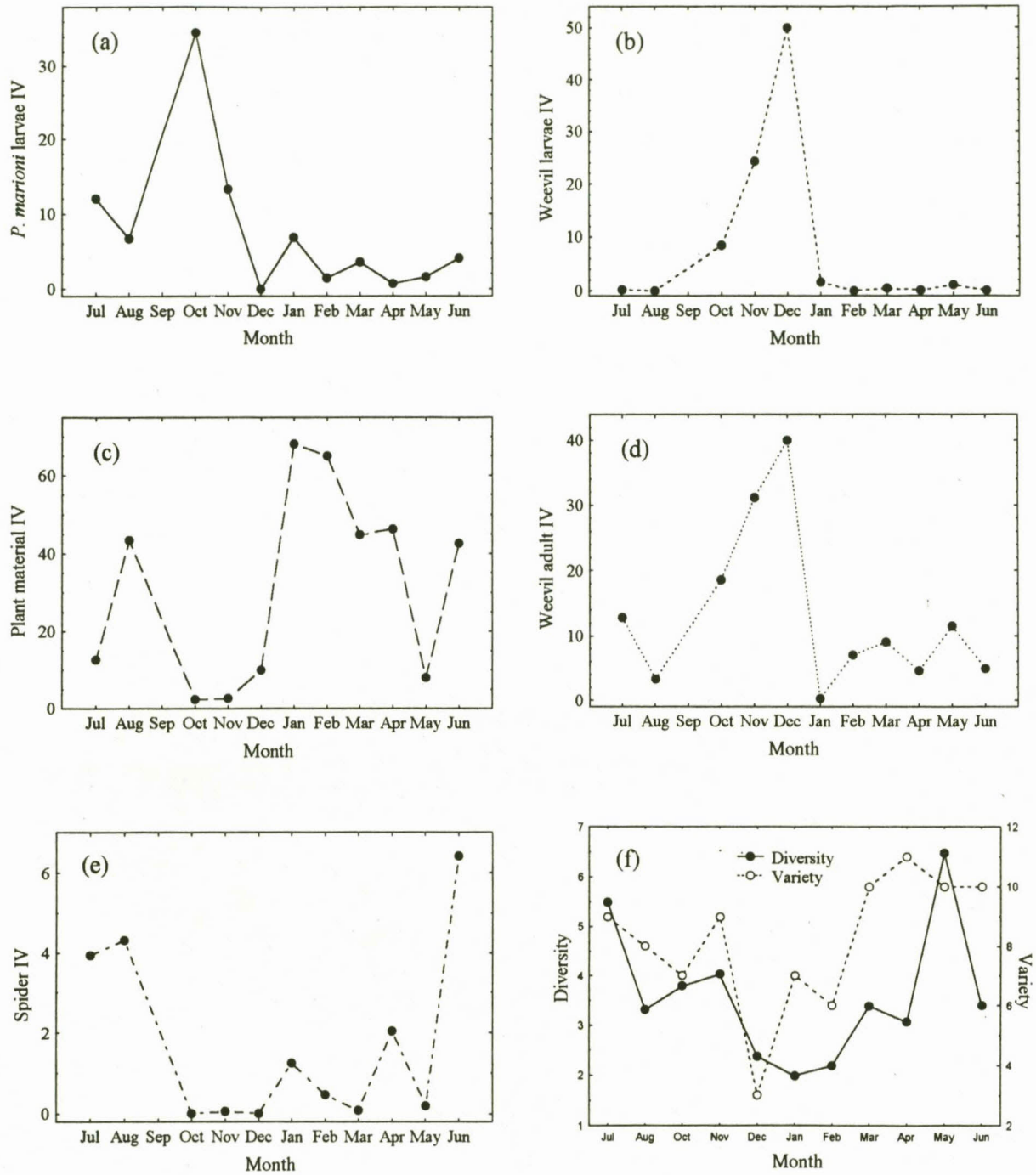

Figure 6.3. (a - e) Seasonal variations in the importance values of the most commonly occuring items in the stomachs of mice from the hummocky mosaic site. (f) Seasonal variations in diet diversity (solid circles, lines) and variety (open circles, stippled lines).

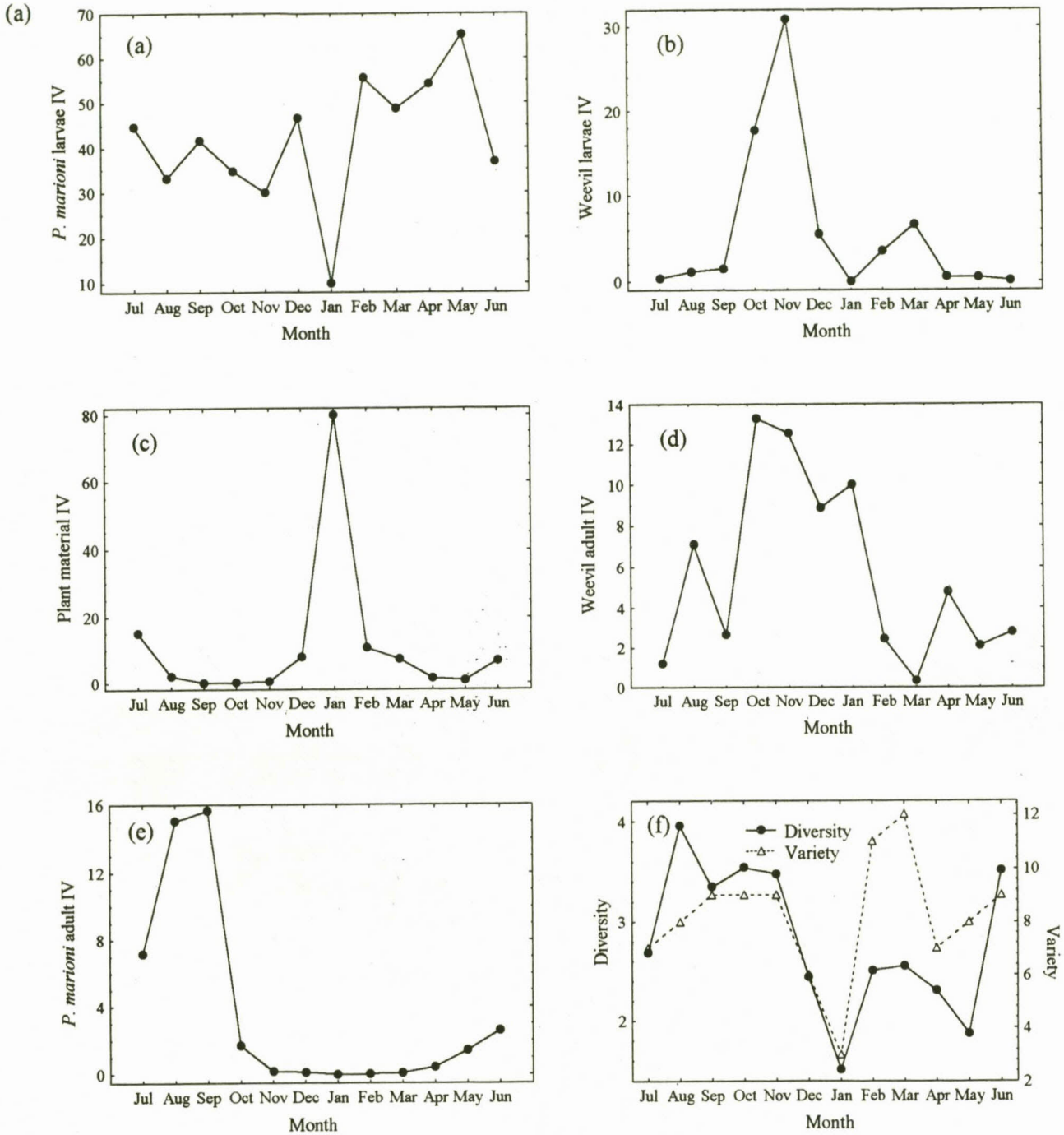

Figure 6.4. (a - e) Seasonal variations in the importance values of the most commonly occuring items in the stomachs of mice from the mire site. (f) Seasonal variations in diet diversity (solid circles, lines) and variety (open circles, stippled lines).

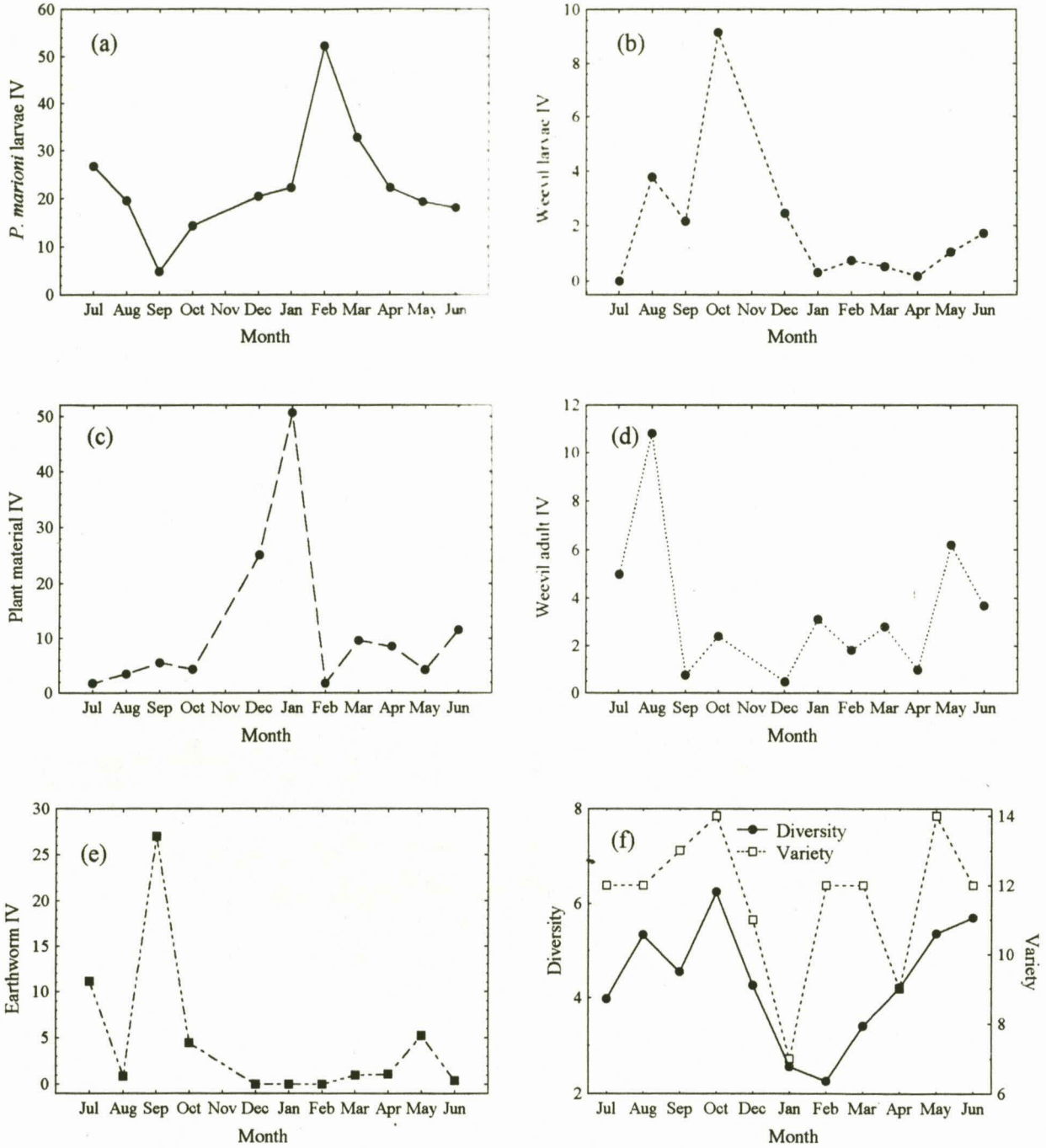

Figure 6.5. (a - e) Seasonal variations in the importance values of the most commonly occuring items in the stomachs of mice from the biotic site. (f) Seasonal variations in diet diversity (solid circles, lines) and variety (open circles, stippled lines).

adults in August, earthworms in September, weevil larvae in October and moth larvae in February, with plant material being important in the mid summer period between the weevil larvae and moth larvae peaks.

There were no clearcut seasonal patterns in diet diversity and variety, as might be expected in a situation where there is a restricted number of diet items to choose from and where most prey species are present for most of the year (and where all plant items were considered as one category). Diversity tended to be lower in summer and autumn (December to April or May) than in late winter and spring (July to November). Variety was lowest in midsummer (December or January) and highest in autumn (hummocky and mire sites) or winter (biotic site).

6.3.3 Prey preference

There were no significant differences between male and female mice in their size selection of moth larvae or earthworms or in time spent in subduing and devouring the prey, so the data from both sexes were considered together (Tables 6.2 and 6.3).

Mice went straight for their first prey item in 86% of the trials; in the other 14% they visited one or more of the petri dishes before making a choice. Moth larvae were selected first in 92% of all 36 trials done in the laboratory, and second in the other 8% (Table 6.2). Either earthworms or weevil adults were generally the second item selected. Weevil larvae were most often the fourth item taken. Only one slug was selected, as the last choice and only a small part of it was eaten before it was discarded. Mean score for moth larvae was significantly greater than those for earthworms and weevil adults, which were, in turn, greater than the score for weevil larvae.

When allowed to choose between *P. marioni* larvae of different mass, mice generally chose the largest (heaviest) individuals first and the smallest individuals last (Table 6.3). The largest larvae were eaten during all thirteen trials, the second largest larvae during 11 trials, the third largest larvae during eight trials, and the fourth largest larvae during seven of the trials. Mean mass was therefore greatest for the first choice and declined significantly between all subsequent choices. For earthworms the heaviest one was most often chosen first, so the mean mass of the

Table 6.2. Prey preference of house mice under laboratory conditions on Marion Island. n is the number of trials in which the particular item was chosen in the particular"Choice" category.

Choice	Points awarded	*P.marioni* larvae	Earth-worms	Weevil adults	Weevil larvae	Slugs
First	5	n=33	n= 2	n= 1	n= 0	n= 0
Second	4	n= 3	n=17	n=11	n= 5	n= 0
Third	3	n= 0	n=13	n=16	n= 7	n= 0
Fourth	2	n= 0	n= 4	n= 8	n=24	n= 0
Fifth	1	n= 0	n= 0	n= 0	n= 0	n= 1
Not eaten	0	n= 0	n= 0	n= 0	n= 0	n=35
Total score		177	125	113	89	1

Table 6.3. Prey size (g) preference of seven male and six female house mice and the amount of time (seconds) needed to subdue and eat three prey items under laboratory conditions on Marion Island and the Spearman rank correlation coefficient of mass with time.

	N	Mass	Time	Correlation*
Pringleophaga marioni larvae				
First choice	13	0.257 ± 0.092	50.5 ± 14.3	R=0.6612; p=0.0139
Second choice	11	0.164 ± 0.045	31.4 ± 9.2	R=0.7234; p=0.0180
Third choice	8	0.140 ± 0.062	31.4 ± 16.7	R=0.8260; p=0.0114
Fourth choice	7	0.088 ± 0.029	72.3 ± 81.1	R=0.3930; p=0.3833
Mean	39	0.177 ± 0.090	45.4 ± 38.0	R=0.5867; p=0.0001
Earthworms				
First choice	13	0.156 ± 0.079	61.6 ± 31.3	R=0.6740; p=0.0115
Second choice	12	0.130 ± 0.071	40.3 ± 27.1	R=0.7193; p=0.0084
Third choice	10	0.136 ± 0.071	48.6 ± 27.8	R=0.6483; p=0.0426
Fourth choice	4	0.123 ± 0.056	60.0 ± 58.0	-
Mean	39	0.139 ± 0.071	51.1 ± 30.4	R=0.7694; p<0.0001
Weevil adults				
Mean	68	0.010 ± 0.002	5.87 ± 3.25	R=0.3668; p=0.0021

first choice was higher than for subsequent choices. However, the order of individuals taken after the first choice did not depend on size so there was no difference in mean mass of subsequent choices.

On average, mice spent 45.4 seconds to subdue and eat a *P. marioni* larve and 51.1 seconds to eat an earthworm. With the larvae and the earthworms, for the first three selections, but not the fourth, there was a significant correlation between prey mass and time needed to subdue and eat the prey. The correlation was poor where moth larvae were the fourth choice, partly because the mice took a longer, and more variable, time to eat them and partly because moth larvae were seldom only the fourth choice amongst the prey items offered, so sample size was low. Earthworms were the fourth choice in four instances and in two of them the mouse did not finish eating the worm, so a time: mass correlation was not calculated.

Mice offered weevil adults one at a time, took on average 5.9 seconds to eat the weevil (data not shown). Slugs of different sizes were offered to 13 hungry mice but none were eaten when first offered. After 10 hours without food each mouse was given a *P. marioni* larvae, which was immediately devoured, and then a slug. In one case the slug was eaten (22 seconds for a 0.235g individual) and in another the mouse bit the slug but then left it alone. The other 11 mice ignored the slugs.

In the trials in which mice were offered only plant material (*Acaena magellanica, Pringlea antiscorbutica* and *Uncinia compacta* seed) it proved impossible to accurately estimate the mass of seed consumed since mice communited and scattered the seed, defecated and urinated on it and used it for nesting material. Never the less, these trial gave interesting and in some cases, unexpected, results. In all the trials the condition of the mice deteriorated (in some instances severely) during the trials, yet in none of them was more than 50% of the seed mass eaten. *P. antiscorbutica* seed was eaten in the largest quantity; on average about 40% of the mass offered was devoured and in all the trials at least some *P. antiscorbutica* seed was eaten. In about $^1/_3$ of the trials the *A. magellanica* and *U. compacta* seed was untouched and, on average, less than 30% of the seed of these two species was consumed. During all the trials with *P. antiscorbutica,* seed was used to build nests. *A. magellanica* seed was used for this purpose in three trials but *U. compacta* seed was not used in any of them.

After 6 hours, two of the mice provided with *A. magellanica* had died and four were in a very poor condition so they were removed from the trial. After another six hours three of the remaining mice were dead and the other three very close to death. Two of the mice given *U. compacta* seed nearly died in the first 6 hours and were removed; two died over the next 6 hours and the remainder were in poor condition. The mice fared slightly better on *P. antiscorbutica* seed; four of the 13 were still in reasonably good condition after 12 hours, but seven were in poor condition and one had died.

6.4 DISCUSSION

Gleeson (1981) carried out his 1979/80 diet study in six habitat types and pooled his results, which makes comparison with the results presented here difficult. Fiducial limits or other distribution statistics are also not provided for the stomach content values from 1979/80 data so statistical comparisons are impossible. However, there are some conspicuous dissimilarities in the results of the two studies. The most striking is that in 1979/80 *Pringleophaga marioni* larvae overwhelmingly dominated the diet – it occurred in about 75% of the stomachs and contributed, on average, about 50% of the stomach content volume. Overall, these larvae were still found to be the most important diet item in 1992/93 but, at the hummocky and biotic sites their occurrence and volumetric contribution were both less than in 1979/80. In contrast, weevil larvae increased in importance since 1979/80. The mean volume contribution of weevil larvae in 1979/80 was *c.*2%, compared with 7% at the biotic site and 10% at the hummocky and mire sites in 1992/93. The annual mean volume contributions of weevil adults at all three sites (8 to 19%) were also higher than what was found overall in 1979/80 (7%).

The importance of plant material has also increased; mean volume contribution of plants was not more than 30% for any of the six sampling periods in 1979/80, whereas for the 1992/93 sampling periods it was sometimes more than 30%, frequently so at the hummocky site. Certainly, the incidence of plant items in the stomachs has greatly increased, from a 36% overall mean in 1979/80 to 49 - 78% for the three sites in 1992/93.

Earthworms were only occasionally found in the stomachs in 1979/80, suggestedly because their subterranean habit makes them relatively unavailable (Gleeson & Van Rensburg 1982). In 1992/93, earthworms were found in 13% of the stomachs and were an important diet item at the biotic site in winter.

The seasonal contribution of particular items to the stomach contents seems also to have changed since 19979/80. For instance, in 1979/80 weevil adults were most important in the diet in late winter (August to October) whereas at the hummocky and mire sites in 1992/93 they were most important in early summer (October to December, or January).

In the 1979/80 study flies, aphids, mites and marine amphipods were all lumped in the "other" category, whereas in the 1992/93 study these were considered as separate diet items, so the diversity indices in Table 6.1 cannot be compared with the corresponding 1979/80 values. Recomputation using the same diet categories as in 1979/80 gives a diversity index of 3.4 ± 0.7 for the three sites overall, similar to the value (3.6) for 1979/80. However, unlike in 1979/80, when diet diversity was lowest from July to October (winter and early spring), in 1992/93 it was highest then.

Stomach contents were found to be heavier in winter than in spring or summer in both studies, and it was shown here that this is not because mice are heavier in winter. Gleeson (1981) ascribed it to longer winter nights allowing for a longer foraging period. Mice have also been shown to increase their food consumption markedly when faced with lower temperature (Myrcha 1975).

Site- and season-specific estimates of the impact of mice on their invertebrate prey are presented in Table 6.4. Definition of seasons is the same as that in earlier chapters, i.e. spring is October & November, summer is December to March, autumn is April and May and winter is June to September. The estimate of Rowe-Rowe et al. (1989) that the island's mice each consume, on average, 3.5 g dry mass of food per day was multiplied by the seasonal mean mouse density and by the seasonal mean contribution of a particular prey item to estimate the mean daily and total annual consumption of that item. Mouse densities (Petersen estimates corrected using assessment lines) were those measured in 1991/92 by Matthewson (1993) - density in April was

Table 6.4. Daily consumption, A (g $ha^{-1}d^{-1}$) and daily consumption as percentage of mean biomass, B (%) of macroinvertebrate prey items at the biotic and mire sites.

	Days	Mouse density (mice ha^{-1})	Moth larvae		Moth adults		Weevil larvae		Weevil adults		Earthworms		Flies		Spiders		Total
			A	B	A	B	A	B	A	B	A	B	A	B	A	B	A
Biotic site																	
Spring	61	33	31.3	0.4	6.1	-	23.3	0.4	8.2	0.4	18.3	0.01	2.4	-	3.3	1.1	92.9
Summer	121	80	126.8	1.6	1.2	-	14.8	0.3	15.3	0.7	5.8	0.01	2.3	-	3.8	1.3	170.0
Autumn	61	211	267.4	3.4	31.0	-	26.1	0.5	63.0	13.1	92.1	0.11	20.5	-	6.2	1.0	506.3
Winter	122	42	44.1	0.6	5.2	-	10.3	0.2	15.9	3.3	29.0	0.03	4.3	-	2.7	0.5	111.5
Year			106.7	1.3	8.3	-	16.6	0.3	22.3	1.6	30.1	0.03	6.0	-	3.7	0.8	193.7
Annual consumption (kg ha^{-1} y^{-1})			38.9		3.0	-	6.1		8.1		11.0		2.2		1.4		70.7
Annual mean biomass (kg ha^{-1})			7.94		?		5.2		1.4		10.8		?		0.4		
Annual consumption / biomass			4.9x		-		1.2x		5.8x		1.0x		-		3.1x		
Mire site																	
Spring	61	7	9.6	0.1	0.8	-	7.8	0.1	3.6	0.1	0.4	0.02	0.1	-	0.7	0.2	23.0
Summer	121	5	8.2	0.1	0.1	-	1.6	0.1	1.4	0.1	0.1	0.01	0.1	-	0.3	0.1	11.8
Autumn	61	35	83.1	2.0	5.0	-	4.3	0.4	12.0	-	1.4	0.03	0.1	-	3.9	0.7	109.8
Winter	122	18	30.2	0.7	9.4	-	2.4	0.2	5.4	-	8.1	0.17	0.5	-	0.6	0.1	56.6
Year			28.3	0.3	4.2	-	3.4	0.3	4.8	0.3	3.0	0.09	0.2	-	1.1	0.2	45.0
Annual consumption (kg ha^{-1} y^{-1})			10.3		1.5	-	1.2		1.8		1.1		0.08		0.4		
Annual mean biomass (kg ha^{-1})			11.1		-		4.8		1.6		3.4		?		0.5		
Annual consumption / biomass			0.9x		-		0.3x		1.1x		0.3x		-		0.8x		

not measured so it was estimated from the seasonal curve. Since mouse densities at the mire were only measured every second month, but were similar to those at the "vegetated lava" site, for which monthly measurements were made, pooled values from the two sites were used to estimate densities at the mire. Seasonal mean contributions of prey items to mouse stomach contents were calculated from the monthly measurements made in 1992/93 and reported in this chapter. Macroinvertebrate biomasses given for summer in Chapter 3 were assumed to also be those in spring (they were measured in December/January), and the autumn values were assumed to be the same as those given for winter (measured in June/July). The macroinvertebrate species considered together accounted for >90% of the total animal remains in the stomach contents at the two sites; moth larvae and adults, weevil larvae and adults, earthworms, spiders and flies.

Mean estimated daily impact of mice on all invertebrates during this study was 194 g ha^{-1} (dry mass) at the biotic site and 45 g ha^{-1} at the mire (Table 6.4), or total annual consumptions of 70.7 kg ha^{-1} and 16.3 kg ha^{-1} respectively. Moth larvae made up a substantial proportion of this; at the biotic site the average daily consumption was 107 g ha^{-1} or 1.3% of the annual average biomass of larvae, while at the mire 28 g ha^{-1}, or 0.3% of the average biomass, were consumed per day. Mice impacted most on moth larvae in summer and autumn at the mire site, but in autumn and winter at the mire. The average daily consumption of moth larvae for both sites over the year (67.5 g ha^{-1}) is very similar to that reported for the island's coastal plain as a whole (65 g ha^{-1}) by Rowe-Rowe et al. (1989).

In terms of mass consumed, earthworms were the item taken next most heavily after moth larvae at the biotic site, where they were most impacted on in autumn. However, the average amount consumed per day over the year was only a small fraction of the amount available so that, overall, mice consume about the annual average biomass of earthworms in a year at the biotic site. At the mire site, mice mostly impacted on the earthworm population in winter, but overall in the year only consumed about $^1/_3$ of the average biomass.

At both sites, the heaviest impact of mice, in terms of the amount consumed in relation to biomass, was for weevil adults – up to 5 times the annual average biomass was consumed at the biotic site, and daily consumption in winter 13% of the average biomass. This confirms previous reports that mice are having an especially severe impact on weevils, especially adults, at the island (Chown and Smith 1993).

CHAPTER 7: CONCLUSIONS AND SUGGESTIONS FOR FURTHER RESEARCH

7.1 Conclusions

This study showed that house mice on Marion Island try, through the construction of simplex and complex burrow systems and above-ground runways, evade the worst extremes of a harsh climate. Burrow temperatures seldom drop below 2°C and ground surface temperatures seldom below 0°C. Burrowing is thus an important factor in the survival of the island's house mouse population. However, the mouse's life within these burrows is still unknown and studies on social behavioural aspects (e.g. territoriality, huddling) as well as *in situ* physiological studies (thermogenesis, diurnal range in metabolic rates, energy demands of reproduction, possible torpor) are needed.

This study reinforced all previous findings that biotically influenced (seabird and seal manuring) habitats contain the highest numbers of macroinvertebrates, almost certainly the reason why they also support the highest mouse populations. The relative contributions of the various prey species to the macroinvertebrate populations have changed over 15 years. One major change is that the relative importance of earthworms has decreased. Another is that an exotic slug (*Deroceras caruanae*) has become well established and may be displacing some of the indigenous species, such as the sub-Antarctic land snail *Notodiscus hookeri*. The slug is probably the only macroinvertebrate species on the island that was exposed to mammalian predation in its evolution and it seems to have developed an adaptation that makes it unpalatable to mice since they rarely eat slugs in the laboratory. Overall, mean macroinvertebrate density in summer was about 45% lower during this study (1992/93) than the mean density of 1976/77, while summer biomass is about 60% lower than in 1976/77, which could mean that either macroinvertebrates as a whole became smaller (some did, e.g. weevil adults and spiders, and possibly moth larvae) or that smaller species are becoming more important at the expense of larger ones.

All these changes have been shown before and it is most often suggested that house mice are their cause. The composition of the mouse diet has changed since it was first investigated in

1979/80. Mostly the change was associated with a lowering in importance of moth larvae in the diet, although they are still the most important item, overall. This decrease was compensated for by increases in the importance of earthworms (winter) and plant material (summer), and also weevil adults and larvae

Differences in the diversity and variety of food ingested over a 12 month period strengthen the idea that the percentage contribution of the different prey types, and therefore the composition and/or density and/or composition of size classes of invertebrates, have changed since the 1979/80 study. Where in1979/80 diversity and variety were both lowest during winter, this study found the lowest diversity and variety in summer.

Mean estimated daily impact of mice on all invertebrates during this study was 194 g ha^{-1} (dry mass) at the biotic site and 45 g ha^{-1} at the mire, or total annual consumptions of 70.7 kg ha^{-1} and 16.3 kg ha^{-1} respectively. Moth larvae made up a substantial proportion of these values.

The mice are almost certainly size selective feeders that switch to other prey items when the preferred (or major) prey item is not available. This "prey-switching" probably plays an important role in their survival under the harsh conditions on the island. During the colder periods of low prey density mice were observed to eat a wider variety of prey, with a higher percentage contribution of less favoured food (such as plant matter, aphids, mites, ticks and slugs).

The cold, wet and windy conditions, together with the seasonal fluctuations in prey quality and quantity also have an influence on house mouse reproduction on Marion Island. Here mice reach sexual maturity at a later age than generally found elsewhere. Numerous authors have showed that the rate of maturation decreases at low temperatures, poor food quality and/or availability, high density, or a combination of these and other factors. Also, reproductive activities of sexually mature Marion Island males and females from the younger and very old age classes were found to be the first to stop at the onset of adverse conditions (such as low temperature, scarcity of food and population density). This is interpreted as these mice being less competitive for food and space and experiencing higher levels of social stress than mice in the prime of their lives.

House mice are seasonal breeders on Marion Island. Here it is assumed that temperature, food supply and social stress level determine the timing of the breeding season. The breeding season is associated collectively with warmer temperatures and higher prey density and -biomass. Female reproductive activity at all vegetation types were significantly correlated with mean daily mean and mean daily minimum temperatures at nearly all positions sampled. Reproductive state of house mouse females, however, correlated best with the temperature where the mice forage (on the ground outside the burrow system, below the vegetation cover). The start of the breeding season is, therefore, associated with an increase in temperature after winter, when mouse densities are low. The cessation of breeding at the end of April is associated with a decrease in temperature and an expected simultaneous seasonal decline in food supply (qualitative and quantitative) and high mouse density. The fact that male mice on Marion Island become reproductively active earlier in the season than females can be explained by the fact that the basic energy requirements for reproduction are lower for males than for females. Male reproduction is, therefore, consequently less affected by harsh environmental conditions. The fact that male reproductive condition declined from late autumn to late winter on Marion Island is further proof of the severe environmental stress that Marion mice experience during this time of year. The fact that not all males at the mire site were non-scrotal during the mid-winter months, as well as the fact that mire females became reproductively active one month before those at any of the other sites may prove that mire mice experience less stress during winter than mice at the other vegetation types.

From the period when a significant proportion of females were pregnant or lactating it is concluded that breeding started earlier in 1992 than in 1979/80, and stopped later; the length of the breeding season has therefore increased, possibly by as much as 2 months. This is almost certainly due to ameliorating temperatures. The peak season for male reproductive activity lasted for the 7 months of September to April.

The age structure of Marion Island house mice is characteristic of a seasonal breeding population. The very young and old individuals were thus absent during the harshest time of the year. Differences in age composition between habitats can be attributed to differences in the survival rate of mice at the different sites, as well as differences in the time of onset of reproduction (indirectly attributed to possible differences in temperature experienced, refuge availability and differences in prey density and biomass). Differences in age structure and onset

and cessation of reproduction between specific mice groups suggest that Marion mice experience stress differently at different sites, at different times of year, at different ages, between sexes and in different reproductive states. We can deduce that mice experience the least stress at the mire site in winter. Males and subadult female experience the highest levels of stress in winter. Lactating and pregnant females experience the highest, but non-reproductive females the lowest, stress levels towards the end of the breeding season (February - April).

Morphometrical measurements (body mass and length, intestine length and composition, and kidney and adrenal mass) confirmed the fact that the mice on Marion Island experience stress differently at different sites, at different times of year, at different ages, between sexes and in different reproductive states. The information on the seasonal variation and sex- or reproduction related differences in body mass and length, or in intestinal parameters are consistent with the conclusions based on the seasonal changes in reproductive status. The morphometric results suggest that mice experience the least stress during winter and spring at the mire but during summer at the biotic site. Throughout the year the hummocky mosaic site is the most stressful of the three investigated. Adult females experience higher stress levels than males during the breeding season only. Males and subadult females experience the highest levels of stress in winter, while adult females experience the highest stress levels in the period October – January, when a high percentage are either pregnant or lactating. At the beginning of the reproductive season, in late August to October, the older males (age classes 4 - 7) experience high stress levels. Towards the end of the breeding season (February - April) the younger adult (age class 3) and oldest (age class 7) males are most stressed. In the period April - June the very young (age class <3) and very old (age class 7) males experience highest stress and there is a high rate of mortality amongst them.

Other factors that may have an influence on stress levels are the relative availability of food, high mouse density and social structure .

7.2 Suggestions for further research:

The Prince Edward Islands Management Plan requires that attention be given to the removal of aliens from these islands. In February 1995 a workshop on "the impact of feral house mice at sub-Antarctic Marion Island and the desirability of eradication" (Chown & Cooper 1995) was held where I made a contribution based on the work presented in this thesis. It was decided that the eradication of mice is feasible but would be prohibitively expensive. It was urged that control measures should be investigated. In the meantime, the presence of a relatively easily studied, alien mammal in a well understood ecosystem that has developed in the absence of mammalian predators and herbivores, and that is experiencing pronounced climate change, offers a wonderful opportunity to carry out fundamental studies on alien invasive biology. With mouse-free Prince Edward as a control, the response of an ecosystem to a highly successful alien organism such as the house mouse, and the adaptations shown by the mouse to what is still a fairly inhospitable ecosystem, are fascinating and profitable topics of investigation.

Considering the current situation of a changing temperature regime on the island, and the cardinal and interdependent roles of both mice and their invertebrate prey in the island's ecology, it is imperative that, at minimum, a monitoring programme be put in place to measure mouse densities every year, preferably in April/May when values are highest, and at two low- and one high altitude sites. Stomach contents of the captured mice must be documented and invertebrate densities measured at the same time at adjacent, similar sites. Such a monitoring programme would not be too onerous and should not replace current studies on the population biology, energetics and physiological adaptations of the island's house mouse population – it will add to the value of these studies and make the interpretation of their results more meaningful. However, even as a stand-alone effort, the monitoring, although providing a fairly small window of information for each year, will in time yield extremely valuable data for understanding the ecological impacts of mice on the island. Considering our need to understand the island's terrestrial ecosystem so that it can be managed and conserved, there is as much justification for monitoring mice as there is for the current seal and bird monitoring programmes already in place. In fact, it is noteworthy that the bird monitoring ignores the island's Lesser sheathbill population, which is directly threatened by mice.

In addition to this monitoring, there is much to be learnt about the feeding biology and physiology of the mice, such as the timing, method and range of foraging, ingestion, egestion and assimilation rates, transit times of food through the gut, possibility of cellulose and chitin digestion, energy allocation patterns and how they are influenced by season, reproductive state and intra-specific competition. Concentrated studies defining the spatial and temporal patterns in the densities and distributions of the soil invertebrate populations, not only for the macroinvertebrates studied to date, but also for groups such as enchytraeids, nematodes, mites and Collembola must be undertaken. This will lead to a very large increase in our understanding of many aspects of the island's biology, much more than merely telling us something more about the island's house mouse population.

SUMMARY

This thesis presents the results of a study of the biotic and abiotic conditions experienced by house mice on Marion Island, their morphological and reproductional adaptations to island conditions, the seasonal changes in their diet, and of the densities and biomasses of their prey items.

By establishing burrow systems and sheltered aboveground runways mice experience a microclimate that is far less harsh than the macroclimatic regime. In terms of warmth, this extends the season of mouse activity significantly compared with what would be allowed by the macroclimate.

House mice are opportunistic feeders and this plays a major role in their survival under the harsh conditions on Marion Island. The mice are primarily carnivores and impact severely on soil macroinvertebrate populations, annually removing up to several times the average instantaneous standing crop of some macroinvertebrate populations. Since macroinvertebrates are cardinal agents of ecosystem functioning by being the main mediators of nutrient cycling on the island, their predation by mice has severe ecological implications. Between 1979/80 and 1992/93 the densities and biomasses of the mouse's major invertebrate prey species have decreased. The percentage composition of the various prey types in the macroinvertebrate population has also changed. These changes have caused changes in the composition of the mouse's diet.

Seasonal changes in reproductive status, sex ratio, age structure, body mass and length, kidney- and adrenal mass, and length and shape of intestines were determined, in order to provide information concerning the house mouse's response to fluctuating environmental parameters and to assess the levels of stress experienced by mice at different times of the year. Stress levels are influenced by population density, sex, reproductive status, temperature and availability of food. In 1992/93 mice had significantly larger body to tail length ratios than in 1979/80, despite the fact that the island warmed considerably in the interim. This warming has allowed a significantly longer breeding season, perhaps by as much as two months. It is

suggested that this is the reason that end of season densities are now considerably higher than in 1979/80.

OPSOMMING

Hierdie tesis toon die resultate van 'n studie van die biotiese en abiotiese toestande wat deur die huismuis op Marioneiland (46°54' S, 37°45' E) ondervind word – hulle morfologiese en voortplantings-aanpassings by eiland toestande, die seisoenale veranderinge in die dieët, asook die digtheid en biomassas van hulle prooi.

Deur die daarstelling van 'n tonnelsisteem en beskutte bogrondse gange, ondervind die muise 'n mikroklimaat wat baie minder vel is as die mikroklimaat regime. In terme van hitte laat dit die seisoen, sover muisaktiwiteite aangaan, toe om baie langer te wees as wat deur die mikroklimaat toegelaat word.

Muise is opportunistiese voeders en dit speel 'n groot rol in hulle oorlewing onder die uiterste toestande op Marioneiland. Muise is hoofsaaklik karnivore en het 'n geweldige impak op die grond mikro-invertebraatbevolkings en verwyder jaarliks tot verskeie kere die onmiddelike opbrengs van sekere van die mikro-invertebraatbevolkings. Aangesien mikro-invertebrata van kardinale belang is in die funksionering van die ekosisteem deurdat hulle die beskikbaarstellers van voedingstof-sirkulering op die eiland is, het die feit dat hulle die prooi van muise is, geweldige ekologiese implikasies. Tussen 1979/80 en 1992/3 het die digthede en biomassas van die invertebraatspesies wat hoofsaaklik die muis se prooi is, verminder. Die persentasie samestelling van die verskeie prooitipes in die mikro-invertebraatbevolkings het ook verander. Hierdie veranderinge het veranderinge in die muis se dieët tot gevolg gehad.

Seisoenale veranderinge in geslagtelike status, geslagsverhoudings, ouderdomstruktuur, liggaamsmassa en –lengte, nier- en adrenaalgewig en lengte en die mates van die ingewande is bepaal om inligting ten opsigte van die muis se reaksie op wisselende omgewingsparameters te verkry, asook die stresvlakke deur die muis ondervind op verskeie tye van die jaar. Stresvlakke word beinvloed deur bevolkingsdigtheid, geslag, voortplantingstatus, temperatuur en beskikbaarheid van voedsel. In 1992/93 is betekenisvolle groter liggaam-tot stertlengte verhoudings bepaal as in 1979/80, ten spyte van die feit dat die eiland intussen aansienlike hoër temperature ondervind. Hierdie verwarming het 'n aansienlike langer broeiseisoen tot gevolg,

omtrent tot soveel as twee maande. Dit is waarom die veronderstelling daar is dat die digthede aan die einde van die teelseisoen nou aansienlik hoër is as die in 1979/80.

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